Daily variation in net primary production and net calcification in coral reef communities exposed to elevated pCO$_2$

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

5   [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

10   [3]Southern Cross University School of Environment, Science, and Engineering, Military

Road Lismore NSW 2480 Australia

Correspondence to: Steve Comeau (steve.comeau@uwa.edu.au)

Abstract

15

The threat represented by ocean acidification (OA) for coral reef has received

considerable attention because of the sensitivity of calcifiers to changing water carbonate

chemistry. However most studies have focused on the organismic response of

20   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 CO_2 enrichment affects

25   the relationships between PAR and community net 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 Moorea, French Polynesia, (ii) the

fore reef of Moorea, and (iii) the reef flat of Oahu, Hawaii. The results were used to test

the hypothesis that OA affects the relationship between P_{net} and G_{net}. For the three

30   communities tested, pCO_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 Moorea (but not in Oahu). 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 pCO_2 on G_{net}. Our result

35   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

40   Ocean acidification (OA), which is caused by the dissolution of atmospheric CO_2 in surface seawater, leads to profound changes in seawater carbonate chemistry, involving an increased concentration of bicarbonate ions and dissolved CO_2, and a decrease in 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

45   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 organism, and have focused on calcification as a

50   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, 2016a). The few experiments addressing the effects of OA on intact coral reef communities have confirmed the threat to calcification rates previously reported for

55   individual organisms, notably by showing a decreased capacity of communities to maintain positive net calcification under conditions mimicking future ocean in which seawater pH will be depressed 0.15 – 0.3 units relative to present-day conditions (e.g., Dove et al. 2013; Comeau et al. 2015, 2016a). These community-level studies have focused mostly on the response of calcification to low pH (Dove et al. 2013; Comeau et

60   al. 2015, 2016a) and, in contrast, the effect of increasing pCO_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 pCO_2 (to ~ 1000 µatm) (Leclerc et al.

2002; Langdon and Atkinson 2005, Dove et al. 2013), while a positive effect of pCO_2 on

the net production of photosynthetically fixed organic carbon has been reported during a

65   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

70   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

75   carbon substrates (Comeau and Cornwall 2016). However, a stimulatory effect of OA on

photosynthesis have 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. 2016b).

80   One reason why studies of the effect of pCO_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 non-linear (e.g., Borowitzka 1981; Chalker et al. 1988; Muscatine 1990;

Chisholm 2000). In symbiotic reef corals, the relationships between photosynthesis and

85   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

90   investigated the effect of pCO_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

95   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

100   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.

105   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

110   chemistry on the G_{net} - P_{net} relationhip of reef communities, it is therefore necessary to

first 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 pCO_2 due

115   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 pCO_2. Because the shape of these relationships likely depends on the community

120   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

125   on a back reef community assembled in Moorea, French Polynesia, during the Austral

spring 2013 (Comeau et al. 2015); one experiment focused on a reef flat community

assembled in Kaneohe Bay, Oahu, during the winter 2014; and one experiment focused

on a fore reef community assembled in Moorea, during the Austral spring 2014 (Comeau

et al. 2016a). For the communities analysed in Moorea, the present contribution describes

130   in more detailed 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, 2016a); the study conducted in Oahu has not been described before. The three

communities were incubated in outdoor flumes of similar designs, and were operated

under ambient and elevated pCO_2 (~ 400 µatm and ~1300 µatm, respectively). When the

135   experiments were conducted, community P_{net} and G_{net} were measured simultaneously.

2. Materials and Methods

2.1 Collection and sample preparation

140

           This study utilizes results from three experiments conducted between August

2013 and October 2014. The first and third experiments were carried out in Moorea,

French Polynesia, at the Richard B. Gump South Pacific Research Station, and the second

experiment was conducted in Oahu, Hawaii, on Coconut Island at the Hawaii Institute of

145   Marine Biology.

           The first experiment took place in August-October 2013, and focused on a back

reef community from 1–2 m depth on the north shore of Moorea (Comeau et al. 2015).

This community consisted of massive *Porites* spp. (11% cover), *Porites rus* (6%),

150   *Montipora* spp. (3%), *Pocillopora* spp. (2%), and crustose coralline algae (6%), and the

coverage of each taxon in the flume was scaled to represent the community structure

measured in this habitat in 2013 (Carpenter 2014; Edmunds 2014). To create benthic

communities that were ecologically relevant to the back reef of Moorea (Carpenter 2014;

Edmunds 2014), two-third of the area of the working section of the flume was occupied

155 by sediments collected from the lagoon at 2-m depth using custom made sediment boxes

(0.4 × 0.3 m in area and 0.3 m deep).

The second experiment was carried out in Oahu in January-February 2014 and

focused on a benthic community similar to that found at 1-2 m depth on the Kaneohe Bay

160 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 Oahu (as designed and

165 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.

170 The third experiment was carried out from August to October, 2014 in Moorea,

and focused on outer reef benthic communities prepared from specimens collected from ~

15–17-m depth (Comeau et al. 2016a). This community consisted of *Pocillopora* spp.

(11% cover), massive *Porites* spp. (8%), and *Acropora* spp. (8%), and the crustose

coralline alga *Porolithon onkodes* (5%), and the coverage of each taxon was scaled in the

175 flumes to match community structure recorded in this habitat (at the same depth) in 2006

(Carpenter 2014; Edmunds 2014). Because the benthos on the fore reef of Moorea

consisted mostly of reef pavement in 2006 (i.e., cemented calcium carbonate substratum

covered by algal turf and coralline algae (Carpenter 2014; Edmunds 2014), 55% of the

floor of the flume was covered by ~ $20 \times 20 \times 5$ cm pieces of reef pavement collected

180   from ~15-m depth to match the % cover of the benthic community. Sediments were not

included in this experiment, as they are not common on the fore reef at the investigated

depth.

In Moorea, the two experiments were performed in four outdoor flumes consisting

185   of a working section of $5.0 \times 0.3 \times 0.3$ m (as in Comeau et al. 2015) in which water was

re-circulated at a constant speed of 10 ± 0.5 cm s^{-1} (mean ± SE; 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 2014; Comeau et al. 2016). Two flumes were

maintained at ambient pCO_2 (~ 400 µatm), and two at elevated pCO_2 (~1200–1300 µatm,

190   see below). Fresh sand-filtered seawater (nominal pore size of ~ 100 µm) was dispensed

continuously into the flumes at 5 L min^{-1}, and the experiments lasted eight (Experiment

1) or seven weeks (Experiments 3).

In Oahu, the benthic community was constructed in two outdoor flumes, one with

195   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 pCO_2 and one at elevated pCO_2. To

address the confounding effect of flumes in 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 three weeks, the pCO_2 treatments were switched between flumes,

200 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 Moorea, was maintained using electric trolling motors (Minnkota Riptide

205 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 Experiment 1 and 2, the maximum PAR was set at ~ 1000 μmol

210 quanta m^{-2} s^{-1} to represent light levels at ~ 1–2m 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 Moorea 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

215 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 Experiment 1 and 3 (both conducted during Austral

spring) and ~ 24 °C in Experiment 2 (conducted in winter).

220

2.2 Carbonate chemistry manipulations and measurements

For the three experiments, pCO_2 levels were chosen to match ambient pCO_2 (~

400 µatm) and the pCO_2 expected in the atmosphere by the end of the present century

225   under a pessimistic scenario of further anthropogenic activity (Representative

Concentration Pathway 8.5, ~1300 µatm, Moss et al., 2010). pCO_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;

230   Comeau et al., 2014a), in Experiment 1 and 2, seawater pH was maintained 0.1 unit lower

at night (from 18:00 to 6:00) than during the day. Diel variation in pH was not applied

during Experiment 3, because seawater pH varies < 0.1 between day and night on the fore

reef of Moorea (S. Comeau unpublished data).

235   For the three experiments, pH on the total scale (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). pH_T also was measured every 2 weeks spectrophotometrically

using m-cresol dye (Dickson et al., 2007). Mean values of pH_T measured

240   spectrophotometrically and using a pH electrode differed < 0.02 pH units. Total alkalinity

(A_T) was measured using open-cell potentiometric titrations (Dickson et al., 2007) on 50-

mL samples of seawater collected every 2-3 d. 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 ~ 4 µmol kg^{-1} of the nominal value. Parameters of

245 the carbonate system in seawater were determined with the R package seacarb (Gattuso et

al., 2015) using measured values of 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

250 alkalinity anomaly method (Chisholm and Gattuso 1991; Schoepf et al. 2016), and net

community primary production (P_{net}) was measured using oxygen sensors (TROLL 9500,

In-Situ) that measured the O_2 concentration at 60-second intervals. Measurements of

changes in dissolved inorganic carbon (DIC) were not meaningful with our experimental-

design because DIC was held constant by adding pure CO_2 during the incubations to

255 maintain pCO_2 at target values.

For the three experiments, community metabolism was measured every 7 d 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,

260 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 O_2 was constantly monitored. Since only two O_2

sensors were available, and experiments were conducted in four flumes in Moorea, P_{net}

was measured for each incubation in one ambient and one elevated pCO_2 flumes that

were picked randomly. In Oahu, one O_2 sensor was used in each flume during the

265 incubations. Acrylic covers placed on top of the flumes limited gas exchange with the

atmosphere but did not prevent it. However, gas exchange, which was similar between

treatments, was estimated (using the methods of Langdon and Atkinson [2005]) to be

minimal (i.e. < 5%) and, therefore, was not taken into account in the present study. To

maintain A_T, nutrient concentrations, and pO_2 at values close to ambient seawater in the

270   sampled habitats, ~ 50% of the flume volume was replaced every 3 h during the day, and

every 6 h at night (i.e., at 6:00, 9:00, 12:00, 15:00, 18:00, and 00:00). Light was

monitored constantly during the incubations using cosine-corrected PAR sensors

(Odyssey, Dataflow Systems Pty Ltd, Christchurch, New Zealand).

275   *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 (6:00, 9:00, 12:00, 15:00,

18:00, and 00:00 hrs). 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

280   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 Moorea in only one flume per treatment at a time,

285   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

Oahu were considered replicates.

An Akaike Information Criterion (AIC) approach was used to determine if a

290   linear, logarithmic, or hyperbolic tangent functions 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

295   reef corals (Chalker 1981; Marubini et al. 2001), also were fit to the data in cases where

photosynthesis (or calcification) initially rapidly increased with PAR, then approached an

asymptote at saturating PAR.

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

300   to:

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

where $P_{net\,max}$ is the maximum photosynthetic rate, I is the 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

305   G_{net} in the light was:

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

where $G_{net\,max}$ is the maximum calcification rate, I is the 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 function

310   *nls* 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

315   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

320   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.

325

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$_2$

330   treatments during Experiments 1, 2, and 3, respectively (all $\pm$ SE, n = 42–56). In all

experiments and both treatments, aragonite saturation states (Ω_{arag}) was ~ 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

Biogeosciences

Discussions

EGU

Open Access

Experiment 2 in Oahu compared to Experiments 1 and 3 in Moorea because of naturally

335   lower A_T (~ 2160 μmol kg^{-1}) and temperature (~24°C) in this location (cf in Moorea

where A_T is ~2340 μmol kg^{-1} at 27°C).

For the three experiments, benthic community structure was not measured during

these short experiments, but we assume that changes were minor as there was no coral

340   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

345   logarithmic functions) to fit the relationship between P_{net} and PAR during the day for the

three experiments under the two pCO_2 conditions (Fig. 1A, B, and C). For the back reef

community of Moorea, the back reef community of Oahu, and the fore reef community of

Moorea, there was no effect of pCO_2 on any of the parameters of the relationship between

P_{net} and PAR (Table 2).

350

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. 2A, B, and C). For the Moorea back reef community, there was no difference

in maximum calcification ($G_{net\ max}$), and slope of the initial portion of the relationship (α)

355   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

Oahu was not statistically affected by pCO$_2$ (Table 2). For the fore reef community of

Moorea, $G_{net\ max}$ and α did not differ between treatments, but C_0 was higher (2.77 mmol

360   O$_2$ m^{-2} h^{-1}) at ambient versus elevated pCO$_2$ (0.58 mmol O$_2$ m^{-2} h^{-1}) (Table 2).

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

For the back reef communities of Moorea, the relationship between P_{net} and G_{net}

were significantly and positively correlated (p < 0.001 under ambient and elevated pCO$_2$)

365   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. 3A). There was

no difference between treatments in slopes (ANCOVA, p = 0.749, Table 3), but

elevations were 61% greater under ambient versus elevated pCO$_2$ (p < 0.001, Table 3).

370   G_{net} and P_{net} for the back reef communities of Oahu also were positively

correlated (p < 0.001 under both ambient and elevated pCO$_2$) and their relationships

exhibited slopes of 0.14 ± 0.02 mmol CaCO$_3$ mmol O$_2$$^{-1}$ under ambient pCO$_2$, and 0.17 ±

0.02 mmol CaCO$_3$ mmol O$_2$$^{-1}$ (both ± SE, n = 36) under elevated pCO$_2$ (Fig. 3B). There

was no difference between treatments in slopes (ANCOVA, p = 0.286, Table 3), but the

375   elevations were 32% greater under ambient versus elevated pCO$_2$ (p < 0.001).

For the fore reef community of Moorea, the relationships between G_{net} and P_{net}

were significant under ambient and elevated pCO$_2$ (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 ±

380   SE, n = 28). For the back reef communities, there were no difference of the slopes

between G_{net} and P_{net} between treatments (ANCOVA, p = 0.623, Table 3), but elevations

were 48% greater under elevated versus ambient pCO_2 (p = 0.002).

4. Discussion

385

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 pCO_2. Our results also

demonstrate that the slope of the relationship between P_{net} and G_{net} was unaffected by

390   increasing pCO_2, 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 tested, pCO_2 did not affect the functional

395   relationship between PAR and P_{net} as modelled using a hyperbolic tangent function. This

result suggests that for the organisms composing the three communities investigated, 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

400   cannot be sure whether the results are consistent throughout the year, as seasonal

variations in community and organismic P_{net} and G_{net} are common on coral reefs (e.g.,

Falter et al. 2012). Whether increasing pCO_2 has beneficial consequences for rates of

Biogeosciences
Discussions

EGU
Open Access

photosynthesis of marine organisms is equivocal (Connell and Russell 2010; Britton et al.

2016) and, indeed, the absence of an effect of pCO_2 on photosynthesis may have

405   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

410   (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

415   and calcified algae) (Schneider & 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 O_2 changes, in response to OA arising from pCO_2 values as

high as 2000 µatm. Stimulatory effects of pCO_2 on P_{net} probably were not detected in our

communities (i.e., where coral cover ranged form 22–27%), because such effects are

420   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 pCO_2 on

community carbon production, but not oxygen production, for shallow water coral reefs

have been reported by Langdon & Atkinson (2005), who found a 20–50% increase in

425   carbon production of coral assemblages composed of *Porites compressa* and *Montipora*

capitata. 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 it favors the production of carbohydrates over proteins and lipids (Langdon &

Atkinson 2005). While this hypothesis is appealing, it was not possible to test in the

430   present study because P_{net} was determined through measurements of O_2 (see Material and

Methods).

       In our three experiments, maximal community G_{net} was coincident with the

highest PAR. Similar to P_{net}, the relationships of G_{net} with PAR at the two pCO_2 levels

435   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 pCO_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 Moorea were affected by high pCO_2, and in

this case their reduction relative to ambient pCO_2 demonstrates that G_{net} consistently was

440   lower, regardless of PAR, at high pCO_2. Comparative data on the effect of PAR on the

response of community calcification to pCO_2 are currently not available, but the few

studies of these effects that have been conducted at the organism scale report equivocal

results (Marubini et al. 2001; Comeau et al. 2013; Dufault et al. 2013; Sugget et al. 2013;

Comeau et al. 2014b; Enochs et al. 2014).

445

       The consistently lower G_{net} in the high pCO_2 treatments for the three experiments

could have resulted from either a decrease in gross calcification, an increase in

dissolution, or a combination of both. The constant offset (i.e., difference in elevation of

the response) between G_{net} under ambient and high pCO$_2$ at any given PAR suggests the

450   effect cannot be accounted for solely by changes in gross calcification (G_{gross}). Indeed, if

only G_{gross} was affected, a proportional effect G_{net} would be expected, with the reduction

of G_{net} associated with high pCO$_2$ 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 pCO$_2$, it is

455   likely that PAR would have only a small influence in G_{net}. Thus, it is likely that

increasing dissolution/bierosion in the high pCO$_2$ treatment caused most of the observed

decreases in G_{net}.

Although the two coral reef communities studied in Moorea differed in

460   substratum composition (i.e., sand in the back reef versus pavement in the outer reef),

community structure, and the quality and quantity of light applied (i.e., blue-biased at

depth and a 40% reduction at 17-m versus 2-m depth), both communities exhibited a 50-

60% decline in G_{net} at 1300 µatm pCO$_2$. In contrast, mean G_{net} for the Oahu back reef

community was less affected by pCO$_2$ than for the communities of Moorea. The reduced

465   sensitivity of G_{net} to ~ 1200 µatm pCO$_2$ for back reef communities in Oahu 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 Oahu experiment were collected from Kaneohe Bay where seawater

pCO$_2$ (up to ~450-500 µatm) is higher than current atmospheric levels (~400 µatm), and

470   there are strong diurnal cycles in pCO$_2$, and rapid changes in pCO$_2$ during storm events

(Fagan and Mackenzie 2007; Drupp et al. 2011). These conditions potentially could have

Biogeosciences
Discussions

Open Access

EGU

created the opportunity for physiological acclimatization that might reduce their

sensitivity to high pCO_2 in the experimental trials.

475   The relationship between community P_{net} and G_{net} is used commonly to evaluate

the "state" of a coral reef (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_{net} - G_{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 (Oahu) (this and all

480   following slope values have units of mmol $CaCO_3$ mmol O_2^{-1}) and 0.27 (Moorea fore

reef). In Moorea, 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 calcifier cover.

The slopes of the P_{net} - G_{net} relationships for the communities tested are within the range

485   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.

490   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 pCO_2 for which currently there is no in situ data.

495   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 elevations of the

P_{net} - G_{net} relationships varied between treatments and were greater under ambient pCO$_2$.

The absence of changes in slopes as a function of pCO$_2$ probably was due to the lack of a

pCO$_2$ effect on P_{net}, and the lack of a PAR-pCO$_2$ interactive effect on P_{net} and G_{net}.

500   Furthermore, the community composition remained the same in the ambient and elevated

pCO$_2$ 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 (C.A. Lantz unpubl.). Thus, this result indicates that elevated CO$_2$ alone

505   (e.g., without considering 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.

Biogeosciences
Discussions

EGU

Open Access

515

References

Albright R., Langdon C., and Anthony K. R.: Dynamics of seawater carbonate chemistry,

   production, and calcification of a coral reef flat, central Great Barrier Reef.

   Biogeosciences, 10, 6747–6758, 2013.

520 Anthony K. R., Kline D. I., Diaz-Pulido G., Dove S., and Hoegh-Guldberg O.: Ocean

   acidification causes bleaching and productivity loss in coral reef builders. Proc Natl.

   Acad. Sci., 105,17442–17446, 2008.

Andersson, A. J., and Gledhill, D.: Ocean acidification and coral reefs: effects on

   breakdown, dissolution, and net ecosystem calcification. Annu. Rev. Mar. Sci., 5, 321–

525   348, 2013.

Atkinson, M. J., Kotler E., and Newton, P.: Effects of water velocity on respiration,

   calcification, and ammonium uptake of a *Porites compressa* community. Pacific Sci.,

   48, 296-303, 1994.

Barkley, H. C., Cohen, A. L., Golbuu, Y., Starczak, V. R., DeCarlo, T. M., and

530   Shamberger, K. E. F.: Changes in coral reef communities across a natural gradient in

seawater pH. Science Advances, 1: e1500328, doi:10.1126/sciadv.1500328, 2015.

Borowitzka, M. A.: Photosynthesis and calcification in the articulated coralline red algae

Amphiroa anceps and *A. foliacea*. Mar. Biol., 62, 17–23, 1981.

Britton, D., Cornwall, C. E., Revill, A. T., Hurd, C. L., and Johnson, C. R.: Ocean

535   acidification reverses the positive effects of seawater pH fluctuations on growth and

photosynthesis of the habitat-forming kelp, *Ecklonia radiata*. Scientific Reports, 6,

26036, doi:10.1038/srep26036, 2016.

Brown, B. E., Ambarsari, I., Warner, M. E., Fitt, W. K., Dunne, R. P., Gibb, S. W., and

Cummings, D. G.: Diurnal changes in photochemical efficiency and xanthophyll

540   concentrations in shallow water reef corals : evidence for photoinhibition and

photoprotection. Coral Reefs, 18, 99–105, 1999.

Carpenter, R. C. of Moorea Coral Reef LTER.: MCR LTER: Coral Reef: Long-term

population and community dynamics: benthic algae and other community components,

ongoing since 2005. knb-lter-mcr.8.27. Available at: http://metacat.lter-

545   net.edu/knb/metacat/knb-lter-mcr.8.27/lter, 2014.

Carpenter, R. C. of Moorea Coral Reef LTER.: MCR LTER: Coral Reef: Benthic

Photosynthetically Active Radiation (PAR), ongoing since 2009. knb-lter-mcr.4005.8

doi:10.6073/pasta/ea06e6d53df8b1cdf7c1d50d025b77fd, 2016.

Chalker, B. E.: Simulating light-saturation curves for photosynthesis and calcification by

550   reef-building corals. Mar. Biol., 63, 135–141, 1981.

Chalker, B. E., Barnes, D. J., Dunlap, W. C., and Jokiel, P. L.: Light and reef-building corals. Interdisciplinary Sci. Rev., 13, 222–237, 1988.

Chisholm, J. R. M., and Gattuso, J.-P.: Validation of the alkalinity anomaly technique for investigating calcification of photosynthesis in coral reef communities. Limnol.

555   Oceanogr., 36: 1232–1239, 1991.

Chisholm, J. R. M.: Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. Limnol. Oceanogr., 45, 1476–1484, 2000.

Comeau S., and Cornwall, C. E.: Contrasting effects of ocean acidification on coral reef "animal forests" versus seaweed "kelp forests". *In*: Marine Animal Forests, Springer,

560   2016.

Comeau, S., Carpenter, R. C., and Edmunds, P. J.: Effects of pCO_2 on photosynthesis and respiration of tropical scleractinian corals and calcified algae. ICES J.Mar. Sci., fsv267, doi:10.1093/icesjms/fsv267, 2016b.

Comeau, S., Carpenter, R. C., Lantz, C. A., and Edmunds, P. J.: Ocean acidification

565   accelerates dissolution of experimental coral reef communities. Biogeosciences, 12, 365–372, 2015.

Comeau, S., Lantz, C. A., Edmunds, P. J., and Carpenter, R. C.: Framework of barrier reefs threatened by ocean acidification. Glob. Change Biol., 22, 1225–1234, 2016a.

Comeau, S., Edmunds, P. J., Spindel, N. B., and Carpenter, R. C.: Diel pCO_2 oscillations

570   modulate the response of the coral *Acropora hyacinthus* to ocean acidification. Mar. Ecol. Progr. Seri., 501, 99–111, 2014.

Connell, S. D., and Russell, B. D.: The direct effects of increasing CO_2 and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. P. Roy. Soc. B, 277, 1409-1415, 2010.

575 Connell, S. D., Kroeker, K. J., Fabricius, K. E., Kline, D. I., and Russell, B. D.: The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance. Philo. Trans. Roy. Soc. B, 368, 20120442, doi:10.1098/rstb.2012.0442, 2013.

Diaz-Pulido, G., Cornwall, C., Gartrell, P., Hurd, C., and Tran, D. V.: Strategies of

580 dissolved inorganic carbon use in macroalgae across a gradient of terrestrial influence: implications for the Great Barrier Reef in the context of ocean acidification. Coral Reefs, 35, 1327, doi:10.1007/s00338-016-1481-5, 2016.

Dickson A. G., Sabine, C. L., and Christian, J. R.: Guide to best practices for ocean CO_2 measurements. PICES Special Publication 3, pp 191, 2007.

585 Dove, S. G., Kline, D. I., Pantos, O., Angly, F. E., Tyson, G. W., and Hoegh-Guldberg, O.: Future reef decalcification under a business-as-usual CO_2 emission scenario. Proc. Natl. Acad. Sci., 110, 15342–15347, 2013.

Drupp, P., DeCarlo, E. H., Mackenzie, F. T., Bienfang, P., and Sabine, C. L.: Nutrient inputs, phytoplankton response, and CO_2 variations in a semi-enclosed subtropical

590 embayment, Kaneohe Bay, Hawaii. Aquatic Geochem., 17, 473–498, 2011.

Dufault, A. M., Ninokawa, A., Bramanti, L., Cumbo, V. R., Fan, T.-Y., and Edmunds, P. J.: The role of light in mediating the effects of ocean acidification on coral calcification. J. Exp. Biol., 216, 1570–1577, 2013.

Edmunds, P. J. of Moorea Coral Reef LTER.: MCR LTER: Coral Reef: Long-term

595   population and community dynamics: corals. knb-lter-mcr.4.31. Available at:

http://metacat.lternet.edu/knb/metacat/knb-lter-mcr.4.31/lter, 2014.

Enochs, I. C., Manzello, D. P., Carlton, R., Schopmeyer, S., Van Hooidonk, R., and

Lirman, D.: Effects of light and elevated pCO_2 on the growth and photochemical

efficiency of *Acropora cervicornis*. Coral Reefs, 33, 477–485, 2014.

600   Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey,C., Noonan, S., De'ath, G. et al.:

Losers and winners in coral reefs acclimatized to elevated carbon dioxide

concentrations. Nature Clim. Change, 1, 165–169, 2011.

Fagan K. E., and Mackenzie, F. T.: Air – sea CO_2 exchange in a subtropical estuarine-coral

reef system, Kaneohe Bay, Oahu, Hawaii. Mar. Chem., 106, 174 – 191, 2007.

605   Falter, J. L., Lowe, R. J., Atkinson, M. J., and Cuet, P.: Seasonal coupling and de-coupling

of net calcification rates from coral reef metabolism and carbonate chemistry at

Ningaloo Reef, Western Australia. J. Geophys. Res., 117, C05003,

doi:10.1029/2011JC007268, 2012.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F.

610   J.: Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science, 305, 362–

366, 2004.

Gattuso, J.-P., and Hansson, L.: Ocean acidification: background and history. Ocean

acidification, 2011.

Gattuso, J.-P., Allemand, D., and Frankignoulle, M.: Photosynthesis and calcification at

615   cellular, organismal and community levels in coral reefs: a review on interactions and

control by carbonate chemistry. Amer. Zool., 39, 160–183, 1999.

Gattuso, J.-P., Epitalon, J.-M., and Lavigne, H.: seacarb: Seawater carbonate chemistry. R

package version 3.0.6. http://CRAN.R-project.org/package=seacarb, 2015.

Giordano, M., Beardall, J., and Raven, J. A.: CO_2 concentrating mechanism in algae:

620   mechanisms, environmental modulation, and evolution. Annual Rev. Plant Biol., 56,

99–131, 2005.

Hepburn, C. D., Pritchard, D. W., Cornwall, C. E., McLeod, R. J., Beardall, J., Raven, J.

A., and Hurd, C. L.: Diversity of carbon use strategies in a kelp forest community:

implications for a high CO_2 ocean. Global Change Biol., 17, 2488–2497, 2011.

625 Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., et al.:

High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PLoS One, 6,

e28983, doi:10.1371/journal.pone.0028983, 2011.

Jokiel, P. L., Jury, C. P., and Ku'ulei, S. R.: Coral-algae metabolism and diurnal changes in

the CO_2-carbonate system of bulk sea water. PeerJ, 2, e378, doi: 10.7717/peerj.378,

630   2014.

Jokiel, P. L., Rodgers, K. S., Brown, E. K., Kenyon, J. C., Aeby, G., Smith, W. R., and

Farrell, F.: Comparison of methods used to estimate coral cover in the Hawaiian

Islands. PeerJ, 3,e954, doi.org/10.7717/peerj.954, 2015.

Kroeker, K. J., Kordas, R. L., Crim, R., Hendriks, I. E., Ramajo, L., Singh, G. S. et al.:

635   Impacts of ocean acidification on marine organisms: quantifying sensitivities and

interaction with warming. Global Change Biol., 19, 1884–1896, 2013.

Langdon, C., and Atkinson, M. J.: Effect of elevated pCO_2 on photosynthesis and

calcification of corals and interactions with seasonal change in temperature/irradiance

and nutrient enrichment. J. Geophys. Res., 110, C09S07, doi:10.1029/2004JC002576,

640   2005.

Langdon, C., Broecker, W. S., Hammond, D. E., Glenn, E., Fitzsimmons, K., Nelson, S.

G., et al.: Effect of elevated CO_2 on the community metabolism of an experimental

coral reef. Global Biogeochem. Cycles, 17, 1011, doi:10.1029/2002GB001941, 2003.

Lantz, C. A., Atkinson, M. J., Winn, C. W., and Kahng, S. E.: Dissolved inorganic carbon

645   and total alkalinity of a Hawaiian fringing reef: chemical techniques for monitoring the

effects of ocean acidification on coral reefs. Coral Reefs, 33, 105–115, 2014.

Leclercq, N., Gattuso, J.-P., and Jaubert, J.: Primary production, respiration, and

calcification of a coral reef mesocosm under increased CO_2 partial pressure. Limnol.

Oceanogr., 47, 558–564, 2002.

650 Mackey, K.R.M., Morris, J.J., Morel, F.M.M., and Kranz, S.A.: Response of

photosynthesis to ocean acidification. Oceanogr., 28,74–91, 2015.

Marubini, F., Barnett, H., Langdon, C., and Atkinson, M. J.: Dependence of calcification

on light and carbonate ion concentration for the hermatypic coral *Porites compressa*.

Mar. Ecol. Prog. Ser., 220, 153–162, 2001.

655 Marubini, F., Ferrier-Pagès, C., Furla, P., and Allemand, D.: Coral calcification responds

to seawater acidification: a working hypothesis towards a physiological mechanism.

Coral Reefs, 27, 491–499, 2008.

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren,

D. P. et al.: The next generation of scenarios for climate change research and

660   assessment. Nature, 463, 747–756, 2010.

Muscatine, L.: The role of symbiotic algae in carbon and energy flux in reef corals, in:

Dubinsky, Z. (Ed), Coral Reefs, Ecosystems of the World, Elsevier, Amsterdam, pp. 75-

87, 1990.

Muscatine, L., Goiran, C., Land, L., Jaubert, J., Cuif, J.-P., and Allemand, D.: Stable

665   isotopes (δ^{13}C and δ^{15}N) of organic matrix from coral skeleton. P. Natl Acad. Sci., 102,

1525–1530, 2005.

Okazaki, R. R., Towle, E. K., van Hooidonk, R., Mor, C., Winter, R. N., Piggot, A. M. et

al.: Species-specific responses to climate change and community composition determine

future calcification rates of Florida Keys reefs. Glob. Change Biol., 13481,

670   doi:10.1111/gcb.13481, 2016.

Raven, J. A., Beardall, J., and Giordano, M.: Energy costs of carbon dioxide concentrating

mechanisms in aquatic organisms. Photosynthesis Res., 121, 111–124, 2014.

Schoepf, V., Grottoli, A. G., Warner, M. E., Cai, W.-J., Melman, T. F., Hoadley, K. D. et

al.: Coral energy reserves and calcification in a high-CO_2 world at two temperatures.

675   PLoS One, 8, e75049. doi:10.1371/journal.pone.0075049, 2013.

Schoepf, V., Hu, X., Holcomb, M., Cai, W.-J., Li, Q., Wang, Y., et al.: Coral calcification

under environmental change: a direct comparison of the alkalinity anomaly and buoyant

weight techniques. Coral Reefs, doi:10.1007/s00338-016-1507-z, 2016.

Shaw, E. C., McNeil, B. I., and Tilbrook, B.: Impacts of ocean acidification in naturally

680   variable coral reef flat ecosystems. J. Geophys. Res., 117, C03038,

doi:10.1029/2011JC007655, 2012.

Shaw, E. C., Phinn, S. R., Tilbrook, B., and Steven, A.: Natural in situ relationships suggest coral reef calcium carbonate production will decline with ocean acidification. Limnol. Oceanogr., 60, 777–788, 2015.

685 Schneider, K., and Erez, J.: The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. Limnol. Oceanogr., 51, 1284–1293, 2006.

Stambler, N.: Zooxanthellae: the yellow symbionts inside animals. In Coral Reefs: An Ecosystem in Transition, pp. 87–106. Ed. by Z. Dubinsky, and N. Stambler. Springer,

690 Berlin, Germany, 2011.

Suggett, D. J., Dong, L. F., Lawson, T., Lawrenz, E., Torres, L., and Smith, D. J.: Light availability determines susceptibility of reef building corals to ocean acidification. Coral Reefs, 32, 327–337, 2013.

Washburn, L.: MCR LTER: coral reef: ocean currents and biogeochemitsry: salinity,

695 temperature and current at CTD and ADCP mooring FOR05 from 2005 ongoing. Knb-lter-mcr.30.30, 2015.

Biogeosciences
Discussions

Open Access

EGU

Table 1: Mean carbonate chemistry and temperature treatments in the flumes during the experiments conducted with back reef communities in Moorea and Oahu, and the fore reef community in Moorea. 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
Moorea Back reef	**Ambient**	8.01	2339	453	2025	3.52	35.9	26.9
		± 0.02	± 2	± 30	± 9	± 0.09		± 0.1
	OA	7.61	2344	1317	2230	1.64	35.9	27.0
		± 0.01	± 1	± 50	± 7	± 0.06		± 0.1
Oahu Back reef	**Ambient**	7.96	2160	490	1936	2.59	33.4	23.9
		± 0.01	± 4	± 23	± 8	± 0.06		± 0.2
	OA	7.62	2164	1233	2074	1.36	33.4	23.9
		± 0.02	± 4	± 76	± 12	± 0.10		± 0.2
Moorea Fore reef	**Ambient**	8.04	2329	400	1992	3.71	36.5	27.1
		± 0.01	± 2	± 14	± 8	± 0.08		± 0.1
	OA	7.65	2330	1176	2198	1.75	36.5	27.0
		± 0.01	± 2	± 37	± 6	± 0.05		± 0.1

Table 2: Results of the t-tests used to compare between pCO_2 treatments the parameters

705 of the hyperbolic tangent functions describing the relationship between community net

photosynthesis (P_{net}) and PAR and net calcification (G_{net}) 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).

710

Parameter	Experiment	Function parameter	*p*-value
Net Photosynthesis	Moorea – Back reef	$P_{net\ max}$	0.558
(P_{net})		α	0.387
		C_0	0.559
	Oahu – Back reef	$P_{net\ max}$	0.840
		α	0.536
		C_0	0.621
	Moorea – Fore reef	$P_{net\ max}$	0.942
		α	0.792
		C_0	0.579
Net Calcification	Moorea – Back reef	$G_{net\ max}$	0.376
(G_{net})		α	0.836
		C_0	0.046
	Oahu – Back reef	$P_{net\ max}$	0.867
		α	0.126
		C_0	0.394
	Moorea – Fore reef	$P_{net\ max}$	0.736
		α	0.715
		C_0	0.002

Table 3: Results of ANCOVA analyses testing for effects of pCO_2 on slopes and elevation of the P_{net} - G_{net} relationships. Results are shown for the experiments with back reef communities in Moorea and Oahu, and the fore reef communities in Moorea.
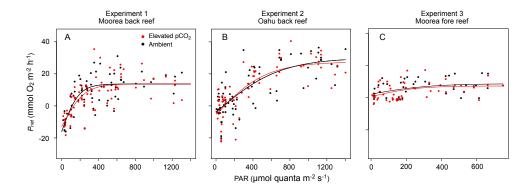
Experiment	Parameter	SS	F-value	P-value
Moorea - back reef	Slope	0.50	$F_{1,92} = 0.10$	0.749
	Elevation	100.48	$F_{1,92} = 20.49$	<0.001
Oahu - back reef	Slope	6.10	$F_{1,74} = 1.15$	0.286
	Elevation	66.40	$F_{1,74} = 12.57$	<0.001
Moorea - fore reef	Slope	0.83	$F_{1,62} = 0.24$	0.623
	Elevation	36.39	$F_{1,62} = 10.61$	0.002

715

Fig. 1. Relationships of net primary production (P_{net}) with PAR in three coral reef communities representing the back reef of Moorea (A), the back reef of Oahu (B), and the fore reef of Moorea (C). Communities were incubated under ambient pCO_2 (~400 μatm, black symbols and lines) and elevated pCO_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.

Fig. 2. Relationships of net calcification (G_{net}) with PAR in three coral reef communities

representing the back reef of Moorea (A), the back reef of Oahu (B), and the fore reef of

Moorea (C). Communities were incubated under ambient pCO_2 (~400 μatm, black

730   symbols and lines) and elevated pCO_2 (~1200 μatm, red symbols and lines). The curves

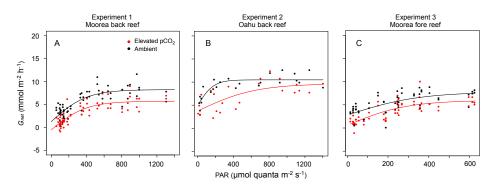represent the best fit of a hyperbolic tangent function for the relationship between G_{net}

and PAR.

Fig. 3. Variations in G_{net} as a function of P_{net} in the three study sites: (A) Moorea back

735   reef, (B) Oahu back reef, and (C) Moorea fore reef. Relationships were determined under

control pCO$_2$ (400 µatm, black points and lines) and elevated pCO$_2$ (~1200 µatm, red

points and lines). For the three communities and the two pCO$_2$ levels the slopes of the

linear relationships between P_{net} and G_{net} were significant.

740