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 conditions (Erez et al. 2011; Chan and Connolly, 2012), while recent laboratory work describes species-specific responses with some corals and calcifying algae resistant to decreasing pH (Comeau et al., 2013; Takahashi and Kurihara, 2013). Differential organismic sensitivities to OA potentially could lead to changes in coral community structure, and in turn this could affect habitat complexity (Fabricius et al. 2011, 2014).

Critically, most of the studies on coral reef organisms have been performed on individuals maintained in isolation in laboratory conditions, and studies performed at the scale of whole communities are scarce (Leclercq et al., 2002; Jokiel et al., 2008; Andersson et al., 2009; Dove et al., 2013). Generally there are three complementary approaches for studying the responses of coral reef communities to OA. Firstly, *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). Secondly, carbonate chemistry can be manipulated directly *in situ* (Kline et al., 2012), although this

47 approach is challenging technically and has not yet been used to study intact
48 communities. Thirdly, reef communities can be constructed *ex situ* (Andersson et al.,
49 2009; Dove et al., 2013) to allow precise control of the physical parameters predicted
50 under future OA conditions. For our experiment, we chose to construct *ex situ*
51 communities and used, for the first time, large outdoor flumes (after Atkinson and Bilger,
52 1992) to investigate the effects of OA on coral reef communities.
53 In addition to corals and macroalgae, it is important to incorporate sediments in
54 OA experiments, as this component of reef ecosystems may be sensitive to decreasing pH
55 (Cyronak et al. 2013a, b; Andersson et al., 2009). Dissolution occurs on coral reefs in
56 sediment pore-waters, or in particular microenvironments where $pCO_2$ is elevated due to
57 biological activity (Andersson and Gledhill, 2013). Observations in Bermuda have shown
58 that the dissolution of Mg-calcite sediments occurs in a location with seawater $pCO_2$
59 naturally elevated to values expected by the end of the century (Andersson et al., 2007).
60 Further*, in situ* manipulations show that elevated $pCO_2$ (~ 800 µatm) can transition the
61 calcification budget of coral reef sediments from net precipitation to net dissolution
62 (Cyronak et al., 2013a). Increasing $pCO_2$ likely will lead to increasing dissolution and
63 decreased precipitation of calcium carbonate, resulting in coral reef community
64 calcification changing from net precipitation to net dissolution (Yates and Halley, 2006;
65 Silvermann et al., 2009; Andersson et al., 2009). Given the aforementioned results that
66 highlight the importance of sediments in the community calcification of entire coral reefs,
67 we included reef carbonate sediments into the constructed communities.
68 We investigated the response of constructed reef communities in flumes to OA
69 filled with seawater maintained either at ambient $pCO_2$ (i.e., ~ 400 µatm) or elevated

70 $pCO_2$. Net calcification rates were measured at three levels of biological function: whole
71 community, sediments, and macro-calcifiers to determine the sensitivity to OA of each
72 compartment of the community.
73
74 **2 Materials and methods**
75 **2.1 Collection and sample preparation**
76 This study was carried out in August-October 2013 in Moorea, French Polynesia,
77 using organisms collected from the back reef of the north shore at ~ 1–2 m depth. The
78 organisms used to construct communities in outdoor flumes were assembled to match the
79 contemporary (in 2013) mean cover of a back reef in Moorea (Carpenter, 2014;
80 Edmunds, 2014). Coral communities were built from the four dominant coral taxa found
81 on the back reefs of Moorea: massive *Porites* spp. (11% cover), *Porites rus* (6%),
82 *Montipora* spp. (3%), and *Pocillopora* spp. (2%), that together accounted for 98% of the
83 coral cover in this habitat. In addition to corals, 6% of the planar floor surface of the
84 flumes was covered by crustose coralline algae (66% *Porolithon onkodes* and 33%
85 *Lithophyllum flavescens*), and 5% by rubble (dead coral skeletons). After collection of
86 corals and algae (all ~ 10 × 10 cm), they were returned to the Richard B. Gump South
87 Pacific Research Station and attached to plastic supports using epoxy glue. Following
88 preparation, samples were left to recover in a seawater table for 3 d.
89 Sediments were collected from the lagoon on the north shore, ~ 200 m from the
90 reef crest, at 2-m depth using 24 custom made boxes (0.4 × 0.3 × 0.3 m). Sediment boxes
91 were inserted into the sediment and left *in situ* for 4 d to allow chemical stratification in

92 the sediment to re-establish (note that chemical stratification was not monitored) before
93 transferring the boxes to the flumes.
94 The four outdoor flumes consisted of a working section measuring 5.0 × 0.3 × 0.3
95 m. Water was re-circulated using water pumps (W. Lim Wave II 373 J $s^{-1}$) to obtain a 10
96 cm $s^{-1}$ flow. Flow was measured across the working section of the flume using a Nortek
97 Vectrino Acoustic Doppler Velocimeter. At each end of the flume, seawater passed
98 through an 88-cm long transition section (circular to rectangular) that housed 20-cm
99 (length) flow straighteners made of stacked, 3 cm (inner diameter) PVC pipe, and then
100 into a 12.5 cm (inner diameter) return section. Fresh sand-filtered seawater, pumped from
101 Cook's Bay at 12-m depth, was dispensed continuously into the flume at 5 L $min^{-1}$.
102 Flumes experienced natural sunlight that was attenuated using fiberglass screens to
103 maintain irradiances similar to ambient irradiances in the back reefs of Moorea (daily
104 maximum of ~ 1500 µmol photons $m^{-2}$ $cm^{-1}$ over the incubation period determined with a
105 4π quantum sensor LI-193 and a LiCor LI-1400 meter). Temperature in the flumes was
106 maintained at ~ 27 °C to match the ambient temperature in the back reef of Moorea in
107 September-October.
108
109 **2. 2 Carbonate chemistry control and measurements**
110
111 As the $pCO_2$ in seawater flowing over the back reef of Moorea is close to open-
112 ocean and current atmospheric values (e.g., Comeau et al. 2014a), $pCO_2$ levels for the
113 incubations were chosen to match ambient $pCO_2$ (~ 400 µatm) and the $pCO_2$ expected in
114 the atmosphere by the end of the present century under a pessimistic scenario of further
115 anthropogenic activity (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).

**2.3 Calcification measurements and sediment analysis**

Net calcification rates were measured using the total alkalinity anomaly method (Chisholm and Gattuso, 1991), which is based on the stoichiometric relationship of 2 moles of $A_T$ being removed/added for each mole of $CaCO_3$ precipitated/dissolved. Calcification measurements were made every 7 d on the constructed community, and in the analysis of sediments alone, after 7, 30, and 56 d of treatments. During incubations,

139 the addition of seawater was stopped so that each flume operated in a closed loop;
140 seawater samples for $A_T$ then were taken every 3 h during the day and every 6 h at night.
141 To maintain $A_T$ and nutrients close to ambient levels, water in the flumes was refreshed
142 every 3-6 h for 30 min. Regular refreshing limited changes in alkalinity during
143 incubations to < 50-100 μmol $kg^{-1}$, which corresponded to variations in aragonite
144 saturation state (Ω) of < 0.1-0.2. Nutrient changes in the flumes were monitored during
145 four incubations and the changes in nitrate and ammonium during incubations were < 2
146 μmol $L^{-1}$. To conduct incubations with sediments alone, corals and coralline algae were
147 removed from the flumes for 24 h and held in a separate tank where conditions were
148 identical to those in the flumes. Corals and coralline algal calcification was calculated by
149 subtracting the mean light and dark net calcification of the sediments from the
150 community calcification. For both corals and algae, buoyant weight (Davies, 1989) was
151 recorded before and after the 8-week treatments and converted to dry weight to quantify
152 the contribution of each functional group to the calcification budget. Sediment grain size
153 of each flume was analyzed in triplicate using sediment sieves. Three vertical cross
154 sections of sand (~ 600g) were collected from each flume sediment chamber and dried at
155 60 °C to remove moisture. Sand then was sieved through five separate sediment sieves
156 (149 μm, 420 μm, 840 μm, 3360 μm) yielding six size class fractions for each flume (n =
157 3).
158
159 **2.4 Statistical analysis**
160 All analyses were performed using R software (R Foundation for Statistical
161 Computing), and assumptions of normality and equality of variance were evaluated

through graphical analyses of residuals. Calcification rates were analyzed using a repeated measures 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 measures 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 (*Phestilla* spp.), which consumed *Porites* spp. tissue. Most coralline algae (~ 70%) had died by 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.

### 3.2 Community

184 Net calcification was higher at ambient versus high $pCO_2$ (Fig. 2A), both during
185 the day and night (repeated measures ANOVA, $F_{1, 2} = 84.9$, $p = 0.012$ and $F_{1, 2} = 44.9$,
186 0.022, respectively); there were no differences between flumes within each treatment so
187 the nested factor was removed from the final analysis. At night, treatment effects were
188 more striking than during the day, as calcium carbonate dissolution exceeded
189 precipitation at high $pCO_2$ (-1.6 ± 0.9 $gCaCO_3$ $m^{-2}$ $d^{-1}$), whereas net calcification
190 remained positive at ambient $pCO_2$ (2.6 ± 0.6 $gCaCO_3$ $m^{-2}$ $d^{-1}$) (both means ± SE, n =
191 16). Calcification integrated over 24 h highlighted the difference between treatments ($F_{1, 2}$
192 = 869.2, $p = 0.001$), with calcification 59% lower at high $pCO_2$ than at ambient $pCO_2$.
193
194 **3.3 Sediments**
195 Sediment grain sizes in the flumes were similar between flumes and fractionated
196 (by weight) to 5.3 ± 0.5% < 149 μm grain size, 56.5 ± 1.4% > 149 μm and < 420 μm,
197 25.9 ± 0.4 % > 420 μm < 840 μm, 10.1 ± 0.5% > 840 μm and < 3360 μm, and 2.2 ± 0.9%
198 > 3360 μm. Net calcification of the sediments alone differed between treatments, during
199 the day and night ($F_{1, 2} = 344.2$, $p = 0.003$ and $F_{1, 2} = 282.6$, $p = 0.003$, respectively) (Fig.
200 2B), but there were no differences between flumes within each treatment, hence the
201 nested factor was removed from the final analysis. Net calcification pooled among
202 treatments was negative during the day (-0.7 ± 0.5 $gCaCO_3$ $m^{-2}$ $d^{-1}$) and night (-2.5 ± 0.4
203 $gCaCO_3$ $m^{-2}$ $d^{-1}$) at high $pCO_2$, whereas net calcification was positive during the day (0.9
204 ± 0.7 $gCaCO_3$ $m^{-2}$ $d^{-1}$) and negative at night (-0.6 ± 0.8 $gCaCO_3$ $m^{-2}$ $d^{-1}$) in the ambient
205 treatment. When calcification was integrated over 24 h, $pCO_2$ effects were significant ($F_{1,}$
206 $_2 = 886.5$, $p = 0.001$), with dissolution exceeding precipitation at high $pCO_2$ (-1.6 ± 0.8

207 $gCaCO_3\ m^{-2}\ d^{-1}$), and a nearly balanced calcification budget under ambient $pCO_2$ (0.1 ±

208 0.6 $gCaCO_3\ m^{-2}\ d^{-1}$).

209

210 **3.4 Corals and calcifying algae**

211 The total net calcification of corals and calcifying algae was estimated by

212 subtracting the mean sediment calcification rates from the total community calcification

213 in each flume. Net calcification of the corals and calcifying algae differed between

214 treatments during the day ($F_{1, 2} = 32.3$, $p = 0.030$) and night ($F_{1, 2} = 22.9$, $p = 0.041$) (Fig.

215 2C). In contrast to the whole community and the sediments alone, net calcification of

216 corals and calcifying algae was positive at night at high $pCO_2$ (0.9 ± 0.5 $gCaCO_3\ m^{-2}$ in

217 12 h), but was 24% and 44% lower at high $pCO_2$ compared to ambient $pCO_2$ during the

218 day and night, respectively. Net calcification integrated over 24 h also differed between

219 treatments ($F_{1, 2} = 2569$, $p < 0.001$) with calcification at ambient $pCO_2$ 29% higher than at

220 high $pCO_2$.

221 Calcification of the constructed reef communities was driven principally by

222 corals, since their contribution to the calcification budget, based on dry weight calculated

223 from the changes in buoyant weight, was ~ 98% of the total (Fig. 3). Massive *Porites* spp.

224 was the main contributor among the corals, with an increased contribution to the

225 calcification budget at high $pCO_2$ (40% at ambient $pCO_2$, and 48.5% at high $pCO_2$, Fig.

226 3). In contrast, the importance of *P. rus*, *Montipora* spp., and *Pocillopora* spp. was

227 reduced at high $pCO_2$. The small contribution of coralline algae to the calcification

228 budget was due to high mortality perhaps leading to potential dissolution during the last

229 weeks of the incubation. Furthermore, while the ratio of planar area to surface area for

crustose coralline algae is close to one, corals have a disproportionately large surface area to planar area ratio due to their three-dimensional structure. With such a large actual surface area, the corals made a large contribution to the calcification budget of the communities assembled in the flumes.

## 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 the community level, the reduction 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 $pCO_2$) based on the consequences of high $pCO_2$ on organismic calcification (Chan and Connolly, 2013). This discrepancy likely is not caused by experimental bias, as rates of net community calcification in the flumes in the ambient treatment were similar to rates measured for back reef communities on the north shore of Moorea. For instance, in 2012 and 2013 we measured calcification rates during the day that ranged from 5 to 25 $gCaCO_3\ m^{-2}\ d^{-1}$ (R.C. Carpenter, unpublished data), which spans the rates measured in flumes during the present study (i.e., 13.9 $gCaCO_3\ m^{-2}\ d^{-1}$ in the light, Fig. 2A). Net community calcification for the back reef of Moorea in 1991 (~ 19–25 $gCaCO_3\ m^{-2}\ d^{-1}$; Gattuso et al., 1996) was also similar to the rates measured in the flumes (this study) and in the field as described above. Rates of calcification in the present study under ambient conditions are also similar to the 7.9 $gCaCO_3\ m^{-2}\ d^{-1}$ reported by Andersson et al. (2009)

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

276 ratio. Size-frequency distribution of sediment grain was not different between treatments
277 at the end of our incubations and therefore is unlikely to have affected the treatment
278 effects we detected. Sensitivity of coral reef communities to dissolution has been shown
279 previously for communities constructed in mesocosms in Hawaii, where dissolution (-3.6
280 mmol $CaCO_3$ $m^{-2}$ $h^{-1}$) was detected at night when $CO_2$ levels in the mesocosm where
281 equivalent to 2-fold $pCO_2$ in ambient air (Andersson et al., 2009). In this case, dissolution
282 was attributed to the thin layer of sediment that accumulated at the bottom of the
283 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 previously has been
287 show to occur when blocks of *Porites lobata* are incubated under 750 µatm $pCO_2$ for 3-
288 month (Tribollet et al. 2009). In future work it will be important to census the fragments
289 of coral and rock to quantify the presence of bioeroders and their relative contribution to
290 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 accounted for a decrease in net calcification of 29% over 24 h at elevated $pCO_2$
294 versus ambient $pCO_2$. Such a decrease falls within the range of values we have
295 previously reported for organismic effects of high $pCO_2$, in which the calcification rates
296 of 16 calcifiers in Moorea declined 0–40% at 1300 µatm $pCO_2$ compared to ambient
297 $pCO_2$ (Comeau et al., 2013; Comeau et al., 2014b). It is also within the range of the
298 predicted changes for calcification of corals under a tripling of $pCO_2$ (relative to present

299 values) estimated by meta-analysis (i.e., a ~ 26% reduction; Chan and Connolly, 2012).
300 The proportional decrease (i.e., ~ 29%) in calcification rate for corals and coralline algae
301 recorded in the present study under a tripling of present $pCO_2$ alone supports the validity
302 of our experimental approach, which assumes that calcification of macro-calcifiers is
303 equal to the difference between net sediment calcification and net community
304 calcification. This "subtraction method" for calculating the calcification rate of corals and
305 coralline algae included in community experiments has some limitations, as it assumes
306 that the calcification of the sediments and the macro-calcifiers are independent. This
307 assumption might be violated if, for example, sediment dissolution locally enhances total
308 alkalinity that could favor calcification of near-by macro-calcifiers. Testing for such
309 feedback mechanisms among the different compartments of the communities we built
310 was beyond the scope of the present study, but it will be important to consider such
311 effects in future experiments.
312 Our results demonstrate the suitability of large outdoor flumes for investigating
313 the responses of coral reef communities to OA. Similar rates of calcification in the field
314 and in the flumes suggest that the communities assembled in the flumes effectively
315 mimicked both the biological communities and the physical and chemical conditions
316 characterizing the back reef of Moorea. The ability to create ecologically relevant flow
317 conditions in the flumes is likely to be especially important for establishing ecological
318 relevance, as flow is critical in modulating mass transfer and metabolism of coral reef
319 organisms (Atkinson and Gilmer, 1992; Carpenter and Williams, 2007, Comeau et al.
320 2014c). In the case of stony corals, for example, high flow speeds are suspected to
321 enhance coral calcification by favoring proton export from coral tissue through boundary

322 layers (Jokiel, 2011; Jokiel et al., 2014), and for coralline algae, might increase sensitivity
323 to OA by reducing the capacity to maintain high pH in the diffusion boundary layer
324 adjacent to the algal thallus (Cornwall et al., 2013, 2014).
325
326 **5 Conclusion**
327 The present results suggest that, despite a reduction in calcification, calcifying reef
328 organisms may maintain net positive calcification under $pCO_2$ as high as 1300 µatm.
329 However, at the scale of coral reef communities in back reef habitats, community net
330 calcification will be affected strongly and negatively, at least for reefs similar in
331 community structure to those in Moorea in 2013. The present experiments demonstrate
332 the importance of living organisms on benthic surfaces in maintaining a positive balance
333 between precipitation and dissolution of calcium carbonate. Whereas several reefs around
334 the world are already at the threshold between precipitation and dissolution of calcium
335 carbonate (Silverman et al., 2009, 2014), the susceptibility of coral reefs to net
336 dissolution in the future likely will be linked directly to the proportion of the reef covered
337 by macro-calcifiers and sediments. In addition to dissolution, it also is possible that coral
338 reefs will be exposed to increased bioerosion at high $pCO_2$ (Wisshak et al., 2012; Crook
339 et al., 2013) that will decrease the integrity of the carbonate framework. In addition to the
340 direct effects of OA on reef builders, the associated loss of three-dimensional framework
341 might impact a large variety of marine organisms by reducing habitat complexity, and the
342 availability of refuges (Fabricius et al., 2014). Our results suggest that under OA
343 conditions anticipated by the end of the current century, at least some tropical corals and
344 calcifying algae will persist, but the function of the coral reef community as a net

345 precipitator of calcium carbonate and as a physical structure to protect coasts against

346 erosion (Ferrario et al., 2014) will be challenged.

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**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 aragonite saturation state ($\Omega_{arag}$) and the calcite saturation state ($\Omega_{calc}$) were calculated from $pH_T$, total alkalinity ($A_T$), temperature and salinity. The values presented are mean ± SE (n = 56). SE for salinity was < 0.1.

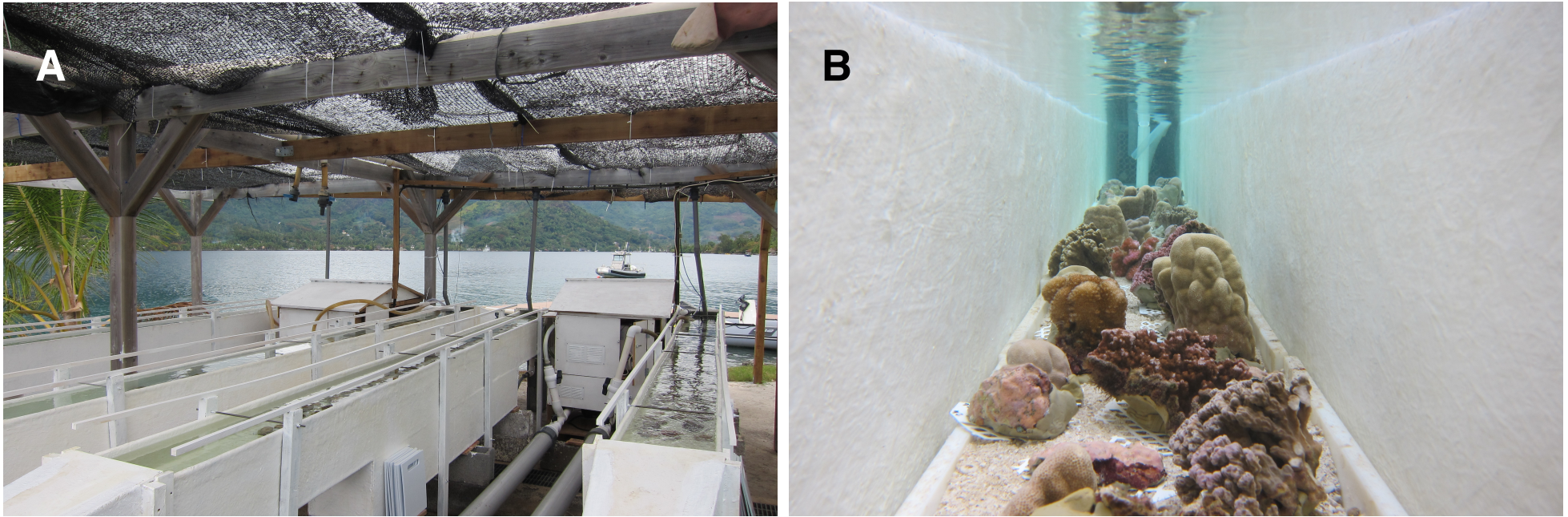
| Flume | Treatment | $pH_T$ | $A_T$ (µmol. kg$^{-1}$) | $pCO_2$ (µatm) | $\Omega_{arag}$ | $\Omega_{calc}$ | Temperature (°C) | Salinity |
|---|---|---|---|---|---|---|---|---|
| F1 | High $pCO_2$ | 7.603 ± 0.008 | 2343 ± 1 | 1329 ± 28 | 1.60 ± 0.03 | 2.41 ± 0.04 | 27.0 ± 0.1 | 35.9 |
| F2 | Ambient | 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 |

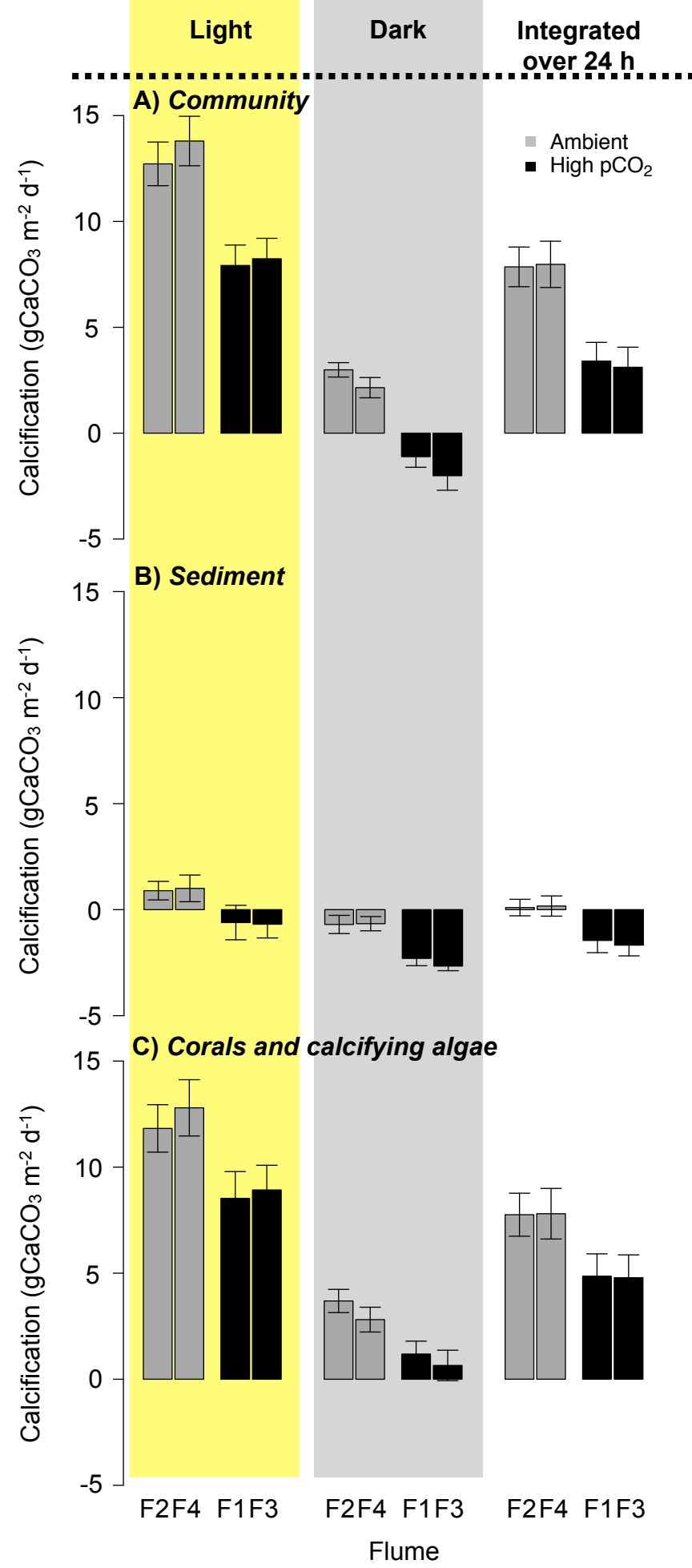
## Figure legends

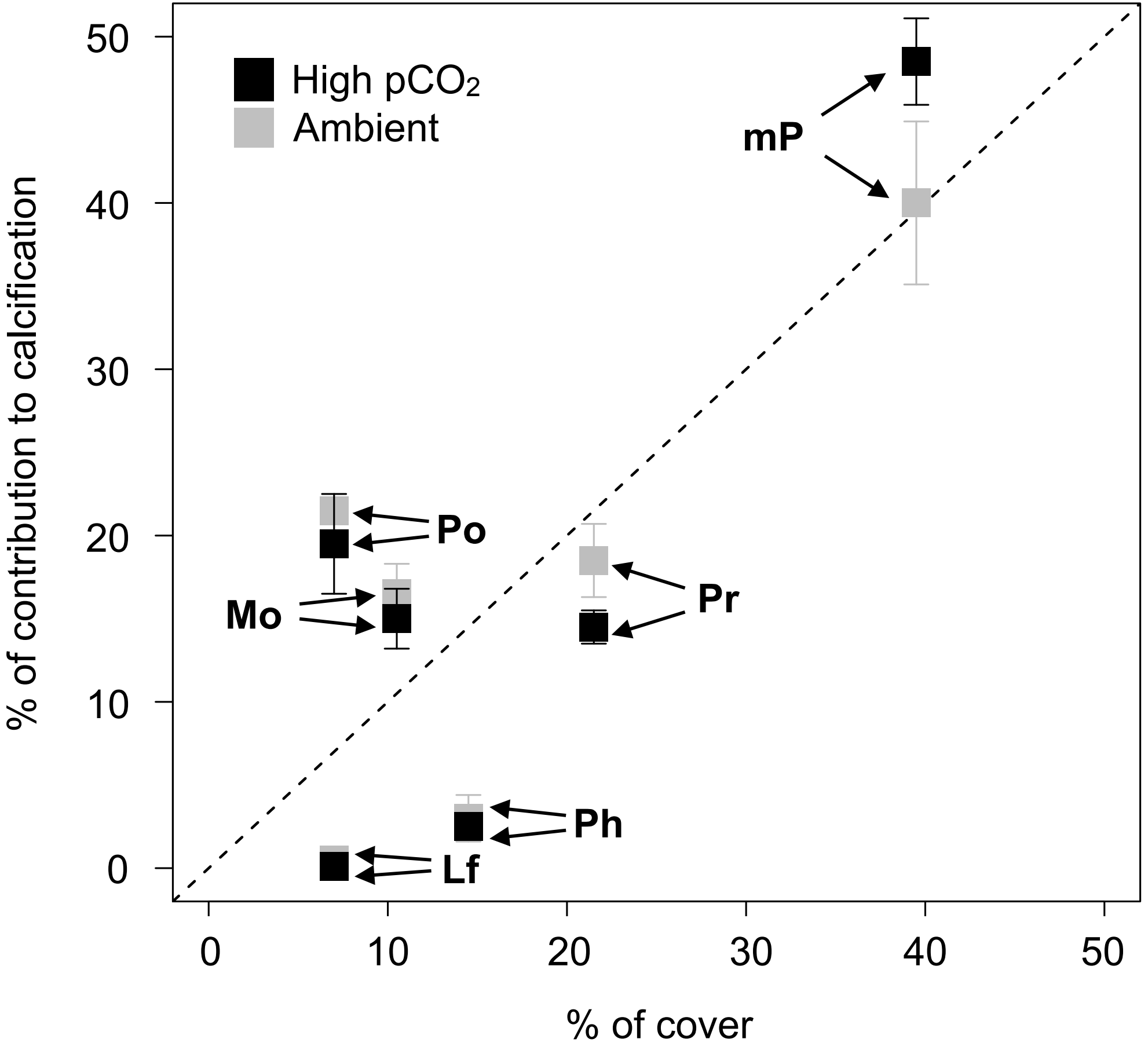
**Figure 1.** Photographs of the outdoor flumes. a) The flumes consisted of a 5.00 × 0.30 × 0.30 m working section, and a lower sediment chamber (2.50 × 0.30 × 0.25 m) in which sediments were maintained, and together contained ~ 600 L of seawater. b) Communities matching the average composition (in 2013) 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. F1, F2, F3, and F4 indicate the different flumes.

**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