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Ocean warming drives decline in coral metabolism while acidification highlights species-specific responses

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ABSTRACT
Ocean warming and acidification can have negative implications on coral reefs. This mechanistic study aims to evaluate the proximal causes of the observed negative response of Hawaiian corals to climate change scenarios. Net calcification ($G_{\text{net}}$), gross photosynthesis, and dark respiration were measured in three species of Hawaiian corals across a range of temperature and acidification regimes using endpoint incubations. Calcification rates showed a curvilinear response with temperature, with the highest calcification rates observed at 26°C. Coral response to ocean acidification (OA) was species dependent and highly variable. OA enhanced calcification rates by 45% in the perforate coral, Montipora capitata, but had no short-term effect on the calcification or photosynthetic rates of imperforate corals, Pocillopora damicornis or Leptastrea purpurea. Further investigations revealed M. capitata to effectively dissipate protons (H$^+$) while increasing uptake of bicarbonate (HCO$_3^-$), therefore maintaining high rates of $G_{\text{net}}$ under acute OA stress. This study demonstrates the first experimental evidence of the ability of a coral species to take advantage of increased dissolved inorganic carbon and overcome an increasing proton gradient in the boundary layer under OA conditions. These observed differences in coral metabolism may underlie the species-specific responses to climate change.

Introduction

Increases in anthropogenic carbon dioxide in the atmosphere warm the planet, increase sea surface temperatures, and increase the acidity of the ocean. Ocean acidification (OA) and warming have been shown to have severe negative effects on coral reef organisms (Jokiel et al. 2008; Erez et al. 2011; Kroeker et al. 2013). Coral calcification rates are predicted to decrease by 40% by the end of the century unless anthropogenic emissions of greenhouse gasses are sharply curtailed (Gattuso et al. 1999; Kleypas et al. 1999; Langdon et al. 2000; Marubini et al. 2001, 2003; Müller et al. 2004; Langdon and Atkinson 2005; Kleypas and Langdon 2006; Hofmann et al. 2010; Erez et al. 2011). As ocean warming and acidification increase in unison, we must understand the independent and interactive effects of these stressors on marine organisms.

Corals experience dynamic fluctuations in environmental parameters over seasonal and diurnal timescales. For example, oxygen concentrations on coral reefs fluctuate from hyperoxic during the day to hypoxic at night (Shashar et al. 1993; Kühl et al. 2008). Tidal fluctuations drive daily temperature variations between 1–2°C or up to 6°C in more extreme reef environments such as Ofu Island, American Samoa (Craig et al. 2001). Additionally, pH may fluctuate daily between 7.8 and 8.2 due to photosynthesis and respiration of reef organisms (Jokiel et al. 2014). These dynamic environmental conditions may constrain the corals’ ability to exchange gas and solutes with the environment (dependent on the size of the boundary layer) or the effect of the presence of an endolithic community within the skeleton (Kühl et al. 2008). In fact, larger than those changes related to the external environment are the internal changes in pCO$_2$ that occur within coral tissues every day as resulting from the activation or suppression of coral photosynthesis. Photosynthesis by symbiotic zooxanthellae provide up to 90% of the energy for tropical and subtropical reef-building corals (Chalker and Taylor 1975). Extreme and sub-optimal temperatures negatively impact net photosynthesis ($P_{\text{net}}$) and elevate respiration (R) of the coral holobiont (Coles and Jokiel 2006).
Thus, metabolism can be used as an indicator of coral tolerance (Castillo and Helmuth 2005). The effects of elevated temperature have been well documented but less is known about OA implications and the combined effects of temperature and OA on these essential processes. It is possible that OA may enhance photosynthesis by reducing the high energetic cost of carbon delivery via carbon concentration mechanisms to the algal symbionts as well as the coral host. However, previous studies have shown that some corals and other calcifying marine invertebrates have depressed metabolism under OA conditions (Reipschläger and Pörtner 1996; Michaelidis et al. 2005; Anthony et al. 2008; Edmunds 2012; Hoadley et al. 2015). Additionally, calcification is limited by the diffusion of the calcification waste product (H+) through the boundary layer. The increasing proton gradient under OA conditions limits proton diffusion through the boundary layer and increases acidosis in the coral tissues (Proton Flux Hypothesis) (Jokiel 2011).

Numerous studies have demonstrated differences in responses to temperature and OA among various coral genera and species (Erez et al. 2011; Bahr et al. 2016). Previous work has shown little or no effect of OA on the calcification of certain coral species such as Stylophora pistillata (Reynaud et al. 2003), Porites spp. (Edmunds et al. 2012) and Montipora capitata (Bahr et al. 2016). Cryptic and slow growing species (e.g. Leptastrea purpurea) have been typically found to be more resistant to thermal stress (Loya et al. 2001; Bahr et al. 2016). Species-specific responses observed in these studies and others may be attributed to differences in the coral host metabolism, respiration rates, tissue composition and thickness, lipid concentration, or physiological and photosynthetic differences among the symbionts (Baird et al. 2009). Additionally, temperature and OA sensitivity within the coral-algal complex is highly variable among symbiont clade, coral species, and associated genotypes (Fitt et al. 2009; Hoadley et al. 2015), and may change seasonally (Scheuflen et al. 2017). Studies have attempted to assess the physiological tolerance and characteristics of the algal symbiont, but these studies fail to account for the coral host metabolism, which may play an equally important role in determining coral tolerance (Fitt et al. 2009; Hoadley et al. 2015).

Therefore, we conducted a series of manipulative experiments to test the metabolic plasticity of common coral species in Hawai‘i under short-term exposure to OA and elevated temperature. The objectives of this study were to (1) characterize the relationship between coral calcification, photosynthesis, and respiration across a range of temperature and OA regimes and (2) quantify the interactive effect of temperature and OA on the metabolism of selected coral species.

**Materials and methods**

This research was conducted at the Hawai‘i Institute of Marine Biology (HIMB) at Moku o Lo‘e, Kāne‘ohe Bay, Hawai‘i (21.4°N, 157.8°W). Water temperatures inside Kāne‘ohe Bay range from 22–23°C in the winter to 27–28°C in the summer with daily temperature fluctuations between 1–2°C (Bahr et al. 2015). Three species of corals were selected for this study. *Pocillopora damicornis* is a small branching coral that is common in shallow water throughout the bay and is among the most sensitive to high temperature (Bahr et al. 2016). This species is widely distributed throughout the Indo-Pacific and has been the subject of much research throughout its range (Richmond 1987). *M. capitata* is a major reef-forming coral in Kāne‘ohe Bay and possesses many growth forms (i.e. encrusting, plating, branching) (Maragos 1972; Forstman et al. 2010). The most abundant branching morphology was used in this study. *L. purpurea* is a small, cryptic encrusting coral that shows tolerance to environmental extremes (Bahr et al. 2015, 2016). Corals used in this investigation were collected at a depth of 1 m from the adjacent reef flat surrounding Moku o Lo‘e.

**Acclimation holding tank**

Five different individuals within each of the 3 species (i.e. *P. damicornis*, *M. capitata*, and *L. purpurea*) were fragmented (5 cm branches), tagged and affixed onto clear acrylic plastic squares (2.5 cm²) in an upright position. The corals (*n* = 15) were then cultured in a 10 L recirculating holding tank under optimal control conditions of temperature (26°C), pH (8.0) and salinity (35 ppt) for four weeks. The seawater was filtered (0.22 μm) to limit the contribution of heterotrophic feeding to the metabolic rates of the experimental corals (Szmant-Froelich and Pilson 1984). Complete water changes occurred every other day throughout the experimental period. A submersible aquarium titanium heater and chiller (CSXC-1, Chill Solutions LLC) controlled temperature in the holding tank. Light was provided by 250 W metal halide lamps at an irradiance of 500 μmol photons m⁻² s⁻¹ on a 12 h light:dark cycle controlled by a timer. A submersible pump and air stone provided a high rate of circulation and turbulence in the holding tank. Before each experimental
run, the corals were acclimated to experimental temperature and pCO₂ treatments for 48 h in the 10 L recirculating holding tank. Coral acclimation to new chemistry conditions can occur in <3 h (Furla et al. 2000; Langdon and Atkinson 2005).

**Experimental setup and incubation procedures**

The five different individuals (n = 15) of each coral species (i.e. *P. damicornis*, *M. capitata*, and *L. purpurea*) were exposed to six replicated treatments consisting of two CO₂ levels (present day Kāne‘ohi Bay levels and 2X present) and three temperature regimes (23°C, 26°C, and 30°C) under constant light levels (∼500 µmol photons m⁻² s⁻¹) (Table I).

During the incubations, temperature was maintained using submersible aquarium titanium (Finnex, TH-08005) heaters and a titanium coil water chiller (Aqua Logic Cyclone, model CY-4, 115 V) in a large 200 L temperature-controlled water bath. Irradiance during the incubations was supplied by four 250 W metal halide lamps at an intensity of 500 µmol photons m⁻² s⁻¹. Carbonate chemistry was manipulated through direct bubbling of CO₂ into stock filtered seawater. This filtered seawater was then aliquoted into eighteen 1 L glass incubation beakers. Each experimental run contained eighteen 1 L glass beakers: fifteen contained one of the five individuals of each species (*M. capitata*, *L. purpurea*, and *P. damicornis*), and three served as controls to correct for non-coral changes in seawater chemistry during the incubations.

Incubations proceeded by placing each coral fragment into a single 1 L glass beaker. Each beaker was fitted with a floatation collar and contained the targeted experimental seawater treatments (Table I). Beakers (n = 18) were placed inside the large 200 L temperature-controlled water bath to allow for coral acclimation to experimental conditions and irradiance regime (i.e. light or dark). Incubation chambers were left open to the atmosphere to allow pH and temperature to be monitored. A submersible pump vigorously agitated the water in the water bath such that the floating incubation beakers bobbed and circulated the water bath for no possibility of a position effect. The constant motion created sufficient mixing within the beakers to cause visible swaying in the coral polyps (Coles and Jokiel 1977).

After a one-hour acclimation to the light regime (i.e. light or dark), total alkalinity (TA), dissolved oxygen (DO), pH, and temperature measurements were taken as the initial reading of the incubation. Corals were then incubated for 1 h under treatment conditions in the same light regime (e.g. light). Samples were collected (i.e. TA, DO, temperature, pH), the light was turned off, and the corals were acclimated for 1 h in darkness, which was followed by a dark incubation for 1 h. Each experimental run consisted of a 1 h light acclimation followed by a 1 h incubation with samples of TA, DO, pH and temperature collected at the beginning and end of each incubation period. Initial and final water samples were also taken from each of the three seawater-only control beakers, the results of which were averaged and used to correct for non-biologically related changes in chemistry.

After the experimental run was complete, all coral samples were returned to the 10 L holding tank and allowed (48 h) to re-adjust to optimal conditions (26°C and pH = 8.0) before starting the next experimental run. One experimental run (1 light and 1 dark incubation) was performed every 3 days for a 30 d period. Each treatment was performed twice and the mean response was used for statistical analysis. The order of the treatment incubations (experimental conditions) and light regimes (light or dark) were randomized. The same coral colonies were measured repeatedly throughout the randomized series of treatment and light incubations such that each colony was measured under each set of conditions. This allowed comparison of individual coral performance of the same coral in the different treatments. This experimental design was accounted for in the repeated measure statistical analyses. In order to account for any carry-over effect, the order of treatment exposure was included as a random factor in the mixed model approach.

**Analytical procedures**

Measurements of temperature (°C), polarographic dissolved oxygen (mg l⁻¹), and salinity (‰) were taken before and after each incubation using a YSI multiparameter metre (YSI 556MPS, accuracy ± 0.15°C ± 0.2 mg l⁻¹, ±2 ‰). An Accumet AP72 pH/mV/temperature metre (accuracy ± 0.01 pH and ±0.02 mV) was used to measure pH₇. Filtered seawater samples for TA measurements were collected and stored in 120 mL clear borosilicate glass bottles and analyzed within 2 h of collection. TA was measured independently using an automatic titrator (Titirno Plus 877, Metrohm) with pH glass electrode (9101 Herisau, Metrohm). Precision of the automatic titrator was confirmed with certified reference materials (Batch 127 from A. Dickson Laboratory, Scripps Institution of Oceanography). Temperature, TA, pH₇ and salinity were used to calculate pCO₂, dissolved inorganic
carbon (DIC), and proton concentration (H+) in CO2SYS (Pierrot et al. 2006) with the stoichiometric dissociation constants (K1, K2) defined by Mehrbach (1973) and refit by Dickson and Millero (1987). Irradiance reaching the corals within each beaker was measured using a cosine corrected quantum sensor (LI-250A metre, LI-7792 sensor).

**Measurements of photosynthesis, respiration and calcification rates**

Coral calcification (G<sub>net</sub>), net photosynthesis (P<sub>net</sub>) at 500 μmol photons m<sup>−2</sup> s<sup>−1</sup>, and respiration in dark (R) were measured. The techniques used in this study were nondestructive and allow for repeated measurements using the same individual under different experimental conditions (Chisholm and Gattuso 1991; Jury et al. 2010). All response variables were normalized to the dry weight of each colony via buoyant weight (Jokiel et al. 1978).

**Measurements of net calcification (G<sub>net</sub>)**

G<sub>net</sub> was calculated from the changes in alkalinity during the incubation periods using the TA anomaly method (Smith and Kinsey 1978). Calcification produces an excess of H<sup>+</sup> and thus reduces TA by two moles for every mole of CaCO<sub>3</sub> precipitated (Smith and Kinsey 1978; Murillo et al. 2014). Initial and final TA values collected during the incubations were used to calculate G<sub>net</sub>. Changes in TA were corrected for any change in the TA in the seawater-only (control) beakers (Jury et al. 2010). G<sub>net</sub> represents the sum of all the calcification processes minus the sum of all the dissolution processes. Thus, all positive numbers are net calcification and all negative numbers are net dissolution. All calcification rates are presented as mg g<sup>−1</sup> CaCO<sub>3</sub> h<sup>−1</sup>.

**Photosynthesis (P<sub>net</sub>) and respiration (R)**

Dissolved oxygen concentrations remained between 80–100% throughout incubation periods. P<sub>net</sub> and R were calculated from changes in dissolved oxygen concentration (mg L<sup>−1</sup>) in the chambers during the incubation period and corrected using the controls. Photosynthetic and respiration rates are expressed as mg O<sub>2</sub> g<sup>−1</sup> CaCO<sub>3</sub> h<sup>−1</sup>. P<sub>net</sub> represents oxygen production in the light and R refers to oxygen consumption when corals were incubated in the dark. P:R as used herein refers to the ratio of the 1 h P<sub>net</sub> in light to 1 h R in darkness.

**Statistical analyses**

In an attempt to reduce variation between experimental units, which may obscure the effects of the treatment, the same individual coral was exposed to the experimental treatment structure that was applied randomly over time. Therefore, the biological response variables (i.e. photosynthesis and respiration, P:R and G<sub>net</sub>) were analyzed using a Repeated Measures Mixed Model. The models embraced a full factorial of fixed factors (i.e. temperature, pH), and their interactions. Individual was included as a random factor to account for the repeated measures design (Table II). To account for any potential carry over effects, sequence order of treatments and trial was included as a random factor in the model. This model was fitted for each species. Analysis of G<sub>net</sub> also included a quadratic term for temperature designed to model curvature of the line fitted to the data (sensu Bahr et al., 2017). Assumptions of normal distribution and homoscedasticity were assessed through graphical analyses of the residuals. Descriptive and statistical analyses were conducted using JMP 13 Pro (SAS Institute Inc., USA).

**Results**

**Treatment conditions**

Incubations were conducted in a dark room that eliminated all external light. In all cases, corals received either constant irradiance levels of 500 μmol photons m<sup>−2</sup> s<sup>−1</sup> during light incubations or total darkness during dark incubations. Manipulations of temperature at 23°C (One way ANOVA; F<sub>1,46</sub> = 2.7106; p = 0.1071), 26°C (One way ANOVA; F<sub>1,46</sub> = 2.7345; p = 0.1050) and 30°C (One way ANOVA; F<sub>1,46</sub> = 0.0236; p = 0.8787) did not differ among pH treatments. Also,
treatments of pH 8.0 (One way ANOVA; $F_{(2, 69)} = 2.7876; p = 0.0685$) and pH 7.7 (One way ANOVA; $F_{(2, 69)} = 2.0518; p = 0.1363$) did not differ across temperatures (Table I). Salinity did not change over the course of the 1 h incubations. Treatment conditions were maintained; therefore, no off-gassing occurred in the high pCO$_2$ treatments.

**Photosynthetic rates (P$_{net}$)**

Photosynthetic rates generally decreased with increasing temperatures, but response varied among species (Figure 1). The largest declines in photosynthetic rates (mean difference ± SE) occurred in *L. purpurea* (−27%; $-0.013 ± 0.006$ mg O$_2$ g$^{-1}$ CaCO$_3$ h$^{-1}$; $p = 0.0099$) under elevated temperature stress (30°C). Significant declines in photosynthetic rates were not observed in *M. capitata* ($p = 0.131$), or *P. damicornis* ($p = 0.368$) (Table II). Acute acidification stress (48 h) alone or in combination with temperature had no influence on the photosynthetic rates of any of the tested species (*L. purpurea*, $p = 0.5522$, $p = 0.309$; *M. capitata*, $p = 0.183$, $p = 0.500$; *P. damicornis*, $p = 0.2075$, $p = 0.707$) (Table II).

**Dark respiration rates (R)**

Temperature had a significant influence on the respiration rates of *P. damicornis* ($p = 0.0078$) (Figure 1). In comparison to 23°C, respiration rates (mean difference ± SE) increase by 48% in *P. damicornis* (+0.014 ± 0.004 mg O$_2$ g$^{-1}$ CaCO$_3$ h$^{-1}$; $p = 0.0275$) at 30°C. Respiration rates of *L. purpurea* ($p = 0.086$) and *M. capitata* were not significantly influenced by temperature ($p = 0.259$) (Table II). Acidification increased respiration rates (mean difference ± SE) by 31% in *M. capitata* (+0.012 ± 0.004 mg O$_2$ g$^{-1}$ CaCO$_3$ h$^{-1}$; $p = 0.0156$), and by 26% in *P. damicornis* (+0.0083 ± 0.003 mg O$_2$ g$^{-1}$ CaCO$_3$ h$^{-1}$; $p = 0.0275$). The respiration rates of *L. purpurea* was not impaired by acute exposure to acidification ($p = 0.086$). The combined effect of temperature and acidification did not influence respiration rates of the tested species (*L. purpurea*, $p = 0.991$; *M. capitata*, $p = 0.905$; *P. damicornis*, $p = 0.551$).

**P:R ratios**

P:R ratios decline linearly with increasing temperature (Figure 1). Elevated temperature (30°C) drove the largest declines (mean difference ± SE) in *L. purpurea* (−37%; $-0.61 ± 0.11$; $p = 0.0031$) and in *P. damicornis* (−28%; $-0.37 ± 0.14$; $p = 0.0481$). Depressed P:R ratios were also observed in *M. capitata* (−19%; $-0.27 ± 0.12$; $p = 0.0074$) (Table II). Acidification suppressed P:R ratios in all species. The largest declined in P:R ratios was observed in *P. damicornis* (−20%; $-0.31 ± 0.11$; $p = 0.0255$), followed by *L. purpurea* (−17%; $-0.29 ± 0.11$; $p = 0.0218$) and *M. capitata* (−14%; $-0.22 ± 0.10$; $p = 0.0480$). No interactive effects between temperature and acidification were observed on the P:R ratios of the tested species.

**Calcification rates (G$_{net}$)**

Calcification rates showed a curvilinear response with temperature (Temperature$^2$: *L. purpurea*, $p = 0.0010$; *M. capitata*, $p = 0.0090$; *P. damicornis*, $p = 0.0106$). All species showed an optimum growth rate at 26°C (Figure 1). Elevated temperatures (30°C) reduced calcification rates (mean difference ± SE) in *P. damicornis*...
M. capitata (−57%; −0.15 ± 0.05 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0343\)), and L. purpurea (−53%; −0.06 ± 0.02 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0247\)) (Figure 1). Similarly, lower temperatures (23°C) suppress growth rates in P. damicornis (−80%; −0.15 ± 0.04 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0223\)), M. capitata (−62%; −0.17 ± 0.05 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0258\)), and L. purpurea (−97%; −0.10 ± 0.02 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0021\)) compared to optimal growth rates at 26°C.

The influence of short-term exposure acidification on calcification rates differed across species. Increased acidification enhanced calcification rates (mean difference ± SE) of M. capitata by 45% compared to corals under ambient conditions (+0.10 ± 0.04 mg g\(^{-1}\) h\(^{-1}\); \(p = 0.0453\)). Acidification did not have an effect on the
calcification rates of *L. purpurea* (*p* = 0.762) and *P. damicornis* (*p* = 0.767) (Figure 1). Short-term exposure to temperature and acidification did not interact to influence calcification rates of tested species.

**Discussion**

Results of this work identify species-specific physiological responses to warming and acidification stress. Acute exposure to elevated temperature drove declines in photosynthetic rates of *L. purpurea*, which drove declines in P:R. Acidification had little to no impact on *L. purpurea*. Short-term exposure to acidification increased calcification rates in *M. capitata* but at a cost of high respiration rates and impacting P:R ratios. Lastly, short-term exposure to warming and acidification increased respiration rates, therefore impacting P:R ratios of *P. damicornis*.

Elevated temperature had a significant effect on physiological responses, while acidification mainly drove species-specific responses. Autotrophic capacity (P:R ratio) was suppressed across all tested coral species. Overall, P:R ratios decreased with increasing temperature, which is consistent with previous work conducted on Hawaiian species (Coles and Jokiel 1977; Porter et al. 2004; Al-Horani 2005; Castillo and Helmuth 2014). Sub-optimal temperatures negatively impact net photosynthesis and elevate respiration of the coral holobiont (Coles and Jokiel 1977; Porter et al. 1989). Elevated temperatures cause the light reactions of photosynthesis to malfunction and reduce autotrophic capacity (P:R ratio) of the coral (Lesser 1997; Jones et al. 1998; Saxby et al. 2003; Tchernov et al. 2004; Al-Horani 2005; Castillo and Helmuth 2005). This impairment of the photosynthetic system causes corals to rely on heterotrophic feeding and stored lipids to meet their energy needs (Iglesias-Prieto 1997; Jokiel 2004). Low P:R ratios may restrict coral calcification and maintenance of energy reserves (e.g. lipids), which are essential for sustaining homeostatic functions as well as sexual reproduction and biophysical stress resistance (Wooldridge 2014).

Calcification rates show a curvilinear response with temperature, with the highest calcification rates observed at 26°C. This is in agreement with others (Jokiel and Coles 1977; Cantin et al. 2010; Castillo et al. 2014; Bahr et al. 2017) where *G*$_{\text{net}}$ shows a parabolic response to temperature. Acute elevated temperatures (30°C) reduced calcification between 50–60% among the tested species, while suboptimal exposure at 23°C reduced by 60–97%.

Coral response to acute exposure to acidification was species dependent and highly variable among the response variables. It has been hypothesized that OA may enhance photosynthesis by reducing the high energetic cost of carbon delivery via carbon concentration mechanisms to the algal symbionts as well as the coral host. Acidification did not enhance photosynthetic rates, but OA was observed to increase dark respiration rates (in *M. capitata* and *P. damicornis*, but not *L. purpurea*) and decrease P:R ratios across species. Conversely, high pCO$_2$ had no effect on the dark respiration of *S. pistillata* (Reyna et al. 2003) or *Acropora eurystoma* (Schneider and Erez 2006) further revealing a species-specific response. These results are somewhat in agreement with previous studies that have shown ocean acidification (OA) conditions reduced coral metabolism, decrease calcification, increase loss of *Symbiodinium* populations and increase oxidative stress (Reipschläger and Pörtner 1996; Michaelidis et al. 2005; Anthony et al. 2008; Jokiel et al. 2008; Cantin et al. 2010; Edmunds 2012; Kaniewska et al. 2012; Hoadley et al. 2015).

The interactive effects of temperature and acidification did not influence the physiological responses of the tested coral species. Elevated temperature and acidification have been documented to have negative synergistic effects on *S. pistillata* (Reyna et al. 2003) and *Porites panamensis* (Anlauf et al. 2011) and on the partial mortality rates of Hawaiian endemic, *Porites compressa* (Bahr et al. 2016). In contrast, high pCO$_2$ mitigates the negative effect of elevated temperature on photosynthetic rates of *Galaxea fascicularis* (Agostini et al. 2013) and on the calcification of *P. damicornis* after long-term (42 d) exposure (Bahr et al. 2016).

The varied responses in respiration and photosynthesis across the species under elevated temperature and OA conditions indicates a shift of energy allocation to repair and/or stabilize impacted physiological processes (Gates and Edmunds 1999). In mature corals, somatic maintenance constitutes the majority of the energy budget and takes priority over growth and reproduction when influx of energy is low (Rombough 1994; Kooijman 2010). It is likely these physiological processes are more impaired under long term exposure to OA and warming stress.

The response of corals to environmental challenges depends on the frequency, severity, and duration of the disturbance. Subsequently, the physiological responses to such perturbations can range from subtle to severe. Short-term (48 h) exposure to OA showed enhanced calcification rates in *M. capitata* and no influence on *P. damicornis* or *L. purpurea*. Also, elevated temperatures reduced calcification among the tested species. Conversely, *L. purpurea* was shown
to not respond to long-term exposure to acidification or temperature stress (Bahr et al. 2016). Additionally, calcification rates in *M. capitata* were not influenced by long-term exposure (42 d) to lowered pH and acidification ameliorated the negative effect of high temperature on the calcification rates of *P. damicornis* (Bahr et al. 2016). Clearly, biological responses vary among species and between acute and chronic environmental stress, however differences in calcification response can be attributed to methodology for measuring calcification. Chan and Connolly (2013) found that studies using buoyant weighting found significantly smaller decreases in calcification under ocean acidification scenarios (~10%) compared with studies using the alkalinity anomaly technique (~25%). The differences between these methods have been attributed to the tendency for the buoyant weighing methods to integrate over light and dark calcification. Moreover, seasonality in environmental factors (i.e. temperature and irradiance) will directly influence coral metabolic and calcification rates. During sea surface temperature anomalies (i.e. bleaching events) corals rely on a combination of alternative sources of fixed carbon (e.g. energy reserves, heterotrophy) to recover from bleaching (Levas et al. 2016). However, heterotrophic plasticity is highly species specific. For example, *M. capitata* and *Porites astreoides* can increase their zooplankton consumption to meet their metabolic demand during bleaching events (Rodrigues and Grottoli 2007; Grottoli et al. 2014), while Caribbean corals, *Porites divaricata* and *Orbicella faveolata*, have significantly lower heterotrophic contribution to their energy needs (Grottoli et al. 2014).

As processes, photosynthesis and calcification compete for dissolved inorganic carbon (DIC) (Jokiel et al. 2016). Under OA conditions, dissolved inorganic carbon (DIC) concentrations increase, therefore we may observed increases in photosynthetic rates, as illustrated in *M. capitata* (Figure 1). Calcification rates are expected to increase as well due to the increased availability of DIC; however, this did not occur across all species. During calcification, precipitation of calcium carbonate from Ca\(^{2+}\) and HCO\(_3^-\) generates excess protons inside the calcification compartment. In order to maintain acid-base regulation, this compartment requires these excess calcification waste products (H\(^+\)) to be pumped out of this space. The flux of protons across the biological coral membrane is diffusion limited by the net proton transport through the boundary layer, which is hindered by increasing proton concentration due to OA in the seawater (Jokiel 2011). Although OA conditions increase DIC availability, calcification is ultimately limited by the removal of protons from the zone of calcification. We expect larger reduction in calcification rates among fast growing species because these coral must dissipate greater quantities of protons through the boundary layer against the increasingly steep proton gradient. Conversely, if organisms are able to compensate (e.g. evolved mechanisms, skeletal morphology, etc.) for this unfavourable proton gradient, then they may be able to exploit the increased availability of bicarbonate to increase calcification in the CO\(_2\)-acidified cellular spaces. Therefore, organisms with effective morphological and metabolic means of dissipating H\(^+\) while increasing uptake of HCO\(_3^-\) would be able to maintain high rates of G\(_{\text{net}}\) as the [DIC]:[H\(^+\)] ratio of seawater decreases. Further investigation of the [DIC]:[H\(^+\)] during light and dark processes reveal *M. capitata* to maintain significantly higher influx of DIC in the light and high efflux and dissipation of H\(^+\) in the dark (Figure 2). This study demonstrates the first experimental evidence of a coral’s ability to deal with this proton problem.

**Figure 2.** Flux of dissolved inorganic carbon (DIC) as a function of the flux of protons (H\(^+\)) in the light and dark (shaded) under ambient pH (8.0, white) and acidified pH (7.7, blue) across all temperatures for the corals *L. purpurea*, *M. capitata* and *P. damicornis*. Error bar represent SE of mean (\(n = 10\)).
Elevated calcification rates (+ 45%) were observed in the perforate coral, *M. capitata*, but had no short-term effect on the calcification rates of imperforate corals, *P. damicornis* or *L. purpurea*. Short-term exposure to OA allows *M. capitata* to take advantage of increase DIC availability and maintain high $G_{net}$ at the cost of high respiration rates. However, *M. capitata* is not able to withstand increased metabolic cost of acidification during prolonged exposure (Bahr et al. 2016). We believe that *M. capitata* has evolved mechanisms to compensate for increased protons (e.g. high surface to volume ratio, thin tissue, small polyps, perforate skeleton) and is able to dissipate protons out of its zone of calcification at a rate sufficient to avoid acidosis of the tissues (Jokiel 2011). Some insights into the relationship between porosity and calcification can be gained by examining the reverse reaction of dissolution. Dead skeletons of the foliose perforate coral *Montipora* and dead foliose skeletons of imperforate *Pectinia* coral were compared under conditions of increased OA (van Woesik et al. 2013). The skeletons of foliose, perforate *Montipora* coral colonies dissolved significantly faster than the skeletons of foliose, imperforate *Pectinia* coral colonies. Apparently the high surface to volume ratio of the perforate coral allowed for more rapid exchange of materials ($H^+$ and DIC) between the skeleton and the surrounding sea water which presumably would work in the favour of perforate corals undergoing the reverse process of calcification. Future studies should focus on examining the intracellular as well as the extracellular pH to assess the capacity of corals to maintain acid–base balance in the face of OA. This will provide insights into the mechanisms underlying the sensitivity of higher-level processes such as development, growth, and reproduction.

In summary, future scenarios of global warming and OA will lead to severe effects on coral calcification and respiration rates long before visible signs of bleaching and mortality are detected. Temperature has the greatest influence on coral calcification and *M. capitata* shows enhanced calcification under short-term exposure to OA conditions, while the other imperforate coral species show no reponse. This study revealed *M. capitata* to uptake DIC at a rate to avoid acidosis of the tissue and sufficiently remove $H^+$ from its tissue under OA conditions. This unique ability to overcome this proton problem may be prevalent in other Acroporidae corals, which are the most abundant and species-rich ($n = 149$ described species) group of corals in the world (Fukami et al. 2000). Therefore, corals with evolved mechanisms to mitigate the proton diffusion problem may have a competitive advantage over other corals under conditions of global warming and OA. However, other factors (e.g. reproductive strategies, settlement preferences, etc.) may influence overall species composition shifts on future reefs. Nonetheless, predicted increases in sea surface temperatures will have a stronger impact on coral physiological processes and will shape the future reefs.

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No potential conflict of interest was reported by the authors.

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**References**


