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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-02193013>

Submitted on 24 Sep 2019

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Carbonate dissolution by reef microbial borers:

A biogeological process producing alkalinity under different pCO₂ conditions

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Keywords: Biogenic carbonate dissolution, microborers, euendoliths, coral reefs, ocean acidification, seawater alkalinity

Acknowledgments

We would like to dedicate this paper to our colleague and friend Marlin Atkinson who passed away in 2013. A.T. and P.C. conceived the experimental design. A.T., P.C. and A.C. collected samples and analysed data. A.T. and P.C. wrote the article and A.C. gave assistance on figure preparations and for formatting. We thank the Plateforme Alizes (IRD Bondy) for SEM access and S. Pyneeandy for her help with measurements of biogenic rates on coral blocks. We thank the Center IRD in Nouméa for its support in the field. Finally, this work was supported by the French Ministry of Ecology (program 'MIDACOR', 2011-2014) and the Institut de Recherche pour le Développement. The funding sponsors had no involvement in the present study development (design, collection, analysis, etc.).

Abstract

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

1. Introduction

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

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

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

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

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

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

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

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

2. Methods

2.1. Experimental design

Experimental blocks of dead coral skeleton ($7 \times 5 \times 5$ cm) were cut in the center of a massive live coral colony of *Porites lobata* collected in the lagoon of New Caledonia at Larégnère reef. This location was chosen to collect large, healthy, massive colonies of *Porites* to prepare experimental blocks (with negligible initial bioerosion). Blocks were bleached (at least one week), rinsed with fresh water (one week) and then dried (two weeks). In October 2009, 6 blocks were fixed on an aluminium grid with bolts and nuts to be laid at 14 m depth on the reef of Casy (Southern lagoon of Grande Terre, New Caledonia). This reef was selected to study biogenic dissolution under nearshore conditions. Water surrounding Casy is regularly impacted by terrigenous inputs rendering visibility underwater very limited (0–4 m). After 1 year of colonization by epilithic and endolithic organisms (2009–2010), 3 colonized blocks were randomly collected and brought back to the Institut de Recherche pour le Développement in Nouméa (2 h transport) and put in a 150 l tank. The tank was filled with filtered seawater (Whatman GF/C) pumped at Casy. A 12:12 h daylight to night photoperiod was applied with a light intensity of $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ delivered by two Solar simulator Arrays (Tailored lighting). A heater-chiller provided a constant temperature in the tank (25.2 ± 0.1 °C). Three different saturation states were tested, $\Omega_{\text{Arag}} = 2, 3$ and 3.5 with a constant 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 $53 \pm 3 \%$, 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).

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

2.2. Seawater chemistry analysis

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

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

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

2.3. Net dissolution and organic carbon metabolism calculation

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

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

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

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

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

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

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

2.4. Statistical analysis

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

3. Results

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

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

At constant light and temperature (Table 1), CaCO_3 dissolution measured by the alkalinity anomaly technique was simultaneously affected by light (daylight vs. night conditions: $p < 0.0003$) and Ω_{Arag} ($p < 0.02$), with no interaction between the two factors (Fig. 2). CaCO_3 dissolution was higher at night than at $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (on average $8.4 \pm 1.1 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{h}^{-1}$ and $1.9 \pm 1.1 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{h}^{-1}$, respectively) (Fig. 2). CaCO_3 dissolution was the highest at $\Omega_{\text{Arag}} \sim 2$ with an average of $8.3 \pm 1.5 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{h}^{-1}$ (vs. $3.6 \pm 1.2 \mu\text{mol CaCO}_3 \text{ block}^{-1} \text{h}^{-1}$ at $\Omega_{\text{Arag}} \sim 3\text{-}3.5$). Besides, the difference in CaCO_3 dissolution between night and daylight conditions did not differ significantly among treatments. Taking into account the exposed surface area of the blocks (5 sides = 155 cm^2), the daily CaCO_3 dissolution was $12.8 \pm 0.7 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{d}^{-1}$ (corresponding to an alkalinity production of $25.6 \pm 1.4 \text{ mEq m}^{-2} \text{d}^{-1}$) and $5.6 \pm 0.4 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{d}^{-1}$ ($11.2 \pm 0.8 \text{ mEq m}^{-2} \text{d}^{-1}$) at $\Omega_{\text{Arag}} \sim 2$ and $\Omega_{\text{Arag}} \sim 3\text{-}3.5$, respectively.

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

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

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

4. Discussion

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

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

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

4.2. Daily cycle of biogenic dissolution

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

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

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

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

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

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

Similarly to zooxanthellate boring sponges under high $p\text{CO}_2$ (Wisshak et al. 2012), increased biogenic dissolution by microborers could be explained by an enhancement of photosynthetic energy, and/or the lowering of the pH gradient between ambient seawater and the site of dissolution, thereby lowering the metabolic cost required for CaCO_3 dissolution. Providing acidified seawater near the dissolution front of euendolithic filaments could make interstitial water thermodynamically more favourable to chemical dissolution. Changes in extracellular pH have also been shown to directly drive changes in intracellular pH of some marine microalgae and in turn affect H^+ gradients and cellular pH homeostasis (Taylor et al. 2011). That such processes are used at the dissolution front in *Ostreobium* remains to be determined. Basic knowledge of the process of CaCO_3 dissolution is currently lacking to fully understand mechanisms behind *Ostreobium* response to acidification.

4.4. Significance of biogenic dissolution in coral reefs

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

Considering all biogenic dissolution rates for hard substrates in Table 2, the average rate is 11 mmol m^{-2} of reef d^{-1} . This average is assumed to be representative of the process occurring on 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

427 **References**

428 Adey WH (1998) Review. Coral reefs: algal structured and mediated ecosystems in shallow,
429 turbulent, alkaline waters. *J Phycol* 34:393–406

430 Andersson AJ, Bates NR, Mackenzie FT (2007) Dissolution of carbonate sediments under
431 rising pCO₂ and ocean acidification: observations from Devil’s Hole, Bermuda. *Aquat*
432 *Geochem* 13:237-264

433 Andersson AJ, Gledhill D (2013) Ocean acidification and coral reefs: effects on breakdown,
434 dissolution, and net ecosystem calcification. *Annual Review Mar Sci* 5:321-348

435 Andersson AJ, Mackenzie FT (2012) Revisiting four scientific debates in ocean acidification
436 research. *Biogeosciences* 9 :893-905

437 Barat R, Montoya T, Borrás L, Ferrer J, Seco A (2008) Interactions between calcium
438 precipitation and the polyphosphate-accumulating bacteria metabolism. *Water Res* 42:3415-
439 3424

440 Caldeira K, Wickett ME (2003) Oceanography: anthropogenic carbon and ocean pH. *Nature*
441 425:365

442 Carreiro-Silva M, McClanahan TR, Kiene WE (2005) The role of inorganic nutrients and
443 herbivory in controlling microbioerosion of carbonate substratum. *Coral Reefs* 24 :214-221

444 Chan N, Connolly SR (2013) Sensitivity of coral calcification to ocean acidification: a
445 meta-analysis. *Global Change Biol* 19:282-290

446 Chauvin A, Denis V, Cuet P (2011) Is the response of coral calcification to seawater
 447 acidification related to nutrient loading? *Coral Reefs* 30:911-923

448 Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M (1995) Bioerosion rates on coral
 449 reefs: interactions between macroborers, microborers and grazers (Moorea, French
 450 Polynesia). *Palaeo3* 113:189-198

451 Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M, Cuet P (2002) The effects of
 452 eutrophication-related alterations to coral reef communities on agents and rates of bioerosion
 453 (Reunion Island, Indian Ocean). *Coral Reefs* 21:375-390

454 Comeau S, Carpenter RC, Lantz CA, Edmunds PJ (2015) Ocean acidification accelerates
 455 dissolution of experimental coral reef communities. *Biogeosciences* 12 :365-372

456 Cyronak T, Schulz KG, Santos IR, Eyre BD (2014) Enhanced acidification of global coral
 457 reefs driven by regional biogeochemical feedbacks. *Geophys Res Lett* 41:5538-5546

458 Dickson AG (1990) Standard potential of the reaction: $\text{AgCl(s)} + \frac{1}{2} \text{H}_2\text{(g)} = \text{Ag(s)} + \text{HCl(aq)}$,
 459 and the standard acidity constant of the ion HSO_4^- in synthetic sea water from 273.15 to
 460 318.15 K. *J Chem Thermodynamics* 22:113-127

461 Dickson AG, Sabine CL, Christian JR (2007) Guide to best practices for ocean CO₂
 462 measurements. *PICES Spec Pub* 3:1-191

463 Enochs IC, Manzello DP, Tribollet, A et al (2016) Elevated colonization of microborers at a
 464 volcanically acidified coral reef. *PLoS One* 11:e0159818

465 Eyre BD, Andersson AJ, Cyronak T (2014) Benthic coral reef calcium carbonate dissolution
 466 in an acidifying ocean. *Nature Climate Change* 4:969-976

467 Eyre BD, Cyronak T, Drupp P, De Carlo EH, Sachs JP, Andersson AJ (2018) Coral reefs will
 468 transition to net dissolving before end of century. *Science* 359:908-911

469 Falter JL, Lowe RJ, Atkinson MJ, Cuet P (2012) Seasonal coupling and de-coupling of net
 470 calcification rates from coral reef metabolism and carbonate chemistry at Ningaloo Reef,
 471 Western Australia. *J Geophysic Res* 117:C05003
 472 Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of
 473 anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305:362-366
 474 Garcia-Pichel F, Ramírez-Reinat E, Gao Q (2010) Microbial excavation of solid carbonates
 475 powered by P-type ATPase-mediated transcellular Ca²⁺ transport. *PNAS* 107:21749-21754
 476 Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular,
 477 organismal and community levels in coral reefs: a review on interactions and control by
 478 carbonate chemistry. *Amer Zool* 39:160-183
 479 Golubic S, Friedmann I, Schneider J (1981) The lithobiontic ecological niche, with special
 480 reference to microorganisms. *J Sediment Res* 51:475-478
 481 Grange JS, Rybarczyk H, Tribollet A (2015) The three steps of the carbonate biogenic
 482 dissolution process by microborers in coral reefs (New Caledonia). *Environmen Sci Pollut*
 483 *Res* 22:13625-13637
 484 Guinotte JM, Fabry VJ (2008) Ocean acidification and its potential effects on marine
 485 ecosystems. *Annals of the New York Academy of Sciences* 1134:320-342
 486 Hepburn CD, Pritchard DW, Cornwall CE, McLeod RJ, Beardall J, Raven JA, Hurd CL
 487 (2011) Diversity of carbon use strategies in a kelp forest community: implications for a high
 488 CO₂ ocean. *Global Change Biol* 17:2488-2497
 489 Hoskin CM, Reed JK, Mook DH (1986) Production and off-bank transport of carbonate
 490 sediment, Black Rock, southwest Little Bahama Bank. *Mar Geol* 73 :125-144
 491 Hurd CL, Hepburn CD, Currie KI, Raven JA, Hunter KA (2009) Testing the effects of ocean
 492 acidification on algal metabolism: considerations for experimental designs. *J Phycol* 45:1236-
 493 1251

494 Johnson MD, Price NN, Smith JE (2014) Contrasting effects of ocean acidification on tropical
 495 fleshy and calcareous algae. *PeerJ* 2:e411
 496 Kinsey DW (1978) Productivity and calcification estimates using slack-water periods and
 497 field enclosures. In: Stoddart DR, Johannes RE (eds) *Monographs on oceanographic*
 498 *methodology, Coral reefs: research methods*. UNESCO, pp 439-468.
 499 Krumins V, Gehlen M, Arndt S, Cappellen PV, Regnier P (2013) Dissolved inorganic carbon
 500 and alkalinity fluxes from coastal marine sediments: model estimates for different shelf
 501 environments and sensitivity to global change. *Biogeosciences* 10:371-398
 502 Kuffner IB, Andersson AJ, Jokiel PL, Ku'ulei SR, Mackenzie FT (2008) Decreased
 503 abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience* 1:114
 504 Kobluk DR, Risk MJ (1977) Calcification of exposed filaments of endolithic algae, micrite
 505 envelope formation and sediment production. *J Sediment Res* 47:517-528
 506 Langdon C, Atkinson MJ (2005) Effect of elevated pCO₂ on photosynthesis and calcification
 507 of corals and interactions with seasonal change in temperature/irradiance and nutrient
 508 enrichment. *J Geophysic Res* 110:C09S07
 509 Le Campion-Alsumard T, Golubic S, Hutchings PA (1995a) Microbial endoliths in skeletons
 510 of live and dead corals: *Porites lobata* (Moorea, French Polynesia). *Mar Ecol Progress Ser*
 511 117:149-157
 512 Milliman JD (1993) Production and accumulation of calcium carbonate in the ocean: budget
 513 of a nonsteady state. *Global Biogeochem Cycles* 7:927-957
 514 Morse JW (1983) The kinetics of calcium carbonate dissolution and precipitation. *Rev*
 515 *Mineral Geochem* 11:227-264
 516 Noisette F, Duong G, Six C, Davoult D, Martin S (2013) Effects of elevated pCO₂ on the
 517 metabolism of a temperate rhodolith *Lithothamnion corallioides* grown under different
 518 temperatures. *J Phycol* 49:746-757

519 Nothdurft LD, Webb GE (2009) Earliest diagenesis in scleractinian coral skeletons:
 520 implications for palaeoclimate-sensitive geochemical archives. *Facies* 55 :161-201
 521 Nothdurft LD, Webb GE, Bostrom T, Rintoul L (2007) Calcite-filled borings in the most
 522 recently deposited skeleton in live-collected *Porites* (Scleractinia): implications for trace
 523 element archives. *Geochim Cosmochim Acta* 71:5423-5438
 524 Orr JC, Fabry VJ, Aumont O et al (2005) Anthropogenic ocean acidification over the twenty-
 525 first century and its impact on calcifying organisms. *Nature* 437: 681-686
 526 Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under
 527 global warming and ocean acidification. *Science* 333:418-422
 528 Pierrot D, Lewis E, Wallace DWR (2006) MS Excel program developed for CO₂ system
 529 calculations. ORNL/CDIAC-105 Carbon Dioxide Information Analysis Center
 530 Radtke G (1993) The distribution of microborings in molluscan shells from recent reef
 531 environments at Lee Stocking Island, Bahamas. *Facies* 29 :81-92
 532 Ramirez-Reinat EL, Garcia-Pichel F (2012) Prevalence of Ca²⁺-ATPase-mediated carbonate
 533 dissolution among cyanobacterial euendoliths. *Appl Environ Microbiol* 78:7-13
 534 Reyes-Nivia C, Diaz-Pulido G, Dove S (2014) Relative roles of endolithic algae and
 535 carbonate chemistry variability in the skeletal dissolution of crustose coralline algae.
 536 *Biogeosciences* 11:4615-4626
 537 Reyes-Nivia C, Diaz-Pulido G, Kline D, Guldberg OH, Dove S (2013) Ocean acidification
 538 and warming scenarios increase microbioerosion of coral skeletons. *Global Change Biol*
 539 19 :1919-1929
 540 Roy RN, Roy LN, Vogel KM et al (1993) The dissociation constants of carbonic acid in
 541 seawater at salinities 5 to 45 and temperatures 0 to 45°C. *Mar Chem* 44:249-267
 542 Sabine CL, Feely RA, Gruber N et al (2004) The oceanic sink for anthropogenic CO₂. *Science*
 543 305:367-371

544 Schönberg CH, Fang JK, Carreiro-Silva M, Tribollet A, Wisshak M (2017) Bioerosion: the
 545 other ocean acidification problem. *ICES J Mar Sci* 74:895-925
 546 Shamberger KEF, Feely RA, Sabine CL et al (2011) Calcification and organic production on
 547 a Hawaiian coral reef. *Mar Chem* 127:64-75
 548 Shashar N, Stambler N (1992) Endolithic algae within corals-life in an extreme environment.
 549 *JEMBE* 163:277-286
 550 Shaw EC, McNeil BI, Tilbrook B (2012) Impacts of ocean acidification in naturally variable
 551 coral reef flat ecosystems. *J Geophys Res* 117 :C03038
 552 Silverman J, Lazar B, Erez J (2007) Community metabolism of a coral reef exposed to
 553 naturally varying dissolved inorganic nutrient loads. *Biogeochemistry* 84 :67-82
 554 Stocker TF, Qin D, Plattner GK et al (2013) Technical summary. In: *Climate change 2013:*
 555 *the physical science basis. Contribution of Working Group I to the Fifth Assessment Report*
 556 *of the Intergovernmental Panel on Climate Change. Cambridge, UK and New York, NY,*
 557 *USA: Cambridge University Press, pp 33-115*
 558 Stubler AD, Peterson BJ (2016) Ocean acidification accelerates net calcium carbonate loss in
 559 a coral rubble community. *Coral Reefs* 35:795-803
 560 Stumm W, Morgan JJ (1996) *Aquatic chemistry: chemical equilibria and rates in natural*
 561 *waters, New York, NY, USA: John Wiley & Sons*
 562 Taylor AR, Chrachri A, Wheeler G, Goddard H, Brownlee C (2011) A voltage-gated H⁺
 563 channel underlying pH homeostasis in calcifying coccolithophores. *PLoS Biology*
 564 9:e1001085
 565 Tribollet A (2008a) Dissolution of dead corals by euendolithic microorganisms across the
 566 northern Great Barrier Reef (Australia). *Microbial Ecol* 55:569-580

567 Tribollet A (2008b) The boring microflora in modern coral reef ecosystems: a review of its
 568 roles. In: Wisshak M, Tapanila L (eds) Current Developments in Bioerosion. Berlin,
 569 Heidelberg: Springer, pp 67–94

570 Tribollet, A., Godinot, C., Atkinson, M., & Langdon, C. (2009). Effects of elevated pCO₂ on
 571 dissolution of coral carbonates by microbial euendoliths. *Global Biogeochem Cycles*
 572 23(3):GB3008

573 Tribollet A, Golubic S (2005) Cross-shelf differences in the pattern and pace of bioerosion of
 574 experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef,
 575 Australia. *Coral Reefs* 24:422–434

576 Tribollet A, Golubic S, Radtke G, Reitner J (2011) On microbiocorrosion. In: Reitner J,
 577 Queric N-V, Arp G (eds) Advances in Geobiology of Stromatolite Formation, Lecture Notes
 578 in Earth Sciences, 131:265-276, Berlin, Heidelberg: Springer

579 Tribollet A, Langdon C, Golubic S, Atkinson M (2006) Endolithic microflora are major
 580 primary producers in dead carbonate substrates of Hawaiian coral reefs. *J Phycol* 42:292-303

581 Tribollet A, Payri C (2001) Bioerosion of coralline alga *Hydrolithon onkodes* by microborers
 582 in the coral reefs of Moorea French Polynesia. *Oceanologica Acta* 24:329-342

583 Trnovsky D, Stoltenberg L, Cyronak T, Eyre BD (2016) Antagonistic effects of ocean
 584 acidification and rising sea surface temperature on the dissolution of coral reef carbonate
 585 sediments. *Frontiers in Marine Science*. [https://doi: 10.3389/fmars.2016.00211](https://doi.org/10.3389/fmars.2016.00211)

586 Tudhope AW, Risk MJ (1985) Rate of dissolution of carbonate sediments by microboring
 587 organisms, Davies Reef, Australia. *J Sediment Res* 55:440-447

588 Vogel K, Gektidis M, Golubic S, Kiene WE, Radtke G (2000) Experimental studies on
 589 microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier
 590 Reef, Australia: implications for paleoecological reconstructions. *Lethaia* 33:190-204

591 Vooren CM (1981) Photosynthetic rates of benthic algae from the deep coral reef of Curacao.
 592 Aquatic Botany 10 :143-159

593 Wisshak M, Schönberg CH, Form A, Freiwald A (2012) Ocean acidification accelerates reef
 594 bioerosion. PloS One 7:e45124

595 Wisshak M, Tribollet A, Golubic S, Jakobsen J, Freiwald A (2011) Temperate bioerosion:
 596 ichnodiversity and biodiversity from intertidal to bathyal depths (Azores). Geobiology 9:492-
 597 520

598 Wu H, Dissard D, Douville E, Blamart D, Bordier L, Tribollet A, Le Cornec F, Pons-Branchu
 599 E, Dapoigny A, Lazareth CE (2018) Surface ocean pH variations since 1689 CE and recent
 600 ocean acidification in the tropical South Pacific. Nature Communications. 9:2543.
 601 <https://doi:10.1038/s41467-018-04922-1>

602 Yates, K. K., & Halley, R. B. (2006) CO_3^{2-} concentration and pCO_2 thresholds for
 603 calcification and dissolution on the Molokai reef flat, Hawaii. Biogeosciences Discussions,
 604 3:123-154

605 Zou D, Gao K, Luo H (2011) Short- and long-term effects of elevated CO_2 on photosynthesis
 606 and respiration in the marine macroalga *Hizikia fusiformis* (Sargassaceae, phaeophyta) grown
 607 at low and high N supplies. J Phycol 47:87-97
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Tables

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

		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

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

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

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

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

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

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