# Effects of *p*CO$_2$ on spatial competition between the corals *Montipora aequituberculata* and *Porites lutea*

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ABSTRACT: We tested the hypothesis that ocean acidification (OA) affects spatial competition among scleractinian corals. Competitive ability was evaluated indirectly by linear extension of *Porites lutea* and *Montipora aequituberculata* placed in intraspecific, interspecific, and control pairings (paired with dead coral skeleton) and exposed to ambient (~400 µatm) and elevated (~1000 µatm) *p*CO$_2$ in experiments conducted in Moorea, French Polynesia, and Okinawa, Japan. High *p*CO$_2$ had no effect on linear extension of *M. aequituberculata* in Moorea, but in Okinawa, it reduced linear extension 37 %; high *p*CO$_2$ had no significant effect on linear extension of *P. lutea* in Okinawa. Much of the negative effect of high *p*CO$_2$ on linear extension for *M. aequituberculata* in Okinawa was due to reduced extension in control pairings, with corals engaged in intra- and interspecific competition unaffected by OA. Linear extension of *M. aequituberculata* and *P. lutea* in interspecific pairings decreased relative to control pairings at ambient *p*CO$_2$ by 39 and 71 %, respectively, indicating a strong effect of competition on extension rates. These differences however disappeared at elevated *p*CO$_2$ when the linear extension of controls was depressed. Together, our results show that OA can negatively affect the linear extension of corals not engaged in competition, as shown in the control pairings, and suggest that OA does not directly affect the ability of corals to compete with one another for space.

KEY WORDS: Ocean acidification · Scleractinia · Competitive interactions · Linear extension

## INTRODUCTION

Despite strong interest in the effects of ocean acidification (OA) on coral calcification (Chan & Connolly 2013), only a few studies have addressed the impacts of OA on ecological processes structuring benthic communities (Gaylord et al. 2015). On coral reefs, competition for space has begun to be studied in the context of OA, because OA is important in mediating coral–macroalgal interactions (Diaz-Pulido et al. 2011) that are ubiquitous on contemporary reefs. The outcome of such interactions are determined by a diversity of mechanisms initiated by both competitors, with corals employing rapid growth or the deployment of sweeper tentacles and mesenterial filaments (Lang 1973, Lapid & Chadwick 2006), and macroalgae employing rapid growth, allelochemicals, and bacteria (McCook et al. 2001, reviewed in Chadwick & Morrow 2011). With multiple pathways through which OA could affect competitive interactions among corals, it is challenging to predict how the outcome of these encounters will change under acidified conditions.

For reef corals, growth rate is an important mechanism of spatial competition (Lang & Chornesky 1990), with fast-growing corals outcompeting slow-

growing corals, unless slow-growing corals deploy alternative mechanisms of competition (Lang & Chornesky 1990, Chadwick & Morrow 2011). Because OA affects coral growth in generally negative ways (Kroeker et al. 2013), it is reasonable to hypothesize that it will modify the abilities of some corals to compete for space. Since OA affects the ability of corals to deposit $CaCO_3$ in ways that differ among species (Comeau et al. 2014), it is likely that these effects will translate to differential abilities to extend linearly (Jokiel et al. 2008, De'ath et al. 2009). In turn, effects of OA on linear extension could alter the capacity to compete through overgrowth (Lang & Chornesky 1990), and therefore could alter the ways in which corals species assemble to form communities (sensu Madin et al. 2008).

The objective of this study was to test the hypothesis that OA affects the ability of scleractinian corals to engage in spatial competition with one another, through differential effects of elevated $pCO_2$ on linear extension. Two laboratory experiments were completed using *Porites lutea* and *Montipora aequituberculata* from back and fringing reef habitats. First, in Moorea, French Polynesia, we evaluated the efficacy of linear extension as a dependent variable characterizing the response of corals in competitive encounters, as well as a means to test for an effect of elevated $pCO_2$ on linear extension. Second, at Sesoko Island, Okinawa, we applied the techniques developed in Moorea to test the effects of elevated $pCO_2$ on the ability of corals to compete with one another for space. This experiment tested the effects of elevated $pCO_2$ on the linear extension of small corals placed ~5 mm apart under laboratory conditions. The results were used to infer how OA might affect the ability of corals to compete in the field for space.

## MATERIALS AND METHODS

### Study species

*Porites lutea* and *Montipora aequituberculata* were used for both experiments, as these species are common throughout the tropical Indo-Pacific (Veron 2000), including in the shallow back reefs of Moorea and the fringing reefs of Okinawa (van Woesik 2000, Comeau et al. 2015) where they often come into contact with one another (Fig. 1a). Inspection of contact zones between colonies of *P. lutea* and *M. aequituberculata in situ* suggested there were competitive 'standoffs' (sensu Connell et al. 2004), because one
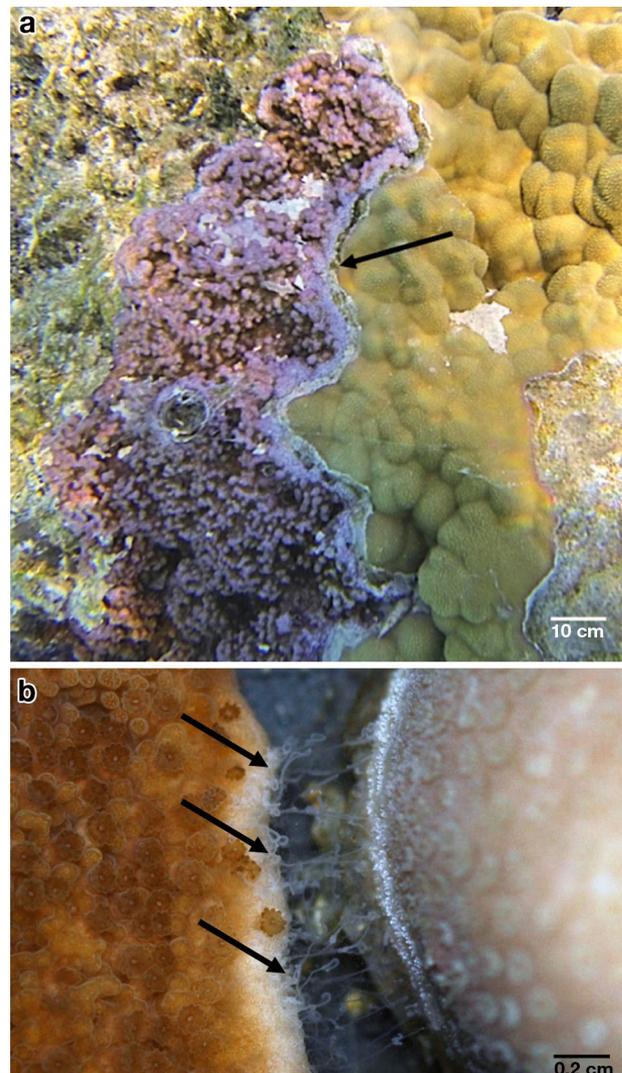


Fig. 1. Interactions between colonies of *Montipora aequituberculata* (left) and *Porites lutea* (right). (a) At ~1 m depth in the back reef of Moorea, French Polynesia, in 2013. A margin of contact (shown with arrow) occurs between the corals marking a zone where coral growth appears to have ceased. (b) After 4–5 d of being paired under laboratory conditions. Numerous mesenterial filaments (white, shown with arrows) are extruded by *M. aequituberculata* and interact with the tissue of *P. lutea*

colony was not clearly overgrowing the other, and opposing colony margins were slightly raised. In studies of competitive networks established among corals on Indo-Pacific reefs, *Montipora* are competitively dominant over massive *Porites* spp. (e.g. Sheppard 1979, Dai 1990), although the mechanistic basis of this hierarchy remains unknown. The commonly-used mechanisms of aggression in corals—for example, mesenterial filaments, sweeper polyps, and sweeper tentacles (Chadwick & Morrow 2011)—

have not been reported for either *M. aequitubercu-lata* or massive *Porites.*

Massive *Porites* consists of multiple species that are difficult to resolve in the field, and their identification classically has relied on features of individual coral-lites (Veron 2000) that require magnification to resolve. In the present study, we focused on collect-ing small colonies of massive *Porites* that were uni-form in color and morphology, and were tentatively assigned to the *P. lobata/P. lutea* complex (Edmunds 2009). Subsequently we used macro photographs to resolve species based on corallite structure (after Veron 2000), and all sampled colonies were identi-fied as *P. lutea.* However, as genetic analyses have revealed that distinguishing species of massive *Porites* based on morphology is problematic (Fors-man et al. 2009), we cannot exclude the possibility that our '*P. lutea*' included other species. We suspect the implications of this possibility are small for our study because the growth rates of massive *Porites* from the Indo-Pacific are similar among species (Lough & Barnes 2000). In contrast to *P. lutea*, *M. aequituberculata* was easily discernable from other *Montipora* spp. in the field, based on conspicuous skeletal features (i.e. fusion of the thecal papillae around the corallites), and corallum morphology (encrusting in high-flow environments, laminar in low-flow environments; after Veron 2000).

The ecological relevance of interactions between *M. aequituberculata* and *P. lutea* lies in the common occurrence of these corals in shallow reef habitats, and the frequency with which they encounter one another, as observed during preliminary field obser-vations. To quantify these effects, we evaluated coral community structure in the back reef of Moorea along the East and West shores that are sampled annually as part of the Moorea Coral Reef LTER (Edmunds 2013). Photoquadrats recorded in the back reef of these shores (at LTER sites 3 and 6) in 2010, and analyzed for coral cover using Coral Point Count (CPCe) software (Kohler & Gill 2006), were used to quantify the abundance of *Montipora* and massive *Porites.* These images were also used for an addi-tional analysis in which colonies of *Porites* and *Mon-tipora* were scored for contact with one another. All colonies of *Porites* and *Montipora* were evaluated for contact, with contact scored when colonies were <5 mm from one another, and these points of contact inferred to be sites of interspecific competition. The number of colonies of each taxon involved in inter-specific competition was expressed as a percentage of the total number of colonies in each taxon that were present in all the photoquadrats evaluated. It

was however not possible to determine the outcome (i.e. which colony was dominant versus subordinate) of most competitive encounters in the planar photo-graphs.

## Expt 1 (Moorea)

The first study in Moorea was conducted in April 2013 at the Richard B. Gump South Pacific Research Station, and lasted 24 d. Juvenile massive *Porites* (~2 cm diameter) and fragments of *Montipora aequitu-berculata* (~1.5 × 1.5 cm) were collected from the back reef at ~2–3 m depth. Colonies were epoxied (Z-Spar A788) into competitive pairings on PVC tiles (4 × 2.5 cm). Fragments of adult colonies of *M. aequituberculata* were used instead of intact juvenile colonies, as preliminary sampling revealed that such small colonies occurred in cryptic microhabitats and could not be collected without damaging the tissue. Following collection, fragments of *M. aequitubercu-lata* secreted mucus for about 2 d, but thereafter behaved normally and started to produce new tissue to cover the skeleton exposed during collection. After 6 d of recovery in flowing seawater, coral tissue had almost fully overgrown the exposed skeleton and fragments were considered sufficiently healed to be used in the experiment.

The experiment staged 3 types of pairings repre-senting those found naturally on the shallow reefs of Moorea (Fig. 2): (1) interspecific pairings of *M. aequi-tuberculata* versus *P. lutea*, (2) intraspecific pairings of *M. aequituberculata* versus *M. aequituberculata*, and (3) control pairings of *M. aequituberculata* ver-sus a piece of dead coral skeleton. Only the linear extension of massive *M. aequituberculata* was scored in this experiment, because the rapid growth of this species (ca. 29 mm yr$^{-1}$ [Browne 2012]) suggested it would show a measurable response to the treat-ments. In contrast, based on slower growth rates of 11 mm yr$^{-1}$ for *P. lutea* (Lough & Barnes 2000), we suspected it would not be possible to measure short-term linear extension for this species.

Scleractinians can extrude mesenterial filaments (Fig. 1b) to digest the tissue of nearby competitors prior to overgrowth (Lang 1973), and therefore corals were placed within reach of these structures (i.e. ~5 mm; Nugues et al. 2004). Control pairings tested for changes in linear extension due to pairing with an inert object that physically impaired growth normal to the colony margin. Twelve replicates were created for each type of pairing, and 2 replicates of each pair-ing type were randomly allocated to one of six 150 l
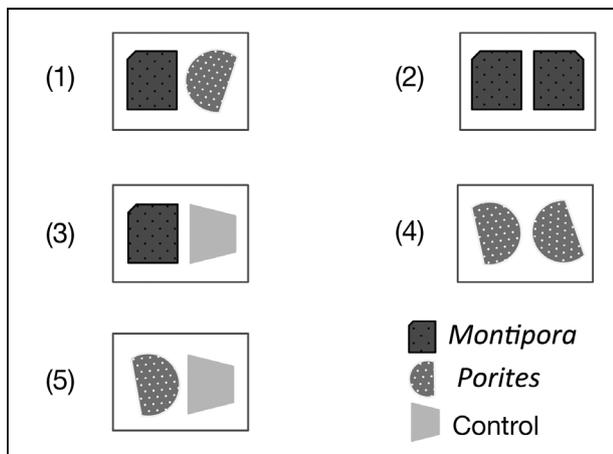
Fig. 2. Competitive pairings that represented treatments in the present study: (1) interspecific pairings of *Montipora aequituberculata* versus *Porites lutea*, (2) intraspecific pairings of *M. aequituberculata* versus *M. aequituberculata*, (3) control pairings of *M. aequituberculata* versus a piece of dead coral skeleton, (4) intraspecific pairings of *P. lutea* versus *P. lutea*, and (5) control pairings of *P. lutea* versus dead coral skeleton. Treatments 1–3 were created in Moorea, but all 5 treatments were created in Okinawa. Replicates of each treatment were allocated to each tank, with replicate tanks nested within each $pCO_2$ treatment

indoor tanks (n = 2 tank$^{-1}$) receiving sand-filtered flowing seawater (~400 ml min$^{-1}$) pumped from Cook's Bay, with $CO_2$ bubbled into 3 of the tanks to create a $pCO_2$ treatment. The tanks were maintained at ecologically relevant light intensities and temperature, and the position of the coral pairings in each tank was changed randomly every 2 d to eliminate position effects.

Tanks were illuminated with a 75 W light emitting diode (LED) module (Sol White LED Module, Aqua-Illumination, 6500 K) that produced a natural diel light cycle, with the intensity rising gradually for 4 h from 06:00 h, stabilizing for 4 h at maximum intensity, then declining for the last 4 h of the 12 h cycle. Light intensities averaged ~500 µmol quanta m$^{-2}$ s$^{-1}$ during maximum intensity (measured using a 4-π Li-Cor LI-193SA sensor), providing an intensity similar to that found where the corals were collected at 3–4 m depth in the back reef (Edmunds et al. 2012). The monitoring of the physical and chemical conditions in the tanks is described in 'Carbonate chemistry', below.

## Expt 2 (Okinawa)

The second study in Okinawa was conducted from May to June 2013 at Sesoko Station (Tropical Biosphere Research Center, University of the Ryukyus),

with the experiment lasting 21 d. Juvenile massive *Porites* (~3 cm diameter) and fragments of *M. aequituberculata* (~3 × 3 cm) were collected from ~3–4 m depth from the fringing reef adjacent to the station. A total of ~40 corals of each taxon was collected, and each colony was cut into pieces (~1.5 × 1.5 cm) that were used as replicates in experimental pairings (described below). Each colony was cut into 2–3 pieces using a band saw (Fujiwara model SWB-250), and the pieces from all colonies were randomized in a tank before selecting pieces to be arranged in experimental pairings. While each genotype was therefore replicated, genotype was not used as a factor in the experiment, and the randomization procedure reduced the implications of this effect on the experimental design. Fragments were left overnight in a flow-through outdoor seawater table to recover, and were glued into competitive pairings on acrylic tiles (5 × 2 cm) using cyanoacrylate adhesive (Aron-Alpha, Konishi). Colonies were cut into small fragments to fit onto the acrylic tiles, and to ensure the desired number of replicate pairings would fit into the small tanks (12 l) available. To obtain clean coral skeleton for use in control pairings, pieces of coral skeleton were cut from beach rock, immersed in dilute bleach (sodium hypochlorite) to remove microorganisms, and soaked for 24 h in freshwater to remove the bleach.

In Okinawa, 2 additional pairing types were added to the experimental design employed in Moorea, with these additions providing a broader selection of the types of pairings in which *P. lutea* engages on the reef: (4) intraspecific pairings of *P. lutea* versus *P. lutea*, and (5) control pairings of *P. lutea* versus a piece of dead coral skeleton. The outcomes for the corals of the pairings were assessed for *M. aequituberculata* and *P. lutea* because the experiment in Moorea revealed that our technique had the resolution to measure growth in both species. However, as both corals in each pairing were not independent of one other, the results from each taxon were analysed separately. The control pairings again were used to test for changes in linear extension due to pairing with an inert object that physically impaired lateral growth.

Sixteen replicates were created for each competitive pairing and were placed in an outdoor seawater table for 2 d for recovery. After this period, fragments had stopped secreting mucus, and coral tissue had begun to grow over the exposed skeleton. While some bare skeleton typically remained when the incubations started, there was no exposed skeleton at the competitive margin between the corals 3–4 d

after the start of the incubations. Two replicates of each of the 5 pairing types were randomly allocated to one of eight 12 l tanks (10 pairings per tank) receiving flowing seawater (~400 ml min$^{-1}$). Coral pairings were moved in each tank every 2 d to eliminate position effects.

Tanks were outside and exposed to a naturally fluctuating light regime, but were sheltered from rain. To avoid corals being damaged by high light intensities, the experiment was shaded using mesh to provide a midday irradiance of ~250 µmol quanta m$^{-2}$ s$^{-1}$ (measured using a 4-π Li-Cor LI-193SA sensor). This irradiance was however ~24 % lower compared to the ambient light intensity (Hayashi et al. 2013), and thus likely to be lower than what the corals experience on the fringing reef at ~2 m depth.

## Carbonate chemistry

$CO_2$ treatments in both experiments consisted of 2 $pCO_2$ levels corresponding to present day conditions (400 µatm), and a high level projected for atmospheric values expected by the end of the 21st century under a 'worst-case' projection of anthropogenic $CO_2$ emissions (~1000 µatm), from representative concentration pathway 8.5 (Moss et al. 2010). $pCO_2$ was maintained at a constant level in both experiments.

In the experiment conducted in Moorea, $pCO_2$ treatments were created by bubbling ambient air or $CO_2$-enriched air into the tanks. $CO_2$-enriched air was obtained with a solenoid-controlled gas regulation system (Model A352, Qubit Systems) that mixed pure $CO_2$ and ambient air at the $pCO_2$ desired. The flow of air and $CO_2$-enriched air was delivered continuously in each tank and adjusted independently by needle valves. Adjustments were conducted twice daily following pH measurements to ensure that the seawater pH was close to the target value. Temperature and pH were measured twice daily (08:00 and 18:00 h) in each tank. In the experiment conducted in Okinawa, $CO_2$ treatments were created by bubbling ambient air, or $CO_2$-enriched air (with a direct $pCO_2$ control system; Kimoto) into 178 l header tanks that drained at 0.36 l min$^{-1}$ into the tanks where the corals were incubated. A single header tank was used for each $CO_2$ treatment, one for the ambient treatment, and one for the high $CO_2$ treatment. Temperature, pH, and light intensity were measured 3 times daily in each tank (08:00, 12:30, and 17:00 h).

For both experiments, seawater pH was measured using a pH meter (Orion, 3-stars mobile coupled with a Mettler DG 115-SC pH electrode) calibrated every 2 d on the total scale using Tris/HCl buffers (A. Dickson, Scripps Institute of Oceanography [SIO], San Diego, CA, USA). Total alkalinity ($A_T$) was measured using ~50 ml samples of seawater collected daily from each tank at 08:00 h, and processed in open-cell, potentiometric titrations using an automatic titrator in Moorea (Model T50, Mettler-Toledo), and a $A_T$ titration analyzer in Okinawa (Kimoto ATT-05). The accuracy and precision of the titrations were evaluated by analyzing certified reference materials (CRM, batch 122 from A. Dickson, SIO) with analyses <5 µmol kg$^{-1}$ from the certified value. Parameters of the carbonate system, including $pCO_2$ and the aragonite saturation state ($\Omega_{arag}$), were calculated from salinity, temperature, $A_T$ and pH$_T$ using the R package seacarb (Lavigne & Gattuso 2013). Based on the calculated carbonate chemistry values, the supply of $CO_2$ to the tanks was adjusted to better match the actual $pCO_2$ values to the target $pCO_2$ values. The supply of $CO_2$ to the tanks was modified in Moorea using the solenoid valve to adjust the air-$CO_2$ mixture, and in Okinawa by adjusting the flow of $CO_2$ gas into each header tank.

## Linear extension

Linear extension of the margins of coral colonies placed into competitive pairings was measured from photographs taken before and after incubation. All measurements were recorded along ~1.5 cm of the colony margin at the site of interaction (Fig. 3), with 3
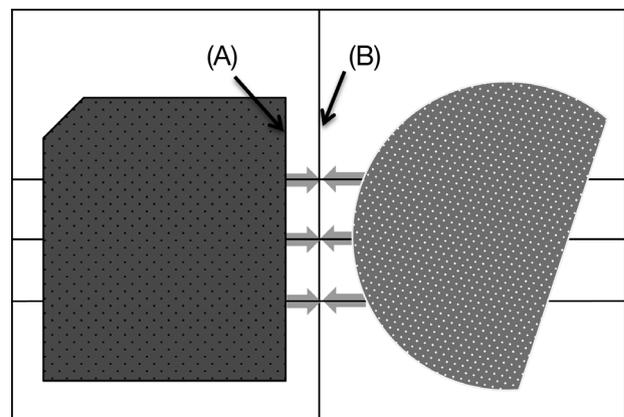


Fig. 3. Interspecific pairing showing how linear extension was measured for corals in all 3 competitive pairings, with the arrows showing measurements that were made. Using ImageJ v1.46 software (Rasband 1997), extension rates were obtained by measuring the distance of the coral margin (A) to the reference line (B) before and after incubations (final units of µm d$^{-1}$)

replicate measures for each coral in each pairing. The 3 measures were scattered evenly along the margin of contact and were averaged by coral to characterize the linear extension of each replicate. Photographs were taken using a digital camera (Nikon D70, 6.1 Megapixel resolution) fitted with a macro lens (Nikon 60 mm f/2.8D). Corals were photographed under natural lighting in seawater in planar view before and after 21–24 d in the treatments. Extension rates were obtained using ImageJ software (Rasband 1997) to measure the distance of the coral margin from reference lines marked on the tile with this distance measured normal to the reference lines. The change in the distance of the margin from the reference lines was used as a measure of growth ($\mu$m d$^{-1}$).

## Statistical design and analyses

Chemical conditions in the tanks were compared among tanks with a 2-way ANOVA, with treatment as a fixed effect, and tank a random factor nested in each treatment. The tank effect was dropped from the analyses when not significant at $p \geq 0.250$ (Quinn & Keough 2002). Competitive pairings in both experiments were used in a split-plot ANOVA with one between-plot effect ($p\mathrm{CO}_2$), one within-plot effect (type of pairing), and replicate tanks (treated as plots, with 3 in Moorea and 4 in Okinawa) nested in each $p\mathrm{CO}_2$ treatment. Treatment effects were assessed after 24 d in Moorea and after 21 d in Okinawa using linear extension as the dependent variable. Planned comparisons of differences between control and interspecific pairings in both the ambient and elevated $\mathrm{CO}_2$ treatments, for *M. aequituberculata* in Moorea and both corals in Okinawa, were selected to test explicitly for an effect of OA on the growth of corals engaged in interspecific competition. Planned comparisons were completed following Sokal & Rohlf (1995). The assumptions of normality and homoscedasticity required for the ANOVAs were evaluated through graphical analyses of residuals. SYSTAT 11 running on a Windows operating system was used for all analyses.

## RESULTS

### Competitive interactions on the reef

In Moorea, photoquadrats recorded in the back reef in 2010 showed that massive *Porites* spp. covered 12.6 ± 3.3 % of the benthos, and *Montipora* spp. covered 14.9 ± 2.1 % of the benthos (both mean ± SE, n = 71). Most (51 %) colonies of massive *Porites* (n = 296 colonies) and 40 % of the colonies of *Montipora* spp. (n = 379 colonies) were in contact with either intraspecific or interspecific colonies (*Montipora* spp. or massive *Porites* spp.), and were inferred to be competing for space. While it was not possible to identify *P. lutea* and *M. aequituberculata* to species in the photoquadrats, it is likely that the interactions between massive *Porites* spp. and *Montipora* spp. included many examples of interactions between *P. lutea* and *M. aequituberculata* because both are common in the back reef of Moorea (Bosserelle et al. 2014).

## Expt 1

All corals appeared to have fully recovered from manipulations after the recovery period, at least as evaluated by the absence of bleaching or tissue death, and the presence within 4 d of the $\mathrm{CO}_2$ treatments beginning of normal nighttime polyp expansion. Five corals showed signs of poor health during the experiment (pale tissue with algal growth), and were removed from the analysis. The rest of the *M. aequituberculata* colonies maintained a healthy appearance, and grew over their epoxy bases as well as towards the adjacent coral or dead coral skeleton (i.e. controls). The tissue of *P. lutea* adjacent to *M. aequituberculata* (but not the tissue of *M. aequituberculata*) became pale by the end of the experiment, though agonistic mechanisms (e.g. mesenterial filaments, and sweeper polyps) were not observed.

Analysis of seawater chemistry revealed that pH, $p\mathrm{CO}_2$, and $\Omega_{\mathrm{arag}}$ differed between treatments, but not between tanks, while temperature and $A_\mathrm{T}$ did not differ among tanks or between treatments (Table 1). Light intensity did not vary among tanks or treatments, with mean (±SE) values of 448 ± 44 $\mu$mol quanta m$^{-2}$ s$^{-1}$ in the ambient $p\mathrm{CO}_2$ treatment, and 451 ± 47 $\mu$mol quanta m$^{-2}$ s$^{-1}$ in the elevated $p\mathrm{CO}_2$ treatment (n = 5). Overall, the treatments contrasted ambient $p\mathrm{CO}_2$ at 388 ± 7 $\mu$atm with elevated $p\mathrm{CO}_2$ at 972 ± 9 $\mu$atm (mean ± SE, n = 45).

There was no overall effect of $p\mathrm{CO}_2$ on linear extension for *Montipora aequituberculata* (Table 2), with mean (±SD) values of 40 ± 7 $\mu$m d$^{-1}$ (n = 24) and 32 ± 9 $\mu$m d$^{-1}$ (n = 19) in ambient and elevated $p\mathrm{CO}_2$, respectively (Fig. 4). Neither the type of competitive pairing nor the interaction between $p\mathrm{CO}_2$ and competitive pairing affected linear extension (Table 2). Planned comparisons revealed that the linear extension was reduced for corals in interspecific pairings compared

Table 1. Parameters of carbonate chemistry in seawater during incubations in Moorea and Okinawa, with results of a 2-way nested ANOVA (between CO$_2$ treatments and among the tanks within CO$_2$ treatments) comparing conditions at each location. Experimental values are mean ± SE (n). SE was <0.01 for pH$_T$ and temperature ($T$) at both locations. Ambient $p$CO$_2$ target was 400 µatm, high $p$CO$_2$ target was 1000 µatm; df: degrees of freedom; $A_T$: total alkalinity; $\Omega_{arag}$: aragonite saturation state

| Parameter | $p$CO$_2$ treatment | | Between CO$_2$ treatments | | | Within CO$_2$ treatments | | |
| | Ambient | High | df | $F$ | p | df | $F$ | p |
|---|---|---|---|---|---|---|---|---|
| **Moorea** | | | | | | | | |
| $T$ (°C) | 28.3 (50) | 28.3 (50) | 1,4 | 0.499 | 0.480 | 4,104 | 0.978 | 0.323 |
| pH$_T$ | 8.05 (45) | 7.72 (45) | 1,4 | 404.201 | >0.001 | 4,270 | 0.934 | 0.445 |
| $p$CO$_2$ (µatm) | 388 ± 7 (45) | 972 ± 9 (45) | 1,4 | 1017.452 | >0.001 | 4,270 | 0.878 | 0.350 |
| $A_T$ (µmol kg$^{-1}$) | 2298 ± 2 (18) | 2297 ± 2 (18) | 1,4 | 0.186 | 0.667 | 4,104 | 1.123 | 0.292 |
| $\Omega_{arag}$ | 3.80 ± 0.03 (45) | 2.07 ± 0.05 (45) | 1,4 | 473.144 | >0.001 | 4,270 | 0.919 | 0.453 |
| **Okinawa** | | | | | | | | |
| $T$ (°C) | 26.8 (42) | 26.8 (42) | 1,6 | 0.187 | 0.667 | 6,364 | 0.003 | 0.959 |
| pH$_T$ | 8.03 (42) | 7.68 (42) | 1,6 | 10473.466 | >0.001 | 6,332 | 0.003 | 0.955 |
| $p$CO$_2$ (µatm) | 401 ± 1 (42) | 1016 ± 2 (42) | 1,6 | 6354.494 | >0.001 | 6,332 | 0.012 | 0.914 |
| $A_T$ (µmol kg$^{-1}$) | 2231 ± 1 (10) | 2232 ± 1 (10) | 1,6 | 0.554 | 0.457 | 6,364 | 0.178 | 0.673 |
| $\Omega_{arag}$ | 3.38 ± 0.01 (42) | 1.79 ± 0.01 (42) | 1,6 | 9011.305 | >0.001 | 6,332 | 0.009 | 0.924 |

to control pairing at ambient $p$CO$_2$, but not at elevated $p$CO$_2$ (Table 3). In ambient $p$CO$_2$, the mean rate of extension decreased 75% from 71.9 ± 18.5 µm d$^{-1}$ (n = 5) in the control pairings, to 17.7 ± 8.16 µm d$^{-1}$ (n = 7) in the interspecific pairings (Fig. 4).

## Expt 2

All corals appeared to recover from manipulations, with no sign of bleaching or tissue death following the recovery period (apart from tissue death as a result of competition), and the corals maintained a healthy color throughout the experiment. Full polyp expansion occurred at night for both species within 3 d of the treatments beginning, with polyps of *P. lutea* touching the polyps of the opposing colony in the intraspecific pairings. Colonies of *M. aequituberculata* regrew tissue over the exposed skeletons along the fractured edges of each fragment within 3–4 d of the incubations starting, and grew towards adjacent corals within 1 wk of the experiment beginning. For *P. lutea*, tissue grew over the edges where the colonies were cut, and at the competitive margin, although it did not fully overgrow the exposed skeleton facing away from the zone of interaction. In some cases, the tissue of *P. lutea* grew onto the acrylic tiles to which they were secured, and towards the competitors, within 10 d of the experiment beginning. In the interspecific pairings, colonies of *M. aequituberculata* extruded up to 20 mesenterial filaments (~3–4 mm long), that were applied to the tissue of the adjacent coral during the night, at least after the corals had grown within 2–3 mm of each other after

~7 d of incubation (Fig. 1b). Subsequently, colonies of *P. lutea* adjacent to *M. aequituberculata* showed signs of tissue paling and tissue necrosis where the mesenterial filaments had attacked the tissue. Agonistic structures were not observed for *P. lutea*.

The CO$_2$ system created stable conditions within the tanks (Table 1), and contrasted ambient $p$CO$_2$ at

Table 2. Comparison of linear extension (µm d$^{-1}$) in Moorea and Okinawa for *Montipora aequituberculata* and *Porites lutea*. Analyses were completed using a split-plot ANOVA with one between-plot effect ($p$CO$_2$) and one within-plot factor (pairing type). Tanks served as plots with 2 tanks nested within each combination of temperature and $p$CO$_2$; tank effects were removed from the model when they were not significant (p > 0.250). df: degrees of freedom; MS: mean sum of squares

| Coral taxon Effect | df | MS | $F$ | p |
|---|---|---|---|---|
| **Moorea** | | | | |
| *M. aequituberculata* | | | | |
| $p$CO$_2$ | 1 | 2.98 | 0.003 | 0.959 |
| Pairing type | 2 | 877.51 | 3.312 | 0.232 |
| $p$CO$_2$ × Pairing type | 2 | 264.91 | 0.253 | 0.783 |
| Residual | 24 | 1031.01 | | |
| **Okinawa** | | | | |
| *M. aequituberculata* | | | | |
| $p$CO$_2$ | 1 | 15435.25 | 11.142 | 0.016 |
| Pairing type | 2 | 5862.71 | 2.987 | 0.089 |
| $p$CO$_2$ × Pairing type | 2 | 1516.28 | 1.153 | 0.326 |
| Residual | 40 | 1315.62 | | |
| *P. lutea* | | | | |
| $p$CO$_2$ | 1 | 69.58 | 0.191 | 0.678 |
| Pairing type | 2 | 401.88 | 0.816 | 0.551 |
| $p$CO$_2$ × Pairing type | 2 | 492.20 | 1.364 | 0.293 |
| Residual | 40 | 171.74 | | |

Moorea Okinawa
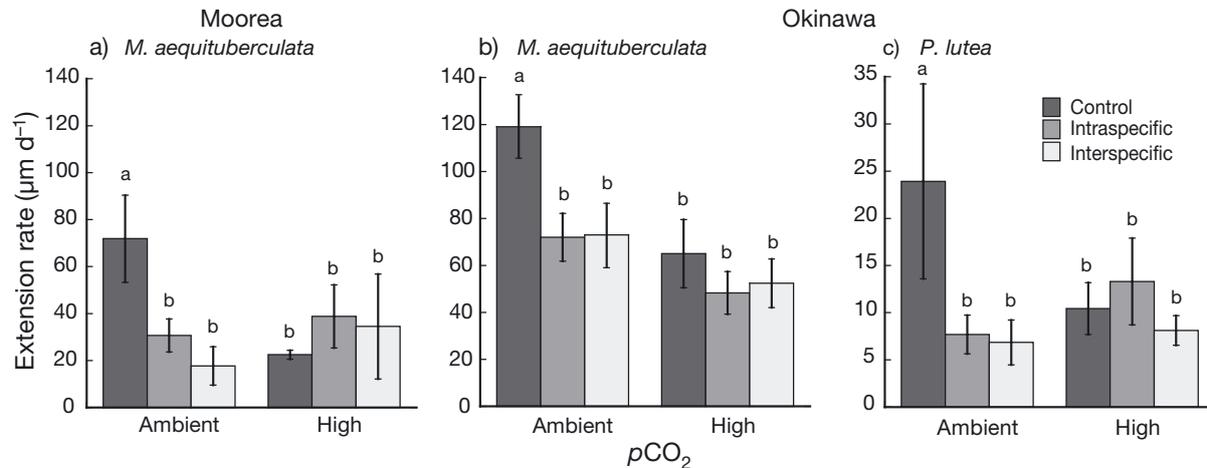


Fig. 4. Linear extension of fragments of *Montipora aequituberculata* and *Porites lutea* placed into competitive pairings (simulating interactions on the reef) and incubated in ambient (~400 µatm) or elevated $pCO_2$ (~1000 µatm). Expt 1 was conducted in Moorea during April 2013, during which pairings were incubated for 24 d; Expt 2 was conducted over 21 d in Okinawa in June 2013. (a) Linear extension of *M. aequituberculata* in Expt 1 (n = 4–6 for each bar). (b) Linear extension of *M. aequituberculata* and (c) linear extension of *P. lutea* (n = 8 for each bar) during Expt 2. Values are mean ± SE. Different letters indicate statistical differences between bars, as revealed by planned comparisons

Table 3. Planned comparisons of linear extension (µm d$^{-1}$) for *Montipora aequituberculata* and *Porites lutea* in Moorea and Okinawa. Planned comparisons of differences between control and interspecific pairings in the ambient and elevated $pCO_2$ treatments were completed according to Sokal & Rohlf (1995). df: degrees of freedom; MS: mean sum of squares

| Coral taxon Contrast | df | MS | F | p |
|---|---|---|---|---|
| **Moorea** | | | | |
| *M. aequituberculata* | | | | |
| Ambient | 1,24 | 8812.15 | 8.409 | <0.050 |
| Elevated | 1,24 | 325.01 | 0.310 | >0.050 |
| **Okinawa** | | | | |
| *M. aequituberculata* | | | | |
| Ambient | 1,40 | 8656.39 | 6.469 | <0.050 |
| Elevated | 1,40 | 638.57 | 0.477 | >0.050 |
| *P. lutea* | | | | |
| Ambient | 1,40 | 1164.45 | 6.780 | <0.050 |
| Elevated | 1,40 | 21.34 | 0.124 | >0.050 |

401 ± 1 µatm with elevated $pCO_2$ at 1016 ± 2 µatm. pH and $pCO_2$ differed between treatments, but not among the 4 tanks within each $CO_2$ treatment. $A_T$, temperature, and light intensity did not vary among tanks or between treatments, and mean (±SE) light intensities were 104 ± 7 µmol quanta m$^{-2}$ s$^{-1}$ in ambient $pCO_2$, and 102 ± 6 µmol quanta m$^{-2}$ s$^{-1}$ in the elevated $pCO_2$ (n = 65).

Linear extension of *M. aequituberculata* was affected by $pCO_2$, but not the pairing combinations, or the interaction between the 2 (Table 2). When linear extension was pooled among competitive pairings,

an effect of $pCO_2$ emerged (t = 2.283, df = 22, p = 0.032) with mean (±SE) extension decreasing 37 % at elevated $pCO_2$ (55 ± 6.3 µm d$^{-1}$) compared to ambient $pCO_2$ (88 ± 7.9 µm d$^{-1}$) (n = 24) (Fig. 4). Planned comparisons revealed a reduction in linear extension of corals in interspecific versus control pairings in ambient $pCO_2$, but not at elevated $pCO_2$ (Table 3). At ambient $pCO_2$, mean (±SE) rates of linear extension decreased 39 % from 119.3 ± 14.3 µm d$^{-1}$ in the control pairings, to 72.7 ± 14.5 µm d$^{-1}$ (n = 8) in the interspecific pairing (Fig. 4).

For *P. lutea*, linear extension was unaffected by $pCO_2$ (Table 2), with mean (±SE) values of 11.5 ± 3 µm d$^{-1}$ at ambient $pCO_2$, and 11.3 ± 2.4 µm d$^{-1}$ at elevated $pCO_2$ (n = 24, pooled among competitive pairings) (Fig. 4). Neither the type of competitive pairing nor the interaction between $pCO_2$ and competitive pairing affected linear extension (Table 2). Planned comparisons revealed a reduction in linear extension of corals placed in interspecific versus control pairings in ambient but not at elevated $pCO_2$ (Table 3). In ambient $pCO_2$, mean (±SE) extension decreased 72 % from 23.9 ± 10.3 µm d$^{-1}$ in the control pairings, to 6.9 ± 2.4 µm d$^{-1}$ (n = 8 for each) in the interspecific pairing (Fig. 4).

## DISCUSSION

In Moorea, there was no overall effect of $pCO_2$ or competitive pairings on *M. aequituberculata*, although under ambient $pCO_2$ linear extension in

interspecific pairings was reduced 75 % compared to controls. This effect disappeared, however, under high $pCO_2$ because the growth of corals in control pairings was greatly reduced, while corals in competitive pairings remained similar under both ambient and elevated $pCO_2$. In Okinawa, elevated $pCO_2$ depressed linear extension of *M. aequituberculata*, though control pairings accounted for 55 % of this effect. In contrast, there was no statistically significant effect of $pCO_2$ on linear extension of *P. lutea*. Our results suggest that OA has no effect on competitive interactions between these corals, at least when these were staged between small corals (or coral fragments) and evaluated over 21–24 d under laboratory conditions. One implication of this outcome is that the effects of OA on linear extension of at least some corals is likely to depend on whether they are engaged in competition with other corals. In our study, corals engaged in coral–coral competition were unaffected by OA, potentially because their growth rates were already depressed by competition, whereas those not in competitive encounters were strongly and negatively affected by OA.

While OA had no apparent effect on competitive interactions between *M. aequituberculata* and *P. lutea*, the corals responded differently to the treatments. *M. aequituberculata* in Okinawa was affected by $pCO_2$, while *P. lutea* in the same location was not. Though it is unclear why the 2 corals responded differently to elevated $pCO_2$, massive *Porites* (i.e. *P. lutea* and *P. lobata*) are tolerant of $pCO_2$ as high as 950 µatm (Fabricius et al. 2011, Edmunds et al. 2012). Conversely, although the effects of OA on *M. aequituberculata* have not been determined, at least one species in this genus (*M. capitata* in Hawaii) is susceptible to high $pCO_2$ (~750 µatm) (Jokiel et al. 2008). It is also possible that *M. aequituberculata* and *P. lutea* differ in their capacity to reduce skeletal density in order to maintain linear extension under conditions favouring reduced deposition of $CaCO_3$ (i.e. under OA). If correct, this hypothesis would suggest that *P. lutea* has a stronger capacity than *M. aequituberculata* to alter skeletal porosity in order to maintain linear extension. *Stylophora pistillata*, for example, exploits this strategy when growing at low pH (7.2), which results in depressed calcification, by increasing skeletal porosity (Tambutté et al. 2015). A similar trend has been reported for the temperate coral *Balanophyllia europaea* (Fantazzini et al. 2015).

Additionally, interpretation of the present results requires an appreciation of the limitations of using planar images (as in the present study) to evaluate linear extension. Critically, this method excludes the possibility of detecting treatment effects attributed to changes in 3-dimensional growth as occurs when corals increase in height. This limitation is unlikely to be important for *M. aequituberculata*, which forms encrusting colonies. However, for *P. lutea*, this limitation could be important as colonies of massive *Porites* grow faster in height than diameter. For example, massive *Porites* at 3–5 m depth on the Great Barrier Reef grow vertically at 13 mm yr$^{-1}$ but extend in radius by 11 mm yr$^{-1}$ (Lough & Barnes 2000). Future studies would therefore benefit from capturing 3-dimensional growth (i.e. both horizontal and vertical growth), as well as measuring mass deposition, for corals such as *P. lutea*.

Despite the different statistical outcomes for *M. aequituberculata* and *P. lutea* in Okinawa, the results for each coral (and *M. aequituberculata* in Moorea) follow similar trends, with interspecific competition depressing linear extension relative to controls under ambient but not elevated $pCO_2$ in all cases. The results suggest that OA does not modify competitive interactions among corals, although corals growing more slowly under OA would take longer to grow towards, and eventually encounter, potential competitors. Furthermore, OA did not prevent the extrusion of agonistic structures (i.e. mesenterial filaments) by *M. aequituberculata* when placed adjacent to *P. lutea*. The results presented here thus provide documentation of one mechanism, mesenterial filaments used by *Montipora* to damage *Porites* colonies, to support the classification of *Montipora* as dominant over *Porites* in some competitive hierarchies on coral reefs (Sheppard 1979, Dai 1990). Because extension rates of both corals were maintained at similar rates when they were placed in interspecific pairings under elevated $pCO_2$, it appears that the inhibitory effects of high $pCO_2$ on coral growth were alleviated when corals were adjacent (i.e. ~5 mm apart) to other corals and competitive interactions were initiated. It is therefore possible that the negative effects that competitive interactions often have on coral growth (examples in Chadwick & Morrow 2011) may have been alleviated by exposure to OA in the present study, at least in the early stages of competition that occurs within the first 21–24 d of coral–coral encounters. While it was beyond the scope of our study to test for the causal basis of this effect, it is likely that the mechanism(s) can be explained by 3 non-exclusive hypotheses.

(1) The decrease in growth of corals in competitive versus control pairings under ambient $pCO_2$ could reflect the way in which high $pCO_2$ affects coral tissues. Such an effect could operate through the meta-

bolic costs of competition (McCook et al. 2001), to which resources are allocated in a trade-off against the needs of other processes such as growth and reproduction (Rinkevich & Loya 1983). While the energetic costs of aggressive mechanisms have not been quantified in corals, trade-offs among multiple energy-requiring processes are well known in metazoans (Edmunds & Spencer-Davies 1986, Anthony et al. 2002), and among corals engaged in competition with other taxa, there are trade-offs in allocating energy to meet the costs of competition, which reduce energy allocation to growth and reproduction (Tanner 1997, Lapid & Chadwick 2006). Under an 'energy trade-off model' (sensu Stearns 1989) the lack of effect of competition on linear extension of *M. aequituberculata* and *P. lutea* under high $pCO_2$ (i.e. no difference between control and competitive pairings) implies that the putative energy limitation to which the trade-off applies has been removed. The negative effects of OA and competition on coral growth do not appear to be additive, as corals engaged in competitive interactions under OA were able to maintain the same rates of linear extension as under ambient $CO_2$ conditions. This outcome suggests that either the effects of OA or competition were removed, or attenuated, in intra- and interspecific pairings under OA.

Additionally, as competition among corals typically involves mechanisms associated both with their tissue (e.g. mesenterial filaments) and skeleton (i.e. linear extension), it is feasible that OA could modify competitive encounters by acting directly on their tissue as well as through the well-known effects on calcification (e.g. Doney et al. 2009). While it is unknown how OA affects key aspects of coral biomass, there is evidence that such effects could be important. For example, massive *Porites* responds to high $pCO_2$ (~800 µatm) with changes in biomass (Edmunds 2011), and shifts in the energy content of tissue characterize the response of at least 2 coral species to elevated $pCO_2$ (Schoepf et al. 2013). Moreover, there is indirect evidence that high $pCO_2$ (760 µatm) affects the protein metabolism of *Seriatopora caliendrum* (Edmunds & Wall 2014).

(2) The absence of an effect of OA on the growth of corals engaged in competition could reflect a direct consequence of the ways in which corals interact with one another. One way such effects could appear is through a small-scale modification of chemical conditions in the seawater between the colonies (see Anthony et al. 2013, Mumby & van Woesik 2014). Collectively, the corals in competitive pairings are likely to release more photosynthetically fixed car-

bon per volume of seawater (i.e. dissolved and particulate organic carbon; Muscatine et al. 1984) than the single corals placed in control pairings adjacent to carbonate rock. When placed within a few millimetres of another coral, as in the staged encounters employed in the present study, organic carbon released by the corals might be retained in the seawater between the juxtaposed colonies, and ultimately be exploited as a food resource by the corals themselves (Houlbrèque & Ferrier-Pagès 2009). Further, carbon released into the seawater could stimulate microbial metabolism (Kline et al. 2006) that has the potential to modify the chemical conditions (i.e. DOC and oxygen availability) in seawater between competing corals (Haas et al. 2011). The fixation of inorganic $CO_2$ through photosynthesis of the *Symbiodinium* within the coral tissue (Muscatine et al. 1981) may have further modified the seawater between competing corals, with $CO_2$ uptake causing a localized increase in seawater pH that could lessen the negative effects of OA on coral growth (see Anthony et al. 2013, Hurd 2015).

(3) Finally, the depressed linear extension rate of control corals at high $pCO_2$ could be a consequence of rapid growth itself, which might have enhanced sensitivity to OA (Comeau et al. 2014). In the study of Comeau et al. (2014), corals growing >1 mg cm$^{-2}$ d$^{-1}$ (i.e. 'fast' growers) were 44% more susceptible to high $pCO_2$ (between 380 and 1970 µatm) than corals growing <1 mg cm$^{-2}$ d$^{-1}$ (i.e. slow growers). The reasons for these effects are unknown, but it is possible that they reflect the quantity of protons that must be removed from the site of calcification (i.e. beneath the calicoblastic ectoderm) to support $CaCO_3$ deposition (McCulloch et al. 2012, Comeau et al. 2014). Massive *Porites* spp. was classified as a 'fast calcifier' by Comeau et al. (2014), and while they did not study *M. aequituberculata*, this species grows at 1.52 mg cm$^{-2}$ d$^{-1}$ at 1–3 m depth on the Great Barrier Reef (Browne 2012), which suggests it is also a 'fast growing' species (sensu Comeau et al. 2014). Although the deposition of $CaCO_3$ was not directly measured in the present study, if *M. aequituberculata* and *P. lutea* in the control pairings calcified at rates similar to those previously recorded (as in Browne 2012, Comeau et al. 2014), and ~2-fold faster than corals in competitive pairings (as evaluated by the linear extension; Fig. 2), then the corals in the control pairings in the present study effectively were fast growers relative to those in competitive pairings. Therefore, the control corals might have been more susceptible to high $pCO_2$ (sensu Comeau et al. 2014), thereby explaining why

their growth (but not corals in competitive pairings) was greatly depressed by our OA treatment. Additionally, the overall reduction in growth under high $pCO_2$ for *M. aequituberculata*, but not for *P. lutea*, may be explained by the higher intrinsic extension rates of *M. aequituberculata*.

An important assumption of the present analysis is that the linear extension of corals competing for 28 d is a good predictor of the outcome of coral–coral encounters occurring on the reef and playing out over many months. The initial stages of coral–coral encounters may, for example, change as the interactions mature, as the passage of time allows agonistic structures like sweeper tentacles to be produced (Chornesky 1989), and as the full suite of actions, re-actions, and competitive reversals (Chornesky 1989) culminates in a clear competitive winner. Clearly, experimental tests of the effects of OA on coral–coral competition must test for such effects over longer periods, but regardless of the outcome of such tests, the present results suggest that the early stages of these effects will not be affected by OA. Indeed, in terms of resistance to the effects of OA, there may be advantages for small corals to occur in aggregates in which competition for space occurs versus occurring as spatially isolated colonies.

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