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# Coral resistance to ocean acidification linked to increased calcium at the site of calcification

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## Research



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Electronic supplementary material is available online at [rs.figshare.com](http://rs.figshare.com).

Ocean acidification threatens the persistence of biogenic calcium carbonate (CaCO<sub>3</sub>) production on coral reefs. However, some coral genera show resistance to declines in seawater pH, potentially achieved by modulating the chemistry of the fluid where calcification occurs. We use two novel geochemical techniques based on boron systematics and Raman spectroscopy, which together provide the first constraints on the sensitivity of coral calcifying fluid calcium concentrations ([Ca<sup>2+</sup>]<sub>cf</sub>) to changing seawater pH. In response to simulated end-of-century pH conditions, *Pocillopora damicornis* increased [Ca<sup>2+</sup>]<sub>cf</sub> to as much as 25% above that of seawater and maintained constant calcification rates. Conversely, *Acropora youngei* displayed less control over [Ca<sup>2+</sup>]<sub>cf</sub>, and its calcification rates strongly declined at lower seawater pH. Although the role of [Ca<sup>2+</sup>]<sub>cf</sub> in driving calcification has often been neglected, increasing [Ca<sup>2+</sup>]<sub>cf</sub> may be a key mechanism enabling more resistant corals to cope with ocean acidification and continue to build CaCO<sub>3</sub> skeletons in a high-CO<sub>2</sub> world.

## 1. Introduction

Since the start of the industrial era, atmospheric CO<sub>2</sub> concentrations have increased from approximately 280 to over 400 ppmv today, primarily due to burning of fossil fuels and deforestation [1]. Although CO<sub>2</sub> levels in the geologic past (e.g. during the Eocene) were likely several times higher than today, it is the speed of CO<sub>2</sub> rise that dictates the severity of ocean acidification [2,3], with the current rate of CO<sub>2</sub> released by human activities being unprecedented even over million-year timescales [4]. However, despite its rapid rise, more than one quarter of anthropogenic CO<sub>2</sub> emissions have already been absorbed by the oceans [5], causing declines in seawater pH and hence aragonite saturation state ( $\Omega_{Ar} = [\text{CO}_3^{2-}][\text{Ca}^{2+}]/K_{sp}$ ). Shallow-water coral reefs, which are found only within a relatively narrow range of open-ocean  $\Omega_{Ar} > 3$  conditions [6], are likely to be among the most sensitive marine ecosystems to ocean acidification [6–8]. Under ‘business-as-usual’ CO<sub>2</sub> emissions, climate models project that the surface open ocean could be devoid of regions with  $\Omega_{Ar} > 3$  by the end of the twenty-first century [9], potentially driving a rapid decline of corals and the CaCO<sub>3</sub>-based reef ecosystems that they build.

Crucial to interpreting the sensitivity of corals to ocean acidification is the mechanism by which calcification occurs. Scleractinian corals transport seawater to a micro-scale internal calcifying space [10–12], thereby supplying some of the calcium (Ca<sup>2+</sup>) and carbonate (CO<sub>3</sub><sup>2-</sup>) ions needed to build their aragonitic (CaCO<sub>3</sub>) skeletons. However, as seawater pH declines, the concentration of carbonate ions ([CO<sub>3</sub><sup>2-</sup>]) in seawater decreases, making precipitation of CaCO<sub>3</sub> less favourable due to lower  $\Omega_{Ar}$  [13]. In laboratory experiments, many corals repeatedly show decreased calcification rates in response to lower- $\Omega_{Ar}$  conditions achieved by manipulating seawater pH or, less commonly, [Ca<sup>2+</sup>] [14–17]. Yet, it is increasingly recognized that not all corals are affected equally. Some species are highly sensitive ‘losers’ and others appear to be more resistant ‘winners’ that

may potentially benefit from reduced competition for space or resources [8]. Differential sensitivities to  $\Omega_{Ar}$  among coral species imply that ocean acidification has the potential to irrevocably alter coral assemblages for centuries to come. Despite this, little is known about how resistant species are better able to cope with acidification. Elevating pH (and thus  $[\text{CO}_3^{2-}]$ ) at the internal site of calcification is one potential mechanism to maintain high  $\Omega_{Ar}$  that may confer resistance [18–21], but the ability to raise pH is not limited to resistant species [22]. Alternatively, or in combination, corals could theoretically elevate internal  $\text{Ca}^{2+}$  to increase  $\Omega_{Ar}$ , even though concentrations of  $\text{Ca}^{2+}$  in ambient seawater (approx.  $10 \text{ mmol kg}^{-1}$ ) far exceed those of  $\text{CO}_3^{2-}$  (approx.  $0.2 \text{ mmol kg}^{-1}$ ). The utility of elevating  $[\text{Ca}^{2+}]$  is, however, potentially limited to less than a factor of approximately two increase relative to seawater because decreases in Mg/Ca will begin to favour the precipitation of calcite over aragonite [23] and the  $\text{Ca}^{2+}/\text{CO}_3^{2-}$  stoichiometry will become less optimal for crystal growth [24]. Nevertheless, while at least some corals can actively pump  $\text{Ca}^{2+}$  [25,26], no study has quantified changes in calcifying fluid  $\text{Ca}^{2+}$  ( $[\text{Ca}^{2+}]_{cf}$ ) in response to seawater pH, and thus, the role of  $\text{Ca}^{2+}$  relative to  $\text{CO}_3^{2-}$  in defining resistance to ocean acidification remains unknown.

We apply a novel technique to derive  $[\text{Ca}^{2+}]_{cf}$  in the corals *Acropora youngei* and *Pocillopora damicornis* cultured under simulated ocean acidification conditions. In the absence of direct or non-invasive techniques to measure  $[\text{Ca}^{2+}]_{cf}$ , we use the information provided by combining two recently developed geochemical proxies. First, the boron systematics ( $\delta^{11}\text{B}$  and B/Ca) of aragonite quantify calcifying fluid carbonate chemistry, including  $\text{pH}_{cf}$  and  $[\text{CO}_3^{2-}]_{cf}$  [27,28]. Second, Raman spectroscopy can be used to determine calcifying fluid  $\Omega_{Ar}$  [29]. As  $\Omega_{Ar}$  is a function of both  $[\text{CO}_3^{2-}]$  and  $[\text{Ca}^{2+}]$ , boron systematics and Raman spectroscopy can be applied in tandem to derive  $[\text{Ca}^{2+}]_{cf}$  (electronic supplementary material, table S1). Here, we use this approach to investigate the response of  $[\text{Ca}^{2+}]_{cf}$  to seawater pH and its potential role in controlling the calcification sensitivity to ocean acidification.

## 2. Material and methods

The coral culturing experimental design was described previously by Comeau *et al.* [30]. Briefly, branches of *A. youngei* and *P. damicornis* were collected from Rottnest Island in Western Australia and transported to the Waterman's Bay experimental aquaria facility in Perth, Australia. The corals were allowed to recover for two weeks before exposure to treatments in 36 aquaria divided among three pH (total scale) treatments of 7.63, 7.81 and 8.09 maintained by  $\text{CO}_2$  bubbling. After eight weeks, the apical tips of the skeletons were crushed to powders for geochemical and Raman analyses. B/Ca and  $\delta^{11}\text{B}$  measurements and data are reported in Comeau *et al.* [30]. Mg/Ca and Sr/Ca ratios were measured on a Q-ICP-MS (X-series II, Thermo Fisher Scientific) following the methods of Holcomb *et al.* [31]. Precisions of Mg/Ca and Sr/Ca were  $0.01 \text{ mmol mol}^{-1}$  and  $0.009 \text{ mmol mol}^{-1}$ , respectively, based on repeated analyses of an in-house coral skeleton consistency standard.

Raman spectroscopy was conducted on the same powders used for geochemical analyses. Measurements were made on a WITec Alpha 300RA+ system with an Andor iDUS 401 CCD maintained at  $-60^\circ\text{C}$ , and a  $20\times$  objective with 0.5 numerical aperture. An infrared (785 nm) laser was used with a  $1200 \text{ mm}^{-1}$  grating and the spectral centre placed at a Raman shift of  $830 \text{ cm}^{-1}$ . Coral skeleton powders were spread onto a

glass slide and multiple grains (typically five) were sampled with 1 s integration times. A target for replication was set at 25 spectra per sample (i.e. per individual coral branch), although this was not always achieved as some spectra with poor signal (i.e. arbitrary intensity units less than 100) were subsequently filtered during data processing (electronic supplementary material, tables S2–S3). For each spectrum, the aragonite  $\nu_1$  peak was fit with a Gaussian curve, and the resulting full width at half maximum (FWHM) intensity was converted to  $\Omega_{Ar}$  following the methods of DeCarlo *et al.* [29]. We note that  $\Omega_{Ar}$  was estimated by Comeau *et al.* [30] based only on boron-derived  $[\text{CO}_3^{2-}]_{cf}$  and assuming a constant  $[\text{Ca}^{2+}]_{cf}$ . Here, we use only the directly derived  $[\text{CO}_3^{2-}]_{cf}$  from Comeau *et al.* [30], and instead, we calculate  $[\text{Ca}^{2+}]_{cf}$  as follows:

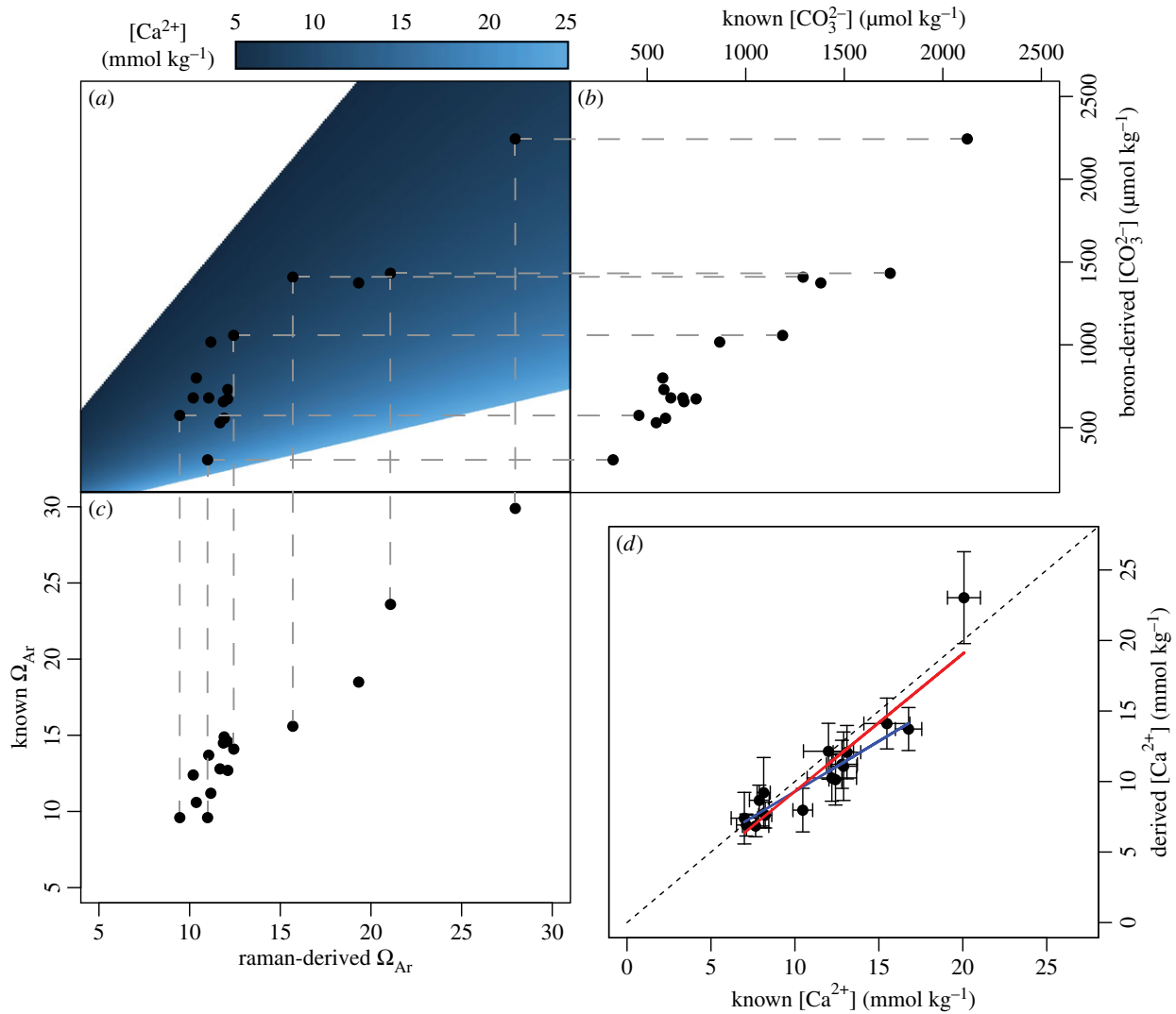
$$[\text{Ca}^{2+}]_{cf} = \frac{\Omega_{Ar} * K_{sp}}{[\text{CO}_3^{2-}]_{cf}}, \quad (2.1)$$

where  $[\text{CO}_3^{2-}]_{cf}$  and  $\Omega_{Ar}$  are derived from boron systematics [28] and Raman spectroscopy, respectively. This equation is simply a rearrangement of the definition of aragonite saturation state shown in the Introduction.  $\text{Ca}_{cf}^{2+}/\text{Ca}_{sw}^{2+}$  ratios were calculated by normalizing to  $[\text{Ca}^{2+}]_{sw}$ , which was estimated from salinity as  $10.58 \text{ mmol kg}^{-1}$  [32].

Precisions of derived  $[\text{Ca}^{2+}]_{cf}$  were estimated with a Monte Carlo method. We repeated the calculation of  $[\text{Ca}^{2+}]_{cf}$   $10^4$  times, and in each iteration, we added random errors to the measured  $\delta^{11}\text{B}$  ( $1\sigma$  analytical uncertainty of  $0.17\%$ ), B/Ca ( $1\sigma$  analytical uncertainty of  $18 \mu\text{mol mol}^{-1}$ ) and Raman FWHM (standard error of replicates per sample; electronic supplementary material, tables S2–S3), assuming Gaussian distributions. We estimated the  $1\sigma$  uncertainty of  $[\text{Ca}^{2+}]_{cf}$  by taking the standard deviation of the  $10^4$  Monte Carlo iterations.

We also tested whether our technique could be accurately applied to abiogenic (i.e. synthetic or inorganic) aragonites. These aragonites were precipitated from seawater with  $[\text{Ca}^{2+}]$  manipulated by the addition of  $\text{CaCl}_2$  and concentrated seawater [27], allowing us to check if our combined boron and Raman approach is sensitive to variations in  $[\text{Ca}^{2+}]$ . We used the seven abiogenic aragonite samples that were repeatedly analysed in DeCarlo *et al.* [29] for calibration of the Raman- $\Omega_{Ar}$  proxy, in addition to new Raman measurements on nine more abiogenic aragonite samples that were precipitated from fluids with  $[\text{Ca}^{2+}]$  exceeding  $12 \text{ mmol kg}^{-1}$ , as described in [27]. Eight of the abiogenic aragonite samples were precipitated using a 'degassing' method in which  $\text{CaCO}_3$  was dissolved in acidified seawater and precipitation occurred as the seawater  $\text{pCO}_2$  equilibrated with the atmosphere. The degassing experiments were not used in calibrating the Raman- $\Omega_{Ar}$  proxy. The other eight experiments were conducted by pumping  $\text{Na}_2\text{CO}_3/\text{NaHCO}_3$  solutions into filtered seawater. For each sample, we used the fluid pH, and the aragonite B/Ca and Raman FWHM to calculate  $[\text{Ca}^{2+}]$  as described above. We then compared our derived  $[\text{Ca}^{2+}]$  with that reported from measurements during the aragonite precipitation experiments [27].

Coral  $[\text{Ca}^{2+}]_{cf}$  dynamics were separately estimated using Mg/Ca and Sr/Ca ratios of the coral skeletons. Coral calcification models that invoke seawater as the ultimate source of the calcifying fluid,  $\text{Ca}^{2+}$  addition to the fluid and precipitation from a closed or semi-closed reservoir have been successful at explaining much of the variability in the elemental composition of the skeleton [12,29,33,34]. Although such models have not been validated in terms of accurately predicting  $[\text{Ca}^{2+}]_{cf}$  variability, they can provide insights into whether  $\text{Ca}^{2+}$  addition to the calcifying fluid is required to explain the skeletal geochemistry. We used the model described in [29] that predicts  $[\text{Ca}^{2+}]_{cf}$  enrichment based on paired Mg/Ca and Sr/Ca data. The model is based on the abiogenic partitioning of these two element ratios between aragonite and seawater, and it solves for the combination of  $[\text{Ca}^{2+}]_{cf}$  enrichment (which dilutes both Mg/Ca and



**Figure 1.** Test of deriving  $[Ca^{2+}]$  from abiogenic aragonites precipitated under various  $Ca^{2+}$  concentrations. (a) Derived  $[Ca^{2+}]$  (colours) as functions of  $\Omega_{Ar}$  (x-axis) and  $[CO_3^{2-}]$  (y-axis). Each black point shows the derived  $[Ca^{2+}]$  of a separate abiogenic precipitation experiment. The boron-derived  $[CO_3^{2-}]$  and Raman-derived  $\Omega_{Ar}$  measurements that are used together to calculate  $[Ca^{2+}]$  are shown in (b) and (c), respectively. The dashed grey lines each connect to the boron and Raman data from a single experiment, indicating how combining these data enables estimates of  $[Ca^{2+}]$ . For clarity, only a subset of these lines is plotted. (d) Comparison of derived  $[Ca^{2+}]$  to the  $[Ca^{2+}]$  known from fluid measurements during the aragonite precipitation experiments. The dashed black line indicates a 1 : 1 relationship, and the solid lines show regressions fit to all the data (red) and to all the data except the highest  $[Ca^{2+}]$  point (blue). Error bars show 95% confidence intervals.

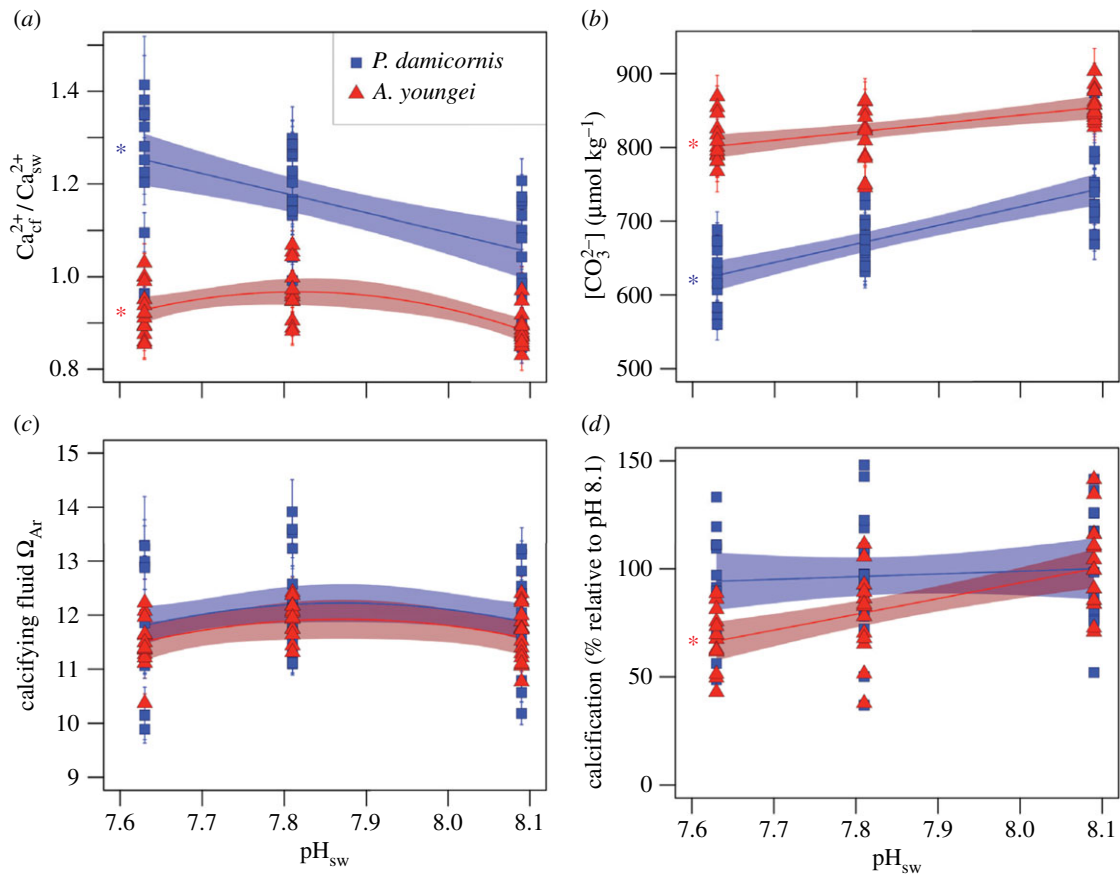
Sr/Ca) and Rayleigh fractionation (which increases Mg/Ca and decreases Sr/Ca) that match the measured element ratios. We performed two separate model runs: one in which addition to the calcifying fluid is 100% selective for  $Ca^{2+}$  and another in which addition is 50% 'leaky' with respect to  $Mg^{2+}$  and  $Sr^{2+}$  (i.e.  $[Sr^{2+}]_{fluid} = (0.5Ca_{addition}^{2+})(Sr_{sw}/Ca_{sw}) + [Sr^{2+}]_{sw}$ ). Both produce the same patterns of variability, but the latter requires twice the  $[Ca^{2+}]_{cf}$  enrichment to explain the measured element ratios.

All parameters ( $[CO_3^{2-}]_{cf}$ ,  $[Ca^{2+}]_{cf}$ ,  $\Omega_{Ar}$ , calcification rate and modelled  $[Ca^{2+}]_{cf}$ ) for each species were checked for normality with Kolmogorov–Smirnov tests and homogeneity of variances across pH treatments with Levene's tests. Regressions were performed using the linear model (*lm*) function in R [35] with species treated as factors as described in the text. Residuals of all regressions were also checked for normality with Kolmogorov–Smirnov tests.

### 3. Results and discussion

Our application of the Raman and boron proxies to the abiogenic aragonites produced  $[Ca^{2+}]$  estimates that were

correlated with the known  $[Ca^{2+}]$  during the experiments (figure 1). A regression between derived and known  $[Ca^{2+}]$  has a slope of  $1.0 \pm 0.1$  ( $r^2 = 0.82$ ) (figure 1d). Although excluding the highest  $[Ca^{2+}]$  data point decreases the slope to  $0.71 \pm 0.09$  ( $r^2 = 0.82$ ), the data still indicate a sensitivity of the combined Raman-boron proxy to fluid  $[Ca^{2+}]$ . This result supports the overall reliability of our approach because the derived versus known  $[Ca^{2+}]$  plot close to a 1 : 1 line, demonstrating that the Raman and B/Ca proxies differ primarily by their sensitivities to  $[Ca^{2+}]$ . The root-mean-square error of the derived to known  $[Ca^{2+}]$  regression is  $1.7\ mmol\ kg^{-1}$ , and comparing this with the average standard deviation of derived  $[Ca^{2+}]$  ( $0.9\ mmol\ kg^{-1}$  for abiogenic data and  $0.5\ mmol\ kg^{-1}$  for our corals) indicates that at least half of the scatter in the regression is explained by propagation of errors from the boron and Raman measurements. That not all the scatter around the regression is accounted for by the propagated uncertainties may suggest that other factors have minor influences on either the boron or Raman proxies, but it is unlikely that we would be able to successfully reconstruct 82% the  $[Ca^{2+}]$  variance of the



**Figure 2.** Sensitivity of calcifying fluid chemistry and calcification to seawater pH. (a)  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$ , (b)  $[\text{CO}_3^{2-}]_{\text{cf}}$ , (c)  $\Omega_{\text{Ar}}$  and (d) calcification responses to pH<sub>sw</sub> treatments for both *P. damicornis* (blue squares) and *A. youngae* (red triangles). Bounded lines indicate regression fits  $\pm 1$  s.e. Coloured asterisks indicate which regressions are statistically significant ( $p < 0.01$ ). Error bars on individual points represent 1 s.e.m.

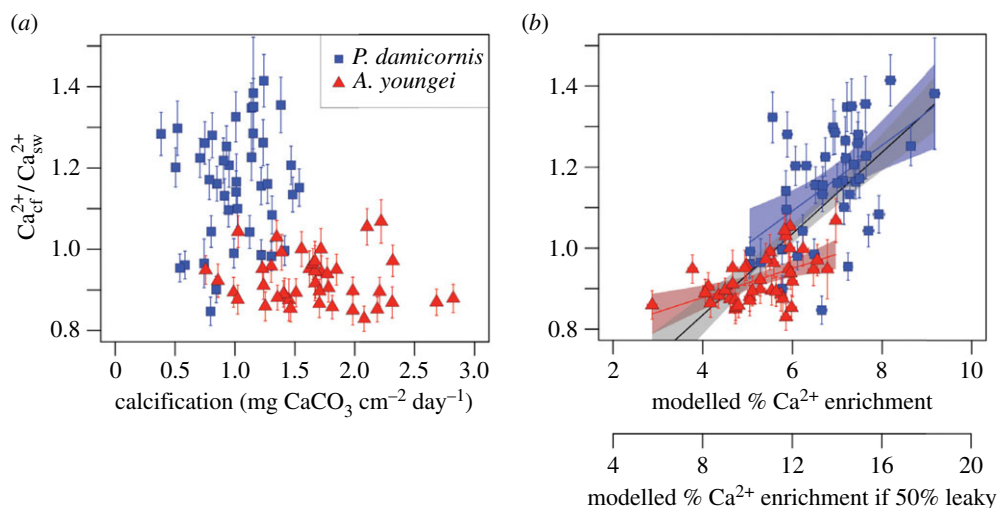
experimental fluids if the primary controls of B/Ca and Raman FWHM were factors other than  $[\text{CO}_3^{2-}]$  and  $\Omega_{\text{Ar}}$  respectively. Therefore, while each individual data point carries substantial uncertainty, our abiogenic test suggests that this approach is successful in capturing changes in  $[\text{Ca}^{2+}]$  given suitable sample replication (figure 1).

In our culturing experiment, *P. damicornis* displayed a strong ability to control  $[\text{Ca}^{2+}]_{\text{cf}}$ , whereas *A. youngae* was unable to elevate  $[\text{Ca}^{2+}]_{\text{cf}}$  in response to low pH. The ratio of  $[\text{Ca}^{2+}]_{\text{cf}}$  to  $[\text{Ca}^{2+}]_{\text{sw}}$  of the external seawater ( $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$ ) ranged from 0.85 to 1.41 for *P. damicornis* and increased significantly with decreasing seawater pH (pH<sub>sw</sub>;  $r^2 = 0.31$ ,  $n = 42$ ,  $p < 0.01$ ,  $F_{1,40} = 19.3$ ; figure 2a). *Pocillopora damicornis* maintained  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  of  $1.06 \pm 0.06$  (s.e.) at present-day pH<sub>sw</sub> (8.09), but it increased  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  to  $1.25 \pm 0.06$  at simulated end-of-century pH<sub>sw</sub> (7.63) under a business-as-usual emissions scenario. Conversely, *A. youngae* did not consistently increase  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  with decreasing pH<sub>sw</sub>. Although *A. youngae* increased  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  slightly from  $0.89 \pm 0.03$  at the highest pH<sub>sw</sub> to  $0.97 \pm 0.03$  at the mid-pH<sub>sw</sub> treatment, there was no further change in  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  at the lowest pH<sub>sw</sub> treatment (figure 2a). Calcifying fluid  $\Omega_{\text{Ar}}$  was maintained at nearly constant levels across treatments for both species, with only slight declines at the lowest pH<sub>sw</sub> (figure 2c). The ability of *P. damicornis* to control  $[\text{Ca}^{2+}]_{\text{cf}}$  resulted in similar  $\Omega_{\text{Ar}}$  compared with *A. youngae*, even though  $[\text{CO}_3^{2-}]_{\text{cf}}$  was lower in *P. damicornis* (figure 2b) [30].

The species' differences in  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  are mirrored in their calcification responses to acidification (figure 2d). While *A. youngae* calcification declined at lower pH<sub>sw</sub> ( $r^2 =$

$0.36$ ,  $n = 42$ ,  $p < 0.01$ ,  $F_{1,40} = 24.3$ ), *P. damicornis* calcification was insensitive to pH<sub>sw</sub> ( $r^2 = 0.01$ ,  $p = 0.58$ ). These contrasting responses appear to be driven not by calcifying fluid carbonate chemistry [30], but rather by  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$ . In fact,  $[\text{CO}_3^{2-}]_{\text{cf}}$  was significantly more sensitive to pH<sub>sw</sub> for *P. damicornis* than for *A. youngae* ( $r^2 = 0.83$ ,  $n = 84$ ,  $p < 0.01$ ,  $F_{3,80} = 134.9$ ), contrasting their calcification sensitivities to pH<sub>sw</sub> (figure 2). Similarly, *P. damicornis* calcification has been shown to be insensitive to acidification across multiple locations in the Pacific Ocean [36], whereas *A. youngae* is highly sensitive [37,38]. Although the mechanisms underlying these different sensitivities have so far remained largely unresolved, our results suggest that resistant corals are those with the ability to elevate  $[\text{Ca}^{2+}]_{\text{cf}}$ , and more susceptible species are those which cannot.

There are two non-mutually exclusive hypotheses to explain the changes in  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  that we observed: (i) passive precipitation of  $\text{CaCO}_3$  and (ii) active upregulation by the coral polyps. Mass balance considerations imply that accretion of  $\text{CaCO}_3$  skeleton consumes  $[\text{Ca}^{2+}]_{\text{cf}}$ , but this does not exclude the possibility that upregulation of processes controlling  $[\text{Ca}^{2+}]_{\text{cf}}$  is also involved. Indeed, several lines of evidence support that much of the  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  variability in our experiment was driven by the activity of the corals. First, while there is a weak inverse correlation between  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  and calcification when data for both species are combined ( $r^2 = 0.22$ ,  $n = 84$ ,  $p < 0.01$ ,  $F_{1,82} = 24.0$ ), there are no significant correlations within each species (figure 3a). Second, the  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  exceeding 1 for *P. damicornis* cannot be explained by  $\text{CaCO}_3$  precipitation and requires some



**Figure 3.** Factors driving  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  variability. Sensitivity of  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  to (a) calcification and (b)  $[\text{Ca}^{2+}]_{\text{cf}}$  elevation estimated by modelling with Mg/Ca and Sr/Ca ratios. In (b), the upper x-axis values show the model assuming 100% selectivity for  $\text{Ca}^{2+}$ , and the lower x-axis values show the model that is 50% leaky with respect to  $\text{Mg}^{2+}$  and  $\text{Sr}^{2+}$  ions. The black line with grey error bound in (b) corresponds to regressions fit to the data from both species. The coloured lines and error bounds in (b) show species-specific regressions. Colours are the same as in figure 2.

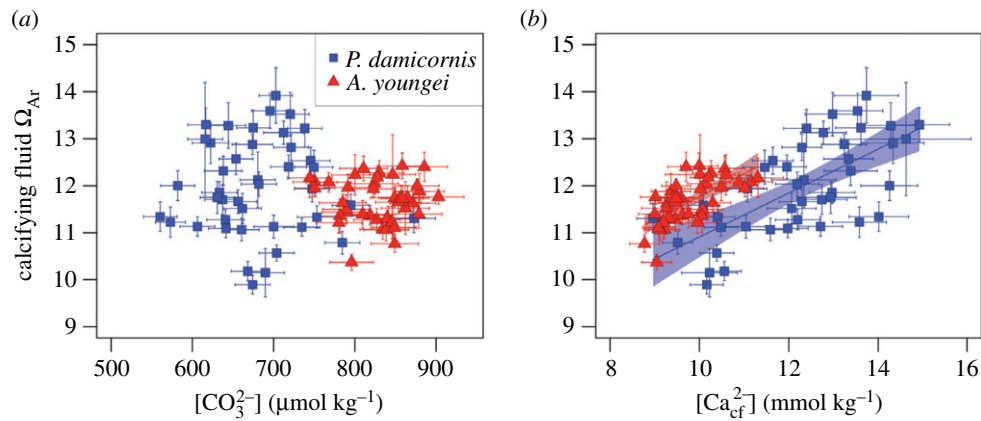
mechanism of increasing  $[\text{Ca}^{2+}]_{\text{cf}}$ . Finally, we independently estimated  $[\text{Ca}^{2+}]_{\text{cf}}$  using skeletal Mg/Ca and Sr/Ca ratios and a simple model [29] in which these element/Ca ratios are explained by initial  $[\text{Ca}^{2+}]_{\text{cf}}$  elevation followed by precipitation from a closed reservoir. The elevation of  $[\text{Ca}^{2+}]_{\text{cf}}$  estimated from this modelling exercise is strongly correlated ( $r^2 = 0.53$ ,  $n = 84$ ,  $p < 0.01$ ,  $F_{1,82} = 93.0$ ) with our derived  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  ratios, and significant positive correlations are found within each species (figure 3b). However, the model implies that  $[\text{Ca}^{2+}]_{\text{cf}}$  is elevated up to 10% with respect to seawater, which is less than the upper limit of 25% indicated by our maximum derived mean  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  of 1.25 for *Pocillopora* at the lowest  $\text{pH}_{\text{sw}}$ . One possible reason for this is that the model assumes that the addition of  $\text{Ca}^{2+}$  to the calcifying fluid is 100% selective for  $\text{Ca}^{2+}$ . Allowing this process to be partially leaky with respect to  $\text{Sr}^{2+}$  and  $\text{Mg}^{2+}$  ions [39] brings the modelled  $[\text{Ca}^{2+}]_{\text{cf}}$  elevation into closer agreement with our derived  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  (figure 3b). Transporting  $\text{Mg}^{2+}$  along with  $\text{Ca}^{2+}$  to the calcifying fluid may allow  $[\text{Ca}^{2+}]_{\text{cf}}$  to be elevated without favouring calcite growth over aragonite. Further geochemical evidence for active  $[\text{Ca}^{2+}]_{\text{cf}}$  elevation comes from calcium isotope ratios in modern and fossil coral skeletons, which cannot be reconciled with direct precipitation from seawater [40,41]. Rather, the calcium isotopic offset between coral skeletons and seawater supports strong biological modulation of  $[\text{Ca}^{2+}]_{\text{cf}}$  [40] and potentially some effects of Rayleigh fractionation or  $\text{Ca}^{2+}$  diffusion between the calcifying fluid and the external environment [41].

Corals may influence their  $[\text{Ca}^{2+}]_{\text{cf}}$  via multiple mechanisms. These potentially include Ca-channels [25,39,42–44],  $\text{Ca}^{2+}/\text{Na}^{+}$  exchange [43],  $\text{Ca}^{2+}$ -ATPase [26] and precipitation/dissolution of amorphous calcium carbonate [45]. The only previous measurements of coral  $[\text{Ca}^{2+}]_{\text{cf}}$  were made by cutting an incision in living *Galaxea fascicularis* polyps and inserting a  $\text{Ca}^{2+}$  microsensor near the skeleton surface [26]. Although potentially invasive, these previous data showed elevation above seawater concentrations by up to 10%, within the range of our  $\text{Ca}_{\text{cf}}^{2+}/\text{Ca}_{\text{sw}}^{2+}$  ratios. Importantly, the microsensor data allowed for continuous measurements, which revealed a strong sensitivity of  $[\text{Ca}^{2+}]_{\text{cf}}$  to light, likely because the polyp uses energy provided by its photosynthetic

symbionts to drive the activity of various  $\text{Ca}^{2+}$ -transport mechanisms [26,44]. In additional laboratory experiments that exposed corals to Ca-channel and  $\text{Ca}^{2+}$ -ATPase inhibitors,  $[\text{Ca}^{2+}]_{\text{cf}}$  variability was dampened and calcification rates were decreased [26,39,43]. These multiple lines of evidence make it clear that some corals have cellular mechanisms in place to modulate  $[\text{Ca}^{2+}]_{\text{cf}}$ , and our results demonstrate that resistant species such as *Pocillopora* can upregulate these processes to resist the effects of ocean acidification and to maintain normal calcification rates even at low  $\text{pH}_{\text{sw}}$ . Conversely, our data indicate that *A. youngei* exerts less control on  $[\text{Ca}^{2+}]_{\text{cf}}$ , consistent with a previous experiment that found gene expression for ion transporters in *Acropora* did not change in response to seawater pH [46].

Our unique characterization of  $[\text{CO}_3^{2-}]_{\text{cf}}$  and  $[\text{Ca}^{2+}]_{\text{cf}}$  enables the first evaluation of their relative influences on calcifying fluid  $\Omega_{\text{Ar}}$ . Most models of coral calcification rely on the assumption that  $\Omega_{\text{Ar}}$  is controlled by  $[\text{CO}_3^{2-}]_{\text{cf}}$  and that variability in  $[\text{Ca}^{2+}]_{\text{cf}}$  is negligible [20,47]. However, we found no significant correlations between  $[\text{CO}_3^{2-}]_{\text{cf}}$  and  $\Omega_{\text{Ar}}$ , neither within nor between species (figure 4a). Rather,  $\Omega_{\text{Ar}}$  is positively correlated ( $r^2 = 0.47$ ,  $n = 84$ ,  $p < 0.01$ ,  $F_{2,81} = 37.8$ ) with  $[\text{Ca}^{2+}]_{\text{cf}}$  for both *A. youngei* and *P. damicornis* (figure 4b). This finding should, however, be viewed with some caution because our technique of deriving  $[\text{Ca}^{2+}]_{\text{cf}}$  in part from proxy measurements of  $\Omega_{\text{Ar}}$  means that they are not independent, and thus, it is difficult to determine if this correlation represents a causal relationship. Nevertheless, for a given  $[\text{Ca}^{2+}]_{\text{cf}}$ , calcifying fluid  $\Omega_{\text{Ar}}$  is higher in *A. youngei* than *P. damicornis*, which may explain the overall faster calcification of *A. youngei* [30]. Critically though,  $[\text{Ca}^{2+}]_{\text{cf}}$  for *A. youngei* remains within a relatively narrow range, whereas *P. damicornis* is capable of driving  $\Omega_{\text{Ar}}$  higher, potentially by elevating  $[\text{Ca}^{2+}]_{\text{cf}}$ . This ability may account for the relative insensitivity of *P. damicornis* calcification to seawater pH, although we cannot exclude some influence of other factors such as changes in calcifying time or surface area within the calyx.

Ocean acidification, combined with warming, threatens to disrupt coral growth and survival [6–8,38]. Although some resistant species are likely to persist, the differential responses



**Figure 4.** Relative influences on coral calcifying fluid  $\Omega_{Ar}$ . Sensitivity of  $\Omega_{Ar}$  to (a)  $[CO_3^{2-}]_{cf}$  and (b)  $[Ca^{2+}]_{cf}$ . Colours are the same as in figure 2.

to ocean acidification will potentially create novel configurations of species occupying coral reefs. If coral communities shift in favour of species resistant to ocean acidification [8], there are likely to be cascading effects in reef ecosystems due to the associations of other reef biota with the habitat created by susceptible coral genera such as *Acropora* [48]. Furthermore, declines in  $\text{CaCO}_3$  production by susceptible genera are expected to be exacerbated by increasing bioerosion and carbonate dissolution rates as seawater pH declines [49–53]. In tandem, these changes in  $\text{CaCO}_3$  budgets could inhibit some reefs from keeping pace with rising sea levels [54]. Identifying which corals can cope with ocean acidification by increasing  $[Ca^{2+}]_{cf}$  provides a new perspective in identifying more resistant species, which may help efforts to forecast the changing state and viability of coral reefs as anthropogenic  $\text{CO}_2$  continues to invade the oceans.

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

**Data accessibility.** Datasets supporting this article have been uploaded as the electronic supplementary material, and the raw data and code

are available at <https://codeocean.com/2018/03/12/code-for-amp-num-34-semi-resistant-coral-increase-calcium-to-cope-with-ocean-acidification-amp-num-34-semi/code>.

**Authors' contributions.** S.C. and C.E.C. performed the culturing experiments and measured the skeletal geochemistry. T.M.D. performed the Raman analyses, designed the technique for quantifying calcium concentrations, and wrote the manuscript. All authors contributed to interpreting data and editing the manuscript.

**Competing interests.** The authors declare that they have no competing interests.

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## References

- IPCC. 2013 Climate Change 2013: The Physical Science Basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds TF Stocker *et al.*), pp. 1535. Cambridge, UK: Cambridge University Press.
- Tyrrell T, Zeebe RE. 2004 History of carbonate ion concentration over the last 100 million years. *Geochim. Cosmochim. Acta* **68**, 3521–3530. (doi:10.1016/j.gca.2004.02.018)
- Hönisch B *et al.* 2012 The geological record of ocean acidification. *Science* **335**, 1058–1063. (doi:10.1126/science.1208277)
- Zeebe RE, Ridgwell A, Zachos JC. 2016 Anthropogenic carbon release rate unprecedented during the past 66 million years. *Nat. Geosci.* **9**, 325–329. (doi:10.1038/ngeo2681)
- Sabine CL *et al.* 2004 The oceanic sink for anthropogenic  $\text{CO}_2$ . *Science* **305**, 367–371. (doi:10.1126/science.1097403)
- Hoegh-Guldberg O *et al.* 2007 Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742. (doi:10.1126/science.1152509)
- De'ath G, Lough JM, Fabricius KE. 2009 Declining coral calcification on the Great Barrier Reef. *Science* **323**, 116. (doi:10.1126/science.1165283)
- Fabricius KE *et al.* 2011 Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat. Clim. Chang.* **1**, 165–169. (doi:10.1038/nclimate1122)
- IPCC. 2014 Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. *Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds V Barros *et al.*), pp. 688. Cambridge, UK: Cambridge University Press.
- Barnes DJ. 1970 Coral skeletons: an explanation of their growth and structure. *Science* **170**, 1305–1308. (doi:10.1126/science.170.3964.1305)
- Clode PL, Marshall AT. 2002 Low temperature FESEM of the calcifying interface of a scleractinian coral. *Tissue Cell* **34**, 187–198. (doi:10.1016/S0040-8166(02)00031-9)
- Gagnon AC, Adkins JF, Erez J. 2012 Seawater transport during coral biomineralization. *Earth Planet. Sci. Lett.* **329**, 150–161. (doi:10.1016/j.epsl.2012.03.005)
- Burton EA, Walter LM. 1987 Relative precipitation rates of aragonite and Mg calcite from seawater: Temperature or carbonate ion control? *Geology* **15**, 111–114. (doi:10.1130/0091-7613(1987)15<111:RPROAA>2.0.CO;2)
- Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW. 1998 Effect of calcium carbonate saturation of seawater on coral calcification. *Glob. Planet. Change* **18**, 37–46. (doi:10.1016/S0921-8181(98)00035-6)
- Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, Marubini F, Aceves H, Barnett H, Atkinson MJ. 2000 Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Glob. Biogeochem. Cycles* **14**, 639–654. (doi:10.1029/1999GB001195)
- Chan NCS, Connolly SR. 2013 Sensitivity of coral calcification to ocean acidification: a meta-analysis.



- 379 *Glob. Chang. Biol.* **19**, 282–290. (doi:10.1111/  
380 gcb.12011)
- 381 17. Swart PK. 1979 The effect of seawater calcium  
382 concentrations on the growth and skeletal composition  
383 of a scleractinian coral: *acropora squamosa*. *SEPM*  
384 *J. Sediment. Res.* **49**, 951–954. (doi:10.1306/  
385 212F7888-2B24-11D7-8648000 102C1865D)
- 386 18. Wall M, Fietzke J, Schmidt GM, Fink A, Hofmann LC,  
387 de Beer D, Fabricius KE. 2016 Internal pH regulation  
388 facilitates in situ long-term acclimation of massive  
389 corals to end-of-century carbon dioxide conditions.  
390 *Sci. Rep.* **6**, 30688. (doi:10.1038/srep30688)
- 391 19. Ries JB, Cohen AL, McCorkle DC. 2009 Marine  
392 calcifiers exhibit mixed responses to CO<sub>2</sub>-induced  
393 ocean acidification. *Geology* **37**, 1131. (doi:10.1130/  
394 G30210A.1)
- 395 20. Ries JB. 2011 A physicochemical framework for  
396 interpreting the biological calcification response  
397 to CO<sub>2</sub>-induced ocean acidification. *Geochim.*  
398 *Cosmochim. Acta* **75**, 4053–4064. (doi:10.1016/  
399 j.gca.2011.04.025)
- 400 21. Venn A, Tambutte E, Holcomb M, Allemand D,  
401 Tambutte S. 2011 Live tissue imaging shows reef  
402 corals elevate pH under their calcifying tissue  
403 relative to seawater. *PLoS ONE* **6**, e20013. (doi:10.  
404 1371/journal.pone.0020013)
- 405 22. McCulloch MT, Falter J, Trotter J, Montagna P. 2012  
406 Coral resilience to ocean acidification and global  
407 warming through pH up-regulation. *Nat. Clim.*  
408 *Chang.* **2**, 623–627. (doi:10.1038/nclimate1473)
- 409 23. Ries JB, Stanley SM, Hardie LA. 2006 Scleractinian  
410 corals produce calcite, and grow more slowly, in  
411 artificial Cretaceous seawater. *Geology* **34**, 525.  
412 (doi:10.1130/G22600.1)
- 413 24. Nehrke G, Reichart G, Van Cappellen P, Meile C,  
414 Bijma J. 2007 Dependence of calcite growth rate  
415 and Sr partitioning on solution stoichiometry: Non-  
416 Kossel crystal growth. *Geochim. Cosmochim. Acta*  
417 **71**, 2240–2249. (doi:10.1016/J.GCA.2007.02.002)
- 418 25. Zoccola D, Tambutté E, Sénégas-Balas F, Michiels  
419 J-F, Failla J-P, Jaubert J, Allemand D. 1999 Cloning  
420 of a calcium channel  $\alpha 1$  subunit from the reef-  
421 building coral, *Stylophora pistillata*. *Gene* **227**,  
422 157–167. (doi:10.1016/S0378-1119(98)00602-7)
- 423 26. Al-Horani FA, Al-Moghrabi SM, De Beer D. 2003 The  
424 mechanism of calcification and its relation to  
425 photosynthesis and respiration in the scleractinian  
426 coral *Galaxea fascicularis*. *Mar. Biol.* **142**, 419–426.  
427 (doi:10.1007/s00227-002-0981-8)
- 428 27. Holcomb M, DeCarlo TM, Gaetani GA, McCulloch M.  
429 2016 Factors affecting B/Ca ratios in synthetic  
430 aragonite. *Chem. Geol.* **437**, 67–76. (doi:10.1016/j.  
431 chemgeo.2016.05.007)
- 432 28. McCulloch MT, D'Olivo Cordero JP, Falter J, Holcomb  
433 M, Trotter JA. 2017 Coral calcification in a changing  
434 World: the interactive dynamics of pH and DIC up-  
435 regulation. *Nat. Commun.* **8**, 15686. (doi:10.1038/  
436 ncomms15686)
- 437 29. DeCarlo TM, D'Olivo JP, Foster T, Holcomb M, Becker  
438 T, McCulloch MT. 2017 Coral calcifying fluid  
439 aragonite saturation states derived from Raman  
440 spectroscopy. *Biogeosciences* **14**, 5253–5269.  
441 (doi:10.5194/bg-14-5253-2017)
30. Comeau S, Cornwall CE, McCulloch MT. 2017  
Decoupling between the response of coral calcifying  
fluid pH and calcification to ocean acidification. *Sci.*  
*Rep.* **7**, 7573. (doi:10.1038/s41598-017-08003-z)
31. Holcomb M, DeCarlo TM, Schoepf V, Dissard D,  
Tanaka K, McCulloch M. 2015 Cleaning and pre-  
treatment procedures for biogenic and synthetic  
calcium carbonate powders for determination of  
elemental and boron isotopic compositions. *Chem.*  
*Geol.* **398**, 11–21. (doi:10.1016/j.chemgeo.  
2015.01.019)
32. Riley JP, Tongudai M. 1967 The major cation/  
chlorinity ratios in sea water. *Chem. Geol.* **2**,  
263–269. (doi:10.1016/0009-2541(67)90026-5)
33. Gaetani GA, Cohen AL. 2006 Element partitioning  
during precipitation of aragonite from seawater: a  
framework for understanding paleoproxies. *Geochim.*  
*Cosmochim. Acta* **70**, 4617–4634. (doi:10.  
1016/j.gca.2006.07.008)
34. DeCarlo TM, Gaetani GA, Holcomb M, Cohen AL.  
2015 Experimental determination of factors  
controlling U/Ca of aragonite precipitated from  
seawater: implications for interpreting coral  
skeleton. *Geochim. Cosmochim. Acta* **162**, 151–165.  
(doi:10.1016/j.gca.2015.04.016)
35. R Core Team. 2016 R: A language and environment  
for statistical computing.
36. Comeau S, Carpenter RC, Nojiri Y, Putnam HM, Sakai  
K, Edmunds PJ. 2014 Pacific-wide contrast  
highlights resistance of reef calcifiers to ocean  
acidification. *Proc. R. Soc. B* **281**, 20141339. (doi:10.  
1098/rspb.2014.1339)
37. Schneider K, Erez J. 2006 The effect of carbonate  
chemistry on calcification and photosynthesis in the  
hermatypic coral *Acropora eurystoma*. *Limnol.*  
*Oceanogr.* **51**, 1284–1293. (doi:10.4319/lo.2006.51.  
3.1284)
38. Anthony KRN, Kline DI, Diaz-Pulido G, Dove S,  
Hoegh-Guldberg O. 2008 Ocean acidification causes  
bleaching and productivity loss in coral reef  
builders. *Proc. Natl Acad. Sci. USA* **105**,  
17 442–17 446. (doi:10.1073/pnas.0804478105)
39. Allison N, Cohen I, Finch AA, Erez J, EIMF F. 2011  
Controls on Sr/Ca and Mg/Ca in scleractinian corals:  
the effects of Ca-ATPase and transcellular Ca  
channels on skeletal chemistry. *Geochim.*  
*Cosmochim. Acta* **75**, 6350–6360. (doi:10.1016/j.  
gca.2011.08.012)
40. Inoue M, Gussone N, Koga Y, Iwase A, Suzuki A,  
Sakai K, Kawahata H. 2015 Controlling factors of Ca  
isotope fractionation in scleractinian corals evaluated  
by temperature, pH and light controlled culture  
experiments. *Geochim. Cosmochim. Acta* **167**,  
80–92. (doi:10.1016/j.gca.2015.06.009)
41. Gothmann AM, Bender ML, Blättler CL, Swart PK,  
Giri SJ, Adkins JF, Stolarski J, Higgins JA. 2016  
Calcium isotopes in scleractinian fossil corals since  
the Mesozoic: implications for vital effects and  
biomineralization through time. *Earth Planet.*  
*Sci. Lett.* **444**, 205–214. (doi:10.1016/j.epsl.2016.  
03.012)
42. Allemand D, Ferrier-Pagès C, Furla P, Houlbrèque F,  
Puverel S, Reynaud S, Tambutté É, Tambutté S,  
Zoccola D. 2004 Biomineralisation in reef-building  
corals: from molecular mechanisms to  
environmental control. *C. R. Palevol* **3**, 453–467.  
(doi:10.1016/j.crpv.2004.07.011)
43. Marshall AT. 1996 Calcification in hermatypic and  
ahermatypic corals. *Science* **271**, 637–640. (doi:10.  
1126/science.271.5249.637)
44. Marshall AT, Clode PL, Russell R, Prince K, Stern R.  
2007 Electron and ion microprobe analysis of  
calcium distribution and transport in coral tissues.  
*J. Exp. Biol.* **210**, 2443–2463. (doi:10.1242/jeb.  
003343)
45. Mass T *et al.* 2017 Amorphous calcium carbonate  
particles form coral skeletons. *Proc. Natl Acad. Sci.*  
*USA* **114**, E7670–E7678. (doi:10.1073/pnas.  
1707890114)
46. Moya A *et al.* 2012 Whole transcriptome analysis of  
the coral *acropora millepora* reveals complex  
responses to CO<sub>2</sub>-driven acidification during the  
initiation of calcification. *Mol. Ecol.* **21**, 2440–2454.  
(doi:10.1111/j.1365-294X.2012.05554.x)
47. Allison N, Cohen I, Finch AA, Erez J, Tudhope AW.  
2014 Corals concentrate dissolved inorganic carbon  
to facilitate calcification. *Nat. Commun.* **5**, 5741.  
(doi:10.1038/ncomms6741)
48. Bonin MC. 2012 Specializing on vulnerable habitat:  
acropora selectivity among damselfish recruits and  
the risk of bleaching-induced habitat loss. *Coral*  
*Reefs* **31**, 287–297. (doi:10.1007/s00338-011-  
0843-2)
49. Wisshak M, Schönberg CHL, Form A, Freiwald A.  
2012 Ocean acidification accelerates reef bioerosion.  
*PLoS ONE* **7**, e45124. (doi:10.1371/journal.pone.  
0045124)
50. Silbiger NJ, Guadayol O, Thomas FIM, Donahue MJ.  
2014 Reefs shift from net accretion to net erosion  
along a natural environmental gradient. *Mar. Ecol.*  
*Prog. Ser.* **515**, 33–44. (doi:10.3354/meps10999)
51. DeCarlo TM, Cohen AL, Barkley HC, Cobban Q,  
Young C, Shamberger KE, Brainard RE, Golbuu Y.  
2015 Coral macrobioerosion is accelerated by ocean  
acidification and nutrients. *Geology* **43**, 7–10.  
(doi:10.1130/G36147.1)
52. Schönberg CHL, Fang JKH, Carreiro-Silva M, Tribollet  
A, Wisshak M. 2017 Bioerosion: the other ocean  
acidification problem. *ICES J. Mar. Sci.* **74**,  
895–925. (doi:10.1093/icesjms/fsw254)
53. Ries JB, Ghazaleh MN, Connolly B, Westfield I,  
Castillo KD. 2016 Impacts of seawater saturation  
state ( $\Omega_A = 0.4–4.6$ ) and temperature (10, 25°C)  
on the dissolution kinetics of whole-shell biogenic  
carbonates. *Geochim. Cosmochim. Acta* **192**,  
318–337. (doi:10.1016/J.GCA.2016.07.001)
54. Yates KK, Zawada DG, Smiley NA, Tiling-Range G.  
2017 Divergence of seafloor elevation and sea level  
rise in coral reef ecosystems. *Biogeosciences* **14**,  
1739–1772. (doi:10.5194/bg-14-1739-2017)