Carbonate dissolution by reef microbial borers: a biogeological process producing alkalinity under different pCO2 conditions

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A biogeological process producing alkalinity under different pCO_2 conditions

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Abstract

Rising atmospheric CO_2 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 ($2 \leq \Omega_{arag} \leq 3.5$ corresponding to $440 \leq pCO2\ (\mu atm) \leq 940$) at 25°C under night and daylight (200 µmol photons m^{-2} 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 $\Omega_{Arag} \sim 2$ and 5.6 ± 0.4 mmol $CaCO_3$ m^{-2} d^{-1} at $\Omega_{Arag} \sim 3\text{-}3.5$ 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 ($pCO_2 \geq 920$ µatm 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 (pCO_2) is rising exponentially due to burning of fossil fuels and changing land-use, and is expected to double (~750 µatm) 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 pCO_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 (Radtke 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 0.1-1.8 mmol m^{-2} 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 pCO_2 increase rates of gross biogenic dissolution, i.e. rates of $CaCO_3$ 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 pCO_2 (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 × 5 × 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 terrigeneous 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 µmol photons m^2 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, Ω_{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

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

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

At the end of the experiment, the 3 colonized blocks were preserved in a seawater buffered formaldehyde solution (3%) prior microscopy analysis in the laboratory. Using microscopy techniques similar to those used by Tribollet et al. (2009), gross rates of biogenic dissolution were quantified (microdensity and porosity of the coral colony skeleton were 2.58 ±0.06 g cm^{-3} and 53 ±3 %, respectively). Rates were expressed in kg $CaCO_3$ m^{-2} y^{-1} or mmol $CaCO_3$ m^{-2} d^{-1} for comparison with net dissolution rates obtained with the alkalinity anomaly technique. The block surface area used in the calculation was the surface area 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 pCO_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 ±2 µequiv 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 µmol l^{-1}, respectively. Conversions between µmol l^{-1} and µmol 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 mmol $CaCO_3$ m^{-2} 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 mmol C m^{-2} h^{-1} was calculated according to the following equation:

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

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 mmol $CaCO_3$ m^{-2} d^{-1}) was obtained by multiplying the average of daylight and night rates (in mmol $CaCO_3$ m^{-2} h^{-1}) by 24. Daily respiration (in mmol C m^{-2} d^{-1}) was calculated as 24 times the night respiration rate (in mmol C m^{-2} h^{-1}). Daily gross production (in mmol C m^{-2} d^{-1}) was calculated by adding night respiration and net photosynthesis (both positive, in mmol C m^{-2} 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 ± 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 µmol photons m^{-2} s^{-1} (on average 8.4 ± 1.1 µmol $CaCO_3$ $block^{-1}$ h^{-1} and 1.9 ± 1.1 µmol $CaCO_3$ $block^{-1}$ h^{-1}, respectively) (Fig. 2). $CaCO_3$ dissolution was the highest at Ω_{Arag} ~ 2 with an average of 8.3 ± 1.5 µmol $CaCO_3$ $block^{-1}$ h^{-1} (vs. 3.6 ± 1.2 µmol $CaCO_3$ $block^{-1}$ h^{-1} at Ω_{Arag} ~ 3-3.5). 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 ± 0.7 mmol $CaCO_3$ m^{-2} d^{-1} (corresponding to an alkalinity production of 25.6 ± 1.4 mEq m^{-2} d^{-1}) and 5.6 ± 0.4 mmol $CaCO_3$ m^{-2} d^{-1} (11.2 ± 0.8 mEq m^{-2} d^{-1}) at Ω_{Arag} ~ 2 and Ω_{Arag} ~ 3-3.5, respectively.

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

The mean depth of penetration of alive euendolithic filaments was 1.81 ± 0.05 mm and the mean surface area bioeroded at the surface of the blocks was 12.85 ± 1.1 %. The estimated

gross rate of biogenic dissolution using microscopy techniques averaged 0.240 ± 0.002 kg m^{-2} y^{-1}, which converts to 7.40 ± 0.05 mmol m^{-2} 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 µmol photons m^{-2} s^{-1} and Ω_{Arag} ~ 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 Ω_{Arag} 3-3.5 (7.4 ± 0.1 mmol $CaCO_3$ m^{-2} d^{-1} versus 5.6 ± 0.4 mmol m^{-2} 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

297 communities in coral blocks were responsible for the bulk of alkalinity production in our
298 experiment.
299
300 *4.2. Daily cycle of biogenic dissolution*
301 Surprisingly 20% of the daily rate of biogenic dissolution was occurring during daylight.
302 Although it seems a paradox to measure simultaneously carbonate dissolution (i.e. release of
303 seawater alkalinity) and photosynthesis, Garcia-Pichel et al. (2010) clearly showed that
304 biogenic dissolution of experimental carbonate substrates by the cultured cyanobacterium *M.*
305 *testarum* was coupled to the photosynthetic energy production. In our experiment, higher rates
306 of net biogenic dissolution were quantified under night conditions than at
307 200 µmol photons.m^{-2}.s^{-1}. The decrease of the interstitial pH with increasing depth into a
308 *Porites cylindrica* skeleton colonized mainly by *Ostreobium* was also particularly important
309 in the dark in Reyes-Nivia et al. (2013)'s study, suggesting that night respiration by
310 microborers could be an important factor involved in $CaCO_3$ dissolution.
311
312 *4.3. Effect of ocean acidification on microborer metabolism and alkalinity production*
313 A 33% increase in gross production was recorded at Ω_{Arag} ~ 2 (pCO_2 of 936 µatm) relative to
314 Ω_{Arag} ~ 3-3.5 (pCO_2 of 437-570 µatm), suggesting that endolithic communities dominated by
315 *Ostreobium* were limited by DIC availability at Ω_{Arag} ~ 3-3.5. Photosynthesis limitation at
316 Ω_{Arag} ~ 3-3.5 was also highlighted by the low Pg/R ratio (0.67 ± 0.02). Although *Ostreobium*
317 presents carbonic anhydrases (CAs) that may serve as a mechanism to supply inorganic
318 carbon at the required rate for photosynthesis (Shashar and Stambler 1992), it remains
319 unknown if it possesses Carbon Concentrating Mechanisms (CCMs) involving active
320 transport of HCO_3^- and/or CO_2. In general, photosynthetic rates of algae that have CCMs are
321 not carbon limited, at least under most environmental conditions (e.g. Hurd et al. 2009). Some

322 species that have CCMs may however, be dependent on CO_2 and positively respond to
323 elevated pCO_2 at sub-saturating irradiance, because light limitation of active carbon uptake
324 increases reliance on CO_2 diffusion (Hepburn et al. 2011).
325
326 To the contrary of photosynthesis, night respiration was not affected by acidification (Fig. 2).
327 Most studies to date have reported no or little effect of elevated CO_2 on dark respiration rates
328 of macroalgae (e.g. Zou et al. 2011; Noisette et al. 2013). Because the responses to elevated
329 CO_2 of respiration and photosynthesis were different in our experiment, pCO_2 increase
330 resulted in an increase in the P_g/R ratio. Zou et al. (2011) reported that CO_2 enrichment
331 decreased the respiratory carbon lost per unit algal biomass in a low-N-grown macroalga, and
332 suggested that CO_2 enrichment may thereby enhance carbon sequestration capacity of this
333 organism.
334
335 The amount of alkalinity released in seawater doubled at $\Omega_{Arag} \sim 2$ compared to $\Omega_{Arag} \sim 3$-3.5
336 (25.6 ± 1.4 and 11.2 ± 0.8 mEq m^{-2} d^{-1}, respectively). Net biogenic dissolution rates did not
337 vary significantly between $\Omega_{Arag} \sim 3$ and 3.5 (pCO_2 = 570 and 437 µatm respectively)
338 suggesting that a threshold somewhere between $\Omega_{Arag} \sim 2$ and 3 must be reached before
339 promoting increased $CaCO_3$ dissolution by microboring communities from New Caledonia.
340 The increase in net biogenic dissolution under elevated pCO_2 in New Caledonia confirms the
341 increase of gross biogenic dissolution reported by Tribollet et al. (2009) and Reyes-Nivia et
342 al. (2013) for dead coral skeletons which were exposed during a few months to high pCO_2
343 (48% at 750 µatm and 46-89% at 1000 µatm relative to ambient pCO_2 depending on coral
344 species, respectively). A similar trend was also observed for pioneer euendolithic
345 communities dominated by the chlorophyte *Phaeophila* sp. under naturally acidified
346 conditions at Maug Island (Mariana Archipelago; Enochs et al. 2016).

Similarly to zooxanthellate boring sponges under high pCO_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

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

Conclusions

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

Data availability

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

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609 **Tables**

610

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

		T *in situ* (°C)	pH_T	A_T (µmol kg^{-1})	DIC (µmol kg^{-1})	pCO_2 (µatm)	Ω_{Arag}
Ω_{Arag} = 2	*night*	25.2	7.740 ±0.002	2304 ±1	2143 ±1	919 ±5	2.08 ±0.01
	daylight	25.2	7.725 ±0.002	2303 ±2	2149 ±1	954 ±4	2.02 ±0.01
Ω_{Arag} = 3	*night*	25.2	7.921 ±0.003	2320 ±1	2069 ±2	568 ±4	2.97 ±0.01
	daylight	25.2	7.919 ±0.003	2322 ±1	2072 ±2	571 ±4	2.97 ±0.01
Ω_{Arag} = 3.5	*night*	25.3	8.010 ±0.002	2296 ±1	1997 ±1	438 ±2	3.46 ±0.01
	daylight	25.2	8.012 ±0.001	2297 ±1	1996 ±1	436 ±1	3.48 ±0.01

613 pH_T (total hydrogen ion concentration scale) and total alkalinity (A_T, in units of µequiv kg^{-1}) were used to
614 calculate the other CO_2 chemistry parameters with the software CO_2Sys (Pierrot *et al.*, 2006): dissolved
615 inorganic carbon (DIC), partial pressure of CO_2 (pCO_2) and aragonite saturation state (Ω_{Arag}), using Roy et al.
616 (1993) values for carbonic acid constants K_1 and K_2, and K_{SO4} as determined by Dickson (1990)

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628 **Table 2.** Rates of biogenic dissolution from our study and from literature at ambient pCO_2, in
629 mmol $CaCO_3$ dissolved per m² per day. Rates from literature where converted, when
630 necessary, using microdensity and porosity of coral skeletons according to Tribollet *et al.*
631 (2009). Here, square meters refer to m² of substrate exposed to colonization by euendoliths
632 when coral substrates were used.
633 * rates measured using microscopy techniques. ** rates measured using the alkalinity
634 technique. *** rates measured using the buoyant weight technique. Cyano.: Cyanobacteria
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Source	**Location**	**Type of reef**	**Depth** (m)	**Type of substrate** (& dominant microborers)	**Dissolution rate** (mmol $CaCO_3$ m^{-2} d^{-1})
Tudhope and Risk (1985)	Australia	Barrier reef	5 – 27	**Sediments** (undetermined algae/fungi)	10*
Hoskin et al. (1986)	Bahamas	Intertidal	2 – 32	**Limestone** (undetermined)	7***
Chazottes et al. (1995)	French Polynesia	Flat reef	2	***Porites lobata*** (cyano., *Ostreobium*, 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, *Ostreobium)*	0.5 – 2*
Carreiro-Silva et al. (2005)	Belize	Patch reef	2	***Strombus* shells** (*Plectonema*, *Phaeophila*)	1*
Tribollet (2008a)	Australia	Inshore reef	14	***P. lobata*** (*Plectonema*, *Ostreobium*, fungi)	3*
		Barrier reef	14	***P. lobata*** (*Plectonema*, *Ostreobium*, fungi)	8 − 16*
		Offshore pinnacle	14	***P. lobata*** (*Plectonema*, *Ostreobium*, fungi)	30 *
Tribollet et al. (2009)	Hawaii	Barrier back reef	3	***P. lobata*** (*Plectonema*, *Ostreobium*)	7-9*
Reyes-Nivia et al. (2013)	Australia	Barrier reef	Shallow	***P. cylindrica, Isopora cuneate*** (*Plectonema*, *Ostreobium*)	26 − 42***
Present study (TA method)	New Caledonia	Bay (inshore reef)	14	***P. lobata*** (*Plectonema*, *Ostreobium*)	6**
Present study (microscopy)	New Caledonia	Bay (inshore reef)	14	***P. lobata*** (*Plectonema*, *Ostreobium*)	7*

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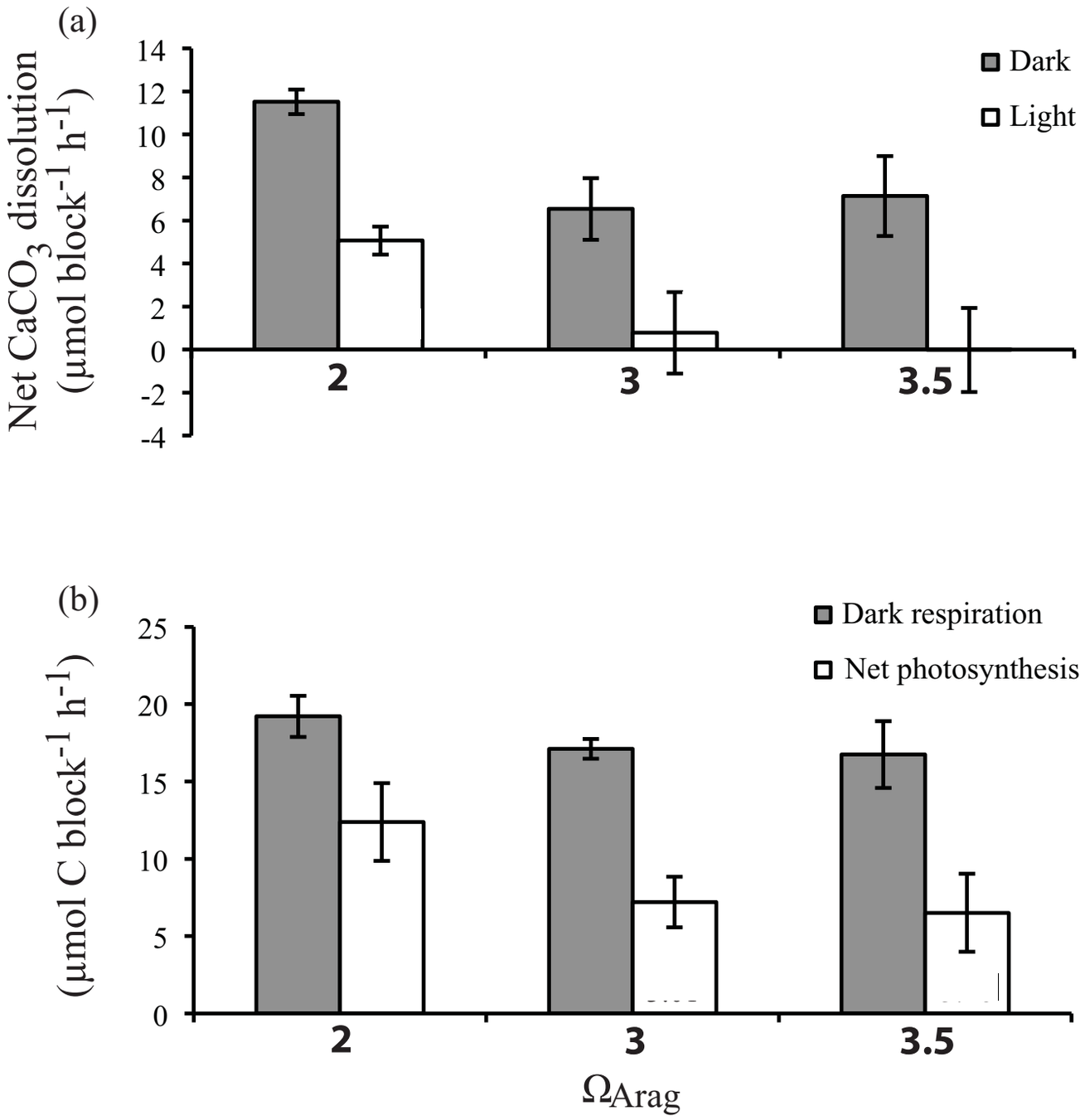
Figures

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 µm.

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.


(a)
Net $CaCO_3$ dissolution
(µmol block^{-1} h^{-1})
14
12
10
8
6
4
2
0
-2
-4
2
3
3.5
Dark
Light
(b)
(µmol C block^{-1} h^{-1})
25
20
15
10
5
0
2
3
3.5
Ω_{Arag}
Dark respiration
Net photosynthesis