1 **Ocean acidification accelerates dissolution of experimental coral reef communities**

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**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 reduced by 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 by 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 transition 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 (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; Jokiel et al., 2008; Andersson et al., 2009; Dove et al., 2013; Edmunds et al., 2013). Generally there are three complementary approaches to studying 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), although this approach is challenging technically and has yet to be used to study

47 intact communities. Third, reef communities can be created *ex situ* (Andersson et al.,
48 2009; Dove et al., 2013) to allow precise control of the physical parameters predicted
49 under future OA conditions. For our experiment, we chose to construct *ex situ*
50 communities and used, for the first time, large outdoor flumes (after Atkinson and Bilger,
51 1992) to investigate the effects of OA on coral reef communities.

52 In addition to corals and macroalgae, it is important to incorporate sediments in
53 OA experiments, as this component of reef ecosystems may be sensitive to decreasing pH
54 (Cyronak et al. 2013a, b; Andersson et al., 2009). Dissolution occurs on coral reefs in
55 sediment pore-waters, or in particular microenvironments where $pCO_2$ is elevated due to
56 biological activity (Andersson and Gledhill, 2013). Observations in Bermuda have shown
57 that the dissolution of Mg-calcite sediments occurs in a location with seawater $pCO_2$
58 naturally elevated to values expected by the end of the century (Andersson et al., 2007).
59 Further*, in situ* manipulations show that elevated $pCO_2$ (~ 800 µatm) can transition the
60 calcification budget of coral reef sediments from net precipitation to net dissolution
61 (Cyronak et al., 2013a). Increasing $pCO_2$ likely will lead to increasing dissolution and
62 decreased precipitation of calcium carbonate, resulting in coral reef community
63 calcification changing from net precipitation to net dissolution (Yates and Halley, 2006;
64 Silvermann et al., 2009; Andersson et al., 2009). Given the aforementioned results that
65 highlight the importance of sediments in the community calcification of entire coral reefs,
66 we included sediment chambers in our flumes (Fig. 1) to integrate reef carbonate
67 sediments into the analysis of OA effects on communities under ecologically relevant
68 conditions.

Our experiment investigated the response to OA of constructed reef communities representative of present day back reef communities of Moorea. Communities were incubated for 8 weeks in two flumes at ambient seawater $pCO_2$ (~ 400 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 used to construct communities in outdoor flumes were assembled to match 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 in 2013), *Porites rus* (6%), *Montipora* spp. (3%), and *Pocillopora* spp. (2%), that together accounted for 98% of the coral cover in this habitat in 2013. In addition to corals, 6% of the surface was covered by crustose coralline algae (66% *Porolithon onkodes* and 33% *Lithophyllum flavescens*), and 5% by rubble (dead coral skeletons). After collection of corals and algae (all ~ 10 × 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 × 0.3 × 0.3 m). Sediment boxes were inserted into the sediment and left *in situ* for 4 d to allow chemical stratification in the sediment to re-establish before transferring the boxes to the flumes. It was not possible to subsample these boxes to quantify the stratification of the sediment, and therefore we assume that 4 d was adequate for stratification to be re-established.

The four outdoor flumes consisted of a working section measuring 5.0 × 0.3 × 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 long transition section (circular to rectangular) that housed 20-cm (length) flow straighteners made of stacked, 3-cm diameter PVC pipe, and then into a 12.5-cm (diameter) 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 fiberglass screens 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). Temperature in the flumes was maintained at ~ 27 °C to match the ambient temperature in the back reef of Moorea in September-October.

## 2. 2 Carbonate chemistry control and measurements

As the $pCO_2$ level in the back reef of Moorea is close to open-ocean and current atmospheric values (e.g., Comeau et al. 2014a), $pCO_2$ levels for the incubations were chosen to match ambient $pCO_2$ (~ 400 µatm) and the $pCO_2$ expected in the atmosphere by the end of the present century under a pessimistic scenario (Representative Concentration Pathway 8.5, ~1300 µatm, Moss et al., 2010). $pCO_2$ in the flumes was controlled using a pH-stat (Aquacontroller, Neptune systems, USA) that actuated the bubbling of either pure $CO_2$ or $CO_2$-free air into the seawater. To match the natural diel variation in pH in the back reef of Moorea (Hofmann et al., 2011; Comeau et al., 2014a) pH was maintained 0.1 unit lower at night (from 18:00 to 6:00) than during the day.

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. pH measured spectrophotometrically or using a pH electrode provided similar results with means differing < 0.01 pH unit. 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. Titrations of certified reference materials provided by A. G. Dickson (batch 122) yielded $A_T$ values within 3.5 µmol $kg^{-1}$ of the nominal value (SE = 3.1 µmol $kg^{-1}$; n = 14). Parameters of the carbonate system in seawater were calculated using the R package seacarb (Lavigne and Gattuso, 2013).

138 **2.3 Calcification measurements and sediment analysis**

139 Calcification rates were measured using the total alkalinity anomaly method
140 (Chisholm and Gattuso, 1991). Calcification measurements were made every 7 d on the
141 constructed community, and in the analysis of sediments alone, after 7, 30, and 56 d of
142 treatments. During incubations, the addition of seawater was stopped so that each flume
143 operated in a closed loop; seawater samples for $A_T$ then were taken every 3 h during the
144 day and every 6 h at night. To maintain $A_T$ and nutrients close to ambient levels, water in
145 the flumes was refreshed every 3-6 h for 30 min. Regular refreshing limited changes in
146 alkalinity during incubations to < 50-100 μmol $kg^{-1}$, which corresponded to variations in
147 aragonite saturation state (Ω) of < 0.1-0.2. Nutrient changes in the flumes were monitored
148 during four incubations and the changes in nitrate and ammonium during incubations
149 were < 2 μmol $L^{-1}$. To conduct incubations with sediments alone, corals and coralline
150 algae were removed from the flumes for 24 h and held in a separate tank where
151 conditions were identical to those in the flumes. Corals and coralline algal calcification
152 was calculated by subtracting the mean light and dark net calcification of the sediments
153 from the community calcification. For both corals and algae, buoyant weight (Davies,
154 1989) was recorded before and after the 8-week treatments and converted to dry weight
155 to quantify the contribution of each functional group to the calcification budget. Sediment
156 grain size of each flume was analyzed in triplicate using sediment sieves. Three vertical
157 cross sections of sand (~ 600g) were collected from each flume sediment chamber and
158 dried at 60 °C to remove moisture. Sand then was sieved through five separate sediment
159 sieves (149 μm, 420 μm, 840 μm, 3360 μm) yielding six size class fractions for each
160 flume (n = 3).

### 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 was a nested effect.

## 3 Results

### 3.1 Carbonate chemistry and organism condition

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). $pCO_2$ differed between treatments (repeated measure ANOVA, $F_{1,232} = 734.38$, $p < 0.001$), but there was no difference within treatments ($F_{2,232} = 0.16$, $p = 0.852$). Communities were maintained in conditions within the flumes that were super-saturated with respect to aragonite, as $\Omega_{arag} \sim 3.5$ under ambient conditions, and ~ 1.6 in the high $pCO_2$ treatment.

No *Pocillopora* spp. and *Montipora* spp. colonies died during the 8-week treatments, but 10% of the *Porites* pooled across flumes died by the end of the experiment, regardless of treatment, because of an outbreak of corallivorous nudibranchs feeding on this taxon (*Phestilla* spp.). Coralline algae (~ 70%) died at the end of the incubation, which was likely due to sediment abrasion. No difference in mortality or bleaching was observed between treatments for corals and calcified algae.

184 **3.2 Community**

185 Net calcification was higher at ambient versus high $pCO_2$ (Fig. 2A), both during
186 the day and night (repeated measures ANOVA, $F_{1, 2} = 84.9$, $p = 0.012$ and $F_{1, 2} = 44.9$,
187 0.022, respectively); there were no differences between flumes within each treatment so
188 the nested factor was removed from the final analysis. At night, treatment effects were
189 more striking than during the day, as calcium carbonate dissolution exceeded
190 precipitation at high $pCO_2$ (-1.6 ± 0.9 $gCaCO_3\ m^{-2}\ d^{-1}$), whereas net calcification
191 remained positive at ambient $pCO_2$ (2.7 ± 0.6 $gCaCO_3\ m^{-2}\ d^{-1}$) (both means ± SE, n =
192 16). Calcification integrated over 24 h highlighted the difference between treatments ($F_{1, 2}$
193 = 869.2, $p = 0.001$), with calcification 59% lower at high $pCO_2$ than at ambient $pCO_2$.
194
195 **3.3 Sediments**

196 Sediment grain sizes in the flumes were similar between flumes and fractionated
197 (by weight) to 5.3 ± 0.5% < 149 μm grain size, 56.5 ± 1.4% > 149 μm and < 420 μm,
198 25.9 ± 0.4 % > 420 μm < 840 μm, 10.1 ± 0.5% > 840 μm and < 3360 μm, and 2.2 ± 0.9%
199 > 3360 μm. Net calcification of the sediments alone differed between treatments, during
200 the day and night ($F_{1, 2} = 344.2$, $p = 0.003$ and $F_{1, 2} = 282.6$, $p = 0.003$, respectively) (Fig.
201 2B), but there were no differences between flumes within each treatment, hence the
202 nested factor was removed from the final analysis. Net calcification pooled among
203 treatments was negative during the day (-1.0 ± 1.3 $gCaCO_3\ m^{-2}\ d^{-1}$) and night (-3.72 ± 0.6
204 $gCaCO_3\ m^{-2}\ d^{-1}$) at high $pCO_2$, whereas net calcification was positive during the day (1.4
205 ± 1.1 $gCaCO_3\ m^{-2}\ d^{-1}$) and negative at night (-1.0 ± 0.8 $gCaCO_3\ m^{-2}\ d^{-1}$) in the ambient
206 treatment. When calcification was integrated over 24 h, $pCO_2$ effects were significant ($F_{1,}$

207 $_2$ = 886.5, $p$ = 0.001), with dissolution exceeding precipitation at high $pCO_2$ (-2.3 ± 1.1
208 $gCaCO_3$ $m^{-2}$ $d^{-1}$), and a nearly balanced calcification budget under ambient $pCO_2$ (0.2 ±
209 0.9 $gCaCO_3$ $m^{-2}$ $d^{-1}$).
210
211 **3.4 Corals and calcifying algae**
212 The total net calcification of corals and calcifying algae was estimated by
213 subtracting the mean sediment calcification rates from the total community calcification
214 in each flume. Net calcification of the corals and calcifying algae differed between
215 treatments during the day ($F_{1, 2}$ = 32.3, $p$ = 0.030) and night ($F_{1, 2}$ = 22.9, $p$ = 0.041) (Fig.
216 2C). In contrast to the whole community and the sediments alone, net calcification of
217 corals and calcifying algae was positive at night at high $pCO_2$ (1.1 ± 0.5 $gCaCO_3$ $m^{-2}$ in
218 12 h), but was 24% and 44% lower at high $pCO_2$ compared to ambient $pCO_2$ during the
219 day and night, respectively. Net calcification integrated over 24 h also differed between
220 treatments ($F_{1, 2}$ = 2569, $p$ < 0.001) with calcification at ambient $pCO_2$ 29% higher than at
221 high $pCO_2$.
222 Calcification of the constructed reef communities was driven principally by
223 corals, since their contribution to the calcification budget, based on dry weight calculated
224 from the changes in buoyant weight, was ~ 98% of the total (Fig. 3). Massive *Porites* spp.
225 was the main contributor among the corals, with an increased contribution to the
226 calcification budget at high $pCO_2$ (40% at ambient $pCO_2$, and 48.5% at high $pCO_2$, Fig.
227 3). In contrast, the importance of *P. rus*, *Montipora* spp., and *Pocillopora* spp. was
228 reduced at high $pCO_2$. The small contribution of coralline algae to the calcification
229 budget was due to high mortality perhaps leading to potential dissolution during the last

230 weeks of the incubation. Furthermore, while the ratio of planar area to surface area for
231 crustose coralline algae is close to one, corals have a disproportionately large surface area
232 to planar area ratio due to their three-dimensional structure. With such a large actual
233 surface area, the corals made a large contribution to the calcification budget of the
234 communities assembled in the flumes.
235
236 **4 Discussion**
237 Using outdoor flumes, we show that the effects of OA on coral reef communities
238 are greater than estimates obtained by summing results obtained by incubating organisms
239 in isolation under similar conditions and assuming their contribution to community
240 calcification is proportional to their planar cover. Indeed, at the community level, the
241 reduction in net calcification attributed to high $pCO_2$ was greater than the mean reduction
242 of 26% calculated in a recent meta-analysis of the effects of future conditions (~1300
243 μatm $pCO_2$) based on the consequences of high $pCO_2$ on organismic calcification (Chan
244 and Connolly, 2013). This discrepancy likely is not caused by experimental bias, as rates
245 of net community calcification in the flumes in the ambient treatment were similar to
246 rates measured for back reef communities on the north shore of Moorea. For instance, in
247 2012 and 2013 we measured calcification rates during the day that ranged from 5 to 25
248 $gCaCO_3\ m^{-2}\ d^{-1}$ (R.C. Carpenter, unpublished data), which spans the rates measured in
249 flumes during the present study (i.e., 13.9 $gCaCO_3\ m^{-2}\ d^{-1}$ in the light, Fig. 2A). Net
250 community calcification for the back reef of Moorea in 1991 (~ 19–25 $gCaCO_3\ m^{-2}\ d^{-1}$;
251 Gattuso et al., 1996) also was similar to the rates measured in the flumes (this study) and
252 in the field as described above. Rates of calcification in the present study under ambient

253 conditions also are similar to the 7.9 $gCaCO_3\ m^{-2}\ d^{-1}$ reported by Andersson et al. (2009)
254 for a reef community from Kaneohe Bay (Hawaii) that was assembled and incubated in
255 mesocosms. However, while community calcification was still positive under high $pCO_2$
256 in the present study, Andersson et al. (2009) measured negative calcification (i.e., net
257 dissolution) in their coral reef communities incubated at a $pCO_2$ twice that of current
258 ambient values. The differences between the present study and that of Andersson et al.
259 (2009) may be due to methodological effects. Andersson et al. (2009) manipulated pH
260 through acid additions (we used $CO_2$ bubbling), and also used a different assemblage of
261 species and sediments in dissimilar proportions compared to the present study.
262 The discrepancy in the evaluation of the effects of high $pCO_2$ at the community
263 level (the present study) versus organismic level (previous studies) was the result of
264 dissolution of sediments that represented up to 50% of the decrease in calcification at
265 high $pCO_2$. Increased dissolution of sediments at high $pCO_2$ likely was caused by the
266 reduction of the seawater saturation state in the flumes, as we did not detect any
267 difference in respiration and photosynthesis under elevated $pCO_2$ (results not shown) that
268 could also affect sediment dissolution (Andersson and Gledhill, 2013). Our results reveal
269 the sensitivity of carbonate sediments to dissolution at elevated $pCO_2$, and they are in
270 agreement with a recent manipulative experiment conducted on Heron Island, where
271 dissolution of in situ areas of sand (1.7 m depth) exceeded precipitation at $pCO_2 > 500$
272 μatm (Cyronak et al., 2013a). During a mesocosm experiment, Dove et al. (2013) also
273 demonstrated that a pH of 7.7 caused a change in sediment granularity to favor small-
274 grained (i.e., ≤ 1 mm) sediments as a result of dissolution or increased bioerosion of
275 larger grains. In this case, bioerosion was more likely than dissolution, as dissolution

276 would favor a loss of the smallest grains as a result of their higher surface area to volume
277 ratio. Size-frequency distribution of sediment grain was not different between treatments
278 at the end of our incubations and therefore is unlikely to have affected the treatment
279 effects we detected. Sensitivity of coral reef communities to dissolution has been shown
280 previously for communities constructed in mesocosms in Hawaii, where dissolution (-3.6
281 mmol $CaCO_3$ $m^{-2}$ $h^{-1}$) was detected at night under conditions of double ambient $pCO_2$
282 (Andersson et al., 2009). In this case, dissolution was attributed to the thin layer of
283 sediment that accumulated at the bottom of the mesocosms (Andersson et al., 2009).
284 In addition to chemical dissolution occurring in the communities constructed in
285 the present study, we cannot exclude the possibility that at least some of the apparent
286 community dissolution was caused by enhanced bioerosion, which for example
287 previously has been show to occur when blocks of *Porites lobata* are incubated under 750
288 µatm $pCO_2$ for 3-month (Tribollet et al. 2009). In future work it will be important to
289 census the fragments of coral and rock to quantify the presence of bioeroders and their
290 relative contribution to dissolution under ambient and OA conditions.
291 When the effect of sediment dissolution was subtracted from the overall net
292 calcification rate for the communities assembled in our flumes, corals and coralline algae
293 alone exhibited a decrease in net calcification of 29% over 24 h at elevated $pCO_2$ versus
294 ambient $pCO_2$. Such a decrease falls within the range of values we have previously
295 reported for organismic effects of high $pCO_2$, in which the calcification rates of 16
296 calcifiers in Moorea declined 0–40% at 1300 µatm $pCO_2$ compared to ambient $pCO_2$
297 (Comeau et al., 2013; Comeau et al., 2014b). It is also within the range of the predicted
298 changes for calcification of corals under a tripling of $pCO_2$ (relative to present values)

299 estimated by meta-analysis (i.e., a ~ 26% reduction; Chan and Connolly, 2012). As the
300 decrease in calcification recorded in the present study for corals and coralline algae alone
301 was within the range of previous studies, this supports our assumptions that calcification
302 of macro-calcifiers is equal to the difference between net sediment calcification and net
303 community calcification. This "subtraction method" for calculating the calcification rate
304 of corals and coralline algae included in community experiments has some limitations, as
305 it assumes that the calcification of the sediments and the macro-calcifiers are
306 independent. Such interactions might occur, for example, if dissolution of the sediment
307 would locally enhance total alkalinity that would, in turn, favor calcification by macro-
308 calcifiers. Testing for such feedback mechanisms among the different compartments of
309 the communities we built was beyond the scope of the present study, but it will be
310 important to consider such effects in future experiments.

311 Our results demonstrate the utility of large outdoor flumes for investigating the
312 responses of coral reef communities to OA. Similar rates of calcification in the field and
313 in the flumes suggest that the communities assembled in the flumes effectively mimicked
314 both the biological communities and the physical and chemical conditions characterizing
315 the back reef of Moorea. The ability to create ecologically relevant flow conditions in the
316 flumes is likely to be especially important for establishing ecological relevance, as flow is
317 critical in modulating mass transfer and metabolism of coral reef organisms (Atkinson
318 and Gilmer, 1992; Carpenter and Williams, 2007, Comeau et al. 2014c). In the case of
319 stony corals, for example, high flow speeds are suspected to enhance coral calcification
320 by favoring proton export from coral tissue through boundary layers (Jokiel, 2011; Jokiel
321 et al., 2014), and for coralline algae, might increase sensitivity to OA by reducing the

capacity to maintain high pH in the diffusion boundary layer adjacent to the algal thallus (Cornwall et al., 2013, 2014).

## 5 Conclusion

The present results suggest that, despite a reduction in calcification, calcifying reef organisms may maintain net positive calcification under $pCO_2$ as high as 1300 µatm. However, at the scale of coral reef communities in back reef habitats, community net calcification will be affected strongly and negatively, at least for reefs similar in community structure to those in Moorea in 2013. The present experiments demonstrate the importance 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, 2014), the susceptibility of coral reefs to net dissolution in the future likely will be linked directly to the proportion of the reef covered by macro-calcifiers and sediments. In addition to dissolution, it also is possible that coral reefs 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 as a physical structure to protect coasts against erosion (Ferrario et al., 2014) will be challenged.

343 **Authors contributions:** S.C. designed and performed experiments, analyzed data and
344 wrote the paper; C.L. performed experiments and wrote the paper; B.C. and P.E.
345 designed experiments, analyzed data and wrote the paper.
346
347 **Acknowledgments**
348 We dedicate this paper to Dr. Marlin Atkinson who pioneered the use of large outdoor
349 flumes for the analysis of coral community metabolism, and whose work inspired our
350 science and the present experiments. This study was funded by the National Science
351 Foundation (OCE 10-41270) and the Moorea Coral Reef LTER (OCE 04-17413 and 10-
352 26852). This is contribution number xxx of the CSUN Marine Biology Program.

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494 **Table 1.** Mean carbonate chemistry in the four flumes (F1-4) during the 8-week incubation. The partial pressure of $CO_2$ ($pCO_2$), the
495 aragonite saturation state ($\Omega_{arag}$) and the calcite saturation state ($\Omega_{calc}$) were calculated from $pH_T$, total alkalinity ($A_T$), temperature and
496 salinity. The values presented are mean ± SE (n = 56). SE for salinity was < 0.1.
497
498

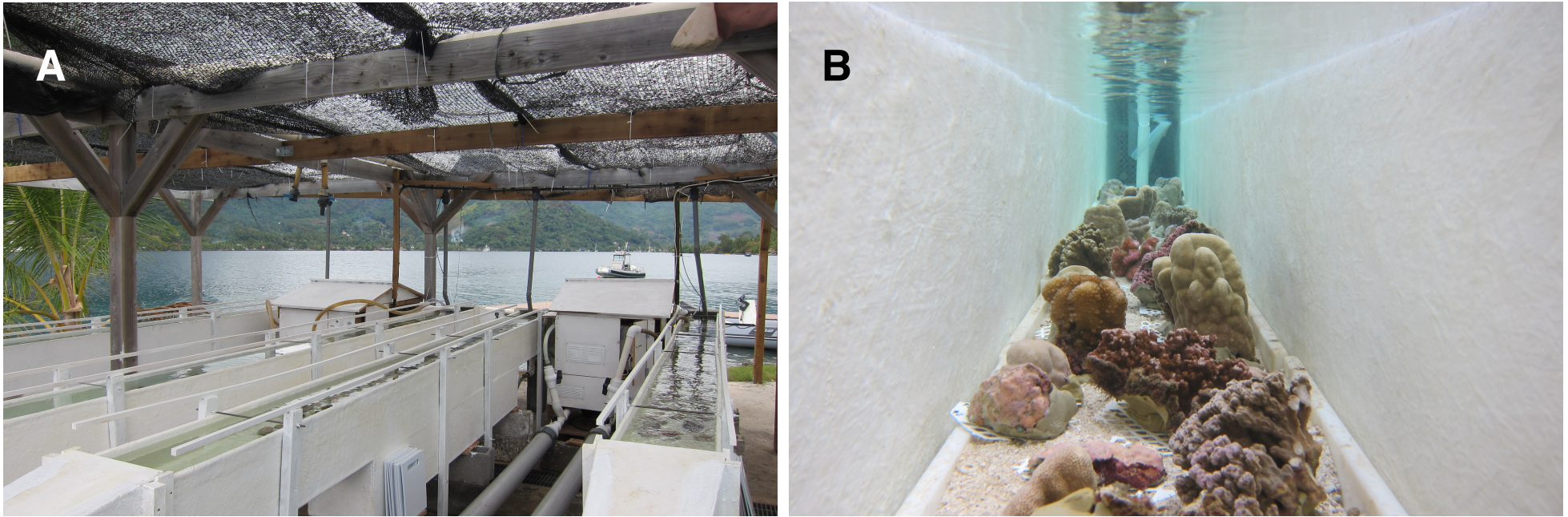
| Flume | Treatment | $pH_T$ | $A_T$ ($\mu mol.\ kg^{-1}$) | $pCO_2$ ($\mu atm$) | $\Omega_{arag}$ | $\Omega_{calc}$ | Temperature (°C) | Salinity |
|---|---|---|---|---|---|---|---|---|
| F1 | High $pCO_2$ | 7.603 ± 0.008 | 2343 ± 1 | 1329 ± 28 | 1.60 ± 0.03 | 2.41 ± 0.04 | 27.0 ± 0.1 | 35.9 |
| F2 | Ambient | 8.010 ± 0.012 | 2339 ± 1 | 456 ± 19 | 3.49 ± 0.07 | 5.26 ± 0.11 | 26.8 ± 0.1 | 35.9 |
| F3 | High $pCO_2$ | 7.617 ± 0.014 | 2345 ± 1 | 1306 ± 42 | 1.68 ± 0.05 | 2.53 ± 0.08 | 27.1 ± 0.1 | 35.9 |
| F4 | Ambient | 8.015 ± 0.013 | 2339 ± 1 | 451 ± 18 | 3.53 ± 0.07 | 5.32 ± 0.11 | 26.9 ± 0.1 | 35.9 |

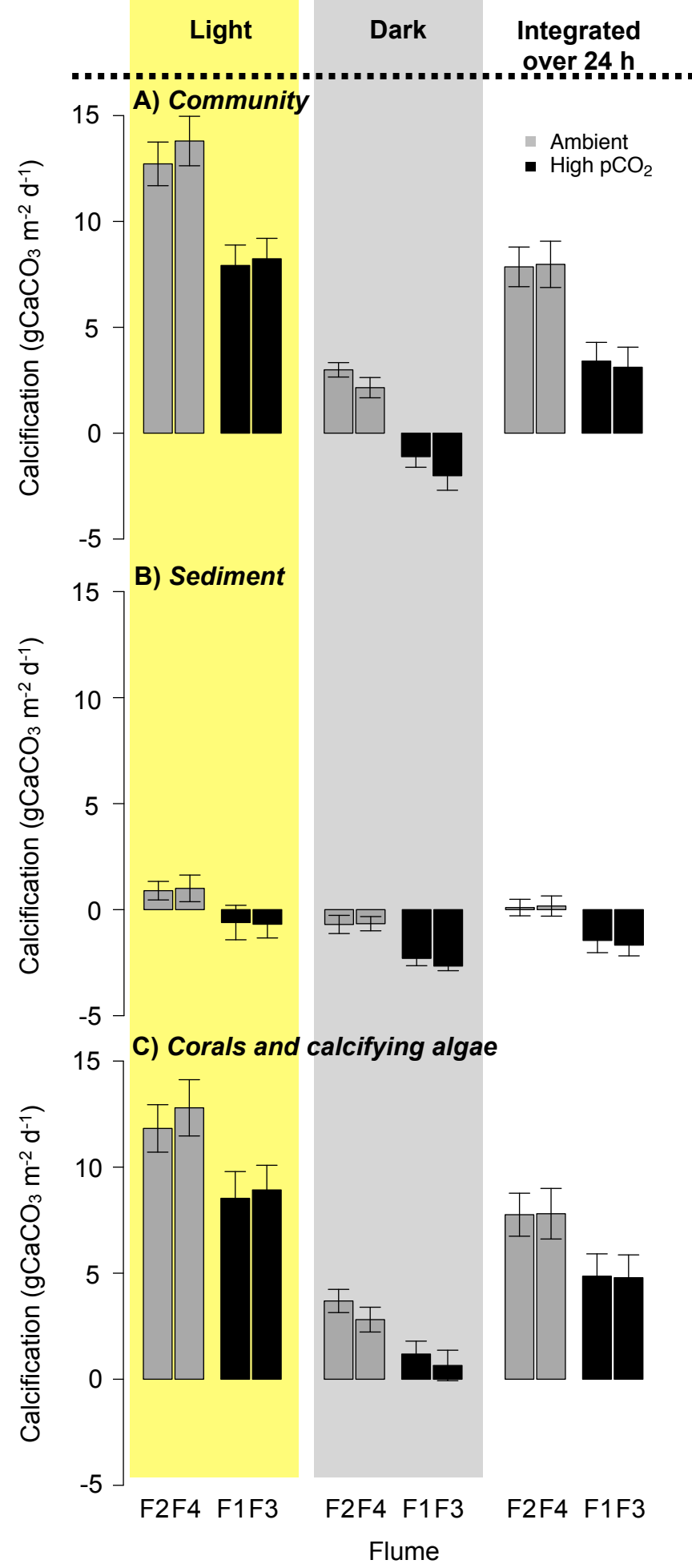
**Figure legends**

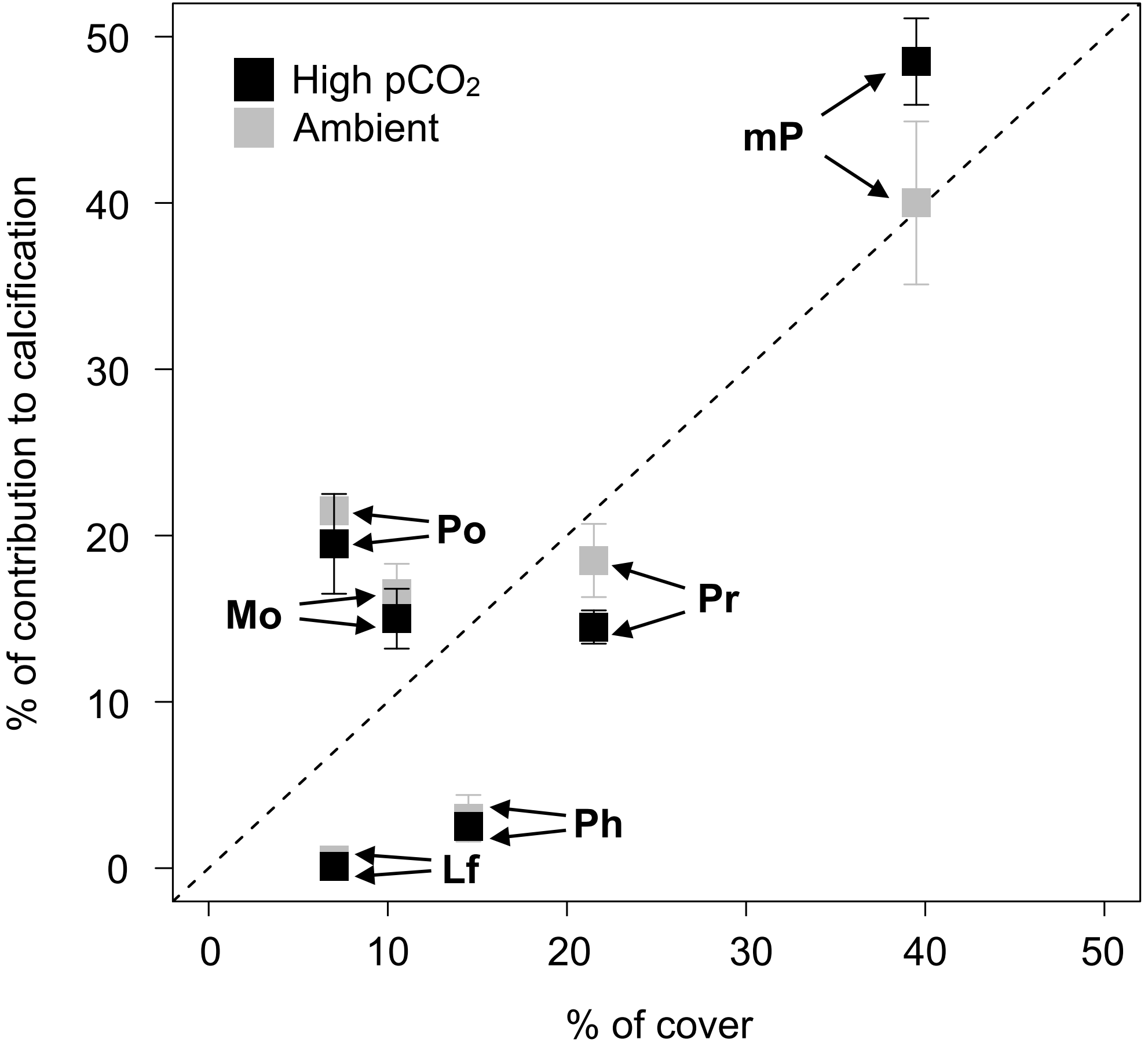
**Figure 1.** Photographs of the outdoor flumes. a) The flumes consisted of a 5.00 × 0.30 × 0.30 m working section, and a lower sediment chamber (2.50 × 0.30 × 0.25 m) in which sediments were maintained, and together contained ~ 600 L of seawater. b) Communities matching the average composition (in 2013)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

**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 $pCO_2$ (~ 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.

**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.


A
B


Light
Dark
Integrated over 24 h
A) Community
B) Sediment
C) Corals and calcifying algae
Ambient
High pCO2
Calcification (gCaCO3 m-2 d-1)
15
10
5
0
-5
F2F4
F1F3
Flume


High pCO2
Ambient
mP
Po
Mo
Pr
Ph
Lf
% of contribution to calcification
% of cover
0
10
20
30
40
50