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Stable Adult Growth but Reduced Asexual Fecundity in *Marginopora vertebralis*, under Global Climate Change Scenarios

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ABSTRACT: Large benthic foraminifera are an integral component of shallow-water tropical habitats and like many marine calcifiers, are susceptible to ocean acidification (OA) and ocean warming (OW). In particular, the prolific Symbiodiniaceae-bearing and high-magnesium calcite *Marginopora vertebralis* has a low threshold compared to several diatom-bearing and low-magnesium calcite species. In this multi-year mesocosm experiment, we tested three RPC 8.5 climate change scenarios (i) present day, (ii) the year 2050, and (iii) 2100. To enable a realistic epiphytic association, these experiments were uniquely conducted using natural carbonate substrate, living calcifying alga, and seagrass. In contrast to previous studies, we detected no reduction in surface-area growth under future climate conditions compared with present day conditions. In terms of calcification, *M. vertebralis*' epiphytic association to primary producers (i.e., calcifying algae and seagrasses) potentially ameliorates the effects of OA by buffering against declines in boundary layer pH during periods of photosynthesis (i.e., CO_2 removal). Importantly for population maintenance, we observed a strong reduction in asexual fecundity under the 2100 scenario. We propose the additional energy needed to maintain growth might be one reason for drastically reduced asexual reproduction. An alternative explanation could be that the 2 °C temperature increase interfered with the environmental synchronization that triggered asexual multiple fission. We conclude that the low levels of reproduction will reduce populations in a high CO_2 environment and reduce a valuable source of $CaCO_3$ sediment production.
KEY WORDS: mesocosm experiment, ocean acidification, ocean warming, large benthic foraminifera, carbonate production, tropical reef, asexual reproduction, climate change.

0 INTRODUCTION

The large benthic foraminifera genus *Marginopora* Quoy & Gaimard, 1830 (Family Soritidae) is present throughout the Indo-Pacific Ocean and Temperate Australasian marine realms (Hayward et al., 2021). They are known to inhabit reef zones from intertidal and lagoons to the outer margins between a depth of 0–45 m (Hayward et al., 2021) and typically have an epiphytic association with seagrass, turf algae, and coral rubble. Population density can reach up to 100 individuals/m^2 (Ross, 1972) or the equivalence to 300 g/m^2 $CaCO_3$ (Doo et al., 2017; Langer et al., 1997) making *Marginopora* spp. one of the most prominent shallow-water carbonate-producing foraminifera in the tropics. Similar to corals, *Marginopora* spp. host unicellular dinoflagellate algae (Momigliano and Uthicke, 2013; Garcia-Cuetos et al., 2005), which contributes to their ability to produce large $CaCO_3$ exoskeleton (test) (e. g., Lee and Hallock, 1987). The flat disc-shaped tests range from 0.2 to 300 mm^3 (Hayward et al., 2021; Ross, 1972), while fossilised Soritidae are known to have grown to 500 mm^3 (Beavington-Penney and Racey, 2004). The porcelaneous high-magnesium calcite exoskeletons are the most soluble $CaCO_3$ polymorph (12.5%; Chave, 1954), rendering the dinoflagellate-bearing porcelaneous LBF families, such as Soritidae, the most vulnerable to climate change and, in particular, to ocean acidification (OA) (Doo et al., 2014; Reymond et al., 2013).

Results from previous studies investigating the response of *Marginopora* spp. to OA and ocean warming (OW), alone or in combination with other stressors, were not always consistent (Table 1). The photobiology (photosynthetic yield, chlorophyll content, or oxygen production) and calcification (surface-area growth rate and alkalinity anomaly) of *Marginopora* spp. have both indicated a general negative response to OW and OA (as reviewed in Narayan et al., 2022). The calcification threshold for *Marginopora* spp. is considered to be pH_{total} ~7.9 or pCO_2 ~800–900 μatm (Naidu et al., 2017; Sinutok et al., 2014, 2011;

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Reymond et al., 2013; Uthicke and Fabricius, 2012). These laboratory and field studies on *Marginopora* spp. include the use of recirculation, flow-through, or closed system, in addition to onboard (vessel) and natural CO_2 vent experiments. Reduced calcification was assumed to be the cause for the absence of *Marginopora* spp. near the Papua New Guinea CO_2 vents (Uthicke et al., 2013, 2012; Fabricius et al., 2011). Below pH_{total} 7.9 one study found that Mg-ATPase activity was inhibited but resulted in no growth difference compared to ambient conditions (Prazeres et al., 2015), while another study measured a 63% growth rate increase when exposed to extremely low pH_{total} <7.5 (pCO_2 ~1 925 μatm) compared to ambient conditions (Vogel and Uthicke, 2012), indicating a possible parabolic trend to OA. Short-term temperature peaks above 31 or 32 °C cause an inhibiting and destabilising effect on the photosymbionts of *Marginopora* spp. (Uthicke et al., 2012; van Dam et al., 2012). While, Schmidt et al. (2014) and Sinutok et al. (2014) found negative synergistic interactions between increased pCO_2 (between ~790 and 1 000 μatm) and temperature (above 31 or 32 °C) for photosynthetic yield (*Fv*/*Fm)*, chlorophyll content (Chl *a*), or oxygen production (O_2). Overall, in isolation or in combination, the effects of global change will likely impair the health and survivorship of *Marginopora* spp.

Reproduction exerts a strong influence on the adaption,

Table 1 Summary of the known responses of *Marginopora* spp. to different experimental methodologies and parameters

Collection location	Experimental conditions	Methods	Responses	References
Heron Is. GBR, Australia 0.3 mwd	Recirculated SW_A mesocosms, 5 wk *T*: 28, 30, 32, 34 °C pCO_2: 350 (pH 8.1), 650 (pH 7.9), 1 000 (pH 7.7), 2 400 (pH 7.4) Irradiances: 300	Calcification: Buoyant weight Photobiology: O_2 microsensors PAM	Calcification: Negative effect in elevated pCO_2 and *T*; high mortality in elevated pCO_2 (>1 000) and *T* (>30 °C) Photosynthetic capacity: Negative O_2 concentrations profile in elevated pCO_2 and *T*; negative Chl *a* and Chl c_2 levels in elevated pCO_2 and elevated *T*	Sinutok et al. (2011)
Milne Bay, Papua New Guinea 0.5–5 mwd	*In situ* volcanic CO_2 vents Point measurements *T*: 23–29 °C (annual range) pCO_2: 290–950 (pH 8.1–7.8) Irradiances: ~12	Population: Abundance appearance	Population: Low to no abundance close to the CO_2 vents (elevated pCO_2); evidence of corroded tests close to CO_2 vents (~pH 7.8)	Fabricius et al. (2011)
Whitsunday Is. and Orpheus Is. GBR, Australia 5 mwd	*In situ* transplants and SW_F closed-aquarium, 5–6 wk *T*: 22 and 28 °C pCO_2: 380 (pH 8.1) +0.2 μM DIP; +2 μM DIN Irradiances: 6–9	Calcification: Surface-area	Calcification: Reduced growth in elevated *T* (28 °C) and nutrients (DIN and DIP)	Reymond et al. (2011)
Milne Bay, Papua New Guinea Orpheus Is. GBR, Australia <1 mwd	*In situ* volcanic CO_2 vents and transplants* Point measurements *T*: ~28–30 °C pCO_2: <500 (>pH 7.95), ~420–2 300 (pH 8.01–7.36) Irradiances: ~12	Calcification: Surface-area Photobiology: O_2 microsensors PAM Population: Abundance reproduction	Calcification: Negative growth rate in elevated pCO_2 (16%–30% reduction) Photobiology: Positive net O_2 production in elevated pCO_2 (55%–150% greater) Population: No populations in elevated pCO_2 (>pH 7.95) zones; densities in control pCO_2 where >thousand individuals m^{-2}; reproduction was only observed in ambient conditions	Uthicke and Fabricius (2012)
Orpheus and Lizard Is. GBR, Australia 2–4 mwd	Flow-through SW_F incubations plates, 96 h *T*: 26; 28; 30; 32; 34 °C Diuron: 0.1 or 3 μg L^{-1} Irradiances: 10	Photobiology: Spectrometer cell count PAM	Photobiology: *T* and diuron inhibited quantum PSII; no significant effect of diuron on Chl *a*; reduced Chl *a* concentration in elevated *T*	van Dam et al. (2012)
Orpheus Is. GBR, Australia <2 mwd	Flow-through SW_F incubation plates, 6 wk *T*: 27 °C pCO_2: 470 (pH 8.1); 780 (pH 7.9); 1 170 (pH ~7.7); 1 660 (pH 7.5) Irradiances: ~30	Calcification: Surface-area and weight Photobiology: O_2 microsensors spectrometer cell count PAM	Calcification: No significant difference in elevated pCO_2 Photobiology: No significant effect on O_2, Chl *a* or PS II in elevated pCO_2	Vogel and Uthicke (2012)
Heron Is. GBR, Australia 30 mwd	Closed-aquariums SW_F, 5 wk *T*: 25 °C pCO_2: 380 (pH 8.1); 700 (pH 7.8); 1 100 (pH 7.6) +0.2 μM DIP; +2 μM DIN Irradiances: between 45–50	Calcification: Surface area Photobiology: O_2 microsensors spectrometer cell count	Calcification: Reduced interactive effect in elevated pCO_2 with DIN or DIP Photobiology: No significant difference to P : R in elevated pCO_2; negative effect on P_{gross} in elevated pCO_2; decreased cell count and increased Chl *a* in elevated DIN and pCO_2	Reymond et al. (2013)

Table 1 Continued

Collection location	Experimental conditions	Methods	Responses	References
Orpheus Is. GBR, Australia 0–1 mwd	Flow-through SW_F incubation plates, 7.5 wk *T*: 28 and 31 °C pCO_2: 490 (pH 8.1); 790 (pH 7.9) Irradiances: 100–140	Calcification: Surface-area Photobiology: O_2 microsensors PAM	Calcification: Negative synergistic interaction in elevated pCO_2 and *T*; no individual factor effect in elevated pCO_2 or *T* Photobiology: Reduced O_2 production in elevated pCO_2 and *T* (synergistic interaction); increased O_2 production in elevated pCO_2; reduced O_2 production in elevated *T*; reduced Chl *a* in elevated pCO_2 and *T* (synergistic interaction); reduced Chl *a* in elevated *T*; increased Chl *a* in elevated pCO_2	Schmidt et al. (2014)
Heron Is. GBR, Australia 0.3 mwd	Recirculated SW_A aquariums, 5 wk *T*: 28 and 32 °C pCO_2: 400 (pH 8.1) 1 000 (pH 7.7) Irradiances: 150	Calcification: Buoyant weight Photobiology: O_2 microsensors PAM	Calcification: Increased calcification in control pCO_2 and elevated *T*; reduced calcification in elevated pCO_2 and control *T*; reduced calcification in elevated pCO_2 and *T* Photobiology: Negative O_2 profile in elevated pCO_2, and *T*; reduced Chl *a* in elevated pCO_2 and *T*; no effect of Chl c_2 in elevated pCO_2 and *T*	Sinutok et al. (2014)
Green Is. GBR, Australia <1 mwd	Flow-through SW_F aquariums, 4 wk *T*: 24 °C pCO_2: 430 (pH 8.15); 2 015 (pH 7.63) Irradiances: 40	Calcification: Buoyant weight Surface-area Density Biochemical: Ca- Mg-ATPase	Calcification: No effect on surface-area, buoyant weight, or density in elevated pCO_2 Biochemical: No effect on Ca-ATPase activity in elevated pCO_2; Mg-ATPase activity inhibition in elevated pCO_2	Prazeres et al. (2015)
Makuluva and Nukubuco reefs, Fiji <1 mwd	Flow-through SW_F aquariums, 11 wk *T*: 27 °C pCO_2: 310 (pH 8.1); 740 (pH 7.8); 1 700 (pH 7.5) Irradiances: ~190	Calcification: Wet weight Surface area Population: Reproduction	Calcification: Reduced weight and surface-area in elevated pCO_2 (>740) Population: Reproduction was only observed in the control treatment	Naidu et al. (2017)
Lizard Is. GBR, Australia 1–3 mwd	Flow-through SW_F incubations, 2 wk *T*: 26 and 29 °C pCO_2: ~1 000 (pH 7.7) Host algae Irradiances: ~100	Calcification: Wet weight Total alkalinity Photobiology: O_2 microsensors cell count PAM	Calcification: Reduced weight in elevated pCO_2 without host algae; no weight difference in elevated pCO_2 with host algae; no different in weight in elevated *T*, with or without host algae; increased dissolution in elevated *T*, ambient and elevated pCO_2 and without host algae Photobiology: Reduced Chl *a* in elevated pCO_2 without host algae; increased Chl *a* in elevated *T* without host algae; decreased O_2 production in elevated *T* without host algae; increased O_2 production and respiration with host algae; decreased O_2 respiration in elevated *T* and without host algae reduced *Fv*/*Fm* in elevated pCO_2 and *T* with host algae; increased *Fv*/*Fm* in elevated pCO_2 with host algae	Doo et al. (2020)
Fantome Is. GBR, Australia 5–10 mwd	Mesocosms SW_F, 2 yr *T*: 26, 27, 28 °C pCO_2: 400 (pH 8.06); 680 (pH 7.9); 940 (pH 7.8) Irradiances integrals: 4.5	Microbiome: DNA sequences	Microbiome: Adults specimens had a reduced abundance of oxyphotobacteria in elevated pCO_2 and *T*; juveniles had a reduced abundance of Proteobacteria in elevated pCO_2 and *T*	Botté et al. (2020)

To date, most studies have focused on local (eutrophication and herbicides) and global (rising temperature and lowering carbonate saturation) stressors. All studies worked on the shallow-water species except the deeper dwelling of *M. rossi* (Reymond et al., 2013). There is a need to clearly distinguish the taxonomy of *Marginopora* spp. as there are likely more cryptic species (e.g., Renema, 2018; Lee et al., 2016; Pawlowski and Holzmann, 2008). pCO_2 values are given in micro-atmospheres (µatm) and are rounded values; mwd, meters water depth; irradiances are given as µmol photons $m^{-2} \cdot s^{-1}$ and set to a 12 h : 12 h light : dark cycle for aquariums experiments; irradiances integrals, photons $m^{-2} \cdot d^{-1}$; PAM, Pulse Amplitude Modulated fluorometry; GBR, Great Barrier Reef; Chl, chlorophyll; PS II, photosystem two; P, photosynthesis; P : R, ratio of photosynthesis to respiration; SW_F, filtered natural seawater; SW_A, artificial seawater; DIP, dissolved inorganic phosphorous (KH_2PO_4); DIN, dissolved inorganic nitrogen (KNO_3); *T*, temperature in °C; h, hours; wk, weeks; yr, years; salinity among all studies ranged between 33 and 36. *Large natural variation across all experiments from the various locations.

diversification, and evolution of organisms (Nilsson and Svensson, 1996; Kirkwood and Rose, 1991). Sexual and asexual reproduction is known to be widespread among protists, of which the life-cycle of foraminifera is one of the most varied (reviewed in Mirzaghaderi and Hörandl, 2016; Goldstein, 1999). For example, obligatory alternating generations, trimorphism, apogamic, binary fission, budding, nuclear dimorphism, and test dimorphism life-cycles have all been described among foraminifera (reviewed in Beavington-Penney and Racey, 2004; Goldstein, 1999). The mode of reproduction has a major influence on the flow of genetic material throughout the population and the acclimatization to local environmental conditions (Weinkauf et al., 2020). Most LBF reach reproductive maturity after 6 – 12 months and commonly longer depending on the growth rate, for example Ross (1972) proposed that *M. vertebralis* needs to be 5–12 mm in diameter before producing ~60–150 offspring. Under optimal environmental conditions this usually occurs during late spring (Fujita et al., 2000; Ross, 1972).

Growth rate and mode of reproduction have a major influence on population genetics and the potential for local morphological and physiological adaptation. We conducted a multi-year mesocosm experiment in a near natural mesocosm setup as described in Uthicke et al. (2020) to understand the growth and reproduction potential of *Marginopora vertebralis* to projected RCP 8.5 ocean warming (OW) and acidification scenarios (OA) for 2050 and 2100 (Meinshausen et al., 2011). The aims of this study are (1) to measure the effect on adult growth (calcification) under combined OW and OA in a near natural mesocosm system, and (2) to determine the influence of projected climate change scenarios on the reproductive success of *M. vertebralis* to OW and OA. Understanding the combined effects of global threats can guide policies, legislations, and management directives to prioritise a stronger and more coordinated approach to build environmental, economic, and social resilience to anticipated changes associated with coastal marine systems (e.g., Galdies et al., 2020).

1 METHODOLOGY AND DATA

1.1 Collection and Acclimatization

Marginopora vertebralis were collected during two subsequent years from Fantome Island (Great Barrier Reef, Australia, 18°41′8″S; 146°30′44″E), from depths between 1–3 m. Most of the specimens were epiphytic on *Halimeda opuntia*, with the calcifying alga also included in the mesocosm system. In the first year, the collection was conducted on February 20, 2016 and the Foraminifera were added into the experimental system on March 9, 2016 (17-day acclimation period). In the second year, samples were collected on May 25, 2017 and added into the experimental system on May 30, 2017 (4-day acclimation period). All specimens were collected by SCUBA divers and maintained in ambient seawater conditions prior to being placed in acclimation tanks (working volume 250 L) in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS, Townsville). Before entering the experimental conditions, all *M. vertebralis* specimens were stained for 24 h in calcein (10 $mg \cdot L^{-1}$), a fluorochrome marker (Fig. 1a), which becomes embedded in newly precipitated $CaCO_3$ (Bernhard et al., 2004). Subsequent to calcein staining, 100 – 150 *M. vertebralis* specimens were placed into the shallow 'B' tanks of each mesocosm system with access to *H. opuntia* (Fig. 1b) and natural habitats (Fig. 1c).

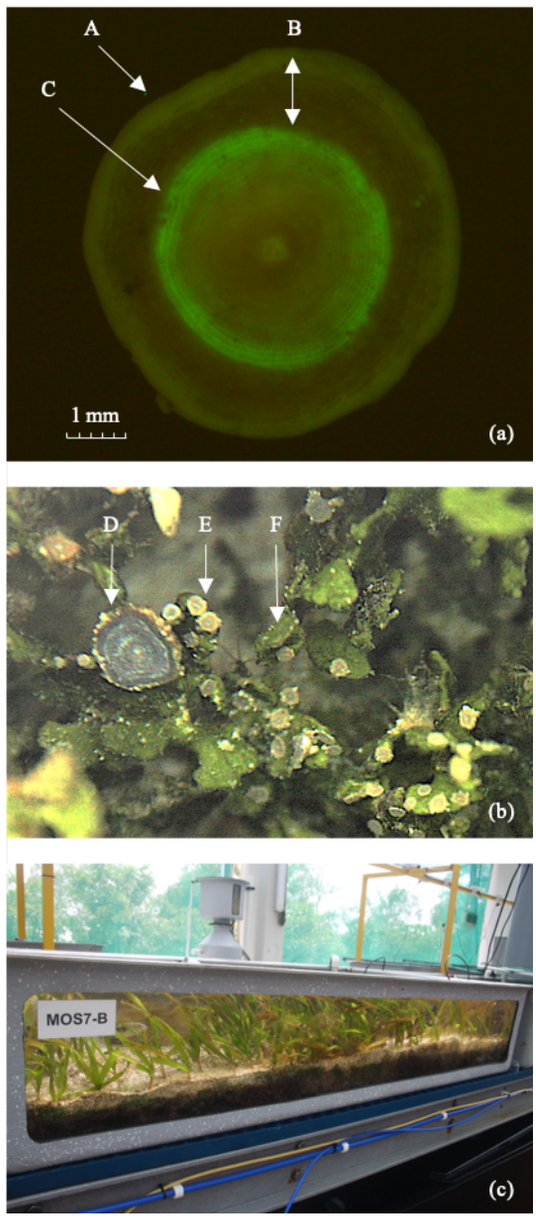

Figure 1. (a) An example of a calcein stained *Marginopora vertebralis*; A indicates the recently calcified outer rim of the disc-shaped foraminifera; B is the calcified area during the experiment; and, C the bright green area demarks the size of the foraminifera at the time of staining and indicates the start of the experiment. (b) An image inside the mesocosm; D points to an epiphytic adult *M. vertebralis* (~9 mm in diameter); E indicates juveniles (2–3 mm diameter); and, F points to the green alga *Halimeda opuntia*, which was also part of the benthic community. (c) One of the outdoor mesocosm aquaria (78 cm × 142 cm × 28 cm).

1.2 Mesocosm System and Treatment Levels

A detailed description of the outdoor mesocosm system can be found in Uthicke et al. (2020). In summary, nine independent flow-through mesocosm tanks (78 cm × 142 cm × 28 cm) replicated the natural habitat of the shallow-water reef where

the foraminifera were collected, and included corals (*Platygyra daedalea*, *Acropora* spp.), sponges (e.g., *Carteriospongia foliascens*), echinoderms (*Echinometra* sp. A, *Linkia laevigata*, and *Holothuria atra*), seagrasses (e.g., *Cymodocea* sp.), green alga (*Halimeda opuntia*), along with carbonate sediment. Three replicate tanks simulated water temperature and pCO_2 levels projected for 2050 (+1 °C and 670 µatm), another three projected for 2100 conditions (+2 °C and 900 µatm), following RCP 8.5 projections (Meinshausen et al., 2011), and three represented the control treatment held at ambient conditions (a summary of the experimental parameters is described in Table S1). To simulate natural pCO_2 diel variation, which is greater than seasonal variation, the target pCO_2 was set to ±60 ppm as observed from the southern Great Barrier Reef (Shaw and McNeil, 2014). The mesocosm temperatures followed seasonal and annual trend-based averages from Davies Reef, a mid-shelf reef in the GBR, which range from 23.4 °C during winter to 28.3 °C during summer (AIMS data centre from 1991 to 2012, which is available at: https://apps.aims.gov.au/metadata/view/38f2c8ae-bdab-47fe-99fe-2b4513938fa5). Throughout both experiments, the measurements of pCO_2, temperature, and light were logged continuously (Fig. 2), while weekly water samples were collected to monitor dissolved inorganic nutrients and the carbon chemistry (dissolved inorganic carbon and total alkalinity). Summary of the target and measured experimental conditions is given in Table S1. In particular, the average recorded temperature for each pCO_2 treatment varied between experiments but it did reflect the natural seasonal variation and was maintained at ambient, +1, and +2 °C above ambient values (detailed in Table S1). The full details of the nutrient and seawater carbonate chemistry analysis can be found in Uthicke et al. (2020). The Mesocosm Outdoor System (MOS) was covered by a clear polymethyl methacrylate (PMMA) roof, which allowed natural sun and the full visible light spectrum and UV component into each mesocosm. Irradiance was reduced to emulate GBR mid-shelf reef lighting levels of approximating 2–5 m water depth. Each MOS contained a PAR sensor (LiCOR), which logged the light intensity data every 20 seconds. Based on those measurements, the daily light integral (DLI) was calculated.

1.3 Growth Measures and Offspring Asexual Reproduction

The first experiment in 2016 finished after 5.5 months (all specimens were recollected from the mesocosm between August 23 and September 7, 2016), while the second experiment ended after 4.5 months (all specimens were recollected between October 10–17, 2017). All living specimens of the adult population were collected, washed in freshwater, air dried and photographed under a fluorescent microscope (Leica DMI6000 B inverted microscope equipped with I3 filter cube). Initial size, final size, and growth were then calculated from area measurements using ImageJ or Photoshop software. Growth (daily percentage of growth) was calculated from the initial size (area from the nucleus to the outer calcein stain) and size when removed from the experiment (total area) using the equation given in ter Kuile and Erez (1984). During collection at the end of the experiment, in both years many specimens asexually reproduced. After multiple fission the parent specimens were subsequently found bleached and dead. To quantify reproduction in the second year, we counted the total number of juveniles (<3 mm) and adults on October 10, 2017. This was achieved by two observers spending at least 30 min at each mesocosm, carefully removing and searching all *Halimeda opuntia* alga, followed by a search of the sediment surface. Prior to that, we scored presence of juveniles six times over 2.5 months into broad categories after checking each aquarium for at least 10 min with two experienced observers. Categorical reproductive index scores were scored on five occasions in August and September 2017: 0. no juveniles detected, 1. few present (<5), 2. some present (5–40), 3. many (40–100), 4. >100.

1.4 Statistical Analyses

The combined effects of climate change scenarios (OA and OW) on calcification and reproduction were tested using Linear Mixed Effects Models (LMER). The three climate scenarios, ambient, 2050, and 2100, were fixed variables, whereas individual mesocosms were regarded as random variables. Binomial models were used to test for significant differences in the probability of foraminifera reproducing depending on the climate change scenario. When applicable, posthoc Tukey's comparisons were performed to understand the differences among individual treatments. Analyses were performed in R (R Core Team, 2020) using libraries lme4 (Bates et al., 2015) and multicomp (Hothorn et al., 2008).

2 RESULTS

2.1 Mesocosm Outdoor System (MOS) Physio-Chemical Parameters

Throughout the two experimental periods, temperature and pCO_2 remained constant and met the target value outlined in Table S1. The pCO_2 values throughout both experiments remained at 410 ppm (±50 ppm), 685 ppm (±50 ppm), and 940 ppm (±50 ppm) for the control, 2050, and 2100 treatments, respectively. Due to a computer glitch in the first two months of the first experiment, the temperatures did not adjust to the daily ambient averages but remained at the level of the start of the experiment. However, the temperature was within the expected seasonal range and difference between treatments remained at target levels of +1 and +2 °C above ambient temperatures (Fig. 2). Daily light integrals showed a diurnal and seasonal fluctuation between 0–10 mol $m^{-2}d^{-1}$ but no difference between treatments. Dissolved inorganic nutrients (NO_2, NO_4, NH_4, PO_4 and SiO_4) remained within expected mid-shelf concentration levels (Table S1).

2.2 *Marginopora vertebralis* Growth Rate between Climate Change Treatments

The number of *M. vertebralis* found with a tag and measured in both years is given in Table S2. Based on surface-area increase, the daily growth rate of *M. vertebralis* did not vary significantly between treatments during the experiment in 2016 ($p = 0.338$, df = 2, $X^2 = 2.17$) nor in 2017 ($p = 0.557$, df = 2, $X^2 = 1.17$). Growth rates during the first experiment in 2016 ranged between 0.4%–0.7% d^{-1} (total average = 0.63% d^{-1}, SD = 0.24 % d^{-1}) during the second experiment in 2017, growth rates ranged between 0.1%–0.3% d^{-1} (total average = 0.27% d^{-1}, SD = 0.20% d^{-1},Fig. 3). There was a significant negative relationship between initial size of the foraminifera and the total area

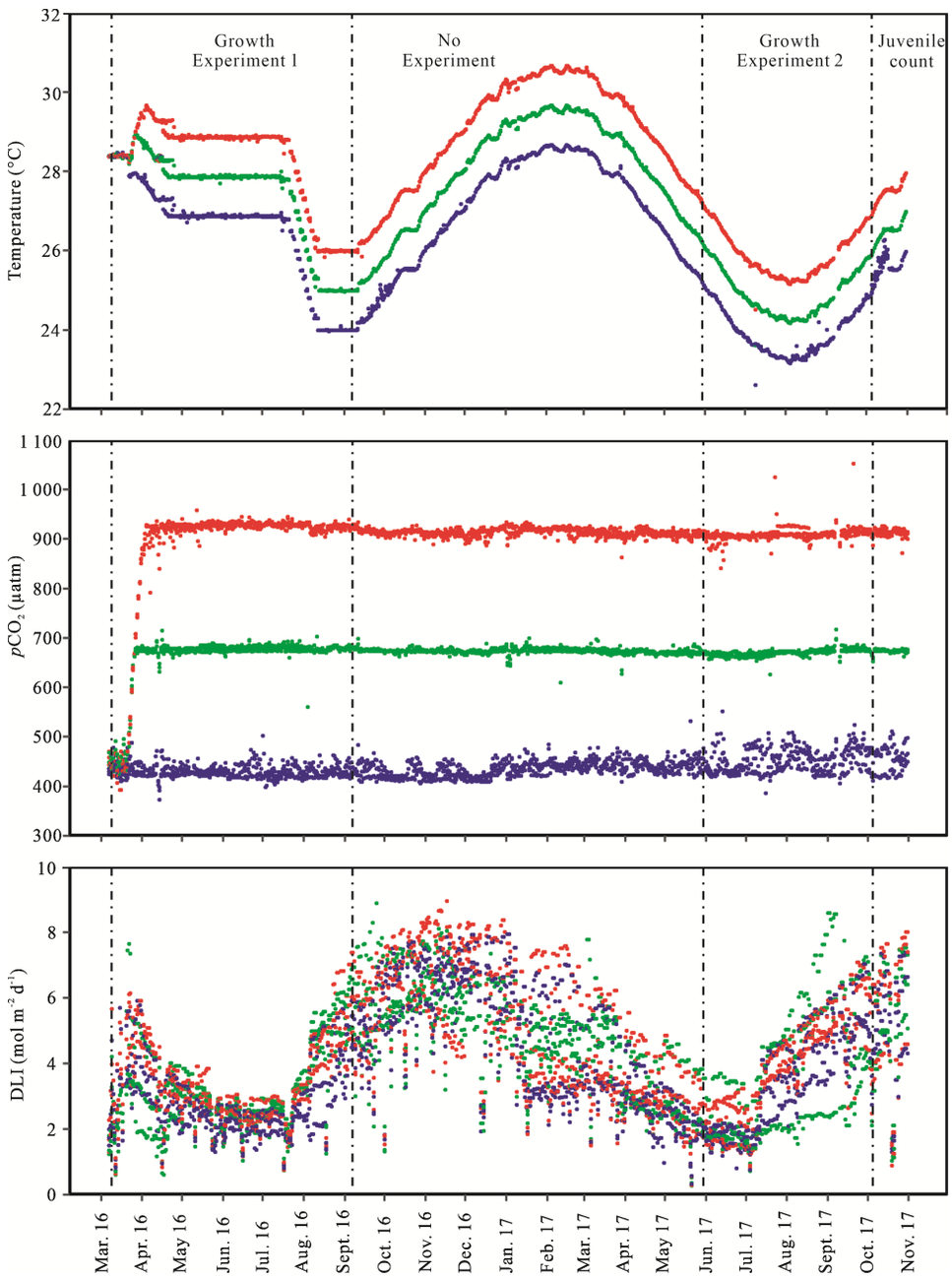

Figure 2. Environmental parameters in the mesocosm outdoor system. Red points indicate data collected from the three replicate 2100 scenario, green points are from the three replicate 2050 scenario, and blue is the three control replicates. The vertical dash lines indicate the start and end of experiments (N = 3 per treatment). DLI. Daily Light Integral.

change at the end of the experiments, which was not affected by treatment (linear model, $F_{1, 311} = 95.10$, $p < 2.2 \times 10^{-16}$, adjusted $R^2 = 0.23$, Fig. 4). In 2016, Growth Experiment 1 was started in mid-March, with foraminifera on average 18.07 mm^2 (SD = 7.25, N = 221). In 2017, Growth Experiment 2 was started in mid-May when *M. vertebralis* were on average larger 38.78 mm^2 (SD = 11.98, N = 92).

2.3 Fecundity in Early Austral Spring

Towards the end of both experiments multiple fission of juveniles from the mother cells were observed in the early austral spring (August) (Fig. 1b). Juveniles were pigmented while still attached to a bleached section of the mother cell, indicating that there was a vertical transfer of photosymbionts (Symbiodiniaceae) from the mother cell to the juveniles. The mother cells eventually became entirely bleached and died. As this was an unexpected event, juveniles were not scored at the end of the 2016 experiment, however at the end of the second growth experiment juveniles were scored to test the effect of climate change scenarios on fecundity.

From the first occurrence of multiple fission on August 3, 2017, the categorical index scores were consistently higher in the 2050 treatment (total average 3.8) and the control (average 1.7) compared with the 2100 treatment (average 0.7). This trend was constant for 6-weeks leading up to the termination of the experiment on October 17, 2017 (Table 2). The total aver-

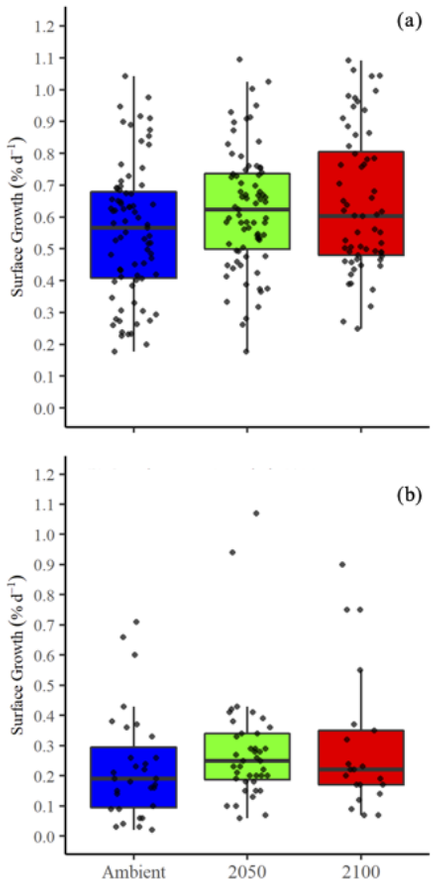

Figure 3. Surface-area growth rate of adult *Marginopora vertebralis* from the long-term mesocosm study. Box plots indicate the data range, 95% confidence intervals, and means for each treatment. (a) Growth Experiment 1 in 2016 for ~5.5 months. (b) Growth Experiment 2 in 2017 for ~4.5 months.

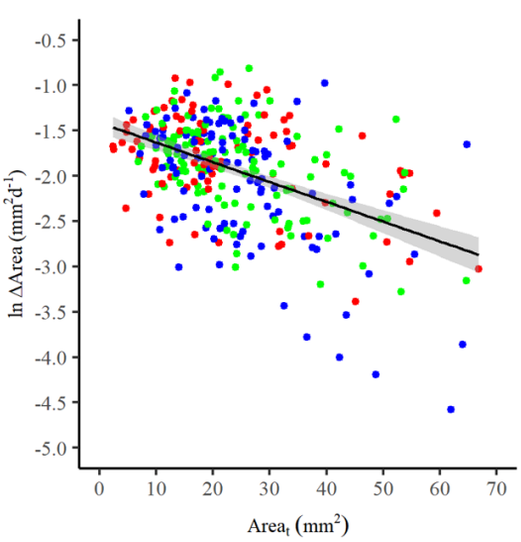

Figure 4. Growth of *Marginopora vertebralis* in the two experiments with respect to the initial size shown on the x-axis. Colours indicate the three treatments (blue points, ambient; green points, 2050 scenario; and red points, 2050 scenario). The black line depicts a linear model fit through all data points (irrespective of treatment and year), the grey band depicts the standard error ($F_{1, 311} = 95.10$, $p < 2.2 \times 10^{-16}$, adjusted $R^2 = 0.23$).

age score of the 2100 treatment was nearly 5.4 times lower than in the 2050 treatment and 2.4 times lower than in the control treatment. Overall there were more juveniles detected in the 2050 treatment, whereas two replicates systems in 2100 had almost no juveniles. All juveniles and remaining live adults were fully counted between October 10–17, 2017. Binomial models demonstrated significant differences in the probability of the occurrence of juveniles ($X^2 = 12.12$, df = 2, $p = 0.002\,3$, Fig. 5). Posthoc comparisons reveal that the probability of an individual being a juvenile was significantly smaller in the 2100 treatment group when compared to the control ($p = 0.003$) or 2050 ($p = 0.020$). There was no significant difference between the control and the 2050 treatment ($p = 0.612$).

3 DISCUSSION

Large benthic foraminifera are the most important calcifying microorganism within tropical marine shallow-water environments. Their densities can reach into the thousands per m^2 and produce up to 10 000 g m^{-2} yr^{-1} $CaCO_3$ locally (e.g., One tree Island, GBR, Doo et al., 2017; the Marshall Islands, Fujita et al., 2009). Similar to many other calcifying marine organisms, LBF are considered threatened by the adverse influence of rising temperature and atmospheric CO_2, alongside other compounding local factors such as, eutrophication, sedimentation, and sewage discharge (reviewed in Narayan et al., 2022; Reymond et al., 2012). The multi-year mesocosm experiments presented in our study give a holistic understanding of the potential impacts of future OW and OA on LBF $CaCO_3$ productivity and fecundity.

3.1 Methodological Considerations

Within the past decade, a number of experimental and observational studies have been conducted on *Marginopora* population (*M. vertebralis* and *M. rossi*) from the central Indo-Pacific (Table 1). The majority of these studies focused on the singular or combined effects of elevated temperature, pCO_2, and/or nutrients to calcification and photobiology of the holobiont. Only one study has investigated the short-term (96 h) impacts of a common pesticide (Diuron), which was found to disrupt photophysiological productivity (van Dam et al., 2012). Typically, these experiments were conducted over a 1–2 month period by placing single species within closed or reticulation aquariums or modified cell plates, while few studies have conducted *in situ* observation, measures, and transplant experiments (Uthicke et al., 2013; Uthicke and Fabricius, 2012; Fabricius et al., 2011; Reymond et al., 2011). One previous short-term study investigated calcification and photobiology performance in association with a host alga (Doo et al., 2020), however the present study is the first to quantitatively record growth rate and fecundity under mesocosm conditions with the epiphyte's host. Besides *in situ* observations, point measurement, and transplants, this mesocosm experiment presents one of the most realistic long-term evaluations of the effect of projected future (2050 and 2100) OW and OA (RCP 8.5 scenarios; Meinshausen et al., 2011) on LBF.

3.2 Calcification and Epiphyte pCO_2 Buffering

A significant negative relationship between initial size of

Table 2 Categorical reproductive-index scores were scored on five occasions in August and September 2017

Treatment	Categorical score and date						Avg. score	Final count
	Aug. 3	Aug. 10	Aug. 29	Sept. 12	Sept. 25	Oct. 10		Oct. 10–17
	0	1	0	3	0	2		21
Control	2	3	3	3	3	4		123
	0	0	0	2	1	3		43
Avg.	0.7	1.3	1.0	2.7	1.3	3.0	1.7	62
	4	4	4	4	4	4		734
2050	0	1	4	2	0	2		18
	3	3	3	3	4	4		303
Avg.	2.3	2.7	3.7	3.0	2.7	3.3	3.8	352
	0	0	0	0	0	1		1
2100	1	2	0	2	3	4		265
	0	0	0	0	0	0		0
Avg.	0.3	0.7	0.0	0.7	1.0	1.7	0.7	89

0. No juveniles detected; 1. few present (<5); 2. some present (5–40); 3. many (40–100); 4. >100; the control, 2050, and 2100 treatments references to the conditions outlined in Table S1 and Fig. 2.

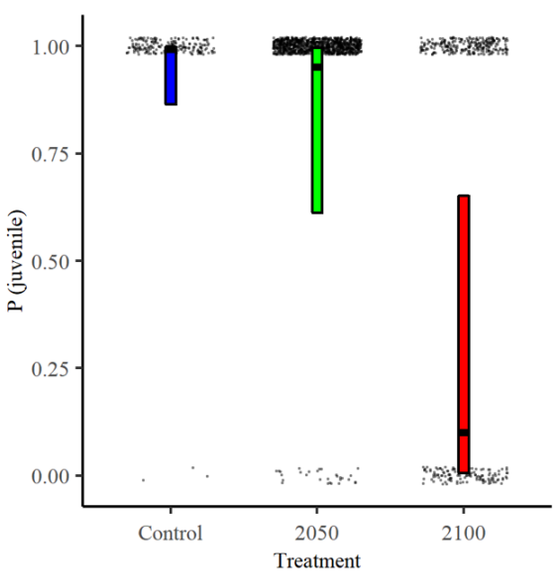

Figure 5. The probability of individuals scored in 2017 of being a juvenile, between the treatments. Black bars indicate the expected mean square means and coloured bars depict asymmetric 95% confidence intervals as determined by the binomial models.

the foraminifera and the log-scale (of the change in total area) explains the difference in growth rates between the two experiments (Fig. 4). Growth Experiment 1 was started in mid-March, with specimens on average ~18 mm^2, while Growth Experiment 2 was started in mid-May with larger specimens on average ~39 mm^2. The season and initial size of the individuals likely contributed to the variation between the two growth experiments. This also indicates that, as in many other phyla, growth rates are greatest in the earlier life stage compared to the later (or pre-reproduction) stages, however it could also relate to the lower temperature range (~24–26 °C; because individuals were added later in the year) in the second experiment, conducted in 2017, compared with the warmer temperature during first experiment in 2016 (~26–28 °C).

Among previous studies, there are a number of discrepancies in calcification results that can largely be attributed to the experimental conditions and methodologies. For example, previous studies have used a combination of surface-area, weight, and alkalinity (e. g., Doo et al., 2020), as well as three-dimensional biometry (Briguglio and Hohenegger, 2014) and logistic differential equations (e.g., Hohenegger and Briguglio, 2014; Hosono et al., 2014) to measure changes in growth rates. When *Marginopora* spp. are cultured in isolation, there is a calcification threshold around pH_{total} ~7.9 or pCO_2 ~800–900 µatm (Naidu et al., 2017; Sinutok et al., 2014, 2011; Reymond et al., 2013; Uthicke and Fabricius, 2012), which is equivalent to the year 2100 RCP 8.5 scenario. Additionally, recent studies have indicated that $CaCO_3$ precipitation rate and polymorph are also likely influenced by organic molecules, Mg concentration, and $CaCO_3$ stoichiometry of the calcifying fluid (e. g., Reymond and Hohn, 2021; Hohn and Reymond, 2019). Also, the findings of Prazeres et al. (2015) suggest *Marginopora* spp. can actively adjust the ion concentration at the site of calcification. Overall, the present long-term study (Fig. 3) and Doo et al. (2020) short-term study show no significant changes in calcification under elevated pCO_2 when cultured with alga (*H. opuntia* or *Laurencia intricate*, respectively). In terms of calcification, this epiphytic relationship seems to ameliorate the effect of elevated pCO_2, possibly due to the alga ability to regulate its' diffusion boundary layer (DBL). This likely provides a beneficial buffering zone for the epiphytic *Marginopora* spp. (e.g., Stuhr et al., 2021; Glas et al., 2012). Additionally, previous studies have proposed the importance of seagrass habitat as carbon sinks, particularly during the Eocene-Oligocene boundary (Brandano et al., 2016). This provides a strong case for monitoring and protecting calcifying and non-calcifying algae and seagrasses to build long-term resilience of LBF under rising pCO_2 and including epiphytic foraminiferal indices into ecological monitoring programs, as recommended by Mateu-Vicens et al. (2014).

3.3 Calcification and Temperature Tolerance

Future RCP 8.5 scenarios predict the average ocean temperatures will rise +1 °C by 2050 and +2 °C by 2100 (Meinshausen et al., 2011). For tropical shallow-water species living close to their temperature threshold, this scenario can present a tipping point, particularly in synergy with other global and local stressors. Previous studies have shown increased temperature can reduce the efficacy of the photosymbiont to translocation photosynthate-derived carbohydrates to the host, and subsequently to energy building blocks used to maintain cell function. In extreme cases, photo-oxidative stress is exhibited by bleaching, which is the death and digestion of the photosymbionts (Schmidt et al., 2011; Talge and Hallock, 2003) or, in a milder form, by the loss of photosynthetic pigment (e.g., Chl *a*), photosynthetic cells residing in the host LBF, or reduced O_2 metabolic production (Fujita et al., 2014). It greatly depends on local adaption to seasonal variability and irradiance tolerance to solar radiation reaching the seafloor (Hallock et al., 2006). As demonstrated by Talge and Hallock (2003), damaging levels of irradiance was far more problematic than temperature, even above 32 °C. However, most studies suggest the threshold for optimal cellular function is <30 °C (e.g., Schmidt et al., 2014, 2011). In these ecologically realistic mesocosm conditions, we showed repeatedly that calcification was not inhibited by the dual effect of pCO_2 and temperatures at 1 or 2 °C above ambient values. It is worth noting that the temperature did not exceed the known threshold (30 °C), which typically causes photobiological damage after a prolonged period, so an average 2 °C temperature increase will likely not pass threshold conditions in reefs that on average are currently below 28 °C. As the experiment did not continue during the summer (peak temperature) months, it is unknown if the juveniles would bleach in >30 °C mesocosm conditions.

3.4 Shifts in Fecundity under Climate Change Scenarios

Understanding the biology of reproduction is important for retracing key evolutionary and paleoecological processes (Hohenegger et al., 2019; Kinoshita et al., 2017; Fujita et al., 2000), yet limited studies on LBF have investigated the role of changing local or global environmental conditions on population dynamics. Similar to other populations of *Marginopora* spp. (Fujita et al., 2000; Ross, 1972), the present study also found that populations of *M. vertebralis* start to reproduce during early austral spring (i.e., during Growth Experiment 2). Throughout the last ~10-weeks of the experiment, observation of asexual reproduction from the RCP 8.5 treatment scenario for 2050 (average from the MOS 27 °C; pCO_2 670 µatm) consistently produced more juveniles. If the host alga could potentially buffer epiphytic foraminifera against higher pCO_2, then the ±1 °C temperature rise along with increased light might trigger reproduction, provided the foraminifera had reached the minimum diameter necessary for reproduction. We propose that the increase in temperature likely mimicked the early onset of spring. Perhaps given extra time, *M. vertebralis* in the ambient conditions may have reached the same fecundity levels as the RCP 8.5 treatment scenario for 2050, however this is unlikely, given the yearly life-cycle of *Marginopora* spp., which eventuates in cessation toward early summer. Similarly, the RCP 8.5 treatment scenario for 2100 (28 °C; pCO_2 900 µatm) likely missed the optimal window between the minimum diameter, temperature, and light to trigger reproduction rates comparable to the ambient or the 2050 RCP 8.5 scenario. This suggests that environmental synchronization is inevitable for the maintenance of *M. vertebralis* populations, particularly where calcareous (green) algae are present and the dissolution of early-stage amorphous $CaCO_3$ (e.g., pre-aragonite crystallization) can provide buffering potential at night.

4 CONCLUSIONS

Understanding the reproductive potential and strategies of a populations is key to retracing evolutionary processes and future divergence. Life-cycle flexibility may offer a selective advantage to environmental variably provided individuals can reach maturity. The present study captures an ecologically realistic scenario of *M. vertebralis* growth and fecundity in a multi-year OA and OW mesocosm experiment. In contrast to other growth studies, this mesocosm experiment shows reduced surface-area growth in elevated climate change scenarios, which is likely ameliorated by the epiphytic pCO_2 buffering by calcifying green algae or seagrasses. However, the additional energy required to maintain higher pH levels, particularly during the night (where respiration increases CO_2 levels) might be one reason for drastically reduced asexual reproduction. An alternative explanation could be that the 2 °C temperature increase interfered with the environmental synchronization that triggered asexual multiple fission. This has implications for calculating current and future $CaCO_3$ contribution to shallow-marine environments, therefore the habitat and population dynamics of LBF is an essential consideration for future coastal-marine planning.

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