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Daily variation in net primary production and net calcification in coral reef communities exposed to elevated $p\mathrm{CO_2}$

Steeve Comeau[1,2], **Peter J. Edmunds**[1], **Coulson A. Lantz**[1,3], **and Robert C. Carpenter**[1]

[1]Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA
[2]School of Earth Sciences, Oceans Institute and ARC Centre of Excellence for Coral Reef Studies, The University of Western Australia, Crawley, Western Australia 6009, Australia
[3]Southern Cross University School of Environment, Science, and Engineering, Military Road Lismore NSW 2480, Australia

Correspondence to: Steeve Comeau (steeve.comeau@uwa.edu.au)

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Abstract. The threat represented by ocean acidification (OA) for coral reefs has received considerable attention because of the sensitivity of calcifiers to changing seawater carbonate chemistry. However, most studies have focused on the organismic response of calcification to OA, and only a few have addressed community-level effects, or investigated parameters other than calcification, such as photosynthesis. Light (photosynthetically active radiation, PAR) is a driver of biological processes on coral reefs, and the possibility that these processes might be perturbed by OA has important implications for community function. Here we investigate how $\mathrm{CO_2}$ enrichment affects the relationships between PAR and community net $\mathrm{O_2}$ production (P_{net}), and between PAR and community net calcification (G_{net}), using experiments on three coral communities constructed to match (i) the back reef of Mo'orea, French Polynesia, (ii) the fore reef of Mo'orea, and (iii) the back reef of O'ahu, Hawaii. The results were used to test the hypothesis that OA affects the relationship between P_{net} and G_{net}. For the three communities tested, $p\mathrm{CO_2}$ did not affect the P_{net}–PAR relationship, but it affected the intercept of the hyperbolic tangent curve fitting the G_{net}–PAR relationship for both reef communities in Mo'orea (but not in O'ahu). For the three communities, the slopes of the linear relationships between P_{net} and G_{net} were not affected by OA, although the intercepts were depressed by the inhibitory effect of high $p\mathrm{CO_2}$ on G_{net}. Our result indicates that OA can modify the balance between net calcification and net photosynthesis of reef communities by depressing community calcification, but without affecting community photosynthesis.

1 Introduction

Ocean acidification (OA), which is caused by the dissolution of atmospheric $\mathrm{CO_2}$ in surface seawater, induces profound changes in seawater carbonate chemistry, involving an increased concentration of dissolved $\mathrm{CO_2}$ and bicarbonate ions, and a decrease in the concentration of carbonate ions and pH (Feely et al., 2004). The effects of these changes on tropical coral reefs are beginning to be understood in detail, with most studies reporting a decrease in calcification of scleractinian corals and coralline algae at reduced seawater pH (Gattuso and Hanson, 2011; Kroeker et al., 2013).

To date, studies addressing the effects of OA on coral reefs have been performed mostly at the scale of individual organisms, and have focused on calcification as a response variable (Schoepf et al., 2013; Comeau et al., 2013; Okazaki et al., 2016), while studies focusing on larger spatial scales (i.e., whole communities) have remained rare, mostly because of technical constraints (e.g., Dove et al., 2013; Comeau et al., 2015, 2016b). The few experiments addressing the effects of OA on intact coral reef communities have confirmed the threat to calcification rates previously reported for individual organisms, notably by showing a decreased capacity of communities to maintain positive net calcification under conditions mimicking a future ocean in which seawater pH will be depressed 0.15–0.30 units relative to present-day conditions (e.g., Dove et al., 2013; Comeau et al., 2015, 2016b). These community-level studies have focused mostly on the response of calcification to low pH (Dove et al., 2013; Comeau et al., 2015, 2016b) and, in contrast, the effect of increasing $p\mathrm{CO}_2$ on community net O_2 production has rarely been investigated. Where this issue has been addressed, community O_2 production has been found to be insensitive to $p\mathrm{CO}_2$ (to ∼ 1000 µatm) (Leclerc et al., 2002; Langdon and Atkinson, 2005, Dove et al., 2013), while a positive effect of $p\mathrm{CO}_2$ on the net production of photosynthetically fixed organic carbon has been reported during a flume experiment (Langdon and Atkinson, 2005).

Investigating the combined response to OA of primary production and calcification of benthic coral reef communities is critical, because increasing dissolved CO_2 and bicarbonate ion concentrations potentially could "fertilize" photosynthesis of marine organisms (Connell and Russell, 2010; Hepburn et al., 2011; Connell et al., 2013), thereby perturbing ecosystem trophodynamics. A stimulatory effect of OA on photosynthesis could, for calcifying taxa such as corals and coralline algae, support higher rates of calcification by increasing the ease with which the metabolic costs of these events could be met through enhanced respiration fuelled by greater availability of carbon substrates (Comeau and Cornwall, 2016). However, a stimulatory effect of OA on photosynthesis has not been clearly established for coral reef organisms, and to date, the evidence in support of this possibility is equivocal (e.g., Anthony et al., 2008; Kroeker et al., 2013; Comeau et al., 2016a).

One reason why studies of the effect of $p\mathrm{CO}_2$ on the relationship between primary production and calcification are technically challenging is that the relationships between light (photosynthetically active radiation, PAR) and both photosynthesis and calcification are nonlinear (e.g., Borowitzka, 1981; Chalker et al., 1988; Muscatine, 1990; Chisholm, 2000). In symbiotic reef corals, the relationships between photosynthesis and PAR, and between calcification and PAR, generally are best fit by a hyperbolic tangent function (Chalker, 1981; Marubini et al., 2001), which is characterized by a rapid rise of photosynthesis (or calcification) with initial increases in PAR from darkness, followed by a plateau of response at saturating light, and sometimes a reduction in response at the highest PAR intensity (i.e., photoinhibition, e.g., Brown et al., 1999). No studies have investigated the effect of $p\mathrm{CO}_2$ enrichment on the mathematical parameters defining the hyperbolic tangent relationship between PAR and photosynthesis (or calcification) for coral reef organisms and communities.

Because calcification of coral reef communities is coupled to photosynthesis on timescales of hours to days (Gattuso et al., 1999), examination of high-frequency variation in the net O_2 production (P_net)–net calcification (G_net) relationships for these communities has the potential to reveal the capacity to respond dynamically to varying conditions (i.e., Jokiel et al., 2014). The relationship between P_net and G_net for coral reefs is relatively well known at the community level, and generally describes a positive linear relationship (Gattuso et al., 1999; Falter et al., 2012). Such a relationship reflects emergent properties arising from the stimulation of G_net by P_net at the organism scale (i.e., for corals and calcified algae) (Jokiel et al., 2014), most likely because P_net can supply the carbon resources necessary as substrates for aerobic respiration (Stambler, 2011), modify the intracellular and surrounding seawater chemistry (Marubini et al., 2008; Jokiel et al., 2014), and provide the building blocks necessary to construct the organic matrix found within coral skeletons (Muscatine et al., 2005). Unfortunately, it is difficult to test the hypothesis that the G_net–P_net relationship for reef communities is affected by carbonate chemistry, because the seawater chemistry varies with P_net in the natural environment (Jokiel et al., 2014; Shaw et al., 2015). To test for an effect of seawater carbonate chemistry on the G_net–P_net relationship of reef communities, it is therefore necessary to conduct experiments in a controlled environment to assess how seawater carbonate chemistry alone affects the G_net–P_net relationship.

The present study tests the hypothesis that the enrichment in seawater $p\mathrm{CO}_2$ due to OA will affect the relationships between P_net and PAR, and between G_net and PAR for intact reef communities fabricated in outdoor flumes (sensu Atkinson et al., 1994). The second hypothesis tested is that the P_net–G_net relationships would be affected by OA, based on the rationale that community P_net and G_net would respond in dissimilar ways to high $p\mathrm{CO}_2$. Because the shape of these relationships likely depends on the community composition (i.e., the taxa present and their relative abundances, Gattuso et al., 1999), we used results from three independent experiments to explore variations in the relationships caused by differences in environmental conditions and differences in the taxonomic assemblages composing the communities tested. Data from three experiments conducted in flumes in two locations in the tropical Pacific were combined; one experiment focused on a back reef community assembled in Mo'orea, French Polynesia, during the austral spring of 2013 (Comeau et al., 2015); one experiment focused on a reef flat (back reef) community assembled in Kāne'ohe Bay, O'ahu, during the winter of 2014; and one experiment focused on a fore reef community assembled in Mo'orea, during the austral spring of 2014 (Comeau et al., 2016b). For the communities analysed in Mo'orea, the present contribution describes in more detail the results for net calcification, as well as new results for photosynthesis that originate from experiments that are described in part in previous papers (Comeau et al., 2015, 2016b); the study conducted in O'ahu has not been described before. The three communities were incubated in outdoor flumes of similar designs, and were operated under ambient and elevated $p\mathrm{CO}_2$ (∼ 400 and ∼ 1300 µatm, respectively). When the experiments were conducted, community P_net and G_net were measured simultaneously.

2 Materials and methods

2.1 Collection and sample preparation

This study utilizes results from three experiments conducted between August 2013 and October 2014. The first and third experiments were carried out in Mo'orea, French Polynesia, at the Richard B. Gump South Pacific Research Station, and the second experiment was conducted in O'ahu, Hawaii, on Coconut Island at the Hawaii Institute of Marine Biology (Fig. 1).

The first experiment took place in August–October 2013, and focused on a back reef community from 1 to 2 m depth on the northern shore of Mo'orea (Comeau et al., 2015). When the study was completed, this community consisted of 22 % coral cover and 6 % coralline alga cover. Two-thirds of the area of the working section of the flume was occupied by sediments collected from the lagoon at 2 m depth.

The second experiment was carried out in O'ahu in January–February 2014 and focused on a benthic community similar to that found at 1–2 m depth on the Kāne'ohe Bay barrier reef flat in 2013. This community consisted of *Porites compressa* (7 % cover), *Montipora capitata* (12 %), massive *Porites* spp. (3 %), and *Pocillopora damicornis* (2 %), and the crustose coralline alga *Porolithon onkodes* (4 %) (Jokiel et al., 2015). As described above for Experiment 1, sediments were inserted into the floor of the flume to recreate ecologically relevant communities. Since the flumes in O'ahu (as designed and utilized by M. Atkinson, e.g., Atkinson et al., 1994) were not designed to include sediments, a custom-made sediment box was inserted into the floor of the flumes to provide an area occupying two-thirds of the floor of the working section of the flume with sediment to a depth of ~ 5–8 cm.

The third experiment was carried out from August to October 2014 in Mo'orea, and focused on outer reef benthic communities prepared from specimens collected from ~ 15 to 17 m depth (Comeau et al., 2016b). This community consisted of 27 % cover of corals and 5 % cover of coralline algae; 55 % of the floor of the flume was covered by ~ $20 \times 20 \times 5$ cm pieces of reef pavement collected from ~ 15 m.

In Mo'orea, the two experiments were performed in four outdoor flumes consisting of a working section of $5.0 \times 0.3 \times 0.3$ m (as in Comeau et al., 2015) in which water was recirculated at a constant speed of 10 ± 0.5 cm s^{-1}(mean ± SE (standard error); Experiment 1) or 8 ± 0.5 cm s^{-1} (Experiment 3) that represented the mean in situ flow speed over the year measured in the two habitats (Washburn and MCR LTER, 2015; Comeau et al., 2016b). Two flumes were maintained at ambient $p\text{CO}_2$ (~ 400 µatm) and two at elevated $p\text{CO}_2$ (~ 1200–1300 µatm; see below). Fresh sand-filtered seawater was dispensed continuously into the flumes at 5 L min^{-1}, and the experiments lasted 8 (Experiment 1) or 7 weeks (Experiment 3).

In O'ahu, the benthic community was constructed in two outdoor flumes, one with a working section of $9 \times 0.6 \times 0.3$ m and one with a working section of $4 \times 0.4 \times 0.4$ m; one of these flumes was maintained at ambient $p\text{CO}_2$ and one at elevated $p\text{CO}_2$. To address the confounding effect of flumes on this design (i.e., the flumes were allocated to one of two treatments and the flumes were not of an identical design), the first experiment ended after 3 weeks, the $p\text{CO}_2$ treatments were switched between flumes, and new communities (with the same taxon composition including sediment) were placed in the two flumes for a second trial of the same experiment lasting 3 weeks. Fresh sand-filtered seawater was dispensed continuously into both flumes (at 5–10 L min^{-1}), and a flow speed of 10 cm s^{-1}, similar to that employed in the earlier trial with the back reef communities of Mo'orea, was maintained using electric trolling motors (Minnkota USA Riptide 55, Minnkota, USA).

The three experiments were performed outdoors under natural sunlight that was attenuated using shade cloth to maintain PAR values similar to ambient PAR recorded in situ in each habitat. In Experiments 1 and 2, the maximum PAR was set at ~ 1000 µmol quanta m^{-2} s^{-1} to represent light levels at ~ 1–2 m depth in the back reef (Carpenter et al., 2016), and in Experiment 3, maximum PAR was set at ~ 600 µmol quanta m^{-2} s^{-1} to mimic light levels recorded at 17 m depth on the fore reef of Mo'orea around noon on a cloudless day (Carpenter et al., 2016). For Experiment 3 (with an outer reef community from deeper water), blue acetate filters (Lee Filters 183 Moonlight Blue) were placed over the flumes to filter ambient sunlight in the 600–800 nm range to approximate the light spectrum found at 17 m depth (Comeau et al., 2016a). Temperature in all flumes was maintained at ambient seawater temperature when the experiments were conducted, which corresponded to ~ 27 °C in Experiments 1 and 3 (both conducted in austral spring) and ~ 24 °C in Experiment 2 (conducted in winter).

2.2 Carbonate chemistry manipulations and measurements

For the three experiments, $p\text{CO}_2$ levels were chosen to match ambient $p\text{CO}_2$ (~ 400 µatm) and the $p\text{CO}_2$ expected in the atmosphere by the middle of the next century (~ 1300 µatm, Moss et al., 2010). $p\text{CO}_2$ in the flumes was controlled using pH controllers (Aquacontroller, Neptune systems, USA) that controlled the delivery of either pure CO_2 or CO_2-free air into the seawater. To match the natural diel variation in seawater pH in shallow back reef communities (Hofmann et al., 2011; Comeau et al., 2014), in Experiments 1 and 2, seawater pH was maintained 0.1 units lower at night (from 18:00 to 06:00 LT (UTC−10) than during the day. It is expected that diel fluctuations in pH will be larger in the future due to changes in the buffering capacity of seawater. However, similar fluctuations were chosen here to apply similar pH fluctuations between ambient and elevated $p\text{CO}_2$ flumes to

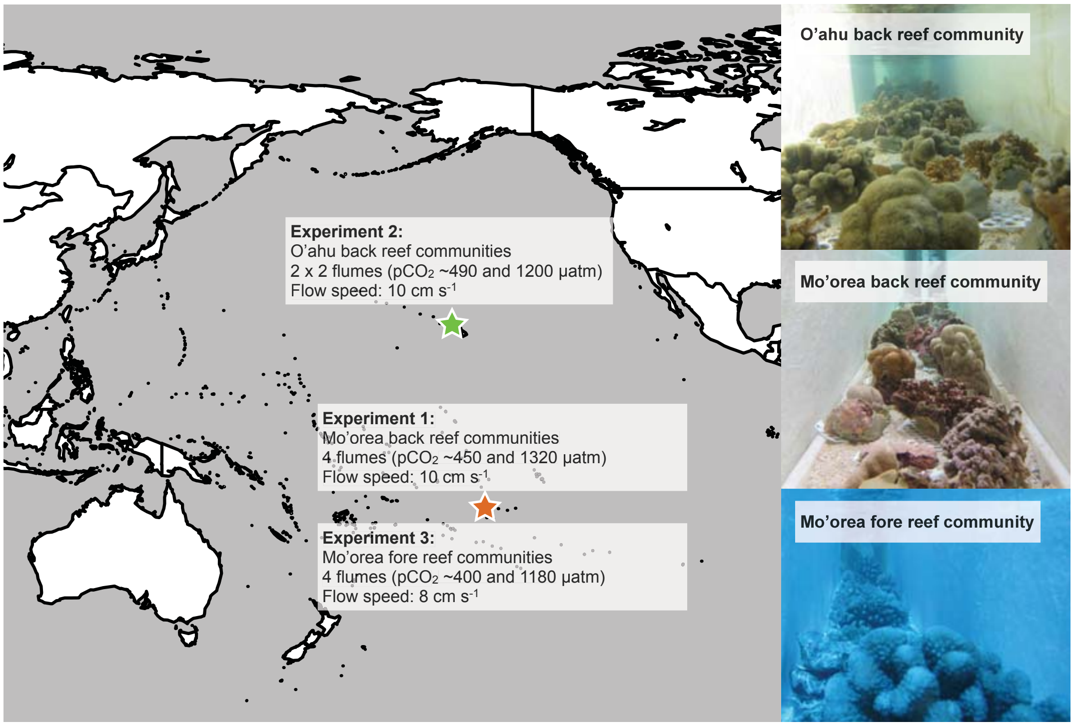

Figure 1. Map showing the study locations and photos of the three assembled communities. Experiments were performed on three coral reef communities representing the back reef of Mo'orea (Experiment 1), the back reef of O'ahu (Experiment 2), and the fore reef of Mo'orea (Experiment 3). The respective $p\mathrm{CO_2}$ levels and flow speeds used are indicated.

avoid confounding effects. Diel variation in pH was not applied during Experiment 3, because seawater pH varies by < 0.1 between day and night on the fore reef of Mo'orea (S. Comeau, unpublished data).

For the three experiments, pH on the total scale ($\mathrm{pH_T}$) was measured daily using a portable pH meter (Orion 3-stars, Thermo-Scientific, USA) fitted with a DG 115-SC pH probe (Mettler Toledo, Switzerland) calibrated every other day with Tris/HCl buffers (Dickson et al., 2007). $\mathrm{pH_T}$ also was measured every 2 weeks spectrophotometrically using m-cresol dye (Dickson et al., 2007). Mean values of $\mathrm{pH_T}$ measured spectrophotometrically and using a pH electrode differed by < 0.02 pH units. Total alkalinity (A_T) was measured using open-cell potentiometric titrations (Dickson et al., 2007) on ~ 50 g samples of seawater collected every 2–3 days. Accuracy of A_T measurements was checked by titrating certified reference materials provided by A.G. Dickson (batch 122 and 140) that yielded A_T values within $\sim 4\,\mu\mathrm{mol\,kg^{-1}}$ of the nominal value. Parameters of the carbonate system in seawater were determined with the seacarb R package (Gattuso et al., 2015) using measured values of $\mathrm{pH_T}$, A_T, temperature, and salinity.

2.3 Net calcification and primary production measurements

Net community calcification (G_net) in the flumes was measured using the total alkalinity anomaly method (Chisholm and Gattuso 1991; Schoepf et al., 2017), and net community primary production (P_net) was measured using oxygen sensors (TROLL 9500, In-Situ) that measured the $\mathrm{O_2}$ concentration at 60 s intervals with an accuracy of $0.2\,\mathrm{mg\,L^{-1}}$. Oxygen sensors were calibrated at the beginning of the experiment using a two-point calibration (0 and 100 % $\mathrm{O_2}$ seawater solutions). Measurements of changes in dissolved inorganic carbon (DIC) were not meaningful with our experimental design because DIC was held constant by adding pure $\mathrm{CO_2}$ during the incubations to maintain $p\mathrm{CO_2}$ at target values.

For the three experiments, community metabolism was measured every 7 days using single 24 h incubations during which the addition of seawater to the flumes was stopped, and the flumes were operated in a closed circuit mode. During these incubations, seawater samples for the determination of A_T were taken every 3 h during the day, and every 6 h at night, to estimate G_net, while $\mathrm{O_2}$ was constantly monitored. To maintain A_T, nutrient concentrations, and $p\mathrm{O_2}$ at values close to ambient seawater in the sampled habitats, $\sim 50\,\%$ of the flume volume was replaced every 3 h during the day, and every 6 h at night (i.e., at 06:00, 09:00, 12:00, 15:00, 18:00, and 00:00 LT). A_T and DIC changed by $< 5\,\%$ (~ 40–

50 µmol kg^{-1}) during the incubations, which likely did not affect the metabolism of organisms. Since only two O_2 sensors were available, and experiments were conducted in four flumes in Mo'orea, P_{net} was measured for each incubation in one ambient flume and one elevated pCO$_2$ flume that were randomly picked. In O'ahu, one O_2 sensor was used in each flume during the incubations. Acrylic covers placed on top of the flumes limited gas exchange with the atmosphere but did not prevent it. Gas exchange between seawater and the atmosphere was estimated based on the flume surface areas, the flow speed, and the differences between the O_2 concentration measured in seawater and the theoretical O_2 concentrations when in equilibrium with the atmosphere following equations of Langdon and Atkinson (2005). Wind effects on gas exchange across the air–water interface were assumed to be negligible because acrylic covers protected flumes. Gas exchange was estimated to be small (i.e. < 5–10 %) because ~ 50 % of the flume volume was replaced every 3 h during the day. Gas exchange was similar between treatments and was therefore not taken into account in the present study. Light was monitored constantly during the incubations using cosine-corrected PAR sensors (Odyssey, Dataflow Systems Pty Ltd, Christchurch, New Zealand).

2.4 Calculations and statistical analysis

P_{net} was estimated hourly by calculating the change in O_2 during the incubations, except for the hours during which the seawater was refreshed (06:00, 09:00, 12:00, 15:00, 18:00, and 00:00 LT). G_{net} was estimated at 3 h intervals during the day and 6 h intervals at night by collecting A_{T} samples at the beginning (after seawater refreshing) and at the end of each incubation (before adding fresh seawater).

Because there were no significant differences in calcification between flumes for each treatment (Comeau et al., 2015, 2016a), G_{net} was pooled among replicate flumes in each treatment. P_{net} was measured in Mo'orea in only one flume per treatment at a time, and it was assumed that the measurements represented the average response to the conditions experienced in each treatment. Individual measurements of G_{net} and P_{net} in O'ahu were considered replicates.

A corrected Akaike information criterion (AIC) approach was used to determine whether a linear, logarithmic, or hyperbolic tangent function best described the functional relationships between P_{net} and PAR, and between G_{net} and PAR, for each community (see details in Comeau et al., 2013). A linear relationship was fit to explore a "proportional effect" model for increasing PAR. A logarithmic function and a hyperbolic tangent function that are commonly used to describe the relationship between P_{net} and PAR for reef corals (Chalker, 1981; Marubini et al., 2001) were also fit to the data in cases where photosynthesis (or calcification) initially rapidly increased with PAR, and then approached an asymptote at saturating PAR.

The hyperbolic tangent function between PAR and P_{net} in the light corresponded to

$$P_{\mathrm{net}} = C_0 + P_{\mathrm{net\,max}} \tanh \frac{(\alpha I)}{P_{\mathrm{net\,max}}}, \tag{1}$$

where $P_{\mathrm{net\,max}}$ is the maximum photosynthetic rate, I is PAR, α is the slope of the initial portion of the P_{net} versus I relationship, and C_0 is the intercept.

Similarly, the hyperbolic tangent function for the relationship between PAR and G_{net} in the light was

$$G_{\mathrm{net}} = C_0 + G_{\mathrm{net\,max}} \tanh \frac{(\alpha I)}{G_{\mathrm{net\,max}}}, \tag{2}$$

where $G_{\mathrm{net\,max}}$ is the maximum calcification rate, I is PAR, α is the slope of the initial portion of the G_{net} versus I relationship, and C_0 is the intercept.

The best fits of the functions (least squares) were determined using the *nls* function in R, and t-tests were used to compare the curve parameters between pCO$_2$ treatments.

To test the hypothesis that P_{net} and G_{net} were associated, mean P_{net} corresponding to the G_{net} determination intervals (3 h periods during the day and 6 h at night) were calculated, and the relationship between P_{net} and G_{net} was investigated using a correlation approach (sensu Gattuso et al., 1999). When the linear associations between G_{net} on P_{net} were significant, analyses of covariance (ANCOVA), with P_{net} as the covariate, were used to test the effects of pCO$_2$ (a fixed effect) on the P_{net}–G_{net} relationship for each experiment. All analyses were performed using R software (R Foundation for Statistical Computing). In this design, both P_{net} and G_{net} are random variables for which a test of association is best accomplished with correlation. Evaluating the slope and intercept is problematic as it is not appropriate to use Model I (least squares) approaches for the purpose of describing the functional relationship between two random variables. In the present case, we report Model I slopes because we are interested in the capacity to predict G_{net} from P_{net} and because Model I slopes are integral to the ANCOVA approach.

3 Results

Carbonate chemistry was tightly controlled during the three experiments, with mean pCO$_2$ maintained at 453 ± 30, 460 ± 23, and 400 ± 14 µatm in the ambient treatments, and 1317 ± 50, 1233 ± 76, and 1176 ± 37 µatm in the elevated pCO$_2$ treatments during Experiments 1, 2, and 3, respectively (all ± SE, $n = 42$–56). In all experiments and both treatments, aragonite saturation states (Ω_{arag}) were ~ 3.52, 2.59, and 3.71 in the ambient treatments, and 1.64, 1.36, and 1.75 in the elevated pCO$_2$ treatments during Experiments 1, 2, and 3, respectively (Table 1). Ω_{arag} was lower during Experiment 2 in O'ahu compared to Experiments 1 and 3 in Mo'orea because of naturally lower A_{T} (~ 2160 µmol kg^{-1})

Table 1. Mean carbonate chemistry and temperature treatments in the flumes during the experiments conducted with back reef communities in Mo'orea and O'ahu, and the fore reef community in Mo'orea. The mean ± SE partial pressure of CO_2 (pCO_2) and the saturation states of aragonite (Ω_{arag}) were calculated from pH_T, total alkalinity (A_T), salinity (S), and temperature (T). SE for salinity was < 0.1.

Experiment	Treatment	pH_T	A_T	pCO_2	C_T	Ω_{arag}	S	T
Mo'orea back reef	Ambient	8.01 ± 0.02	2339 ± 2	453 ± 30	2025 ± 9	3.52 ± 0.09	35.9	26.9 ± 0.1
	OA	7.61 ± 0.01	2344 ± 1	1317 ± 50	2230 ± 7	1.64 ± 0.06	35.9	27.0 ± 0.1
O'ahu back reef	Ambient	7.96 ± 0.01	2160 ± 4	490 ± 23	1936 ± 8	2.59 ± 0.06	33.4	23.9 ± 0.2
	OA	7.62 ± 0.02	2164 ± 4	1233 ± 76	2074 ± 12	1.36 ± 0.10	33.4	23.9 ± 0.2
Mo'orea fore reef	Ambient	8.04 ± 0.01	2329 ± 2	400 ± 14	1992 ± 8	3.71 ± 0.08	36.5	27.1 ± 0.1
	OA	7.65 ± 0.01	2330 ± 2	1176 ± 37	2198 ± 6	1.75 ± 0.05	36.5	27.0 ± 0.1

and temperature (~ 24 °C) in this location (cf. in Mo'orea where A_T is ~ 2340 $\mu mol\,kg^{-1}$ at 27 °C).

Benthic community structure in the flumes was not measured during these short experiments, and we assume that changes were minor as there was no major coral mortality and planar growth would have been trivial over several weeks.

3.1 Relationships of P_{net} and G_{net} with PAR

AIC analyses justified the use of a hyperbolic tangent function (versus linear or logarithmic functions) to fit the relationship between P_{net} and PAR during the day for the back reef communities of Mo'orea and O'ahu under the two pCO_2 conditions (Fig. 2a, b, and c; Table S1 in the Supplement). Since the hyperbolic tangent function could not be rejected for the fore reef community of Mo'orea, this model was also chosen to facilitate comparisons between experiments. For the back reef community of Mo'orea, the back reef community of O'ahu, and the fore reef community of Mo'orea, there was no effect of pCO_2 on any of the parameters of the relationship between P_{net} and PAR (Table 2).

Similar to P_{net}, AIC tests also confirmed that the relationships of G_{net} with PAR could be fit with a hyperbolic tangent function for the three experiments under the two pCO_2 conditions tested (Fig. 3a–c; Table S2). For the Mo'orea back reef community, there was no difference in maximum calcification ($G_{net\,max}$) and the slope of the initial portion of the relationship (α) between pCO_2 treatments (Table 2). However, pCO_2 affected the intercepts (C_0, $p = 0.046$), with C_0 at ambient pCO_2 (1.26 $mmol\,m^{-2}\,h^{-1}$) greater than C_0 at elevated pCO_2 (−0.52 $mmol\,m^{-2}\,h^{-1}$). The relationship of G_{net} with PAR for the back reef communities in O'ahu was not statistically affected by pCO_2 (Table 2). For the fore reef community of Mo'orea, $G_{net\,max}$ and α did not differ between treatments, but C_0 was higher (2.77 $mmol\,O_2\,m^{-2}\,h^{-1}$) at ambient versus elevated pCO_2 (0.58 $mmol\,O_2\,m^{-2}\,h^{-1}$) (Table 2).

Table 2. Results of the t-tests used to compare between pCO_2 treatments the parameters of the hyperbolic tangent functions describing the relationship between community net photosynthesis (P_{net}) in the light and PAR and net calcification (G_{net}) in the light and PAR. Parameters of the hyperbolic function are the maximum rate ($P_{net\,max}$ and $G_{net\,max}$), the slope of the initial portion of the relationship (α), and the intercept (C_0).

Parameter	Experiment	Function parameter	p-value
Net photosynthesis (P_{net})	Mo'orea – back reef	$P_{net\,max}$	0.558
		α	0.387
		C_0	0.559
	O'ahu – back reef	$P_{net\,max}$	0.840
		α	0.536
		C_0	0.621
	Mo'orea – fore reef	$P_{net\,max}$	0.942
		α	0.792
		C_0	0.579
Net calcification (G_{net})	Mo'orea – back reef	$G_{net\,max}$	0.376
		α	0.836
		C_0	0.046
	O'ahu – back reef	$P_{net\,max}$	0.867
		α	0.126
		C_0	0.394
	Mo'orea – fore reef	$P_{net\,max}$	0.736
		α	0.715
		C_0	0.002

3.2 Relationships between P_{net} and G_{net}

For the back reef communities of Mo'orea, the relationship between P_{net} and G_{net} was significantly and positively correlated ($p < 0.001$ under ambient and elevated pCO_2) with slopes of 0.17 ± 0.03 $mmol\,CaCO_3\,mmol\,O_2^{-1}$ under ambient pCO_2, and 0.18 ± 0.03 $mmol\,CaCO_3\,mmol\,O_2^{-1}$ (both ± SE, $n = 48$) under elevated pCO_2 (Fig. 4a, Table 3). There was no difference between treatments in slopes (ANCOVA, $p = 0.749$), but intercepts were 61 % greater under ambient versus elevated pCO_2 ($p < 0.001$).

Table 3. Results of the linear regressions modeling the P_{net}–G_{net} relationships under ambient and elevated $p\text{CO}_2$. Results are shown for the experiments with back reef communities in Mo'orea and O'ahu, and fore reef communities in Mo'orea.

Experiment	Treatment	Slope	Slope *p*-value	Intercept	Intercept *p*-value
Mo'orea – back reef	Ambient	0.27 ± 0.05	< 0.001	3.85 ± 0.33	< 0.001
	Elevated	0.30 ± 0.05	< 0.001	1.99 ± 0.31	< 0.001
O'ahu – back reef	Ambient	0.14 ± 0.02	< 0.001	6.1 ± 0.38	< 0.001
	Elevated	0.17 ± 0.02	< 0.001	4.12 ± 0.37	< 0.001
Mo'orea – fore reef	Ambient	0.27 ± 0.05	< 0.001	3.85 ± 0.33	< 0.001
	Elevated	0.30 ± 0.06	< 0.001	1.99 ± 0.31	< 0.001

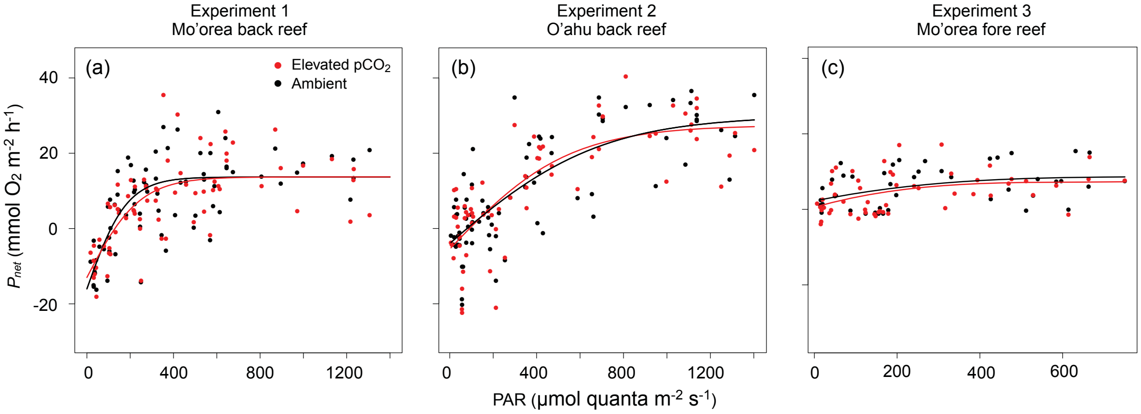

Figure 2. Relationships of net primary production (P_{net}) in the light with PAR in three coral reef communities representing the back reef of Mo'orea **(a)**, the back reef of O'ahu **(b)**, and the fore reef of Mo'orea **(c)**. Communities were incubated under ambient $p\text{CO}_2$ (~ 400 µatm, black symbols and lines) and elevated $p\text{CO}_2$ (~ 1200 µatm, red symbols and lines). The curves represent the best fit of a hyperbolic tangent function for the relationship between P_{net} with PAR.

G_{net} and P_{net} for the back reef communities of O'ahu also were positively correlated ($p < 0.001$ under both ambient and elevated $p\text{CO}_2$) and their relationships exhibited slopes of 0.14 ± 0.02 mmol CaCO_3 mmol O_2^{-1} under ambient $p\text{CO}_2$, and 0.17 ± 0.02 mmol CaCO_3 mmol O_2^{-1} (both ± SE, $n = 36$) under elevated $p\text{CO}_2$ (Fig. 4b, Table 3). There was no difference between treatments in slopes (ANCOVA, $p = 0.286$), but the intercepts were 32 % greater under ambient versus elevated $p\text{CO}_2$ ($p < 0.001$).

For the fore reef community of Mo'orea, the relationships between G_{net} and P_{net} were significant under ambient and elevated $p\text{CO}_2$ ($p < 0.001$) and had respective slopes of 0.27 ± 0.05 mmol CaCO_3 mmol O_2^{-1} and 0.30 ± 0.06 mmol CaCO_3 mmol O_2^{-1} (both ±SE, $n = 28$; Table 3). For the back reef communities, there were no differences in the slopes between G_{net} and P_{net} between treatments (ANCOVA, $p = 0.623$), but intercepts were 48 % greater under elevated versus ambient $p\text{CO}_2$ ($p = 0.002$).

4 Discussion

By testing the response of three coral reef communities to OA under natural PAR, our study demonstrates that the relationships between P_{net} and PAR and G_{net} and PAR for back reef and outer reef communities are not affected by $p\text{CO}_2$. Our results also demonstrate that the slope of the relationship between P_{net} and G_{net} was unaffected by increasing $p\text{CO}_2$, but in contrast, the intercepts were more elevated in the ambient treatments. Such results were caused by a constant effect of OA on G_{net} for the range of P_{net}values measured in the three communities.

For the three assembled communities, $p\text{CO}_2$ did not affect the functional relationship between PAR and P_{net} as modeled using a hyperbolic tangent function. This result suggests that for the organisms composing the three communities, the additional quantities of bicarbonate and dissolved CO_2 available under OA conditions did not enhance photosynthesis across the range of light intensities and community structures tested. However, as our results come from experiments completed in a single season, we cannot be sure whether the results are consistent throughout the year, as seasonal varia-

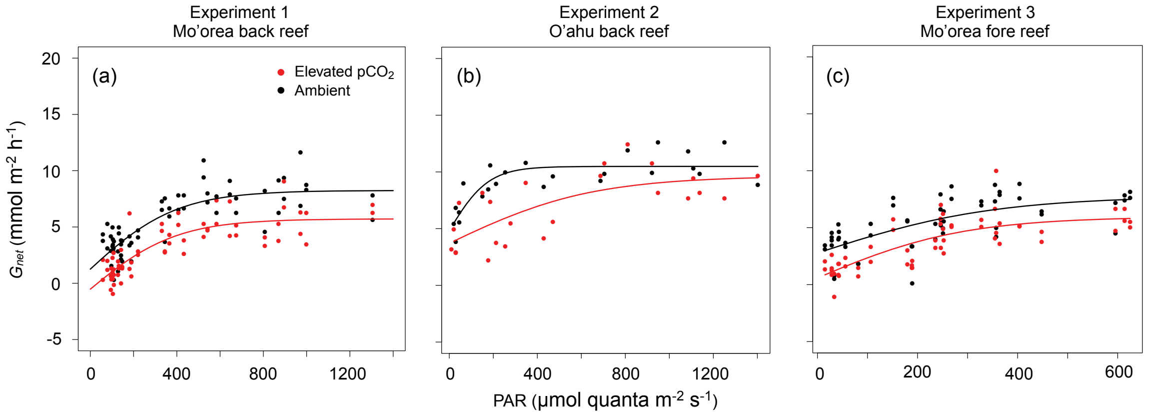

Figure 3. Relationships of net calcification (G_{net}) in the light with PAR in three coral reef communities representing the back reef of Mo'orea **(a)**, the back reef of O'ahu **(b)**, and the fore reef of Mo'orea **(c)**. Communities were incubated under ambient $p\mathrm{CO}_2$ ($\sim 400\,\mu$atm, black symbols and lines) and elevated $p\mathrm{CO}_2$ ($\sim 1200\,\mu$atm, red symbols and lines). The curves represent the best fit of a hyperbolic tangent function for the relationship between G_{net} and PAR.

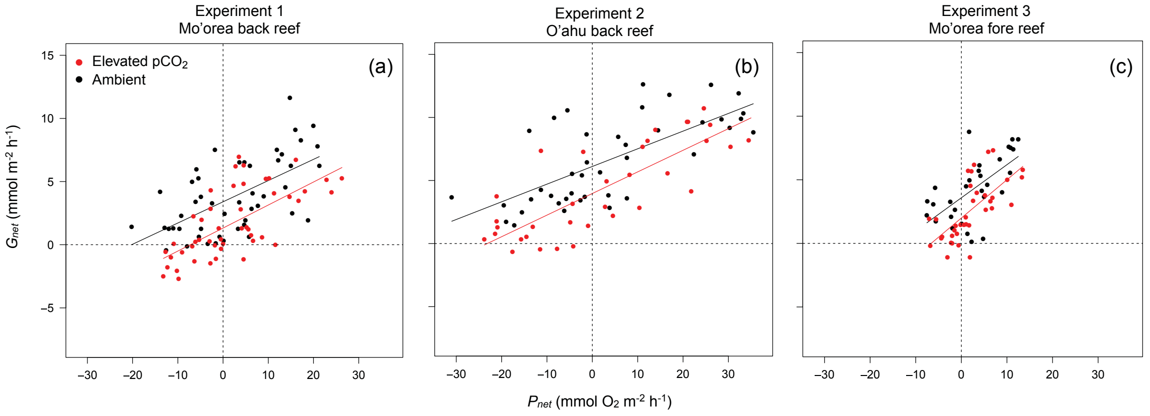

Figure 4. Variations in G_{net} as a function of P_{net} at the three study sites: **(a)** Mo'orea back reef, **(b)** O'ahu back reef, and **(c)** Mo'orea fore reef. Relationships were determined under control $p\mathrm{CO}_2$ ($400\,\mu$atm, black points and lines) and elevated $p\mathrm{CO}_2$ ($\sim 1200\,\mu$atm, red points and lines). For the three communities and the two $p\mathrm{CO}_2$ levels, the slopes of the linear relationships between P_{net} and G_{net} were significant.

tions in community and organismic P_{net} and G_{net} are common on coral reefs (e.g., Falter et al., 2012). Whether increasing $p\mathrm{CO}_2$ has beneficial consequences for rates of photosynthesis of marine organisms is equivocal (Connell and Russell, 2010; Britton et al., 2016) and, indeed, the absence of an effect of $p\mathrm{CO}_2$ on photosynthesis may have important biological meaning (e.g., Kroeker et al., 2013). For instance, such an outcome could reflect the presence of diverse carbon concentrating mechanisms (CCM), which allow organisms to actively concentrate CO_2 at the site of Rubisco activity by actively transporting HCO_3^- across internal membranes (Giardano et al., 2005; Raven et al., 2014). Increases in concentration of dissolved CO_2 in seawater that occur as a result of OA (Feely et al., 2004) could have beneficial consequences for photosynthetic rates of species that currently are DIC limited (Diaz-Pulido et al., 2016), because these organisms often rely on inefficient and energetically costly CCMs to access CO_2 (Raven et al., 2014).

The present study, as well as previous studies of both coral reef organisms (corals and calcified algae) (Schneider and Erez, 2006; Comeau et al., 2016b) and coral reef communities (Leclercq et al., 2002; Langdon et al 2003; Dove et al., 2013), showed no change in P_{net}, measured by changes in O_2 concentrations, in response to OA arising from $p\mathrm{CO}_2$ values as high as $2000\,\mu$atm. Stimulatory effects of $p\mathrm{CO}_2$ on P_{net} probably were not detected in our communities (i.e., where coral cover ranged from 22 to 27 %), because such effects are likely to be minimal for endosymbiotic *Symbiodinium* in corals that possess a CCM (Mackey et al., 2015) and, moreover, are able to exploit some of the host respiratory CO_2 as an alternative DIC source (Stambler, 2011). Beneficial effects of high $p\mathrm{CO}_2$ on community carbon production, but not oxygen production, for shallow water coral reefs have been reported by Langdon and Atkinson (2005), who found a 20–50 % increase in carbon production of coral assemblages composed of *Porites compressa* and *Montipora capitata* in

Hawai'i. This result led to the hypothesis that increasing CO_2 causes a decrease in the photosynthetic quotient of corals, which could be a product of the metabolism of the coral host, if CO_2 favors the production of carbohydrates over proteins and lipids (Langdon and Atkinson, 2005). While this hypothesis is appealing as a means to resolve discrepancy between studies, it was not possible to test in the present study because P_{net} was determined through measurements of O_2 (see Sect. 2, "Materials and methods"). In order to reconcile these apparently contradictory results regarding a potential "CO_2 fertilization" effect, it would be necessary for future studies to simultaneously measure changes in O_2, DIC, and A_{T}. In such an experiment, fluxes in DIC should be corrected for changes in A_{T} due to calcium carbonate precipitation and dissolution (because 0.5 moles DIC is equivalent to 1 mole A_{T} (Gattuso et al., 1999). DIC data corrected by this means could then be compared against contemporaneous measurements of O_2 in an experimental setup to ascertain whether the expected 1 : 1 molar flux ratio (of DIC : O_2) changes under elevated seawater $p\mathrm{CO_2}$. Changes in the value of this ratio, relative to ambient conditions, may provide insight into the possibility that coral reef calcifiers alter the allocation of photosynthetically fixed carbon among carbohydrate, lipid, and protein pools as a result of exposure to elevated seawater $p\mathrm{CO_2}$.

In our three experiments, maximal community G_{net} was coincident with the highest PAR. At low PAR ($\sim < 50\,\mu\mathrm{mol\,quanta\,m^{-2}\,s^{-1}}$) only the fore reef community in Mo'orea exhibited positive P_{net} at both $p\mathrm{CO_2}$ levels, demonstrating the capacity of this deeper community to photosynthesize at lower intensities of PAR. Similar to P_{net}, the relationships of G_{net} with PAR at the two $p\mathrm{CO_2}$ levels were best fit by a hyperbolic tangent function. The lack of changes in the parameters of these relationships as a result of the treatment conditions demonstrated that $p\mathrm{CO_2}$ and light did not have interactive effects on G_{net} (Table 2). Only the elevations of the hyperbolic functions for the two habitats in Mo'orea were affected by high $p\mathrm{CO_2}$, and in this case their reduction relative to ambient $p\mathrm{CO_2}$ demonstrates that G_{net} was consistently lower, regardless of PAR intensity, at high $p\mathrm{CO_2}$. Comparative data on the effect of the intensity of PAR on the response of community calcification to $p\mathrm{CO_2}$ are not available, but of the few studies of similar effects that have been conducted at the organism scale, contradictory results have been found (Marubini et al., 2001; Comeau et al., 2013, 2014b; Dufault et al., 2013; Suggett et al., 2013; Enochs et al., 2014).

The consistently lower G_{net} in the high $p\mathrm{CO_2}$ treatments for the three experiments could have resulted from either a decrease in gross calcification, an increase in calcium carbonate dissolution, or a combination of both. The constant offset (i.e., difference in elevation of the response) between G_{net} under ambient and high $p\mathrm{CO_2}$ at any given PAR suggests the effect cannot be accounted for solely by changes in gross calcification (G_{gross}). Indeed, if only G_{gross} were affected by high $p\mathrm{CO_2}$, a proportional effect on G_{net} would be expected, with the reduction of G_{net} associated with high $p\mathrm{CO_2}$ varying with G_{gross} and, therefore, PAR. In contrast, if dissolution and bioerosion, which are mostly chemically and mechanically driven (Andersson and Gledhill, 2013), were responsible for the reduced G_{net} at high $p\mathrm{CO_2}$, it is likely that PAR would have only a small influence in G_{net}. Thus, it is likely that increasing dissolution and chemical bioerosion in the high $p\mathrm{CO_2}$ treatment caused most of the observed decreases in G_{net}. However, the method used in the present study (the alkalinity anomaly technique) did not permit quantification of mechanical bioerosion, which could also be affected by OA (Enochs et al., 2016).

Although the two coral reef communities studied in Mo'orea differed in substratum composition (i.e., with sand present in the back reef versus pavement in the outer reef, and differences in coral cover), community structure, and the quality and quantity of light applied (i.e., blue-biased at depth, and a 40 % reduction in intensity at 17 m versus 2 m depth), both communities exhibited a 50–60 % decline in G_{net} at 1300 µatm $p\mathrm{CO_2}$. In contrast, mean G_{net} for the O'ahu back reef community was less affected by $p\mathrm{CO_2}$ than for the communities of Mo'orea. The reduced sensitivity of G_{net} to ~ 1200 µatm $p\mathrm{CO_2}$ for back reef communities in O'ahu may reflect different sediment composition and legacy effects associated with environmental conditions in the bay from which the organisms and sediment were collected. Critically, the organisms for the O'ahu experiment were collected from Kāne'ohe Bay where seawater $p\mathrm{CO_2}$ (up to ~ 450–500 µatm) is higher than current atmospheric levels (~ 400 µatm) because of heterotrophy and calcification (Fagan and Mackenzie, 2007; Drupp et al., 2011). Kāne'ohe Bay is also affected by strong diurnal cycles in $p\mathrm{CO_2}$ and rapid changes in $p\mathrm{CO_2}$ during storm events (Fagan and Mackenzie, 2007; Drupp et al., 2011). These conditions potentially could have created the opportunity for physiological acclimatization or local adaptation that might reduce their sensitivity to high $p\mathrm{CO_2}$ in the experimental trials.

The relationship between community P_{net} and G_{net} is commonly used as a measure of the coral reef "state" (Gattuso et al., 1999; Lantz et al., 2014), with coral reefs dominated by high coral cover and low cover of macroalgae characterized by elevated slopes of the $P_{\mathrm{net}} - G_{\mathrm{net}}$ relationship. In the present study, the slopes of the relationships between P_{net} and G_{net} in the ambient treatment were between 0.14 (O'ahu) (this and all following slope values have units of $\mathrm{mmol\ CaCO_3\ mmol\ O_2^{-1}}$) and 0.27 (Mo'orea fore reef). In Mo'orea, the slopes were higher for the fore reef (0.27 and 0.30) versus the back reef (0.17 and 0.18) community, which demonstrated that G_{net} was more sensitive to changes in P_{net} in fore reef communities, probably because of a higher cover of calcifiers. The slopes of the P_{net}–G_{net} relationships for the communities tested are within the range estimated from in situ "reef-scale" measurements, which indicate a mean value of 0.22 based on 52 reefs (Gattuso et al., 1999). More recently, Shaw et al. (2012) reported a P_{net}–G_{net} slope of 0.24 for the reef flat of Lady Elliot Island, Australia, and a slope of 0.14 was reported for Ningaloo Reef, Australia (Falter et al., 2012). The consistency between the slopes reported herein, and values determined in situ (e.g., Shaw et al., 2012; Gattuso et al., 1999), suggest that our constructed communities, and the conditions to which they were exposed, reproduced conditions found in situ on coral reefs. This outcome lends support to the inferences we are able to make regarding the response of reef communities to elevated $p\mathrm{CO}_2$, for which currently there are no in situ data.

Our results are consistent with the hypothesis that OA will affect the relationship between community P_{net} and G_{net} (sensu Gattuso et al., 1999) because intercepts of the P_{net}–G_{net} relationships varied between treatments and were more elevated under ambient $p\mathrm{CO}_2$. The absence of changes in slopes as a function of $p\mathrm{CO}_2$ probably was due to the lack of a $p\mathrm{CO}_2$ effect on P_{net} and the lack of a PAR–$p\mathrm{CO}_2$ interactive effect on P_{net} and G_{net}. Furthermore, the community composition remained the same in the ambient and elevated $p\mathrm{CO}_2$ conditions, with no mortality or loss of benthic cover of living organisms during the course of the experiment, which could potentially have modified the community P_{net}–G_{net} relationship (Lantz et al., 2014; Shaw et al., 2015) due to taxon-specific P_{net}–G_{net} relationships (Page et al., 2016). Thus, this result indicates that elevated CO_2 alone (e.g., without considering global warming) can modify the balance between calcification and photosynthesis at the scale of a whole reef, because of a decrease in coral reef community calcification while photosynthesis remains constant.

Data availability. All the data presented in the manuscript were deposited in the PANGAEA database and will be available at: https://www.pangaea.de/?q=Comeau&f.author%5B%5D=Comeau%2C+Steeve.

The Supplement related to this article is available online at https://doi.org/10.5194/bg-14-3549-2017-supplement.

Competing interests. The authors declare that they have no conflict of interest.

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