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REPORT

Effects of light and elevated pCO_2 on the growth and photochemical efficiency of *Acropora cervicornis*

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Abstract The effects of light and elevated pCO_2 on the growth and photochemical efficiency of the critically endangered staghorn coral, *Acropora cervicornis*, were examined experimentally. Corals were subjected to high and low treatments of CO_2 and light in a fully crossed design and monitored using 3D scanning and buoyant weight methodologies. Calcification rates, linear extension, as well as colony surface area and volume of *A. cervicornis* were highly dependent on light intensity. At pCO_2 levels projected to occur by the end of the century from ocean acidification (OA), *A. cervicornis* exhibited depressed calcification, but no change in linear extension. Photochemical efficiency (F_v/F_m) was higher at low light, but unaffected by CO_2. Amelioration of OA-depressed calcification under high-light treatments was not observed, and we suggest that the high-light intensity necessary to reach saturation of photosynthesis and calcification in *A. cervicornis* may limit the effectiveness of this potentially protective mechanism in this species. High CO_2 causes depressed skeletal density, but not linear extension, illustrating that the measurement of extension by itself is inadequate to detect CO_2 impacts. The skeletal integrity of *A. cervicornis* will be impaired by OA, which may further reduce the resilience of the already diminished populations of this endangered species.

Keywords *Acropora cervicornis* · Ocean acidification · Light · Calcification

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Introduction

Coral cover has experienced marked declines throughout the Caribbean due to a variety of acute and chronic stressors (Gardner et al. 2003). This decline has contributed to a decrease in structural complexity and led to a loss in essential habitat, influencing a myriad of reef-associated species (Alvarez-Filip et al. 2009). Staghorn coral, *Acropora cervicornis*, once an abundant and important habitat builder in the Caribbean has been particularly impacted, as widespread die-offs have been documented since the 1980s primarily due to disease and physical disturbance by hurricanes (Aronson and Precht 2001). Declines of *A. cervicornis* have been so alarming that it was one of the two reef-building corals first categorized as threatened under the US Endangered Species Act (ESA) (Hogarth 2006) and critically endangered by the International Union for Conservation of Nature (IUCN) (Aronson et al. 2008). These listings have drawn attention to the marked decline of this

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important species, underscoring the need for effective management strategies to curtail population collapse.

Sexual recruitment (Vargas-Angel et al. 2003) and dispersal (Vollmer and Palumbi 2007) are limited for *A. cervicornis*, which instead relies on rapid growth and asexual fragmentation (Tunnicliffe 1981). Because of this, factors influencing coral growth and structural integrity (e.g., porosity) have the potential to strongly influence population dynamics and ultimately recovery. For example, high branch extension with depressed carbonate deposition could result in a weak skeleton, more susceptible to physical disturbance from storms (Tunnicliffe 1979).

Given this, one stressor of particular concern for *A. cervicornis* is ocean acidification (OA), which describes the oceanic uptake of anthropogenic (CO_2), resulting in lower seawater pH and a reduction in the saturation state of carbonate mineral phases precipitated by various calcifying taxa (e.g., aragonite by scleractinian corals). Ocean acidification (OA) is expected to reduce the calcification rate of corals (Langdon and Atkinson 2005) but some species may be less affected than others (McCulloch et al. 2012; Takahashi and Kurihara 2013). Previous work by Renegar and Riegl (2005) has demonstrated that calcification of *A. cervicornis* is negatively influenced by OA.

Light has been shown to be strongly linked to calcification in numerous species of scleractinian corals (Schutter et al. 2008). Recent evidence from a Pacific species of *Acropora* (Suggett et al. 2012) and from *Pocillopora damicornis* recruits (Default et al. 2013) suggests that the effects of OA are more pronounced in low- and intermediate-light conditions, respectively. Suggett et al. (2012) hypothesize that under high-light levels, elevated pCO_2 may ameliorate CO_2 limitation of the symbiotic zooxanthellae, thus enhancing photosynthesis. Shading has been shown to be directly detrimental to calcification rates in *A. cervicornis* in both field (Rogers 1979; Kendall Jr et al. 1985) and laboratory experiments (Chalker and Taylor 1975). Therefore, sea-level rise, increasing runoff, and other changes in light conditions predicted to be associated with climate change may further influence declines of *A. cervicornis* populations (Baker et al. 2008; Suggett et al. 2012).

Numerous efforts are currently underway to culture and outplant *A. cervicornis* fragments in an attempt to restore wild populations and increase genetic diversity (Lirman et al. 2010; Young et al. 2012). To this end, natural gradients in seawater carbonate chemistry may provide refugia from OA, potentially allowing localized populations of calcifying organisms to escape the deleterious effects of decreasing seawater pH (Manzello et al. 2012). Seagrass beds, which reduce CO_2 due to their photosynthetic activity, may provide one such refuge and are thus of interest to coral nursery efforts that aim to maximize growth and calcification. However, the effects of covarying factors that can occur with depressed CO_2, such as lower light, need to be determined in order to evaluate the efficacy of this management strategy. This study was conducted to investigate the combined effects of OA and shading on the growth and photochemical efficiency of *A. cervicornis* to better understand the interacting influences of light and pCO_2 so that these factors may be considered not only in modeling the persistence of wild stocks, but also in the planning and efficient deployment of restoration efforts.

Materials and methods

Small fragments ($\sim$10 cm in length) of *A. cervicornis* were collected from the University of Miami *Acropora* nursery in Dade County, FL, United States (depth = 6 m). Fragments ($n = 77$) from four genetically unique parent colonies were transported to the University of Miami by boat, epoxied to PVC bases, and divided among eight experimental aquaria. Corals were maintained in ambient CO_2 conditions for 7 d and observed to be healthy. CO_2 levels were increased to treatment levels over 9 d at which point the experiment was initiated.

Experimental treatments

Corals were maintained in eight separate indoor 150-l semi-recirculating aquaria throughout the duration of the experiment. Fresh seawater was dripped into each aquarium at a rate of 12 l h^{-1}. Seawater was obtained from Biscayne Bay where high precipitation likely reduced salinity below oceanic averages. Biscayne Bay has high total alkalinity, likely due in part to seagrass mediated sediment dissolution that occurs in this shallow embayment (e.g., Burdige and Zimmerman 2002, Burdige et al. 2008). The temperature within the experimental aquaria was maintained at 28 °C with a combination of cold-water baths and submersible heaters. Light was provided by two parallel 48 inch 216 W T5 high output fluorescent fixtures with 2 daylight and two actinic bulbs. Low-light conditions were created with shade cloths.

CO_2 treatments were maintained by separately injecting gas (0.4 l min^{-1}) with a venturi valve into air–gas reaction chambers plumbed into each recirculating system. The concentration of CO_2 in the elevated CO_2 treatments was precisely set using air and CO_2 mass flow controllers. This design is additive in nature, and there was some natural variability in carbonate chemistry due to differences in source water over time.

Water samples were taken weekly in borosilicate bottles and poisoned with mercuric chloride. Samples were

analyzed for dissolved inorganic carbon (DIC; Apollo SciTech AS-C3) and total alkalinity (TA; Apollo SciTech AS-ALK2). DIC and TA, in conjunction with temperature and salinity, were input into CO2SYS (Lewis and Wallace 1998) to solve the carbonic acid system and calculate aragonite saturation state (Ω_{Arag}) using the dissociation constants of Mehrbach et al. (1973) as refit by Dickson and Millero (1987) and Dickson (1990) for boric acid.

Downwelling photosynthetically active radiation (PAR; 400–700 nm) was measured with an in-water BIC2104x cosine irradiance radiometer (Biospherical Instruments). The instrument was placed in the center on the bottom of each tank so that the sensor was adjacent to the corals. In each tank, 100 measurements were taken and the average daily dose of Photosynthetic Photon Flux Density was reported in mol quanta m^{-2} d^{-1}.

Sample analysis

The maximum quantum yield of photosystem II fluorescence (F_v/F_m) was measured using pulse-amplitude-modulated (PAM) fluorometry with the PAM monitoring head positioned at a fixed distance of approximately 1 cm away from the coral. All corals were dark adapted for 30 min prior to measuring.

Calcification was measured via buoyant weight (Jokiel et al. 1978) at the beginning and end of the experiment (42-d duration). Additionally, fragments were scanned at the beginning of the experiment and after 28 d of growth using a white light 3D scanner (HDI Advance R2, 3D3 Solutions) configured with dual 2-megapixel monochrome cameras (Point Grey) and calibrated with a 5-mm square glass calibration board. Care was taken to minimize the amount of time the coral samples were out of the water during the scanning process and corals were not subjected to aerial exposure >1 min. Aerial exposure and briefly elevated light levels associated with the patterns projected onto the corals' surfaces were observed to minimally affect coral health, as no mortality occurred and corals were observed to extend their tentacles within hours of reintroduction to their experimental aquaria. Each sample was scanned every 20° around the central axis. The resulting 18 scans were aligned and compiled into a single model using the FlexScan3D software package. Coral height was measured by selecting a minimum and maximum point in the 3D space of the model and calculating the distance between those points. Identical points, as determined by model geometry and coralite position, were selected to calculate height in the initial and final 3D scan.

Three-dimensional scans were manually trimmed to digitally remove the sample base, epoxy, and all non-coral material. Care was taken to trim initial and final scans at exactly the same location to reduce error in surface area and volume measurements caused by improperly defining the 3D extent of the coral sample. Once trimmed, sample meshes were resampled to reduce small openings in the model. Finally, sample scans were loaded into the Leios 2 software, remaining model holes were filled, and coral surface area and volume were measured (Fig. 1).

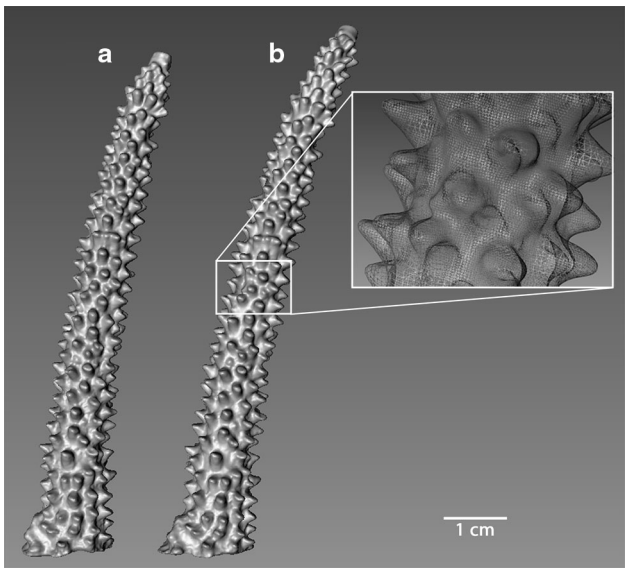

Fig. 1 Three-dimensional scans of *A. cervicornis* at the start of the experiment (*a*) and after 28 d (*b*). Detail shows the resolution of digital mesh composing the model

While other studies have used 3D scanning to quantify coral morphology and test the accuracy of various methodologies for estimating surface area (Courtney et al. 2007; Razbahat et al. 2009), this is the first study we are aware of that has used this technique to monitor the growth rates of living corals. While other methods exist for quantifying surface area (e.g., aluminum foil, Marsh Jr 1970; wax dipping, Stimson and Kinzie 1991; dye absorption, Hoegh-Guldberg 1988), they are often lethal or require dead and clean coral skeletons. Our methodology resulted in highly accurate measurements of surface area, volume, and linear extension on living tissues (Electronic Supplementary Material, ESM 1). This procedure is minimally invasive, accurate, and a time-effective method for monitoring coral growth.

Statistical analysis

In order to balance sample size per treatment, eight replicates were randomly selected per tank, resulting in 16 replicates per treatment combination (light and CO_2) and a total of 64 fragments. Treatments (Ω_{Arag} and PAR) were analyzed using a two-way ANOVA with tanks as a random effect nested within a fixed treatment effect. Eight samples were selected from each tank for the analysis. All the data

Table 1 Mean treatment conditions (±SEM)

Treatment	Tank	Salinity (psu)	Temp (°C)	PAR (mol quanta m^{-2} d^{-1})	TA (μmol kg^{-1})	DIC (μmol kg^{-1})	pCO_2 (μatm)	Ω_{Arag}
LL-LCO_2	1	32.3 ± 0.2	28.0 ± 0.0	4.84 ± 0.22	2,506.21 ± 25.72	2,206.66 ± 19.28	501.1 ± 23.9	3.69 ± 0.17
LL-LCO_2	2	32.1 ± 0.3	28.1 ± 0.0	4.36 ± 0.70	2,498.45 ± 24.71	2,211.70 ± 24.74	524.9 ± 22.1	3.55 ± 0.09
LL-HCO_2	3	32.0 ± 0.3	28.1 ± 0.0	4.39 ± 0.13	2,504.35 ± 26.26	2,298.64 ± 39.31	824.7 ± 114.6	2.70 ± 0.21
LL-HCO_2	4	32.2 ± 0.2	28.4 ± 0.0	4.04 ± 0.54	2,505.09 ± 25.09	2,321.23 ± 30.20	917.1 ± 80.8	2.47 ± 0.13
HL-LCO_2	5	32.2 ± 0.2	28.1 ± 0.0	15.14 ± 1.08	2,476.27 ± 24.86	2,185.54 ± 24.58	505.8 ± 16.1	3.58 ± 0.07
HL-LCO_2	6	32.3 ± 0.2	28.4 ± 0.0	15.42 ± 1.26	2,483.66 ± 28.93	2,168.16 ± 33.62	462.1 ± 25.0	3.86 ± 0.08
HL-HCO_2	7	32.3 ± 0.2	28.1 ± 0.0	15.32 ± 0.77	2,490.10 ± 26.34	2,276.86 ± 36.71	774.5 ± 79.4	2.76 ± 0.15
HL-HCO_2	8	32.2 ± 0.2	28.4 ± 0.0	15.62 ± 1.05	2,485.94 ± 25.83	2,285.27 ± 33.18	827.4 ± 73.2	2.63 ± 0.13

LL-LCO_2, low light, low CO_2; LL-HCO_2, low light, high CO_2; HL-LCO_2, high light, low CO_2; HL-HCO_2, high light, high CO_2

were analyzed for normality (Shapiro–Wilk) and homoscedasticity. Change in volume and surface area was analyzed using a fully crossed two-way ANOVA to test the effects of light and elevated CO_2 (SigmaPlot 12.0). Change in weight, linear extension, and F_v/F_m data did not conform to the assumptions of a parametric ANOVA. For these growth metrics, univariate permutational analysis of variance (PERMANOVA) was used as it allows a two-factor design and tests the interaction effect without the requirements of similar parametric procedures. PERMANOVA was run with 9,999 permutations on resemblance matrices constructed from Euclidian distances. PERMANOVA was conducted with the PRIMER 6 software package with the PERMANOVA add-on.

Results

Water chemistry and light conditions are given in Table 1. PAR (ln transformed, $F = 0.397$, $P = 0.808$) and Ω_{Arag} ($F = 1.157$, $P = 0.342$) were not significantly different between tank replicates nested within treatments. Mean growth rates and F_v/F_m values for *Acropora* replicates are given in Table 2. Calcification was significantly impacted by high CO_2, but linear extension was not (Fig. 2; Tables 2, 3). Thus, high CO_2 had no effect on branch elongation, but depressed the density of the skeleton deposited. Light, on the other hand, significantly impacted both extension and calcification. Similarly, high-light treatments, irrespective of CO_2, were found to have the highest increases in both surface area and volume (Fig. 2c, d; Tables 2, 4). Low-light treatments had a small but significant increase in F_v/F_m versus high-light treatments (Fig. 3; Tables 2, 5).

Discussion

Elevated pCO_2 significantly affected calcification, but not linear extension, surface area, or volume, suggesting that CO_2 levels influence the growth of *A. cervicornis* by altering skeletal density. This could have broad implications for the structural integrity and longevity of branching coral colonies that must withstand natural physical and biological disturbances under increased OA scenarios (Chamberlain 1978; Tunnicliffe 1981).

While *A. cervicornis* branches are stronger than congenerics, mechanical stress is often concentrated at their more-slender base, resulting in snapping and fragmentation (Schuhmacher and Plewka 1981). An increase in skeletal porosity due to OA could therefore decrease the force needed to break colony branches, leading to more frequent fragmentation and potentially decreased maximum colony size. Furthermore, breakage of *A. cervicornis* is often enhanced by the infestation of the basal region colonies by bioeroding clionaid sponges (Tunnicliffe 1979). The erosive potential of these sponges is expected to be accelerated by OA (Wisshak et al. 2012) and may therefore act in concert with OA-weakened skeletons to further increase fragmentation.

Acropora cervicornis relies heavily on asexual propagation to maintain and expand local populations (Tunnicliffe 1981; Vargas-Angel et al. 2003). While it has been argued that high skeletal density could negatively influence *Acropora* populations by limiting asexual reproduction (Chamberlain 1978), the reverse is not necessarily true. Asexual reproduction of *Acropora* is a product of both breakage and the survivability of the resulting fragments. Following disturbance events, survivability and recruitment success are strongly dependent on fragment size, with

Table 2 Mean *A. cervicornis* growth rates and final photochemical efficiency (±SEM)

Treatment	Weight (mg d^{-1})	Linear (mm d^{-1})	SA (mm^2 d^{-1})	Volume (mm^3 d^{-1})	Photo. effic.
LL-LCO_2	8.41 (3.092)	0.01 (0.002)	6.80 (0.989)	11.68 (1.797)	0.64 (0.008)
LL-HCO_2	2.56 (2.375)	0.01 (0.002)	6.59 (0.528)	8.66 (1.409)	0.65 (0.004)
HL-LCO_2	29.19 (2.938)	0.21 (0.020)	12.08 (1.054)	17.59 (2.028)	0.62 (0.008)
HL-HCO_2	21.65 (1.441)	0.21 (0.018)	11.47 (0.882)	18.10 (1.868)	0.62 (0.010)

LL-LCO_2, low light, low CO_2; LL-HCO_2, low light, high CO_2; HL-LCO_2, high light, low CO_2; HL-HCO_2, high light, high CO_2

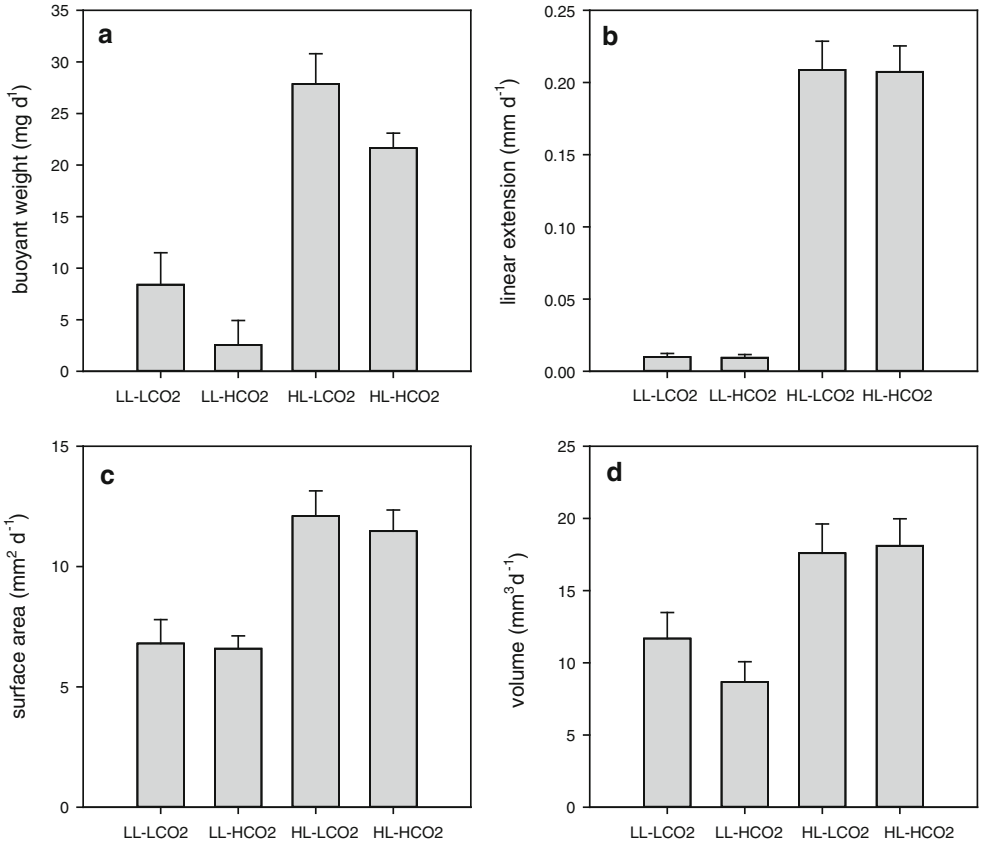

Fig. 2 Growth parameters of *A. cervicornis* subjected to light and CO_2 treatments (LL-LCO_2, low light, low CO_2; LL-HCO_2, low light, high CO_2; HL-LCO_2, high light, low CO_2; HL-HCO_2, high light, high CO_2). **a** Change in buoyant weight, **b** linear extension, **c** change in surface area, **d** change in volume

larger fragments experiencing lower mortality (Highsmith et al. 1980; Lirman 2000; Lirman et al. 2010). A decrease in structural integrity could therefore lead to a decrease in asexual reproduction potential by reducing the length at which branches fragment and the average size of fragments produced. Moreover, a decline in calcification would likely delay the recovery of skeletal lesions and the time it takes for fragments to cement to the bottom. Lesion recovery and re-attachment to the benthos have been shown to be important for the long-term growth and survivorship of *Acropora* fragments (Lirman 2000). Additionally, OA is also known to negatively influence both the fertilization and settlement success of the congeneric *Acropora palmata* (Albright et al. 2010) and may similarly affect *A. cervicornis*. Together, these impacts of OA could spell trouble for increasingly isolated *Acropora* populations throughout the Caribbean (Vollmer and Palumbi 2007).

We did observe a lower proportional reduction in calcification in high-light (15.4 mol quanta m^{-2} d^{-1}) versus low-light (4.4 mol quanta m^{-2} d^{-1}) treatments due to CO_2 (70 vs. 26 %), but the interaction of light and CO_2 on calcification was not significant. Suggett et al. (2012), however, did observe a significant difference in OA-reduced daytime calcification between light treatments

Table 3 Summary of two-way PERMANOVA examining the effects of light and CO_2 on the change in buoyant weight and linear extension

Source	Weight						Linear extension					
	DF	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms	*DF*	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
Light	1	5,941.80	5,941.80	57.32	<0.001	9,836	1	0.63	0.63	217.63	<0.001	9,830
CO_2	1	581.16	581.16	5.61	0.021	9,830	1	1.48E−5	1.48E−5	5.12E−3	0.944	9,856
Light × CO_2	1	0.51	0.51	4.92E−3	0.944	9,835	1	2.67E−6	2.67E−6	9.22E−4	0.976	9,826
Residual	60	6,219.6	103.66				60	0.17	2.89E−3			
Total	63	12,743					63	0.80				

Table 4 Summary of two-way ANOVA examining the effects of light and CO_2 on the change in surface area and volume

Source	Surface area					Volume				
	DF	SS	MS	*F*	*P*	*DF*	SS	MS	*F*	*P*
Light	1	413.45	413.45	32.85	<0.001	1	942.41	942.41	18.38	<0.001
CO2	1	2.82	2.812	0.22	0.638	1	25.16	25.16	0.49	0.486
Light × CO_2	1	0.68	0.68	0.05	0.817	1	49.94	49.94	0.97	0.328
Residual	60	755.27	12.59			60	3,076.10	51.27		
Total	63	1,172.22	18.61			63	4,093.60	64.98		

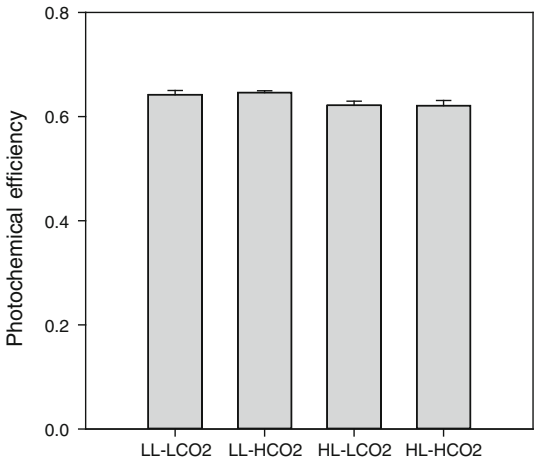

Fig. 3 Photochemical efficiency of *A. cervicornis* replicates subjected to light and CO_2 treatments (LL-LCO_2, low light, low CO_2; LL-HCO_2, low light, high CO_2; HL-LCO_2, high light, low CO_2; HL-HCO_2, high light, high CO_2)

(34.6 vs. 8.6 mol quanta m^{-2} d^{-1}). These authors have hypothesized that in scenarios where symbiont photosynthesis is enhanced to the point of CO_2 limitation (e.g., high light), elevated pCO_2 may help to overcome this limitation, in turn enhancing calcification and potentially buffering the deleterious influences of OA. Default et al. (2013) proposed that whereas OA-associated declines in CO_3^{2-} will decrease both day and nighttime calcification, the increase in HCO_3^- associated with moderate levels of OA may offset potential limitation during high-light daytime utilization of HCO_3^-.

Marubini et al. (2001) measured the buoyant weight of *Porites compressa* under four light (23.3, 12.6, 8.1, and 3.5 mol quanta m^{-2} d^{-1}) and three CO_2 (286, 336, and 641 µatm) treatments over a 3-week period, encompassing natural day/night cycles. Unlike Suggett et al. (2012), the authors observed stronger OA-depressed calcification in high-light versus low-light treatments. This result occurred at light levels far below the high-light treatment of Suggett et al. (2012; 34.6 mol quanta m^{-2} d^{-1}) and therefore was not likely due solely to light-related stress.

Default et al. (2013) subjected *P. damicornis* recruits to two trial runs of two CO_2 and five light treatments. The negative effects of OA on calcification were observed to be the most pronounced at intermediate-light levels (6.0 and 4.8 mol quanta m^{-2} d^{-1}, trials 1 and 2, respectively), and no significant effect of OA was recorded at low-light levels (2.7 and 1.2 mol quanta m^{-2} d^{-1}). While the shape of calcification–irradiance response curves was different for the high-CO_2 treatment between trials, OA-depressed calcification was less pronounced in the highest light treatments (19.5 and 16.5 mol quanta m^{-2} d^{-1}). These studies, combined with the different magnitude of responses observed for *Porites cylindrica* and *Acropora horrida* in the Suggett experiments, suggest that the effects of light and CO_2 on coral calcification may be species-dependent and subject to the specific light requirements of the specimen in question.

It is possible that our high-light treatments (15.4 mol quanta m^{-2} d^{-1}) were not intense enough to result in CO_2 limitation and consequently did not

Table 5 Summary of two-way PERMANOVA examining the effects of light and CO_2 on photochemical efficiency

Source	*DF*	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
Light	1	1.05E−2	1.05E−2	8.94	0.003	9,841
CO_2	1	6.48E−5	6.48E−5	5.53E−2	0.817	9,833
Light × CO_2	1	9.25E−5	9.25E−5	7.88E−2	0.783	9,812
Residual	76	8.91E−2	1.17E−3			
Total	79	9.98E−2				

significantly demonstrate the high-light treatment (34.6 mol quanta m^{-2} d^{-1}) buffering of OA proposed by Suggett et al. (2012). Indeed, Chalker (1981) created calcification and photosynthesis saturation curves for *A. cervicornis* collected from 12 to 18 m in the Bahamas. According to these relationships, our light treatments did not reach saturation of photosynthesis (I_k = 20.4 mol quanta m^{-2} d^{-1}, where I_k is the irradiance at which a line with the initial slope of the function intersects the function's asymptote) or light-enhanced calcification (I_k = 27.3 mol quanta m^{-2} d^{-1}). This raises an interesting point. Given the high irradiance required for *A. cervicornis* to reach saturation, it is unlikely that wild populations will experience light levels intense enough to buffer the effects of OA. Indeed, coral species adapted to high-light conditions, which rarely reach complete light saturation, may be more susceptible to OA. Corals grown in high-light treatments displayed similar linear extension rates (7.7 cm yr^{-1}) to those recorded in the US Virgin Islands (7.1 cm yr^{-1}, Gladfelter et al. 1978) and the Florida Keys (11.5 cm yr^{-1}, Eastern Sambo, Jaap 1974; Key Largo, 3.4–11.0 cm yr^{-1}, Shinn 1966). This suggests that experimentally manipulated light levels in this study were adequate to yield similar rates of growth to what is observed in the field.

In a field experiment involving shading of a natural reef, *A. cervicornis* was the first species to respond to lowered light levels, which significantly reduced growth rate and caused bleaching, ultimately resulting in mortality (Rogers 1979). The calcification rate of *A. cervicornis* has previously been shown to be strongly linked to light intensity and can be inhibited by various photosynthesis antagonists (Chalker and Taylor 1975). It is cautioned, however, that not all light is beneficial. Translocation of *A. cervicornis* colonies to shallower areas can lead to a greater increase in UV radiation than PAR and may result in lower skeletal extension, bleaching, and a reduction in skeletal density (Torres et al. 2007).

In this study, there was a slight but significant drop in photochemical efficiency under high-light treatments. This was in agreement with the previous studies, which have observed lower photochemical efficiency under higher light conditions and proportionally greater translocation of photosynthetically fixed carbon to host corals by shade-adapted zooxanthellae (Muscatine et al. 1984). It is likely, however, that the much greater irradiance in the high-light versus low-light treatments resulted in similar or greater total fixation of carbon in the high-light treatments. Thus, high-light conditions could have resulted in a greater availability of photosynthetically fixed carbon for growth and calcification despite lower photochemical efficiency.

While linear extension was nearly zero in the low-light treatment, we observed a significant increase in volume, surface area, and buoyant weight over the duration of the experiment. This corroborates other studies that have observed that light influences skeletal morphology (Chappell 1980; Falkowski and Dubinsky 1981; Crabbe and Smith 2005).

The effects of light and CO_2 operate in concert with a suite of environmental parameters, both natural and anthropogenic, which influence coral calcification and growth. Several studies have documented a reduction in coral calcification as a result of nutrient enrichment (Tomascik and Sander 1985; Stambler et al. 1991; Marubini and Davies 1996; Ferrier-Pagès et al. 2000) and *A. cervicornis* is no exception (Renegar and Riegl 2005). In these situations, it is hypothesized that dissolved inorganic nitrogen can stimulate zooxanthellae populations leading to elevated gross photosynthesis and either stronger competition for DIC necessary for calcification or reduced organic carbon provided to the host (Stambler et al. 1991).

Sedimentation, turbidity, and light are often linked in the field. However, artificially elevated sedimentation rates (200 mg cm^{-1}) applied to *A. cervicornis* colonies over a period of 45 d resulted in no significant change in growth rate, and the elongate cylindrical form of this species may be especially adept at preventing the deleterious accumulation of sediments (Rogers 1979). In natural environments, where suspended sediments are sufficiently high to reduce light availability, they may negatively influence coral growth (Shinn 1966).

Additionally, evidence suggests that heterotrophy may help to offset the negative effect of elevated pCO_2 on calcification (Edmunds 2011). Given that calcification is an energetically costly process (e.g., Cohen et al. 2009), high light and increased heterotrophy may be similar in that they could satisfy the necessary metabolic carbon demand for calcification and potentially ameliorate the effects of OA. It is cautioned that these are complex processes and that the relationship between heterotrophy and carbon translocation between symbionts and hosts may be in fact complicated

by light intensity (Tremblay et al. 2013). The degree to which these factors interact to influence the calcification of *A. cervicornis* was not tested in this experiment and is, as of yet, unknown. Similarly, several studies have shown that elevated temperature can increase calcification provided that they do not surpass an optimal value (Cooper et al. 2012; Edmunds et al. 2012). In controlled situations, where seasonal thermal maxima do not induce stress or bleaching (Baker et al. 2008), this could provide a mechanism for enhancing coral calcification and possibly offsetting OA.

The results of this study and that of Renegar and Riegl (2005) show that calcification of *A. cervicornis* is negatively influenced by seawater pCO_2 levels projected to occur by the end of the century. Decreased calcification can be expected to negatively impact the recovery of wild populations and detrimentally influence restoration operations. The need for environmental refugia was evident during the 2010 cold-water anomaly that affected the Florida Keys. During this event, coral nurseries deployed in deeper habitats experienced lower mortality than those sites established in shallower habitats closer to shore where temperature extremes were more pronounced (Lirman et al. 2011; Schopmeyer et al. 2012). Thus, we recommend that future plans for the expansion of coral restoration programs consider the possibility of targeting potential OA refugia as part of their long-term activities to buffer the impacts of elevated CO_2 (Manzello et al. 2012). The underwater light environment must also be considered as it had a stronger effect on calcification in this study. Nurseries located in areas with high water clarity and high light will yield the greatest rates of calcification and production of *A. cervicornis* for restoration efforts. It is cautioned, however, that these areas may often be prone to periodic temperature extremes that can cause bleaching and mortality (Shinn 1966; Lirman et al. 2011), and in many regions, they may be located closer to land-based sources of pollution. Further investigation is necessary to identify environmental conditions that maximize coral growth and calcification, minimize mortality, and promote the rapid restoration of threatened coral species.

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References

Albright R, Mason B, Miller M, Langdon C (2010) Ocean acidification compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. Proc Natl Acad Sci USA 107:20400–20404

Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proc R Soc Lond, B 276:3019–3025

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38

Aronson RB, Bruckner A, Moore J, Precht WF, Weil E (2008) *Acropora cervicornis*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>

Baker AC, Glynn PWP, Riegl BM (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471

Burdige DJ, Zimmerman RC (2002) Impact of sea grass density on carbonate dissolution in Bahamian sediments. Limnol Oceanogr 47:1751–1763

Burdige DJ, Zimmerman RC, Xinping H (2008) Rates of carbonate dissolution in permeable sediments estimated from pore-water profiles: The role of sea grasses. Limnol Oceanogr 53:549–565

Chalker BE (1981) Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. Mar Biol 63:135–141

Chalker BE, Taylor DL (1975) Light-enhanced calcification, and the role of oxidative phosphorylation in calcification of the coral *Acropora cervicornis*. Proc R Soc Lond, B 190:323–331

Chamberlain JA (1978) Mechanical properties of coral skeleton: compressive strength and its adaptive significance. Paleobiology 4:419–435

Chappell J (1980) Coral morphology, diversity and reef growth. Nature 286:249–252

Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA (2009) Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into the biomineralization response to ocean acidification. Geochemistry Geophysics Geosystems 10:1–12

Cooper TF, O'Leary RA, Lough JM (2012) Growth of Western Australian corals in the anthropocene. Science 335:593–596

Courtney LA, Fisher WS, Raimondo S, Oliver LM, Davis WP (2007) Estimating 3-dimensional colony surface area of field corals. J Exp Mar Biol Ecol 351:234–242

Crabbe MJC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24:437–441

Default AM, Ninokawa A, Bramanti L, Cumbo VR, Fan T-Y, Edmunds PJ (2013) The role of light in mediating the effects of ocean acidification on coral calcification. J Exp Biol 216:1570–1577

Dickson AG (1990) Thermodynamics of the dissociation of boric acid in synthetic seawater from 273.15 to 318.15 K. Deep-Sea Res 37:755–766

Dickson AG, Millero FFJ (1987) A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep-Sea Res 34:1733–1743

Edmunds PJ (2011) Zooplanktivory ameliorates the effects of ocean acidification on the reef coral *Porites* spp. Limnol Oceanogr 56:2402–2410

Edmunds PJ, Brown D, Moriarty V (2012) Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. Global Change Biol 18:2173–2183

Falkowski P, Dubinsky Z (1981) Light-shade adaptation *of Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature 289:172–174

Ferrier-Pagès C, Gattuso JP, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. Coral Reefs 19:103–113

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gladfelter EH, Monahan RK, Gladfelter WB (1978) Growth rates of five reef-building corals in the northeastern Caribbean. Bull Mar Sci 28:728–734

Highsmith RC, Riggs AC, D'Antonio CM (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322–329

Hoegh-Guldberg O (1988) A method for determining the surface area of corals. Coral Reefs 7:113–116

Hogarth WT (2006) Endangered and threatened species: final listing determinations for the elkhorn coral and staghorn coral. Fed Register 71:26852–26872

Jaap WC (1974) Scleractinian growth rate studies. Proc Fl Keys Coral Reef Wrkshp. FL Dept Nat Res Coastal Coordinating Council. p 17

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. In: Stoddart DR, Johannes RE (eds) Coral Reefs: Research Methods. UNESCO monographs on oceanographic methodology, Paris, pp 529–542

Kendall JJ Jr, Powell EN, Connor SJ, Bright TJ, Zastrow CE (1985) Effects of turbidity on calcification rate, protein concentration and the free amino acid pool of the coral *Acropora cervicornis*. Mar Biol 87:33–46

Langdon C, Atkinson MJ (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. J Geophys Res C 110:C09S07.1–C09S07.16

Lewis E, Wallace D (1998) Program developed for CO_2 system calculations. ORNL/CDIAC-105, Oak Ridge National Laboratory

Lirman D (2000) Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. J Exp Mar Biol Ecol 251:41–57

Lirman D, Thyberg T, Herlan J, Hill C, Young-Lahiff C, Schopmeyer SA, Huntington B, Santos R, Drury C (2010) Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. Coral Reefs 29:729–735

Lirman D, Schopmeyer SA, Manzello DP, Gramer LJ, Precht WF, Muller-Karger F, Banks K, Barnes B, Bartels E, Bourque A, Byrne J, Donahue S, Duquesnel J, Fisher L, Gilliam D, Hendee J, Johnson M, Maxwell K, McDevitt E, Monty J, Rueda D, Ruzicka R, Thanner S (2011) Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. PloS ONE 6:1–10

Manzello DP, Enochs IC, Melo N, Gledhill DK, Johns EM (2012) Ocean acidification refugia of the Florida Reef Tract. PloS ONE 7:1–10

Marsh JA Jr (1970) Primary productivity of reef-building calcareous red algae. Ecology 51:255–263

Marubini F, Davies PS (1996) Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. Mar Biol 127:319–328

Marubini F, Barnett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. Mar Ecol Prog Ser 220:153–162

McCulloch M, Falter J, Trotter J, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH up-regulation. Nature Climate Change 2:623–627

Mehrbach C, Culberson CH, Hawley JE, Pytkowicx RM (1973) Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. Limnol Oceanogr 18:897–907

Muscatine L, Falkowsky PG, Porter JW, Dubinsky Z, Falkowski PG (1984) Fate of photosynthetic fixed carbon in light-and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proc R Soc Lond, B 222:181–202

Raz-bahat M, Faibish H, Mass T, Rinkevich B (2009) Three-dimensional laser scanning as an efficient tool for coral surface area measurements. Limnol Oceanogr-Meth 7:657–663

Renegar DA, Riegl BBM (2005) Effect of nutrient enrichment and elevated CO_2 partial pressure on growth rate of Atlantic scleractinian coral *Acropora cervicornis*. Mar Ecol Prog Ser 293:69–76

Rogers CS (1979) The effect of shading on coral reef structure and function. J Exp Mar Biol Ecol 41:269–288

Schopmeyer SA, Lirman D, Bartels E, Byrne J, Gilliam DS, Hunt J, Johnson ME, Larson EA, Maxwell K, Nedimeyer K, Walter C (2012) In situ coral nurseries serve as genetic repositories for coral reef restoration after an extreme cold-water event. Restor Ecol 20:696–703

Schuhmacher H, Plewka M (1981) The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora plamata* and *Acropora cervicornis* (Cnidaria, Scleractinia). Proc 4th Int Coral Reef Symp 2:121–128

Schutter S, van Velthoven B, Janse M, Osinga R, Janssen M, Wijffels R, Verreth J (2008) The effect of irradiance on long-term skeletal growth and net photosynthesis *in Galaxea fascicularis* under four light conditions. J Exp Mar Biol Ecol 367:75–80

Shinn EA (1966) Coral growth-rate, an environmental indicator. J Paleontol 40:233–240

Stambler N, Popper N, Dubinsky Z, Stimson J (1991) Effects of nutrient enrichment and water motion on the coral *Pocillopora damicornis*. Pac Sci 45:299–307

Stimson J, Kinzie RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis*(Linnaeus) under nitrogen-enrichment and control conditions. J Exp Mar Biol Ecol 153:63–74

Suggett DJ, Dong LF, Lawson T, Lawrenz E, Torres L, Smith DJ (2012) Light availability determines susceptibility of reef building corals to ocean acidification. Coral Reefs 32:327–337

Takahashi A, Kurihara H (2013) Ocean acidification does not affect the physiology of the tropical coral *Acropora digitifera* during a 5-week experiment. Coral Reefs 32:305–314

Tomascik T, Sander F (1985) Effects of eutrophication on reef-building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. Mar Biol 87:143–155

Torres JL, Armstrong RA, Corredor JE, Gilbes F (2007) Physiological responses of *Acropora cervicornis* to increased solar irradiance. Photochem Photobiol 83:839–850

Tremblay P, Grover R, Maguer JF, Hoogenbroom M, Ferrier-Pagès (2013) Carbon translocation from symbiont to host depends on irradiance and food availability in the tropical coral Stylophora pistillata. Coral Reefs. doi:10.1007/s00338-013-1100-7

Tunnicliffe V (1979) The role of boring sponges in coral fracture. In: Levi C, Boury-Esnault N (eds) Biologie des spongiares. Coll Int, Centre National de la Recherche Scientifique, 291:309–315

Tunnicliffe V (1981) Breakage and propagation of the stony coral *Acropora cervicornis*. Proc Natl Acad Sci USA 78:2427–2431

Vargas-Angel B, Thomas JD, Hoke SM (2003) High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. Coral Reefs 22:465–473

Vollmer SV, Palumbi SR (2007) Restricted gene flow in the Caribbean staghorn coral *Acropora cervicornis*: implications for the recovery of endangered reefs. J Hered 98:40–50

Wisshak M, Schönberg CHL, Form A, Freiwald A (2012) Ocean acidification accelerates reef bioerosion. PloS ONE 7:1–8

Young CN, Schopmeyer SA, Lirman D (2012) A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and western Atlantic. Bull Mar Sci 88:1075–1098