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Resistance of corals and coralline algae to ocean acidification: physiological control of calcification under natural pH variability

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Ocean acidification is a threat to the continued accretion of coral reefs, though some undergo daily fluctuations in pH exceeding declines predicted by 2100. We test whether exposure to greater pH variability enhances resistance to ocean acidification for the coral *Goniopora* sp. and coralline alga *Hydrolithon reinboldii* from two sites: one with low pH variability (less than 0.15 units daily; Shell Island) and a site with high pH variability (up to 1.4 pH units daily; Tallon Island). We grew populations of both species for more than 100 days under a combination of differing pH variability (high/low) and means (ambient pH 8.05/ocean acidification pH 7.65). Calcification rates of *Goniopora* sp. were unaffected by the examined variables. Calcification rates of *H. reinboldii* were significantly faster in Tallon than in Shell Island individuals, and Tallon Island individuals calcified faster in the high variability pH 8.05 treatment compared with all others. Geochemical proxies for carbonate chemistry within the calcifying fluid (cf) of both species indicated that only mean seawater pH influenced pH_{cf} . pH treatments had no effect on proxies for Ω_{cf} . These limited responses to extreme pH treatments demonstrate that some calcifying taxa may be capable of maintaining constant rates of calcification under ocean acidification by actively modifying Ω_{cf} .

1. Introduction

Ocean acidification is a growing threat to marine ecosystems [1,2], particularly those heavily reliant on calcifying taxa, such as coral reefs [3–5]. Coral reefs provide billions of dollars annually to the world’s economy through tourism and fisheries [6], and they are a hotspot of biodiversity [7]. Therefore, determining the impacts of future ocean acidification on these ecosystems is of paramount importance. Both the habitat-forming corals and their settlement substrate of preference, coralline algae, are expected to be vulnerable to the effects of ocean acidification [5,8,9]. However, predictions of coral reef futures are often based on open ocean pH regimes (e.g. [4,10]), but the seawater pH on coral reefs encountered by resident taxa can be drastically different from that of the surrounding open ocean [11]. Corals and coralline algae can encounter large daily fluctuations in pH when they reside in habitats with high biomasses of macroalgae or seagrass, and with low seawater exchange with the open ocean [12–14]. This has led to suggestions that organisms living within highly variable pH environments will be less vulnerable to ocean acidification compared to those that encounter more constant seawater pH [15–17].

Despite the dramatic daily pH oscillations that occur on many coral reefs, little is known regarding how pH variability influences the physiology of

calcifying taxa, especially when superimposed upon declines in mean seawater pH. It has been proposed that higher pH during the day could offset some of the negative effects of ocean acidification for organisms living in diurnally variable pH regimes [12,15,17]. However, experimental evidence supporting this hypothesis is ambiguous. Roughly half of all coral and coralline algal species tested to date have responded positively to increased pH variability, while half of the coralline algal species respond negatively to greater pH variability [12,18–24]. Thus, while elevated pH during the day could potentially offset the impacts of ocean acidification, it is equally plausible that reductions in pH at night within these habitats could exacerbate night-time dissolution [12,25,26].

Individuals or populations residing in more variable environmental regimes are typically more tolerant to mean changes in these parameters. For example, corals residing in environments with greater thermal variability can be more tolerant to the effects of increasing mean temperature [14,27,28]. Environments with greater variability can also favour populations with greater phenotypic plasticity, while stable environments eliminate the selection pressure for these traits, resulting in their eventual loss from the population [29]. Similarly, individuals exposed to greater extremes in environmental variables throughout their lifetime could also be acclimatized to such effects [30]. The role of prior exposure to greater pH variability to promote resistance to ocean acidification has been observed in some temperate invertebrate species from upwelling systems [16]. However, whether prior exposure to greater pH variability promotes tolerance or complete resistance to ocean acidification in corals and coralline algae is unknown [14]. Coral reef habitats typically do not contain the large biomasses of resident autotrophs required to shift pH significantly, when compared with other ecosystems such as temperate kelp forests in well-flushed reefs [31]. Therefore, it is possible that the coral reef taxa used in studies determining how an organisms' past pH history could affect responses to ocean acidification (e.g. [18–20]) were from conditions that were too constant to elicit detectable responses (though see [20]). To further understand whether greater pH variability or past exposure to pH variability influences responses of calcification to ocean acidification, we need to use larger oscillations in pH and to further explore the mechanisms responsible. One possible mechanism that has been evoked is a greater capacity to maintain elevated pH in the calcifying fluid (pH_{cf}) of corals exposed to natural pH variability under ocean acidification [32].

The capacity to elevate pH in the calcifying fluid (pH_{cf}) has been linked with greater resistance to ocean acidification in both corals and coralline algae [33,34]. How the elevation of pH_{cf} is influenced by natural pH variability is poorly known. When the coral *Porites cylindrica* was exposed to variable pH regimes both during and prior to a long-term ocean acidification experiment, they demonstrated relatively constant calcification rates and pH_{cf} under ocean acidification treatments [32]. Therefore, exposure of corals to natural pH variability could promote elevated pH_{cf} under ocean acidification [32]. However, the correlation between declines in pH_{cf} and calcification rates under ocean acidification does not occur for all corals under constant pH regimes [35]. Reconstructions of $\text{Ca}_{\text{cf}}^{2+}$ using recently developed geochemical proxies show that the capacity to elevate Ω_{cf} through either

increased Ca^{2+} pumping or elevating pH_{cf} could be two different strategies for maintaining faster calcification rates and higher Ω_{cf} in the face of ocean acidification [36]. If current (or prior) exposure to elevated seawater pH variability promotes pH_{cf} upregulation or increased Ca^{2+} uptake, and subsequent resistance to ocean acidification, then this will have important ramifications regarding how we predict the impacts of ocean acidification based on the majority of prior laboratory studies where it is unknown how the pH variability employed matches that of the organisms' site of collection [14].

Here, we assess the responses of two populations of corals (*Goniopora* sp.) and coralline algae (*Hydrolithon reinboldii*) from two sites with markedly different pH regimes (Shell Island, less than 0.05 units; and Tallon Island, 1.4 units daily pH variability) to four different experimental treatments each. These treatments are the fully factorial interaction between pH variability (low (approx. 0.11) and high (approx. 0.75 unit) daily variability) and mean pH (ambient (approx. 8.05) and ocean acidification (7.65)). In the highly variable pH environment of Tallon Island, oxygen concentrations also covary with pH. Therefore, we also assess the responses of *Goniopora* sp. to these treatments over both constant and variable oxygen concentrations during two time periods. We hypothesize that (i) both corals and coralline algae from highly variable pH regimes will be more resistant to the effects of ocean acidification than those from more constant pH regimes; and (ii) that both corals and coralline algae will be more resistant to the effects of ocean acidification when grown under pH regimes that vary on diurnal cycles, compared with those grown under constant regimes. We also hypothesize that (iii) any resistance to ocean acidification will be driven by favourable carbonate chemistry in the calcifying fluid (pH_{cf} and Ω_{cf}), which will promote faster calcification rates.

2. Material and methods

(a) Sample collection, site characterization and physiological measurements

pH, temperature, oxygen concentration and light data were all collected from two focal sites in the Buccaneer Archipelago of the Kimberley region, Western Australia, Australia from April 2016 until October 2016 as part of several long-term monitoring projects. This region is macrotidal and possesses an approximately 10 m tidal range that creates a highly dynamic environmental regime at many of the exposed tidal pools [37]. The two locations were Tallon/Jalan Island (16°40S, 123°14E) and Shell Island (16°48S, 123°04E). These *in situ* data will be explored in a complementary study [38]; see electronic supplementary material, SI 1 for more details on data collection.

Seventy *Goniopora* sp. and *H. reinboldii* individuals were collected from each site and transported to the Indian Ocean Marine Research Centre at Watermans Bay, Perth. Six individuals per treatment and site combination were placed into the four pH treatments in this experiment (figure 1), two low variability and two high variability treatments for each of the two mean pH treatment levels (8.05 and 7.65). These four treatments were: (i) ambient mean and constant pH (hereafter 'AC', mean $\text{pH } 8.05 \pm 0.06$ units daily variability), similar to Shell Island today; (ii) ambient mean and fluctuating pH ('AF', $\text{pH } 8.05 \pm 0.31$ units), similar to Tallon Island today; (iii) an ocean acidification scenario with constant pH ('OAC', mean $\text{pH } 7.65 \pm 0.06$ units), similar to an end of century scenario at Shell Island;

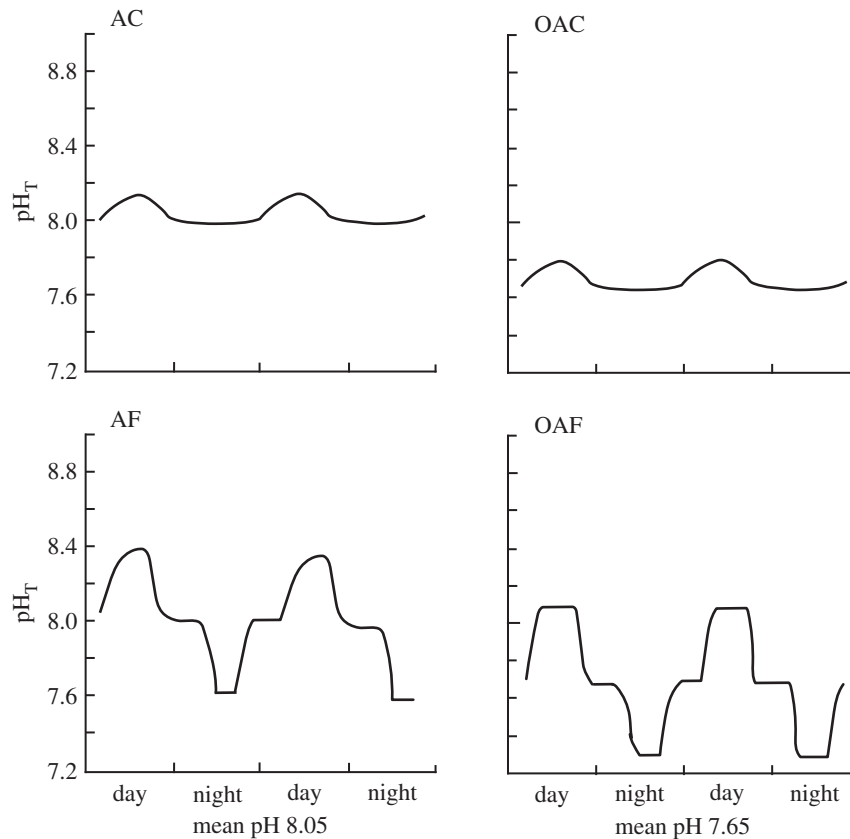


Figure 1. Schematic of pH treatments achieved within the experimental tanks in this study. AC, ambient mean and constant pH; AF, ambient mean and fluctuating pH; OAC, ocean acidification scenario with constant pH; OAF, ocean acidification scenario with fluctuating pH.

and (iv) an ocean acidification scenario with fluctuating pH ('OAF', mean $\text{pH } 7.65 \pm 0.40$ units), similar to an end of century Tallon Island scenario. For more experimental design details, see electronic supplementary material, S1. Calcification, photosynthetic and respiration rates were all measured. These are also detailed in electronic supplementary material, S1. See electronic supplementary material, S2 for the full range of seawater carbonate chemistry in each treatment during this experiment.

(b) pH_{cf} , dissolved inorganic carbon (DIC_{cf}) and Raman spectroscopy

Calcifying fluid pH (pH_{cf}) for all organisms and dissolved inorganic carbon (DIC_{cf}) for corals were calculated using the $\delta^{11}\text{B}$ proxy method for pH_{cf} [39] and the $\delta^{11}\text{B}$ and B/Ca method for DIC_{cf} [40,41]. Further details beyond these references are presented in electronic supplementary material, S1. We also used confocal Raman spectroscopy to determine sample mineralogy and as a proxy of calcifying fluid Ω [42], where Ω_{cf} decreases as full width at half peak maximum (FWHM) decreases. These methods are detailed in DeCarlo *et al.*, but for specific details also see electronic supplementary material, S1 1.

(c) Statistical analysis

We used linear mixed models to detect differences caused by the interaction between the mean and variability of pH treatments and the site of origin on the measured metrics. For *Goniopora* sp. under low oxygen concentration variability, these were: calcification rates, pH_{cf} , DIC_{cf} , B/Ca, $\text{Ca}_{\text{cf}}^{2+}$ and Ω_{cf} . For *H. reinboldii* under high oxygen concentration variability, these were calcification rates, photosynthetic rates, respiration rates, pH_{cf} , B/Ca, and Raman-derived residual FWHM. *Goniopora* sp. calcification, photosynthetic and respiration rates under low oxygen concentration variability were also analysed in this way. The site of

origin (Tallon or Shell Islands), seawater pH variability (constant or fluctuating) and seawater mean pH (8.05 and 7.65) were fixed factors in a fully factorial model, where header tank identity was also included as a random factor. The mean of responses for experimental tanks containing more than one individual was used as the raw data in the model. All data conformed to assumptions of normality and homogeneity of variance. Turkey's post hoc tests were conducted when significant differences were detected in linear mixed models that were not due to main effects.

3. Results

(a) *In situ* seawater carbonate chemistry

Mean pH was 8.08 at Tallon Island and 7.96 at Shell Island. The variability in seawater pH was orders of magnitude greater at Tallon Island compared with Shell Island (figure 2 and electronic supplementary material, figure S1). pH ranged from 7.8 to 8.2 at Shell Island, and the greatest variability in any given day was 0.14 units. On all other days pH varied by less than 0.1 units. By contrast, at Tallon Island, pH varied between 7.51 and 9.15, with the greatest pH variability being 1.4 units on any given day. The ranges between the lowest and highest standard deviations of seawater pH at any given hour of the day, e.g. 95.45% of all pH values encountered at either site, were 0.10 at Shell Island and 1.06 pH units at Tallon Island (electronic supplementary material, figure S1).

(b) Experimental seawater carbonate chemistry

Experimental treatments were achieved within 0.01–0.09 pH units of the target for all treatments at any given time phase

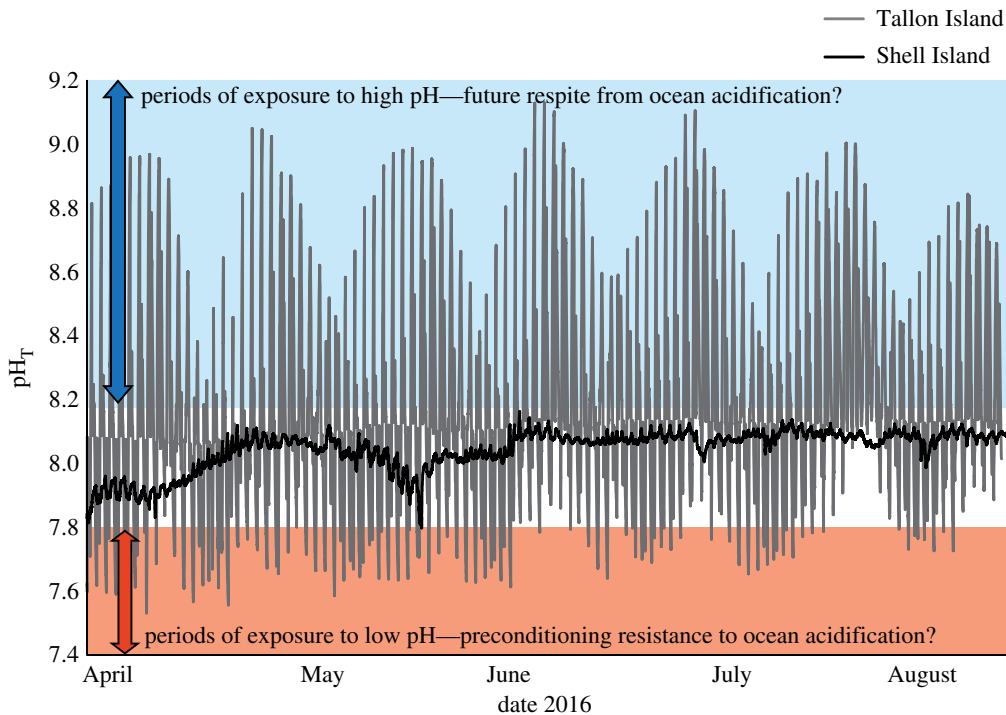


Figure 2. Example of pH variability measured at the collection sites. Tallon Island (in grey) being a coralline algal platform and Shell Island (in black) being a large coral-dominated intertidal pool. Note that early April corresponds to the coral bleaching even described in Le Nohaïc *et al.* [37]. Blue denotes pH range above those encountered at Shell Island, and red indicates those encountered below those at Shell Island. (Online version in colour.)

over 24 h cycles, except for during the 'day' time period for the AF treatment, where pH was on average 0.18 pH units lower than initially desired (electronic supplementary material, table S2). This treatment reached a mean of 8.37 by the end of its time phase, but was much slower than the other treatments to reach its 'day' time phase target, hence the lower mean during this time phase. As this is a variable treatment, the impact of differences in the AF treatment is not likely to be as notable as if this were a stable pH treatment.

(c) Calcification rates

Calcification rates did not vary by the treatment or site of origin for *Goniopora* sp. under both high and low oxygen concentration variability (figure 3*a,b*; electronic supplementary material, S2 and table S2). However, calcification rates of *H. reinboldii* from Tallon Island were significantly faster than those from Shell Island under high oxygen concentration variability. Calcification rates of *H. reinboldii* from Tallon Island were also significantly faster in the AF treatment than in any other treatment (figure 3*c*; electronic supplementary material, SI 2 and table S3).

(d) Photosynthetic and respiration rates

Goniopora sp. and *H. reinboldii* photosynthetic and respiration rates were unaffected by pH treatments (electronic supplementary material SI 3, figure S2, S2 materials and tables S2 and S3). However, *Goniopora* sp. from Shell Island had significantly higher gross photosynthetic rates compared with those from Tallon Island, and respiration rates of Tallon Island *H. reinboldii* were significantly higher than those from Shell Island. Respiration rates of *Goniopora* sp. within constant treatments were nearly significantly higher ($p = 0.053$) than those within fluctuating treatments when an α -value of 0.05 was employed.

(e) Geochemistry

pH_{cf} was significantly lower in both taxa when grown in the ocean acidification treatments compared with the treatments with ambient mean pH, irrespective of pH variability or site of origin (figure 4; electronic supplementary material, SI 2 and tables S4 and S5). This equated to a mean 0.07 unit decrease in *Goniopora* sp. (8.45–8.38) and a 0.10 unit decrease in pH_{cf} for *H. reinboldii* (8.71–8.61). This equates to slopes of 0.21 and 0.30 unit declines in pH_{cf} per unit pH of seawater for *Goniopora* sp. and *H. reinboldii*, respectively. There was no significant effect of variability in pH or site of origin on pH_{cf} for either taxa.

DIC_{cf} was significantly lower for *Goniopora* sp. individuals in the AF treatments compared with the OAF treatments (figure 5*a*; electronic supplementary material, S2 table S5, Tukey HSD $p = 0.03$), equating to a mean reduction of $342 \mu\text{mol kg}^{-1}$. DIC_{cf} was also significantly lower in *Goniopora* sp. from Tallon Island when grown under both ambient mean pH treatments (AF and AC) in general compared with ocean acidification treatments (OAC and OAF; figure 5*a*; electronic supplementary material, S2 table S5, Tukey HSD $p < 0.01$). There was no significant effect of treatments or site of origin on the B/Ca of *H. reinboldii* (figure 5*b*), nor on *Gonopora* sp. Ω_{cf} or $\text{Ca}_{\text{cf}}^{2+}$ (figure 6*a*; electronic supplementary material, SI 3 and figure S3). *H. reinboldii* residual FWHM, a potential proxy for Ω_{cf} , was significantly lower in individuals from Tallon Island, but did not vary by pH treatment (figure 6*b*).

4. Discussion

Here, we demonstrate that corals and coralline algae from locations with greater variability in pH are not more tolerant to the impacts of ocean acidification than those from sites with lower pH variability. In addition, experimental exposure

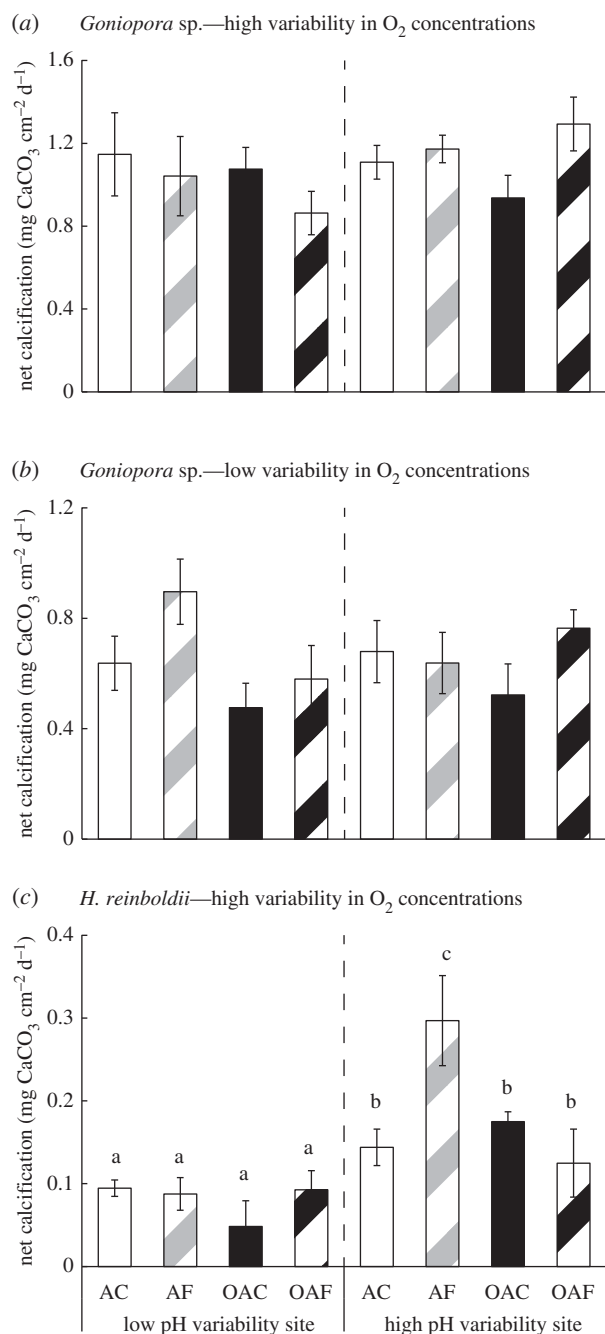


Figure 3. Calcification rates of coral (a,b) (*Goniopora* sp.) and (c) crustose coralline algae (*H. reinboldii*) during the laboratory experiment under the four treatments from two different populations. The following details apply to this figure and all subsequent figures: the treatments are: AC, ambient mean and constant pH; AF, ambient mean and fluctuating pH; OAC, ocean acidification scenario with constant pH; OAF, ocean acidification scenario with fluctuating pH. Collected from a low pH variability site, Shell Island and a high pH variability site, Tallon Island in the presence of high variability in oxygen concentrations (a,c) and under low oxygen concentration variability (b). Means \pm s.e., $n = 4-6$ per treatment and site combination. Treatments with different letters above the error bars are statistically different from one another.

to greater pH variability does not provide resistance against the impacts of ocean acidification for the taxa examined. This applies to both the calcification rates and chemistry within the calcifying fluid. Here, physiological control over calcification rates in these two species from different biological kingdoms limited the capacity to detect an effect of pH variability promoting tolerance or providing respite against

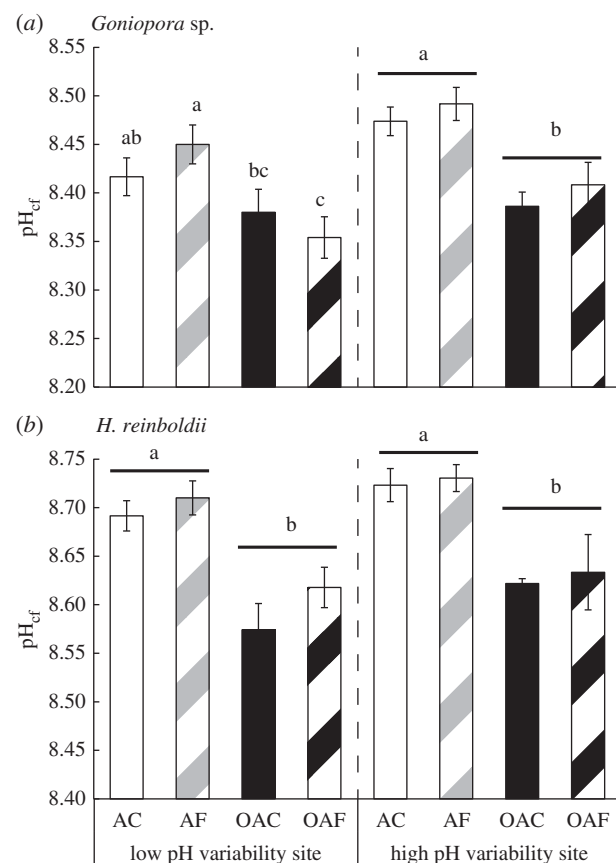


Figure 4. pH_{cf} of (a) coral (*Goniopora* sp.) and (b) crustose coralline algae (*H. reinboldii*) grown under the four treatments from two different populations.

the impacts of ocean acidification. This was irrespective of high or low variability in oxygen concentrations for *Goniopora* sp. Thus, while pH variability still had some effects, species-specific physiological control over calcification appears more important than pH variability in determining responses to ocean acidification in these two key coral reef taxa with vastly different calcification mechanisms.

Our results contrast with the general ecological theory that exposure to greater envelopes of variability in an environmental parameter will provide greater tolerance to shifts in means of that factor [30], a point that has been questioned previously in respect to pH where conflicting results have been observed [14]. While we did observe some effects—mainly in the form of faster calcification and respiration in the coralline alga *H. reinboldii* from Tallon Island (particularly under the AF treatment) and faster photosynthetic rates in *Goniopora* sp. from Shell Island, we observed limited interactive effects between changes in mean pH and either site of origin or pH variability. Both the corals and coralline algae displayed resistance to the effects of ocean acidification through the regulation of calcifying fluid carbonate chemistry.

The lack of strong responses to pH variability here supports the overall trend that the interplay between pH variability and ocean acidification is complex, often yielding contrasting responses in these two calcifying coral reef taxa [14]. The calcification of three coral [19,21,22] and three coralline algal species [20,23] have responded positively to increased pH variability under ocean acidification. By contrast, experimental pH variability did not influence the other half of coral species examined [18,21] and negatively impacted both the adults and F1 recruits of a temperate

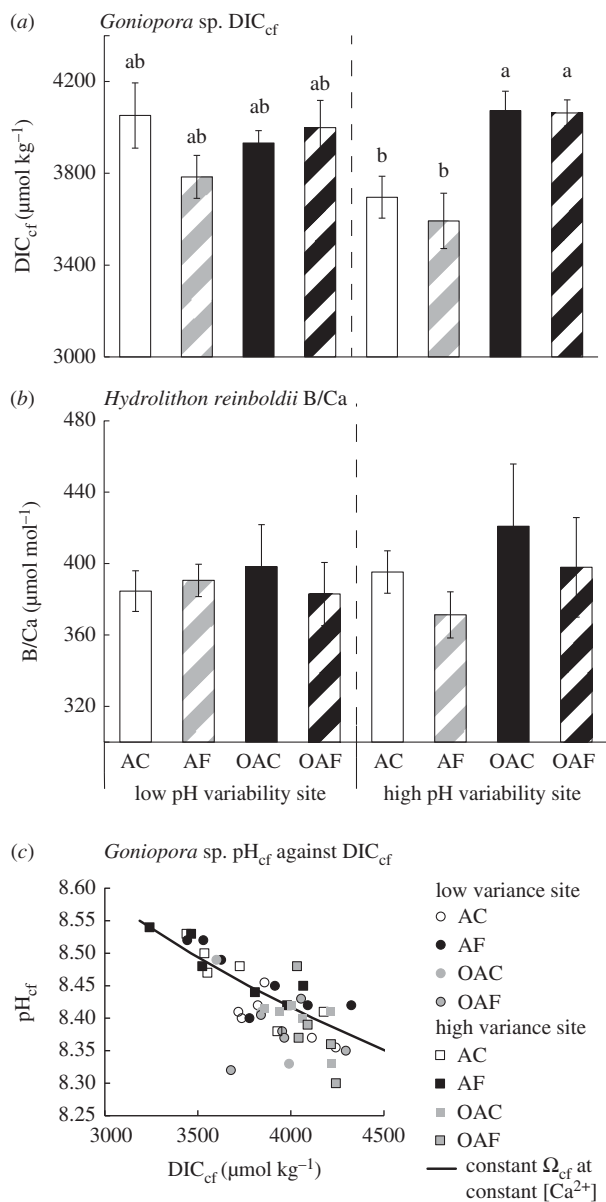


Figure 5. DIC_{cf} of (a) coral (*Goniopora* sp.) and (b) B/Ca of crustose coralline algae (*H. reinboldii*) grown under the four treatments from two different populations. (c) Relationship between *Goniopora* sp. pH_{cf} and DIC_{cf} , demonstrating how modifications of both under different treatments result in near constant Ω_{cf} .

coralline algal species [12,24]. However, strong effects of pH variability were not observed here, except for its impacts on Tallon Island *H. reinboldii* at mean pH 8.05, i.e. once out of a possible eight treatment combinations. This is surprising, particularly for the coralline algae whose sites of calcification are likely more 'open' to seawater than corals. Coralline algae calcify in the top three cell layers [33], whereas the calcifying fluid of corals is separated from seawater by four layers of tissues [43]. This indicates that both taxa are capable of physiological control over calcification, regardless of their very distinct calcification mechanisms.

Our findings therefore add to the understanding that there are multiple considerations that must be taken into account when determining how pH variability will affect corals and coralline algae. All species have differential susceptibilities to changes in seawater carbonate chemistry [44], which seem to be more related to species-specific controls over carbonate chemistry than to their kingdom of

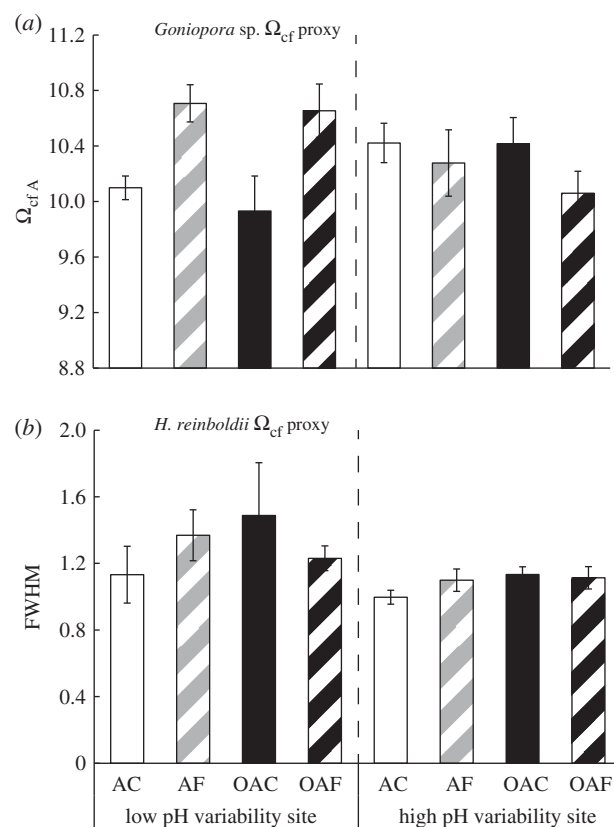


Figure 6. Raman spectroscopy-derived Ω_{cfA} of (a) coral (*Goniopora* sp.) and (b) FWHM intensity of crustose coralline algae (*H. reinboldii*) grown under the four treatments from two different populations. Note: as Ω_{cf} decreases as FWHM decreases.

origin when corals and coralline algae are compared [33,35,45,46]. Species with limited physiological control over their calcification physiology would be expected to respond more dramatically to changes in seawater pH, while species with greater physiological control would respond more robustly [33,35,45], as shown here.

It is possible that a proportion of the inconsistencies between the responses of different species to the effects of greater pH variability could also be elicited by methodological differences between laboratory studies. Only by employing fully factorial assessments of pH variability and ocean acidification will their isolated and combined effects be known. For example, if the response of calcification to declines in mean seawater pH is parabolic in a particular population (i.e. increases first before eventually decreasing) [47], then treatments with higher pH variability and lower mean pH than the 'control' low pH variability treatments (e.g. [20,21]) could elicit faster calcification rates that are in response to mean seawater pH. Similarly, differences in seawater carbonate chemistry between the collection site of organisms could elicit vastly different responses to the same treatments (e.g. [48]). This could explain why many organisms from diurnally variable sites (high pH variability and higher mean pH) do not respond as consistently robust to the effects of ocean acidification as those from upwelling locations (high pH variability, but lower mean pH) [14,16].

Understanding the impacts of variability in seawater carbonate chemistry could be more complex than the effects of other parameters like temperature. This is due to the covarying nature of different components of seawater carbonate chemistry, all of which could have differing physiological

effects on marine species. Treatments with differing variability in pH and identical means will not have the same mean in $p\text{CO}_2$ or Ω and vice versa. This is because of the nonlinear relationship between these parameters. For example, the mean $p\text{CO}_2$ (in μatm) in our AC treatments was 385, AF = 557, OAC = 1095 and OAF = 1454. This nonlinearity is especially problematic given the poor understanding of drivers of calcification, particularly regarding the causal mechanism and exact component of carbonate chemistry responsible for decreases in calcification under ocean acidification/reduced seawater pH [49]. Therefore, treatments that manipulate one component of variability in carbonate chemistry could find different results if means in another aspect of carbonate chemistry drives changes calcification. Furthermore, predicting the combined impacts of changes in variability in these parameters will be even more difficult unless larger multi-treatment experimental designs are employed if more than one parameter of seawater carbonate chemistry influences calcification [25,50] and/or other physiological processes such as photosynthesis [51,52]. These same problems exist when comparing the past exposure of marine species with different ranges of seawater carbonate chemistry.

Exposure to greater pH variability did not promote a greater capacity to maintain elevated pH_{cf} or Ω_{cf} within the calcifying fluid in either corals or coralline algae examined here. This is in contrast to prior observations that the coral *P. cylindrica* from a highly dynamic pH environment was capable of maintaining constant pH_{cf} when exposed simultaneously to low/variable pH and ambient/variable pH [32]. Here, we tested the two hypotheses that could be responsible: (i) that the corals used by Georgiou *et al.* [32] were pre-conditioned to low pH events, having come from the highly dynamic Heron Island reef flat (e.g. the red in our figure 2) or (ii) that the benefit of elevated daytime pH equalled or outweighed any detrimental effects of low night-time pH (e.g. the blue in our figure 2). However, we found neither such response in our experiment, ruling out the possibility that this is a ubiquitous response to pH variability among coral species. Similar to the findings of Georgiou *et al.* [32], is the fact that numerous species of corals have also displayed limited declines in pH_{cf} when reductions in seawater pH are not extreme (i.e. not more than 0.3–0.4 units [35,48,53]). This points to the more likely possibility that declines in pH_{cf} do not occur in every coral species under ocean acidification, or that these declines are not always linked to decreased calcification rates under ocean acidification [35].

It was interesting that mean seawater pH in our study, and not variability in pH, was the driver of mean pH_{cf} . This indicates that when changes in mean seawater pH are larger, such as here and in some other studies [33,35,53], mean conditions are more important in driving mean pH_{cf} in both corals and coralline algae. pH_{cf} calculated using $\delta^{11}\text{B}$ records both day- and night-time precipitation (when night-time precipitation does occur). Here, the contrasting effects of day and night seawater pH on pH_{cf} were averaged over a 24 h cycle in our fluctuating treatments. This is likely because of the similar seawater pH means in both the constant and variable pH treatments. This might not occur for all species, such as in those with limited precipitation during the night. However, further work in either the field or the laboratory should aim to use methods that allow high frequency or real-time determination of changes in

seawater carbonate chemistry within the calcifying fluid, perhaps by using Raman microscopy, pH-sensitive dye or even well-replicated microsensors measurements, to determine changes in calcifying fluid carbonate chemistry over day- and night-time scales under diurnally fluctuating pH conditions.

Reduced mean seawater pH and not pH variability increased *Goniopora* sp.'s DIC_{cf} , particularly those from Tallon Island. This higher DIC_{cf} was not related to elevated photosynthetic rates. It has been previously proposed that the maintenance of higher overall Ω_{cf} relative to seawater in coral, and not simply pH_{cf} , could promote resistance to the effects of ocean acidification [35]. It is possible that increases in *Goniopora* sp. DIC_{cf} partially offset its declining pH_{cf} in the ocean acidification treatments, resulting in constant Ω_{cf} (figure 5c). This increase in DIC_{cf} and decline in pH_{cf} likely resulted in the constant calcification rates, as seen previously in *Porites compressa* from Kāne'ohe Bay in Hawaii [48], which maintained constant $[\text{CO}_3^{2-}]_{\text{cf}}$ and calcification rates when grown in reduced seawater pH.

Constant Ω_{cf} under the ocean acidification treatments in *Goniopora* sp. could have led to its resistance to ocean acidification here. *Pocillopora damicornis* from Rottneest Island, Australia had lower $[\text{CO}_3^{2-}]_{\text{cf}}$ when grown under conditions simulating ocean acidification, but Ω_{cf} was maintained at a constant value by increased $[\text{Ca}^{2+}]_{\text{cf}}$ [35,36,46]. Here, we did not find increased $[\text{Ca}^{2+}]_{\text{cf}}$ in *Goniopora* sp. under ocean acidification, and their $[\text{Ca}^{2+}]_{\text{cf}}$ was lower than that of seawater ($10.64 \text{ mmol kg}^{-1}$) in all treatments. However, constant Ω_{cf} and calcification rates of *Goniopora* sp. with declining mean pH support the overall hypothesis that the capacity to maintain constant and elevated Ω_{cf} could be linked to resistance to the effects of ocean acidification. While we cannot as yet quantify Ω_{cf} in high magnesium calcite, no changes in *H. reinboldii* FWHM also suggest overall constant Ω_{cf} . Combined with the pH_{cf} sensitivity, this indicates a likely increase in DIC_{cf} and/or $\text{Ca}_{\text{cf}}^{2+}$ in *H. reinboldii*.

Together, these recent results indicate that resistance of these two key coral reef taxa to the impacts of ocean acidification is related to the maintenance of constant Ω_{cf} , which can occur via three possibly complementary mechanisms under ocean acidification: (i) maintenance of constant pH_{cf} ; (ii) elevation of DIC_{cf} ; and (iii) elevation of $\text{Ca}_{\text{cf}}^{2+}$, for which the capacity of all processes differs between species [32,35,36,46,48]. Additionally, these processes were not strongly influenced by variability in seawater pH or past exposure to greater pH variability, with the only effects caused by pH variability being higher DIC_{cf} for *Goniopora* sp. under the OAF treatments compared to AF treatments. While past environmental variability and exposure to greater pH variability may be important in driving the resistance of temperate upwelling species to ocean acidification [16], this is not ubiquitous in the two calcifying coral reef taxa examined here. Our two focal calcifying species were the only two common at both study sites. Therefore, further research should explore whether the trends observed here hold for other locations, and other coral and coralline algal species. We demonstrate that physiological control over calcification physiology can be more important in predicting the responses of coral reef taxa to ocean acidification than either past or current exposure to pH variability. This study has revealed that many pertinent questions regarding the calcification physiology of corals and coralline algae remain

unanswered, while at the same time supporting the conclusion that physiological controls on calcification drive resistance to ocean acidification in corals and coralline algae.

Ethics. All local regulations and permit requirements were followed during this study.

Data accessibility. All geochemical data are within the electronic supplementary material; all else are accessible in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.250q1g7> [54].

Authors' contributions. C.E.C. and S.C. conceived the research and wrote the paper. C.E.C., S.C., B.M. and Q.D. ran the experiment. C.E.C., S.C. and B.M. conducted fieldwork. C.E.C. and S.C. conducted boron isotope and trace element analysis. T.M.D. conducted the Raman spectroscopy analysis. M.T.M. provided essential laboratory equipment, facilities and analyses. C.E.C. conducted the statistical analyses. All authors edited the manuscript, or provided intellectual input, and agreed to its submission.

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