Long-term effects of nutrient and CO₂ enrichment on the temperate coral Astrangia poculata (Ellis and Solander, 1786)

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1. Introduction

As the level of CO₂ in the atmosphere and surface-ocean continues to rise, there is increasing concern about the impact of ocean acidification on corals and the diverse ecosystems they sustain. Many experimental studies have documented that scleractinian corals respond to ocean acidification and the consequent decline in aragonite saturation state (Ω) (e.g. Langdon and Atkinson, 2005), and most suggest that coral calcification decreases with decreasing saturation state. However, the saturation state of the surrounding seawater alone does not control coral calcification as corals can continue to calcify in under-saturated conditions (e.g. Marubini and Atkinson, 1999; Cohen et al., 2009) or dissolve in super-saturated conditions (e.g. Herfort et al., 2008).

In zooxanthellate corals, calciﬁcation appears tightly linked to photosynthesis by the symbiotic zooxanthellae. The median coral calcification rate in the light is three times that in the dark, and symbiotic corals calcify at higher rates than non-symbiotic corals (e.g. Gattuso et al., 1999). When corals bleach and lose their zooxanthellae, calcification rates decline (e.g. Rodrigues and Grottoli, 2006).

Photosynthesis generally responds positively to elevated CO₂ and enhanced nutrient levels. Thus, high CO₂ and high nutrient levels could enhance coral calcification. However, this is not necessarily the case. Elevated concentrations of inorganic nitrogen can increase zooxanthellae photosynthesis but cause calcification by the host coral to decline. Marubini and Davies (1996) suggested coral calcification and zooxanthellae photosynthesis compete for a limited supply of carbon. While nutrient enrichment favors growth of the zooxanthellae and increased photosynthetic activity, photosynthesis may outcompete calcification for a limited supply of dissolved inorganic carbon (DIC), so calcification declines.

Studies of ocean acidification show that coral calcification generally declines under higher pCO₂ conditions, even in those studies where photosynthesis increases (e.g. Langdon and Atkinson, 2005). Thus, elevated CO₂ levels and elevated nutrient levels each tend to negatively affect coral calcification. However, if the CO₂ limitation model (Marubini and Davies, 1996) is correct, then the combined effects of elevated CO₂ and nutrients could be positive. Nutrient addition may enhance photosynthesis while elevated DIC could relieve the competition between photosynthesis and calcification for DIC.

To date, four studies have specifically addressed the interaction of nutrients and carbonate chemistry on calcification (Marubini and Atkinson, 1999; Marubini and Thake, 1999; Langdon and Atkinson, 2005; Renegar and Riegl, 2005). Both the work of Marubini and Thake (1999) and of Marubini and Atkinson (1999) looked only at nitrogen.
yet other nutrients, such as P and Fe have been found to be limiting in many systems (e.g. Sakka et al., 1999). In three of the four studies, carbonate chemistry was manipulated by the addition of acid/base and bicarbonate. However, the effects of CO₂ may differ from those of acid addition (e.g. Jury et al., 2008). The one study to combine CO₂ and nutrients incurred high rates of coral mortality (Renegar and Riegl, 2005), which makes interpretation of calcite cation rates difficult.

To assess how CO₂ and nutrients (N, P, Fe) interact to affect coral calcification, this study examines a temperate coral A stangia ploculata, which is shown to naturally experience a wide range in aragonite saturation state. Both zooxanthellate and azooxanthellate colonies were used to examine the influence of symbiosis on the calcification response to nutrients and CO₂. Corals were grown under long-term conditions of nutrient enrichment and reduced carbonate ion concentration, with aqueous carbonate chemistry manipulated by CO₂ enrichment.

2. Methods

2.1. Corals

Five zooxanthellate and six azooxanthellate A. ploculata colonies were collected from the Woods Hole Oceanographic Institution (WHOI) pier near the peak summer time water temperature in early August (23.5 °C) at depths from 3–9 m. Specimens were returned to the lab in seawater, fragmented into four or eight pieces and trimmed of visibly bored skeleton. The fragments were attached to acrylic slides using cyanoacrylate adhesive. Once the corals were attached to the slide, the slides were suspended vertically using cable ties. Specimens were divided amongst treatments such that either one or two specimens from each parent colony were in every treatment. No mortality was observed during the course of the experiment. Corals were allowed to acclimate to aquarium conditions for 1 month, then CO₂ and nutrient levels were gradually increased over a period of 10 days to reach treatment levels.

2.2. Aquaria

Coral fragments were maintained in a ow-through aquarium system. Two 450 L reservoirs were 1led daily with Vineyard Sound seawater (UV sterilized, 20 μm iterated); water from a given reservoir was continuously pumped to a header tank. From each header tank, water was fed into gas mixing chambers to equilibrate the water with a CO₂/air mixture, and from there into valve manifolds used to deliver water to individual aquaria. Individual aquaria consisted of 1 L PET food service containers (Solo) held in 25.8 ± 0.1 °C water baths (temperature controlled by an Omega CN1504 controller using aquarium heaters and thermometer temperature probes). Each container was covered with a tight-fitting PET lid with 3 holes in the lid—1 for water, one for air, and one for feeding. Incoming water passed through a loop of tubing inside the water bath, then dripped in from the top of the container. Outgoing water exited by a hole in the side which limited the total volume held to 800 ml. Flow rates to each container were 8 L/day. Each container was continuously bubbled using aquarium air-stones. Lighting was provided by three T5-HO bulbs (2 10,000 K bulbs, 1 actinic), on a 12 h L/D cycle; light levels ranged from 40 to 115 μmol photons/m²/s (Apogee quantum sensor), no systematic differences existed between light levels received by different treatments. Each container contained two corals, one zooxanthellate and one azooxanthellate. However, since the azooxanthellate corals acquired symbionts over the course of the experiment, no comparison of zooxanthellate and azooxanthellate colonies could be made, thus the results from the originally azooxanthellate colonies are not extensively discussed. Corals were fed daily. On alternating days, corals were fed either freshly hatched brine shrimp or frozen brine shrimp supplemented with Selcon (American Marine). Every few weeks, containers were cleaned of algal growth.

Based on previous studies in Vineyard Sound seawater (e.g. Gilbert et al., 1985) dissolved inorganic nitrogen is expected to be b1 M, and is most likely to be the limiting nutrient species. A level of 5 M NO₃⁻ has been found to reduce calcification in other coral species (Marubini and Davies, 1996). Thus a target enrichment of 5 M NO₃⁻ was chosen for the nutrient treatment to provide a concentration which should affect calcification and exceed the natural background level. As a precaution against inducing PO₄³⁻ or Fe limitation, both were introduced in approximate Red eld ratios based on the NO₃ enrichment. Nutrient levels were elevated by adding NaNO₃, K₂HPO₄, and FeCl₂ stock solutions to one of the reservoirs to increase concentrations of NO₃⁻, PO₄³⁻, and Fe⁺² by 5 μM, 0.3 μM and 2 μM respectively. Water samples were taken every few days from each reservoir. Samples were stored frozen until analyzed for ammonium, nitrate/nitrite (expressed as NO₂) and phosphate by the WHOI Nutrient Analytical Facility (using a Lachat Instruments QuickChem 8000 ow injection system). Mean levels were 3 ± 4 μM NH₄, 6 ± 1 μM NO₂, 0.7 ± 0.2 μM PO₄ in the nutrient enriched treatment; ambient conditions were 3 ± 5 μM NH₄, 0.8 ± 0.7 μM NO₂, 0.5 ± 0.3 μM PO₄, iron was not measured. The average difference between nutrient enriched and ambient samples collected on the same day were 0 ± 6 μM NH₄, 5 ± 1 μM NO₂, 0.3 ± 0.1 μM PO₄. Average nutrient levels experienced by the corals may have been lower due to algal growth between cleanings.

CO₂ levels were increased for one set of gas mixing chambers and their corresponding individual aquaria using ambient air (provided by an air-compressor) and CO₂. Flow rates for CO₂ and air were controlled by rotameters (Alborg Instruments), to provide an air/CO₂ mixture with CO₂ levels 400 ppm above ambient, this value was chosen to provide an enrichment greater than daily variations in aquarium pCO₂ while still being a value atmospheric pCO₂ may reach within the next 100 years (e.g. Ioo et al., 1999). A Qubit s151 CO₂ analyzer and a commercially prepared CO₂ standard (Corp Brothers) were used daily to assess the stability of CO₂ levels. Average ambient CO₂ levels were 386 ± 9 ppmv, CO₂ enriched levels were 780 ± 40 ppmv. A dial barometer (Fisher) was used to measure atmospheric pressure at the time of each CO₂ measurement (766 ± 7 mHg). Alkalinity was measured as follows: Large volume alkalinity samples were taken periodically from the WHOI pier (in Great Harbor, Woods Hole, MA) at a depth of 1.5 m starting before the start of experiments and continuing after the completion of experiments to monitor ambient conditions. A single large volume sample was taken from the water supply used to fill the reservoirs feeding the coral tanks during the course of experiments (alkalinity: 2086 μmol/kg, dissolved inorganic carbon (DIC): 1930 μmol/kg, salinity: 32.02, sample taken Feb. 13, 2008). Samples were collected in 250 ml glass bottles and poisoned with 70 μl of a saturated HgCl₂ solution. Alkalinity and DIC were determined by closed vessel titration of 100 ml aliquots using an automated titration system (Bradshaw et al., 1981; Brewer et al., 1986). Alkalinity and DIC concentrations were determined using a nonlinear curve fitting approach (Department of Energy, 1994), and standardized using certi ed reference materials obtained from Dr. A. Dickson ( Scripps Institution of Oceanography).

Samples for salinity measurements were taken at the same time as large volume alkalinity samples and were analyzed using aGuildline autosol model 8400B salinometer. Small volume alkalinity samples were taken four times over the course of the experiment from the reservoirs feeding the coral tanks. Small volume samples were stored at 4 °C in screw cap vials (Evergreen Scienti c) until analysis. Aliquots of 1 ml were used for Gran titration with 0.01 N HCl, values ranged from 2050–2150 μmol/kg, average 2110 ± 40 μmol/kg.

2.3. Buoyant weights

Buoyant weight measurements (based on Davies, 1989) were made 1 month after the start of treatments, and again 5 months later.
An Acclulab Vicon-123 balance (accurate to 0.01 g) with weigh-below hook was used to weigh corals in ambient seawater. Glass and aluminum weights were used to estimate water density. Temperature and salinity were recorded at the same time. Corals were handled entirely underwater during buoyant weights to minimize stress or introduction of bubbles. Mass changes are assumed to re ect changes in the mass of aragonite; an aragonite density of 2.93 was used to calculate the dry weight of calcium carbonate deposited.

2.4. Alkalinity depletion

At the beginning and end of the experiment, water ow to all containers was stopped. A Ba isotope spike was added (138Ba or 139Ba, suf cient to double the ambient Ba concentration), and containers held without water ow for 2 days. Small volume alkalinity samples were taken from every container at the end of the incubation to estimate calcification rates. Calcium ion was assumed to be the only process affecting alkalinity, with 2 mol alkalinity consumed for every mole of carbonate produced. Alkalinity samples were stored prior to measurement during which time some samples evaporated. Salinity was checked using a refractometer at the time of measurement, and samples which had evaporated during storage were excluded.

2.5. Surface area

Coral specimens were photographed using a Canon Digital Rebel XTı camera, images were saved in a raw le format. Photoshop CS3 was used to estimate the surface area of coral specimens. 2D surface areas and average diameters were determined for each specimen from images taken looking down on the coral; from side views, specimen height was determined. The total number of polyps was also counted. In addition, average calyx diameter and depth was obtained by sectioning some of the specimens. The data presented are normalized to an estimated 3D surface area using an average radius from the 2D surface area and colony height to calculate the surface area of a cone (π×radius×height). To account for the additional area contributed from individual polyps, the polyps were assumed to add an additional conical area minus the area of the base (to avoid double counting) (π×calice radius×calice depth × π×(calice radius)²). The average calice radius was 3.6±0.5 mm, depth 4.5±1.3 mm. Individual calices are closely approximated by a cone, while coral fragments displayed considerable variability, ranging from nearly planar to roughly cylindrical, with most specimens representing a form in between planar and cylindrical; a cone was chosen as an intermediate form which could be applied to all specimens.

2.6. Statistics

A factorial ANOVA model, including the parent colony as a blocking variable, was run on rank transformed data using SAS. To make pairwise comparisons, each treatment combination was considered a unique treatment for use in a 1-way ANOVA, Dunnett’s procedure was used to compare each treatment combination to ambient; comparisons with p<0.05 are considered statistically signi cant. For each ANOVA model, residuals were plotted against predicted values, against measured values, and on normal probability plots to assess violations of ANOVA assumptions. Linear regressions were performed using Systat. All data are given as mean±standard deviation.

3. Results

Alkalinity, DIC, salinity and temperature measurements from the A. poculata collection site in Woods Hole, MA are reported in Fig. 1 and the Supplementary Table. These data correspond to an annual cycle in seawater aragonite saturation state ranging from 1.5 in the winter to 2.5 in the summer.

Carbonate chemistry and saturation state of the seawater for each treatment, calculated from average alkalinity, salinity, phosphate and pCO2 values are shown in Table 1. The elevated CO2 treatments have higher bicarbonate concentrations (1840 μmol HCO3/kg for CO2 treatment, 1660 μmol HCO3/kg for ambient) and lower saturation state (1.8 ± 3.0) than ambient or nutrient only treatments.

Coral calcification rates determined using alkalinity depletion are compared with calcification rates determined from buoyant weight measurements in Fig. 2. Data obtained by the two methods are signi cantly correlated (p<0.001), with a relationship described by the equation: buoyant weight value = 1.08* alkalinity depletion value. Alkalinity depletion measurements were made for each container, thus the values represent the combined calcification by the zooxanthellate and the originally azooxanthellate colony in each container. The alkalinity depletion value presented is the average of measurements made at the beginning and end of each treatment. To allow comparison of the alkalinity depletion and buoyant weight methods of estimating calcification, the buoyant weights of the zooxanthellate and originally azooxanthellate colonies have been combined. Since both alkalinity depletion and buoyant weight based calcification estimates show similar patterns, it is possible to compare results of different studies in which only one of the two methods has been employed.

Fig. 3 shows the average calcification rates for zooxanthellate A. poculata colonies grown for 6 months under each of the nutrient and CO2 treatments normalised to surface area. Average growth rates were 2.1±0.1, 0.7±0.1, 1.4±0.1, and 1.3±0.1 g/m2/d for ambient, CO2 treated, nutrient treated, and CO2+nutrient treated corals respectively. Relative to ambient conditions, growth rates were reduced signi cantly by CO2 treatment (p<0.05) to 34% of the ambient rate, however with the addition of nutrients, growth rates were 61%–65% of ambient regardless of CO2 level. Table 2 shows the
associated factorial ANOVA table. Treatment with CO₂ resulted in lower calci cation rates (p = 0.0212). Nutrients alone appear to have a slightly negative effect, though this is not signi cant (p = 0.7273). However, when combined with CO₂, nutrients appear to reduce the negative effects of CO₂, suggesting a potential interaction of nutrients with CO₂, though the interaction term is not signi cant (p = 0.0562).

4. Discussion

Elevated pCO₂ levels negatively impacted calci cation by A. poculata. However, the degree to which elevated pCO₂ impacted calci cation was affected by inorganic nutrients. The decline in calci cation with elevated pCO₂ at ambient nutrient levels most likely indicates a calci cation response to changing carbonate chemistry (declining saturation state). Nutrient addition alone resulted in an apparent reduction in calci cation of 35%, consistent with suggestions of carbon limitation under nutrient enriched conditions (e.g. Marubini and Davies, 1996). The combination of moderate nutrient addition and elevated pCO₂, however, counteracted the negative effects of elevated pCO₂ alone. This response is similar to that reported by Langdon and Atkinson (2005) for tropical corals (Fig. 4). Despite using different methodologies (HCl addition, constant DIC vs. pCO₂ elevation, elevated DIC) and coral species (temperate vs. tropical), both studies show that elevated nutrient conditions reduce the degree to which reduced saturation state impacts coral calci cation. This suggests that coral calci cation can be nutrient limited under elevated DIC conditions (or elevated HCO₃⁻ + CO₃²⁻aq), the two carbon species generally used for photosynthesis), while elevated nutrients can lead to DIC limitation. Thus, the response of A. poculata to changing pCO₂ levels depends on the nutritional status of the coral holobiont, and the response to nutrients is similarly dependent upon DIC. Conversely, Renegar and Riegler (2005) found no bene t from adding nitrate or phosphate under elevated CO₂ conditions, however, in their study, DIC was lower in the high CO₂ treatment. Similarly, Marubini and Atkinson (1999) found no bene t from adding nutrients under acidified conditions, however, their acidified treatment was also associated with lower DIC.

Based on the results reported here, and by Langdon and Atkinson (2005), it may be possible to make a general prediction as to how otherwise healthy corals could respond to elevated pCO₂ depending on the availability of nutrients or their nutritional status. Nutritionally replete corals should be able to compensate for reduced saturation state under elevated pCO₂ conditions. As pCO₂ increases and seawater saturation state declines, availability of DIC to the zooxanthellae will increase, potentially allowing increased photosynthesis which provides both alkalinity and energy to help drive calci cation. If the coral is experiencing carbon limitation, elevated pCO₂ could even positively impact calci cation. Thus, so long as other factors such as light do not limit photosynthesis, nutritionally replete corals are expected to be relatively insensitive to modest reductions in saturation state, and can potentially bene t from higher DIC levels. Conversely, elevation of nutrient levels may negatively impact calci cation by nutritionally replete corals by increasing zooxanthellae growth which could increase photosynthesis leading to DIC limitation of calci cation, or increase self shading of the zooxanthellae leading to light limitation and reduced photosynthetic ef ciency (see Marubini and Davies, 1996). Calci cation by nutritionally limited corals will be strongly affected by reduced saturation state since DIC is already available at suf cient levels to support photosynthesis and calci cation, thus the decline in saturation state should drive the calci cation response. Nutritionally limited corals may thus respond in a manner more similar to the way inorganic aragonite precipitation responds to changing seawater saturation state (e.g., Burton and Walter, 1987). Nutritionally limited corals could bene t from modest nutrient

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**Table 1**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>T (°C)</th>
<th>S</th>
<th>PO₄</th>
<th>Alk</th>
<th>pCO₂</th>
<th>pH total</th>
<th>CO₂</th>
<th>HCO₃⁻</th>
<th>CO₃⁻</th>
<th>Ω aragonite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ambient</td>
<td>25.8 (0.1)</td>
<td>31 (0.9)</td>
<td>0.5 (0.3)</td>
<td>2110 (40)</td>
<td>390 (10)</td>
<td>8.03</td>
<td>11</td>
<td>1662</td>
<td>182</td>
<td>3</td>
</tr>
<tr>
<td>CO₂</td>
<td>25.8 (0.1)</td>
<td>31 (0.9)</td>
<td>0.5 (0.3)</td>
<td>2110 (40)</td>
<td>780 (40)</td>
<td>7.78</td>
<td>22</td>
<td>1837</td>
<td>111</td>
<td>1.8</td>
</tr>
<tr>
<td>Nutrient</td>
<td>25.8 (0.1)</td>
<td>31 (0.9)</td>
<td>0.7 (0.2)</td>
<td>2110 (40)</td>
<td>390 (10)</td>
<td>8.03</td>
<td>11</td>
<td>1662</td>
<td>182</td>
<td>3</td>
</tr>
<tr>
<td>Nutrient &amp; CO₂</td>
<td>25.8 (0.1)</td>
<td>31 (0.9)</td>
<td>0.7 (0.2)</td>
<td>2110 (40)</td>
<td>780 (40)</td>
<td>7.78</td>
<td>22</td>
<td>1837</td>
<td>111</td>
<td>1.8</td>
</tr>
</tbody>
</table>

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**Fig. 2.** Relationship between growth rates based on alkalinity depletion and buoyant weight measurements. Each point represents a measurement for an individual pair of corals, the line represents the best t line (buoyant weight = 1.084⁴ alkalinity depletion, R² = 0.523).

**Fig. 3.** Average growth rates of zooxanthellate A. poculata colonies exposed to nutrient and CO₂ treatments for 6 months. Bars represent mean of six replicates, error bars are standard deviation. * indicates treatments signi cantly different from ambient p<0.05.
increases so long as factors such as light availability, available space, and a lack of competition with other organisms (e.g. Lapointe, 1997) can allow an increase in nutrients to translate into increased photosynthesis and increased transfer of photosynthetic to the coral host, while still having sufficient DIC to support calcification.

The interaction between nutritional status of the coral, DIC availability, and saturation state may help to explain the wide range of calcification responses seen in published acidi cation and nutrient enrichment studies. Figs. 5 and 6 summarize data from several studies using a range of methods to manipulate carbonate chemistry and estimate calcification rates of both corals and coral communities. Only studies which provided sufficient data to calculate carbonate speciation are included. The change in coral calcification rates is presented as a function of saturation state, carbonate species, and nutrient levels. Across these studies, calcification rates were determined using one of four methods: alkalinity depletion and buoyant weight techniques, shown in this study to be comparable (Fig. 2), and radioisotope and calcium uptake techniques, also shown to be comparable to alkalinity depletion values by Tambutte et al. (1995) and Chisholm and Gattuso (1991).

In Fig. 5, all but two studies show a positive relationship between saturation state and relative calcification rate. In inorganic precipitation studies, saturation state is closely tied to precipitation rate (e.g. Burton and Walter, 1987; Holcomb et al., 2009), thus it might be expected that precipitation of aragonite by corals would show a similar dependence on saturation state, and some studies do show a similar relationship (e.g. Langdon and Atkinson, 2005; Herfort et al., 2008; the current study) (Figs. 4 and 5a). However, amongst those studies showing a positive response of calcification to saturation state, the calcification response differs by orders of magnitude. Such high levels of variability suggest that saturation state alone is not an effective predator of coral calcification. Calcification rate responses to carbonate ion follow a similar pattern to the response to saturation state (Fig. 6A). For bicarbonate (Fig. 6B), aqueous CO₂ (Fig. 6C), and DIC (Fig. 6D) some studies show positive relationships between calcification and bicarbonate, aqueous CO₂, or DIC, while others show negative relationships. Such a wide range of responses suggests that no carbonate system parameter alone can be used as an effective predictor of coral calcification.

In studies which have examined the effects of feeding, nutrients, light, and temperature without manipulating carbonate chemistry, calcification rates changed substantially in the absence of substantial changes in seawater saturation state (e.g. Marubini and Davies, 1996; Reynaud et al., 2003; Houblouque et al., 2004; Tanaka et al., 2007). Such results point to the importance of multiple factors in determining rates of coral calcification.

It has been suggested that bicarbonate may be the carbonate species controlling calcification rates (Herfort et al., 2008; Jury et al., 2008). However, Fig. 6B–D show no clear correlation between bicarbonate, aqueous CO₂, or DIC and calcification. Most of the studies showing positive calcification rate responses to elevated bicarbonate,

\begin{table}
\centering
\begin{tabular}{|l|l|l|l|l|}
\hline
Source & DF & SS & Mean square & F & p \\
\hline
Model & 7 & 620.708 & 88.67 & 2.68 & 0.0485 \\
Error & 16 & 529.291 & 33.08 & & \\
\text{CO}_2 & 1 & 216 & 216 & 6.53 & 0.0212 \\
\text{Nutrients} & 1 & 4.16666 & 4.17 & 0.13 & 0.7273 \\
\text{CO}_2 mat} & 1 & 140.166 & 140.17 & 4.24 & 0.0562 \\
\hline
\end{tabular}
\end{table}
aqueous CO$_2$, or DIC are studies in which saturation state is positively correlated with bicarbonate, aqueous CO$_2$, or DIC. Thus saturation state may be the controlling factor. The work of Reynaud et al. (2003) done at 25 °C and Anthony et al. (2008) done at 28.5 °C are exceptions, in which saturation state and calcification are not correlated. Anthony et al. (2008) used three CO$_2$ levels, only the highest of which was associated with a decline in calcification. Both of these studies manipulated carbonate chemistry by use of CO$_2$, and DIC increases as saturation state declines. These studies may represent nutrient replete conditions in which DIC is limiting calcification, thus a moderate elevation of DIC allows calcification to increase despite the decline in saturation state.

This study shows that elevated pCO$_2$ negatively impacts calcification, but that modest additions of nutrients (N, P, and Fe) can reduce that impact. The interactions amongst "nutrients", DIC, and saturation state yield results different from those seen when any one variable is manipulated. Aquarium-based experiments can therefore produce a wide range of coral responses to changes in seawater saturation state, all or none of which may be applicable to reef communities. In the studies discussed, only a small handful of the variables known to affect calcification and/or photosynthesis have been tested in combination with other variables, but how representative the species values used may be to natural reef environments is unknown. Additional complications arise in aquarium systems with low pH which may be much lower than encountered in a reef environment, creating diffusive boundary layers which could artifically limit transport of ions to the coral, or removal of metabolic wastes thus altering the apparent sensitivity of corals to nutrient, DIC and saturation state changes. Aquarium experiments also fail to capture how reefs, which contain countless species, will respond to changes in nutrients and CO$_2$ due to shifts in species abundance — macroalgae in particular are one group of organisms commonly artifically controlled in aquarium environments which may well benefit from higher nutrient levels and lead to a shift in community composition. Further laboratory-based work is needed to better understand how nutrients and/or enhanced nutritional status impact the calcification response.
to ocean acidification, and to identify measurable parameters, such as tissue composition, C:N:P ratios, etc. that may predict the "nutritional" status of corals in natural settings. Ultimately, manipulation of carbonate chemistry in natural reef environments is needed to accurately quantify the coral calcification response to elevated CO2.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2010.02.007.

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