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Living coral tissue slows skeletal dissolution related to ocean acidification

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Climate change is causing major changes to marine ecosystems globally, with ocean acidification of particular concern for coral reefs. Using a 200 d in situ carbon dioxide enrichment study on Heron Island, Australia, we simulated future ocean acidification conditions, and found reduced pH led to a drastic decline in net calcification of living corals to no net growth, and accelerated disintegration of dead corals. Net calcification declined more severely than in previous studies due to exposure to the natural community of bioeroding organisms in this in situ study and to a longer experimental duration. Our data suggest that reef flat corals reach net dissolution at an aragonite saturation state (Ω_{AR}) of 2.3 (95% confidence interval: 1.8–2.8) with 100% living coral cover and at $\Omega_{AR} > 3.5$ with 30% living coral cover. This model suggests that areas of the reef with relatively low coral mortality, where living coral cover is high, are likely to be resistant to carbon dioxide-induced reef dissolution.

The oceans are warming, deoxygenating, rising and the ocean's surface pH is predicted to decline by 0.3–0.4 by 2100, depending on global carbon emission scenarios[1], with similar average pH drops expected for coral reef waters[2]. Ocean acidification (OA) impacts a range of ecologically and economically important calcifying organisms[3], although impacts are confounded by factors including food supply[4], temperature[3], nutrients[5], flow[6], natural carbon system variability[7] and altered species interactions such as competition[8]. Coral reefs exist in a delicate balance between growth/calcification and erosion/dissolution forces[9], and most available evidence suggests that reefs will probably shift to net dissolution this century without a major reduction in carbon dioxide (CO_2) emission rates[10,11]. Furthermore, future declines in net coral reef calcification suggest that many coral reefs will not be able to keep up with predicted levels of sea level rise[12]. OA resistance and resilience for coral reefs are also confounded by relative resistance and resilience to thermal stress and bleaching-related mortality in corals[13,14]. The oceans are warming up to 40% faster than previously believed[15] and coral bleaching events are becoming more severe and frequent[16]. The third global bleaching event in 2014–2017 resulted in up to 50% coral mortality on the northern Great Barrier Reef (GBR) and caused high levels of coral mortality on many reefs globally due to unprecedented thermal stress and bleaching[16,17]. The dramatic global decline in coral reefs raises profound concerns about reef resilience to global stressors and behooves the research community to better understand the variability of reef responses to global stressors[3,14,17–19].

Coral reefs have been a key area of OA research due to their high ecological and economic value and for their potential vulnerability to OA[20]. However, controlled, long-term in situ experiments on the effect of OA on the skeletal growth and dissolution of corals with natural food, nutrients, flow, carbon system variability and species interactions are largely absent from the literature. Most of our knowledge about the impact of OA on coral reefs are derived from manipulative experimental studies under laboratory or aquarium conditions where organisms are isolated from their natural ecosystem, the natural communities of bioeroders, and placed under relatively artificial environmental conditions[18]. Some flow-through mesocosm systems (for example, ref. [21]) come close to stimulating the natural variability and complexity expected as elevated concentrations of CO_2 affect coral reef waters, and findings from naturally elevated CO_2 environments, such as vent/seep and upwelling regions, have improved our understanding of the long-term impacts of OA on organisms, communities and ecosystems (for example, refs. [18,22]). There is little control over the exposure to the carbonate chemistry in these research settings, however, and there may be unaccounted-for variables (for example, methane) that are likely to influence the results. In the short-term, fully enclosed in situ studies across different coral reef zones suggest that reef flats will probably shift to net dissolution at partial pressure of CO_2 carbon dioxide(P_{CO_2}) levels between 470 and 1,000 ppm (refs. [2,23]). The duration of this approach is limited, however, because the enclosed community has major biogeochemical feedbacks to the seawater chemistry and the waste products build up after 1–2 d. Recently, there have also been short-term, repeated 1 d community-level in situ OA experiments that have revealed that OA depresses net community calcification[10] while increasing seawater pH elevates it[24]. These are critical community-level OA studies but the experimental duration, replication and dosing accuracy are limited.

Our understanding of OA dynamics on coral reefs can be vastly improved by an emerging and highly promising approach

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involving controlled in situ manipulative experiments with semi-enclosed replicate Free Ocean Carbon Enrichment (FOCE) flumes that have been deployed in a range of environments from the deep ocean, to Antarctica, to the Mediterranean and on coral reefs[25–30]. In terrestrial systems, such studies have been conducted for over 20 yr using Free Air Carbon Enrichment (FACE) technologies, leading to key and unexpected discoveries about ecological responses and carbon cycling in forests and grasslands[31]. We designed a similar systems for near-shore coral reef environments to understand whether living coral structures can maintain reef and reef dwellers' resilience to OA better than dead coral structures subjected to the same future conditions.

Results

Here we present the results of a FOCE study on a coral reef, which serves to close a major knowledge gap in our understanding of how bioerosion and calcification may interact under future OA conditions. The FOCE system was set up on the southern GBR at the Heron Island reef flat for 200 d with the four replicate flumes parallel to the shore in accordance with the natural flow regime (Fig. 1a). Each flume was open to the environment at both ends and at the bottom. Five replicate living *Porites cylindrica* colonies and five airbrushed dead colonies were in each flume (Fig. 1b). The system successfully maintained reduced pH and aragonite saturation state (Ω_{AR}) in treatment flumes as an offset below the environmental conditions: the pH offset was reduced in a stepwise process over 3 months to −0.25 total pH (Fig. 2a) to approximately simulate the Intergovernmental Panel on Climate Change 2100 representative concentration pathway (RCP) 8.5 scenario[1]. The mean pH was significantly lower in the treatments flumes compared to the controls during all experimental phases: phase I (single-factor analysis of variance (ANOVA), $P=2.3\times10^{-6}$, $n=202$, $F=23$), phase II (single-factor ANOVA, $P=0.0002$, $n=79$, $F=14.4$), phase III (single-factor ANOVA, $P=5.5\times10^{-30}$, $n=244$, $F=147.7$), phase IV (single-factor ANOVA, $P=1.4\times10^{-12}$, $n=230$, $F=53.1$,), phase V (single-factor ANOVA, $P=0.00127$, $n=21$, $F=11.3$). Throughout the experiment, the mean pH was reduced incrementally from one phase to the next in the treatment, while the average treatment and the control flumes pH remained offset and significantly different (Fig. 2). This demonstrates that our FOCE system accurately reduced the pH from the environmental conditions throughout the 200 d experiment.

Discrete seawater samples were collected periodically from the treatment and control flumes during the day and night to measure dissolved inorganic carbon (DIC) and total alkalinity (ALK), which were used with temperature and salinity at the time of sampling to calculate Ω_{AR} using CO_2 system calculations (CO_2SYS) (Table 1). The carbonate conditions on the Heron Island reef flat had high diel variability in DIC and ALK[32]. The ALK and DIC were not sampled frequently enough to show statistical differences between the dosing phases across treatments, but are included here for illustration purposes.

We used linear mixed effects models to test whether changes in weight differed among ambient versus reduced pH treatments, for live versus dead corals and for the interaction of the two. To account for the potential artefacts of replicated use of individual genotypes and FOCE experimental apparatuses, coral genotype and FOCE units were included as separate random grouping variables (that is, intercepts varied among these groups). Using the estimated full model, we tested whether changes in weight differed among pH treatments within each coral status (live versus dead) and whether change in weight differed among coral status within each pH treatment.

The reduced pH treatment in the FOCE (Fig. 2a) led to stunted growth in living corals and intensified bioerosion and/or dissolution in dead corals (Fig. 2b). There was a significant effect of both

Fig. 1 | The CP-FOCE system deployed on the Heron Island reef flat. **a**, The system was deployed between May and December 2010, with four replicate open-ended and bottomed flumes that were accessible at low tide. **b**, Inside each flume were five living fragments of *P. cylindrica* and five recently dead fragments, which were airbrushed with seawater to remove their living tissue and collected from different mother colonies. Inside each open-bottomed flume was a pH sensor, flow sensor and photosynthetically active radiation sensor.

pH treatment ($\chi^2=8.09$, d.f. = 1, $P=0.004$) and status ($\chi^2=30.22$, d.f. = 1, $P<0.001$) but no significant interaction ($\chi^2=2.1$, d.f. = 1, $P=0.14$). Specifically, all dead corals, apart from one, lost carbonate material at both levels of Ω_{AR} (ambient or reduced) in the experiment. The mean rate of loss of carbonate material for the dead coral colonies in the control and reduced pH treatment flumes were −8.12% (±3.22 s.e.m.) and −11.48% (±1.55 s.e.m.), respectively (Fig. 3a); however, the differences in buoyant weight loss of dead corals in the control and treatment flumes was not significant ($z=1.002$, $P=0.78$). In contrast, the treatment had a significant effect on weight loss in live corals ($z=3.18$, $P=0.0058$). Living corals in ambient conditions yielded net calcification (8.66%, ±1.83 s.e.m., Fig. 3a), while living corals in the reduced pH yielded almost zero net calcification (Fig. 3a). When comparing coral status within each pH treatment, we found a significant effect for both pH treatments (ambient pH: $z=4.92$, $P<0.001$; reduced pH: $z=3.98$, $P<0.001$).

Our findings reveal that the reduced pH treatment significantly stunted living coral growth while potentially intensifying bioerosion/dissolution of dead colonies, which is consistent with serious threats to skeletal integrity in a high CO_2 world (Fig. 4). The results show that living colonies suffered a much less drastic buoyant weight loss in the treatment flumes compared to the buoyant weight loss sustained by the dead colonies in the treatment. There was no significant difference in weight loss in the dead corals between the control and treatment flumes; however, this probably indicates that even at ambient pH levels, dead coral substrate has already exceeded a tipping point, leading to rapid bioerosion/dissolution. It is also acknowledged that the responses measured in this experiment do not have an accompanying high-temperature signal, which exacerbates the impact of reduced pH exposure.

We used our experimental results to estimate how the proportion of dead corals interacts with Ω_{AR} to determine the point of net dissolution (that is, when overall calcification turns from positive to negative) in habitats containing these corals. The relationship between net calcification (ΔC) and aragonite saturation can range from linear to saturating, and the degree of saturation therein can depend in part on nutrient availability and other conditions[5]. Our data is not designed to estimate the shape of the functional response. Thus, we conducted several conditional analyses with assumptions that range

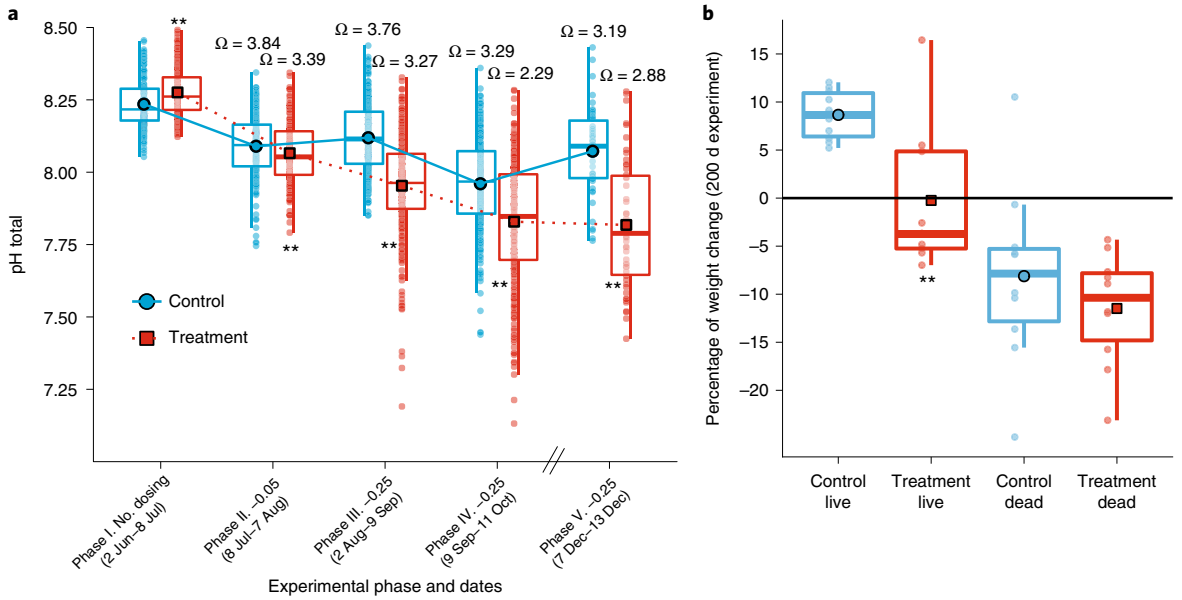

Fig. 2 | pH levels in the FOCE flumes and controls throughout the experiment and the changes in coral annual buoyant weights. a, Total pH measured in the two control treatment flumes (blue) and the two reduced pH treatment flumes (red). In these box plots the bold middle line is the median, the outlined dot is the mean, the boxes represent the quartiles and the whiskers represent the quartile ± the quartile range. The large variability in pH is due to diel variability related to photosynthesis and respiration. The dosing started with approximately 1 month of no dosing to allow the coral to acclimatize to the flumes. The dosing was then increased over 2 months to a −0.25 pH offset from the measured environmental pH. Asterisks indicate when the treatment pH conditions were significantly lower than the control and environmental pH during that period ($P<0.05$, single factor ANOVA). The mean pH was significantly lower in the treatment flumes compared with the controls during all experimental phases: phase I (single-factor ANOVA, $P=2.3\times10^{-6}$, $n=202$, $F=23$), phase II (single-factor ANOVA, $P=0.0002$, $n=79$, $F=14.4$), phase III (single-factor ANOVA, $P=5.5\times10^{-30}$, $n=244$, $F=147.7$), phase IV (single-factor ANOVA, $P=1.4\times10^{-12}$, $n=230$, $F=53.1$,), phase V (single-factor ANOVA, $P=0.00127$, $n=21$, $F=11.3$). The mean Ω_{AR} for the dosing periods are shown, except in the initial no dosing period when discrete seawater samples were not collected. **b**, Change in buoyant weight data over the 200 d experiment for the living and dead control and treatment corals. The living treatment corals corals had a significantly lower net growth rate than the controls (**$z=3.18$, $P=0.0058$, linear mixed effect model). In these box plots the bold middle line is the median, the outlined dot is the mean, the boxes represent the quartiles and the whiskers represent the quartile ± the quartile range.

Table 1 | Means for the pH, temperature, DIC, ALK and Ω_{AR} over the different phases of the FOCE experiment in 2010.

Controls versus treatments	pH (mean ± s.e.m.)	Temperature (mean ± s.e.m.)	DIC (mean ± s.e.m.)	ALK (mean ± s.e.m.)	Ω_{AR} (mean ± s.e.m.)
Control					
Phase II (9 July–2 August)	8.09 ± 0.01 ($n=163$)	21.73 ± 0.22 ($n=28$)	1966.1 ± 110 ($n=28$)	2309.1 ± 48 ($n=28$)	3.84 ± 0.17 ($n=28$)
Phase III (3 August–9 September)	8.09 ± 0.01 ($n=247$)	20.68 ± 0.10 ($n=8$)	2001.2 ± 52 ($n=8$)	2337.7 ± 29 ($n=8$)	3.76 ± 0.18 ($n=8$)
Phase IV (10 September–11 October)	7.99 ± 0.01 ($n=184$)	22.34 ± 0.30 ($n=10$)	1961.1 ± 70.2 ($n=10$)	2211.5 ± 40 ($n=10$)	3.29 ± 0.19 ($n=10$)
Phase V (22 October–13 December)	8.07 ± 0.02 ($n=46$)	25.26 ± 0.20 ($n=24$)	1941.5 ± 108.6 ($n=24$)_	2218.7 ± 151 ($n=24$)	3.19 ± 0.22 ($n=24$)
Treatment					
Phase II (9 July–2 August)	8.07 ± 0.01 ($n=147$)	21.74 ± 0.21 ($n=26$)	2016.0 ± 92.3 ($n=28$)	2311.9 ± 65.1 ($n=28$)	3.39 ± 0.19 ($n=26$)
Phase III (3 August–9 September)	7.94 ± 0.01 ($n=221$)	20.68 ± 0.10 ($n=8$)	2106.3 ± 71.3 ($n=8$)	2391.6 ± 77.5 ($n=8$)	3.27 ± 0.21 ($n=8$)
Phase IV (10 September–11 October)	7.82 ± 0.01 ($n=222$)	22.86 ± 0.33 ($n=6$)	2092.5 ± 86.3 ($n=10$)	2263.2 ± 114.8 ($n=10$)	2.29 ± 0.47 ($n=6$)
Phase V (22 October–13 December)	7.82 ± 0.03 ($n=50$)	25.26 ± 0.20 ($n=24$)	2039.9 ± 136.3 ($n=24$)	2279.7 ± 128.5 ($n=24$)	2.88 ± 0.29 ($n=24$)

pH was sampled every second but analyses were performed on 3 h averages of the data. The temperature was recorded at the same time as the samples for DIC and ALK were collected. For each phase, the number of samples for the control and treatment values represent the two control flumes combined and the two treatment flumes combined, respectively. A total of 134 discrete samples were collected for DIC and ALK data, which were then combined, using CO_2SYS, with temperature data to estimate the Ω_{AR}.

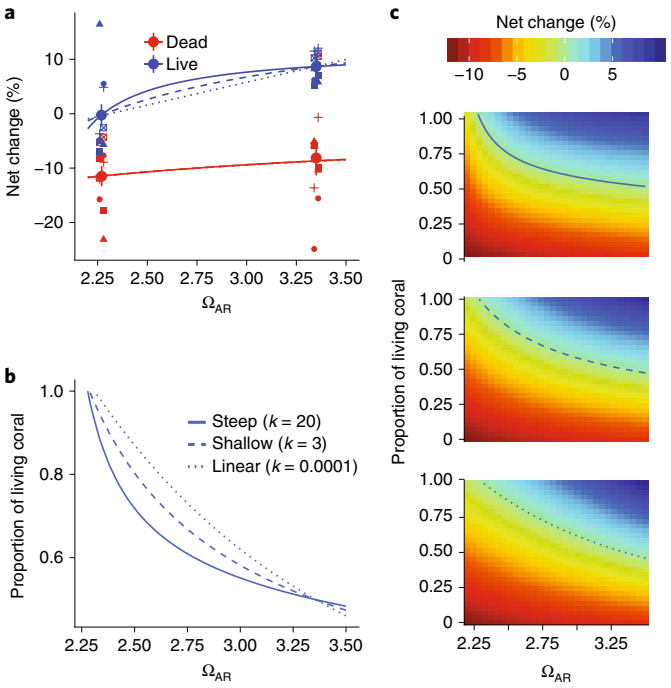

Fig. 3 | Observed and estimated responses of changes in annual buoyant weight as a function of Ω_{AR} and coral status (live versus dead). a, Observed individual (small shapes) and mean (large shapes) changes in buoyant weight as a function of Ω_{AR} in living (red) and dead (blue) colonies used in the experiment. The living corals reached net dissolution at an Ω_{AR} = 2.3 (95% CI 1.8–2.8), while the dead colonies reached it above ambient Ω_{AR}. Lines represent models fit with different assumptions for the non-linear response to Ω_{AR} (ref. [5]) and shapes represent individual genotypes. **b**,**c**, Estimated zero growth isoclines (**b**) and net change in buoyant weight (**c**) as a function of the proportion of living coral on the reef and Ω_{AR} given models fit under different assumptions of nonlinearity (k) in Ω_{AR} (based on curves shown in (**a**) where k is defined in equation (1)). The zero growth isoclines (lines in (**b**) and (**c**)) show the threshold for net dissolution under the model assumptions. Under these scenarios, net dissolution occurs when all corals are living at Ω_{AR} = 2.3 (95% CI 1.8–2.8). Net dissolution occurs at higher Ω_{AR} with lower proportions of dead coral and steeper non-linearity in the Ω_{AR}-dissolution relationship.

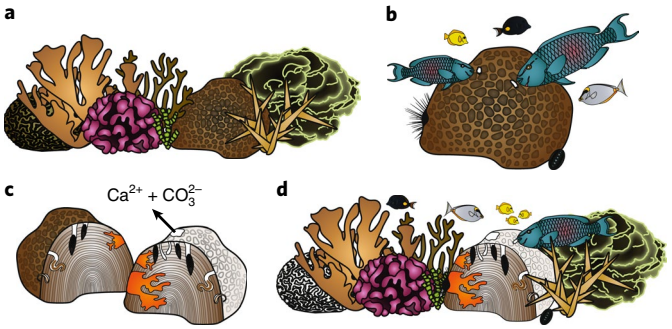

Fig. 4 | Illustration revealing the drivers of the dynamic balance between growth and dissolution on a coral reef. a–**c**, Representation of net reef calcification that includes growth by the main calcifiers (corals and calcareous algae (**a**)) but often does not consider external bioeroders such as fish (for example, parrotfish and surgeonfish), urchins and chitons (**b**) or internal bioeroders on living and dead colonies such as boring molluscs, sponges, worms or bacteria or chemical dissolution (shown by arrow (**c**)). Our results suggest that bioerosion and/or dissolution are greater in dead coral colonies (white colony on the right in **c**) than in living colonies. **d**, Net reef calcification is a balance between calcification and dissolution/erosion of the living and dead components of the reef. This study suggests that maintaining living coral cover increases the likelihood of maintaining net reef calcification by both increasing the calcification component and reducing the bioerosion/dissolution component. Credit: Illustrations copyright Adi Khen 2019.

from strong saturation (strong curvature) to no saturation (linear) using a modified Michaelis–Menten equation[5]. We assume no calcification for dead corals, but use a power function so that dissolution can approach zero (equation (1)):

$$\Delta C = \begin{cases} -d(\Omega_{AR})^{\gamma} & \text{if dead} \\ \beta_1[\Omega_{AR} - \beta_0] / \left(\frac{1}{k\beta_1} + [\Omega_{AR} - \beta_0]\right) & \text{if alive} \end{cases} \quad (1)$$

Here, the parameter k controls the strength of saturation, β_0 represents the x-intercept and β_1 represents the slope when $\Omega_{AR} = \beta_0$. d represents the slope for dead corals when $\Omega_{AR} = 0$ and γ sets the curvature. We estimate the model with random genotype effects for d and β_1 using non-linear mixed effects models. On the patch scale, given a proportion of the reef that is dead or alive (p) under the experimental environmental conditions and surface area to volume ratio of the corals, this means that the net calcification rate is:

$$\frac{\delta C}{\delta t} \propto (p)\beta_1[\Omega_{AR} - \beta_0] / \left(\frac{1}{k\beta_1} + [\Omega_{AR} - \beta_0]\right) - (1-p)d(\Omega_{AR})^{\gamma}, \quad 0 \le p \le 1 \quad (2)$$

Numerically solving for the zero isocline gives the point of net dissolution. We used three assumptions for saturation: approximately linear ($k = 10^{-4}$, solid lines in Fig. 3), shallow saturation ($k = 3$, dashed lines in Fig. 3) and steep saturation ($k = 20$, dotted lines in Fig. 3).

Our empirically informed model illustrates that the threshold at which dissolution is expected to overtake calcification is strongly affected by the proportion of living corals on a reef and also by the impact of Ω_{AR} on the net rate of calcification/dissolution. The three models give similar results for 100% live coral at Ω_{AR} = 2.3 (linear = 2.3, 95% confidence interval (CI) 1.8–2.8; shallow saturation = 2.29, 95% CI 2.0–.6; steep saturation = 2.28, 95% CI 2.1–2.4). Our results reveal that for a reef with 30% living coral the reef would reach net dissolution at an $\Omega_{AR} > 3.5$ (but estimated at Ω_{AR} = 4.35–7.67) (k = linear to steep saturation), with 60% living coral at Ω_{AR} = 3.05–2.94 and 90% living coral at Ω_{AR} = 2.45–2.33 (Fig. 3c). Given that the Ω_{AR} for the 30% living coral is an extrapolation beyond the Ω_{AR} measured in our study, we could only suggest that net dissolution would occur at an $\Omega_{AR} > 3.5$. Note that these are transient solutions (that is, as dead corals dissolves, the proportion of living coral increases) and represent extrapolations from our results with one coral species at one reef location.

Given that the present day average Ω_{AR} for tropical surface waters ranges between 3.6 and 3.9 (ref. [33]) and live coral cover is already less than 30% on many reefs globally, maximizing living coral cover is already essential to avoid reaching net dissolution on many coral reefs today. These estimates are sensitive to assumptions about the shape of the relationship between calcification, dissolution and Ω_{AR}; however, because net calcification equals dissolution at the reduced Ω_{AR} treatment, the results provide qualitatively similar conclusions: in future OA scenarios net dissolution begins to rapidly overtake and exceed calcification, and this effect is expected to be more extreme with higher proportions of dead corals on the reef.

Discussion

These findings suggest that any proximal (for example, disease, coral predator outbreaks, sedimentation) or ultimate (for example,

bleaching) stressors that lower living coral coverage would lower the reefs' resilience to OA, shifting the reef towards net dissolution sooner, but that the shift to net dissolution would be delayed for living coral structures when compared to dead coral structures. This in situ data driven model further suggests that there is an Ω_{AR} threshold below which living coral coverage cannot overcome the loss from bioerosion and dissolution. This threshold will depend on the ratio of living to dead corals on the reef (Fig. 3b). The results suggest that having a higher fraction of a reef ecosystem occupied with living rather than dead coral structures would maintain reef integrity and resistance to OA for longer, thus pointing to a necessity to protect living corals in marine reserves and using reef restoration methods such as coral farming and possibly even genetically modified climate resistant corals or 'Super Corals'[34,35].

Our in situ FOCE experiment has demonstrated that reduced pH resulted in drastic carbonate skeleton weight loss in the living and dead coral specimens. Living corals were significantly affected by the reduced pH treatment; however, the living corals in the reduced pH treatment did not lose as much of their mass as dead corals in the same treatment. The 100% reduction in living coral calcification rate to no net growth in our study was more extreme than previous OA studies. For example, a meta-analysis of 25 OA studies by Chan and Connolly[5] found that that there was a ~10% decline in calcification rate per unit decline in Ω_{AR} when calcification rate was measured with the buoyant weight method[5]. Net calcification declined more severely than in previous studies, probably due to exposure to the natural community of bioeroding organisms in this in situ study and to a longer experimental duration.

Bioerosion/dissolution for dead corals was roughly 8.1% at ambient conditions and 11.5% at reduced pH (a 41% increase). This effect was not statistically significant and probably due to substantial variation among colony variability and the already high ambient background bioerosion/dissolution, but it is similar to that of Tribollet et al.[36] who measured a 48% increase. Our linear threshold estimates suggest dead corals would reach net dissolution at $\Omega_{AR} > 3.5$, while living corals show more structural resilience, effectively reaching a net calcification rate of zero at much lower Ω_{AR} values, theoretically down to $\Omega_{AR} = 2.3$ (95% CI 1.8–2.8) (Fig. 3).

These results suggest that a long-term integration effect of a decrease in calcium carbonate precipitation due to OA is moderate compared to short-term experiments[3,30]. It also further confirms that coral skeletons will dissolve due to the effect of OA. The threshold of $\Omega_{AR} = 2.3$ is a value that reefs routinely reach during the night[32] and could become the daily average Ω_{AR} on most reefs by 2100 under a RCP8.5 scenario[37]. The relative high threshold of Ω_{AR} for dead corals suggests that the reef dissolution during the night[23,38] may be due to dissolution of dead coral skeletons and the calcium carbonate infrastructure of the reef. Methods that determine calcification rates from changes in seawater chemistry do not distinguish between the dissolution of different reef components, while in the method used in this study it is possible to determine the effect of the chemistry on the corals and to obtain a long-term integration that represents the effect of OA on corals, which are the base of the coral reef infrastructure.

This study posits that although the rate of carbonate dissolution/bioerosion may not be significantly affected by OA conditions, the driver of declining net calcification rates could be the slow decline in the calcification rates of living corals with declining Ω_{AR}. This suggests that having a higher percentage of living coral would slow down the rate of reef disintegration under projected OA. It remains uncertain, however, how zero net calcification is affected by the relative amount of organic versus inorganic carbon cycling on the reef. Furthermore, as this study is based on the response of one coral species in a single location, it also remains to be seen how a coral reef made up of multiple coral species with different susceptibilities to OA will respond. This coral reef FOCE study is one of the longest FOCE experiments conducted, and sets the stage for future coral reef FOCE experiments that include multiple species in different locations.

Slow-flow habitats such as wave-sheltered reef flats may provide a refugia from OA by defining a thick diffusion boundary layer of corals and other calcifying organisms[39]. Additionally, studies from a Mediterranean CO_2 vent system have found that corals living under elevated CO_2 conditions (total pH 7.7–7.9) maintained their linear extension rates but had lower net calcification rates, reduced bulk density and higher skeletal porosity[40]. The higher skeletal porosity and lower bulk density would probably increase rates of bioerosion and/or dissolution, which could lower the net calcification rates as we observed in this study. A study performing geochemical analyses on the living corals from this experiment found that the corals from the highly variable pH environment of the reef flat were able to maintain their extension rates, skeletal density and internal pH even under OA conditions[41]. These studies, along with this study, suggest that corals living in highly variable pH environments may be able to maintain their growth rates under OA conditions, but at the cost of increased bioerosion/dissolution and therefore reduced net calcification.

In situ reef biogeochemistry studies[11,42,43], naturally high CO_2 reef sites (for example, ref. [22]) and in situ short-term community-scale OA experiments[10] suggest that coral reefs will shift to net dissolution under future high CO_2 conditions. Dove et al.[21] used mesocosms containing coral reef communities to reveal that there will be reef dissolution under business-as-usual CO_2 emission scenarios and there were elevated net calcification rates under preindustrial conditions. An in situ study by Albright et al.[24] expanded upon these findings by revealing that net reef calcification increased significantly when the pH was experimentally elevated in situ and declined when it was reduced[10]. Importantly, aquarium studies have recently begun to reveal the mechanisms underlying the increases in dissolution and bioerosion under elevated CO_2 conditions (for example, ref. [44]). These findings highlight the importance of using a combination of experimental approaches[18] to understand the impacts of elevated CO_2 on coral reefs. In situ approaches such as the FOCE make it possible to do long-term controlled CO_2 manipulation studies with the corals exposed to the natural environmental conditions, seawater, food and nutrient conditions while exposed to the surrounding reef community[18].

This study presents a unique combination of long-term in situ measurements, in situ manipulative studies, laboratory measurements and modelling that together confirm that lower Ω_{AR}, associated with OA, will lead to net reef dissolution on many coral reefs globally. Findings from this study, however, imply that any cause of living coral cover decline may make a reef more prone to experiencing faster rates of localized dissolution/bioerosion, whereas areas maintaining high living coral cover may be able to resist dissolution/bioerosion impacts from OA longer (Fig. 4). Maintaining higher living coral cover would be associated with keeping net community calcification high with respect to net community production. In this way, marine reserves protecting living coral cover will also be climate reserves, serving to secure more climate-resistant reefs among global reefs.

Our study suggests there may be a relationship between OA vulnerability and bleaching vulnerability. Even areas where living coral cover is strongly protected, such as UNESCO (United Nations Educational, Scientific and Cultural Organization) Marine World Heritage Sites, have experienced severe bleaching in the recent global bleaching event of 2014–2017 (refs. [14,16,17]). The variation in bleaching mortality responses across protected sites, however, is important to document. In relation to heat stress and bleaching-related mortality and reduction in living coral cover, it is possible that coral reef areas of comparatively highest resistance to bleaching may also be more resistant to carbonate dissolution as OA

progresses globally. Conservation efforts to protect living coral cover and areas of lowest bleaching-related mortality would therefore delay the gradual OA-induced loss of three-dimensional reef structure, which is critical for reef biodiversity, fisheries habitat, fisheries production, coastal protection and food security for coastal communities in many tropical island nations.

Methods

CP-FOCE. The Coral Proto-FOCE (CP-FOCE) was set up on the Heron Island reef flat (23° 27′ S, 151° 55′ E), a coral cay in the Capricorn-Bunker group at the southern end of the GBR, in front of the University of Queensland's research station as previously described[25,30,32]. The Heron Island reef flat has a semidiurnal tidal cycle that has depths between 0.3 and 1.0 m in the shallowest reef flat areas at low tide[45]. The CP-FOCE's four open-bottomed and open-ended flumes were positioned parallel to shore in a sandy bottomed area of a shallow section of the reef flat, approximately 2 m away from each other. Fluorescein dye was used to ensure that the outflow from a flume could not be taken into any of the other flumes. Two of the flumes were designated as control flumes and unmodified seawater was pumped in at the same rates as in the reduced pH treatment flumes; nothing else was manipulated. In the reduced pH treatment flumes there was initially no treatment from 2 June to 8 July 2010 to allow the corals to acclimate to the flumes, and then there was a −0.05 pH offset below the pH measured in the environment[32] from 8 July to 2 August, followed by a −0.15 pH offset from 2 August to 9 September and then a −0.25 pH offset starting on 9 September through to the completion of the experiment on 13 December (Fig. 2a). A powerful tropical storm in November 2010 disabled many of the CP-FOCE instruments and limited access to the site, resulting in a data gap in November. A detailed description of the surrounding seawater carbonate chemistry and environmental conditions throughout the experiment was published previously[32].

Coral collection. *P. cylindrica* (Dana, 1846) is a branching coral that is one of the dominant corals on the Heron Island reef flat and also of reef flats across the GBR[46]. *P. cylindrica* colonies approximately 10 cm in diameter were carefully collected using stainless steel bone clippers, making sure that cuts were only made on dead sections of the colony. Eight replicate heads were collected from five large *P. cylindrica* mother colonies, which were at least 10 m apart, and immediately labelled using a colour-coded, numbered vinyl fish tag (Floy Tags). The corals were sampled from five mother colonies at least 10 m apart to ensure there were five replicate genets (or genetically distinct individuals) represented in each replicate flume. Half of the collected *P. cylindrica* colonies were transported to the research station and airbrushed with filtered seawater to remove all living tissue. The tagged corals were then allowed to recover for 1 month at the experimental sites on Heron Island reef flat to ensure that the living corals had not suffered damage associated with collecting and that no coral tissue could grow back in the recently dead, airbrushed corals. The corals were never removed from seawater and were only briefly held in the Heron Island flow-through aquarium system during the airbrushing to minimize the impacts on the corals' internal bioeroding communities. One living and one recently dead *P. cylindrica* head from each of the five mother colonies was randomly placed in each of the four CP-FOCE flumes, establishing a total of five living and five recently dead coral colonies in each flume (Fig. 1). The corals were allowed to acclimate to the CP-FOCE flumes for 1 month until the pH dosing started on 8 July 2010.

This study was carefully designed to be representative of a reef flat environment. The reef flat on Heron Island hosts vibrant and healthy coral colonies, which grow on a sandy bottom with dead coral reef substrate occurring under the sediment. Our experimental set up was designed to represent a typical coral colony growing on the reef flat that included turf and other algae, which were naturally growing on the sediments and corals in the FOCE flumes. The physical oceanography and hydrodynamics on the Heron Island reef flat and connectivity to nearby reef environments, which also host various corals and reef algae that affect seawater chemistry signals, guarantees the reef flat where we performed our experiment was bathed in these waters naturally with the tides, in effect integrating the seawater chemistry signal.

Continuous and discrete environmental and carbonate chemistry measurements. The CP-FOCE system included an instrumentation array in the environment and in each of the FOCE flumes that included a Monterey Bay Area Research Institute (MBARI)-modified Sea-Bird 18 digital pH sensor sampling every second (1 s resolution, manufacturer's reported precision of ±0.001 pH units; field precision of approximately ±0.01 pH units, Nido Instruments), a Vector acoustic velocimeter (2 min resolution, Nortek) and a Conductivity, Temperature, Depth instrument (10 s resolution, SBE-16plusV2, Sea-Bird Electronics) with a Satlantic photosynthetically active radiation sensor (Sea-Bird Scientific). The instrument array was connected to a waterproof CompacRIO computer pod (National Instruments) and a 12 V power supply (details of the CP-FOCE instrumentation array can be found in refs. [25,30]). The pH sensors were swapped out with freshly calibrated sensors every 48–72 h and cleaned daily. The pH sensors were calibrated to the seawater scale using a Denver pH metre (UB-10, Denver Instruments) with National Bureau of Standards (NBS) standards and were then used to prepare pH 6 and pH 8.20 filtered seawater standards. The mV readings of the pH sensors in the freshly prepared seawater standards were used for sensor calibration to the seawater pH scale using a spreadsheet developed by MBARI.

Discrete samples for DIC, ALK and pH were collected at variable frequencies throughout the study. In June and December, the availability of personnel allowed for the capture of the full diel cycle in DIC and ALK through 3–4 h interval sampling on the reef flat. During the winter and early spring months, we were constrained to sampling once or twice a day, typically at noon and at the daytime low tide due to lack of personnel. DIC samples were measured with a LI-COR 7000 H_2O:CO_2 analyser (LI-COR, Lincoln) coupled to an automated DIC sample introduction unit built by Stanford University's Stable Isotope Laboratory. DIC precision ranged between ±1 and 2 μmol kg^{-1} and the accuracy was determined with certified reference materials from A.G. Dickson (Scripps Institution of Oceanography, Oceanic Carbon Dioxide Quality Control). ALK was measured via potentiometric titrations in accordance with Gran titration procedures[47], using a T50 titrator with a small-volume DGi101-SC pH sensor (Mettler Toledo) as described in previous publications[30,32]. All ALK samples were corrected based on the offset between the measured and certified value of the certified reference materials and ALK precision was ±3 μmol kg^{-1}. DIC, ALK, temperature and salinity were used to compute P_{CO_2} and Ω_{AR} using CO_2SYS[48]. Monte Carlo simulations (5,000 runs) provide error sensitivities of ±3.5 ppm for P_{CO_2}, an error of ±0.03 units for Ω_{AR} and ±0.01 units for pH. We tested the sensitivities of pairs of variables and this analysis demonstrated that the derived values of ALK are most sensitive to salinity changes. DIC and ALK values were normalized to the 6-month average salinity of 35.2 practical salinity unit and presented as DIC and ALK. Non-normalized DIC and ALK values were used with CO_2SYS to compute Ω_{AR} and P_{CO_2}; otherwise, we display salinity-normalized values for the 6-month period to remove the effects of rainfall and evaporation on the DIC and ALK values and observe the effects of the benthos on the water column chemistry.

Statistical analysis. All statistical analyses were conducted in R[49]. Single factor ANOVA was used to determine whether there was statistically significant difference between the pH in the control flumes and the treatment flumes during dosing. Both the statistical model and the process-based models were estimated using linear mixed effects models. For the statistical models, we tested how treatments (live versus dead, reduced pH versus ambient pH, and the interaction) affected change in buoyant weight while accounting for the correlated structure of the experiment (that is, multiple genotypes crossed within multiple FOCE flumes). Specifically, treatments and the interaction were considered fixed effects. We allowed all fixed effects to also vary by genotype and the overall intercept to vary by FOCE flume number as random effects (note that tests of fixed effects were not sensitive to simpler random effects parameterizations). Linear mixed effects models were fit using the lme4 package[50]. The main effects and interactions were tested using likelihood ratio tests (type III tests). The individual contrasts (live versus dead within each pH treatment, and reduced versus ambient pH within live and dead treatments) were tested using the lsmeans package[51]. We found no meaningful deviations from distributional assumptions (that is, residual homoscedasticity among treatments, among subjects or overall normality).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data generated or analysed during this study are included in this published article and its Supplementary information files.

Code availability

Script files and associated data for analysis can be found at https://github.com/dkokamoto.

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Author contributions

D.I.K., S.D. and O.H.-G. conceived of and designed the experiment. D.I.K, T.M., A.C. and M.M. designed and built the CP-FOCE experimental system. D.I.K., L.T., K.S., K.C., T.M., A.C., M.M., R.B.D., B.G.M., S.D. and O.H.-G. collected the data and conducted the field experiments. D.I.K., L.T. and D.K.O. analysed the data. D.I.K. and L.T. wrote the manuscript with input from all co-authors.

Competing interests

The authors declare no competing interests.

Additional information

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☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	All statistical analyses were conducted in R.). Script files for analysis can be found at https://github.com/dkokamoto.

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Study description	Using a 200-day Free Ocean Carbon Enrichment (FOCE) in situ CO2 enrichment system on Heron Island, Australia, we simulated future OA conditions, and found reduced pH led to drastic decline in net calcification of living corals to no net growth, and accelerated disintegration of dead corals. The FOCE system was set up on the southern GBR at the Heron Island reef flat for 200 days with its four replicate flumes oriented parallel to the shore in accordance with the natural flow regime and with each flume open to the environment on either end and on the bottom. Due to logistical and cost limitations ther were 2 replicate control FOCE flumes and 2 replicate low pH treatment flumes. In each flume there were 5 replicate living Porites cylindrica colonies and five airbrushed dead colonies in each flume, that were each collected from a different mother colony.
Research sample	Porites cylindrica (Dana, 1846) is a branching coral which is one of the dominant corals on the Heron Island reef flat and of reef flats across the Great Barrier Reef (47). P. cylindrica colonies that were approximately 10 cm. in diameter were carefully collected using stainless steel bone clippers, making sure that cuts were only made on dead sections of the colony. 8 replicate heads were collected from 5 large P. cylindrica mother colonies, that were at least 10 m apart, and immediately labeled using a color-coded, numbered vinyl fish tag (Floy Tags, Seattle Washington). Half of the collected P. cylindrica colonies were transported to the research station and airbrushed with filtered seawater to remove all living tissue. The tagged corals were then allowed to recover for one month at the experimental sites on Heron Island reef flat to ensure that all of the living corals had no damage associated with collecting and that no coral tissue could grow back in the recently dead, airbrushed corals. The corals were never removed from seawater and were only briefly held in the Heron Island flow through aquarium system during the airbrushing to minimize the impacts on the corals' internal bioeroding communities. One living and one recently dead P. cylindrica head from each of the 5 mother colonies was haphazardly placed in each of the 4 CP-FOCE flumes, establishing a total of 5 living and 5 recently dead coral colonies in each flume.
Sampling strategy	P. cylindrica colonies that were approximately 10 cm. in diameter were carefully collected using stainless steel bone clippers, making sure that cuts were only made on dead sections of the colony. 8 replicate heads were collected from 5 large P. cylindrica mother colonies, that were at least 10 m apart, and immediately labeled using a color-coded, numbered vinyl fish tag (Floy Tags, Seattle Washington). Half of the collected P. cylindrica colonies were transported to the research station and airbrushed with filtered seawater to remove all living tissue. The tagged corals were then allowed to recover for one month at the experimental sites on Heron Island reef flat to ensure that all of the living corals had no damage associated with collecting and that no coral tissue could grow back in the recently dead, airbrushed corals. The corals were never removed from seawater and were only briefly held in the Heron Island flow through aquarium system during the airbrushing to minimize the impacts on the corals' internal bioeroding communities. One living and one recently dead P. cylindrica head from each of the 5 mother colonies was haphazardly placed in each of the 4 CP-FOCE flumes, establishing a total of 5 living and 5 recently dead coral colonies in each flume. The number of replicate treatment and control FOCE flumes was based on logisitical and cost considerations while the 5 living and dead colonies used in each flume were based on how many corals could be placed in each flume without overcrowding. The corals were sampled from 5 mother colonies at least 10 m apart to ensure that there were 5 replicate genets represented in each replicate flume. Given the technical, logisitical and cost limitations of running an in situ FOCE experiment the number of flumes and coral colonies was sufficient.
Data collection	The CP-FOCE system included an instrumentation array in the environment and in each of the FOCE flumes that included a Monterey Bay Area Research Institute (MBARI) modified Sea-Bird 18 digital pH sensor sampling every second (1-second resolution, manufacturer's reported precision of ± 0.001 pH units; field precision of approximately ± 0.01 pH units, Nido Instruments, USA), a Vector acoustic velocimeter (2-minute resolution; Nortek, Norway), and a Conductivity, Temperature, Depth (CTD) instrument (10-second resolution, SBE-16plusV2, Sea-Bird Electronics, USA) with a Satlantic Photosynthetically Active Radiation (PAR) sensor (Sea-Bird Scientific, USA). The instrument array was connected to a waterproof CompacRIO computer pod (National Instruments, USA) and a 12V power supply. The compacRIO computer pod recorded all of the data from the instrument array and sent the data using a radio antennae to a computer in the field station were the data was saved and backed up to an external hard drive.
Timing and spatial scale	The data collection began on June 1, 2010 and ended on December 11, 2010. There was a data gap between October 10 and November 30 because of a major storm that damaged part of the FOCE system and required repair. pH measurements were made every second and averaged in to 3 hour bins for statistical analysis while the acoustic velocimeter, CTD and OAR sensors took measurements every 10 minutes. The one second sampling period for the pH was necessary for feed-back control of the pH treatments.
Data exclusions	pH data was excluded during and immediately after calibrations or 3 hours after new sensors were deployed in order to get rid of unstable or non sense readings as pH sensors need time to stabilize after changing salinity environments. One living coral in one of the treatment flumes, FOCE 3 was excluded from analysis because of breakage of the colony and loss of broken fragments to the environment that would have altered its buoyant weight.
Reproducibility	Due to the long 200 day length of this study and its logistical complexity we were not able to replicate the study.
Randomization	. cylindrica colonies that were approximately 10 cm. in diameter were carefully collected using stainless steel bone clippers, making sure that cuts were only made on dead sections of the colony. 8 replicate heads were collected from 5 large P. cylindrica mother colonies, that were at least 10 m apart, and immediately labeled using a color-coded, numbered vinyl fish tag (Floy Tags, Seattle Washington). The mother colonies were at least 10m apart to maximize the chance that they represented separate genets or genetically distinct colonies. One living and one recently dead P. cylindrica head from each of the 5 mother colonies was haphazardly placed in each of the 4 CP-FOCE flumes, establishing a total of 5 living and 5 recently dead coral colonies in each flume.
Blinding	Each coral colony had a unique coded tag and all measurements on the corals were done blind to that the person performing the measurements did not know the treatment or the colony from which the coral had come from but did everything based on the code.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The field work was done over a 200 day period on the Heron Island reef flat with field conditions ranged from clear and sunny to incredibly challenging and rainy during a massive tropical storm that lasted for several weeks.
Location	The CP-FOCE was set up on the Heron Island reef flat (23°27'S, 151°55'E), a coral cay in the Capricorn-Bunker group at the southern end of the Great Barrier Reef, in front of the University of Queensland's research station at a water depth between 1-2m depending on the tides.
Access and import/export	Permits from the Department of Environment and Resource Management (#CSCE00874010) and the Great Barrier Reef Marine Park Authority (#G09/29996.1) were provided to conduct this research.
Disturbance	As part of the permitting process we had to demonstrate to DERM and GBRMPA that our FOCE installment and CO2 dosing caused no permanent damage to the study site which was verified at the beginning and end of the experiment.

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We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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n/a	Involved in the study
☒	☐ ChIP-seq
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☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	*For laboratory animals, report species, strain, sex and age OR state that the study did not involve laboratory animals.*
Wild animals	Porites cylindrica (Dana, 1846) is a branching coral which is one of the dominant corals on the Heron Island reef flat and of reef flats across the Great Barrier Reef (47). P. cylindrica colonies that were approximately 10 cm. in diameter were carefully collected using stainless steel bone clippers, making sure that cuts were only made on dead sections of the colony. These corals are hermaphroditic and their age is indeterminate due to their clonal nature. Corals were flash frozen in liquid nitrogen at the end of the experiment.
Field-collected samples	*For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.*
Ethics oversight	As corals are invertebrates no ethics oversight was required but we regularly consulted with the Department of Environment and Resource Management and the Great Barrier Reef Marine Park Authority to ensure that we minimized damage to the corals used and to the surrounding environment.

Note that full information on the approval of the study protocol must also be provided in the manuscript.