Journal of Experimental Marine Biology and Ecology 453 (2014) 28–35

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Effects of irradiance on the response of the coral *Acropora pulchra* and the calcifying alga *Hydrolithon reinboldii* to temperature elevation and ocean acidification

Steeve Comeau *, Robert C. Carpenter, Peter J. Edmunds

Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA

ARTICLE INFO

Article history:
Received 12 August 2013
Received in revised form 16 December 2013
Accepted 17 December 2013
Available online 22 January 2014

Keywords:
Biomass
Global warming
Irradiance
Net calcification
Ocean acidification
Reef calcifiers

ABSTRACT

We tested experimentally if irradiance can modulate the response of coral reef calcifiers to seawater warming and ocean acidification. Nubbins of the coral *Acropora pulchra* and individuals of the calcifying alga *Hydrolithon reinboldii* were incubated for 20 d under 2 irradiances (150 and 650 μmol quanta m^{-2} s^{-1}) in a matrix of duplicate treatments crossing 2 temperatures (27.2 °C and 29.8 °C) with 3 pCO_2 levels (400, 750 and 1100 μatm). To determine the effects of the treatments, net calcification was measured in *A. pulchra* and *H. reinboldii*, and biomass in *A. pulchra*. High temperature and low irradiance caused a significant decrease in coral net calcification, whereas only low irradiance resulted in a significant decrease in algal net calcification. The biomass of *A. pulchra* was affected significantly by pCO_2 and light (separately and in synergy), with maximum biomass measured at 750 μatm pCO_2 in 3 out of 4 combinations of light and temperature. Light intensity adds complexity to the response of reef calcifiers to ocean acidification through indirect effects on coral biomass, which will need to be considered in future studies.

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1. Introduction

Anthropogenic activities are affecting Earth by releasing large quantities of carbon dioxide (CO_2) into the atmosphere as a result of the burning of fossil fuels and deforestation (Sabine et al., 2004). As CO_2 is a greenhouse gas, it has driven a warming of the Earth's surface of 0.2 °C decade^{-1} for the past thirty years (Hansen et al., 2006). Oceans are affected by global warming since they have absorbed ~84% of the total heat of the Earth system over the last 40 years (Levitus et al., 2005). The International Panel on Climate Change (IPCC, 2007) projects for the end of the century an increase in ocean surface temperature of 1.8 to 4.0 °C depending on the scenario considered. Aside from global warming, ~25% of the human-produced CO_2 has been absorbed by seawater in the upper surface of the oceans (Sabine et al., 2004) leading to the "other CO_2 problem" known as ocean acidification (OA) (Gattuso and Hansson, 2011). OA is caused by the dissolution of CO_2 in seawater to form carbonic acid, leading to a decrease in ocean pH and a reduction in calcium carbonate saturation state (Ω).

In addition to a multitude of local disturbances (Pandolfi et al., 2003), coral reefs are threatened directly by global warming and OA (Gattuso and Hansson, 2011). Global warming leading to seawater warming is a major driver of mass bleaching episodes of tropical corals (Brown, 1997), which in a persistent state leads to reduced calcification, slow growth, and increased mortality (e.g., Glynn, 1996; Hoegh-Guldberg, 1999). Although, the effects of OA currently are less conspicuous than bleaching, the potential consequences are dire, with pessimistic projections suggesting that coral reefs will start dissolving by 2050 (Hoegh-Guldberg et al., 2007; Silverman et al., 2009). These projections are based in part on studies conducted in mesocosms showing that coral calcification declines ~20% when pCO_2 doubles (Chan and Connolly, 2013; Comeau et al., 2013a; Erez et al., 2011), and to date they have not evaluated whether at least some corals might show signs of resistance to OA as it has been shown in the field (Fabricius et al., 2011) and in short laboratory incubations (Comeau et al., 2013a). OA and global warming also are expected to threaten other important calcifiers on coral reefs, particularly coralline algae, which are significant contributors to the calcium carbonate budget of coral reefs (Chisholm, 2000). As it has been described for scleractinian corals, studies of coralline algae have detected deleterious effects of OA on growth, recruitment and calcification (e.g., Comeau et al., 2013a; Jokiel et al., 2008; Kuffner et al., 2008), although some species are affected less (e.g., Martin et al., 2013).

To date, most studies of the effects of OA and warming on reef calcifiers have tested the effects of these stressors independently, and of the few studies that have employed combinations of increased temperature and decreased pH, the results are equivocal and suggest that the responses are species-specific. For example, some studies report that temperature does not affect the response of corals to OA, including the temperate coral *Cladocora caespitosa* (Rodolfo-Metalpa et al., 2010) and the tropical coral massive *Porites* (Anthony et al., 2008; Edmunds et al., 2012). In other studies however, the interaction between

* Corresponding author. Tel.: +1 818 677 5063.
E-mail address: steve.comeau@csun.edu (S. Comeau).

0022-0981/$ – see front matter. Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.jembe.2013.12.013

increased temperature and high pCO_2 decreases calcification disproportionately as in the coral *Stylophora pistilla* (Reynaud et al., 2003), and reduces growth of primary polyps as in *Porites panamensis* (Anlauf et al., 2011). In tropical coralline algae, the interaction between warming and OA causes an increased sensitivity to bleaching, a decrease in net primary productivity, and a decrease in calcification (Anthony et al., 2008). In temperate coralline algae the effects of increasing pCO_2 and warming alone, and in combination, can be either positive or negative for calcification and photosynthesis as a function of the season (Martin and Gattuso, 2009; Martin et al., 2013).

Aside from seawater temperature and the concentration of dissolved inorganic carbon (DIC), coral and calcifying algal physiology also is strongly affected by irradiance, which drives photosynthesis and the supply of photosynthetically fixed carbon (e.g., Chalker et al., 1988; Muscatine, 1990). In symbiotic corals, the metabolic energy supplied to the host through the catabolism of photosynthetically fixed carbon, as well as the change in internal pH caused by photosynthesis (Allemand et al., 2011; Borowitzka and Larkum, 1987) favors calcification that is on average 3-fold higher in the light than in the dark (Gattuso et al., 1999). Similar to photosynthesis, calcification in corals is associated strongly with irradiance, and the relationship is best fitted with a hyperbolic tangent function (Chalker, 1981). Remarkably few studies have explored the combined effect of irradiance and pCO_2 on the calcification of corals, and the same is true for calcified algae, although it has long been known that their rates of calcification are light-enhanced (Borowitzka, 1981).

In corals, two studies have found no interactive effects of irradiance and pCO_2 (or Ω_a) on the calcification rates of adult *Porites compressa* and *Porites rus* (Comeau et al., 2013b; Marubini et al., 2001). In contrast, juvenile *Pocillopora damicornis* respond strongly to the interactive effect of irradiance and pCO_2, with the calcification–irradiance relationship following a hyperbolic tangent function under ambient pCO_2, but a reversed hyperbolic tangent function under high pCO_2 (Dufault et al., 2013). The inconsistency between the aforementioned studies likely is due to both differences between life stages and differences in the range of irradiances tested. For example, Marubini et al. (2001) used a range of irradiance from 81 to 698 μmol quanta m^{-2} s^{-1}, Comeau et al. (2013b) used 215 and 1000 μmol quanta m^{-2} s^{-1}, and Dufault et al. (2013) used 31 to 226 μmol quanta m^{-2} s^{-1}. A recent study also has shown that high pCO_2 induces a greater decrease in light calcification in corals incubated in low light compared to those incubated in high light, although dark calcification was similarly affected by high pCO_2 in the two light regimes (Suggett et al., 2013). This result supports the hypothesis that corals can use bicarbonate ions, which increase in concentration under OA conditions, to calcify in the light, thereby reducing the deleterious effects of decreasing carbonate ions which also is associated with OA (Comeau et al., 2013c).

In view of the critical role played by the three environmental parameters discussed above (temperature, pCO_2, and irradiance) on the rates of calcification in tropical corals and algae, our study tested the hypothesis that irradiance affects the response of corals and calcified algae to ocean warming and OA. To test this hypothesis, a 3-week incubation on the coral *Acropora pulchra* and the alga *Hydrolithon reinboldii* was performed, during which net calcification was measured under combinations of two light levels, two temperatures, and three pCO_2 levels. Biomass also was measured in the corals to investigate potential effects of treatments on the allocation of resources between tissue and skeleton growth.

2. Material and methods

2.1. Samples collection

Fragments of *A. pulchra* (n = 120) and individual *H. reinboldii* (n = 120) were collected in January 2013 in the lagoon of the North shore of Moorea, French Polynesia, at ~2 m depth. Samples were taken to the Richard B. Gump South Pacific Research Station, and attached to plastic tiles using epoxy glue (Z-Spar, A788 epoxy) to facilitate labeling and handling. After 2 d in a shallow tank supplied with a rapid flow of fresh seawater, samples were transferred to a recovery tank where they remained for 7 d. Lighting in the recovery tank was provided by four 75 W Light Emitting Diode (LED) modules (Sol White LED Module, Aquaillumination) that duplicated light quality and quantity used in the experiment (~150 and ~650 μmol quanta m^{-2} s^{-1} depending on the position in the tank). LEDs delivered most of the light in the spectrum 400–700 nm under the range of intensity utilized. Temperature in the recovery tank was maintained at ~28.5 °C, which was the seawater temperature at the collection site at the time of the experiment, and also was the mean of the temperatures used in the subsequent incubations (27.2 °C and 29.8 °C).

After recovery, samples were transferred to twelve 150 L mesocosms arranged randomly in a matrix of three pCO_2 and two temperature treatments that each were duplicated (see below). The experiment was a split-plot design, in which between-plot effects were pCO_2 and temperature, and the within-plot effect was irradiance that was manipulated in each mesocosm. The experiment was analyzed using analysis of variance (ANOVA). Five corals acclimated to low light and five acclimated to high light were selected randomly and transferred to the corresponding light treatment in each mesocosm. As it was not biologically meaningful to statistically compare taxa, corals and algae were incubated in the same mesocosms. Similarly, five algae acclimated to low light and five acclimated to high light were placed in the same mesocosms. The position of organisms in the mesocosms was changed randomly within a light level every 2 d to eliminate position effects, and seawater was replaced continuously in each mesocosm at ~200 mL min^{-1}.

The two light regimes (150 and 650 μmol quanta m^{-2} s^{-1} at maximum intensity) were created within each mesocosm by shading half of each mesocosm with neutral density mesh. The mesh attenuated ~77% of the irradiance and therefore created a shaded and unshaded portion in each mesocosm. To produce a natural diel light cycle, light intensity was gradually increased from 0 to 100% output over 4 h beginning at 06:00 h, maintained at maximum intensity for 4 h, and then reduced during the last 4 h of the 12-h day. To quantify the consistency of the light treatments, irradiance was measured once weekly below the seawater surface with a 4π quantum sensor (LI-193) and a LiCor LI-1400 meter in all 12 mesocosms during maximum light intensity. Irradiance also was measured in two different mesocosms during a 24 h period to quantify the natural light cycle created by altering the intensity of the lamps. The two irradiances were chosen with respect to photosynthetic performance to expose the organisms to saturating (650 μmol quanta m^{-2} s^{-1}) and light-limited (150 μmol quanta m^{-2} s^{-1}, e. g. Marubini et al., 2001) conditions. These irradiances are experienced on the shallow reefs of Moorea, where light intensity ranges from ~2000 μmol photons m^{-2} s^{-1} in the shallow (0.5 m depth) back reef to ~200 μmol photons m^{-2} s^{-1} in shaded areas of the back reef, and at ~17 m depth on the fore reef (Carpenter and Moorea Coral Reef LTER, 2012). Temperature was maintained at 27.2 °C in 6 of the 12 mesocosms, and at 29.8 °C in the remainder. These temperatures covered the range of temperatures recorded in the back reef of Moorea (e.g., Edmunds et al., 2010).

CO_2 treatments consisted of three pCO_2 levels corresponding to the present day concentration (400 μatm), an average value expected by the end of the century (~750 μatm, from representative concentration pathway [RCP] scenario 6.0, Moss et al., 2010), and a pessimistic value expected by the end of the 21st century (~1100 μatm, ~RCP scenario 8.5). The experiments were performed at constant pCO_2 because natural daily pCO_2 oscillations are limited on the back reef of the North shore of Moorea during this time of year (i.e., ~70 μatm, Comeau et al., in press-a). Either ambient air or CO_2-enriched air was bubbled into the tanks to create CO_2 treatments. A solenoid-controlled gas regulation system (Model A352, Qubit Systems) was used to create the CO_2-enriched air by mixing pure CO_2 and ambient air at the targeted value.