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Relative roles of endolithic algae and carbonate chemistry variability in the skeletal dissolution of crustose coralline algae

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Abstract

The susceptibility of crustose coralline algae (CCA) skeletons to dissolution is predicted to increase as oceans warm and acidify. Skeletal dissolution is caused by bioerosion from endolithic microorganisms and by chemical processes associated with undersaturation of carbonate minerals in seawater. Yet, the relative contribution of algal microborers and seawater carbonate chemistry to the dissolution of organisms that cement reefs under projected CO_2 and temperature (CO_2-T) scenarios have not been quantified. We exposed CCA skeletons (*Porolithon onkodes*) to four CO_2-T treatments (pre-industrial, present-day, SRES-B1 reduced CO_2 emission scenario, SRES-A1FI business-as-usual CO_2 emission scenario) under natural light cycles vs. constant dark conditions for 8 weeks. Dissolution rates of skeletons without photo-endoliths were dramatically higher (200 %) than those colonized by endolithic algae across all CO_2-T scenarios. This suggests that daytime photosynthesis by microborers counteract dissolution by reduced saturation states resulting in lower net erosion rates over day-night cycles. Regardless of the presence or absence of phototrophic microborers, skeletal dissolution increased significantly under the spring A1FI "business-as-usual" scenario, confirming the CCA sensitivity to future oceans. Projected ocean acidity and temperature may significantly disturb the stability of reef frameworks cemented by CCA, but surficial substrates harboring photosynthetic microborers will be less impacted than those without algal endoliths.

1 Introduction

Crustose coralline algae (CCA) contribute significantly to the construction of coral reef frameworks by depositing $CaCO_3$ and binding reef components (Littler and Littler, 1984; Perry and Hepburn, 2008). CCA skeletons are particularly susceptible to increased ocean acidity and temperature, and consequent decrease in seawater saturation state (Ω), as they precipitate a highly soluble form of calcium carbonate (high-

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Mg calcite, HMC) (Feely et al., 2004; Morse et al., 2006). Reduced Ω with respect to HMC appears to increase dissolution rates of CCA threatening the structural integrity of coral reef ecosystems (Andersson et al., 2008). Along with the environmental effect of altered Ω_{HMC}, recent evidence suggests that bioerosional processes driven by endolithic algae further increase the dissolution of CCA as CO_2 and temperature rise (Diaz-Pulido et al., 2012). Although both biological (bioerosional) and environmental (chemical) processes play a role in weakening the structural integrity of reef structures, their relative contribution to the destruction of major reef cements has not been investigated.

Responses of reef frameworks to changes in seawater carbonate chemistry may be projected from ecosystems where low pH and Ω are noted to coincide with observations of poor cementation and high erosion rates (Manzello et al., 2008). Empirical and field studies have further shown how a drop in seawater Ω intensifies the dissolution of reef sediments, particularly those dominated by high-Mg calcites (Yamamoto et al., 2012; Morse et al., 2006). These studies offer valuable insights into the vulnerability of Mg-calcite-rich carbonates due to ocean acidification (OA), but they lack a more realistic approach combining the effect of acidified and warmer oceans on the stability of reef frameworks (Dove et al., 2013). Recent evidence suggests that CCA skeletons also contain a more stable carbonate phase, dolomite (Nash et al., 2011), which appears to be favored under high CO_2 and temperature levels (Diaz-Pulido et al., 2014). While such a response may reduce the effect of altered ocean chemistry on reef framework stability (Nash et al., 2012), it is critical to understand the actual influence of Ω_{HMC} in the dissolution of CCA skeletons and decouple that effect from bioerosional processes.

Endolithic algae are ubiquitous in marine carbonate sediments. In CCA, endolithic algae naturally occur below the living tissue (i.e. pink veneer) (Tribollet and Payri, 2001), and also colonize newly exposed skeletons (e.g, following CCA mortality) (Diaz-Pulido et al., 2012; Webster et al., 2011). These algae are mainly filamentous and coccoid green algae and cyanobacteria (Tribollet and Payri, 2001) and their metabolic activity causes primary dissolution not only of calcitic but also aragonitic substrates

(Ramírez-Reinat and Garcia-Pichel, 2012b; Nothdurft et al., 2007). Ocean acidification and warming conditions can enhance the biomass and respiration rates of endolithic algae, which in turn appear to decrease the interstitial pH and increase dissolution of coral skeletons (Reyes-Nivia et al., 2013; Tribollet et al., 2009). Enhanced dissolution of living CCA under elevated CO_2 and temperature (CO_2-T) conditions has also been related to increased abundance of endolithic algae (Diaz-Pulido et al., 2012), but no empirical studies have quantified their contribution in the dissolution of CCA skeletons.

Here, we used an experimental outdoor system designed to assess the relative contribution of endolithic algae and carbonate chemistry variability on skeletal dissolution of dead CCA fragments exposed to combined OA and warming. Endolithic algae abundance, metabolism, and bioerosion rates increase under OA conditions in corals, therefore we hypothesized that similar responses will occur in CCA skeletons. Further, as endolithic algae contribute considerably to carbonate dissolution, we also hypothesized enhanced dissolution rates when they are present. The biological role of photosynthetic microborers on skeletal dissolution was isolated from the environmental effect of seawater carbonate chemistry (driven by CO_2-T conditions, or by local CO_2 production/consumption from the thermal stimulation of metabolism, i.e. $\Omega_{HMC} < 1$) by maintaining experimental CCA under dark conditions. Ocean chemistry variability included past and present CO_2-T conditions following scenario projections by the Intergovernmental Panel of Climate Change (IPCC) (Meehl et al., 2007).

Our experimental approach did not investigate the independent effect of acidification or temperature but combined both stressors to assess how different climate scenarios may influence CCA dissolution. This allows us to determine whether potential increases in dissolution are greater under future ocean conditions compatible with "business-as-usual" (High, equivalent to SRES-A1FI), as opposed to, "reduced" (Medium, equivalent to SRES-B1) CO_2 emission scenarios; and hence to determine potential risks to reef framework should we not implement strategies to limit CO_2 emissions in the near future (Meinshausen et al., 2009). Our results reveal a remarkable ecological role of phototrophic microborers in counteracting the susceptibility of CCA skeletons to chemically

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driven dissolution (i.e. the isolated effect of Ω_{HMC}), but also reveal a significant increase in skeletal dissolution under future CO_2-T climate scenarios. We further demonstrate that the "business-as-usual" scenario resulted in greater rates of dissolution than the "reduced" CO_2 emission scenario.

2 Methods

2.1 Experimental setup and CO_2-temperature system

The experiment was conducted during the austral spring from October to November 2011 using a flow-through system at Heron Island Research Station. Specimens of the CCA *Porolithon onkodes* were collected from the shallow reef crest (2–3 m depth) at Coral Canyons, Heron Island (23°26.6′ S, 151°54.5′ E), southern Great Barrier Reef (GBR). To obtain recently dead CCA substrates, fragments of ca. 3 cm × 3 cm ($n = 128$) were immersed in hot seawater (50 °C) for 10 min to kill the algae. CCA experimental substrates were then acclimatized in running seawater in outdoor aquaria during 5 days prior to the experiment. No visual signs of CCA recovery (e.g. pigmented-pink tissue) were observed through the acclimation and experimental period.

Samples were exposed to four CO_2-T regimes simulating pre-industrial (−100 µatm, −1 °C), present-day (410 µatm, 24 °C), "reduced" (+200 µatm, +2 °C), and "business-as-usual" (+600 µatm, +4 °C) emission scenarios. Offsets for "reduced" and business-as-usual" conditions were based on IPCC scenarios (SRES B1 and A1FI respectively) projected for the end of the century (Meehl et al., 2007). CO_2-T regimes followed daily and seasonal variability based on a reference field site (Harry's Bommie, http://www.pmel.noaa.gov/co2/story/Heron+Island) and were achieved by a controlled system described previously (Dove et al., 2013; Reyes-Nivia et al., 2013). In short, CO_2 levels were manipulated by bubbling CO_2-enriched and CO_2-depleted air (CO2-Pro™, Pro-Oceanus Systems) into four mixing sumps (8 kL). Reduction of CO_2 concentration was obtained by filtering the air through two soda lime columns. Temperature was

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controlled in each sump by heater-chillers (Rheem HWP017-1BB, Accent Air). pCO_2 and temperature levels were continuously monitored to guarantee a clear separation among scenarios over the experimental period (Table 1).

Each CO_2-T scenario treatment had eight replicate 20 L tanks (glass aquaria); each tank received treated seawater at a constant flow rate ($1\,L\,min^{-1}$) and had small powerheads to ensure water circulation. Each tank contained four dead CCA fragments (subsamples). To avoid endolithic algal growth inside the CCA skeletons, 16 tanks containing the CCA were exposed to constant dark conditions using a black plastic wrap on all the sides. Light level in the dark tanks at midday was $0\,\mu mol$ quanta $m^{-2}\,s^{-1}$ (LI-192 Underwater Quantum Sensor, Li-COR). The remaining 16 tanks experienced natural light regimes. Neutral density filters (ND filter 0.3, LEE Filters, Australia) covered each light tank to reduce exposure by 50 % and compensate for depth variation between shallow reef crests and tanks. CCA fragments were exposed to light levels similar to reef habitat light levels, ranging from 600 to $1200\,\mu mol$ quanta $m^{-2}\,s^{-1}$ at midday depending on cloud cover. Epilithic algae growing on dead CCA under natural light conditions were gently removed three times a week using a soft toothbrush to reduce potential confounding effects caused by algal turf growth and shading. Dark samples were also brushed to keep consistency among light and dark samples.

2.2 Seawater carbonate chemistry

Seawater samples for total alkalinity (A_T) analysis were collected from the light and dark experimental tanks at noon and midnight at the end of the study to include the largest variation in seawater alkalinity and pH. Seawater samples were analyzed by potentiometric titration (T50, Mettler Toledo) with replicates within a sample ($n = 2$–3) having a maximum error of $3\,\mu mol\,kg^{-1}$ (Dickson et al., 2003). Temperature, pCO_2, A_T, and salinity (35.3 ppt) were used to calculate pH, bicarbonate (HCO_3), and carbonate (CO_3) with CO2SYS (Pierrot et al., 2006) using K1, K2 constants (Mehrbach et al., 1973; Dickson and Millero, 1987) and the seawater scale. The saturation state of seawater with respect to high-Mg calcite (Ω_{HMC}) was calcu-

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lated for a 17 mol % $MgCO_3$ Mol % $MgCO_3$ was calculated for 10 *P. onkodes* fragments collected at the study site (17.3 ± 0.25 SEM; $n = 10$), using Powder X-ray diffraction (XRD) techniques described in Nash et al. (2011, 2014). XRD analyses were conducted by M. Nash at the Australian National University. Estimations of Ω_{HMC} were conducted according Diaz-Pulido et al. (2012), which are based on the stoichiometric solubility products using the biogenic "minimally prepared" solubility curve of Plummer and Mackenzie (Plummer and Mackenzie, 1974) and Eq. (8) in Morse et al. (2006).

2.3 Skeletal dissolution

To compare the environmental effect of seawater CO_2-T conditions and the biological effect of phototrophic microborers on rates of skeletal dissolution, dark and light CCA skeletons were buoyant weighed at the beginning and end of the experiment (8-weeks). The difference between these measurements represented the percent of dissolution, which was then expressed as the change in dry weight normalized to the surface area (mg $CaCO_3$ cm^{-2} d^{-1}). For this, the change in buoyant weight was converted into dissolved $CaCO_3$ using *P. onkodes* skeletal density of 2.58 g cm^{-3} (±0.06 s.e.m., $n = 12$, determined in the laboratory using a high precision scale) and seawater density of 1.024 g cm^{-3}. Surface area of each sample was determined by image analysis (ImageJ, NIH US Department of Health and Human Services). Buoyant weight and skeletal density were determined by applying the equations and techniques described in Davies (Davies, 1989). For skeletal density estimation, the organic matter in CCA skeletons was removed using a diluted seawater-sodium hypochlorite solution (NaClO 10–13 %, 9 : 1). To guarantee that NaClO did not affect the carbonate skeletons, samples were buoyant weighed before and after treatment (0.2 % ± 0.03 s.e.m, $n = 12$) and were soaked in the diluted NaClO solution for 5 h.

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2.4 Biomass of photosynthetic microborers

To assess biological responses of photosynthetic microborers, their biomass was calculated as the total organic matter per unit area (mg cm^{-2}) on a subset of light samples at the end of the study. Surfaces of 1 cm^2 were randomly selected and scrapped off to a depth of 1 mm under a dissecting microscope using a scalpel. Collected samples were weighed using a high-precision microbalance (Pro11 Sartorius) to ensure that comparable amounts were obtained by the scraping method. No significant differences were detected in the 1 cm^2 skeletal sample weights among pCO_2-T scenarios (Anova, $df_{3,44} = 2.257$, $p > 0.05$, $n = 12$). Samples were decalcified with 10 % HCl and the solution was filtered through 0.7 µm GF/F glass microfiber filters (Whatman, England), which were pre-combusted at 550 °C and pre-weighed before filtration. Filters containing the endolithic algae were dried at 70 °C until they reached constant weight and then combusted at 550 °C for 4 h to oxidize all organic matter (Heiri et al., 2001). The same procedure was conducted on a set of living CCA substrates ($n = 15$) to estimate the contribution of previous organic compounds (i.e. CCA fleshy tissue) to the endolithic algal biomass estimates. A mean CCA organic content of 28 % was used for correction purposes.

2.5 Community structure of photosynthetic microborers

Composition and relative abundance of endolithic microborers was determined by the method of Diaz-Pulido and McCook (Diaz-Pulido and McCook, 2002) with modifications described in Reyes-Nivia et al. (Reyes-Nivia et al., 2013). In summary, CCA surfaces colonized by endolithic algae were transversally cut to obtain standardized areas of ca. 0.25 cm^2. The relative abundance of endolithic taxa was estimated as the percent cover in 6 microscopic fields (40× magnification) per slide ($n = 3$ per tank). Species were identified based on the literature available (Humm and Wicks, 1980; Le Campion-Alsumard et al., 1995; Lukas, 1974; Tribollet, 2008).

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2.6 Data analysis

A two-way nested ANOVA was applied to test the effect of pCO_2-T scenarios and light on CCA dissolution. The model included pCO_2-T scenario and light as fixed factors, tanks as random replicates, and samples nested within tanks. The same model was applied in one-way nested ANOVA to test the fixed effect of pCO_2-T scenarios on the biomass of photosynthetic microborers. The tank effect was removed from the model only when a conservative significance of $p > 0.25$ was obtained (Underwood, 1997). Subsequently tanks were pooled in a one-way ANOVA using samples as replicates. Post-hoc pairwise analyses were applied using Tukey's tests. The percentage of dissolution was square root-transformed while biomass was log-transformed. Assumptions of variance homogeneity and normality were tested using Levene's and K-S respectively. Analyses were completed using STATISTICA 11.

The community structure of endolithic microborers was compared among pCO_2-T scenarios using multivariate analysis based on a Bray-Curtis similarity measure (Anderson et al., 2008). A resemblance matrix on the square root-transformed percentage of relative abundance was obtained to perform a one-way nested PERMANOVA with pCO_2-T scenario as a fixed factor, tanks as replicates nested within the scenario and subsamples nested within tanks. *P* values for all PERMANOVA main effect and pairwise tests were generated by 9999 permutations when the number of unique permutations was large or by the Monte Carlo asymptotic *P* value otherwise (Anderson, 2005). Canonical analysis of principal coordinates (CAP) was used to spatially discriminate endolithic communities among a priori pCO_2-T groups. Potential indicator species or species assemblages underlying patterns of change among pCO_2-T groups were determined by Pearson correlations (> 0.5) and superimposed on the canonical space. Analyses were done using PERMANOVA+ for PRIMER v6.

Regression analyses using the least-squares approach were applied to assess the relationship between dissolution and the biomass of photosynthetic microborers, and the saturation state of seawater with respect to high-Mg calcite in light and dark tanks.

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3 Results

3.1 Effects of endolithic algae and CO_2-T scenarios on CCA dissolution

As predicted, elevated CO_2-T scenarios consistently enhanced dissolution rates of CCA skeletons over the 8-week experiment (Fig. 1, Table 2). The dissolution was ca. 200 % higher in CCA fragments kept under dark conditions compared to those under light conditions and colonized by endolithic algae (Fig. 1). This result was consistent across all CO_2-T treatments.

3.2 Dissolution response to saturation states

Absolute rates of $CaCO_3$ dissolution for CCA skeletons with photosynthetic microborers increased 37 % in the high CO_2-T scenario relative to present-day (preindustrial = 0.23 ± 0.02; present-day = 0.21 ± 0.02; medium = 0.23 ± 0.06; high = 0.28 ± 0.03 mg $CaCO_3$ cm^{-2} d^{-1}). Dissolution of CCA skeletons without photosynthetic microborers increased ca. 43 % under both elevated CO_2-T scenarios (preindustrial = 0.50 ± 0.04; present-day = 0.54±0.02; medium = 0.77 ± 0.04; and high 0.78 ± 0.04 mg $CaCO_3$ cm^{-2} d^{-1}). The absolute rate of $CaCO_3$ dissolution for CCA skeletons with photosynthetic microborers was only marginally related to the saturation state of seawater with respect to high-Mg calcite (Ω_{HMC}) (R^2 = 0.6211, p = 0.211; Fig. 2a). In contrast, dissolution rate of CCA without photosynthetic microborers was significantly (negatively) related to reduced Ω_{HMC} (R^2 = 0.9062, $p < 0.041$; Fig. 2b).

3.3 Biomass of photosynthetic microborers

The biomass of photosynthetic microborers (mg cm^{-2}) significantly increased in the high CO_2-T scenario relative to preindustrial and medium treatments but not to present-day (Fig. 3a, Table 1). Rates of CCA dissolution (mg $CaCO_3$ cm^{-2} d^{-1}) were positively

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related to the biomass of photosynthetic microborers ($R^2 = 0.1526$, $p < 0.006$; Fig. 3b), particularly in the high CO_2-T scenario ($R^2 = 0.5019$, $p < 0.009$; Fig. 3b).

3.4 Community structure of microborers

The filamentous green algae *Ostreobium* spp. and the cyanobacterium *Mastigocoleus testarum* accounted for 70–85 % of the total abundance among CO_2-T scenarios (Fig. 4). Less abundant species included the cyanobacteria *Plectonema terebrans* and *Hyella* sp., an unidentified coccoid species and fungi. The epilithic cyanobacteria *Oscillatoria* sp. and *Calothrix* sp. (Fig. 4) were also recorded. The community structure of endolithic algae in CCA skeletons significantly varied between the high CO_2-T treatment and the other scenarios (Fig. 4, Table 2). Differences were confirmed by the CAP analysis, where distinctive community structures were associated to CO_2-T regimes (Fig. 5). Correlations between species and CAP multivariate axes indicated that the preindustrial CO_2-T scenario was characterized by the presence of fungi, while present-day treatment by the high abundance of *Ostreobium* sp. and *Hyella* sp., and the medium treatment by *P. terebrans*, coccoid and *Oscillatoria* sp. Samples from the high CO_2-T scenario clearly segregated from the other treatments due to increased abundance of *M. testarum*.

4 Discussion

Combined elevated CO_2 and warming, together with endolithic algal bioerosion have both been suggested to contribute to the dissolution of high-Mg calcite skeletons of tropical reef coralline algae (Diaz-Pulido et al., 2012). However, our study is the first to provide experimental evidence of the relative contribution of these processes to the dissolution of CCA skeletons among a range of CO_2-T scenarios. Contrary to expectation (Reyes-Nivia et al., 2013), our results demonstrated that the effect of reduced seawater saturation state on CCA dissolution was much lower in the presence of endolithic

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algae, suggesting the absence of endolithic algae (under dark conditions) contributed considerably to the environmental dissolution of CCA. Under the high ("business-as-usual") CO_2-T treatment, enhanced endolithic biomass was positively associated to higher CCA dissolution, suggesting that endolithic algae do contribute to carbonate bioerosion. Yet, the absence of algae at the high CO_2-T scenario had a much larger effect on CCA dissolution than their presence. Our findings offer important insights into the contrasting roles of endolithic algae, as they imply dissolution and preservation of structural reef components dominated by high-Mg calcite carbonates.

A plausible explanation for the positive effect of endolithic algae in reducing CCA dissolution caused by reduced Ω may be the stimulation of carbonate cement precipitation associated with photosynthesis. Secondary precipitation of minerals such as brucite and dolomite has been associated with the presence of endolithic algae bands (Buster and Holmes, 2006; Diaz-Pulido et al., 2014; Nothdurft and Webb, 2009). Additionally, the erosional activity of endolithic cyanobacterial filaments include Ca^{2+} removal from surrounding $CaCO_3$ skeletons, which are then transported by the algal filaments and accumulated around the borehole surface where supersaturation and subsequent re-precipitation may occur (Garcia-Pichel et al., 2010). Since the formation of supersaturated zones by boring phototrophs is a light-dependent process (Garcia-Pichel et al., 2010; Ramirez-Reinat and Garcia-Pichel, 2012a), and endolithic algae have the ability to significantly elevate the interstitial pH of reef substrates at daylight (Reyes-Nivia et al., 2013), this may further stimulate supersaturation within light microenvironments, increasing the chances for internal precipitation (Diaz-Pulido et al., 2014) while reducing the dissolution potential. It is also plausible that the photosynthetic activity of endolithic algae consumes CO_2 produced by non-photosynthetic microorganisms (e.g. bacteria), buffering to some extent the interstitial pH and reducing chemical dissolution processes (e.g. as suggested for fleshy macroalgae in reef environments) (Anthony et al., 2013; Smith et al., 2013). Under dark conditions, the absence of algae cannot mitigate the impacts of CO_2 producing organisms on skeletal dissolution.

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Increased CO_2 and temperature enhanced the dissolution of CCA skeletons, both in the presence or absence of endolithic algae, although the magnitude of dissolution was much larger when endolithic algae were absent. Previous studies found that projected changes in ocean acidity and temperature cause mortality and subsequent dissolution of CCA (Anthony et al., 2008; Diaz-Pulido et al., 2012; Martin and Gattuso, 2009), and here we demonstrated the rate of skeletal dissolution is enhanced under elevated OA and warming following CCA mortality. Using comparable experimental treatments, we previously found (Reyes-Nivia et al., 2013) that dissolution of coral skeletons by endolithic algae was also higher at elevated CO_2-T conditions, but skeletons in the dark (without endolithic algae) did not dissolve. The variable response of coral and CCA skeletons to future CO_2-T scenarios may be due to differences in skeletal mineralogy as corals are aragonitic and less prone to dissolution (Morse et al., 2006). Our results confirm a potentially higher susceptibility to dissolution of those reefs where the carbonate framework is mainly composed of CCA skeletons.

Here, we also found that elevated CO_2-T conditions stimulate the biomass production of photosynthetic microborers, which in turn explained the increased dissolution rates of CCA skeletons under the "business-as-usual" scenario. Exposure to elevated CO_2 and/or temperature favors the growth of photosynthetic microborers (Fine and Loya, 2002; Tribollet et al., 2009) and this response has also been associated to higher dissolution rates of coral skeletons and living CCA with partial mortality (Diaz-Pulido et al., 2012; Reyes-Nivia et al., 2013). Thus far, the evidence regarding the effect of OA and/or warming on the abundance of boring phototrophs and coupled dissolution of major reef substrates is quite consistent. Predicted CO_2 and/or temperature scenarios may also weaken the structural integrity of coralline algal skeletons (Ragazzola et al., 2012) whilst increasing their susceptibility to grazing-induced bioerosion (Johnson and Carpenter, 2012). This suggests that the consolidation of surficial reef components cemented by CCA may be compromised as oceans warm and acidify.

Interestingly, CCA skeletons colonized by photosynthetic microborers displayed a non-significant linear response in the dissolution rates to consistently reduced Ω_{HMC}.

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This suggests that the environmental effect of seawater plays a minor role in the dissolution of skeletons with endolithic algae and that the increased biomass of such photosynthetic component likely neutralized the dissolution when HMC became undersaturated (i.e. $\Omega_{HMC} = 0.7$). Endolithic algae contribute to reef accretion processes by calcification of their exposed filaments (Kobluk and Risk, 1977b, a), and our results highlight the importance of these organisms in the accumulation/erosion balance of CCA carbonates under future CO_2-T scenarios. The reduced susceptibility to environmental dissolution we detected may be associated with the potential role of endolithic algae in facilitating the concentration of dolomite at elevated CO_2-T conditions (Diaz-Pulido et al., 2014). Dolomite formation within marine carbonate environments is similarly associated to metabolic processes of cyanobacteria and its stability has been identified over geological time (Andrews, 1991; Rao et al., 2003). While the enhanced abundance of this stable carbonate under greenhouse conditions (Diaz-Pulido et al., 2014) may increase the preservation potential of surficial reef cements at future climate scenarios, it is critical to establish the dissolution to concentration and/or precipitation ratio of secondary carbonates and the contribution of photosynthetic microborers, or particular species, in constructive processes.

We found that the endolithic community structure was altered under the high CO_2-T scenario with a particular increase in the relative abundance of the cyanobacterium *M. testarum* (Fig. 4). This boring alga is a pioneer colonizer of dead CCA substrates and exhibits a moderate abundance at the early stages of bioerosion (Ghirardelli, 2002; Tribollet and Payri, 2001). *M. testarum* largely accounted for the increased abundance of endolithic micoborers in dead portions of living CCA under elevated CO_2-T conditions (Diaz-Pulido et al., 2012). Here, we further quantified the abundance of major endolithic microborers and found a positive response of *M. testarum* to high CO_2-T levels, which may also be associated to the increased dissolution rates of CCA skeletons under this scenario. It is also likely that higher density networks formed by *M. testarum* linked to environmentally weakened high-Mg skeletons may also explain the increased amount of $CaCO_3$ removed in the high CO_2-T treatment.

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Exposure to full dark conditions revealed that dissolution of CCA skeletons within the reef matrix is largely mediated by changes in seawater Ω_{HMC} across all CO_2-T treatments. Since CCA exposed to seawater supersaturated with respect to high-Mg calcite ($\Omega_{HMC} > 1$ for preindustrial, present-day and medium scenarios) also dissolved, this suggests that acidic and undersaturated interstitial seawater were likely generated by heterotrophic microbial metabolism (Dupraz et al., 2009; Andersson and Gledhill, 2013). Processes such as microbial respiration and/or sulfide oxidation have been related to the dissolution of reef carbonate sediments, with a preferential dissolution of the more soluble high-Mg calcite and aragonite phases (Burdige et al., 2010; Rao et al., 2012). Similarly, our results indicated that CCA high-Mg calcite skeletons might undergo persistent environmental and/or heterotrophic metabolic dissolution across a range of CO_2-T scenarios. Our previous work showed that coral skeletons under dark conditions did not undergo dissolution, as aragonite undersaturation was neither chemically nor metabolically reached even under "business-as-usual" CO_2-T levels (Reyes-Nivia et al., 2013). Clearly, alterations in seawater saturation state of different carbonate phases play a critical role in the susceptibility to dissolution of major reef components.

We also demonstrated that CCA skeletons maintained in constant darkness are highly susceptible to OA and warming scenarios as dissolution was increased due to the altered seawater Ω_{HMC} in the elevated CO_2-T treatments. Thermodynamically it is expected that increases in seawater temperature on tropical shallow reef ecosystems slightly counteract the effect of elevated CO_2 in decreasing seawater Ω_{HMC} (Andersson et al., 2008). Yet, we found a linear dissolution response to declined seawater Ω_{HMC} from CCA skeletons which may indicate that environmentally elevated CO_2 conditions, likely exacerbated by microbial metabolism, override the thermal effect at dark environments. Our results suggest that in situ CCA skeletons within the reef matrix may experience rapid dissolution at high CO_2 and temperature levels, compromising the stability of coral reef structures. Furthermore, the dissolution rates observed under the "business-as-usual" CO_2 emission scenario significantly exceed rates of dissolution observed currently, or under "reduced" CO_2 emission scenarios. This result is important because it suggests that mitigation in the form of limiting atmospheric CO_2 production can have a highly positive effect on the carbonate balance of reefs, and hence with the maintenance of the key reef services inclusive of coastal protection.

Combined, our results indicate that endolithic algae play ecologically relevant roles in the carbonate balance of coral reef ecosystems as they act destructively on high-Mg calcite substrates but also reduce the effect of seawater carbonate chemistry in the dissolution of CCA skeletons. This suggests that particular processes mediated by endolithic algae further contribute to the stability of reef frameworks. Because of this, dissolution of high-Mg calcite carbonates within the reef matrix, which is mostly driven by changes in seawater saturation state, appear to be stronger than that of surficial reef components containing photosynthetic microborers. The lowered dissolution of surficial substrates will be relevant for recently dead and/or constantly grazed CCA skeletons in which the epilithic component is reduced and thus the metabolic activity of endoliths is not limited. Irrespective of the presence/absence of endolithic algae, exposure to the "business-as-usual" CO_2 emission scenario increased the dissolution of CCA skeletons. Models also project that Mg-calcite carbonates will undergo significant environmental dissolution under OA and/or warming scenarios as they are currently surrounded by slightly supersaturated seawater (Andersson et al., 2008). This suggests that weakened carbonate deposits are at increased risk of further erosion through wave impact generated by storms or cyclones. Despite the potential ability of endolithic algae to reduce the dissolution caused by declined Ω_{HMC} under warmer and acidic oceans, reef frameworks with a high proportion of Mg-calcite carbonates (e.g. fringing shallow reefs and algal ridges) may experience significant dissolution threatening the architectural complexity and persistency of these ecosystems.

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Table 1. Summary of the physical and chemical seawater parameters kept over 8 weeks to create four distinct pCO_2-T scenarios, along with the carbonate chemistry estimated for each CO_2-T scenario at the end of the experiment. Temperature and pCO_2 are mean values (±SD) recorded at < 30 min intervals over the length of the experiment. Input temperature (T), seawater pCO_2, and total alkalinity (A_T) are means (±SD) of 18 seawater replicates collected at the end of the study. Output pH (seawater scale kg mol^{-1}), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) were estimated using the program CO2SYS (Pierrot et al., 2006). High-Mg calcite saturation state (Ω_{HMC}) was estimated for a 17 % mol magnesite ($MgCO_3$) content as described in Diaz-Pulido et al. (2012).

	pCO_2-T conditions 8-week mean		Seawater carbonate chemistry Input parameters			Output parameters			
Scenarios	T (°C)	pCO_2 (µatm)	T (°C)	pCO_2 (µatm)	A_T (µmol kg^{-1})	pH	Ω_{HMC}	HCO_3^- (µmol kg^{-1})	CO_3^{2-} (µmol kg^{-1})
Preindustrial	23.5 ± 0.8	323 ± 31.2	24.3 ± 0.4	350 ± 1.6	2282 ± 32.5	8.1 ± 0.005	1.4 ± 0.07	1730 ± 19.3	223 ± 6.8
Present-day	24.4 ± 0.8	413 ± 36.4	25.2 ± 0.3	415 ± 1.9	2272 ± 16.7	8.0 ± 0.001	1.3 ± 0.07	1766 ± 8.79	205 ± 3.7
B1	26.6 ± 0.5	608 ± 17.9	27.0 ± 0.5	640 ± 43.4	2270 ± 15.0	7.9 ± 0.027	1.0 ± 0.09	1871 ± 17.7	162 ± 11.7
A1FI	28.0 ± 1.1	1008 ± 19.4	29.0 ± 0.2	1082 ± 75.6	2261 ± 32.7	7.7 ± 0.031	0.7 ± 0.06	1976 ± 19.9	115 ± 9.3

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Table 2. ANOVA results of dissolution (%) and biomass of endolithic algae (mg cm^{-2}), and PERMANOVA results of endolithic community structure (%) in CCA skeletons. Analyses were conducted using 1 – a two-way nested ANOVA to test the effect of CO_2-T scenarios on dissolution of light and dark CCA samples, 2 – a one-way ANOVA to test the effect of CO_2-T scenarios on biomass of endolithic algae and 3 – a one-way nested PERMANOVA to test the effect of CO_2-T scenarios on endolithic community structure. MS = mean square, Photo-micro = photosynthetic microborers, P = Preindustrial, PD = Present-day, M = Medium, H = High CO_2-T.

Source ANOVA	d.f.	MS	F	p	Post-hoc
Dissolution					
Scenario	3	0.512	7.47	< 0.001	$H > M$, PD, and P
Photo-micro	1	12.346	179.97	< 0.001	$D > L$
Scenario × Photo-micro	3	0.039	0.57	0.640	
Tank (Scenario × Photo-micro)	24	0.068	1.17	0.281	
Error	96	0.058			
Biomass of microborers					
Scenario	3	0.017	7.29	< 0.001	$H > M, P$
Error	44	0.002			
Source PERMANOVA	**d.f.**	**MS**	**Pseudo-F**	**P**	**pairwise**
Community structure					
Scenario	3	1722.6	2.94	0.029	$H \neq M$, PD, and P
Tank (Scenario)	12	586.8	2.60	< 0.001	
Residuals	31	225.4			
Total	46				

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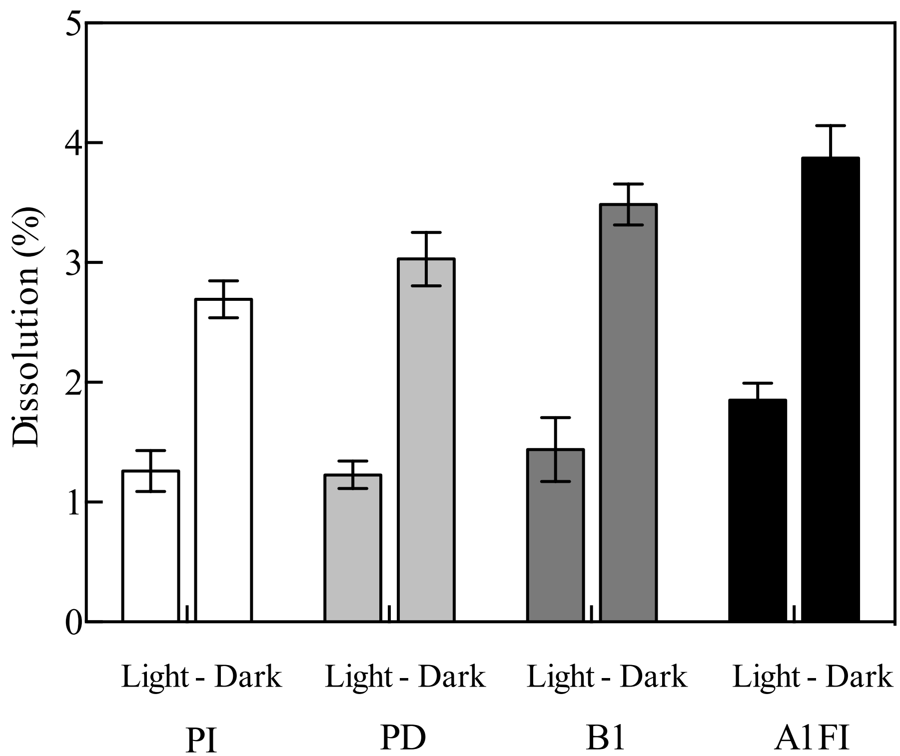

Fig. 1. Dissolution (%) of CCA skeletons exposed to light (with photosynthetic microborers) and dark conditions (without photosynthetic microborers) and four pCO_2-T scenarios over 8 weeks. Data correspond to means ±s.e.m (n = 16 per light condition and pCO_2-T treatment). pCO_2-T levels correspond to preindustrial (320 µatm, 23 °C), present-day (410 µatm, 24 °C), reduced (600 µatm, 26 °C), and business-as-usual (1000 µatm, 28 °C) CO_2 emission scenarios.

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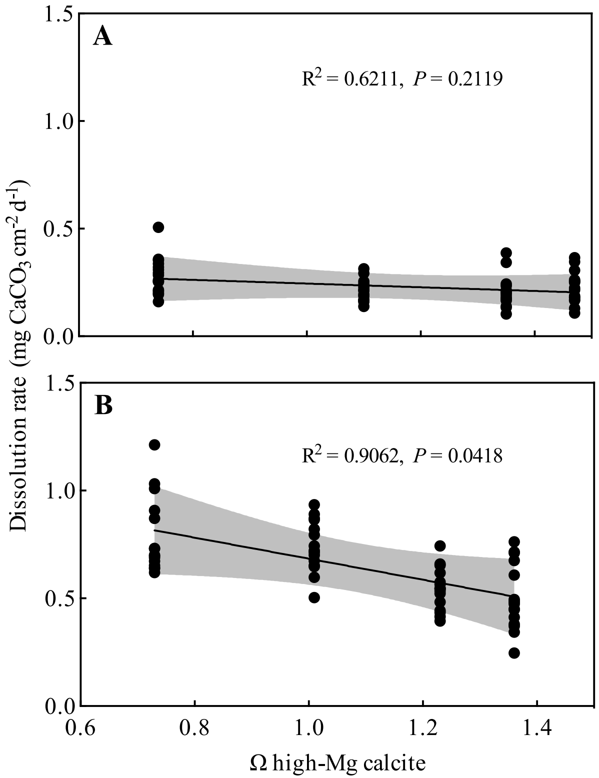

Fig. 2. Linear dissolution response of CCA skeletons to declining saturation state of seawater with respect to high-Mg calcite (Ω_{HMC}) over 8 weeks under **(A)** natural light (photosynthetic microborers + environmental effect) and **(B)** dark conditions (environmental effect). Dissolution data correspond to means ±s.e.m ($n = 16$ samples per light condition and $p\text{CO}_2$-T treatment) and Ω_{HMC}values correspond to means calculated for light and dark tanks ($n = 9$). The solid curves represent the linear regression and the dashed curves correspond to the 95 % confidence interval of the relationship.

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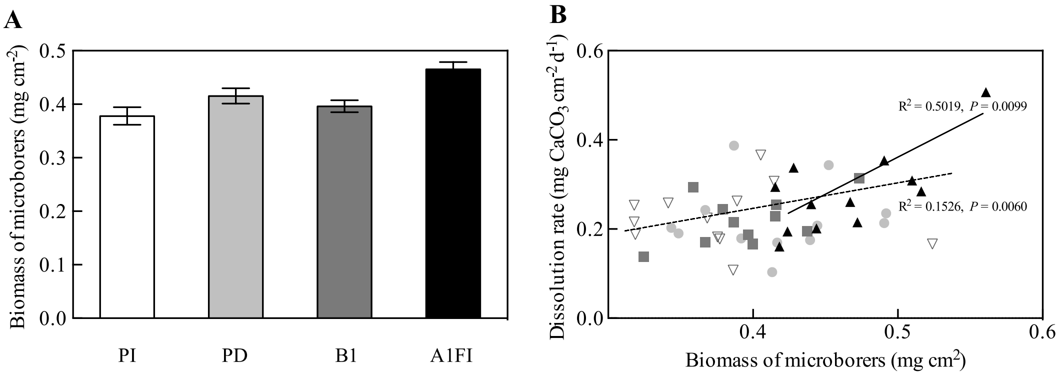

Fig. 3. Photosynthetic microborers in CCA skeletons. **(A)** Biomass of photosynthetic microborers (mg cm^{-2}). **(B)** Relationship between biomass of microborers (mg cm^{-2}) and dissolution rate (mg $CaCO_3$ cm^{-2} d^{-1}). Data correspond to means ±s.e.m (n = 12 per $p$$CO_2$-T treatment). $p$$CO_2$-T levels correspond to preindustrial (320 µatm, 23 °C), present-day (410 µatm, 24 °C), reduced (600 µatm, 26 °C), and business-as-usual (1000 µatm, 28 °C) CO_2 emission scenarios. The dashed line represents the linear regression of the complete data set and the solid line corresponds to the relationship for the A1FI CO_2-T scenario.

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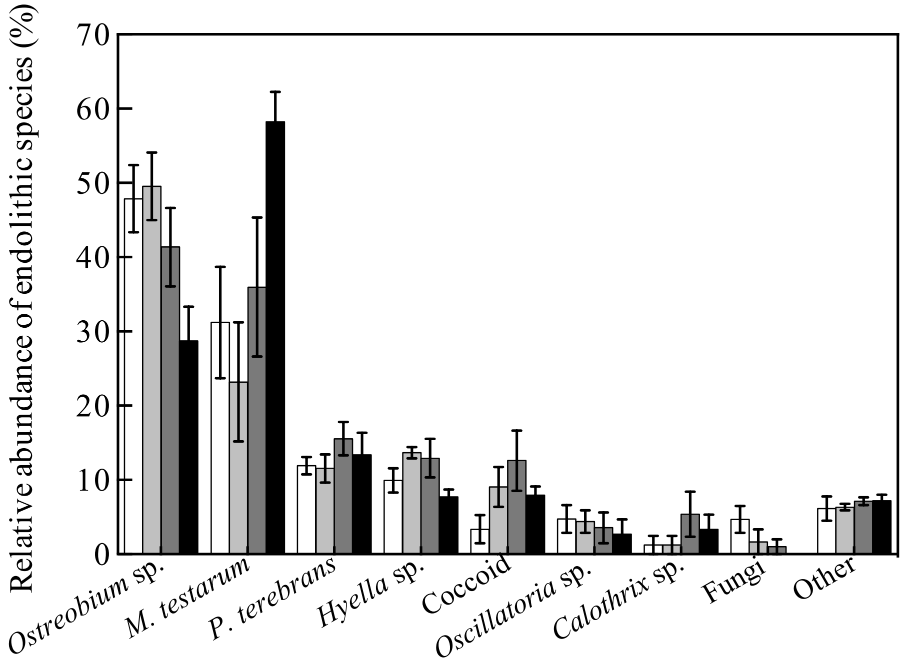

Fig. 4. Relative abundance (%) of endolithic microborers and epilithic cyanobacteria in CCA skeletons after an 8 weeks colonization period under four CO_2-T treatment scenarios. Data correspond to means ±SEM (n = 12 per CO_2-T treatment). CO_2-T levels correspond to preindustrial (320 µatm, 23 °C), present-day (410 µatm, 24 °C), reduced (600 µatm, 26 °C), and business-as-usual (1000 µatm, 28 °C) CO_2 emission scenarios.

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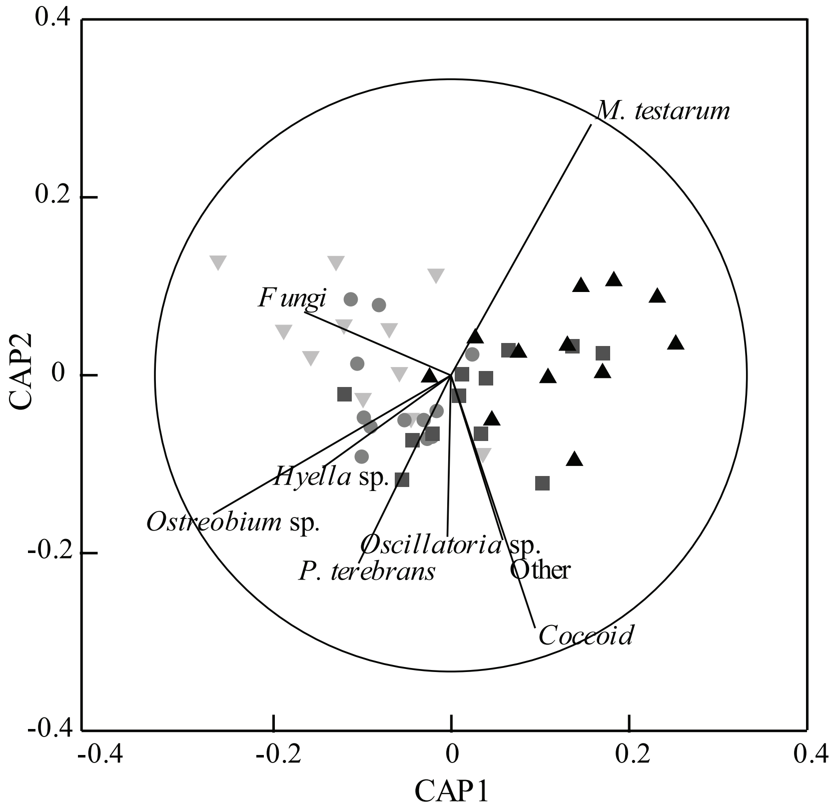

Fig. 5. Canonical analysis of principal coordinates (CAP) of the endolithic community response to four $p\mathrm{CO_2}$-T scenarios over 8 weeks (preindustrial = white triangles, present-day = circles, B1 = squares, A1F1 = black triangles). $p\mathrm{CO_2}$-T levels correspond to preindustrial (320 µatm, 23 °C), present-day (410 µatm, 24 °C), reduced (600 µatm, 26 °C), and business-as-usual (1000 µatm, 28 °C) $\mathrm{CO_2}$ emission scenarios.

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