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1 **The three steps of the carbonate biogenic dissolution process by microborers in coral reefs**  
2 **(New Caledonia)**

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13  
14 **Keywords** Microbioerosion dynamics; biogenic dissolution of calcium carbonate; euendoliths; succession of  
15 microboring communities; coral reefs; New Caledonia

16  
17 **Abstract**

18 Biogenic dissolution of carbonates by microborers is one of the main destructive forces in coral reefs and is  
19 predicted to be enhanced by eutrophication and ocean acidification by 2100. The chlorophyte *Ostreobium* sp.,  
20 the main agent of this process, has been reported to be one of the most responsive of all microboring species to  
21 those environmental factors. However, very little is known about its recruitment, how it develops over  
22 successions of microboring communities and how that influences rates of biogenic dissolution. Thus, an  
23 experiment with dead coral blocks exposed to colonization by microborers was carried out on a reef in New  
24 Caledonia over a year period. Each month, a few blocks were collected to study microboring communities and  
25 the associated rates of biogenic dissolution. Our results showed a drastic shift in community species composition  
26 between the 4<sup>th</sup> and 5<sup>th</sup> months of exposure, i.e. pioneer communities dominated by large chlorophytes such as  
27 *Phaeophila* sp. were replaced by mature communities dominated by *Ostreobium* sp.. Prior the 4<sup>th</sup> month of  
28 exposure, large chlorophytes were responsible of low rates of biogenic dissolution while during the community  
29 shift, rates increased exponentially (x10). After 6 months of exposure, rates slowed down and reached a 'plateau'  
30 with a mean of 0.93 kg of CaCO<sub>3</sub> dissolved per m<sup>2</sup> of reef after 12 months of exposure. Here we show that (a)  
31 *Ostreobium* sp. settled down in new dead substrates as soon as the 3<sup>rd</sup> month of exposure but dominated  
32 communities only after 5 months of exposure, and (b) microbioerosion dynamics comprise 3 distinct steps which  
33 fully depend on community development stage and grazing pressure.

## 41 Introduction

42

43 Coral reefs are highly diverse and complex marine ecosystems, providing many services including commercial  
44 fishing, tourism and coastal protection against storms (Knowlton et al. 2010). Their maintenance results from the  
45 delicate balance between constructive forces, mainly calcification of corals and encrusting coralline algae, and  
46 destructive forces, mostly bioerosion processes (Scoffin et al. 1980, Tribollet & Golubic 2011). Unfortunately,  
47 this equilibrium is increasingly threatened by anthropogenic and environmental factors such as eutrophication,  
48 overfishing, rising sea surface temperature and ocean acidification (Hoegh-Guldberg et al. 2007, Pandolfi et al.  
49 2011, Huand 2012). To date, 20% of coral reefs have already disappeared and 20% show signs of imminent  
50 extinction (Wilkinson 2008). Although both constructive and destructive forces are affected by anthropogenic  
51 and climatic stresses (Anthony et al. 2008, Tribollet et al. 2009, Chauvin et al. 2011, Carreiro-Silva et al. 2012,  
52 Andersson & Gledhill 2013, Jessen et al. 2014, Wisshak et al. 2014), much less attention has been given to  
53 bioerosion than reef accretion.

54

55 Reef bioerosion results from the mechanical and/or chemical activity of living organisms (Neumann 1966)  
56 comprising grazers (e.g. urchins and parrotfishes), macroborers (e.g. bivalves and sponges) and microborers or  
57 euendoliths (cyanobacteria, algae and fungi) (Glynn 1997, Tribollet & Golubic 2011). Grazers abrade substrate  
58 surfaces to feed on epilithic and euendolithic algae (Pari et al. 1998, Tribollet & Golubic 2005) while macro- and  
59 micro-borers penetrate actively by mechanical and/or chemical means into substrates to find a shelter (Lazar &  
60 Loya 1991, Zundevich et al. 2007, Garcia-Pichel et al. 2010, Tribollet & Golubic 2011). Previous studies  
61 showed that microbioerosion in synergy with grazing is the main process driving reef bioerosion of dead  
62 carbonates when exposed several months to three years to bioeroding agents (Chazottes et al. 1995, Tribollet &  
63 Golubic 2005). Despite their microscopic size, euendoliths are probably the main agents of reef bioerosion as  
64 they are able to colonize each available micrometer of carbonate surface area, -from carbonate sand to skeletons  
65 of dead and live calcifiers such as corals, mollusks and crustose coralline algae-, and are able to dissolve as much  
66 as 1.1 kg of  $\text{CaCO}_3$  per linear  $\text{m}^2$  of reef per year, which converts to  $30 \text{ mmol CaCO}_3 \cdot \text{m}^2 \cdot \text{d}^{-1}$  (value obtained  
67 from the highest rate of microbioerosion quantified in coral reefs and recalculated using coral microdensity and  
68 porosity; see Tribollet & Golubic 2005). Chazottes et al. (1995) and Tribollet (2008a) highlighted that the  
69 highest rates of carbonate dissolution result mostly from the activity of the chlorophytes of the genus  
70 *Ostreobium*. Recently, experiments realized under controlled conditions or semi-controlled conditions over short  
71 periods of time showed that ocean acidification and eutrophication enhance biogenic dissolution by stimulating  
72 the activity of chlorophytes such as *Ostreobium* sp., suggesting an acceleration of reef framework degradation in  
73 the near future (Chazottes et al. 2002, Tribollet et al. 2009, Carreiro-Silva et al. 2012, Reyes-Nivia et al. 2013,  
74 Tribollet et al. 2014). These experiments strongly suggested the dependence of the response of biogenic  
75 dissolution on species composition of microboring communities (see also Tribollet 2008a). To better understand  
76 dynamics of the biogenic dissolution process under various environmental conditions, it is therefore essential to  
77 determine simultaneously species composition of microboring communities, their successions over time and  
78 their associated rates of biogenic dissolution under natural conditions. Interestingly these aspects have been  
79 rarely studied limiting possibilities of modeling dynamics of the biogenic dissolution process for better  
80 prediction of coral reef future.

81  
82 Very few studies have indeed investigated changes in euendolithic assemblages at different time scales and the  
83 influence of such changes on rates of carbonate biogenic dissolution. Le Campion-Alsumard (1975) was first to  
84 report successions of euendolithic communities in exposed calcite spar in the Mediterranean Sea over a period of  
85 one month. She showed that colonization of calcite by euendoliths starts after 8 days of exposure and that the  
86 early colonizers are cyanobacteria such as *Mastigocoleus testarum*. Unfortunately, she did not quantify rates of  
87 carbonate dissolution. Later, Kiene et al. (1995), Gektidis (1999) and Vogel et al. (2000) reported successions of  
88 euendolithic communities in various reef carbonate substrates after 1, 3, 6, 12, 24 months and very scarce  
89 information on rates of biogenic dissolution associated with those communities. They confirmed that pioneer  
90 euendolithic communities, also called ‘immature communities’, comprise short lived cyanobacteria such as *M.*  
91 *testarum* and the chlorophyte *Phaeophila* sp., and that the long-lived euendolithic chlorophyte *Ostreobium* sp.  
92 appears later to dominate communities after 1 or 2 years of exposure (‘mature communities’). Chazottes et al.  
93 (1995), Tribollet et al. (2006) and Tribollet (2008a) specified later that euendolithic communities in coral reefs  
94 become mature at least after 6-12 months of exposure. However, the exact period of settlement of *Ostreobium*  
95 and when it becomes dominant remain unknown. Among all those studies, only Chazottes et al. (1995) and  
96 Tribollet (2008a) studied and reported simultaneously species composition of euendolithic communities and  
97 rates of reef biogenic dissolution over time, i.e. after 2, 6, 12, 24 months and 12 and 36 months, respectively.  
98 They reported that biogenic dissolution does not vary linearly nor proportionally over time, however those  
99 authors did not present the full dynamics of the process. Thus, to better understand dynamics of biogenic  
100 dissolution of carbonates by euendoliths, we carried out an experiment with a high temporal resolution on a reef  
101 in New Caledonia. Experimental coral blocks were exposed to colonization by euendoliths and were recovered  
102 every month over a year period. The experiment did not last longer to avoid colonization by macroboring  
103 organisms (see review by Tribollet & Golubic 2011) but was long enough to report interactions between  
104 euendoliths and grazers. The specific goals of the present study were to determine (1) when *Ostreobium* sp.  
105 settles on dead carbonate substrates newly available, (2) when exactly it dominates communities, (3) how  
106 euendolithic communities succeed to each other over a year period with a monthly resolution, and (4) how does  
107 that influence biogenic dissolution. In addition we quantified grazing pressure and how it influenced biogenic  
108 dissolution. Then, the first model of the biogenic dissolution process dynamics was developed.

109  
110

## 111 **Material and Methods**

112

### 113 Site and experimental design description

114 This study was carried out on the coral reef of the Island ‘Ile aux Canards’ in New Caledonia (lat. 22°31’S, long.  
115 166°43’E, Fig. 1a, b) located in the lagoon, a few hundred meters away from Nouméa city (South province of the  
116 Island Grande Terre). This site was selected because of its easy access by boat from the laboratory (Center of the  
117 Institut de Recherche pour le Développement), it presents a well developed reef which is relatively healthy  
118 although it is impacted by anthropogenic activities such as tourism. At this site, the tide amplitude is low (~1.5  
119 m) and seawater is weakly turbid over the year due to the hydrodynamism occurring around the island. Local  
120 currents resuspend regularly carbonate sediments and organic matter. The mean seawater temperature during the

121 hot season is  $26 \pm 2$  C° (November-April) and  $23 \pm 1$  C° during the cold season (May-October). Seawater  
122 salinity varies between 35.1 and 35.8 over a year period (monthly measurements with CTD sensors on the reef  
123 during the experiment).

124 To determine successions of euendolithic communities and to quantify associated biogenic dissolution and  
125 grazing rates, 60 experimental coral blocks were fixed on two steel grids (1 m x 1 m) affixed on the reef at 3 m  
126 depth on the 15<sup>th</sup> of December 2010, i.e. during the austral summer season (Fig. 1c). Experimental coral blocks  
127 (~1.5 cm x 2 cm x 2 cm) were cut from the interior of a live colony of the massive coral *Porites* sp. using a band  
128 saw. *Porites* skeletons have been used in several previous bioerosion studies thus allowing for comparison of  
129 results (Kiene & Hutchings 1994, Chazottes et al. 1995, Pari et al. 1998, Edinger et al. 2000, Schonberg 2001,  
130 Chazottes et al. 2002, Tribollet & Golubic 2005, Tribollet 2008a). Micro- and bulk density of the coral skeleton  
131 were measured using the buoyant weight technique as described by Bucher et al. (1998). Between January and  
132 December 2011, 3 coral blocks were collected every month and were preserved in a buffered 4% solution of  
133 formaldehyde in seawater.

134  
135 Sample analyses

136 Colonized blocks were cut in half perpendicular to the upper side. The first halves were used to estimate the  
137 bioeroded surface area by euendoliths (in cm<sup>2</sup>) on the upper side, by taking pictures under a Scanning Electronic  
138 Microscope (SEM, Zeiss EVO LS15, Alizés Platform, IRD, Bondy, France). Twenty pictures were taken per  
139 coral block ( $n = 60$  per month) at panoramic magnification x1500, and were analyzed using the software ImageJ.  
140 The second halves of blocks were used to prepare thin sections according to the technique described by Golubic  
141 et al. (1970), and Tribollet et al. (2002). These thin sections were observed under a light microscope (Nikon  
142 Eclipse LV100) to allow the determination of (1) the species composition of euendolithic communities, (2) the  
143 relative abundance (RA) of living filaments inside substrates ( $n > 120$  measurements per month) expressed in %  
144 ( $\pm$  the confidence interval), and (3) the mean depth of penetration ( $P_{80}$ ) in cm at which 80%-90% of the living  
145 euendolithic filaments could be observed inside coral blocks ( $n > 120$  measurements per month; see technique  
146 description in Tribollet et al. 2009). To complete the identification of euendoliths, small pieces of sample were  
147 decalcified (HCl < 10%) allowing the observations of a few euendolithic filaments at a time. Identification was  
148 based on morphological criteria with the help of Stjepko Golubic, and according to Bornet and Flahault (1889)  
149 and Wisshak et al. (2011). Only species with relative abundance higher than 5% are presented in this paper.  
150 The quantity of carbonate dissolved per month, called here ‘biogenic dissolution’ (BD), was calculated using the  
151 following equation (adapted from Tribollet et al. 2009):

$$152 \quad BD = \frac{\text{Depth of penetration} \times \text{Bioeroded surface area} \times \text{Density}}{\text{Surface area of blocks}}$$

153  
154 where ‘BD’ is expressed in g of CaCO<sub>3</sub> dissolved per linear square meter of reef after a certain time of exposure  
155 (e.g. one month of exposure for blocks colonized by euendoliths during one month), ‘depth of penetration’ is  $P_{80}$   
156 in cm, ‘bioeroded surface area’ is the bioeroded surface area of block surfaces exposed to colonization by  
157 euendoliths multiplied by (100 - (% of porosity of coral skeleton) in cm<sup>2</sup> (here we considered only 5 sides per  
158 block as the bottom side was exposed to a different light regime and porosity was 53%), ‘density’ is the coral  
159 skeleton microdensity ( $2.58 \pm 0.06$  g.cm<sup>-3</sup>) as filaments of euendoliths grow into the microstructure of the

160 skeleton, not in its void spaces, and ‘surface area of block’ is the surface area of the 5 sides of each block  
161 exposed to colonization (the bottom side was discarded). We assumed here that the measured bioeroded surface  
162 area and  $P_{80}$  on the upper sides of blocks were representative of the 5 sides as blocks were small enough to be  
163 exposed to the same light intensity.

164  
165 By knowing the initial dimensions of coral blocks, it was also possible to estimate the percentage of carbonate  
166 removed by grazers on each sample, by analyzing pictures of thin sections taken by a high resolution Nikon  
167 camera (Nikon Camera Digital D5100 with AF-S Micro Nikkor 60mm objective) using the software imageJ ( $n >$   
168 12 measurements per month). Grazing rates were then calculated using the following equation:

$$\text{Grazing} = \frac{\text{Percent of grazing} \times \text{Volume of blocks} \times \text{Density}}{\text{Surface area of blocks}}$$

170  
171 where ‘grazing’ is expressed in g of  $\text{CaCO}_3$  eroded per linear square meter of reef after a certain time of  
172 exposure (i.e. xx months), ‘volume of block’ is expressed in  $\text{cm}^3$  (initial length x height x width), ‘density’ is the  
173 bulk density of the coral skeleton in  $\text{g.cm}^{-3}$  ( $1.86 \pm 0.1 \text{ g.cm}^{-3}$ ) as grazers abrade simultaneously voids and  
174 skeleton, and ‘surface area of block’ is similar to that used for BD, in  $\text{cm}^2$ .

175  
176 Statistical analysis

177 Statistical analyzes were performed under the R statistical framework (R. Development Core Team 2014). All  
178 data sets were analyzed with non-parametric tests because homogeneity of variance and normality distribution  
179 were not met (Bartlett test and Shapiro test, respectively) even after data transformation (Hollander et al. 2014).  
180 The Kruskal-Wallis test (with  $\alpha = 5 \%$ ) was used to determine if measured variables (i.e. relative abundance and  
181 depth of penetration of euendolithic filaments, biogenic dissolution, and grazing) varied significantly among the  
182 different durations of exposure (from 1 month to 12 months). When the Kruskal-Wallis test was significant a  
183 pairwise post-hoc analysis of Mann and Whitney was realized using a correction of Bonferroni (Hollander et al.  
184 2014). To fit biogenic dissolution values and to obtain a rate of the biogenic dissolution after 12 months of  
185 exposure, we used a logistic growth model in R statistical framework with the nls2 library (Grothendieck 2013):

$$\frac{A}{(1 + e^{X-t})/S}$$

187  
188 where ‘A’ is the maximum asymptotic value, ‘X’ is the time where A/2 is observed, ‘S’ is the maximum slope  
189 and ‘t’ is the time of exposure. To see possible correlation between grazing and biogenic dissolution, the  
190 correlation of Spearman was used (Hollander et al. 2014). Finally to determine the main variables driving  
191 biogenic dissolution dynamics over a year period, a hierarchical cluster analysis was performed based on  
192 dissimilarity matrix using Bray-Curtis distances (Murtagh & Legendre 2014). A non-metric multidimensional  
193 scaling analysis (nMDS) was performed using this matrix as well as a hierarchical cluster analysis to graphically  
194 represent results (Faith et al. 1987).

195  
196

197 **Results**

198

199 Euendolithic species

200 Euendoliths observed in the experimental coral blocks comprised (i) chlorophytes including *Phaeophila* sp. (Fig.  
201 2a), *Eugomontia* sp., (Fig. 2b) and *Ostreobium* sp. (Fig. 2c), (ii) two cyanobacteria comprising *Mastigocoleus*  
202 *testarum* (Fig. 2d) and *Plectonema terebrans* (Fig. 2e), and (iii) unidentified fungi (Fig. 2f). Due to relative  
203 morphological similarities between *Eugomontia* sp. and *Phaeophila* sp. and difficulties sometimes to distinguish  
204 these two species from unidentified large chlorophytes, all these euendoliths were grouped in one category  
205 named ‘unidentified chlorophytes’. *Ostreobium* sp. was easily identified as this chlorophyte presents siphonous  
206 and polymorphic filaments. *Plectonema terebrans* and fungi were also grouped in one category named ‘thin  
207 filaments’ as the diameter of their filaments did not exceed 1-2  $\mu\text{m}$  and cells in some filaments of *P. terebrans*  
208 were difficult to distinguish. Moreover perpendicular branches and reproductive organs of fungi were usually  
209 absent rendering difficult their differentiation from *P. terebrans* filaments.

210

211 Successions of communities: abundance and distribution of euendoliths

212 After one month of exposure, euendolithic communities were mostly composed of unidentified chlorophytes  
213 even though thin filaments and the cyanobacterium *M. testarum* were observed (mean RA of 83% for  
214 unidentified chlorophytes, Fig. 3a). Filaments of *M. testarum* and *P. terebrans* as well as fungi were observed in  
215 all blocks during the overall duration of the experiment but their mean relative abundance never exceeded 20%  
216 (Fig. 3c,d). The cyanobacterium *Hyella* sp. was also observed in one month-old blocks but was very rare (RA <  
217 0.5%). In 2 and 3 months-old blocks, the unidentified chlorophytes remained dominant with a mean RA of 52%  
218 (Fig. 3a). About 2% can be attributable to *M. testarum*, 0.5% to thin filaments and the rest to *O. quekettii*. The  
219 unidentified chlorophytes never penetrated deeper than 0.5 mm into coral skeletons (Fig. 3a). Similarly filaments  
220 of *M. testarum* were abundant beneath the surface of substrates although a few filaments could be observed  
221 down to 2 mm (their relative abundance at this depth was less than 2%; Fig. 3d). Between 4 and 6 months, the  
222 relative abundance of unidentified chlorophytes and *O. quekettii* was inversely correlated (Spearman test,  $r = -$   
223 0.81,  $p < 0.01$ ), with RA of unidentified chlorophytes reaching less than 1% after 6 months of exposure (Fig. 3a)  
224 and RA of *O. quekettii* 42% (Fig. 3b). After more than 6 months of exposure, *O. quekettii* dominated  
225 euendolithic communities. Its relative abundance was maximal (> 70%) after 11 months of exposure (Fig. 3b).  
226 The rest of the communities comprised thin filaments (13%) and rare filaments of *M. testarum* (4%). *O. quekettii*  
227 and thin filaments could penetrate deep into coral skeletons reaching sometimes more than 4 mm (Fig. 3b, c). *O.*  
228 *quekettii* was the most abundant species between 0.5 mm and 4 mm below the substrate surface with a mean RA  
229 of 43% (Fig. 3b).

230

231 Surface area bioeroded and depth of penetration ( $P_{80}$ )

232 After one month of exposure, the mean surface area bioeroded by euendoliths was about  $17.6\% \pm 2.1\%$ . During  
233 the first four months of exposure, the surface area bioeroded increased significantly (Mann and Whitney,  $p < 0.01$ ;  
234 Table 1) and reached a mean value of 40%. After 4 months of exposure, the surface area bioeroded was 38% on  
235 average, except between 7 and 9 months of exposure (lowest mean quantified, 28%).

236 The mean depth of penetration of living euendolithic filaments ( $P_{80}$ ) increased slowly during the first four  
237 months of exposure (Table 1). Between the 4<sup>th</sup> and 7<sup>th</sup> months of exposure,  $P_{80}$  increased exponentially and  
238 reached a maximum mean value of  $3.19 \pm 0.19$  mm after 7 months of exposure. Finally, after 8 months of  
239 exposure, depths of penetration tend to stabilize with a mean value of  $2.55 \pm 0.20$  mm.

240

#### 241 Biogenic dissolution rates

242 The quantity of dissolved calcium carbonate by euendoliths increased significantly over time (Mann and  
243 Whitney,  $p < 0.001$ ) but non-linearly (Fig. 4a). The dynamics of the biogenic dissolution process presented indeed  
244 3 steps. First, between 1 and 3 months of exposure, biogenic dissolution increased slowly reaching  $66 \pm 0.8$  g of  
245 dissolved per square meter of reef after 3 months of exposure (Fig. 4a). Within this period of 2 months, the mean  
246 rate of dissolved  $\text{CaCO}_3$  was  $30 \text{ g.m}^{-2}.\text{mo}^{-1}$ . Second, between 4 and 5 months of exposure, biogenic dissolution  
247 increased exponentially reaching a mean of  $739 \pm 11 \text{ g.m}^{-2}$  after 5 months of exposure. During this short period  
248 of time, the mean rate of biogenic dissolution was  $564 \text{ g.m}^{-2}.\text{mo}^{-1}$ . Finally after 6 months of exposure, the  
249 process slowed down dramatically. Biogenic dissolution reached a 'plateau' with a mean value varying between  
250  $742$  and  $1134 \text{ g.m}^{-2}$  after 8 months and 11 months, respectively (Fig. 4a); the mean rate of biogenic dissolution  
251 was  $23 \text{ g.m}^{-2}.\text{mo}^{-1}$  for the period comprised between 7 and 12 months of exposure. This process, as described  
252 above, is typically a logistic growth model in three steps. A preliminary model was then developed to highlight  
253 the process kinetics and to estimate the mean rate of biogenic dissolution for a 12 months period (Fig. 5). The  
254 expression of a logistic model growth was used in R to fit our biogenic dissolution dataset. The asymptotic value  
255 or the maximum value of biogenic dissolution was  $0.91 \pm 0.04 \text{ kg.m}^{-2}$ ; half of the biogenic dissolution was  
256 realized after  $4.5 \pm 0.2$  months and the maximum of slope was  $0.37 \pm 0.15 \text{ kg.m}^{-2}.\text{mo}^{-1}$ . The 3 steps-process was  
257 confirmed by the non-metric multidimensional scaling (nMDS) with the hierarchical cluster analysis (Fig. 6).  
258 The low value of stress indicates that the representation is reliable: the distance between studied months (circle)  
259 correlate well with the dissimilarity of the three clusters (ellipses). In addition, the nMDS showed how the  
260 different measured biological parameters influenced each step. The early step of biogenic dissolution appeared to  
261 be driven by the abundance of unidentified chlorophytes while the second step seemed to be related to the shift  
262 in community species composition. In contrast, the final step was clearly driven by the abundance of the  
263 chlorophyte *Ostreobium quekettii* and the intensity of grazing.

264

#### 265 Grazing pressure

266 Based on observations of block surfaces under a binocular microscope, grazing traces appeared to be due mostly  
267 to parrotfishes, confirming a few *in situ* observations during block collection. Between 1 and 7 months of  
268 exposure, grazing increased almost linearly (from  $35 \pm 11$  to  $365 \pm 51$  g of  $\text{CaCO}_3$  eroded per square meter of  
269 reef, respectively; Fig. 4b). Except for the two peaks at 8 and 10 months of exposure (grazing rate  $> 600 \text{ g.m}^{-2}$ ),  
270 after 7 months of exposure grazing rate values oscillated around the mean obtained after 12 months of exposure,  
271 i.e.  $339 \pm 81 \text{ g.m}^{-2}$  (Fig. 4b). Biogenic dissolution and grazing were strongly negatively correlated after 7 months  
272 of exposure (Spearman correlation,  $r = -0.92$ ,  $p < 0.01$ ).

273

274

#### 275 Discussion



276

277 The present study of euendolithic community successions with a monthly resolution reveals the three main steps  
278 in the colonization of newly available dead carbonate substrates: (i) an early community development stage  
279 between 0 and 3 months where large chlorophytes such as *Phaeophila* sp. are dominant, (ii) an intermediate  
280 stage between 3 and 6 months where the chlorophyte *Ostreobium* sp. the main agent of biogenic dissolution,  
281 starts to settle down and to dominate communities, and (iii) a final stage, after more than 6 months of exposure,  
282 where *Ostreobium* sp. dominates largely microboring communities. The present work confirms that colonization  
283 by euendoliths of newly available carbonate substrates is rapid (a few days or weeks) and is dominated by large  
284 pioneer chlorophytes, especially the green alga *Phaeophila* sp., and cyanobacteria such as *Mastigocoleus*  
285 *testarum* (see Chazottes et al. 1995, Kiene et al. 1995, Le Campion-Alsumard et al. 1995, Gektidis 1999, Vogel  
286 et al. 2000, Tribollet et al. 2006, Tribollet 2008b). Those communities are characteristic of ‘immature  
287 communities’ (Gektidis 1999). Here, the relative abundance of large unidentified chlorophytes, comprising  
288 mostly *Phaeophila* filaments, was higher than 60% during the first 4 months of exposure which is similar to the  
289 findings of Kiene et al. (1995) and Vogel et al. (2000) in limestone in Bahamian and Australian reefs. Although  
290 Chazottes et al. (1995) also found *Phaeophila* in abundance in one-month old coral blocks in French Polynesia,  
291 the relative abundance of this species in communities decreased rapidly after the second month of exposure. This  
292 could result from the intense grazing quantified on blocks in French Polynesia which certainly limited the  
293 development of epiliths and *Phaeophila*, and postponed *Ostreobium* settlement (seen after 6 months of  
294 exposure). In the present study, significant traces of grazing were only observed on blocks after a few months of  
295 exposure suggesting that epilithic and euendolithic communities developed slowly on the studied reef in New  
296 Caledonia compared to those growing in French Polynesian reefs. Grazers are indeed not attracted by substrates  
297 until epilithic (mostly turfs) and euendolithic communities on which they feed, start to be well developed  
298 (Bruggemann et al. 1994). Interestingly in the present study, *Ostreobium* sp. started settling on new dead coral  
299 skeletons as soon as the 3<sup>rd</sup> month of exposure (but represented less than 5% of euendolithic communities). In  
300 mollusc shells Carreiro-Silva et al. (2005) also observed *Ostreobium* filaments after 49 days. To the contrary of  
301 what was suggested in previous studies, this green euendolithic alga appears thus as an early colonist of dead  
302 carbonate substrates in shallow reefs. Most studies have indeed reported the presence of *Ostreobium* sp. in dead  
303 substrates comprising limestone, calcite spar, mollusc shells and coral skeletons, only after more than 6-12  
304 months of exposure (Chazottes et al. 1995, Kiene et al. 1995, Le Campion-Alsumard et al. 1995, Gektidis 1999,  
305 Vogel et al. 2000, Tribollet et al. 2006, Tribollet 2008a).

306

307 All pioneer euendolithic species were located within the first few hundred micrometers beneath the substrate  
308 surface, with the exception of a few filaments of *M. testarum* seen down to 2 mm below the surface. These  
309 species are indeed known as photophile euendoliths which do not penetrate deep into substrates as they require  
310 high light intensities to insure photosynthesis (see review by Tribollet 2008b). In contrast, *Ostreobium* is a  
311 sciaphile or oligophotic euendolith, i.e. that it is adapted to low light intensities (Fork & Larkum 1989, Tribollet  
312 et al. 2006), and thus, can penetrate deep inside substrates (max depth > 4 mm after 6 months of exposure) and  
313 presents a large bathymetric distribution (found down to 300 m depth; Lukas (1978); Kiene et al. (1995); Radtke  
314 et al. 1996). It can also be easily photoinhibited by sudden important light intensities like in the case of a rapid  
315 bleaching event in live corals (Fine et al. 2005). Its light regime requirements may thus explain why it was not

316 observed on one month-old blocks. Like suggested by Vogel et al. (2000), we strongly emphasize that  
317 *Ostreobium* can only settle on substrates once they are colonized by epilithic organisms (biofilms, and then turfs  
318 at the early stages) and pioneer euendoliths, which provide shade (see also Radtke et al. 1996). As soon as those  
319 conditions were met in the present experiment, *Ostreobium* started rapidly to dominate communities. The shift in  
320 euendolithic community species composition in favour of *Ostreobium* occurred between the 4<sup>th</sup> and 5<sup>th</sup> months of  
321 exposure. Although such shift was suggested previously by Chazottes et al. (1995) and Kiene et al. (1995), its  
322 period of occurrence was not highlighted due to the temporal resolution selected in each experiment (2-3 months  
323 and then, 6 months or more). Here, after 6 months of exposure, the relative abundance of *Ostreobium* reached  
324 more than 45% while that of large unidentified chlorophytes (mostly *Phaeophila*) dropped down to 1%. The  
325 outcompetition between *Ostreobium* and *Phaeophila* was first reported by Le Campion-Alsumard et al. (1995) in  
326 shallow waters where light intensity is high. The other species observed in the present study after 6 months of  
327 exposure were essentially the cyanobacterium *P. terebrans* and fungi. The presence of these species in addition  
328 to *Ostreobium* characterizes 'mature communities' (Chazottes et al. 1995, Kiene et al. 1995, Gektidis 1999,  
329 Vogel et al. 2000, Tribollet 2008a). Such community species composition seems to be maintained after 12  
330 months of exposure (Chazottes et al. 1995, Kiene et al. 1995, Tribollet 2008a) unless a major event occurs. An  
331 extreme grazing pressure for instance, can modify dramatically community assemblages by removing most of  
332 settled euendolithic filaments in substrates allowing more light to penetrate inside the carbonate structure. The  
333 remaining filaments can then grow inside substrates until they reach their new depth of compensation  
334 (photosynthesis = respiration) while new pioneer euendoliths colonize substrate surfaces (Schneider & Torunski  
335 1983, Chazottes et al. 1995). In general, grazers do not remove all euendolithic filaments inside coral skeleton  
336 allowing *Ostreobium* to remain the dominant species in substrates exposed more than 6 months to colonization,  
337 but are sufficient to offer new surfaces available to colonization by cyanobacteria such as *Hyella* sp. and *M.*  
338 *testarum*. This is why these pioneer species are often observed within mature communities, but in relatively low  
339 abundance (less than 0.5% for *Hyella* sp. and 20% for *M. Testarum* here; see also Chazottes et al. 1995, Tribollet  
340 et al. 2006, and Tribollet 2008a).

341  
342 With a monthly resolution, we highlight how much the dynamics of euendolithic communities and grazing  
343 pressure controlled the process of biogenic dissolution over a year period. First of all, pioneer communities  
344 within the first 3 months of exposure drove a slow process of biogenic dissolution with a mean rate of 30 g.m<sup>-2</sup>  
345 .mo<sup>-1</sup> although the amount of dissolved CaCO<sub>3</sub> after 3 months of exposure was 66 g.m<sup>-2</sup>, which is similar to  
346 what found Chazottes et al. (1995), and Peyrot-Clausade et al. (1995) in 2 months-old blocks in French  
347 Polynesia (~73 g.m<sup>-2</sup> after recalculation with a microdensity for *Porites* coral skeleton of 2.58 g.cm<sup>-3</sup> and a  
348 porosity of 53%). This was due to the low depth of penetration of euendolithic filaments at this early stage of  
349 community development (< 400 μm), and not to the colonization of surfaces which was already important (>  
350 30% like in Chazottes et al. 1995) and the large diameter of pioneer euendolithic filaments (> 10 μm). Carbonate  
351 biogenic dissolution became a very efficient process during the community shift with a mean rate of 564 g.m<sup>-2</sup>  
352 .mo<sup>-1</sup> (rate obtained the 4<sup>th</sup> and 5<sup>th</sup> month of exposure). The rate of the biogenic dissolution increased  
353 exponentially during this short period of time (one month) and was multiplied by a factor 10. This resulted from  
354 the 3D network development of *Ostreobium* filaments within substrates (increase of filament abundance and  
355 depth of penetration) as described above. Once *Ostreobium*'s population became stable after 6 months of

356 exposure, -i.e. *Ostreobium* filaments reached their depth of compensation (about 4 mm which is similar to that  
357 found by Tribollet 2008a)-, the mean rate of biogenic dissolution slowed down and reached a 'plateau' ( $23 \text{ g.m}^{-2}.$   
358  $\text{mo}^{-1}$ ). Interestingly the estimated average rate of biogenic dissolution provided by the model after 12 months of  
359 exposure ( $0.91 \text{ kg m}^{-2}.\text{y}^{-1}$ ) was of the same order to rates estimated on offshore reefs on the Great Barrier Reef  
360 after one year of exposure, although those reefs were more influenced by oceanic conditions than the present  
361 studied site ( $0.5$  to  $1.1 \text{ kg m}^{-2}.\text{y}^{-1}$  after recalculation with microdensity and porosity of *Porites* skeletons, Tribollet  
362 & Golubic 2005). Those rates are comparable as the same techniques were used for their quantification (SEM  
363 picture analysis and thin sections; see Tribollet 2008a). Tribollet (2008a)'s methodology, although it prevents  
364 from confounding initial microbioerosion like in Chazottes et al. (1995) and avoids subjective estimations like in  
365 Vogel et al. (2000) and Carreiro-Silva et al. (2005), allows only the quantification of the amount of  $\text{CaCO}_3$   
366 dissolved by euendoliths alive at the time of collection. It is like an instantaneous 'snap shot' of a community  
367 activity at a given time. It cannot provide the cumulative effects of euendolithic communities on carbonate  
368 substrates over a given time period and does not reflect the potential long term impact of abiotic factors. The  
369 survey of biogenic dissolution rates at different periods of time like in the present study allows however,  
370 determining the possible impacts of biotic and abiotic factors on the process. Here, biogenic dissolution variation  
371 within the last 7 months of the experiment resulted from grazing activity as a strong inverse correlation between  
372 the two processes was found during this period. Grazing was especially important after 8 and 10 months of  
373 exposure reducing biogenic dissolution by about 30% (the 'residual biogenic dissolution' was thus measured; see  
374 definition in Chazottes et al. 1995). This synergy between grazers and euendoliths has first been well described  
375 by Schneider and Torunski (1983) in the Adriatic Sea and later by Chazottes et al. (1995) in coral reefs. It has  
376 been reported as the main bioerosion process in dead substrates after more than 12 months by Tribollet and  
377 Golubic (2005). Here, it also appears as the main bioerosion process on dead carbonates exposed 6 to 12 months  
378 to colonization.

379  
380 In conclusion, the present experiment revealed the 3 steps in the process of biogenic dissolution over a year  
381 period confirming that it is a neither linear, nor proportional process over time. It also suggested that rates  
382 estimated after 12 months of exposure should be considered as conservative rates (probably minimum values).  
383 This is the first time that such pattern is highlighted under natural conditions with a moderate grazing pressure.  
384 Due to the experimental design, temporal resolution, and biotic conditions (intense grazing), Chazottes et al.  
385 (1995) could only report part of the kinetics of the process. The present study also highlights that the biogenic  
386 dissolution process is particularly efficient during the community shift between the 4<sup>th</sup> and the 5<sup>th</sup> month of  
387 exposure and after a grazing episode (similar slopes). It took indeed about one month for the remaining  
388 *Ostreobium* filaments to reach again their depth of compensation as the amount of calcium carbonate dissolved  
389 per square meter after a high grazing episode (e.g. 8 months) was of the same order to that estimated prior to  
390 grazing (Fig. 7). This fast growth in depth inside substrates may be the result of the avoidance of an increased  
391 light intensity by *Ostreobium* filaments as epiliths and euendoliths near the surface have been scrapped off by  
392 grazers. This reinforces the idea that the chlorophyte *Ostreobium* is a very efficient bioeroding microorganism in  
393 coral reef systems. It should be noticed here however, that euendolithic community dynamics over 12 months  
394 were studied starting in the summer season (December). Biofilms and epilithic covers may develop slowly in  
395 winter due to reduce light intensity and seawater temperature, and thus may slow down euendolith settlement

396 (especially that of *Ostreobium*), successions and therefore, biogenic dissolution. This should be investigated over  
397 several years to highlight possible seasonal and inter-annual variations. Such data would definitely improve our  
398 capacity to better predict the response of biogenic dissolution to climatic and anthropogenic factors, and  
399 therefore to better evaluate coral reef future by 2100.

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**TABLES**

**Table 1** Mean bioeroded surface area and mean depth of penetration  $P_{80}$  by euendoliths in dead coral blocks over a 12 months period.

<b>Time of exposure</b> <i>(Months)</i>	<b>Bioeroded surface area</b> <i>(% ± SEM)</i>	<b>Depth of penetration</b> <i>(mm ± SEM)</i>
<b>1</b>	17.62 ± 2.10	0.08 ± 0.02
<b>2</b>	28.64 ± 2.60	0.10 ± 0.01
<b>3</b>	32.22 ± 2.40	0.19 ± 0.02
<b>4</b>	40.55 ± 2.40	0.42 ± 0.04
<b>5</b>	39.44 ± 3.80	1.63 ± 0.12
<b>6</b>	33.76 ± 2.40	2.12 ± 0.15
<b>7</b>	27.91 ± 2.00	3.19 ± 0.19
<b>8</b>	25.61 ± 2.10	2.66 ± 0.22
<b>9</b>	29.20 ± 2.20	2.77 ± 0.22
<b>10</b>	36.32 ± 2.80	2.35 ± 0.22
<b>11</b>	38.43 ± 2.60	2.69 ± 0.18
<b>12</b>	39.70 ± 2.60	2.29 ± 0.24

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## FIGURES

**Fig. 1** The area of study. a - Position of New Caledonia in the Southwest Pacific Ocean; b - Study site at “Ile aux Canards” in New Caledonia; c - Two experimental exposure grids with 60 experimental coral blocks fixed on the reef at 3 m-depth

**Fig. 2** Euendolithic filaments or borings observed on colored thin sections or after decalcification under light microscopy, or under SEM. A – *Phaeophila* sp. filament (Chlorophyta, on thin section); b – *Eugomontia* sp. filament with a few cells (Chlorophyta, after decalcification); c – *Ostreobium* sp. filaments (Chlorophyta, on thin section) with the white arrow indicating the typical shape of this alga, and the black arrow highlighting filaments of fungi; d – *Mastigocoleus testarum* filaments (Cyanobacteria, after decalcification) with heterocystous cells (black arrow); e – *Plectonema terebrans* filaments (Cyanobacteria, after decalcification); f – Borings of unidentified euendolithic fungi (under SEM). Scale bare = 20  $\mu\text{m}$

**Fig. 3** Mean relative abundance (RA) of euendolithic species as a function of time (in months) and their depth of penetration in substrates (in mm). a - Unidentified chlorophytes (i.e. *Phaeophila* sp. + *Eugomontia* sp. + unidentified species); b - The chlorophyte *Ostreobium* sp., c; Thin filaments (i.e. *Plectonema terebrans* + fungi); d - The cyanobacterium *Mastigocoleus testarum*

**Fig. 4** Bioerosion by euendoliths (a) and grazers (b) as a function of time. Rates are expressed in kg of  $\text{CaCO}_3$  dissolved per linear  $\text{m}^2$  of reef (Mean  $\pm$  standard error)

**Fig. 5** Preliminary logistic growth model of the process of biogenic dissolution in kg of  $\text{CaCO}_3$  dissolved per linear  $\text{m}^2$  of reef as a function of time. Solid line relates to fitted values, and dotted lines show the confidence interval of fitted values

**Fig. 6** Non-metric multidimensional scaling (nMDS) realized after clustering the relative abundance of euendolithic species, biogenic dissolution (BD), and grazing over the duration of the experiment

**Fig. 7** Graphic representation of temporal dynamics of the process of biogenic dissolution of carbonates by euendoliths and interaction with grazers















