UNDERSTANDING THE THREATS OF OCEAN ACIDIFICATION TO CORAL REEFS

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ABSTRACT. The Moorea Coral Reef Long Term Ecological Research program affords a unique opportunity to study the implications of ocean acidification (OA) for coral reefs, as ongoing ecological and physical monitoring there provides a context in which the patterns of community change attributed to OA can be detected. We used mesocosms to study the impacts of OA on corals and calcified algae, and conducted experiments to compare multiple species and evaluate how they are affected by changing concentrations of the different forms of dissolved inorganic carbon. Our results reveal taxonomic variation in the response to OA, with some corals and algae showing signs of resistance to OA conditions. This discovery is informing an urgent debate over the form in which coral reefs will survive (if at all) in the future.

INTRODUCTION

Increased production of CO_2 through anthropogenic activities is causing the ocean to acidify (Feely et al., 2004). The additional dissolved CO_2 being taken up by the ocean reduces its pH and alters its dissolved inorganic carbon (DIC) chemistry (Doney et al., 2009). Coral reefs are a major focus of attention in the debate regarding how ocean acidification (OA) is affecting the health of marine ecosystems (Doney et al., 2012). Scleractinian corals are the best-known calcifiers of reef systems, where they build massive frameworks upon which other taxa rely. Early studies of the effects of OA on reef corals supported the prediction that a doubling of pre-industrial atmospheric CO_2 concentration would cause a 40% reduction in coral calcification (Hoegh-Guldberg et al., 2007). More recent research, including our own, is prompting a reevaluation of the magnitude of the predicted effects of elevated partial pressures of CO_2 (pCO_2) on coral reefs (Chan and Connelly, 2012).

The Moorea Coral Reef Long Term Ecological Research (LTER) program offers an excellent opportunity to study the effects of OA on coral reefs. The program's monitoring of biological and physical conditions provides an unparalleled context within which manipulative analyses of OA effects can be conducted. Here, we summarize the outcomes of our recent experiments designed to quantify the effects of OA on corals, calcified algae, and coral reefs.

EFFECTS ON ORGANISMS

In the mesocosm system we use to explore the effects of OA (Figure 1), we control light and temperature and use gas-mixing technology to create different partial pressures of CO_2 that are bubbled into the seawater. Initially, we characterized organismic responses to elevated pCO_2. Now, we are focusing on ecological processes and how they will be affected by OA, and we have built flumes to achieve this goal (Figure 1).

We tested the effects of OA using a variety of coral and algae taxa from the shallow reefs of Moorea that are representative of a variety of morphologies and functional roles on a Pacific reef. Our results reveal negative effects of OA on the calcification of most species, which is consistent with much of the previous work on this topic (e.g., Kroecker

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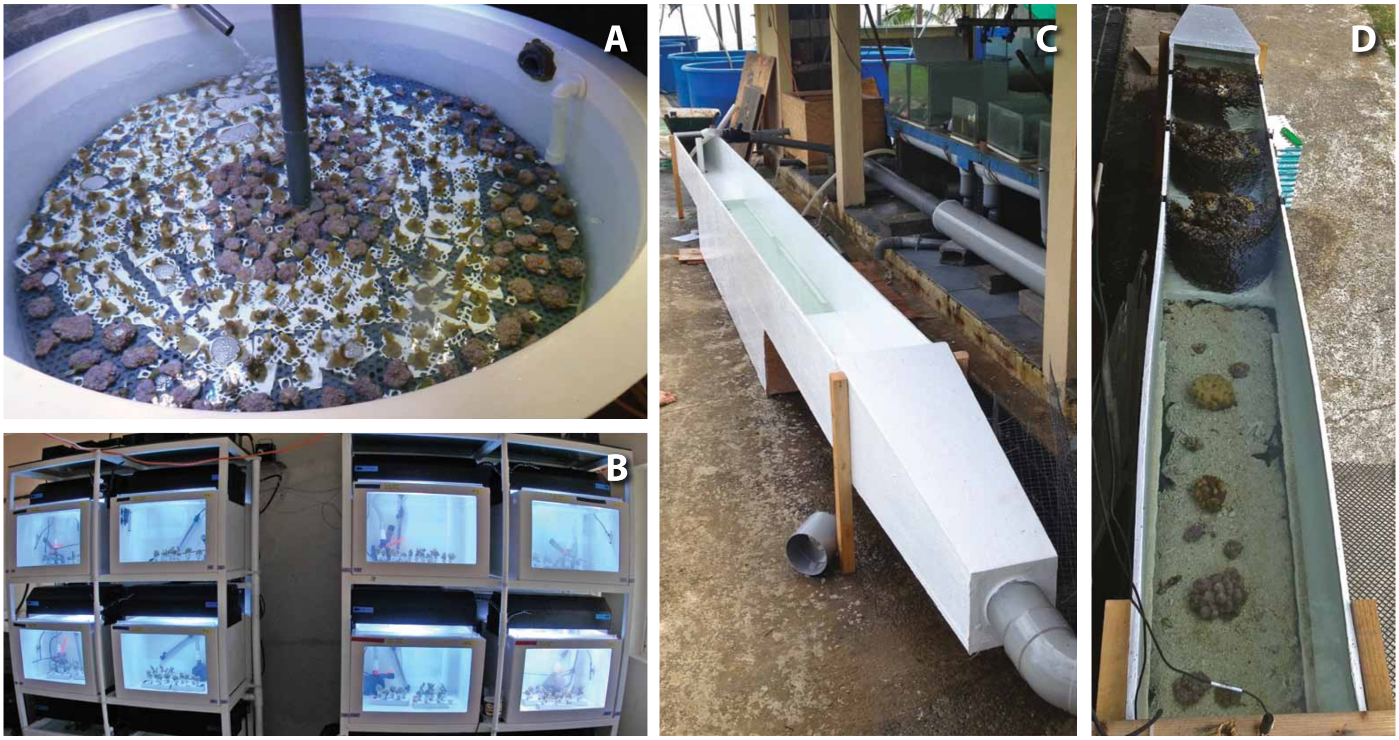

Figure 1. The effects of ocean acidification (OA) on corals and calcified algae in Moorea have so far been conducted in mesocosms, but outdoor experiments with the objective of eventually manipulating pCO_2 on the reef are in early stages. (A) Following collection, corals and algae are acclimated in a tank where light and temperature are controlled. (B) When acclimated, they are placed in mesocosms in which light, temperature, and pCO_2 are regulated. (C, D) Future experiments will be conducted in 5 m long flumes that receive CO_2-manipulated seawater under natural sunlight.

et al., 2010). However, they also support conclusions that are nuanced compared to other studies, and provide some optimism for the future of coral reefs.

Our research has led to four important advances. First, we find that the reduction in net calcification for individual species of corals and algae as a function of pCO_2 corresponds to a 0–14% decline in calcification with a doubling of pCO_2, although these estimates continue to evolve as more data are added to the analysis (Figure 2). These declines are lower than some estimates for an equivalent increase in pCO_2 (Erez et al., 2011; Chan and Connolly, 2012).

Second, we have uncovered taxonomic variation in the response to OA, both for corals and calcifying algae. While increasing pCO_2 greatly affects some taxa (*Acropora pulchra* and *Halimeda minima*), it affects others only weakly (*Porites rus* and massive *Porites*), and a few species appear unaffected (*Pocillopora damicornis* and *Halimeda macroloba*) even as pCO_2 reaches ~ 2,000 µatm (Comeau et al., 2013a). These species-specific responses contribute variance to the response of individual genera to OA, and the relationships between calcification and OA become a little equivocal at the genus level (Figure 2). Overall, calcification is still depressed significantly as pCO_2 rises for corals (pooled among four genera, $P = 0.011$), but calcification is statistically unaffected for each algal genus ($P \geq 0.331$; pooling among genera is not possible as the methods of normalizing differ) due to differences in the responses of species within each genus to OA (Comeau et al., 2013a). The number of corals and algae that have been studied relative to the diversity found on coral reefs still is small, and much more work needs to be done. However, our results suggest that the future of coral reefs will depend on the number of potential "winning" corals and algae (those less affected by OA) versus "losing" corals and algae (those strongly affected by OA) and whether their long-term responses to OA can be predicted reliably from the short-term experiments we conducted.

Third, we have explored the possibility that a tipping point characterizes the response of calcified taxa to rising pCO_2 (Hoegh-Guldberg and Bruno 2010), a tipping point that could signal unpredictable changes in calcification as

pCO_2 rises. Our results do not support this possibility (Comeau et al., 2013a) but instead describe negative linear relations that indicate gradual (and predictable) declines in calcification as pCO_2 rises (Figure 2). Finally, we have started to explore the mechanistic basis of variation in the response of calcified taxa to OA, and have found that light intensity modulates the response to pCO_2 by mediating the daylight uptake of HCO_3^- (Comeau et al., 2013b; Dufault et al., 2013). This discovery is important, as it argues against the generality of the widely accepted direct relationship between the saturation state of $CaCO_3$ in seawater (Ω; which declines under OA) and calcification (Langdon and Atkinson, 2005). In contrast, we found that corals and algae can buffer their responses to declining Ω by utilizing HCO_3^-, at least under high light conditions. Therefore, negative effects of OA on calcification may be accentuated at low light intensities.

IMPORTANCE OF ENVIRONMENTAL CONDITIONS

Light is an important determinant of coral calcification rates as a result of the coupling between *Symbiodinium* photosynthesis and deposition of calcium carbonate by the coral host (Allemand et al., 2011). Similar coupling between photosynthesis and calcification also is observed in calcified algae (Borowitzka and Larkum, 1987). The stimulatory effects of light on calcification, and the synergy with high pCO_2, probably are important factors contributing to the detection of smaller effects of pCO_2 on calcification of corals and algae in our work compared to previous studies (Edmunds et al., 2012).

Temperature is a critical determinant of physiological processes, and while it has typically been controlled in previous experiments on OA, there have been few attempts to explore synergies with pCO_2. Experiments to date provide some support for interactive effects of temperature and pCO_2 on calcification (Rodolfo-Metalpa et al., 2011), but such effects may be dependent on the study species and conditions employed.

Water flow modulates metabolic

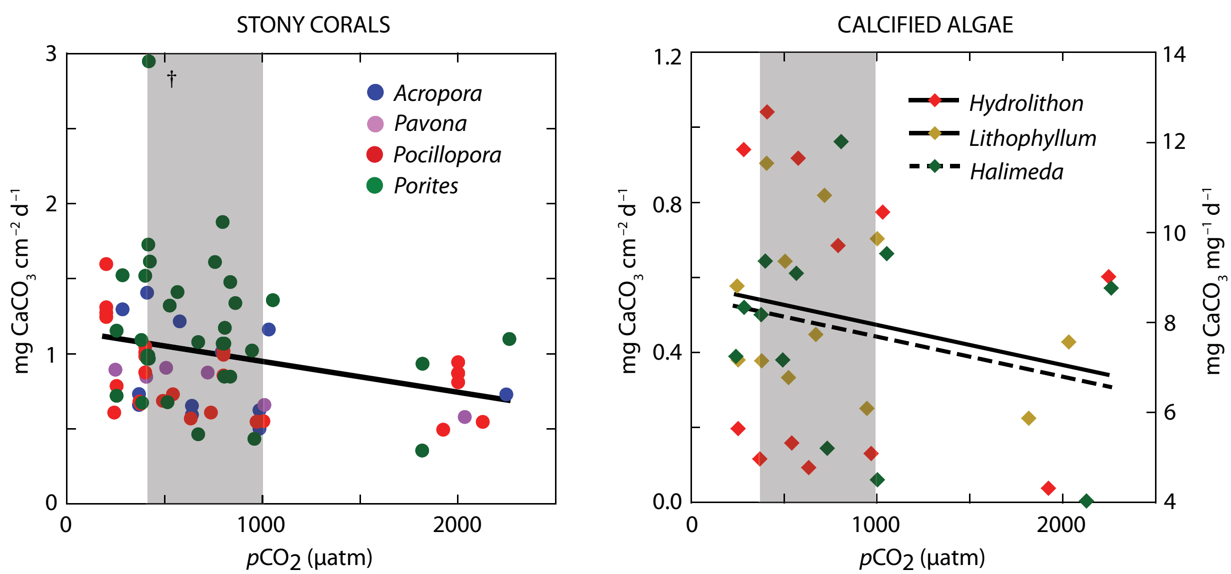

Figure 2. Summary of Moorea experiments in which several genera of stony corals and calcified algae have been incubated under different pCO_2 conditions. Lines represent the best-fit linear solutions: corals, y = 1.148 – 0.000205x (P = 0.011) († = one extreme value for *Porites rus*); algae standardized to area (two genera), y = 0.577 – 0.000106x (P = 0.415); algae standardized to mass (one genus), y = 8.551 – 0.000888x (P = 0.331). The shaded block represents approximately atmospheric pCO_2 at present (left edge) and under a pessimistic scenario for the end of the current century. Based on our estimates of calcification under present atmospheric pCO_2 conditions (~ 400 µatm), calcification rates of "all" corals (pooled among the genera sampled) at ~ 1.068 mg $CaCO_3$ cm^{-2} d^{-1} will be reduced 12% by an increase of atmospheric pCO_2 to 1,000 µatm, which is pessimistic for the end of the current century. The data currently do not show a significant effect of pCO_2 on genera of calcifying algae (which combines variance attributable to individual species, some of which are strongly affected by pCO_2 [Comeau et al., 2013a]). Nevertheless, nonsignificant trends suggest that calcification in algae will be reduced by 12% standardized to area and 7% standardized to biomass with an increase of atmospheric pCO_2 to 1,000 µatm.

processes of coral reef organisms by affecting the dynamics of near-organism boundary layers and controlling rates of mass transfer of metabolites between organisms and seawater (Atkinson and Bilger, 1992). OA results in a modification of the DIC species in seawater, and this has been proposed to underlie the decreases found in the rates of calcification of reef calcifiers (Langdon and Atkinson, 2005).

FUTURE DIRECTIONS

There are several areas that will be fruitful for future research on the effects of OA on coral reefs. At the smallest scale, studies of the mechanisms underlying the effects of elevated pCO_2 on calcification will require a better understanding of the cellular and molecular events involved in the calcification process. Another gap in our understanding of OA effects is evaluating whether the reduced rates of calcification exhibited by most calcifying taxa are the result of lowered calcification or increased dissolution of calcium carbonate. More predictive capability of how coral reef organisms will respond to climate change will be gained from experiments that include multiple stressors such as temperature and pCO_2. The degree to which coral reef calcifying species can acclimatize and perhaps adapt to elevated pCO_2 is an exciting area of OA research that will increase our understanding of organism responses to future conditions (Pespeni et al., 2013). The Moorea Coral Reef LTER is now poised to test for the ecological outcomes of emerging nuances of organismic and community functional responses to OA. Specifically, the time-series analyses at the core of LTER science are the perfect tools to evaluate whether corals and algae categorized as winners when exposed for short periods to low pH will become long-term winners defined by population growth and community dominance in an era strongly affected by climate change and OA.

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