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## Original Article

# Year-long effects of high $pCO_2$ on the community structure of a tropical fore reef assembled in outdoor flumes

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In this study, fore reef coral communities were exposed to high $pCO_2$ for a year to explore the relationship between net accretion ($G_{net}$) and community structure (planar area growth). Coral reef communities simulating the fore reef at 17-m depth on Mo'orea, French Polynesia, were assembled in three outdoor flumes (each 500 l) that were maintained at ambient (396 µatm), 782 µatm, and 1434 µatm $pCO_2$, supplied with seawater at 300 l $h^{-1}$, and exposed to light simulating 17-m depth. The communities were constructed using corals from the fore reef, and the responses of massive *Porites* spp., *Acropora* spp., and *Pocillopora verrucosa* were assessed through monthly measurements of $G_{net}$ and planar area. High $pCO_2$ depressed $G_{net}$ but did not affect colony area by taxon, although the areas of *Acropora* spp. and *P. verrucosa* summed to cause multivariate community structure to differ among treatments. These results suggest that skeletal plasticity modulates the effects of reduced $G_{net}$ at high $pCO_2$ on planar growth, at least over a year. The low sensitivity of the planar growth of fore reef corals to the effects of ocean acidification (OA) on net calcification supports the counterintuitive conclusion that coral community structure may not be strongly affected by OA.

**Keywords:** climate change, Mo'orea, OA, ocean acidification, Scleractinia

## Introduction

Ocean acidification (OA), the consequence of the solution of rising atmospheric concentrations of $CO_2$ in the oceans (Broecker, 1975), gained widespread attention as a global threat to marine ecosystems ~2000 (Kleypas *et al.*, 1999; Langdon *et al.*, 2000). Since this realization, numerous experiments have been conducted in which phylogenetically diverse taxa have been incubated in tanks maintained at high seawater $pCO_2$ (and reduced pH), thus revealing impaired biological functionality that most frequently has involved net calcification (Kroeker *et al.*, 2010). For calcified organisms, net accretion typically is reduced by lowered seawater pH (Chan and Connolly, 2012; Kroeker *et al.*, 2013; Kornder *et al.*, 2018), leading to the conclusion that ecosystems dominated by foundation species having calcified shells and skeletons will be threatened by OA (Doney *et al.* 2009). Tropical coral reefs conform to this prediction (Doney *et al.*, 2009; Kornder *et al.*, 2018), with the most severe of the possibilities (i.e. net ecosystem dissolution) predicted to occur within the current century on sediment-dominated reefs (Eyre *et al.*, 2018).

Much is known of the short-term effects of elevated seawater $pCO_2$ on the net calcification of corals and coral reef communities (Chan and Connolly, 2012; Kroeker *et al.*, 2013; Kornder *et al.*, 2018). However, less is known about the response of coral reef communities to high $pCO_2$ over ecologically relevant time scales of a year or more, with only a few studies conducted in the laboratory (e.g. Horwitz *et al.*, 2017; Edmunds *et al.*, 2019a) or the field (Fabricius *et al.*, 2011). The limited number of studies addressing the response of coral communities to OA over long time scales creates a significant knowledge gap in understanding the effects of OA on coral reefs. Addressing this gap requires information on aspects of the biological effects of OA that have yet to be addressed in detail. One of these effects involves the

processes by which net calcification influences the planar spread of scleractinian skeletons across the benthos, which represents the state variable (i.e. coral cover) through which coral community ecology has advanced for decades (Loya, 1972; Connell, 1973; De'ath *et al.*, 2012). Indeed, the coral reef crisis largely is defined by the decline in coral cover (Bellwood *et al.*, 2004; Hughes *et al.*, 2010) and the gravity of future projections is evaluated by how little coral cover will remain within a century (Edmunds, 2015; Donner *et al.*, 2018), together with low, or negative, rates of net community calcification (van Hooidonk *et al.*, 2014; Eyre *et al.*, 2018). There is a great need, therefore, to express the implications for coral reefs of OA using the same parameter (i.e. coral cover) through which their ecological success typically is evaluated.

Testing for the effects of OA on the benthic ecology of coral reefs can only be accomplished through analyses of natural communities exposed to elevated seawater $pCO_2$ (e.g. volcanic seeps, Fabricius *et al.*, 2011), free ocean $CO_2$ enrichment experiments (FOCE) (Kline *et al.*, 2012; Doo *et al.*, 2019), or laboratory experiments using tanks with the volumetric capacity to accommodate reef communities (Langdon *et al.*, 2000; Jokiel *et al.*, 2008; Carpenter *et al.*, 2018). Analyses of coral reefs naturally enriched by $CO_2$ are subject to the limitations of mensurative experimentation (Hurlbert, 1984; Cornwall and Hurd, 2015), while the ability of FOCE and laboratory experiments to test for effects using ecological response variables (e.g. planar area) requires incubations lasting long enough to allow slow-onset effects to be detected. Despite these challenges, several studies have begun to suggest that negative effects of OA on the ecology of coral reef communities are complex and subtle, even while their net calcification declines (Edmunds *et al.*, 2019a; Rippe *et al.*, 2018).

Dove *et al.* (2013), for example incubated coral communities from Heron Island, Australia, for ∼84 d under four combinations of $pCO_2$ and temperature using 300-l tanks. At 572 µatm $pCO_2$ and +4°C, net community calcification shifted to dissolution and coral cover declined from ∼35% to ∼27%. Horwitz *et al.* (2017) conducted a year-long experiment in 30-l tanks and compared the effects of 400 vs. 1795 ppm $CO_2$ on growth and competition among corals from Eilat, Israel. Coral–coral competition reduced growth to such an extent that there was no further additive effect of high $pCO_2$ on coral growth. High $pCO_2$ altered the competitive hierarchy among six coral species, which was inferred to promote shifts in community structure (Horwitz *et al.*, 2017). Close spacing among coral colonies, also has the potential to modulate the effects of OA on coral growth, as aggregates of *Pocillopora verrucosa* are less affected by ∼1200 µatm $pCO_2$ than single branches (Evensen and Edmunds, 2017). Moreover, multi-branched coral colonies are less susceptible to high $pCO_2$ than single branches (Edmunds and Burgess, 2016). Reef communities in Papua New Guinea naturally exposed to ∼750 ppm $pCO_2$ show changes (but not complete losses) in scleractinian communities relative to reefs at ∼390 ppm $pCO_2$ (Fabricius *et al.*, 2011), and in Japan, reefs are dominated (∼50% cover) by octocorals at 830 µatm $pCO_2$ but depleted of octocorals and scleractinians (∼5% cover) at 1465 µatm $pCO_2$ (Inoue *et al.*, 2013). Working with back reef communities in Mo'orea, French Polynesia, Comeau *et al.* (2015) showed that net community calcification was reduced by 59% over 8 weeks at 1300 µatm $pCO_2$, mostly through sediment dissolution. However, when an experiment with back reef communities that was comparable to that of Comeau *et al.* (2015) was extended over 1 year (employing $pCO_2$ as high as 1067 µatm), this effect did not translate into changes in community structure, even though the net calcification of individual colonies was depressed (Edmunds *et al.*, 2019a).

By revealing the effects of OA on corals that emerge as the scale of investigation changes, for example from coral fragments to coral communities, the aforementioned studies highlight the challenges of inferring ecological consequences from the negative effects of OA on coral calcification and coral reef biogeochemistry. Responding to these challenges provided motivation for extending our analysis of the effects of OA on back reef community structure (Edmunds *et al.*, 2019a) to a coral reef habitat (i.e. the fore reef) that is more complex in terms of species assemblages and physical environmental conditions. The fore reef habitat is vastly different from the back reef in terms of community assemblages (e.g. coral cover and diversity, Done, 1983) and physical environmental conditions (e.g. wave forces, light, and often temperature, Done, 1983). The large aerial extent of the fore reef habitat relative to back reef habitat, and the high rates of net accretion achieved by fore reef communities (Vecsei 2001, 2004), makes them a critical focus for studies of the effects of OA. Unlike our early year-long analysis (Edmunds *et al.*, 2019a), here, we focus on fore reef communities from 17-m depth and extend our 7-week analysis (Comeau *et al.*, 2016) of the effects of high $pCO_2$ on fore reef communities to a year. The experiment tests the null hypothesis that community structure is unaffected by long-term exposure to elevated $pCO_2$ (targeted at 700 and 1300 µatm). By simultaneously measuring net organismic calcification ($G_{net}$), and community structure through two-dimensional planar images, we explored the relationship between a common measure of the effects of OA on coral reef organisms and a common community-based metric by which the ecological consequences of the coral reef crisis are expressed.

## Material and methods

### Overview

Fore reef communities were assembled in three outdoor flumes in Mo'orea, which were assigned randomly to $pCO_2$ treatments targeting ambient (400 µatm) and 700 and 1300 µatm $pCO_2$. The elevated $pCO_2$ treatments approximated atmospheric conditions projected for ∼2140 under representative concentration pathways 2.6, 4.5, and 8.5 (IPCC, 2014), respectively. Treatments were maintained for 1 year beginning in late Austral spring (November 2017), and actual $pCO_2$ treatments over the year differed from target values (described below). The flumes are described elsewhere (Carpenter *et al.*, 2018, Edmunds *et al.*, 2019a). In brief, each flume consisted of a working section that was 5.0-m long and 30-cm wide and filled to ∼30-cm depth with ∼500 l of seawater. The working section contained fore reef community members that either were secured on the floor of the flumes (the "fixed" portion) or were placed on the floor of the flumes (i.e. they were "unfixed"), and together these portions occupied 4.7 m × 0.3 m of the floor of the working section of each flume. Seawater was circulated continually through a return section and was exchanged with fresh seawater at ∼300 l $h^{-1}$. Seawater was pumped from Cook's Bay (14-m depth) and filtered through sand (pore size ∼450–550 µm) before entering the flumes. With this pore size, small particulates passed through the filter and were added to the flumes where they were available as food for heterotrophic organisms. It was not logistically feasible to pump seawater from the fore reef (1.5 km away), but we reasoned that the high flow rate of fore reef water over the reef crest

(Hench *et al.*, 2008), and the pumping of water from 14-m depth would reduce artefacts related to the source of seawater used to fill the flumes.

Our experiment is pseudoreplicated (both "simple" and "temporal", after Hurlbert 1984), but we sought to balance the value of statistical independence against ecological relevance in terms of volume, functional scale, environmental conditions, and experimental duration. The challenges of achieving ecological relevance cannot always be reconciled with statistical perfection (e.g. Kline *et al.*, 2012; Albright *et al.*, 2018), but the experiment can be implemented to alleviate the lack of independence of replication that is the core concept of pseudoreplication. In the present study, the small size of the corals relative to the volume of seawater in the flumes, and the high exchange rate of seawater (~60% $h^{-1}$), reduced the likelihood that corals in any one flume were influenced by other corals in the same flume (i.e. they probably were independent). The inferred independence of corals within each flume reduced the implications of pseudoreplication in the analysis of coral growth (change in the area) over time, in which corals were treated as replicates. In the analysis of the net change in mass of corals, the dependence of measurements on single corals at multiple times was addressed with a repeated measures statistical design (both described in "Statistical Analyses" section).

### *Fore reef communities*

The reef communities were assembled to correspond to the mean percent cover of the major benthic space holders recorded in 2006 at 17-m depth on the fore reef of the north shore of Mo'orea (Carpenter, 2018; Edmunds, 2019). A historic community structure (rather than present-day) was used because 2006 represented the long-term community structure on this reef (Edmunds *et al.*, 2019b), and it created the capacity to compare aspects of the present experiment with a previous experiment (Comeau *et al.*, 2016). Based on six sites sampled around Mo'orea in 2006, the community structure in the flumes was targeted to ~11% cover of *Pocillopora* spp., ~8% massive *Porites* spp., 8% *Acropora* spp., and ~53% reef rock. This construct created a community with ~27% coral cover, which was slightly lower than the actual mean coral cover in 2006 (32%) because the remaining 14 genera of scleractinians and *Millepora* contributed 5% coral cover. The *Pocillopora* conformed to the classic morphology of *P. verrucosa* (Veron, 2000), but it is likely that other *Pocillopora* spp. were present in the flumes (Edmunds *et al.*, 2016). Likewise, *Acropora* spp. were selected to represent *Acropora hyacinthus* and *A. retusa*, which were common on the fore reef when the experiment was completed, and colonies of these species were scattered haphazardly among the flumes. Given the morphological complexity of *Acropora* spp., it is possible that other species were placed into the flumes. Pieces of coral rubble (~11.5-cm diameter) were added to achieve ~29% cover. Coral and rubble were haphazardly scattered along the working section of each flume to approach the targets for percentage cover, and this resulted in portions of the flumes having slightly different covers of coral. This was important for the central 2.4-m portion of the flume, where community members were fixed to allow the community structure to be quantified monthly using planar photographs. In the adjacent portions of the flumes, community members were unfixed so that they could be removed monthly for buoyant weighing (described below).

Corals and rubble were collected from ~17-m depth on the north shore fore reef, epoxied (Z-Spar A788; Pettit Marine Paint, Rockaway, NJ, USA) to plastic bases, and placed in a seawater table for at least 2 d before being added to the flumes. This time allowed the epoxy to cure and for the corals to recover from the collection. Fore reef communities were assembled in the flumes on 27 October 2017, where they were maintained under ambient seawater conditions until 3 November. At this time, treatment $pCO_2$ levels were initiated in two flumes (one remained at ambient $pCO_2$), with $pCO_2$ gradually increased to target values over 24 h.

### *Physical and chemical parameters*

Seawater was circulated in the flumes at ~0.1 m $s^{-1}$ using a pump (Wave II 373 J $s^{-1}$, W. Lim Corp., El Monte, CA, USA), and flow speeds were measured across the working sections using a Nortek Vectrino Acoustic Doppler Velocimeter. This flow speed was ecologically relevant for 15-m depth on the fore reef of Mo'orea (14-year mean = 0.065 m $s^{-1}$, Washburn, 2018). The flumes were exposed to natural sunlight that was reduced with a blue filter (LEE # 183; Lee Filters, Andover, England) to photon flux densities (PFD) in the range of photosynthetically active radiation (400–700 nm) that approximated those at 17-m depth (Comeau *et al.*, 2016). Light in the flumes was measured continuously (at 0.0006 Hz) using cosine-corrected sensors (Odyssey; Dataflow Systems Ltd, Christchurch, New Zealand) that recorded photosynthetically active radiation (PAR). Odyssey sensors were calibrated with a Li-COR meter [LI-1400, Li-COR Biosciences, Lincoln, NE, USA attached to a $2\pi$ sensor (LI 192A)]. Temperatures in the flumes were regulated with chillers (heaters were not required) and were maintained close to the mean monthly seawater temperature at 17-m depth on the fore reef.

Seawater carbonate chemistry was uncontrolled in one flume (ambient, ~400 µatm $pCO_2$), and controlled in two others to simulate conditions arising from seawater $pCO_2$ targeted at 700 and 1300 µatm. Seawater pH was not altered in the ambient flume but was controlled in the treatment flumes by bubbling $CO_2$ into the seawater to alter pH relative to a set point (regulated using an AquaController, Neptune Systems, Morgan Hill, CA, USA) that operated a solenoid supplying pure $CO_2$ gas to a diffuser stone submerged in each flume. A diurnal downward pH adjustment of ~0.1 unit was applied to the two treatment flumes to simulate natural diurnal variation in seawater $pCO_2$ on the reef of Mo'orea (Hofmann *et al.*, 2011). The ambient flume also maintained a diurnal variation in $pCO_2$ with a night-time pH ~0.1 unit lower than in the daytime. Ambient air was bubbled continuously into all flumes. Periodic measurements of $pCO_2$ in the flumes confirmed that nocturnal $pCO_2$ met, or exceeded, day-time target values (described in results).

Throughout the experiment, logging sensors (described above) recorded PAR, and temperature [Hobo Pro v2 (±0.2°C); Onset Computer Corp., Bourne, MA, USA]. pH was measured daily on the total hydrogen ion scale ($pH_T$) using a handheld meter (see below). The values from the temperature and pH measurements were used to adjust the thermostat and pH set points to achieve target $pCO_2$ values. Seawater carbonate chemistry was calculated weekly using pH and $A_T$ measurements recorded once during the day, and once at night. A bench-top conductivity meter (Orion Star A212; Thermo Scientific, Waltham, MA, USA) was used to measure the salinity of the same water samples. The parameters

of the seawater carbonate system were calculated from temperature, salinity, $pH_T$, and $A_T$, using the R package Seacarb (Lavigne and Gattuso, 2013). Calculations were made using the carbonic acid dissociation constants of Lueker *et al.* (2000), the $K_{SO4}$ concentration for the bisulphate ion from Dickson *et al.* (1990) and the $K_f$ constant of Perez and Fraga (1987).

$pH_T$ was measured using a DG 115-SC electrode (Mettler Toledo, Columbus, OH, USA) that was calibrated with a TRIS buffer (SOP 6a, Dickson *et al.*, 2007). $A_T$ was measured using open-cell, acidimetric titration (SOP 3b, Dickson *et al.*, 2007) using certified titrant with an automatic titrator (T50, Mettler Toledo) fitted with a DG 115-SC electrode (Mettler Toledo). The accuracy and precision of measurements were determined by processing certified reference materials (CRMs' batch numbers 158 and 172; A. Dickson Laboratory, Scripps Institution of Oceanography, CA, USA), against which measured values of $A_T$ maintained an accuracy of $2.7 \pm 0.4$ µmol $kg^{-1}$ ($n = 54$) and the precision of $1.8 \pm 0.1$ µmol $kg^{-1}$ ($n = 475$).

### *Response variables*

Net changes in mass ($G_{net}$) of corals in the unfixed portion of the community were measured every month by buoyant weighing (accuracy $\pm 1$ mg $CaCO_3$) (Spencer Davies, 1989). The fixed community members were weighed at the start and end of the experiment. Buoyant weight was converted to dry weight of $CaCO_3$ using empirical seawater density [$1.02278 \pm 0.00475$ g $cm^{-3}$ (mean $\pm$ s.e. based on 17 determinations over the year)] and the density of pure aragonite (2.93 g $cm^{-3}$). As the three-dimensional area of tissue changed throughout the year as a result of growth and partial mortality, the change in mass could not be normalized to the actual surface area of the live coral tissue. $G_{net}$ at each time, therefore, was expressed as the percentage change in mass relative to the initial mass in November 2017.

### *Community structure*

The effects of the treatments on the community structure were described using photographs recorded monthly in the planar view. The image-based technique strengthened the ability to address the effects of OA on the community ecology of coral reefs, which frequently is recorded using planar photographs (including in Mo'orea, Edmunds, 2019). Given the high capacity for corals on the fore reef of Mo'orea to increase in planar cover within a year (e.g. Edmunds, 2019), and the linear extension rates that can be expected for the corals employed in our study (e.g. https://coraltraits.org/), it was reasonable to expect changes in planar area of corals, and the effects of treatments on these areas, to be detected by photography over a year (e.g. Edmunds *et al.*, 2019a). Photographs were recorded in ambient light using a GoPro Hero 4 camera (12 MP, 3-mm focal length) that was fitted to a stand and positioned on the upper edge of the flumes to record the benthic community through the air–water interface. At each sampling, the camera was sequentially moved along the flume to record the community in the middle 2.4 m of the working section using ~15 contiguous photographs.

Photographs were analysed using ImageJ software (Abramoff *et al.*, 2004) after they were stitched together to make a single image for each sampling. This image covered the ~2.4-m length of the central portion of the flume where the corals were secured to a plastic-coated metal grid with a mesh size of 5 cm × 5 cm (see Edmunds *et al.*, 2019a). The stitching of photographs sometimes was imperfect due to parallax errors, and in such cases, separate pictures were evaluated to assess organism size. The planar area of living tissue on corals was quantified by outlining organisms in ImageJ, after scaling the image using the metal grid as a size reference. Organism size ($cm^2$) was expressed as a percentage of the area (7200 $cm^2$) occupied by the fixed portion of the community. The summed area of community members was used to determine the cover of the benthic community, and the areas of each organism were used to quantify growth (and shrinkage). Where organisms died, their area was set to zero.

## Statistical analyses

Mortality of the corals was compared between the fixed and unfixed portions of the flumes, and among treatments, using $\chi^2$ contingency tables. $G_{net}$ was analysed by species using repeated measure permutational multivariate analysis of variance (PERMANOVA) (999 permutations, $\alpha = 0.05$) in which the percentage change relative to the initial mass was the response variable, flume was the fixed effects, and time was the repeated measure. Data were square-root transformed and prepared as a resemblance matrix using Bray–Curtis dissimilarity values.

The rate of change in the planar area for each organism was evaluated by the least squares linear regression of non-zero areas (i.e. when the organisms were alive) on time (months). Growth rates (i.e. the slopes of the regression lines, % $month^{-1}$) were used to compare the planar growth of each taxon among flumes using Kruskal–Wallis tests. Multivariate community structure over time was described with two-dimensional ordinations using non-metric multidimensional scaling (nMDS). The resemblance matrices used for nMDS cannot accommodate missing data, and missing data either were set to zero (where organisms died) or replaced by values interpolated by the least squares linear regressions prepared for each organism using all available data for that organism. Resemblance matrices were based on percentage cover and were prepared independently for each flume. Data were $\log(x+1)$ transformed and converted to Bray–Curtis dissimilarities; nMDS plots were obtained using 100 iterations until stress was <1.0. To test for differences among $pCO_2$ treatments in the temporal variation in multivariate community structure, resemblance matrices were compared using rank correlation coefficients in a pairwise fashion against the resemblance matrix for the community incubated under ambient $pCO_2$; significance was evaluated in a permutational framework (999 iterations) using an $\alpha$ of 0.05.

The roles of chemical and physical conditions (Supplementary Table S1) in driving changing community structure were evaluated using multivariate tests of association for each flume. The BEST routine (in PRIMER, Clark and Gorley, 2006) was used to test for associations between community structure (evaluated using Bray–Curtis dissimilarities) and the chemical and physical conditions (evaluated using Euclidian Distances). Chemical and physical data (Supplementary Table S1) were screened for co-linearity, and one member of each pair of co-linear variables was excluded from the analysis.

Univariate statistics were completed using SYSTAT 13 (SYSTAT Software Inc., San Jose, CA, USA), and multivariate and permutational statistics were completed using Primer 6.0 with the PERMANOVA+ add on (Clark and Gorley, 2006).

## Results

### Overview

The experiment ran for 12 months over which the mean monthly temperature (MMT) ranged from 27.9 ± 0.2°C (1434 µatm flume) to 28.1 ± 0.2°C in the other treatments (± s.e., $n = 12$ months) and MMTs varied from 28.7 ± 0.1°C (January, March, and April) to 26.9 ± 0.1°C October (± s.e., $n = 3$ flumes). PFD in each flume was affected by daily variation in weather, and maximum daily PFD varied from 14 to 1636 µmol quanta $m^{-2}$ $s^{-1}$, with the highest values occurring when the lids of the flumes were removed during cleaning. Overall, mean (± s.e., $n = 328$ d) maximum irradiances were 370 ± 12 µmol quanta $m^{-2}$ $s^{-1}$ (400 µatm flume), 296 ± 7 µmol quanta $m^{-2}$ $s^{-1}$ (700 µatm flume), and 274 ± 9 µmol quanta $m^{-2}$ $s^{-1}$ (1300 µatm flume). The mean monthly maximum daily PFD ranged from 63 ± 8 µmol quanta $m^{-2}$ $s^{-1}$ (February 2018) to 641 ± 145 µmol quanta $m^{-2}$ $s^{-1}$ (June 2018), and daily integrated values ranged from 1.1 ± 0.1 mol quanta $m^{-2}$ $d^{-1}$ (February 2018) to 14.5 ± 1.9 mol quanta $m^{-2}$ $d^{-1}$ (September 2018). The three flumes contrasted mean day-time $pCO_2$ treatments of 375 ± 15 (control), 711 ± 15, and 1315 ± 20 µatm, which corresponded to mean $pH_{Total}$ and $A_T$ of 8.1 ± <0.1 and 2340 ± 2 µmol $kg^{-1}$, 7.8 ± <0.1 and 2344 ± 3 µmol $kg^{-1}$, and 7.6 ± <0.1 and 2349 ± 3 µmol $kg^{-1}$, respectively (all ± s.e., $n = 47$, Supplementary Table S2). The night-time conditions of the three flumes were 416 ± 8 (control), 853 ± 23, and 1553 ± 30 µatm, which corresponded to mean $pH_{Total}$ and $A_T$ of 8.03 ± <0.1 and 2336 ± 3 µmol $kg^{-1}$, 7.76 ± <0.1 and 2338 ± 4 µmol $kg^{-1}$, and 7.54 ± <0.1 and 2350 ± 3 µmol $kg^{-1}$, respectively (all ± s.e., $n = 40$; Supplementary Table S2). Salinity values during the incubation were 35.4 ± <0.1 PSU, 35.5 ± <0.1 PSU, and 35.6 ± <0.1 PSU for the 400, 800, and 1300 µatm flumes, respectively (mean ± s.e., $n = 47$), and did not differ significantly from day to night (Supplementary Table S2).

In November 2017, the working section of each flume contained 9–10 colonies of *Acropora* spp., 14–17 colonies of massive *Porites* spp., and 14–17 colonies of *P. verrucosa*, of which 4–5, 7–8, and 7–8 colonies, respectively, were in the fixed (2.4-m long) community section. Initial coral cover was 20% (in the 396 µatm flume), 19% (782 µatm), and 20% (1434 µatm) in the working section of each flume, with 18%, 20%, and 18% in the fixed community sections. This cover represented 4–7% of *Acropora* spp., 5–7% of massive *Porites* spp., and 6–9% of *P. verrucosa*. One year later, mortality left 9 colonies of *Acropora* spp., 1–3 colonies of massive *Porites* spp., and 11–15 colonies of *P. verrucosa* in each flume, with 4–5, 0–2, and 5–6 colonies, respectively, in the fixed community sections of each flume. The coral cover at the end of the experiment (November 2018) was 14% (396 µatm), 13% (782 µatm), and 12% (1434 µatm), with the fixed communities having a combined coral cover of 11%, 13%, and 11%, respectively.

### Net changes in mass ($G_{net}$)

In November 2017, the mean (± s.e.) mass of the corals in the unfixed portions of the communities was 77 ± 6 g ($n = 25$) for *P. verrucosa*, 104 ± 12 g for *Acropora* spp. ($n = 15$), and 95 ± 10 g for massive *Porites* spp. ($n = 24$); the fixed corals had similar masses [86 ± 7 g ($n = 23$), 116 ± 13 g ($n = 13$), and 86 ± 8 g ($n = 23$), respectively]. Over the year, a few *Acropora* spp. died (7%, $n = 25$ across all treatments), but mortality was higher for *P. verrucosa* (14%, $n = 49$) and highest for massive *Porites* (87%, $n = 47$). Mortality was independent of treatment for massive *Porites* spp. ($\chi^2 = 1.267$, df = 2, $p = 0.531$) and *P. verrucosa* ($\chi^2 = 0.572$, df = 2, $p = 0.768$) and independent of whether they were in the fixed or unfixed portion of the communities (pooled among taxa and treatments, $\chi^2 = 0.654$, df = 1, $p = 0.418$).

By November 2018, among the unfixed members of the community, 96% of the corals in the 396 µatm treatment increased in mass (all of the *Acropora* spp. and massive *Porites* and 89% of the *P. verrucosa*), 74% of the corals in the 782 µatm treatment increased in mass (all of the *P. verrucosa*, 80% of the *Acropora* spp., and 50% of the massive *Porites*), and 68% of corals in the 1434 µatm treatment increased in mass (80% of the *Acropora* spp., 90% of the *P. verrucosa*, and 29% of the massive *Porites*). Among the fixed members of the community, 90% of the corals in the 396 µatm treatment increased in mass (all the *Acropora* spp. and massive *Porites* and 75% of the *P. verrucosa*), 91% of the corals in the 782 µatm treatment increased in mass (all of *Acropora* spp. and *P. verrucosa* and 75% of the massive *Porites*), and 83% of the corals in the 1434 µatm treatment increased in mass (all of the *Acropora* spp., 86% of the *P. verrucosa*, and 71% of the massive *Porites*). $G_{net}$ of the unfixed corals that were weighed monthly varied among taxa and treatments (Figure 1). To statistically test for effects of treatments and time, PERMANOVA requires complete data frames and missing data, therefore, were replaced with values interpolated by linear regression, with 4 of 195 values interpolated for *Acropora* spp., 7 of 312 for massive *Porites* spp., and 8 of 312 for *P. verrucosa*. For all three taxa, $G_{net}$ varied over time and among flumes, but there was no interaction between these effects (Table 1, Figure 1).

### Community structure

At the start of the experiment, the size of the corals in the fixed community varied from 16 to 179 $cm^2$. Most *Acropora* spp. grew, most *P. verrucosa* shrank, and most massive *Porites* spp. shrank and died (Figure 2, Supplementary Figure S1); mortality of massive *Porites* spp. rapidly began in month 5 of the experiment (March 2018) when seawater temperature was reaching its maximum annual value (Supplementary Table S1). Based on the regressions of size on time (months) (Supplementary Table S3), the rates of change in size (i.e. the slopes of these regressions) were unaffected by treatments for *Acropora* spp. ($H = 0.119$, $n_1 = 4$, $n_2 = 5$, $n_3 = 4$, $p = 0.942$), *P. verrucosa* ($H = 1.068$, $n_1 = 7$, $n_2 = 8$, $n_3 = 9$, $p = 0.396$), and massive *Porites* spp. ($H = 1.851$, $n_1 = 7$, $n_2 = 7$, $n_3 = 8$, $p = 0.396$).

When displayed using two-dimensional ordination, the sizes of the colonies in each treatment described multivariate community structures differing among months and the ordinations were similar among treatments (Figure 3). However, based on Spearman rank correlations comparing resemblance matrices for the communities created by *Acropora* spp. and *P. verrucosa* under the two elevated $pCO_2$ treatments vs. the control (i.e. 396 µatm), community dynamics differed from that recorded under 396 µatm for both the 782 µatm ($\rho = 0.606$, $p_{perm} = 0.001$) and 1434 µatm ($\rho = 908$, $p_{perm} = 0.001$) treatments. These effects are expressed in the uniform rate at which monthly community analyses diverged over time at 396 µatm $pCO_2$, the four clusters of monthly community structures at 782 µatm, and the tighter clustering of the first 10 months of community structure at 1434 µatm (Figure 3).

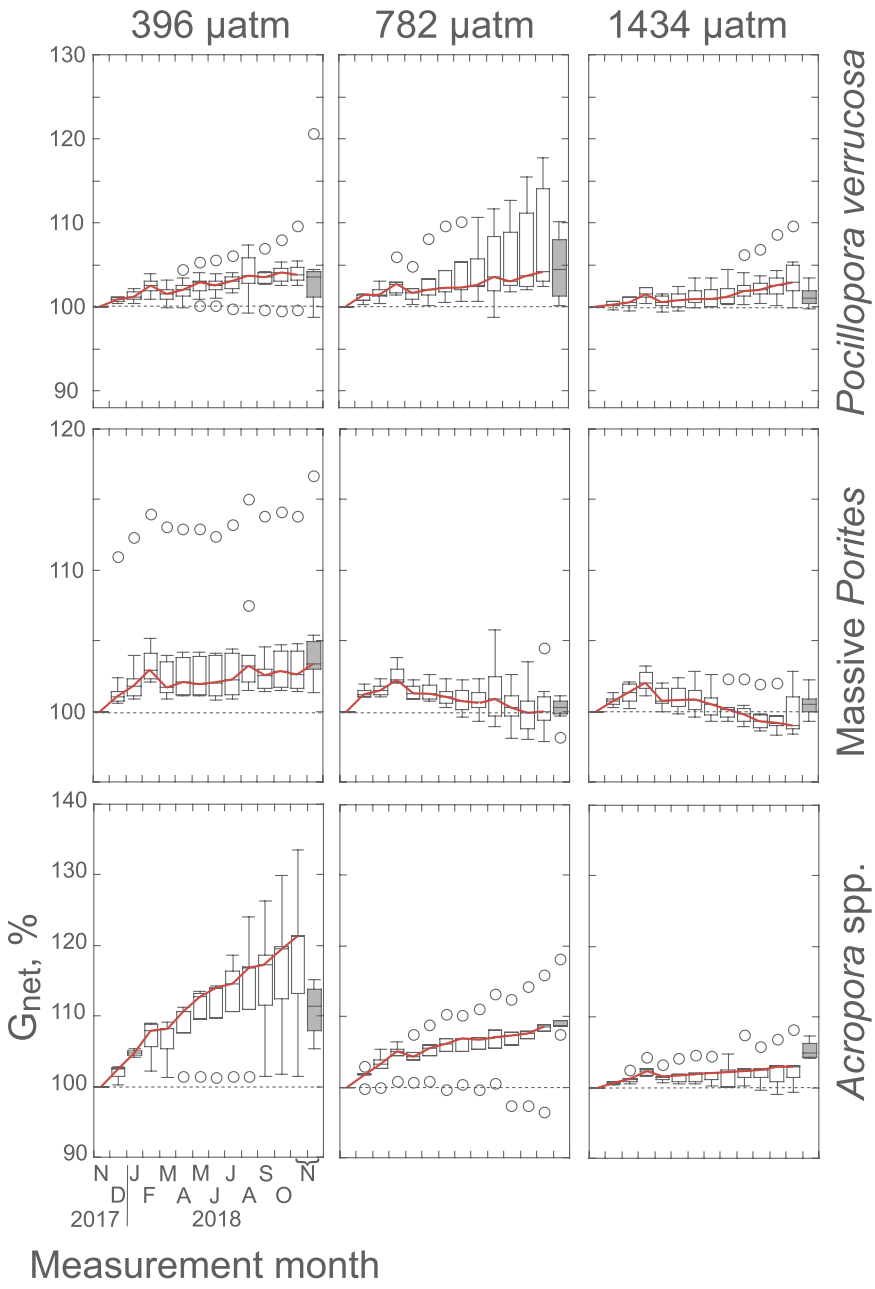


**Figure 1.** Summary of changes in net mass ($G_{net}$) of corals incubated in flumes maintained at three different $pCO_2$ treatments. Values show members of the unfixed community (open boxes, monthly determinations) and fixed community (shaded, November 2018 only) and display dry mass as a percentage of the initial mass of each coral. The percentage scale supports contrasts among corals that differed in initial mass. Box plots report medians as a line within each box (linked by red lines for the unfixed community), boxes show quartiles, and whiskers display ×1.5 the interquartile range, with outliners plotted individually. Sample sizes are shown in each plot frame for unfixed and fixed organisms.

The physical and chemical conditions created over the year within the treatments (Supplementary Table S1) were tested for their ability to explain variation in the biotic data using Spearman rank correlations after screening standardized abiotic data for co-linearity. These analyses were completed for December 2017–September 2018, which corresponded to the 10-month period with a complete set of physical and chemical data in the flumes; the analysis employed seven metrics as predictor variables (Supplementary Table S1). The change in community structure that occurred in the flume maintained at 1434 µatm $pCO_2$ was best explained by MMT ($p_{perm} = 0.003$), although significant explanatory power also was provided by MMT and the slope of changing mean daily temperature prior to sampling (SMDT) ($p_{perm} < 0.050$), and MMT, SMDT and the integrated light intensity on the day of measurement ($p_{perm} < 0.050$); no other combination of variables was significant ($p_{perm} > 0.050$). Variation in community structure in the 396- and 782 µatm flume was not explained by any combination of abiotic drivers ($p\text{-}_{perm} \geq 0.050$) (Supplementary Table S1).

## Discussion

The present study describes a year-long experiment in which fore reef communities with ecological relevance to co-located ecological time-series analyses (Edmunds 2019) were exposed to ambient and high $pCO_2$ under seasonally varying environmental conditions. The outcome demonstrates the effects of high $pCO_2$ on organismic net calcification ($G_{net}$) that reflected largely the inhibitory effects anticipated from previous research (Chan and Connelly 2012; Comeau *et al.*, 2016; Kornder *et al.*, 2018). These effects, however, did not translate into modified rates at which the percentage cover of coral colonies changed over time. Instead, the percentage cover of corals in each flume was strongly affected by common temporal drivers of variation in coral growth, including temperature and light (Knutson *et al.*, 1972; Lough and Barnes, 2000; Pratchett *et al.*, 2015; Scheufen *et al.*, 2017). While the outcomes of the incubations were similar among treatments in terms of final coral cover, the effects of high $CO_2$ were evident in statistically significant, but small, shifts in the extent to which community structure differed between months in each flume (Figure 3).

As we have described for a back reef community incubated for a year in the same flumes (Edmunds *et al.*, 2019a), the present results for a community from a very different habitat and exposed to different environmental conditions are broadly similar in terms of the response of coral community structure to high $pCO_2$. The present results for a fore reef community suggest that the effects of OA on coral community structure, and the contribution of these effects to the coral reef crisis (sensu Hoegh-Guldberg *et al.*, 2007; Hughes *et al.*, 2010), could remain subtle for years to come. While the generality of this conclusion is limited by the year duration of the experiment, longer duration experiments probably will remain intractable in remote tropical locations. To lengthen the effective exposure times in studies of

**Table 1.** Summary of statistical contrasts of $G_{net}$ among treatments (i.e. flumes) and times for corals incubated for a year in three flumes maintained at different $pCO_2$ levels.

| Taxon | Effects | Pseudo-F | df | $p$-perm |
|---|---|---|---|---|
| *Acropora* spp. | Time | 4.504 | 12 180 | 0.001 |
| | Treatment | 40.676 | 2 180 | 0.001 |
| Massive *Porites* spp. | Time | 1.876 | 12 297 | 0.031 |
| | Flumes | 29.414 | 2 297 | 0.001 |
| *Pocillopora verrucosa* | Time | 10.565 | 12 297 | 0.001 |
| | Flumes | 19.968 | 2 297 | 0.001 |

Analyses completed using repeated measures PERMANOVA in which flume was the fixed effects (3 levels), time was the repeated measures effects (13 levels), and relative $G_{net}$ was the dependent variable (and was square-root transformed data).

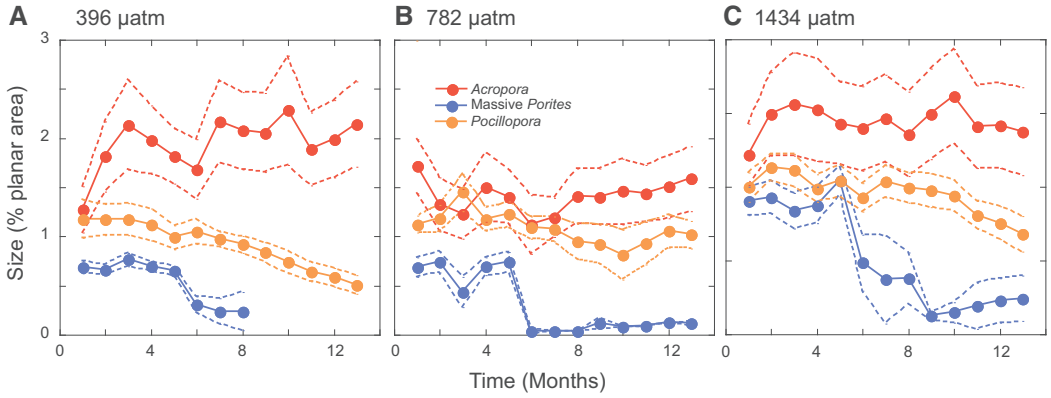


**Figure 2.** Mean (± s.e. confidence belts) percentage cover of live tissue on colonies of *Acropora* spp., *Pocillopora verrucosa*, and massive *Porites* spp. in the fixed portions of three flumes incubated at different $pCO_2$ treatments (A–C). Where corals died, their tissue area became zero and they were not continued in the plots.

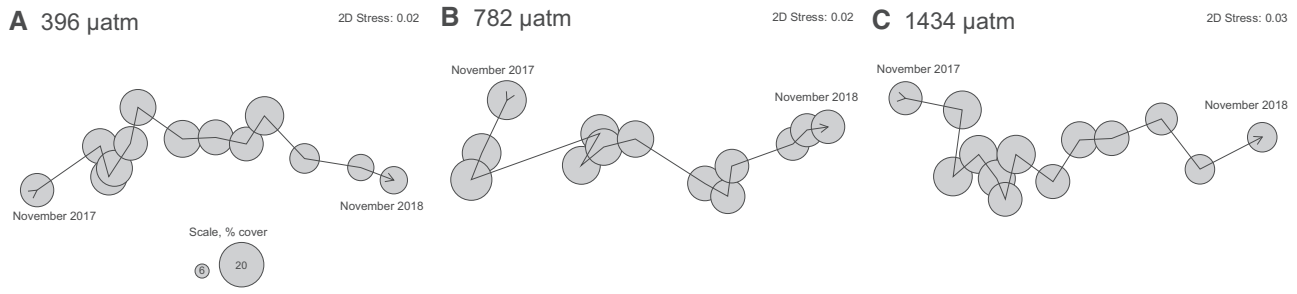


**Figure 3.** nMDS of coral reef communities composed of *Acropora* spp. and *Pocillopora verrucosa* in three flumes incubated under different $pCO_2$ treatments. Analyses are based on the area of individual corals in the fixed portion of the community for each month, with missing values interpolated by linear regression, and areas set to zero if colonies died. Values were log($x + 1$) transformed, and dissimilarities

the effects of OA on coral communities, future work should consider approaches differing from the one employed herein, for example utilizing greater use of predictive modelling (e.g. Evenhuis *et al.*, 2014).

The present study differs from most other studies addressing the effects of OA on corals and coral reefs because we focused on ecological effects in terms of a state variable (i.e. coral cover) that is at the forefront of quantifying the coral reef crisis (e.g. Bruno and Selig, 1970; De'ath *et al.*, 2012; Jackson *et al.*, 2014). Two decades of research on the effects of OA on the net calcification of corals, other coral reef organisms, and reef communities have revealed the implications of this stressor for the persistence of coral reefs as a calcified ecosystem (e.g. Silverman *et al.*, 2009; Eyre *et al.*, 2018). While the focus of this rapid advancement of knowledge is consistent with the importance of calcification for the functional significance of coral reefs (Anderson and Gledhill, 2013; Pratchett *et al.*, 2015), and the role of scleractinians as a foundation taxon (Jones *et al.*, 1994), it has left ecological processes overlooked as targets of OA effects. This has created a disconnect between ecological analyses of coral reefs through which the coral reef crisis has been recorded, largely through the reduction in coral cover (Bruno and Selig, 2007; De'ath *et al.*, 2012; Jackson *et al.*, 2014), and physiological and biogeochemical analyses through which the impairment of calcification by OA has been reported (Doney *et al.*, 2009; Anderson and Gledhill, 2013). While it is likely that calcification of most corals and calcified algae will be depressed in a more acidic future, and that reefs will transition into net dissolution within the current century due to declining seawater pH (Silverman *et al.*, 2009; Eyre *et al.*, 2018), it is unclear how these trends will affect the occupation of planar space by corals.

Within the research community investigating the effects of OA on marine systems, there is a growing recognition of the importance of addressing the effects on ecological processes such as primary production, the energetic costs of consumers, and species interactions (Gaylord *et al.*, 2015). Studies of the effects of OA on ecological processes shaping coral communities is in its infancy, in part because many of these processes unfold over time scales associated with the generation time of the organism involved. The effects of OA on coral reproduction, for example will be expressed only over time scales embracing annual cycles of gametogenesis, spawning, and recruitment (Albright *et al.*, 2010; Albright and Langdon, 2011; Fabricius *et al.*, 2017). The effects on coral–coral competition will appear only if corals have the time to grow towards one another, interact, and develop a dominant and subordinate hierarchy (Horwitz *et al.*, 2017). Despite these experimental difficulties, improved technical competence in conducting OA experiments and the discovery of "natural laboratories" where seawater $pCO_2$ is normally high (Fabricius *et al.*, 2011; Inoue *et al.*, 2013) are starting to reveal how coral community ecology might be affected by OA. For instance, coral recruits show depressed skeletogenesis and deformities at high $pCO_2$ (Foster *et al.*, 2016), yet coral recruitment is unaffected by habitually high $pCO_2$ on at least one reef adjacent to a $CO_2$ seep (Oprandi *et al.*, 2019). As recruits contribute to creating crowded coral communities, competition among adjacent colonies is affected by high $pCO_2$, thereby modifying competitive hierarchies among the component corals (Horwitz *et al.*, 2017). One potential outcome of these kinds of ecological effects is modified coral community structure.

While the state variable most widely used to quantify coral communities, coral cover, remains understudied with respect to OA, there is evidence that it may be less strongly affected by OA than the net calcification of coral colonies. Support for this inference comes from two domains of investigation, one focusing on the ways in which mass deposition of $CaCO_3$ translates into linear skeletal extension and the other focusing on measurements of the cover state variable itself. In terms of $CaCO_3$ deposition and skeletal extension, there are several experimental studies showing that skeletal porosity increases as OA depresses mass deposition in corals, thereby allowing linear extension (and increase in coral colony cover) to be sustained (Fantazzini *et al.*, 2015; Mollica *et al.*, 2018), presumably at the expense of skeletal strength (Hennige *et al.*, 2015). Studies of coral communities at some natural $CO_2$ seeps show that the cover of scleractinians can be maintained (Fabricius *et al.*, 2011), but not always (Inoue *et al.*, 2013). Our previous work with back reef communities in Móorea shows that coral cover can persist while the carbonate framework experiences dissolution, at least over a year (Edmunds *et al.*, 2019a). The present study provides a second example from a very different reef habitat of a similar outcome.

A limitation of the present study is that many of the *P. verrucosa* and massive *Porites* in the flumes shrank in cover or died. As coral cover at 17-m depth on the fore reef of Mo'orea increased over the same period (Edmunds, 2019), it is reasonable to conclude that the declines in coral cover in the flumes were associated with the *ex situ* environment. Corals thrived in the same flumes when a similar experiment was completed with back reef communities over 2015–2016 (Comeau *et al.*, 2015), and also when fore reef communities from 17-m depth were grown for 7 weeks from August to October 2014 (Comeau *et al.*, 2016). Seawater temperature during the present study was slightly warmer in some months compared with the same months in the previous studies (i.e. 0.5°C warmer in January 2018 and 1.6°C warmer in September 2018 compared with the same months in 2016 (Edmunds *et al.*, 2019a; see also Edmunds 2017), but none of the MMTs during 2017–2018 exceeded the bleaching threshold for Mo'orea (30°C, https://coralreefwatch.noaa.gov/). Since seawater temperatures during the present year-long experiment were not extreme relative to the local bleaching threshold, it is unlikely that thermal stress was the cause of coral mortality. While the reasons for the coral mortality in our flumes remain unknown, and despite pumping seawater from 14-m depth in Cook's Bay, we cannot exclude the possibility that the coral mortality was associated with impaired seawater quality, or possibly, the negative effects of short exposure to high PFDs (e.g. Baker 2001) when the lids of the flumes were removed for cleaning.

Previously, Comeau *et al.* (2016) used a 7-week experiment in the austral spring to show that 24-h net calcification of fore reef communities from 17-m depth in Moorea was reduced by 45% at 1176 vs. 401 µatm $pCO_2$. This effect was caused by a 31% depression of daytime net community calcification and a 76% reduction in night-time net community calcification that was attributed to dissolution within reef rock (Comeau *et al.*, 2016). The authors did not address how coral cover was affected by the treatments (because measurable planar growth was not expected over 7 weeks). However, with the similarity of physical and chemical conditions between the treatments in Comeau *et al.* (2016) and the present study, and the steps that were taken to make the fore reef communities similar in both studies (described in "Material and Methods" section), it is reasonable to expect that community

calcification would be similarly depressed by OA in the present study, again, through dissolution within reef rock.

Preliminary analyses (i.e. for November 2017–June 2018) for another aspect of the present study shows an 83% reduction in 24 h net calcification at 1434 vs. 396 µatm $pCO_2$, with the greater effect (cf. Comeau *et al.*, 2016) likely reflecting the decline in coral cover over time in the present study. Against this backdrop, it is striking that the effect of OA on community structure in the present study was confined to subtle shifts in the rate at which multivariate community structure composed of *Acropora* spp. and *P. verrucosa* separated among months over a year. Elucidating the causes of these effects was beyond the scope of the present study and, indeed, analyses of the association between multivariate community structure and multivariate environmental conditions proved equivocal in identifying dominant drivers of the changes in coral community structure. Given the seasonality in environmental conditions captured by the present experiment (Supplementary Table S1), and the growing understanding of interactive effects among OA and other environmental conditions in mediating coral performance (e.g. Chan *et al.*, 2016; Langdon *et al.*, 2018), it is likely that such effects were responsible for the shift in the tempo of variation in community structure in the present study.

The present study contributes to a small number of studies that are experimentally addressing the effects of OA on coral communities over time scales that have ecological relevance for reef corals. Such experiments pose unique logistical challenges for the research community, and as the present study reveals, they can capture unexpected effects such as shrinkage and mortality of the organisms under investigation. Nevertheless, the outcome of such experiments can still be insightful when controls reveal the same trends and, as the present study shows (as well as our previous study, Edmunds *et al.*, 2019a), can reveal findings unobtainable within the scale of short experiments (i.e. lasting weeks to months) conducting in small tanks. The present analysis reveals the extent to which the effects of OA on the planar coral cover (and coral community structure derived therefrom) can be undetected over a year. Further empirical or modelling approaches will be required to extend the time horizon towards the generation time of coral colonies (i.e. years–decades), or the time required for reefs to recover from disturbances in the Anthropocene (i.e. decades–centuries).

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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