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► **To cite this version:**

Aline Tribollet, Anne Chauvin, Pascale Cuet. Carbonate dissolution by reef microbial borers: a biogeological process producing alkalinity under different pCO₂ conditions. *Facies*, 2019, 65 (2), 10.1007/s10347-018-0548-x . hal-02193013

HAL Id: hal-02193013

<https://hal.science/hal-02193013v1>

Submitted on 24 Sep 2019

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1 **Carbonate dissolution by reef microbial borers:**

2 **A biogeological process producing alkalinity under different pCO₂ conditions**

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14
15 **Keywords:** Biogenic carbonate dissolution, microborers, euendoliths, coral reefs, ocean
16 acidification, seawater alkalinity

17
18 **Acknowledgments**

19 We would like to dedicate this paper to our colleague and friend Marlin Atkinson who passed

20 away in 2013. A.T. and P.C. conceived the experimental design. A.T., P.C. and A.C. collected

21 samples and analysed data. A.T. and P.C. wrote the article and A.C. gave assistance on figure

22 preparations and for formatting. We thank the Plateforme Alizes (IRD Bondy) for SEM

23 access and S. Pyneeandy for her help with measurements of biogenic rates on coral blocks.

24 We thank the Center IRD in Nouméa for its support in the field. Finally, this work was

25 supported by the French Ministry of Ecology (program 'MIDACOR', 2011-2014) and the

26 Institut de Recherche pour le Développement. The funding sponsors had no involvement in

27 the present study development (design, collection, analysis, etc.).

28 **Abstract**

29 Rising atmospheric CO₂ is acidifying the world's oceans affecting both calcification and
30 dissolution processes in coral reefs. Among processes, carbonate dissolution by bioeroding
31 microflora has been overlooked, and especially its impact on seawater alkalinity. To date, this
32 biogeological process was only studied using microscopy or buoyant weight techniques. To
33 better understand its possible effect on seawater alkalinity and thus, on reef carbonate budget,
34 an experiment was conducted under various seawater chemistry conditions ($2 \leq \Omega_{\text{arag}} \leq 3.5$
35 corresponding to $440 \leq \text{pCO}_2 (\mu\text{atm}) \leq 940$) at 25°C under night and daylight (200 μmol
36 $\text{photons m}^{-2} \text{s}^{-1}$) with natural microboring communities colonizing dead coral blocks (New
37 Caledonia). Both the alkalinity anomaly technique and microscopy methods were used to
38 study the activity of those communities dominated by the chlorophyte *Ostreobium* sp. Results
39 show that (1) the amount of alkalinity released in seawater by such communities is significant
40 and vary between 12.8 ± 0.7 at $\Omega_{\text{Arag}} \sim 2$ and 5.6 ± 0.4 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ at $\Omega_{\text{Arag}} \sim 3\text{-}3.5$
41 considering a 12:12 photoperiod, (2) although dissolution is higher at night (~80% vs 20%
42 during daylight), the process can occur under a significant photosynthetic activity, and (3) the
43 process is greatly stimulated when an acidity threshold is reached ($\text{pCO}_2 \geq 920 \mu\text{atm}$ vs
44 current conditions at constant light intensity). We show that carbonate dissolution by
45 microborers is a major biogeochemical process that could dissolve a large part of the
46 carbonates deposited by calcifying organisms under ocean acidification.

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54 **1. Introduction**

55 Atmospheric carbon dioxide partial pressure ($p\text{CO}_2$) is rising exponentially due to burning of
56 fossil fuels and changing land-use, and is expected to double ($\sim 750 \mu\text{atm}$) by 2100 (Stocker et
57 al. 2013). Thirty to 50% of anthropogenic CO_2 emissions are presently absorbed by the
58 world's oceans, decreasing seawater pH (Sabine et al. 2004; Wu et al. 2018), with a decrease
59 estimated at 0.3–0.4 pH-units by 2100 in the worst-case scenario (Caldeira and Wickett 2003;
60 Stocker et al. 2013). As a consequence, the saturation state of surface seawater (Ω) with
61 respect to calcium carbonate minerals (CaCO_3) will also decrease, impacting calcification
62 rates of marine organisms (Orr et al. 2005; Guinotte and Fabry 2008), and increasing rates of
63 carbonate dissolution (Feely et al. 2004; Tribollet et al. 2009; Krumins et al. 2013; Enochs et
64 al. 2016; Stubler and Peterson 2016; Trnovsky et al. 2016; Schönberg et al. 2017; Eyre et al.
65 2018).

66

67 A recent model (Cyronak et al. 2014) shows that the average $p\text{CO}_2$ may have increased faster
68 in coral reef ecosystems than in the open ocean (~ 3.5 -fold) over the past 20 years due to
69 additional anthropogenic disturbances (e.g. nutrient and organic matter inputs), putting these
70 carbonate ecosystems even more at risk under ocean acidification (Andersson and MacKenzie
71 2012). Recent studies highlighted the negative effect of ocean acidification (combined or not
72 with a rise in seawater temperature) on growth, abundance and calcification rates of the main
73 reef framebuilders, i.e. corals and calcifying algae (Langdon and Atkinson 2005; Kuffner et
74 al. 2007; Pandolfi et al. 2011; Comeau et al. 2015; Johnson et al. 2014). Although the same
75 trend is usually observed at the global reef scale, the relationship between community
76 calcification and aragonite saturation state varies dramatically from one location to the next
77 (Yates and Halley 2006; Silverman et al. 2007; Shamberger et al. 2011; Chan and Connolly

78 2012; Falter et al. 2012; Shaw et al. 2012). Pandolfi et al. (2011) suggested that the largest
79 variations among ecosystems could result from differences in sediment composition; some
80 being enriched in Mg-calcite are thus the first to be dissolved (see also Yates and Halley
81 2006). Dissolution however includes several processes: chemical dissolution resulting from
82 environmental conditions (i.e. properties of the bulk of seawater), metabolic dissolution
83 driven by bacteria through the remineralisation of organic matter, and metabolic dissolution
84 driven by bioeroders such as microborers and sponges, also called biogenic dissolution
85 (Tribollet et al. 2009; Schönberg et al. 2017). Rates of dissolution and resulting fluxes are
86 therefore highly variable in shallow water sediments and affected by a number of factors other
87 than aragonite saturation state, which may explain part of those variations (Milliman 1993;
88 Pandolfi et al. 2011; Andersson and Gledhill 2013; Eyre et al. 2014).

89
90 Biogenic dissolution due to microborers (or euendoliths; see definition Golubic et al. 1981)
91 received little attention as compared to calcification processes, although microborers which
92 comprise cyanobacteria, algae and fungi, are efficient agents of carbonate dissolution,
93 especially the chlorophyte of the genus *Ostreobium* which dominates mature communities
94 (Tribollet 2008a; Grange et al. 2015). The penetration of microborers into carbonates, both in
95 dead and live substrates such as corals, is an active process (see for instance Figure 1d in
96 Tribollet et al. 2011) and results in CaCO_3 dissolution as these organisms leave traces
97 (galleries or microborings) which conform perfectly to the shape of their filaments (Radtke
98 1993; Tribollet 2008b; Wisshak et al. 2011). The known rates of biogenic dissolution by these
99 communities at ambient pCO_2 measured using microscopy or buoyant weight techniques are
100 on average $0.1\text{-}1.8 \text{ mmol m}^{-2} \text{ h}^{-1}$ in dead coral skeletons (Tribollet 2008a; Reyes-Nivia et al.
101 2013). These values fall within the range provided for net dissolution in coral rubble reported

102 by Andersson and Gledhill (2013) suggesting that microborers could be the main agents of
103 carbonate dissolution in such substrates.

104

105 To date however, it is not known whether the metabolic activity of microborers can contribute
106 significantly to an increase of bulk alkalinity of seawater and therefore, if it can buffer the
107 system. Indeed, the process of biogenic dissolution has always been studied using microscopy
108 or buoyant weight techniques. Biogenic dissolution can either increase seawater alkalinity
109 (net dissolution is measured) or not if calcium carbonate is re-precipitated inside substrates or
110 at their surfaces (micritization process; Kobluk and Risk 1977; Nothdurft and Webb 2009).
111 Intuitively, it is difficult to imagine net carbonate dissolution by microborers (or euendoliths)
112 during daylight as they are mostly photosynthetic micro-organisms rising pH (Vooren 1981;
113 Tribollet et al. 2006), which is thermodynamically not favourable to dissolution.

114

115 The goals of the present study were thus to determine if (1) biogenic dissolution by natural
116 mature microboring communities dominated by *Ostreobium* sp. significantly increases
117 seawater alkalinity, (2) if so, when during the daily cycle, and (3) whether ocean acidification
118 stimulates this potential release of alkalinity as recent studies performed under controlled
119 conditions and *in situ* showed that rising pCO₂ increase rates of gross biogenic dissolution,
120 i.e. rates of CaCO₃ removed by microborers when measured by microscopy and buoyant
121 weight techniques (Tribollet et al. 2009; Reyes-Nivia et al. 2013; Enochs et al. 2016). To
122 achieve these objectives, we carried out an experiment with blocks of dead corals (*Porites*
123 *lobata*) naturally colonized by mature microboring communities from New Caledonia. Blocks
124 were maintained under fully controlled conditions to test the effects of rising pCO₂ (decrease
125 of Ω_{arag}) on microborer metabolism. The metabolic activity of microborers
126 (photosynthesis/respiration and carbonate dissolution/precipitation) was determined by

127 respirometry and the alkalinity anomaly technique. Samples were also studied using
128 microscopy techniques (gross biogenic dissolution) in order to compare rates of biogenic
129 dissolution obtained with the alkalinity anomaly technique (net biogenic dissolution).

130

131 **2. Methods**

132

133 *2.1. Experimental design*

134 Experimental blocks of dead coral skeleton ($7 \times 5 \times 5$ cm) were cut in the center of a massive
135 live coral colony of *Porites lobata* collected in the lagoon of New Caledonia at Larégnère
136 reef. This location was chosen to collect large, healthy, massive colonies of *Porites* to prepare
137 experimental blocks (with negligible initial bioerosion). Blocks were bleached (at least one
138 week), rinsed with fresh water (one week) and then dried (two weeks). In October 2009, 6
139 blocks were fixed on an aluminium grid with bolts and nuts to be laid at 14 m depth on the
140 reef of Casy (Southern lagoon of Grande Terre, New Caledonia). This reef was selected to
141 study biogenic dissolution under nearshore conditions. Water surrounding Casy is regularly
142 impacted by terrigenous inputs rendering visibility underwater very limited (0–4 m). After 1
143 year of colonization by epilithic and endolithic organisms (2009–2010), 3 colonized blocks
144 were randomly collected and brought back to the Institut de Recherche pour le
145 Développement in Nouméa (2 h transport) and put in a 150 l tank. The tank was filled with
146 filtered seawater (Whatman GF/C) pumped at Casy. A 12:12 h daylight to night photoperiod
147 was applied with a light intensity of $200 \mu\text{mol photons m}^2 \text{s}^{-1}$ delivered by two Solar simulator
148 Arrays (Tailored lighting). A heater-chiller provided a constant temperature in the tank (25.2
149 ± 0.1 °C). Three different saturation states were tested, $\Omega_{\text{Arag}} = 2, 3$ and 3.5 with a constant
150 seawater alkalinity A_T (see initial conditions in Table 1), by mixing HCl (0.1 mol l^{-1}) and

151 NaHCO_3 (1 mol l^{-1}) to seawater, simulating a realistic CO_2 enrichment scenario (Chauvin et
152 al. 2011).

153 Prior incubation, colonized blocks were gently brushed to remove all epiliths, including
154 calcifying organisms such as crustose coralline algae (Fig. 1A). Blocks were then incubated
155 for 2 h in the morning (daylight conditions) and in the evening (night conditions) using 1.6 l
156 incubation chambers submerged in the tank. A battery-driven magnetic stirrer homogenized
157 seawater inside chambers. In addition, 3 controls of seawater and 3 controls of bleached
158 uncolonized blocks were incubated in the same conditions per incubation. At the end of the
159 incubations, seawater samples were collected to measure A_T and pH_T according to the
160 methods described below. The mean value obtained for seawater controls at the beginning of
161 the incubations was used as the initial condition in the incubation chambers. No metabolic
162 activity was recorded on seawater controls during incubations. The mean value obtained for
163 bleached uncolonized blocks at the end of incubations was used to correct dissolution rates of
164 colonized blocks. Indeed slightly significant rates of CaCO_3 precipitation were measured
165 under current conditions ('nucleus' effect of bleached coral blocks in a super-saturated
166 seawater; see Morse 1983).

167 At the end of the experiment, the 3 colonized blocks were preserved in a seawater buffered
168 formaldehyde solution (3%) prior microscopy analysis in the laboratory. Using microscopy
169 techniques similar to those used by Tribollet et al. (2009), gross rates of biogenic dissolution
170 were quantified (microdensity and porosity of the coral colony skeleton were 2.58 ± 0.06
171 g cm^{-3} and 53 ± 3 %, respectively). Rates were expressed in $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ or
172 $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ for comparison with net dissolution rates obtained with the alkalinity
173 anomaly technique. The block surface area used in the calculation was the surface area
174 exposed to light i.e. the surface area of 5 colonized sides (0.0155 m^2).

175 As in previous studies of bioerosion, especially microbioerosion, a limited number of samples
176 was used (see Chazottes et al. 1995; Tribollet et al. 2006; Tribollet 2008a; Grange et al. 2015;
177 Enochs et al. 2016). The 3 large coral blocks were however representative of parts of reef
178 framework (i.e. pavement and coral rubble colonized by epilithic and endolithic communities;
179 Chazottes et al. 1995; Adey 1998) and allowed natural microboring communities to develop
180 with their usual patchiness distribution (Tribollet and Golubic 2005). To quantify gross rates
181 of biogenic dissolution, 3 independent pieces of coral skeleton (1 cm x 0.5 cm x 1 cm in
182 depth) were collected at the top surface of each block (i.e. surface facing light on the reef).
183 Each piece was then cut in half perpendicular to the top surface. One half was used for SEM
184 observations and quantification of the bioeroded surface area by microborers (see Tribollet
185 and Golubic 2005), while the other half was used to prepare several thin sections (at least 5)
186 to measure the mean depth of penetration of alive microboring filaments ($n > 100$
187 measurements per piece; see definition in Tribollet et al. 2009). A total of 9 independent
188 pieces of blocks were therefore studied to quantify the average gross biogenic dissolution rate
189 under ambient $p\text{CO}_2$ conditions.

190

191 *2.2. Seawater chemistry analysis*

192 Saturated mercuric chloride was added to the seawater samples to prevent biological activity
193 [46]. Potentiometric determination of pH_T was performed using Tris/HCl and 2-
194 aminopyridine/HCl buffers in synthetic seawater to calibrate the electrode (Dickson et al.
195 2007). Measurements of pH_T were performed at 25.0 ± 0.1 °C using a Radiometer TIM865
196 titrator with combined pH electrode pHC2401-8 and a thermostat bath. A_T samples were
197 filtered through Whatman GF/F prior analysis. Potentiometric titration of A_T was performed
198 using 0.01 mol l^{-1} HCl in NaCl to approximate the ionic strength of seawater. Each day of A_T
199 measurements, Certified Reference Material from the laboratory of A. Dickson (Scripps

200 Institution of Oceanography) was titrated to determinate the acid titrant concentration. A_T was
201 calculated in triplicate from the second inflection point of the titration curve obtained using an
202 automatic titration of 25 ml seawater sample. The precision of the analysis based on triplicate
203 measurements (± 1 standard deviation) was typically $\pm 2 \mu\text{equiv l}^{-1}$.

204 Measured pH_T and A_T were used to calculate the other CO_2 chemistry parameters with the
205 software CO2SYS (Pierrot et al. 2006). In New Caledonia, phosphate and silicate
206 concentrations were 0.03 and $3.1 \mu\text{mol l}^{-1}$, respectively. Conversions between $\mu\text{mol l}^{-1}$ and
207 $\mu\text{mol kg}^{-1}$ were performed based on seawater salinity ($S = 35.33$) and temperature.

208

209 2.3. Net dissolution and organic carbon metabolism calculation

210 Net dissolution rates (G), expressed in $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$ were calculated according to the
211 following equation:

$$212 \quad (1) \quad G = (\frac{1}{2} \Delta A_T \times \text{seawater volume}) / (\text{substrate surface area} \times \text{time})$$

213 where G is positive when net dissolution occurs, ΔA_T is the difference in alkalinity between
214 two measurements (final A_T minus initial A_T), *seawater volume* is the volume of the
215 incubation chambers, *substrate surface area* is the surface of the 5 sides of blocks exposed to
216 light, and *time* was the duration of the incubation.

217

218 Net organic carbon metabolism (NP), expressed in $\text{mmol C m}^{-2} \text{ h}^{-1}$ was calculated according
219 to the following equation:

$$220 \quad (2) \quad NP = ((\Delta \text{DIC} \times \text{seawater volume}) / (\text{substrate surface area} \times \text{time})) - G$$

221 where NP is the rate of net photosynthesis during daylight (negative value, although for
222 simplicity it will be presented as positive in the results) or the rate of night respiration
223 (positive value) and ΔDIC is the difference in DIC between two measurements (final DIC
224 minus initial DIC). The other symbols are as defined in Eq. 1.

225

226 Daily net dissolution (in $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$) was obtained by multiplying the average of
227 daylight and night rates (in $\text{mmol CaCO}_3 \text{ m}^{-2} \text{ h}^{-1}$) by 24. Daily respiration (in $\text{mmol C m}^{-2} \text{ d}^{-1}$)
228 was calculated as 24 times the night respiration rate (in $\text{mmol C m}^{-2} \text{ h}^{-1}$). Daily gross
229 production (in $\text{mmol C m}^{-2} \text{ d}^{-1}$) was calculated by adding night respiration and net
230 photosynthesis (both positive, in $\text{mmol C m}^{-2} \text{ h}^{-1}$) and multiplying by 12.

231

232 2.4. Statistical analysis

233 Statistical tests were performed using STATISTICA 7.1 (Statsoft). Data were tested for
234 homogeneity of variances (Levene test) prior to variance analysis and met this requirement.
235 Differences among treatments were tested using a 2-way ANOVA. Means are reported \pm SE.

236

237

238 3. Results

239

240 Observations under light microscopy confirmed that dead coral blocks were colonized by
241 mature communities of microborers dominated by the chlorophyte of the genus *Ostreobium*
242 (Fig. 1B). In addition to *Ostreobium*, filaments of the euendolithic cyanobacterium
243 *Plectonema terebrans* were observed (in abundance) as well as rare fungal hyphae. Coral
244 blocks were covered mainly by large thalli of the brown alga *Lobophora variegata* and the
245 red alga *Peyssonnelia* sp. Some green turf puffs were also observed with entrapped sediments,
246 as well as a few encrusting coralline algae. No traces of boring polychaetes were observed
247 while a few traces of grazing were observed on block surfaces. These substrates were thus

248 representative of dead coral skeletons recently exposed to bioerosion in shallow reefs (<15 m
249 depth) (Chazottes et al. 1995; Tribollet 2008a; Grange et al. 2015).

250

251 At constant light and temperature (Table 1), CaCO₃ dissolution measured by the alkalinity
252 anomaly technique was simultaneously affected by light (daylight vs. night conditions: $p <$
253 0.0003) and Ω_{Arag} ($p < 0.02$), with no interaction between the two factors (Fig. 2). CaCO₃
254 dissolution was higher at night than at $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (on average $8.4 \pm 1.1 \mu\text{mol}$
255 $\text{CaCO}_3 \text{ block}^{-1} \text{ h}^{-1}$ and $1.9 \pm 1.1 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{ h}^{-1}$, respectively) (Fig. 2). CaCO₃
256 dissolution was the highest at $\Omega_{\text{Arag}} \sim 2$ with an average of $8.3 \pm 1.5 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{ h}^{-1}$
257 (vs. $3.6 \pm 1.2 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{ h}^{-1}$ at $\Omega_{\text{Arag}} \sim 3-3.5$). Besides, the difference in CaCO₃
258 dissolution between night and daylight conditions did not differ significantly among
259 treatments. Taking into account the exposed surface area of the blocks (5 sides = 155 cm^2),
260 the daily CaCO₃ dissolution was $12.8 \pm 0.7 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ (corresponding to an
261 alkalinity production of $25.6 \pm 1.4 \text{ mEq m}^{-2} \text{ d}^{-1}$) and $5.6 \pm 0.4 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ (11.2 ± 0.8
262 $\text{mEq m}^{-2} \text{ d}^{-1}$) at $\Omega_{\text{Arag}} \sim 2$ and $\Omega_{\text{Arag}} \sim 3-3.5$, respectively.

263

264 Under night conditions, respiration rate was not affected by Ω_{Arag} (Fig. 2) and was on average
265 $17.7 \pm 0.8 \mu\text{mol C block}^{-1} \text{ h}^{-1}$, or $27 \pm 1 \text{ mmol C m}^{-2} \text{ d}^{-1}$. Similarly, net photosynthesis was the
266 same regardless Ω_{Arag} ($8.7 \pm 1.5 \mu\text{mol C block}^{-1} \text{ h}^{-1}$ on average). Gross production (P_g),
267 however, was slightly affected by Ω_{Arag} ($p < 0.05$), with a higher value at $\Omega_{\text{Arag}} \sim 2$ than Ω_{Arag}
268 $\sim 3-3.5$ (24 ± 2 versus $18 \pm 1 \text{ mmol C m}^{-2} \text{ d}^{-1}$, respectively). The P_g/R ratio was clearly lower
269 than 1 (0.89 ± 0.08 and 0.67 ± 0.02 at $\Omega_{\text{Arag}} \sim 2$ and $\Omega_{\text{Arag}} \sim 3-3.5$, respectively).

270

271 The mean depth of penetration of alive euendolithic filaments was $1.81 \pm 0.05 \text{ mm}$ and the
272 mean surface area bioeroded at the surface of the blocks was $12.85 \pm 1.1 \%$. The estimated

273 gross rate of biogenic dissolution using microscopy techniques averaged $0.240 \pm 0.002 \text{ kg m}^{-2}$
274 y^{-1} , which converts to $7.40 \pm 0.05 \text{ mmol m}^{-2} \text{ d}^{-1}$.

275

276 **4. Discussion**

277

278 *4.1. Production of alkalinity in seawater by microborers under present conditions*

279 To our knowledge, our experiment is the only study in which dissolution of experimental
280 carbonate substrates colonized by natural microboring communities was simultaneously
281 quantified using microscopy and alkalinity anomaly techniques. Under $200 \mu\text{mol photons m}^{-2}$
282 s^{-1} and $\Omega_{\text{Arag}} \sim 3.5$ (similar to Ω_{Arag} measured at Ilot Casey during an entire day upon block
283 collection; 3.58 ± 0.03 , $n = 14$), the photosynthetic activity of endolithic communities was
284 presumably limited by light and/or DIC availability as the P_g/R ratio was clearly lower than 1
285 (0.67 ± 0.02). Although this may have slightly limited the erosive activity of microborers
286 under controlled conditions, the rates of gross biogenic dissolution (microscopy technique)
287 and net dissolution (alkalinity anomaly technique) were of the same order of magnitude at
288 $\Omega_{\text{Arag}} 3\text{-}3.5$ ($7.4 \pm 0.1 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ versus $5.6 \pm 0.4 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively). Other
289 processes than the microborer activity, such as denitrification, can increase alkalinity in
290 seawater (Stumm and Morgan 1996) but are likely to be insignificant in most hard substrate
291 situations (Kinsey 1978; Gattuso et al. 1999). High-magnesium calcite is also rarely observed
292 in coral skeletons (Nothdurft et al. 2007), therefore dissolution of this form of carbonates was
293 most probably not involved in the measured dissolution process. Although some bacterial
294 activity at the block surfaces cannot be ruled out, bacterial activity inside blocks was not
295 involved in CaCO_3 dissolution as we did not observe random patterns of dissolution on
296 scanning electron microscopy pictures. We thus strongly suggest that alive microboring

297 communities in coral blocks were responsible for the bulk of alkalinity production in our
298 experiment.

299

300 *4.2. Daily cycle of biogenic dissolution*

301 Surprisingly 20% of the daily rate of biogenic dissolution was occurring during daylight.
302 Although it seems a paradox to measure simultaneously carbonate dissolution (i.e. release of
303 seawater alkalinity) and photosynthesis, Garcia-Pichel et al. (2010) clearly showed that
304 biogenic dissolution of experimental carbonate substrates by the cultured cyanobacterium *M.*
305 *testarum* was coupled to the photosynthetic energy production. In our experiment, higher rates
306 of net biogenic dissolution were quantified under night conditions than at
307 200 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$. The decrease of the interstitial pH with increasing depth into a
308 *Porites cylindrica* skeleton colonized mainly by *Ostreobium* was also particularly important
309 in the dark in Reyes-Nivia et al. (2013)'s study, suggesting that night respiration by
310 microborers could be an important factor involved in CaCO_3 dissolution.

311

312 *4.3. Effect of ocean acidification on microborer metabolism and alkalinity production*

313 A 33% increase in gross production was recorded at $\Omega_{\text{Arag}} \sim 2$ (pCO_2 of 936 μatm) relative to
314 $\Omega_{\text{Arag}} \sim 3-3.5$ (pCO_2 of 437-570 μatm), suggesting that endolithic communities dominated by
315 *Ostreobium* were limited by DIC availability at $\Omega_{\text{Arag}} \sim 3-3.5$. Photosynthesis limitation at
316 $\Omega_{\text{Arag}} \sim 3-3.5$ was also highlighted by the low Pg/R ratio (0.67 ± 0.02). Although *Ostreobium*
317 presents carbonic anhydrases (CAs) that may serve as a mechanism to supply inorganic
318 carbon at the required rate for photosynthesis (Shashar and Stambler 1992), it remains
319 unknown if it possesses Carbon Concentrating Mechanisms (CCMs) involving active
320 transport of HCO_3^- and/or CO_2 . In general, photosynthetic rates of algae that have CCMs are
321 not carbon limited, at least under most environmental conditions (e.g. Hurd et al. 2009). Some

322 species that have CCMs may however, be dependent on CO₂ and positively respond to
323 elevated pCO₂ at sub-saturating irradiance, because light limitation of active carbon uptake
324 increases reliance on CO₂ diffusion (Hepburn et al. 2011).

325

326 To the contrary of photosynthesis, night respiration was not affected by acidification (Fig. 2).
327 Most studies to date have reported no or little effect of elevated CO₂ on dark respiration rates
328 of macroalgae (e.g. Zou et al. 2011; Noisette et al. 2013). Because the responses to elevated
329 CO₂ of respiration and photosynthesis were different in our experiment, pCO₂ increase
330 resulted in an increase in the P_g/R ratio. Zou et al. (2011) reported that CO₂ enrichment
331 decreased the respiratory carbon lost per unit algal biomass in a low-N-grown macroalga, and
332 suggested that CO₂ enrichment may thereby enhance carbon sequestration capacity of this
333 organism.

334

335 The amount of alkalinity released in seawater doubled at $\Omega_{\text{Arag}} \sim 2$ compared to $\Omega_{\text{Arag}} \sim 3\text{-}3.5$
336 (25.6 ± 1.4 and 11.2 ± 0.8 mEq m⁻² d⁻¹, respectively). Net biogenic dissolution rates did not
337 vary significantly between $\Omega_{\text{Arag}} \sim 3$ and 3.5 (pCO₂ = 570 and 437 μatm respectively)
338 suggesting that a threshold somewhere between $\Omega_{\text{Arag}} \sim 2$ and 3 must be reached before
339 promoting increased CaCO₃ dissolution by microboring communities from New Caledonia.
340 The increase in net biogenic dissolution under elevated pCO₂ in New Caledonia confirms the
341 increase of gross biogenic dissolution reported by Tribollet et al. (2009) and Reyes-Nivia et
342 al. (2013) for dead coral skeletons which were exposed during a few months to high pCO₂
343 (48% at 750 μatm and 46-89% at 1000 μatm relative to ambient pCO₂ depending on coral
344 species, respectively). A similar trend was also observed for pioneer euendolithic
345 communities dominated by the chlorophyte *Phaeophila* sp. under naturally acidified
346 conditions at Maug Island (Mariana Archipelago; Enochs et al. 2016).

347

348 Similarly to zooxanthellate boring sponges under high pCO₂ (Wisshak et al. 2012), increased
349 biogenic dissolution by microborers could be explained by an enhancement of photosynthetic
350 energy, and/or the lowering of the pH gradient between ambient seawater and the site of
351 dissolution, thereby lowering the metabolic cost required for CaCO₃ dissolution. Providing
352 acidified seawater near the dissolution front of euendolithic filaments could make interstitial
353 water thermodynamically more favourable to chemical dissolution. Changes in extracellular
354 pH have also been shown to directly drive changes in intracellular pH of some marine
355 microalgae and in turn affect H⁺ gradients and cellular pH homeostasis (Taylor et al. 2011).
356 That such processes are used at the dissolution front in *Ostreobium* remains to be determined.
357 Basic knowledge of the process of CaCO₃ dissolution is currently lacking to fully understand
358 mechanisms behind *Ostreobium* response to acidification.

359

360 *4.4. Significance of biogenic dissolution in coral reefs*

361 Gross and net rates of biogenic dissolution measured as part of our experiment fall well
362 within the range of gross and net rates of biogenic dissolution reported in the literature for
363 hard dead reef substrates (Table 2). They are also similar to rates quantified on fringing and
364 lagoon reefs (Tribollet 2008a; Tribollet et al. 2009). Interestingly all rates provided in Table 2
365 fall within the range of net dissolution rates provided for various carbonate substrates by
366 Andersson and Gledhill (2013) suggesting that biogenic dissolution by microborers is a major
367 process of carbonate dissolution in coral reefs.

368

369 Considering all biogenic dissolution rates for hard substrates in Table 2, the average rate is 11
370 mmol m⁻² of reef d⁻¹. This average is assumed to be representative of the process occurring on
371 reefs as it includes rates of biogenic dissolution measured under a full range of biotic and

372 abiotic conditions (e.g. light availability and grazing). At the scale of reefs worldwide (surface
373 area of $0.6 \cdot 10^{12} \text{ m}^2$ including 80% of sand and 20% of hard substrates, Milliman 1993) and
374 because microborers can colonize all types of reef carbonates, gross biogenic dissolution is
375 estimated to be $11 \cdot 10^{-3} \times 365 \times 0.2 \times 0.6 \cdot 10^{12} = 0.5 \cdot 10^{12} \text{ mol CaCO}_3 \text{ y}^{-1}$ in hard substrates
376 (living corals being also colonized by microborers; see Tribollet 2008b). Considering an
377 average gross rate of biogenic dissolution for sediments of $10 \text{ mmol m}^{-2} \text{ d}^{-1}$ (Tudhope and
378 Risk 1985), nearly four times more CaCO_3 seems to be dissolved by microborers in sediments
379 than in hard substrates ($1.8 \cdot 10^{12} \text{ mol CaCO}_3 \text{ y}^{-1}$). If we consider a net CaCO_3 production in
380 coral reefs of $9 \cdot 10^{12} \text{ mol CaCO}_3 \text{ y}^{-1}$ (Milliman 1993), at least $11.3 \cdot 10^{12} \text{ mol CaCO}_3 \text{ y}^{-1}$ (i.e.
381 $9 \cdot 10^{12} + 0.5 \cdot 10^{12} + 1.8 \cdot 10^{12}$) is deposited by calcifying organisms (gross calcification) and at
382 most, 20% of this produced CaCO_3 is probably dissolved by microborers. In the worst case
383 scenario, if we consider a doubling of gross biogenic dissolution rates (Reyes-Nivia et al.
384 2013) and a 40% decrease in gross carbonate production due to ocean acidification by 2100
385 (Pandolfi et al. 2011), $2/3$ of reef carbonates deposited per year may be dissolved by
386 microborers. In the more optimistic scenario, with only a 50% increase in CaCO_3 gross
387 biogenic dissolution and a 20% decrease in gross CaCO_3 production (e.g. Tribollet et al.
388 2009; Chauvin et al. 2011; Chan and Connolly 2012) , 40% of reef carbonates deposited per
389 year may be dissolved by microborers. Those estimations are very conservative as they do not
390 take into account sediment dissolution resulting from bacterial activity which can be
391 important in some areas (Andersson et al. 2007) and hard carbonate dissolution by boring
392 sponges and bivalves (see review by Schönberg et al. 2017). Although more investigations on
393 the dynamics of the biogenic dissolution process are needed, our estimations strongly suggest
394 that biogenic dissolution of carbonates by microborers should no longer be overlooked and
395 should be considered in reef carbonate biogeochemical models to better predict the fate of
396 coral reefs.

397

398 **Conclusions**

399 Results show that microboring communities dominated by the phototrophic microboring
400 chlorophyte of the genus *Ostreobium*, produce significant amount of alkalinity while
401 penetrating actively into coral skeletons. Daily production is increased by a factor 2 under
402 ocean acidification conditions (i.e. when Ω decreases from 3-3.5 to 2). Comparisons of net
403 dissolution rates obtained in our study with those in the literature strongly suggest that (i) the
404 biogenic dissolution process resulting from microborer metabolic activity is a major process
405 of carbonate dissolution in coral reefs, and (ii) that it will probably dissolve a large part of
406 reef carbonate deposited per year by the end of the century if human beings maintain their
407 ‘business as usual’ (IPCC 2013). It is not known however, to which extent this process could
408 help maintaining environmental conditions favourable for calcifying organisms (‘negative
409 feedback to ocean acidification’). This role could be significant, at least at the microscale as
410 microborers colonize also living calcifying organisms such as corals and crustose coralline
411 algae (Le Campion-Alsumard et al. 1995; Tribollet and Payri 2001). Reyes-Nivia et al. (2014)
412 showed that crustose coralline algae (CCA) heavily colonized by microborers are less
413 sensitive to ocean acidification than CCA that are less infested, suggesting that the negative
414 effects of ocean acidification on CCA calcification are mitigated by microborer
415 photosynthetic activity. It remains unknown however, if this negative feedback of
416 microborers results from their photosynthetic activity (rise of pH at the microscale) or their
417 dissolution activity (production of alkalinity) or both. We thus urge the scientific community
418 to study the ‘potential buffering’ effect of microborer metabolic activity on reefs at various
419 spatial scales (micro- to ecosystem scale) and stress the importance to consider the dynamics
420 of carbonate dissolution by microborers to better understand past and future effects of this
421 factor on coral reef biogeomorphology and cycle.

422

423 **Data availability**

424 Datasets are available from the corresponding author (aline.tribollet@ird.fr) on reasonable
425 request, while pending to be deposited on the SEANOE repository.

426

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Tables

610

611 **Table 1.** Initial seawater chemistry conditions of the experiment (mean \pm SD).
612

		T <i>in situ</i> (°C)	pH _T	A _T ($\mu\text{mol kg}^{-1}$)	DIC ($\mu\text{mol kg}^{-1}$)	pCO ₂ (μatm)	Ω_{Arag}
$\Omega_{\text{Arag}} = 2$	<i>night</i>	25.2	7.740 \pm 0.002	2304 \pm 1	2143 \pm 1	919 \pm 5	2.08 \pm 0.01
	<i>daylight</i>	25.2	7.725 \pm 0.002	2303 \pm 2	2149 \pm 1	954 \pm 4	2.02 \pm 0.01
$\Omega_{\text{Arag}} = 3$	<i>night</i>	25.2	7.921 \pm 0.003	2320 \pm 1	2069 \pm 2	568 \pm 4	2.97 \pm 0.01
	<i>daylight</i>	25.2	7.919 \pm 0.003	2322 \pm 1	2072 \pm 2	571 \pm 4	2.97 \pm 0.01
$\Omega_{\text{Arag}} = 3.5$	<i>night</i>	25.3	8.010 \pm 0.002	2296 \pm 1	1997 \pm 1	438 \pm 2	3.46 \pm 0.01
	<i>daylight</i>	25.2	8.012 \pm 0.001	2297 \pm 1	1996 \pm 1	436 \pm 1	3.48 \pm 0.01

613 pH_T (total hydrogen ion concentration scale) and total alkalinity (A_T, in units of $\mu\text{equiv kg}^{-1}$) were used to
614 calculate the other CO₂ chemistry parameters with the software CO₂Sys (Pierrot *et al.*, 2006): dissolved
615 inorganic carbon (DIC), partial pressure of CO₂ (pCO₂) and aragonite saturation state (Ω_{Arag}), using Roy *et al.*
616 (1993) values for carbonic acid constants K₁ and K₂, and K_{SO₄} as determined by Dickson (1990)

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628 **Table 2.** Rates of biogenic dissolution from our study and from literature at ambient pCO₂, in
629 mmol CaCO₃ dissolved per m² per day. Rates from literature where converted, when
630 necessary, using microdensity and porosity of coral skeletons according to Tribollet *et al.*
631 (2009). Here, square meters refer to m² of substrate exposed to colonization by euendoliths
632 when coral substrates were used.

633 * rates measured using microscopy techniques. ** rates measured using the alkalinity
634 technique. *** rates measured using the buoyant weight technique. Cyano.: Cyanobacteria

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Source	Location	Type of reef	Depth (m)	Type of substrate (& dominant microborers)	Dissolution rate (mmol CaCO ₃ m ⁻² d ⁻¹)
Tudhope and Risk (1985)	Australia	Barrier reef	5 – 27	Sediments (undetermined algae/fungi)	10*
Hoskin et al. (1986)	Bahamas	Intertidal	2 – 32	Limestone (undetermined)	7***
Chazottes et al. (1995)	French Polynesia	Flat reef	2	Porites lobata (cyano., <i>Ostreobium</i> , fungi)	3*
Vogel et al. (2000)	Bahamas	Various reefs	6 – 30	Limestone (cyano, algae, fungi)	3 – 7*
				Strombus shells (cyano, algae, fungi)	< 3*
Chazottes et al. (2002)	Reunion	Fringing reef	1 – 3	P. lobata (cyano, <i>Ostreobium</i>)	0.5 – 2*
Carreiro-Silva et al. (2005)	Belize	Patch reef	2	Strombus shells (<i>Plectonema</i> , <i>Phaeophila</i>)	1*
Tribollet (2008a)	Australia	Inshore reef	14	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i> , fungi)	3*
		Barrier reef	14	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i> , fungi)	8 – 16*
		Offshore pinnacle	14	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i> , fungi)	30 *
Tribollet et al. (2009)	Hawaii	Barrier back reef	3	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i>)	7-9*
Reyes-Nivia et al. (2013)	Australia	Barrier reef	Shallow	P. cylindrica, Isopora cuneate (<i>Plectonema</i> , <i>Ostreobium</i>)	26 – 42***
Present study (TA method)	New Caledonia	Bay (inshore reef)	14	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i>)	6**
Present study (microscopy)	New Caledonia	Bay (inshore reef)	14	P. lobata (<i>Plectonema</i> , <i>Ostreobium</i>)	7*

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Figures

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645 **Figure 1.** (A) Photograph of a coral block colonized by 1 year-old euendolithic communities
646 after removal of epiliths. Black arrow indicates a dark green endolithic patch due to
647 *Ostreobium* sp. White arrow indicates a purplish endolithic patch due to euendolithic
648 cyanobacteria. Scale bar = 1 cm. (B) *Ostreobium* sp. filaments (black arrows) observed under
649 light microscopy on a thin section coloured by toluidine blue. Scale bar = 30 μm .

650

651 **Figure 2.** Metabolic activity of microboring communities dominated by *Ostreobium* sp. in
652 experimental dead coral skeletons measured under three different saturation state of aragonite
653 (Ω_{Arag}). (a) Net biogenic dissolution of carbonates under daylight (white) and night conditions
654 (grey). (b) Net photosynthesis and respiration under daylight and night conditions,
655 respectively. For clarity, both net photosynthesis and night respiration are shown as positive
656 values. The number in each bar represents the mean value of Ω_{Arag} during the incubations.
657 The standard error of each mean is indicated.

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