Biogeosciences Discuss., 11, 12323–12339, 2014
www.biogeosciences-discuss.net/11/12323/2014/
doi:10.5194/bgd-11-12323-2014

Biogeosciences Discussions
Open Access

Ocean acidification accelerates dissolution of experimental coral reef communities

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

Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA

Received: 27 June 2014 – Accepted: 31 July 2014 – Published: 15 August 2014

Correspondence to: S. Comeau (steve.comeau@csun.edu)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Ocean acidification (OA) poses a severe threat to tropical coral reefs, yet much of what is know about these effects comes from individual corals and algae incubated in isolation under high pCO_2. Studies of similar effects on coral reef communities are scarce. To investigate the response of coral reef communities to OA, we used large outdoor flumes in which communities composed of calcified algae, corals, and sediment were combined to match the percentage cover of benthic communities in the shallow back reef of Moorea, French Polynesia. Reef communities in the flumes were exposed to ambient (~ 400 µatm) and high pCO_2 (~ 1300 µatm) for 8 weeks, and calcification rates measured for the constructed communities including the sediments. Community calcification was depressed 59 % under high pCO_2, with sediment dissolution explaining ~ 50 % of this decrease; net calcification of corals and calcified algae remained positive, but was reduced 29 % under elevated pCO_2. These results show that despite the capacity of coral reef calcifiers to maintain positive net accretion of calcium carbonate under OA conditions, reef communities might switch to net dissolution as pCO_2 increases, particularly at night, due to enhanced sediment dissolution.

1 Introduction

The calcium carbonate framework produced by coral reefs hosts the highest known marine biodiversity, and protects tropical shores from wave erosion (Ferrario et al., 2014). However, in recent decades coral reefs have been impacted by a diversity of disturbances, and now are threatened by an increase in seawater temperature and ocean acidification (OA) (Hoegh-Guldberg et al., 2007; Kleypas and Yates, 2009). OA is caused by the dissolution of atmospheric CO_2 in seawater, which reduces pH, depresses carbonate ion concentration, and increases bicarbonate ion concentration with no change in total alkalinity (Feely et al., 2004). The net effects of OA on coral reefs remain unclear as most studies show a decrease in organismic calcification under OA

BGD
11, 12323–12339, 2014

(Erez et al., 2011; Chan and Connolly, 2012), while recent work describes species-specific responses with some corals and calcifying algae resistant to decreasing pH (Comeau et al., 2013; Takahashi and Kurihara, 2013). Critically, most of these studies have been performed on individuals maintained in isolation in laboratory conditions.

The results from laboratory studies are valuable, but to examine the potential for emergent properties of coral reefs exposed to OA effects, now it is necessary to scale up from individual- to community-level experiments (Leclercq et al., 2002; Dove et al., 2013; Edmunds et al., 2013). Generally there are three complementary approaches to study the responses of coral reef communities to OA. First, in situ observations of communities living in naturally acidified water (Fabricius et al., 2011) due to volcanic activities or local conditions (Shamberger et al., 2014). Second, carbonate chemistry can be manipulated directly in situ (Kline et al., 2012), but this approach is challenging technically and has yet to be used to study intact communities. Third, reef communities can be created ex situ (Dove et al., 2013) to allow precise control of the physical parameters predicted under future OA conditions. For our experiment, we chose to construct ex situ communities and used, for the first time, large outdoor flumes (after Atkinson and Bilger, 1992) to investigate the effects of OA on coral reefs communities.

In addition to corals and macroalgae, it is important to incorporate sediment in OA experiments, as this component of reef ecosystems may be sensitive to decreasing pH (Cyronak et al., 2013a, b). Observations in Bermuda have shown that the dissolution of Mg-calcite sediments is occurring under present seawater conditions, and might exceed precipitation of calcium carbonate by 2100 (Andersson et al., 2007). Further, in situ manipulations show that elevated pCO_2 (~ 800 µatm) can switch the calcification budget of coral reef sediments from net precipitation to net dissolution (Cyronak et al., 2013a). Given the aforementioned results, we included sediment chambers in our flumes (Fig. 1) in order to integrate reef carbonate sediments into the analysis of OA effects on communities under ecologically relevant conditions.

Our experiment investigated the response to OA of constructed reef communities representative of present day back reef communities of Moorea. Communities were

BGD
11, 12323–12339, 2014

incubated for 8 weeks in two flumes at ambient pCO_2 conditions (~ 450 µatm) and two flumes at an elevated pCO_2 (~ 1300 µatm) under natural lighting, controlled temperature, and water flow similar to those experienced on a shallow reef flat (Atkinson and Bilger, 1992; Carpenter and Williams, 2007). Calcification was measured at three levels of biological function using the alkalinity anomaly technique: whole community, sediments, and macro-calcifiers (i.e., corals and calcified algae as determined by subtraction).

2 Materials and methods

2.1 Collection and sample preparation

This study was carried out in August–October 2013 in Moorea, French Polynesia, using organisms collected from the back reef of the north shore at ~ 1–2 m depth. The organisms were used to construct communities in outdoor flumes matching the contemporary (in 2013) mean cover of a back reef in Moorea (Carpenter, 2014; Edmunds, 2014). Coral communities were built from the four dominant coral taxa found on the back reefs of Moorea: massive *Porites* spp. (11 % cover), *Porites rus* (6 %), *Montipora* spp. (3 %), and *Pocillopora* spp. (2 %), that together accounted for 98 % of the coral cover. In addition to corals, 6 % of the surface comprised crustose coralline algae that consisted of 66 % *Porolithon onkodes* and 33 % *Lithophyllum flavescens*. After collection of corals and algae (10 cm × 10 cm), they were returned to the Richard B. Gump South Pacific Research and attached to plastic supports using epoxy glue. Following preparation, samples were left to recover in a seawater table for 3 d.

Sediments were collected from the lagoon on the north shore, ~ 200 m from the reef crest, at 2 m depth using 24 custom made boxes (0.4 m × 0.3 m × 0.3 m). Sediment boxes were inserted into the sediment and left in situ for 4 d to allow sediment stratification to be established naturally before transfer to the flumes.

BGD
11, 12323–12339, 2014

The 4 outdoor flumes consisted of a working section measuring 5.0 m × 0.3 m × 0.3 m. Water was re-circulated using water pumps (W. Lim Wave II 373 J s^{-1}) to obtain a 10 cm s^{-1} flow. Flow was measured across the working section of the flume using a Nortek Vectrino Acoustic Doppler Velocimeter. At each end of the flume seawater passed through an 88 cm transition section (rectangular to circular) that housed 20 cm (length) flow straighteners made of stacked, 3 cm diameter PVC pipe, and then into a 12.5 cm return section. Fresh sand-filtered seawater, pumped from Cook's Bay at 12 m depth, was dispensed continuously into the flume at 5 L min^{-1}. Flumes experienced natural sunlight that was attenuated using screen to maintain irradiances similar to ambient irradiances in the back reefs of Moorea (daily maximum of ∼ 1500 µmol photons m^{-2} cm^{-1} over the incubation period determined with a 4π quantum sensor LI-193 and a LiCor LI-1400 meter).

2.2 Carbonate chemistry control and measurements

Two flumes were maintained at ambient conditions and two at a pCO_2 expected by the end of the present century under a pessimistic scenario (Representative Concentration Pathway 8.5, ∼1300 µatm, Moss et al., 2010). Control of the pCO_2 was accomplished using a pH-stat (Aquacontroller, Neptune systems, USA) and pH was maintained 0.1 unit lower at night (from 18:00:00 to 6:00:00 LT) than during the day to match the natural diel variation in pH in the back reef of Moorea.

pH 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 also was measured spectrophotometrically using m-cresol dye (Dickson et al., 2007) at regular intervals. Measurement of total alkalinity (A_T) was made using open-cell potentiometric titrations (Dickson et al., 2007) using 50 mL samples of seawater collected every 2–3 d. Parameters of the carbonate system in seawater were calculated using the R package seacarb (Lavigne and Gattuso, 2013).

BGD
11, 12323–12339, 2014

2.3 Calcification measurements

Calcification rates were measured using the total alkalinity anomaly method (Chisholm and Gattuso, 1991). Calcification measurements were made every 7 d on the constructed community, and in the analysis of sediments alone, after 7, 30, and 56 d incubation. During incubations, the addition of seawater was stopped so that each flume was a closed loop; seawater samples for A_T were taken every 3 h during the day and every 6 h at night. To maintain A_T and nutrients close to ambient levels, water in the flumes was refreshed every 6 h for 30 min. Nutrient changes in the flumes were monitored during 4 incubations and the changes in nitrate and ammonium during incubations were $< 2\,\mu mol\,L^{-1}$. To conduct incubations with sediments alone, corals and coralline algae were removed from the flumes for 24 h and held in a separate tank where conditions were identical to those in the flumes. Corals and coralline algal calcification was calculated by subtracting the mean light and dark net calcification of the sediment from the community calcification. For both corals and algae, buoyant weight (Davies, 1989) was recorded before and after incubation and converted to dry weight to quantify the contribution of each functional group to the calcification budget.

2.4 Statistical analysis

All analyses were performed using R software (R Foundation for Statistical Computing), and assumptions of normality and equality of variance were evaluated through graphical analyses of residuals. Calcification rates were analyzed using a repeated measure ANOVA in which the within subject factor was time (week), pCO_2 was a fixed effect, and duplicate flumes were a nested effect.

BGD
11, 12323–12339, 2014

3 Results

3.1 Community

Mean pCO_2 in the four flumes during the 8 week incubation was 456 ± 21 µatm and 451 ± 21 µatm in the ambient treatments, and 1329 ± 28 µatm and 1306 ± 41 µatm in the high pCO_2 treatments (±SE, n = 42). Net calcification was higher at ambient vs. high pCO_2 (Fig. 2a), both during the day and night (p = 0.012 and 0.022, respectively); there were no significant differences between flumes within each treatment. At night, treatment effects were more striking than during the day, as calcium carbonate dissolution exceeded precipitation at high pCO_2 ($-1.6 \pm 0.9\,gCaCO_3\,m^{-2}\,d^{-1}$), whereas net precipitation remained positive at ambient pCO_2 ($2.7 \pm 0.6\,gCaCO_3\,m^{-2}\,d^{-1}$) (both means ±SE, n = 16). Calcification integrated over 24 h highlighted the difference between treatments (p = 0.001), with calcification 59 % lower at high pCO_2 than at ambient pCO_2.

3.2 Sediments

Net calcification of the sediment alone differed between treatments, during the day and night (p = 0.003) (Fig. 2b), but there were no differences between flumes within each treatment. Net calcification pooled among treatments was negative during the day ($-1.0 \pm 1.3\,gCaCO_3\,m^{-2}\,d^{-1}$) and night ($-3.72 \pm 0.6\,gCaCO_3\,m^{-2}\,d^{-1}$) at high pCO_2, whereas net calcification was positive during the day ($1.4 \pm 1.1\,gCaCO_3\,m^{-2}\,d^{-1}$) and negative at night ($-1.0 \pm 0.8\,gCaCO_3\,m^{-2},d^{-1}$) in the ambient treatment. When calcification was integrated over 24 h, pCO_2 effects were significant (p = 0.001), with dissolution exceeding precipitation at high pCO_2 ($-2.3 \pm 1.1\,gCaCO_3\,m^{-2}\,d^{-1}$), and a nearly balanced calcification budget under ambient pCO_2 ($0.2 \pm 0.9\,gCaCO_3\,m^{-2}\,d^{-1}$). These net calcification rates for the sediment were normalized to the entire planar area of the flumes occupied by the community; sediment net calcification rates were then higher

BGD
11, 12323–12339, 2014

when normalized to the planar area of sediment in the sediment box (0.4 ± 1.5 and $-4.0 \pm 1.9\,gCaCO_3\,m^{-2}\,d^{-1}$ at ambient and high pCO_2, respectively).

3.3 Corals and calcifying algae

The total net calcification of corals and calcifying algae was estimated by subtracting the mean sediment calcification rates from the total community calcification in each flume. Net calcification of the corals and calcifying algae differed between treatments during the day ($p = 0.030$) and night ($p = 0.041$) (Fig. 2c). In contrast to the whole community and the sediments alone, net calcification of corals and calcifying algae was positive at night at high pCO_2 ($1.1 \pm 0.5\,gCaCO_3\,m^{-2}$ in 12 h), but was 24 % and 44 % lower at high pCO_2 compared to ambient pCO_2 during the day and night, respectively. Net calcification integrated over 24 h also differed between treatments ($p < 0.001$) with calcification at ambient pCO_2 29 % higher than at high pCO_2.

Calcification of our constructed communities was driven principally by corals, since their contribution to the calcification budget, based on buoyant weight was ~ 98 % of the total (Fig. 3). Massive *Porites* spp. was the main contributor to this effect, with an increased contribution to the calcification budget at high pCO_2 (40 % at ambient pCO_2 and 48.5 % at high pCO_2, Fig. 3). In contrast, the importance of *P. rus*, *Montipora* spp., and *Pocillopora* spp. was reduced at high pCO_2. The low contribution of coralline algae to the calcification budget was due to high mortality by the end of the incubation and because of a disproportionate surface area to planar area relationship in corals.

4 Discussion

Using outdoor flumes, we show that the effects of OA on coral reef communities are greater than estimates obtained by summing results obtained by incubating organisms in isolation under similar conditions and assuming their contribution to community calcification is proportional to their planar cover. Indeed, at community level, the reduction

BGD
11, 12323–12339, 2014

in net calcification attributed to high pCO_2 was greater than the mean reduction of 26 % calculated in a recent meta-analysis of the effects of future conditions (~ 1300 µatm) based on organismic calcification (Chan and Connolly, 2013). This discrepancy is likely not caused by an experimental bias as rates of net community calcification in the flumes in the ambient treatment were similar to rates measured for reefs on the north shore of Moorea where measurements in 2012 and 2013 showed that light calcification ranged from 5–25 $g CaCO_3\, m^{-2}\, d^{-1}$ (R. C. Carpenter, unpublished data), which spans the rates measured in the flumes (i.e., 13.9 $g CaCO_3\, m^{-2}\, d^{-1}$ in the light, Fig. 2a). Net community calcification in Moorea in 1991 (~ 19–25 $g CaCO_3\, m^{-2}\, d^{-1}$; Gattuso et al., 1996) also was similar to the rates measured in both the flumes (this study) and field.

The discrepancy between community level (the present study) and past work at organisms level in fact was caused by dissolution of sediments that represented up to 50 % of the decrease in calcification at high pCO_2. These results demonstrate the sensitivity of carbonate sediments to dissolution at elevated pCO_2, and are in agreement with a recent field manipulation on Heron Island where dissolution exceeded precipitation at $pCO_2 > 500$ µatm (Cyronak et al., 2013a). During a mesocosm experiment, Dove et al. (2013) also have shown that a pH of 7.7 caused a greater percentage representation of small-grained (i.e., ≤ 1 mm) sediments as a resolute dissolution of larger grains. Sediment grain size did not change in our incubations (results not shown).

When the sediment effect was subtracted, corals and coralline algae alone exhibited a decrease in net calcification over 24 h of 29 % between ambient and high pCO_2 treatments. Such decrease is in agreement with our previous work where we have shown that the calcification rates of 16 calcifiers in Moorea declined 0–40 % at 1300 µatmpCO_2 compared to rates under ambient pCO_2 (Comeau et al., 2013, 2014). It is also within the range of the predicted changes for calcification under a tripling of pCO_2 estimated by meta-analysis (i.e., ~ 26 % reduction; Chan and Connolly, 2012).

Our results demonstrate the utility of large outdoor flumes for investigating the responses of coral reef communities to OA. Similar rates of calcification in the field and in the flumes suggest that the communities assembled in the flumes effectively mim-

BGD
11, 12323–12339, 2014

icked communities in the back reef of Moorea and were exposed to conditions simulating natural conditions. The ability to create ecologically relevant flow conditions in the flumes is likely to be especially important for establishing ecological relevance, as flow is critical in modulating mass transfer and metabolism of coral reef organisms (Atkinson and Gilmer, 1992; Carpenter and Williams, 2007). Moreover, high flow speeds are suspected to either enhance coral calcification by favoring proton export through boundary layers (Jokiel, 2011; Jokiel et al., 2014), or to increase sensitivity of coralline algae to OA by reducing their capacity to maintain high pH in the passive boundary layer (Cornwall et al., 2013, 2014).

5 Conclusions

The present results suggest that calcifying organisms may maintain net positive calcification under pCO_2 as high as 1300 µatm, but at the scale of intact reefs in back reef habitats, community net calcification will be affected strongly and negatively. The present experiments demonstrate the importance of high cover of living organisms on benthic surfaces in maintaining a positive balance between precipitation and dissolution of calcium carbonate. Whereas several reefs around the world are already at the threshold between precipitation and dissolution of calcium carbonate (Silverman et al., 2009), the susceptibility of coral reefs to net dissolution in the future will be linked directly to the proportion of the reef covered by macro-calcifiers and sediments. In addition to dissolution, coral reefs also will be exposed to increased bioerosion at high pCO_2 (Wisshak et al., 2012; Crook et al., 2013) that will decrease the integrity of the carbonate framework. Our results suggest that under OA conditions anticipated by the end of the current century at least some tropical corals and calcifying algae will persist, but the function of the coral reef community as a net precipitator of calcium carbonate and a means to protect coasts against erosion (Ferrario et al., 2014) will be challenged.

BGD
11, 12323–12339, 2014

Author contribution. S.C. designed and performed experiments, analyzed data and wrote the paper; C. L. performed experiments and wrote the paper; B. C. and P.E. designed experiments, analyzed data and wrote the paper.

Acknowledgements. We dedicate this paper to Marlin Atkinson who pioneered the use of large outdoor flumes for the analysis of coral community metabolism, and whose work inspired our science and the present experiments. This study was funded by the National Science Foundation (OCE 10-41270) and the Moorea Coral Reef LTER (OCE 04-17413 and 10-26852). This is contribution number xxx of the CSUN Marine Biology Program.

References

Andersson, A. J., Bates, N. R., and Mackenzie, F. T.: Dissolution of carbonate sediments under rising pCO_2 and ocean acidification: observations from Devil's Hole, Bermuda, Aquat. Geochem., 13, 237–264, 2007.

Atkinson, M. J. and Bilger, R. W.: Effects of water velocity on phosphate uptake in coral reef-flat communities, Limnol. Oceanogr., 37, 273–279, 1992.

Carpenter, R. C. of Moorea Coral Reef LTE R.: MCR LTER: Coral Reef: Long-term population and community dynamics: benthic algae and other community components, ongoing since 2005, knb-lter-mcr.8.2, available at: http://metacat.lternet.edu/knb/metacat/knb-lter-mcr.8.27/lter, 2014.

Carpenter, R. C. and Williams, S. L.: Mass transfer limitation of photosynthesis of coral reef algal turfs, Mar. Biol., 151, 435–450, 2007.

Chan, N. C. S. and Connolly, S. R.: Sensitivity of coral calcification to ocean acidification: a meta-analysis, Glob. Change Biol., 19, 282–290, 2013.

Chisholm, J. R. M. and Gattuso, J.-P.: Validation of the alkalinity anomaly technique for investigating calcification and photosynthesis in coral reef communities, Limnol. Oceanogr., 36, 1232–1239, 1991.

Comeau, S., Edmunds, P. J., Spindel, N. B., and Carpenter, R. C.: The responses of eight coral reef calcifiers to increasing partial pressure of CO_2 do not exhibit a tipping point, Limnol. Oceanogr., 58, 388–398, 2013.

BGD
11, 12323–12339, 2014

Comeau, S., Edmunds, P. J., Spindel, N. B., and Carpenter, R. C.: Fast coral reef calcifiers are more sensitive to ocean acidification in short-term laboratory incubations, Limnol. Oceanogr., 59, 1081–1091, 2014.
Cornwall, C. E., Hepburn, C. D., Pilditch, C. A., and Hurd, C. L.: Concentration boundary layers around complex assemblages of macroalgae: Implications for the effects of ocean acidification on understory coralline algae, Limnol. Oceanogr., 58, 58–130, 2013.
Cornwall, C. E., Boyd, P. W., McGraw, C. M., Hepburn, C. D., Pilditch, C. A., Morris, J. N., Smith, A. M., and Hurd, C. L.: Diffusion boundary layers ameliorate the negative effects of ocean acidification on the temperate coralline macroalga *Arthrocardia corymbosa*, PLoS One, 9, e97235, doi:10.1371/journal.pone.0097235, 2014.
Crook, E. D., Cohen, A. L., Rebolledo-Vieyra, M., Hernandez, L., and Paytan, A.: Reduced calcification and lack of acclimatization by coral colonies growing in areas of persistent natural acidification, P. Natl. Acad. Sci. USA, 110, 11044–11049, 2013.
Cyronak, T., Santos, I. R., and Eyre, B. D.: Permeable coral reef sediment dissolution driven by elevated pCO_2 and pore water advection, Geophys. Res. Lett., 40, 4876–4881, 2013a.
Cyronak, T., Santos, I. R., McMahon, A., and Eyre, B. D.: Carbon cycling hysteresis in permeable carbonate sands over a diurnal cycle: implications for ocean acidification, Limnol. Oceanogr., 58, 58–143, 2013b.
Davies, P. S.: Short-term growth measurements of corals using an accurate buoyant weighing technique, Mar. Biol., 101, 389–395, 1989.
Dickson, A. G., Sabine, C. L., and Christian, J. R. (Eds.): Guide to best practices for CO_2 measurements, PICES Special Publication, 3, 191 pp., 2007.
Dove, S. G., Kline, D. I., Pantos, S., Angly, F. E., Tyson, G. W., and Hoegh-Guldberg, O.: Future reef decalcification under a business-as-usual CO_2 emission scenario, P. Natl. Acad. Sci. USA, 110, 15342–15347, 2013.
Edmunds, P. J. of Moorea Coral Reef LTE R.: MCR LTER: Coral Reef: Long-term 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.
Edmunds, P. J., Carpenter, R. C., and Comeau, S.: Understanding the threats of ocean acidification to coral reefs, Oceanogr., 26, 149–152, 2013.
Erez, J., Reynaud, S., Silverman, J., Schneider, K., and Allemand, D.: Coral calcification under ocean acidification and global change, in: Coral Reefs: an Ecosystem in Transition, edited by Dubinsky, Z. and Stambler, N., Springer, Germany, 151–176, 2011.

BGD
11, 12323–12339, 2014

Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., Muehllehner, N., Glas, M. S., and Lough, J. M.: Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations, Nature Clim. Change, 1, 165–169, 2011.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J.: Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans, Science, 305, 362–366, 2004.

Ferrario, F., Beck, M. W., Storlazzi, C. D., Micheli, F., Shepard, C. C., and Airoldi, L.: The effectiveness of coral reefs for coastal hazard risk reduction and adaptation, Nature Comm., 5, doi:10.1038/ncomms4794, 2014.

Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C., and Frankignoulle, M.: Carbon fluxes in coral reefs. I. Lagrangian measurement of community metabolism and resulting air–sea CO_2 disequilibrium, Mar. Ecol.-Progr. Ser., 145, 109–121, 1996.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell, C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R. H., Dubi, A., and Hatziolos M. E.: Coral reefs under rapid climate change and ocean acidification, Science, 318, 1737–1742, 2007.

Jokiel, P. L.: The reef coral two compartment proton flux model: a new approach relating tissue-level physiological processes to gross corallum morphology, J. Exp. Mar. Biol. Ecol., 409, 1–12, 2011.

Jokiel, P. L., Jury, C. P., and Rodgers, K. S.: Coral-algae metabolism and diurnal changes in the CO_2-carbonate system of bulk sea water, PeerJ, 2, e378, doi:10.7717/peerj.378, 2014.

Kleypas, J. and Yates, K.: Coral reefs and ocean acidification, Oceanogr., 22, 108–117, 2009.

Kline, D. I., Teneva, L., Schneider, K., Miard, T., Chai, A., Marker, M., Headley, K., Opdyke, B., Nash, M., Valetich, M., Caves, J. K., Russell, B. D., Connell, S. D., Kirkwood, B. J., Brewer, P., Peltzer, E., Silverman, J., Caldeira, K., Dunbar, R. B., Koseff, J. R., Monismith, S. G., Mitchell, B. G., Dove, S., Hoegh-Guldberg, O.: A short-term in situ CO_2 enrichment experiment on Heron Island (GBR), Scientific Reports, 2, 413, doi:10.1038/srep00413, 2012.

Lavigne, H. and Gattuso, J.-P.: Seacarb, seawater carbonate chemistry with R. R package version 2.4.10, available at: http://CRA~N.R-project.org/package=seacarb, 2013.

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, 47–564, 2002.

BGD
11, 12323–12339, 2014

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., VanVuuren, D. P., Carter, T. R., Emori, S., Kainuma, M., Kram, T., Meehl, G. A., Mitchell, J. F., Nakicenovic, N., Riahi, K., Smith, S. J., Stouffer, R. J., Thomson, A. M., Weyant, J. P., and Wilbanks, T. J.: The next generation of scenarios for climate change research and assessment, Nature, 463, 747–756, 2010.

Shamberger, K. E. F., Cohen, A. L., Golbuu, Y., McCorkle, D. C., Lentz, S. J., and Barkley, H. C.: Diverse coral communities in naturally acidified waters of a Western Pacific reef, Geophys. Res. Lett., 41, 499–504, 2014.

Silverman, J., Lazar, B., Cao, L., Caldeira, K., and Erez, J.: Coral reefs may start dissolving when atmospheric CO_2 doubles, Geophys. Res. Lett., 36, L05606, doi:200910.1029/2008GL036282, 2009.

Takahashi, A. and Kurihara, H.: Ocean acidification does not affect the physiology of the tropical coral *Acropora digitifera* during a 5week experiment, Coral Reefs, 32, 305–314, 2013.

Wisshak, M., Schönberg, C. H. L., Form, A., and Freiwald, A.: Ocean acidification accelerates reef bioerosion, PLoS One, 7, e45124, doi:10.1371/journal.pone.0045124, 2012.

BGD
11, 12323–12339, 2014

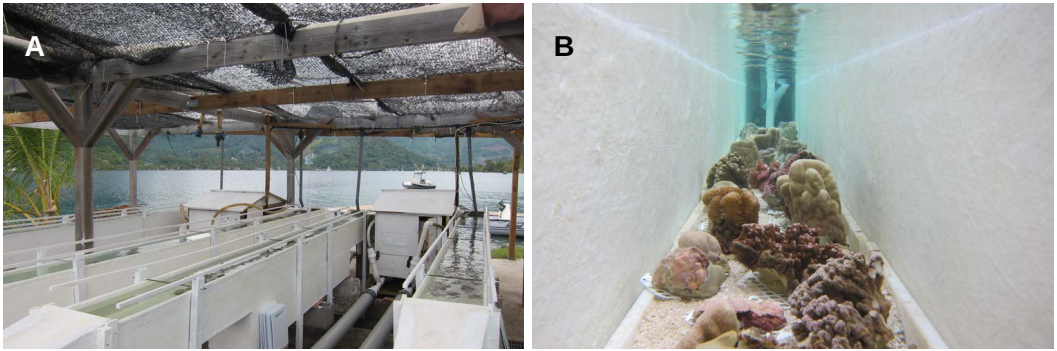

Figure 1. Photographs of the outdoor flumes. **(A)** The flumes consisted of a 5.00 m × 0.30 m × 0.30 m working section, and a lower sediment chamber (2.50 × 0.30 × 0.25 m) in which sediments were maintained, and together contained ~600 L of seawater. **(B)** Communities matching the average composition (in 2013) of the back reef in Moorea were constructed in the flumes.

BGD
11, 12323–12339, 2014

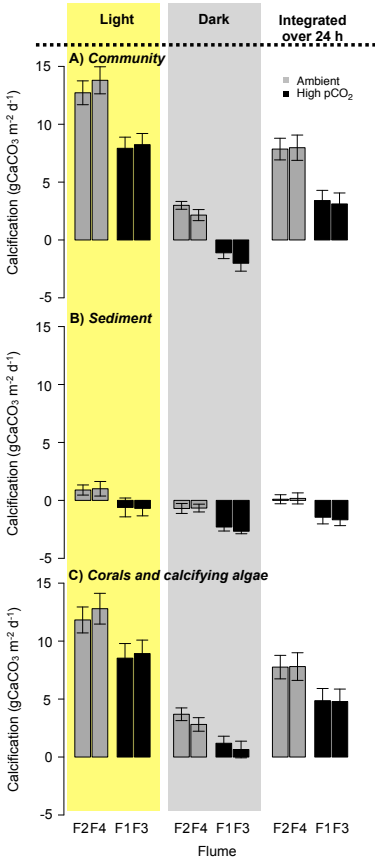

Figure 2. Calcification in the light, dark, and integrated over 24 h for intact communities **(A)**, sediment **(B)**, and corals and coralline algae **(C)** maintained under ambient and high pCO_2 ($\sim$ 1300 µatm). The grey bars represent the calcification measured in the ambient conditions and the black bars are calcification in the elevated pCO_2 treatment.

BGD
11, 12323–12339, 2014

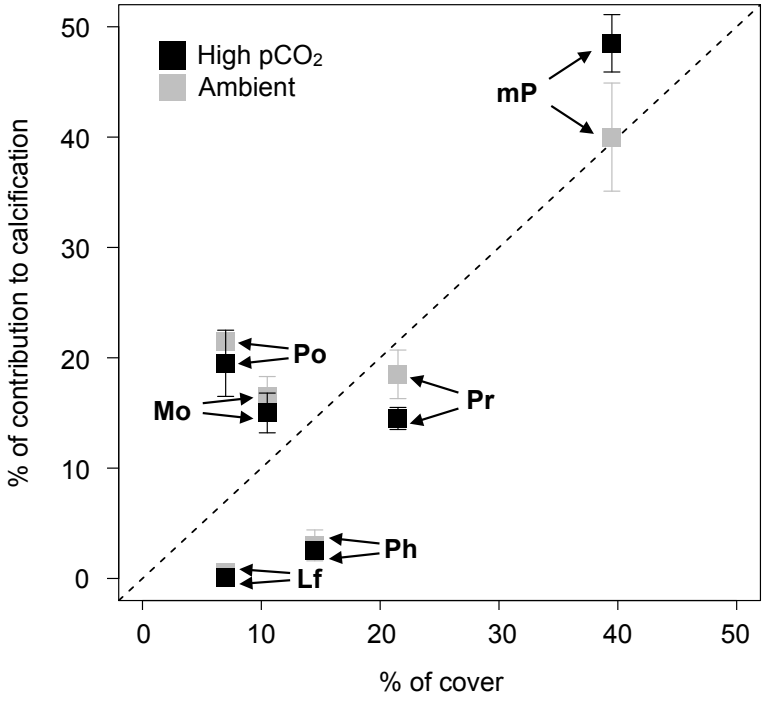

Figure 3. Relative contribution of each functional group of corals and calcifying algae to the calcification budget of communities as a function of their contribution to the planar surface area of calcifiers in the flumes. Contribution to the calcification budget was derived from the buoyant weight measurements made on each individual at the beginning and end of the 8 week incubation. The grey (ambient condition) and black (high pCO_2) squares correspond to the mean ±SD specific contributions of massive *Porites* (mP), *Porites rus* (Pr), *Pocillopora* spp. (Po), *Montipora* spp. (Mo), *Porolithon onkodes* (Ph), and *Lithophyllum flavescens* (Lf). The dashed line corresponds to a contribution to the calcification budget equivalent to the planar surface areas of calcifier in the flumes.

BGD
11, 12323–12339, 2014