Journal of Experimental Marine Biology and Ecology 506 (2018) 135–143

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

The influence of diel carbonate chemistry fluctuations on the calcification rate of *Acropora cervicornis* under present day and future acidification conditions

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ARTICLE INFO

Keywords:
Ocean acidification
Coral
Calcification
Diurnal fluctuation
pH variability
Experimental aquaria

ABSTRACT

Ocean acidification (OA) will result in lower calcification rates for numerous marine taxa, including many species of corals which create important reef habitat. Seawater carbonate chemistry fluctuates over cycles ranging from days to seasons, often driven by biological processes such as respiration and photosynthesis. The magnitude of diel fluctuations varies spatially and may become more pronounced in the future due to OA. Due to technical constraints, OA experiments that incorporate diel variability into treatments are few in number. As a result, the degree to which coral reef organisms are influenced by ambient daily carbonate chemistry variability is poorly understood. Here we describe an experiment conducted in a novel seawater system which can independently manipulate carbonate chemistry in 16 separate aquaria, in real time, allowing precise control of the mean and magnitude of pH oscillations while minimizing pseudoreplication. Five genotypes of the threatened Caribbean coral *Acropora cervicornis* were subjected to a total of five pH treatments, 7.80 ± 0.20, 7.80 ± 0.10, and 7.80 ± 0.00, as well as 8.05 ± 0.10 and 8.05 ± 0.00. Those corals exposed to variable contemporary conditions (8.05 ± 0.10) calcified faster than those in current and future static treatment levels, which did not significantly differ from each other. Variable contemporary pH also resulted in faster growth rates than highly variable future conditions (7.80 ± 0.20), but were not significantly different than future conditions with the same ± 0.10 diel pH oscillation. These findings support the importance of incorporating diel variability into OA experiments and suggest that more variable natural ecosystems may yield higher calcification rates for corals.

1. Introduction

The global acidification of seawater (ocean acidification, OA) due to the anthropogenic increase in atmospheric CO_2 will have widespread ramifications for marine organisms and ecosystems (Fabry et al., 2008). Coral reef habitat, formed by the deposition of calcium carbonate by scleractinian corals, will be adversely affected due to OA-related depression in calcification (Chan and Connolly, 2013), and acceleration of dissolution (Enochs et al., 2016).

While the progressive decline in seawater pH is clear from open-ocean time series (Bates et al., 2014), shallow water systems are complicated by the influence of benthic organisms on carbonate chemistry, especially when water exchange is low (Hofmann et al., 2011). This biological control varies across spatial scales from centimeters (Gagliano et al., 2010) to kilometers (Manzello et al., 2012) and can be influenced by episodic events (Manzello et al., 2013) or by periodic oscillations with periods ranging from days (Price et al., 2012) to seasons (Shaw and Mcneil, 2014). Diel oscillations in pH are primarily due to light-mediated alteration in the balance of photosynthesis/respiration and calcification/dissolution. The magnitude of this fluctuation can vary greatly, and in some reef systems it can contribute to periodic exposure to conditions expected to occur by the end of the century due to OA (Shaw et al., 2012).

The implications of diel pH fluctuations on the organismal responses to OA are poorly understood and may be an important consideration for the persistence of coral reef ecosystems (Hogarth, 2006; Rivest et al., 2017b). If a coral's response to OA is driven by a depression in light enhanced calcification, then dynamic pH oscillations could facilitate

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https://doi.org/10.1016/j.jembe.2018.06.007
Received 23 January 2018; Received in revised form 22 May 2018; Accepted 17 June 2018

more favorable daytime conditions, possibly acting as a temporal OA-buffering refuge. If, however, dark calcification is of paramount importance to a coral's response to OA, a higher amplitude nighttime reduction in pH could lead to a more dramatic OA-related depression in coral growth than previously predicted. The cumulative result of the decline in mean pH from OA, coupled with natural oscillations around that mean, implies that in certain highly variable environments periodic aragonite undersaturation, accompanied by abiotic dissolution, will be reached before the predictions of models that only consider a mean (Shaw et al., 2013b). Further, OA itself may increase the diel amplitude of natural carbonate chemistry oscillations by decreasing the buffering capacity of seawater, potentially leading to unforeseen ecosystem responses (Shaw et al., 2013a).

In order to incorporate natural variability into OA experiments, scientists have conducted in-situ studies on both small (Kline et al., 2012) and large spatial scales (Albright et al., 2018), relying on biological and physical processes to drive diurnal fluctuations. Additionally, naturally high-CO_2 systems due to physical (e.g., Crook et al., 2013; Fabricius et al., 2011) and biological forcing (e.g., Camp et al., 2017; Shamberger et al., 2014) have been employed to investigate dynamic OA conditions. These systems, however, may not always perfectly mimic diel oscillations found on normal reefs (e.g., Enochs et al., 2015).

Laboratory-based studies which experimentally manipulate diurnal pH oscillations are scarce relative to those considering static treatments, primarily due to technical difficulties with controlling carbonate chemistry in real-time. Previously, dynamic pH treatments have been achieved using three approaches. In the first, specimens have been physically transferred back and forth between artificially manipulated high and low pH at dawn and dusk (Comeau et al., 2014a; Dufault et al., 2012; Johnson et al., 2014) or have been automatically refreshed with different pH waters from statically controlled holding tanks (Cornwall et al., 2013). In this approach, the magnitude and phase of dynamic day/night oscillations are controllable but treatments can be artificially abrupt, as specimens are immediately exposed from one extreme to the next during the dawn/dusk transfer process.

In the second approach, diel variability is achieved via an upstream mesocosm containing a community of organisms which biologically force the carbonate chemistry. Both Camp et al. (2016) and Chan and Eggins (2017) have employed this methodology, subjecting corals to carbonate chemistry manipulated via seagrass and coral mesocosms, respectively. In the latter study, static treatments were also achieved by transferring water from the upstream mesocosm to separate aquaria at specific times of day which routinely experience a specific pH set point. While this approach accomplishes gradual diel changes, only one oscillating regime is attainable (that of the mesocosm) and treatment conditions may vary due to biological processes.

The third method of dynamic pH manipulation employees automated dosing of liquid reagents or CO_2 gas, linked with a feedback mechanism to identify when treatment conditions are met. Coupled with moving set points, this approach has been used to depress pH while retaining natural diurnal variability in 1300 L common garden tanks (Putnam et al., 2016), to alter pH fluctuations in 1600 L recirculating tanks (Jarrold and Munday, 2018), as well as to manipulate pH fluctuations (mean and amplitude) in 900 mL phytoplankton culture chambers (Golda et al., 2017). This method is the most flexible of the three, though there can be difficulties with gas delivery and treatment precision (Golda et al., 2017).

Studies which have directly manipulated seawater oscillations have investigated a suite of different taxa including algae (Cornwall et al., 2013; Johnson et al., 2014), coral (Chan and Eggins, 2017; Comeau et al., 2014a; Dufault et al., 2012; Putnam et al., 2016), fishes (Jarrold et al., 2017; Jarrold and Munday, 2018), and isopods (Alenius and Munguia, 2012), among others. Those that have focused on calcification have primarily employed an experimental design comparing responses to variable versus completely static pH. Dufault et al. (2012) found that diurnal oscillations (8.02 to 7.90) increased the calcification of *Seriatopora caliendrum* recruits, relative to static high (8.00) and low (7.88) pH treatments, which yielded non-significant differences. Chan and Eggins (2017) subjected adult *Acropora formosa* to static (7.8, 8.0, 8.2) and a naturally varying pH (7.8 to 8.2). Again, the variable system resulted in higher calcification rates vs. the contemporary (8.0) and future (7.8) treatments, though corals which were subjected to pH variability did not calcify significantly faster than in static 8.2 pH. Similarly, transferring the alga *Porolithon onkodes* across high (8.03) and low pH (7.87) conditions (day and night, respectively) resulted in enhancement of calcification relative to static low pH (7.86) but not static high pH (8.04) treatments (Johnson et al., 2014). Comeau et al. (2014a), however, measured calcification of *Acropora hyacinthus* in three static OA treatments (8.07, 7.88, 7.71), each paired with a variable treatment with a similar daily-averaged mean. The amplitude of the pH variation increased with pH depression and significant differences in calcification were only detected among the samples exposed to the most extreme static OA conditions (7.71) versus the most extreme variable OA conditions (8.07 to 7.47, day to night, respectively).

In contrast to the aforementioned studies, Camp et al. (2016) did not detect a significant influence of variability ($\sim \pm 0.05$ vs. $\sim \pm 0.2$) on present-day and acidified treatments on two species of Caribbean corals, *Acropora palmata* and *Porites astreoides*. Finally, an experiment conducted on a calcifying alga (*Arthrocardia corymbosa*) resulted in lower calcification rates in variable (± 0.4) vs. static pH conditions under present day (8.05) and future (7.65) mean levels (Cornwall et al., 2013). While the results are not always consistent across taxa, these studies indicate that differences in diel oscillation (or lack thereof) between experiments could potentially be responsible for some of the differences in OA-responses observed across prior studies (e.g., Okazaki et al., 2017).

Given the apparent differences between these studies and the limited incorporation of variability treatments into experimental designs, it is presently unclear how diurnal pH oscillation will influence the calcification of important reef-building corals, especially under future OA conditions. Here we describe the construction of a system for the precise manipulation of diurnally fluctuating seawater carbonate chemistry; a system which reproduces gradual diel oscillations (rather than abrupt changes) and does not rely on a biologically-forced header tank. This system was used to test the hypothesis that diel pH variability coupled with present day and future mean pH conditions influences the calcification of the threatened (Hogarth, 2006) staghorn coral *Acropora cervicornis* (Lamarck, 1816).

2. Methods

2.1. Experimental design

Between 40 and 49 fragments of *A. cervicornis* (225 total) were collected from five genotypes (Baums et al., 2009) present at two coral nurseries, south of Key Biscayne, Florida (25.3626 N, 80.1664 W, Genotypes A-C; 25.4888 N, 80.1091 W, Genotypes D,E) in March 2017. Prior to collection, colonies were grown from hanging trees and on cinder blocks in roughly six meters water depth (Lirman et al., 2014; Nedimyer et al., 2011). Fragments were each roughly five cm long and were selected to minimize the presence of multiple apical tips. Corals were transported back to the University of Miami CIMAS and NOAA AOML's Experimental Reef Laboratory, where they were affixed to four cm diameter grey PVC pucks, using cyanoacrylate adhesive. Corals were acclimated to indoor laboratory conditions mimicking those occurring in the field (24.3 °C, 8.05 pH) for two weeks, followed by a week of pH treatment ramping. Initial temperature was obtained from the field at the time of collection, initial pH data from the sites of collection was obtained from 1.5 month SAMI-pH logger (Sunburst Sensors) deployments in 2014 (Fig. S1). Replicates were randomly assigned to tanks and treatments, ensuring at least three corals per