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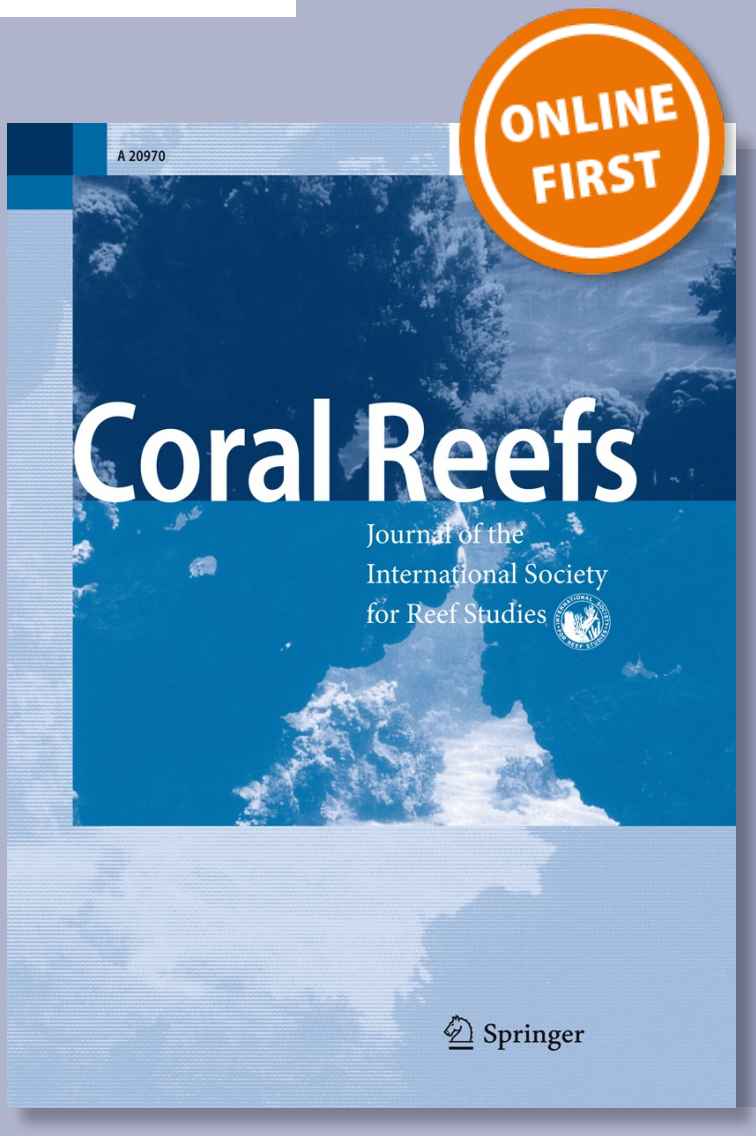

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REPORT

Light availability determines susceptibility of reef building corals to ocean acidification

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Abstract Elevated seawater pCO_2, and in turn ocean acidification (OA), is now widely acknowledged to reduce calcification and growth of reef building corals. As with other environmental factors (e.g., temperature and nutrients), light availability fundamentally regulates calcification and is predicted to change for future reef environments alongside elevated pCO_2 via altered physical processes (e.g., sea level rise and turbidity); however, any potential role of light in regulating the OA-induced reduction of calcification is still unknown. We employed a multifactorial growth experiment to determine how light intensity and pCO_2 together modify calcification for model coral species from two key genera, *Acropora horrida* and *Porites cylindrica*, occupying similar ecological niches but with different physiologies. We show that elevated pCO_2 (OA)-induced losses of calcification in the light (G_L) but not darkness (G_D) were greatest under low-light growth conditions, in particular for *A. horrida*. High-light growth conditions therefore dampened the impact of OA upon G_L but not G_D. Gross photosynthesis (P_G) responded in a reciprocal manner to G_L suggesting OA-relieved pCO_2 limitation of P_G under high-light growth conditions to effectively enhance G_L. A multivariate analysis of past OA experiments was used to evaluate whether our test species responses were more widely applicable across their respective genera. Indeed, the light intensity for growth was identified as a significant factor influencing the OA-induced decline of calcification for species of *Acropora* but not *Porites*. Whereas low-light conditions can provide a refuge for hard corals from thermal and light stress, our study suggests that lower light availability will potentially increase the susceptibility of key coral species to OA.

Keywords Coral · Ocean acidification · Light · *Acropora* · *Porites*

Introduction

Almost one-third of all CO_2 emitted to the atmosphere over the last 200 years has been absorbed by the oceans (Sabine et al. 2004). Importantly, elevated seawater pCO_2 drives a complex change in carbonate chemistry lowering pH (Caldeira and Wickett 2005) and the availability of carbonate (aragonite saturation, Ω) required for coral calcification and growth. Long-term records suggest that coral growth across entire reef systems has already declined in recent decades (De'ath et al. 2009) and hence reductions in ocean pH, or "ocean acidification" (OA), predicted for this century as CO_2 emissions continue to rise (Caldeira and Wickett 2005; IPCC 2007), could potentially be catastrophic for the future form and function of coral reefs (Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011).

A growing wealth of experiments and observations has attempted to quantity the extent with which elevated pCO_2 impacts coral growth (Pandolfi et al. 2011; Chan and Connolly 2012; McCulloch et al. 2012); however, while these efforts provide a strong mechanistic understanding as to how pCO_2 (pH) controls biogeochemical and ecological

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processes, they unlikely yield accurate predictions of future coral growth since additional environmental factors that regulate coral growth and productivity are also predicted to change alongside elevated pCO_2 (Hoegh-Gulberg et al. 2007; Hoegh-Guldberg and Bruno 2010). Factors such as temperature (Anthony et al. 2008; Rodolfo-Metalpa et al. 2011; Edmunds et al. 2012) and organic/inorganic nutrient availability (Langdon and Atkinson 2005; Edmunds 2011; Holcomb et al. 2012) have already been demonstrated to moderate the response of coral growth and/or productivity to pCO_2. However, the direction and extent of this moderating effect is often inconsistent or contradictory between studies highlighting that other factors, such as species (Anthony et al. 2008; Edmunds 2011; McCulloch et al. 2012), life history stage (du Putron et al. 2010; Albright et al. 2012) as well as the approach used to mimic OA scenarios (Marubini et al. 2008; Edmunds et al. 2012) undoubtedly further play a moderating role.

Coral reef growth in modern oceans is fundamentally limited by light availability (Kleypas et al. 1999; Yentsch et al. 2002). Rates of coral calcification and photosynthesis are light dependent and often closely coupled (Gatusso et al. 1999; Langdon and Atkinson 2005), and the light-response for calcification can be similar to that for photosynthesis (Barnes 1982; Marubini et al. 2001; Allemand et al. 2011). Photosynthetic activity has been proposed to directly stimulate calcification (light-enhanced calcification, LEC), most likely via direct modification of internal dissolved inorganic carbon (DIC) pools or indirectly by providing energy required to build organic and inorganic skeletons, although the exact mechanism is still unknown and debated (Furla et al. 2000; Colombo-Palotta et al. 2010; see Allemand et al. 2011). Therefore, it is logical to presume light availability should moderate corals' OA responses; however, aside from two studies suggesting that the OA-driven decline of calcification appears to be independent of light intensity (Langdon et al. (2000) for the BIOSPHERE-2 coral reef community; Marubini et al. (2001) for the species *Porites compressa*), the influence of light upon the OA response of corals has been almost entirely neglected.

While a recent meta-analysis of past coral OA studies suggests light may not influence the response of calcification to pCO_2/pH (Chan and Connolly 2012), these past studies lack any standardization of light availability, e.g., intensities relative to those considered saturating for calcification and or photosynthesis. Such a lack of standardization potentially confounds how well calcification and/or growth can ever be related to Ω and other moderating factors of interest. Light not only regulates calcification but also the susceptibility of corals to stressors such as anomalous temperature (e.g., Dunne and Brown 2001; Anthony et al. 2008; Hoegh-Guldberg and Bruno 2010; Lesser and Farrell 2004); in addition, future light availability to reefs will undoubtedly change as the physical nature of reef environments alters via enhanced river run-off/sedimentation and sea level rise (see Baker et al. 2008) as well as cloud cover (Wild et al. 2011). Fundamentally, light is a key driver of species distributions within tropical ecosystems and thus identifying any role of light in moderating the response to elevated pCO_2 should be a key priority toward better understanding and ultimately predicting future coral growth.

Our present study initially employed a multifactorial experiment to examine the interactive role of light availability and pCO_2 (pH) upon calcification of model reef building coral species *Acropora horrida* and *Porites cylindrica*. The genera *Acropora* and *Porites* have often been the focus of past OA studies (Electronic Supplementary Material (ESM), Table E1), and for our experiment, we chose species occupying a similar ecological niche and thus subjected to the same environmental stressors (both now and in future), but characterized by different physiologies (e.g., Hennige et al. 2010). We combined pCO_2 scenarios that represented present-day ambient (A-CO_2, ca. 400 µatm) and future intermediate A2 (I-CO_2, ca. 700 µatm) IPCC emission scenarios (IPCC 2007) with light intensities that were sub-saturating and saturating for maximum calcification (termed here as low versus high light; LL vs. HL). To fully contextualize the experimental results and evaluate their wider relevance, we constructed a database to examine the influence of growth environment, and specifically light relative to other key factors known to regulate coral growth (temperature, nutrients), for previously published coral OA experiments (28 studies, $n = 125$; until July 2012). Within this database, >50 % of all data has been collected on species of *Acropora* and *Porites* (see ESM, Table E1), and thus, we restricted our analysis to these well-represented and ecologically key genera. A wide range of light conditions have been used across these studies (and hence are not standardized) thus enabling us to examine for any influence of light via a stepwise approach; such an approach is now only possible due to the wide interest in OA and reef systems.

Materials and methods

Experimental setup

Four colonies (genets) of *A. horrida* and *P. cylindrica*, originally from the same parent colony from the Indo-Pacific, were obtained from *Reefworks Ltd.* (Bromley, UK) and *Tropical Marine Centre Ltd.* (Chorleywood, UK), respectively. Each colony was used for one of four replicate experiments (replicated over time) and each

fragmented into 8 nubbins (ramets) of ca. 5–8 cm tall to provide sufficient material for the various treatments within each experiment. Ramets were thus followed throughout the experimental design.

Prior to each experiment, ramets were first attached to 10-mm plastic PVC piping plugs with a non-toxic epoxy resin (Milliput® Standard) and allocated equally to one of two light acclimation tanks set to ca. 100 ± 11 and 400 ± 32 µmol photons m^{-2} s^{-1} (150 W Metal-Halide lamp, 14 Kelvin Bulb *Arcadia Products PLC*, Redhill, UK; and measured at the depth of the nubbins with a bio-spherical micro PAR sensor) on a 12:12 light:dark cycle; these two intensities were determined to be sub-saturating and saturating for calcification based on a previous light-response growth experiment of nubbins from the same colonies grown under a range of light intensities (75–600 µmol photons m^{-2} s^{-1}) for 10–12 weeks (Fig. 1). pCO_2 was not controlled within these initial acclimation tanks but determined as close to 'ambient' of ca. 400 µatm (from periodic pH and alkalinity measurements, not shown). Both acclimation tanks were supplied with Tropic Marin® PRO REEF salt-based seawater supplemented with $NaHCO_3$ maintained at 26 ± 0.9 °C, 35 PSU, a 4 L min^{-1} flow rate circulating between the tanks and a common biological sump of Fijian live rock (*Tropical Marine Centre Ltd.*, Chorleywood, UK). Inorganic nutrient concentrations monitored every two days were undetectable throughout (NO_3^+, PO_4^{3-}, NH_4^+ < 0.1 µM monitored by Multi-test kits, *NT Laboratories Ltd*, Kent, UK but verified by nutrient autoanalysis, *Skalar Analytical B.V.*, The Netherlands). $CaCO_3$ concentrations were maintained at ca. 400 ppm via addition of $CaCl_2$ from a *Schuran 1 Jetstream* calcium reactor monitored using a Ca^{2+} test kit (*Aquarium Pharmaceuticals*, Chalfont, USA). Total alkalinity (TA, as determined from a Titrino titrator, *Metrohm*, Buckingham, UK) achieved throughout was ca. 2.7 ± 0.2 µmol kg^{-1} (e.g., Table 1).

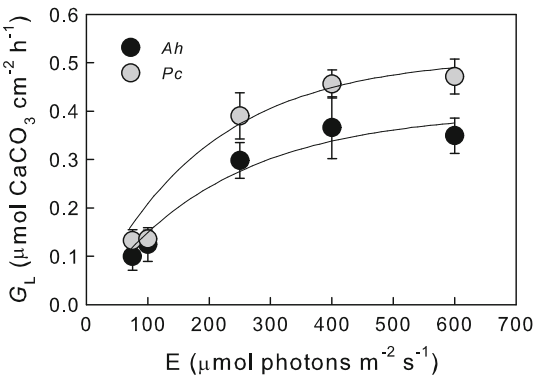

Fig. 1 Calcification rates in the light (G_L, µmol $CaCO_3$ cm^{-2} h^{-1}) for nubbins grown under a range of light intensities (E, µmol photons m^{-2} s^{-1}) for *Acropora horrida* (*Ah*) and *Porites cylindrica* (*Pc*). Each *data point* represents the mean (± SE) of $n = 5$ nubbins grown as part of a preliminary experiment under each intensity and at 26–27 °C in the experimental aquarium system (see main text) for ca. 10–12 weeks. *Solid lines* represent a curve fit of a single exponential function of G_L versus E ($G_L = G_L^{max} \cdot (1 - \exp((-\alpha \cdot E)/G_L^{max}))$; r^2 = ca. 0.95 using Sigmaplot®); the factor G_L^{max}/α describes the light intensity for saturation of G_L and was 274 and 232 µmol photons m^{-2} s^{-1} for *A. horrida* and *P. cylindrica*, respectively

Ramets from the light acclimation tanks were subsequently placed within one of four 750-mL volume CO_2-stat microcosm vessels, that is, two ramets per species per vessel. In principle, the CO_2-stat operates analogously to our pH–stat described previously whereby pH of the medium is continually maintained at a desired value via injections of CO_2-enriched or CO_2-free air using a PC-interface control (Brading et al. 2011); here, we employed a system similar to membrane inlet mass spectrometry whereby a custom-built gas diffusible membrane (standard silicone tubing, 0.31 mm ID–0.64 mm OD; Helix Medical, USA) attached to an external infra red gas analyzer (IRGA, LI-820; LI-COR, Nebraska, USA) was introduced into each vessel. The PC-control interface system was modified so as to maintain constant pCO_2 based on the voltage returned from the IRGA, to achieve a general level of control of ± ca.5–25 µatm (based on the response time of ca. 6 min to reach 95 % of the target pCO_2). A pH probe (combination probe Ross Ultra; *Fisher Scientific*, UK) was also maintained within each vessel and logged continuously alongside pCO_2 such that TA could also be determined and monitored continuously (by feeding online data of pCO_2 and pH into CO2SYS Lewis and Wallace 1998); however, TA was also measured independently using a Titrino titrator (*Metrohm*, Buckingham, UK) to verify the accuracy and precision of the pCO_2-stat approach. Values of TA derived from CO2SYS were always within those 2 % of those directly measured.

The four vessels for each replicate experiment were set as follows to yield the simultaneous light-pCO_2 manipulation: Two set and maintained at ca. 380 and 720 µatm pCO_2 (final mean pCO_2 achieved were ca. 390 and 735 µatm; Table 1) with one of each pCO_2 treatment illuminated at 100 and 400 µmol photons m^{-2} s^{-1}, that is, the same intensities as used to acclimate, via cool white LEDs (Daylights, Farnell, Leeds, UK) modified with neutral density filters (*LEE Filters*, UK) and on a 12:12 light:dark cycle. Final values of aragonite saturation (Ω_T) were slightly (2 %), but consistently, lower for *P. cylindrica* than *A. horrida*; however, Ω_T was always reduced by 30 % between the low and high pCO_2 treatments (Table 1). All vessels were water-jacketed and maintained at 26 °C via a heater-cooler circulator, and seawater was provided continuously from the main aquarium facility at a flow of 70 mL h^{-1}. Aeration and mixing was provided by continuously supplying ambient air, CO_2-free air or pure CO_2;

Table 1 Mean (±SE) carbonate chemistry parameters for the various growth treatments of *A. horrida* and *P. cylindrica* determined at the time of measuring the response variables ($n = 4$)

Treatment	Species	pCO_2 (µatm)	TA (µmol kg^{-1})	pH	TCO_2 (µmol kg^{-1})	HCO_3 (µmol kg^{-1})	CO_3 (µmol kg^{-1})	CO_2 (µmol kg^{-1})	Ω
LL *A*-CO_2	*A. horrida*	398.2 (14.59)	2719 (17.91)	8.207 (0.015)	2304 (4.712)	1975 (5.704)	318.1 (9.922)	11.00 (0.403)	5.071 (0.158)
	P. cylindrica	387.5 (16.11)	2723 (18.39)	8.225 (0.013)	2303 (4.901)	1975 (5.982)	317.1 (10.21)	10.70 (0.444)	5.054 (0.162)
LL *I*-CO_2	*A. horrida*	716.0 (28.16)	2719 (17.91)	7.999 (0.014)	2443 (6.223)	2203 (7.022)	220.3 (8.031)	19.76 (0.543)	3.512 (0.111)
	P. cylindrica	736.4 (32.33)	2723 (18.39)	7.997 (0.012)	2456 (5.143)	2225 (6.475)	211.7 (7.991)	20.33 (0.506)	3.376 (0.094)
HL *A*-CO_2	*A. horrida*	403.6 (12.52)	2719 (17.91)	8.205 (0.011)	2304 (5.020)	1975 (5.811)	317.0 (8.93)	11.14 (0.438)	5.054 (0.164)
	P. cylindrica	393.1 (14.18)	2723 (18.39)	8.220 (0.013)	2307 (4.991)	1981 (6.031)	314.5 (10.18)	10.85 (0.489)	5.015 (0.161)
HL *I*-CO_2	*A. horrida*	726.0 (36.02)	2719 (17.91)	7.994 (0.014)	2446 (6.719)	2208 (6.111)	218.4 (8.439)	20.04 (0.562)	3.482 (0.118)
	P. cylindrica	732.6 (25.79)	2723 (18.39)	8.000 (0.012)	2456 (6.039)	2223 (5.924)	212.5 (8.037)	20.22 (0.497)	3.387 (0.083)

Values for pH, TCO_2, HCO_3, CO_3, CO_2 and Ω were derived from those for pCO_2 and TA using CO2SYS program (Lewis and Wallace (1998), using the constants of Roy et al. (1993) and Dickson for KSO_4)

timing and rate of supply to the vessels were automatically controlled by PC interface to achieve the desired pCO_2 levels. All vessel sides were cleaned every 1–2 days to remove any biofilms. Weekly metabolic drift experiments (see below) demonstrated that a period of 2–3 weeks was required for the metabolic state variables (photosynthesis, calcification) to reach steady state; however, each experiment was terminated after 5–6 weeks. Experiments were repeated over time on separate fragments for both species and each incubated separately to avoid pseudoreplication.

Drift experiments and response variables

Vessels separate to those of the CO_2-stats were used to house nubbins to determine rates of key metabolic processes (calcification, G; photosynthesis P; respiration, R) via TA- and O_2-drifts. Here, vessels were filled with seawater from the appropriate pCO_2 treatment from the main experimental system to incubate the corresponding nubbins, which were maintained under the same light and temperature conditions as described above. Nubbins were then incubated in a closed system for ca. 4 h. Water samples taken at the beginning and end of each incubation were analyzed for TA and oxygen concentrations (using Foxy-R Oxygen Sensor, *Ocean Optics*, USA) to yield rates of calcification (G, mol $CaCO_3$ h^{-1}), via the alkalinity anomaly technique (Smith and Kinsey 1978), as well as photosynthesis and respiration (mol O_2 h^{-1}),

$$G = [0.5 \cdot \Delta \mathrm{TA}] \cdot [v/\Delta T] \quad (1)$$

$$P(R) = [\Delta \mathrm{O_2}/\Delta T] \cdot v \quad (2)$$

where ΔTA, ΔO_2, and ΔT describe the change of TA (µmol L^{-1}), O_2 (µmol O_2 L^{-1}) and time (h) for the incubation period, v is the volume of seawater (L) and 0.5 accounts for the decrease of TA by two equivalents for each mole of $CaCO_3$ precipitated. Both TA- and O_2-drifts were performed during both light and dark periods of the light:dark cycle for each fragment to yield estimates of light-dependant calcification (G_L) and net photosynthesis (P_N) but also dark calcification (G_D) and respiration (R), respectively. Gross photosynthesis (P_G) was determined as $P_N + R$, where R is the sum of dark- (R_D) and light-dependent (R_L) O_2 consumption; for our study, only R_D was measured and we assumed R_L to be constant (and in this case negligible) across species and treatments. Each fragment was subsequently processed for buoyant weight (W, Bucher et al. 1998) and surface area (SA, cm^2; using the paraffin wax technique, Bucher et al. 1998). All metabolic rates were normalized to SA, and thus, G and P (R) were in units of mol $CaCO_3$ cm^{-2} h^{-1} and O_2 cm^{-2} h^{-1}, respectively.

Data analysis

Absolute calcification rates (ESM, Table E2) were used to determine the percentage (%) change of G_L (G_D and P_G) with increasing pCO_2 (i.e., from ambient, A-CO_2, to the treatment, I-CO_2). In this way, we could directly examine the potential influence of growth light intensity, species, and time (since the four independent replicate experiments for the treatments/species were conducted sequentially over time) upon any OA response. Percentage data were initially tested for normality (Shapiro–Wilk) and subsequently arcsine transformed prior to statistical testing. Values for G_L and G_D were consistently negative (since calcification rates always decreased with OA) and therefore were multiplied by a value of -1 prior to transformation. The interactive influence of time, light, and species were tested via three-way ANOVA (Sigmastat®).

To further examine the potential influence of light intensity upon the OA-induced change of G from past OA experiments, a database was constructed to combine calcification or growth (G) with the corresponding growth conditions (carbonate chemistry, light, temperature, whether food or inorganic nutrients were added and elevated nutrient (N and P) concentrations above ambient) (ESM, Table E1). In total, 28 studies were identified with a majority proportion (>50 %) examining species of *Acropora* or *Porites*; many studies employed >1 pCO_2, light, temperature or nutrient treatment to yield a final data set of $n = 125$ (with $n = 29$ *Acropora*, $n = 44$ *Porites*) (herein referred to as the meta-data set). Aragonite saturation (Ω) was used as the carbonate chemistry metric and calculated via CO2SYS (Lewis and Wallace 1998) from the other carbonate chemistry variables where required. Both G and Ω were plotted as the ratio of values in treatment (T) relative to control (ambient, A) pCO_2 concentrations, i.e., $G(\Omega)_T$:$G(\Omega)_A$ such that any residual variability of G_T:G_A not explained by Ω_T:Ω_A must be from other environmental factors and/or species. We do not consider methodologies used within each study (e.g., approach to alter the inorganic carbon chemistry or duration of experiment) since these have recently been shown to not be significant factors affecting variance in calcification/growth among OA studies (Chan and Connolly 2012).

In contrast to light and temperature, nutrient concentrations were not always reported/available, and therefore, we categorized (binary coded) nutrients (N or P) as either high, e.g., via organic or inorganic supplements, versus low/background, e.g., ambient reef/aquarium, concentrations. Multiple stepwise regression (MSR, SPSS® 15.0) was subsequently used to identify variables and variable combinations that are most closely related with the variability of G_T:G_A. Relationships were considered significant for $p < 0.05$. In order to test for the influence of categorization of some but not all variables on the MSR, a subsequent analysis was performed with light, temperature and Ω_T:Ω_A also categorized. As with N and P, these three variables were categorized as either above (high) or below (low) an arbitrary threshold (see Table 2). A 5-factor ANOVA (light, temperature, Ω_T:Ω_A, +N, +P) was then performed via SPSS® to identify the influence of each variable upon G_T: G_A. Any influence upon G_T:G_A was indicated by significant differences ($p < 0.05$) within and/or between variables.

Table 2 Summary of 5-factor ANOVA based on categorized environmental data

Categorization criteria Variable	*Acropora* [$n = 29$]	*Porites* [$n = 44$]
Light (μmol photons m^{-2} s^{-1})	400 [11:18]	400 [24:20]
Temperature (°C)	26.2 [10:19]	26.2 [20:24]
Ω_A:Ω_T (dimensionless)	0.96 [25:4]	0.98 [34:10]
+N	Elevated [22:7]	Elevated [39:5]
+P	Elevated [27:2]	Elevated [42:2]

5-Factor ANOVA	*Acropora*		*Porites*	
	Ω_A:Ω_T	Light	Ω_A:Ω_T	Light
p	<0.001	0.002	<0.001	0.002
F	23.8	15.6	29.5	10.8

To be consistent with the previously categorized nutrient data, where N and P were treated as one of two categories (ambient (low) or elevated (high); Table 1, see also main text), light, temperature, and Ω_A: Ω_T were each categorized as either below (low) or above (high) an arbitrary threshold. The number of data points (n) returned for the low and high categorization is given in brackets, [low:high]. Thresholds were set as (1) a light intensity generally considered as sub-saturating and saturating for maximum calcification from this study (Fig. 1), and (2) the mid value between the minimum and maximum for the data set for temperature and Ω_A:Ω_T. Hence, the degrees of freedom for all variables = 1. The final ANOVA is shown (variables not presented were not returned as significant)

Results

Experiment metabolic responses

Calcification rates under ambient light (G_L) for ambient pCO_2 (A-CO_2) were generally the same for the two species under the light-limited treatment (LL) but higher for *P. cylindrica* than *A. horrida* under the light-saturated (HL) treatment (Table E2; see also Fig. 1). As expected, G_L consistently decreased with increasing pCO_2 for both light treatments and species (see ESM, Table E2). However, under HL, the OA-driven change of G_L (% change of G_L with increased pCO_2) was relatively small (ca. -10 %) for

A. horrida but greater (−50 %) for *P. cylindrica* (Fig. 2a; Table 3). The LL treatment exacerbated the change of G_L with OA by an additional ca. −40 % for both species, to yield values of ca. −50 and −80 % change of G_L with OA for *A. horrida* and *P. cylindrica*, respectively (see Table E2). Thus, reducing the growth light intensity from HL to LL induced a greater loss of G_L with OA for *A. horrida* (a factor of 5) than for *P. cylindrica* (a factor of 1.5).

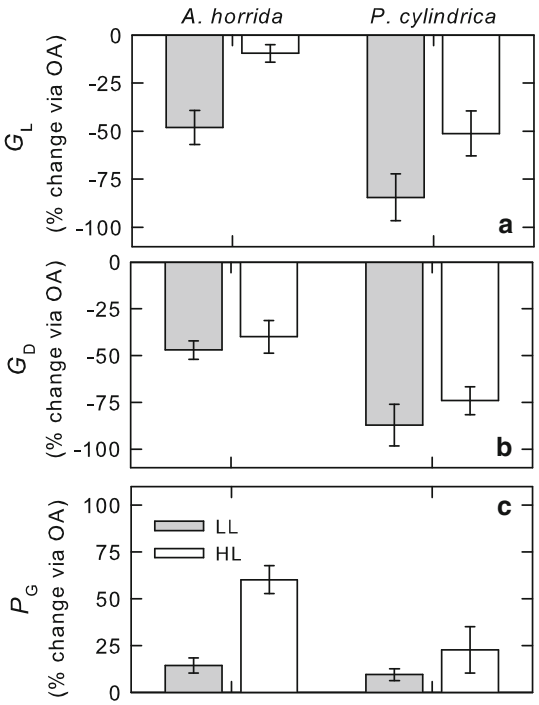

Fig. 2 Mean (±SE) percent change of metabolic rates with increasing pCO_2 (from ambient (A-CO_2) to intermediate (I-CO_2) pCO_2), i.e., ocean acidification. Rates shown are % change of calcification with OA under **a** ambient light (G_L, %) and **b** darkness (G_D, %) and also **c** the % change of gross photosynthesis with OA (P_G, %) for both low-light (LL) and high-light (HL) grown *A. horrida* and *P. cylindrica*. Mean and error values were determined from replicated experiments over time. Statistical differences between the response variable (% change with OA) as a result of time, light, and species were analyzed by 3 way ANOVA (Table 3)

Dark calcification (G_D) responses between pCO_2 treatments were similar as for G_L under light-limited growth (LL) (Fig. 2b). Absolute rates for G_D were ca. 40 and 30 % lower than for G_L for *A. horrida* and *P. cylindrica*, respectively, for all treatments except HL-I-CO_2 where rates were ca. 60 % lower for both species (ESM, Table E2); thus, the ratio of light to dark calcification (G_L:G_D, mol:mol), indicating the extent of light-enhanced calcification, was greater for *A. horrida* than *P. cylindrica* (ca. 1.6 and 1.4) under LL but substantially increased with pCO_2 under HL for both species (ca. 2.6–2.7) (ESM, Table E2).

The change of G_D with OA under light-saturated growth (HL) was the same as for LL, ca. −50 and −80 % for *A. horrida* and *P. cylindrica*, respectively (Fig. 2b; Table 3). Thus, in contrast to G_L, the growth light intensity did not moderate the OA-induced change of G_D for either species. Overall, these trends suggest elevated pCO_2 (OA) facilitates calcification in the light, in particular for *A. horrida* over *P. cylindrica*, under light-saturated growth conditions (such that values of G_L:G_D are highest at ca. 2.7 under the HL I-CO_2 treatment; ESM, Table E2).

We further examined for any potential influence of OA upon gross photosynthesis rates (P_G) that may in turn influence the OA changes of G_L but not G_D observed between the two light treatments (Fig. 2c). Absolute values of P_G were typically higher for *A. horrida* than *P. cylindrica* and consistently increased with pCO_2 treatments (ESM, Table E2, Fig. 2c). OA-induced changes of P_G exhibited reciprocal changes as observed for G_L such that the OA-induced change of P_G was greater for *A. horrida* (ca. 60 %) than *P. cylindrica* (ca. 20 %) under light-saturated growth (HL) (Table 3); this OA-induced change was reduced under light-limited growth conditions (LL), ca. 15

Table 3 Summary of three-way ANOVAs examining for the influence of time, light, and species upon % loss of calcification (G_L and G_D) or % gain of gross photosynthesis (P_G) with ocean acidification (see main text for procedures describing pre-test normalization)

Source of variation	% loss G_L		% loss G_D		% gain P_G	
	F	p	F	p	F	p
Time	0.190	ns	0.442	ns	0.066	ns
Species	30.97	<0.001	14.68	<0.005	13.78	<0.005
Light	30.78	<0.005	1.597	ns	7.031	<0.05
Time × species	1.521	ns	0.210	ns	0.019	ns
Time × light	0.013	ns	0.321	ns	2.789	ns
Species × light	0.053	ns	0.315	ns	4.434	ns
Time × species × light	1.193	ns	0.015	ns	0.420	ns

All significance (p) values are reported for the returned F value relative to the F critical ($F_{0.05,\ 1,\ 15}$)

ns not significant

and 10 % for the two species, respectively. Overall (transformed) % changes of G_L with OA could be closely associated with those of P_G across light treatments and species (% change $G_L = 0.787 \cdot$ % change $P_G + 0.372$; adj. $r^2 = 0.424$, $n = 16$, $p = 0.003$; Sigmastat®). Such reciprocal OA-induced changes of G_L (but not G_D) with P_G is consistent with the notion that gross calcification is likely enhanced by elevated photosynthesis and that P_G, in particular for *A. horrida*, is fundamentally limited by pCO_2 availability (and hence relieved by OA) under HL.

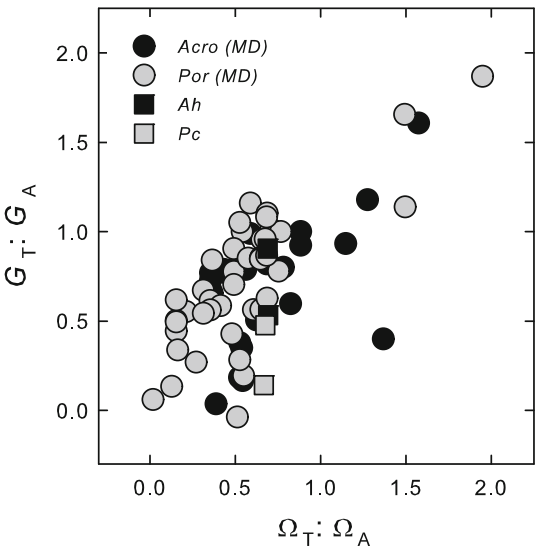

Fig. 3 Relative change of coral calcification/growth (G) under ambient light with aragonite saturation state (Ω) for coral species within the genera *Acropora* (Acro), *Porites* (Por) from the meta-data (MD) set (ESM, Table E1). Both G and Ω are expressed as values determined for treatments (T) relative to the control ('ambient', A; typically present day) conditions (see main text). Linear regression equations were: $G_T{:}G_A = \Omega_T{:}\Omega_A \cdot 0.511$ ($\pm$ 0.124) + 0.369 ($\pm$ 0.168) (adj. $r^2 = 0.282$, $n = 29$, $p = 0.005$) for *Acropora*; $G_T{:}G_A = \Omega_T{:}\Omega_A \cdot 0.808$ ($\pm$ 0.096) + 0.282 ($\pm$ 0.101) (adj. $r^2 = 0.612$, $n = 44$, $p = 0.001$) for *Porites*. A subsequent analysis of covariance (ANCOVA) did not find any significant difference between slope or intercept for these two regressions (not shown). Data from this study for *A. horrida* (*Ah*) and *P. cylindrica* (*Pc*) are overlaid but were not included in the analyses

Dark respiration rates (R_D, μmol $_2$ cm^{-2} h^{-1}) generally increased from the LL to HL treatments by ca. 10 % and were unaffected by the pCO_2 treatment for both species (Table E2; note that elevated pCO_2 did result in a small, ca. 10 %, but insignificant decrease of R_D under HL) treatment for *P. cylindrica*). Overall, the ratio of P_G-to-R_D was consistently higher for *A. horrida* than *P. cylindrica* and was increased by both light and pCO_2 treatments (see Table E2), as a result of the preferential changes to P_G over R_D.

Wider data analysis

Collation of calcification and associated environmental data from previous OA studies (ESM, Table E1) was used to examine the extent with which calcification and/or growth corresponded with aragonite saturation. For this exercise, values for both G and Ω were expressed as treatment (T) relative to the control (typically present day and hence 'ambient', A) values, i.e., $G_T{:}G_A$ and $\Omega_T{:}\Omega_A$, respectively (Fig. 3). Overall, $G_T{:}G_A$ was closely lineally correlated with $\Omega_T{:}\Omega_A$ for both *Porites* ($n = 44$) and *Acropora* ($n = 29$) (see Fig. 3 legend). Values of $G_T{:}G_A$/$\Omega_T{:}\Omega_A$ calculated for both LL and HL growth treatments from our experiments with *A. horrida* and *P. cylindrica* were ca. 0.77–1.31 and 0.21–0.71, respectively, and thus generally within the range for their respective genera from the meta-data set (indicated as the mean $\pm$ SE of the slope of $G_T{:}G_A$ versus $\Omega_T{:}\Omega_A$, Fig. 3 legend).

Subsequent multiple stepwise regression (MSR) analysis confirmed that values of $G_T{:}G_A$ were most strongly linearly correlated with $\Omega_T{:}\Omega_A$ for species of *Porites* ($r^2 = 0.57$) and to a lesser extent for *Acropora* ($r^2 = 0.27$); however, further variance of $G_T{:}G_A$ could be explained by light intensity for *Acropora* ($r^2 = 0.19$) or elevated phosphate (+P) for *Porites* ($r^2 = 0.08$) (Table 4). Note that $G_T{:}G_A$ exhibited a positive and negative relationship with light and +P, respectively, indicating that higher values of $G_T{:}G_A$, i.e., less reduction of G in the treatment relative to

Table 4 Output from Multiple Stepwise Regression (MSR) for covariance between the relative change of calcification/growth ($G_T{:}G_A$) with environmental factors (relative change of Ω ($\Omega_T{:}\Omega_A$), light intensity, temperature, and nutrient availability, +N or +P)

	Acropora		*Porites*	
	$\Omega_T{:}\Omega_A$	Light	$\Omega_T{:}\Omega_A$	+P
Beta	0.603	0.376	0.792	−0.274
r^2	0.267	0.191	0.566	0.082
Significance (p)	0.0004	0.0043	0.001	0.012
Intercept	−0.059		1.096	
Final	$F_{3,\ 26} = 10.57$, $r^2 = 0.448$, $p < 0.001$		$F_{3,\ 43} = 32.43$, $r^2 = 0.613$, $p < 0.001$	

All data were from the meta-data set for species of *Acropora* ($n = 29$) or *Porites* ($n = 44$) and transformed (see main text). Variables not presented were not returned as significant and not further included in the MSR model

ambient corresponded with higher light intensity but lower P. Any residual variance of G_T:G_A not explained by Ω_T:Ω_A could not be accounted for by temperature for either genera or light for *Porites*. Thus, an influence of light upon the OA-induced loss of calcification/growth for species of *Acropora* but not *Porites* from past OA studies is clearly consistent with our experimental results.

As with +N and +P, data for light, temperature, and Ω_T:Ω_A were subsequently categorized to further examine for any potential effects of weighting on the MSR by the categorized nutrient data; this analysis also returned light as a significant variable upon G_T:G_A for *Acropora* (Table 2). In contrast, +P was no longer identified as a significant factor for *Porites* thereby highlighting that the few data available for elevated phosphate (only two data points and hence 5 % of the data) significantly biased the previous MSR. Instead, as with *Acropora*, light was also identified as a significant secondary variable influencing the response of Ω_T:Ω_A upon G_T:G_A for *Porites*. Such a potentially subtler role of light in moderating the OA response of *Porites* would also be consistent with our experimental data.

Discussion

Our data demonstrate that OA impacts upon gross photosynthesis (P_G) and calcification (G_L) were highest where light availability was lower than that required for maximum (light-saturated) calcification, in particular for *A. horrida*. Elevated pCO_2 (OA) appears to primarily play a role in offsetting pCO_2 limitation of P_G under light-saturated growth conditions (HL) (see Muscatine et al. 1989) to in turn facilitate G_L, presumably via light-enhanced calcification (LEC) pathways. It is important to point out here that OA-induced patterns of G_L might not be expected to follow those of daily calcification (i.e., the sum of G_L and G_D weighted to the light–dark cycle), which is also a commonly used metric to evaluate the impact of OA upon coral growth, for example, via changes in buoyant weight (e.g., Anthony et al. 2008; Edmunds 2011). As such, it is perhaps not surprising that a recent meta-analysis of past coral OA experiments has shown that the impact of OA upon coral growth via buoyant weight measurements is less than for G_L measurements (Chan and Connolly 2012). Calculating the % change of daily calcification for our 12 h light:12 h dark cycle [i.e., (% change $G_L \cdot 0.5$) + (% change $G_D \cdot 0.5$) still yielded lower values for *A. horrida* (ca 28 %) over *P. cylindrica* (ca. 62 %) under HL]; thus, daily calcification rates would still likely exhibit the same trends as for G_L but of a slightly different magnitude.

Reduced respiration, in addition/instead of changes to P_G, with elevated pCO_2 has further been suggested to induce a depression of metabolic energy and thus explain reduced calcification/growth (Edmunds 2012). However, in contrast to recent studies, in particular with *Porites* species (*P. cylindrica*, Hii et al. 2009; *Porites* spp., Edmunds 2012), we did not observe significantly reduced dark respiration (R_D) with elevated pCO_2. Interestingly, both Edmunds (2012) and Hii et al. (2009) only observed their decreases of R_D for pCO_2 concentrations that were higher than those employed in our study (note that Hii et al. (2009) employed conditions that induced a similar pH but values of HCO_3^- and CO_3^{-2} that were 2–10 times lower than for our study; TA was not reported and so their actual pCO_2 conditions could not be derived and hence could not be included in the wider analysis). As such, more extreme pCO_2 shifts may be required to induce significant reductions to R_D (but perhaps not light-dependent O_2 consumption, see Crawley et al. Crawley et al. 2010). Overall, our data thus suggest that changes of P_G over R_D most strongly correspond with any changes to G here.

Effective OA-induced stimulation of LEC and in turn G_L would offset dissolution to increase the net calcification rate; however, the underlying processes regulating LEC is still debated (Allemand et al. 2011). Photosynthesis likely enhances the capacity to neutralize protons generated by calcification (Furla et al. 2000; Moya et al. 2008) as well as providing additional energy (ATP) to supplement calcification metabolic costs (Allemand et al. 2011; McCulloch et al. 2012; but see Colombo-Palotta et al. 2010); specifically, OH^- released during conversion of HCO_3^- to CO_2 via *Symbiodinium* cells reacting with H^+ in the sub-calicoblastic space facilitates CO_2 diffusion and $CaCO_3$ precipitation. According to this model, effective OA stimulation of LEC requires that CO_2 becomes limiting at light intensities where photosynthesis is light saturated (Muscatine et al. 1989) and will inevitably be exacerbated where specific *Symbiodinium* phylotypes may be more susceptible to CO_2 limitation of growth and or productivity under present-day condition (Brading et al. 2011); unfortunately, phylotype information is currently unavailable for the coral species examined here. Even so, our results of pCO_2 limited P_G and in turn G_L (by driving cells toward light-saturated P_G) are consistent with relief of resource limitation from inorganic and organic nutrient loading (Langdon and Atkinson 2005; du Putron et al. 2010), which likely also enables enhanced utilization of DIC via carbon fixation. While much photosynthetically fixed inorganic carbon can potentially be supplied by internal sources (Al Horani et al. 2003), it is clear that supplying resources that preferentially stimulate symbiont productivity (light, inorganic nutrients) ultimately come with a cost of increasing CO_2 limitation.

A number of OA-based experiments have effectively mimicked the influence of light-enhanced photosynthesis (and in turn calcification) through HCO_3^- addition

experiments [*Madracis mirabilis* (Jury et al. 2010); *Porites porites* and *Acropora* sp. (Herfort et al. 2008); *Stylophora pistillata* (Marubini et al. 2008)]; in these experiments, supplementary HCO_3^- reduced the decline of calcification (G_L) via Ω by up to a factor of 2. However, only two other studies have previously directly examined whether light moderates how calcification responds to OA-like conditions [from both laboratory and 'wild' grown (Biosphere 2) nubbins of *P. compressa*, Marubini et al. (2001); see also Langdon et al. (2000) for analysis of the whole BIOSPHERE-2 community] and concluded that the influence of Ω upon daily calcification was independent of light. The observations by Marubini et al. (2001) are somewhat consistent with our data, i.e., a much reduced moderation of the OA response by light for *P. cylindrica* compared to *A. horrida*, thereby further confirming that OA responses, including any moderating role of light, are a function of the host coral species in question (e.g., Anthony et al. 2008; McCulloch et al. 2012).

Both species in our experimental study (*A. horrida* and *P. cylindrica*) were chosen as 'model' species of their respective genera. Our data would suggest that those coral species with inherently greater dependency of photosynthesis over respiration to meet their metabolic demands may be most prone to pCO_2 limitation under HL and hence 'benefit' from OA. Other studies indeed show that species with higher photosynthesis rates exhibit a wider range of G_L (and P_G) response to OA-like treatments (*Acropora* sp. vs. *Porites porites*, Herfort et al. 2008). Ultimately, such species level differences may be regulated according to "sensitivities" of species to regulate calcifying fluid pH versus external pH (Ω), including the possible decrease in the efflux of H^+ from corals to surrounding waters as seawater H^+ increases (Jokiel 2011), and is likely independent of energy derived through photosynthesis (McCulloch et al. 2012) but possibly not respiration (Edmunds 2012). In either case, a lower sensitivity of calcification in response to changes in external pH would be indicated by a smaller gradient for the regression of calcification/growth upon Ω; however, the meta-data demonstrated a steeper (but not significantly different) gradient for species of *Porites* over *Acropora* (Fig. 3 legend). No doubt this initial analysis is complicated by variability of the data (15–30 % standard error around the regression coefficient, Fig. 3 legend) but is likely also potentially further compounded by the following two factors.

Firstly, a linear model describing the influence of Ω upon calcification/growth may not be applicable for all species (Ries et al. 2010; Chan and Connolly 2012; see also ESM, Fig. E1), in particular for species largely insensitive to changes of external pH, such as some species of *Porites* (including *P. cylindrica*, McCulloch et al. 2012; although see Hii et al. 2009); our linear model still accounted for >60 % of the variance of G_L from Ω for *Porites* in the MSR (Table 1) suggesting that the influence of sensitive species must therefore outweigh that of insensitive species for *Porites* in the meta-data available. Sensitivity certainly does not appear to be defined at the genera level (McCulloch et al. 2012).

Secondly, that in order to maximize use of available data, we amalgamated calcification and growth rate data. Corresponding mass and growth rates have been shown to demonstrate consistent responses to OA (Ries et al. 2010); however, G_L is potentially decoupled from growth rate, at least where significant LEC modifies the daily integrated calcification rate (above), and therefore growth. Some comparative G_L and G_D data exist within the meta-data set for species of *Acropora* and *Porites* (and *Fungia*) to show that G_L and G_D exhibit similar mean responses to Ω (ESM, Fig. E1) and hence minimum OA stimulation of LEC. Thus, one would in fact expect G_L to be closely coupled to daily calcification/growth; however, the current available data are few and highly variable and reconciliation across various growth metrics warrants further attention.

Importantly, despite possible limitations associated with the meta-data, the MSR analysis returned light as a significant factor influencing the variance of calcification/growth for species of *Acropora* (but not *Porites*) and thus was generally consistent with our independent experimental results. Within the MSR, the actual range of irradiances was lower for species of *Acropora* than *Porites* (ca. 160–1,343 vs. 13–925 μmol photons m^{-2} s^{-1}, or a factor of ca. 10 versus 70, respectively; although median values were similar for the two data sets, 450 and 400 μmol photons m^{-2} s^{-1}, respectively) and yet the moderating influence of light was greatest for *Acropora* over *Porites*. Unfortunately, it was not possible to derive whether the growth irradiances used for the various studies within this wider analysis were limiting or saturating for growth and so determine the strength with which light may ultimately be acting as a moderating factor. The probability determined for light acting as a significant moderating factor was increased for the 'coded' statistical approach (Table 2) compared to the MSR (Table 4) suggesting that an arbitrary categorization of the data as light-limited versus light-saturated can indeed improve the confidence returned for the influence of light upon the OA response. Even so, our experimental data and wider analysis would suggest that only moderate changes in light intensity may ultimately be required to influence the OA response for species more reliant on light availability for growth. Such interpretations clearly differ from the recent meta-data analysis of past coral OA studies by Chan and Connolly (2012) where light was not identified as a factor significantly affecting the OA response of calcification; however, their analysis used a

more temporally restricted database (studies up until 2011) and included many more genera than just *Acropora* or *Porites*.

A surprising result of the MSR (and confirmed by the ANOVA, Table 2) was any lack of influence of temperature for *Acropora* and *Porites*. Temperature is known to influence calcification rates and modify the influence of OA upon calcification/growth (e.g., Anthony et al. 2008; Edmunds et al. 2012). However, the range of temperature in the OA experiments to date is perhaps still relatively small (ESM, Table E1) and thus may not provide a robust test of any influence (positive or negative) on the OA response; this is particularly true where the nature of the growth–temperature responses of the coral species in question is not known prior to choice of experimental treatment. Clearly, the range of values/treatments currently available within the meta-data is still somewhat limited for potentially key environmental variables (temperature but also +P; ESM, Table E1), and their relative role in mediating the OA response certainly requires greater attention.

OA (increased ocean pCO_2) is well acknowledged to accompany increased ocean temperatures via elevated atmospheric pCO_2 (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg and Bruno 2010); however, future light environments of reefs are also at risk from change as a result of altered physical stability (stratification, currents, cloud cover) and land–sea interactions (sedimentation and eutrophication via freshwater runoff) (Baker et al. 2008; Wild et al. 2011). Our results demonstrating that light can significantly moderate the OA-induced decline of calcification, in particular for species of *Acropora*, are therefore potentially critical toward accurately determining the future resistance of coral reefs to climate change. Reduced light availability to reefs can provide resistance against anomalous light–temperature stress to "sensitive" fast growing coral species, e.g., those of *Acropora* (West and Salm 2003). Thus, enhanced susceptibility to OA under low-light growth for such species, as observed in our study, may act to decrease such potential resistance. Alternatively, a requirement for light to play a more positive role in dampening the impact of OA will inevitably require that coral species are able to adapt to high-light (HL) conditions in the face of more immediate stressors, such as thermal anomalies and eutrophication.

Our observations highlight that the influence of light upon corals' OA responses is specific–specific and therefore that OA combined with light availability will likely become one of the key drivers of species distribution. As such, that OA studies must better account for the potential moderating role of light upon growth/diversity if we are to move beyond the current accuracy afforded by predictive algorithms based solely on aragonite saturation (e.g., Pandolfi et al. 2011; McCulloch et al. 2012). Similarly, progressing to ecosystem models that can account for the future underwater light environment of reefs will be fundamental in improving the predictions of future reef resistance to climate change. It is clear that accounting for the net effect(s) of interactions among key environmental variables is critical toward identifying the most effective management solution for coral reef ecosystems.

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