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Branches and plates of the morphologically plastic coral *Porites rus* are insensitive to ocean acidification and warming

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ABSTRACT

This study tested the hypothesis that intraspecific morphological plasticity within a scleractinian coral elicits differential responses to elevated P_{CO2} and temperature. In Mo'orea, French Polynesia, two short-term laboratory experiments (21 and 14 days) were conducted to test the effects of P_{CO2} (400 vs. 700 μatm), and P_{CO2} (400 vs 1000 μatm) combined with temperature (27.0 vs. 29.8 °C), on branches and plates of *Porites rus*. Experiments employed two irradiances (~1000 vs 200 μmol photons m^{-2} s^{-1}), which characterized the microenvironments on the shallow fringing reefs where branching and plating morphologies are common, respectively. Calcification of both morphologies was insensitive to P_{CO2}, as well as the combined effects of elevated P_{CO2} and temperature. Mean calcification rates were faster in high light than in low light for both morphologies, and biomass was greater in plates than branches in all treatments. Together, our results suggest *P. rus* is robust to increased P_{CO2} and high temperature within the constraints of the treatments applied. Morphological plasticity in this species does not mediate physiological resistance to low pH and high temperature.

1. Introduction

Multiple chronic and acute disturbances are threatening tropical scleractinians (De'ath et al., 2012; Jackson et al., 2014), ultimately reducing the ecological resilience (sensu Holling, 1973) of coral reef ecosystems (Bellwood et al., 2004; McClanahan et al., 2002). One of the major chronic disturbances affecting corals is ocean acidification (OA) (Hoegh-Guldberg et al., 2007; Albright et al., 2016), which is the reduction in oceanic pH as a result of atmospheric carbon dioxide (CO_2) dissolving in seawater (Doney et al., 2009). OA changes the concentration of dissolved inorganic carbon (DIC) species in seawater, and reduces the aragonite saturation state, which plays an important role in determining the rate of coral calcification (Cohen and Holcomb, 2009) and reef accretion (Feely et al., 2009; Silbiger et al., 2014). Varied physiological responses to elevated P_{CO2} have been identified both within and among coral taxa (Comeau et al., 2013a, 2014; Kroeker et al., 2010, 2013; Okazaki et al., 2016), which emphasizes the spectrum of sensitivities of corals to reduced pH. Mechanisms supporting higher resistance of individual corals to OA remain largely unknown (Anthony et al., 2008; Cohen and Holcomb, 2009; Comeau et al., 2013a, 2014).

Inter- and intra- specific variation in the sensitivity of scleractinians to OA may be associated with aspects of skeletal phenotype, including skeletal porosity and rate of $CaCO_3$ deposition (Chan and Connolly, 2013; Comeau et al., 2014; Tambutté et al., 2015). Features of the coral holobiont, such as corallum morphology and rates of calcification, have been used in previous studies to distinguish functional groups of corals based on their sensitivity to OA, but the distinction in sensitivity between groups has been equivocal (Comeau et al., 2013a, 2014; Darling et al., 2012; Edmunds, 2011). In natural environments and manipulative studies, mounding corals, such as massive *Porites* spp., are more resistant to elevated P_{CO2} up to 2000 μatm, and temperatures as high as 30 °C, compared to some branching corals, such as *Acropora* spp. and *Pocillopora* spp. (Adjeroud et al., 2009; Comeau et al., 2014; Loya et al., 2001; van Woesik et al., 2011). Organizing corals into functional groups may be helpful in identifying responses to environmental stressors.

Comeau et al. (2014) tested the effects of OA on corals categorized into three functional groups based on: 1) corallum morphology, 2) skeletal porosity, and 3) speed of calcification (e.g., fast vs. slow). After corals were exposed to ~2000 μatm P_{CO2} for 2 weeks, they found that calcification rates of “fast-growing” corals (*Acropora pulchra* and *Psammacora profundacella*) declined, whereas slow-growing corals (*Porites irregularis* and *Pocillopora damicornis*) were unaffected. While Comeau et al. (2014) did not find a strong association between corallum morphology and sensitivity to OA, Anthony et al. (2008) found there

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was higher sensitivity in branching (*A. intermedia*) versus massive (*P. lobata*) coral. The opposing conclusions by these two studies may reflect the use by Comeau et al. (2014) of an experimental design in which species was used as a random factor nested with a contrast of morphology, and thus intrinsic differences between species may have reduced the statistical power of detecting an effect of morphology. Potentially, the results of a test for morphology might be more effective if it was accomplished using a single species that produced multiple morphologies through phenotypic plasticity (e.g., Todd, 2008). To gain further insight into the responses of corals to OA (Comeau et al., 2014; Darling et al., 2012; Edmunds et al., 2014), it might therefore be valuable to consider coral species that are plastic in select traits (e.g., morphology) to test the role of variation within these traits in determining the extent of intraspecific responses to OA.

For this study, two laboratory experiments were conducted to test the hypothesis that corallum morphology in *Porites rus* mediates the response to elevated P_{CO2} and seawater temperature. *P. rus* was selected because it is morphologically plastic, and produces branches and plates within a single colony (Jaubert, 1977; Padillo-Gamiño et al., 2012). In Mo'orea, French Polynesia, where this study was conducted, *P. rus* is abundant in shallow water (<4-m depth) where coral cover in 2012 (when this study was completed) was as high as 28% on fringing reefs along the north shore (Adjeroud and Salvat, 1996; Jaubert, 1977; Padillo-Gamiño et al., 2012); *P. rus* represented ~27–100% of this coral cover (Edmunds, 2016). Morphological plasticity in *P. rus* is largely driven by light (Jaubert, 1977; Padillo-Gamiño et al., 2012), with branches forming in habitats with high light intensities, and plates forming in habitats with low light intensities (Fig. 1).

Experiment 1 tested the response of branches and plates to P_{CO2} values expected to occur by 2100 under representative concentration pathway (RCP) scenario 6.0 (700 μatm), which posits mitigation of fossil fuel production by 2100 (Moss et al., 2010). Experiment 2 compared the response of both morphologies to elevated P_{CO2} predicted to occur by 2100 under a more stringent scenario defined by RCP scenario 8.5 (1000 μatm), which represents a worst-case scenario for the end of the current century (RCP Scenario 8.5; Moss et al., 2010). Additionally, in the second experiment, P_{CO2} treatments were crossed with a temperature treatment that contrasted ambient (27.2 °C) with a temperature 2 °C above ambient, as predicted to occur by 2100 (29.8 °C) (Hoegh-Guldberg et al., 2007). A light treatment was added to both experiments to test for effects of the physical environment on the reef where the two morphologies are found (e.g., Jaubert, 1977), and to avoid generating a bias in the response of a morphology type to the P_{CO2} and temperature treatments.

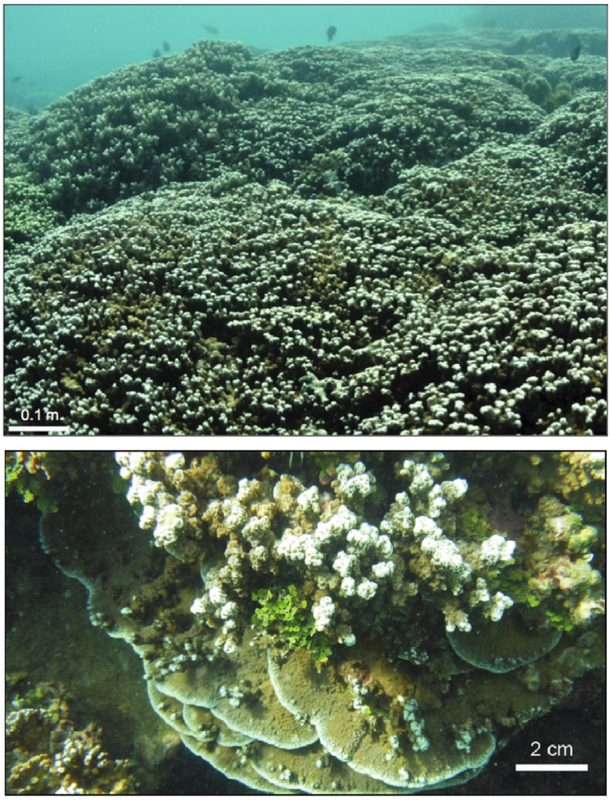

Fig. 1. Branches (top) and plates (bottom) of *Porites rus* in Mo'orea, French Polynesia. Pictures were taken on the fringing reef at 0.5-m depth in 2012.

2. Materials and methods

2.1. Coral collection and acclimation

For each experiment, branches and plates of *Porites rus* were collected haphazardly at 0.5–2.0 m depth along a fringing reef in Cook's Bay, Mo'orea (17°48.96S, 149°81.88 W). Individual branches and plates were placed in plastic bags and brought to the Richard B. Gump South Pacific Station in a cooler filled with seawater. At the lab, branches were trimmed to 3-cm length, and plates to 3-cm width, and attached to plastic bases with marine epoxy (*Z-Spar A-788 Splash Zone Compound* Los Angeles, CA, USA) in either an upright or horizontal position, respectively. After allowing the epoxy to cure for 48 h under high flow, corals were transferred to a 1000 L acclimation tank for 1 week, in which they were exposed to similar conditions to those employed in the subsequent mesocosm experiment. The acclimation period was intended to reduce stress induced from collection and handling, and to allow corals to acclimate to the incubation conditions prior to the start of the experiment.

P_{CO2} and temperature in the acclimation tank were maintained at ambient conditions in Cook's Bay when the experiments were conducted (~400 μatm P_{CO2} for both experiments, 27 °C for Experiment 1 in April–May 2012, and 28 °C for Experiment 2 in January–February 2013). Branches and plates were evenly distributed throughout the circular acclimation tank, either in the center or the perimeter of a circular table that rotated at two revolutions d^{-1} beneath four 75-W Light-Emitting Diode lamps (AquaIllumination® LED System Model: Sol Blue, Ames, IA). The LED lamps operated on a 12:12 h light:dark photoperiod with irradiance gradually increasing from 0 to 100% of maximum irradiance, remaining at 100% for 4 h, and reducing in intensity over the final 4 h of the day to simulate field conditions. Maximum light intensities were ~300 μmol photons m^{-2} s^{-1} and ~700 μmol photons m^{-2} s^{-1} (measured with 4π quantum sensor [LI-193] and a LiCor LI-1400 m) at the perimeter and center of the tank, respectively. These positions were used to mimic high and low light intensity habitats on the fringing reefs of Mo'orea where branches and plates of *P. rus* are most common, respectively. Mean maximum light intensities in the habitats from which the corals were collected were measured close to noon on sunny days in April. Light intensities were measured using two MkV-L logging light sensors (JFE Advantech Co., Kobe, Japan) each equipped with a 4π spherical quantum PAR sensor, and placed at 0.5 m and 2.0 m depth in high and low light environments where branches and plates were collected. The sensors recorded light in 10 min intervals over 2 d (27–28 April 2012). Mean values of light intensities between 11:00–13:30 h were 1472 ± 92 μmol photons m^{-2} s^{-1} where branches were collected, and 226 ± 7 μmol photons m^{-2} s^{-1} where plates were collected (±SE, $n = 64$; Fig. 2).

2.2. Seawater carbonate chemistry and tanks

Tanks used for both experiments contained 150 L of filtered seawater (passed through a sand filter) that was supplied continuously (200