Research Article

**Microalgae, a boring bivalve and a coral. A newly described association between two coral reef bioeroders within their coral host.**

AJ Fordyce¹*, TD Ainsworth², W Leggat¹

¹School of Environmental and Life Sciences, University of Newcastle, Ourimbah NSW 2258, Australia

²School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney NSW 2052, Australia

*Corresponding author: Alexander.Fordyce@uon.edu.au

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**Abstract**

Bioeroding organisms play an important part in shaping structural complexity and carbonate budgets on coral reefs. Species interactions between various bioeroders are an important area of study, as these interactions can affect net rates of bioerosion within a community and mediate how bioeroders respond to environmental change. Here we test the hypothesis that the biomass of endolithic bioeroding microalgae is positively associated with the presence of a macroboring bivalve. We compared the biomass and chlorophyll concentrations of microendolithic biofilms in branches of the coral *Isopora palifera* (Lamarck, 1816) that were or were not inhabited by a macroboring bivalve. Those branches with a macroborer present hosted approximately 80% higher microbial biomass compared to adjacent branches from the same coral with no macroborer. Increased concentrations of chlorophyll *b* indicated this was partly due to a greater abundance of green microalgae. This newly described association has

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important implications for the coral host, as both the bivalve and the microalgae have been hypothesised as symbiotic.

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Keywords: bioerosion, ecological interaction, endolith, coral, lithophagine, microalgae
Abstract

Bioeroding organisms play an important part in shaping structural complexity and carbonate budgets on coral reefs. Species interactions between various bioeroders are an important area of study, as these interactions can affect net rates of bioerosion within a community and mediate how bioeroders respond to environmental change. Here we test the hypothesis that the biomass of endolithic bioeroding microalgae is positively associated with the presence of a macroboring bivalve. We compared the biomass and chlorophyll concentrations of microendolithic biofilms in branches of the coral *Isopora palifera* (Lamarck, 1816) that were or were not inhabited by a macroboring bivalve. Those branches with a macroborer present hosted approximately 80% higher microbial biomass compared to adjacent branches from the same coral with no macroborer. Increased concentrations of chlorophyll *b* indicated this was partly due to a greater abundance of green microalgae. This newly described association has important implications for the coral host, as both the bivalve and the microalgae have been hypothesised as symbiotic.
**Introduction**

The process of bioerosion (the decay, degradation or dissolution of calcium carbonate by living organisms) modulates multiple aspects of reef ecological function. Bioeroders modify the structural complexity of reefs at scales from microns to metres (Davidson et al. 2018; Glynn and Manzello 2015; Roff et al. 2019), which influences coral reef herbivory (Vergés et al. 2011), coral and fish larval settlement (Coker et al. 2012; Kegler et al. 2017), and a reef’s economic value (Graham and Nash 2013; see also Schönberg et al. 2017). Bioeroders can be characterised into guilds depending upon their habitat (epilithic or endolithic), size (micro and macro) and mechanism of bioerosion (Schönberg et al. 2017), with both mechanical and chemical mechanisms being employed by various guilds. Some bioeroding taxa such as excavating parrotfish, scraping urchins and boring sponges physically break down carbonate substrates and produce coarse carbonate sediments on a reef. Sediment turnover is important in maintaining sediment porosity and permeability, which affects the productivity of coral reef sands (Miyajima et al. 2001; Santos et al. 2010). Other bioeroders dissolve, rather than degrade, carbonate substrates and so affect reef carbonate budgets by modulating the availability of dissolved inorganic carbon (Perry et al. 2014). Bioerosion therefore affects both reef growth and productivity.

Importantly, there is evidence that ecological interactions between bioeroders are capable of enhancing or suppressing overall rates of erosion on a coral reef. As such these are key considerations when seeking to understand how bioerosion is shaping a reef environment. For
example, grazing urchins may target endolithic microalgae (i.e. living within rock) as a food source and scrape the substrate as they feed (Chazottes et al. 1995). Despite this, predation by urchins ultimately increases bioerosion by microendoliths due to the increased light field in the substrate which extends the compensation depth for algal colonization (Chazottes et al. 1995; Tribollet and Golubic 2005). Parrotfish and urchin grazing has also been found to control recruitment and succession in endolithic macroborer communities in Kenya, resulting in reduced overall rates of macrobioerosion on the reef (Carreiro-Silva and McClanahan 2012). These inter-guild interactions between microborers, macroborers and grazers can take the form of feedback loops in which one guild might enhance or suppress bioerosion by a different guild (Carreiro-Silva and McClanahan 2012; Schönberg et al. 2017). Environmental change can disrupt the balance between these species and alter pathways in these loops, leading to shifts in ecosystem bioerosion (Perry et al. 2014; Schönberg et al. 2017). Therefore, we can benefit from a greater understanding of the number and structure of bioeroder interactions within an ecological web.

Recently, Rice et al. (2020) identified an interaction between two bioeroding organisms, excavating parrotfish and endolithic lithophagine mussels inhabiting the skeleton of live massive *Porites* spp. corals. Similar to the results presented by Rotjan and Lewis (2005), the authors identified a positive relationship between the density of macroborers in a live coral and the frequency of parrotfish bite scars on the same colony. Both studies suggested that targeted feeding by parrotfish on macroborers drove this association, and Rice et al. (2020) went further to hypothesise that this interaction might be partly mediated by endolithic microalgae living alongside the bivalves inside the coral skeleton. Excretion by the bivalve, which underlies its putative beneficial role to corals (Mokady et al. 1998), could effectively fertilise the surrounding skeleton and so increase the abundance of endolithic microalgae.
The blue mussel, *Mytilus edulis*, has been shown to enrich sediment porewater through the biodeposition of ammonium and phosphates, boosting the growth of co-occurring seagrass (Reusch et al. 1994). By enriching the endolithic habitat of a coral colony with waste products, bivalves are potentially increasing the abundance of endolithic algae which increases the nutritional value of that patch of coral colony for a grazing parrotfish. This is especially true for “microphagous” parrotfish, a termed used to describe their preferential feeding habits on areas abundant in microalgae (Bruggemann et al. 1994; Clements et al. 2017).

Here we investigate the potential for this undescribed association occurring inside the skeleton of a living coral, with the potential to influence coral health and skeletal integrity. We tested the hypothesis of Rice et al. (2020) that the presence of macroborers is associated with an increased biomass of microalgae in the endolithic habitat of *Isopora palifera* (Lamarck, 1816) coral colonies.

**Methods**

**Initial observations**

In October 2019, we observed that the presence of bore holes made by lithophagine bivalves (Fig. 1a - c) were surrounded by a dense green ‘halo’ inside the skeleton of *I. palifera* (Fig. 1b, d). This species of coral has been previously recognised as being frequently infested with lithophagine bivalves (Kleemann 1980). *I. palifera* exhibits variable morphology that can be predominantly encrusting or sub-massive with thick, columnar or plate-like branches (Veron and Stafford-Smith 2000). In the Heron Island reef lagoon, this species is primarily sub-massive with columnar branches, forming stand-alone branching colonies. The green patches within the skeleton were at times macroscopically visible through the live coral tissue as a
green hue (Fig. 1b). In January 2020, we conducted a survey of the Heron Island reef lagoon (0.5 - 2 metres depth; 23.4423° S, 151.9148° E), at low tide, to assess the prevalence of lithophagine macroborer boreholes within *I. palifera* colonies, identified by the conspicuous figure-eight borehole shapes (Kleemann 1980) (Fig. 1a). We haphazardly chose a direction across the reef flat, walked 15 metres, and then surveyed the nearest *I. palifera* colony for the presence of lithophagid boreholes. We then chose another random direction and repeated this step until 45 colonies were surveyed (15 metres was chosen to reduce the chances of surveyed colonies being clonal). The maximum height, width and depth of each colony was measured using a ruler as a coarse estimate of colony volume against which we could estimate macroborer density as the number of individuals per m³ (Fig. 1e).

**Sample collection**

Two branches from each of twenty colonies (n = 40) were collected using a hammer and chisel in January 2020: one branch inhabited by a single lithophagid macroborer and one without any macroborer boreholes. Each coral colony was selected haphazardly and was a minimum of 15 metres apart. When selecting the two branches, we chose two that were adjacent to each other on the horizontal plane and that did not visibly experience significantly different light environments. We hypothesised that microendolithic biomass would be affected by self-shading amongst the branches of the colony, although knowledge of intra-colony variation in endolithic biomass is currently limited. This decision was made to minimise bias from intra-colony variation in endolithic biomass due to variable light environments. The branches were collected under permit G18/41124.1 and did not exceed 7 cm in length or 4 cm in diameter.

**Sample Processing**
To minimise contamination by photosymbiotic dinoflagellates living in the coral tissue, coral tissue was removed using a compressed air gun (Ozito, Australia) attached to a 15 L aluminium SCUBA cylinder. Following this, the macroborers were also removed from those samples they inhabited. This was achieved by cracking open the skeleton using bone cutters and using forceps to remove the bivalve. In the process of removing the bivalve, each sample was also inspected for the presence of other macroborers (e.g. polychaetes). After airbrushing, the skeletal volume of each fragment was measured using Archimedean principles as per the buoyant weight technique (Jokiel 1978). For the split-open samples from which macroborers were removed, the pieces of the skeleton were weighed together in the weighing basket, following the apparatus described by Jokiel (1978). Seawater was supplied from the reef-flat and its density calculated as 1.0245 g cm$^{-3}$, using a stainless steel double-ended snap-bolt as a reference object. The density of the reference object was calculated by comparing its weight in air and distilled water, and this value was used to then calculate seawater density. For every 0.1 °C change in temperature, seawater density was re-calculated.

Samples were weighed while suspended in seawater. After, we back-calculated coral dry weight using the density of pure aragonite which is 2.947 g cm$^{-3}$ (Jokiel 1978). This was used in lieu of a published estimate for the specific skeletal density (termed micro-density) of *I. palifera*. The equation to back-calculate dry weight was:

$$\text{Branch}_{\text{Dry mass}} = \frac{\text{Branch}_{\text{SW mass}}}{(1 - \frac{\text{SW dens}}{2.947})}$$

Then, sample weight in seawater is subtracted from sample dry weight and divided by the density of seawater to produce an estimate of the volume of each coral branch.
After samples were weighed, they were dissolved in acid following modified methods from Fine and Loya (2002). Samples were dissolved in sequential washes using 1.6 M hydrochloric acid within 50 ml plastic centrifuge tubes. Between each acid change, the samples were centrifuged at 3856 x g and 4 °C for ten minutes, in order to separate out the skeletal organic matrix of the coral host. The reacted acid (now calcium chloride), including the organic matrix, was decanted and fresh acid added. The resulting microendolithic pellet was washed twice with 0.22 µm filtered seawater to remove excess acid, was resuspended in 20 ml of filtered seawater and then homogenised by a combination of vigorous shaking and vortexing for up to a minute, in order to break apart the pellet. A 10 ml syringe was used to transfer half of the homogenised endolithic mixture of each sample to a paired centrifuge tube.

**Ash free dry weight**

10 ml of each endolithic sample was first centrifuged and a 10 ml syringe was then used to remove nine ml of the clear supernatant, the remaining pellet was dislodged by gentle shaking and roughly resuspended in the remaining 1 ml of supernatant. The solution was then poured into a sterilised, pre-burned crucible; any particulate still in the tube was washed into the same crucible using filtered seawater. Crucibles were dried in an oven at 70 °C for 18 hours, leaving a combination of dried organic matter and inorganic minerals. These dried crucibles were weighed on a four decimal place balance (Ohaus, New Jersey, USA) and then placed in a muffle furnace at 550 °C for four hours to burn off all organic matter (Reyes-Nivia et al. 2013). After cooling, they were weighed again and the biomass of endolithic phototrophs calculated as the reduction in mass as a result of burning (i.e. ash-free dry weight; AFDW). This was normalised to half the branch volume as the homogenised
endolithic sample was split prior to chlorophyll and biomass analysis. AFDW is measured in grams per centimetre cubed.

**Chlorophyll Concentrations**

The remaining 10 ml of each sample were centrifuged to produce a concentrated endolithic pellet. All of the supernatant was carefully removed and the pellet resuspended in 10 ml of 90% acetone to extract chlorophyll (Ritchie 2008). After adding the acetone, samples were vortexed for 30 seconds and placed in an ultra-sonicator (Unisonics, NSW, Australia) for 20 minutes to break apart cell walls. Suspensions were then vortexed for another 30 seconds and left to extract for 24 hours at 4 °C in the dark. Samples were then centrifuged using the same settings as above to produce a clear green supernatant containing dissolved chlorophyll, and each sample was pipetted in triplicate into a microplate to be analysed using a spectrophotometer (Spectrostar Nano, BMG Labtech, Australia). A paired 90% acetone blank solution was measured between each sample in the microplate read direction. The blank-corrected raw absorbance values were converted to µg cm\(^{-3}\) using the quadrichroic spectrophotometric equations of Ritchie (2008) that measure chlorophylls \(a, b, c\) and \(d\). We selected this method in favour of trichroic equations (e.g. Jeffrey and Humphrey 1975) because chlorophyll \(d\)-containing cyanobacteria have been previously identified from endolithic habitats at this location (Behrendt et al. 2011) and not accounting for the presence of chlorophyll \(d\) can lead to overestimates of chlorophylls \(a\) and \(b\) (Ritchie 2008). The decalcification of the samples using HCl acidified chlorophyll \(a\) in our samples to phaeophytin \(a\), which lowers absorption at 664 nm and broadens the absorption peak, leading to the underestimation of chlorophyll \(a\) by spectrophotometry (Ritchie 2008). Nonetheless, this method still produces results that are well correlated with techniques such as high performance liquid chromatography (Grinham et al. 2007; Ritchie 2008). To normalise
concentrations to branch size, the triplicate sub-samples were first averaged to give a sample-wise concentration in µg cm⁻³ and then multiplied by ten to give an estimate of the total weight of chlorophyll in each 10 ml sample, in µg. These values were then divided by half the fragment volume to give a chlorophyll concentration per cubic centimetre of coral skeleton.

Statistics
All statistics were performed using R version 3.6.0 (R Core Team 2019). We used paired two tailed t-tests to analyse the five parameters (biomass, chlorophylls a-d) of samples with and without macroboring bivalves. To test the assumption that the dependent variables were normally distributed, we used a combination of Shapiro-Wilk tests and Q-Q plots. Potential outliers were identified using a Cook’s distance of 4/n (Cook 1977). When present, we compared the model outcomes with and without the presence of the outlier(s) and in all cases they had no effect upon the results of the t-test. All chlorophyll concentration tests violated the assumption of normality. Log-transforming the data did not address these violations, so we used Wilcoxon signed rank tests to analyse these variables. All reported values are mean ± S.E.

Results
We surveyed 45 I. palifera colonies on the Heron Island reef flat in January 2020 and recorded a median density of 832 lithophagine boreholes per cubic metre of coral (Fig. 1e). When comparing coral branches with and without a bivalve macroborer, we found that branches previously inhabited by a macroborer had an endolithic microbial biomass that was significantly greater than that recorded for branches without a macroborer (t₁₉ = 3.220, p = 0.005; Fig. 2a). The mean chlorophyll a concentration in branches where a macroborer was
present was significantly greater than the concentration recorded for branches without a macroborer ($z = -4.001, p < 0.001$; Fig. 2b). Similarly, the mean chlorophyll $b$ concentration measured from the endolithic microbiome in branches with a bivalve was significantly greater than for branches without a macroborer ($z = -2.383, p = 0.017$; Fig. 2b). The concentrations of chlorophylls $c$ and $d$ did not differ significantly between groups (chl $c$: $z = -1.658, p = 0.097$; chl $d$: $z = -0.018, p = 0.985$).

**Discussion**

Lithophagine bivalve macroborers, identified by the figure-eight shape of their boreholes (Kleemann 1980), were present in all but one of the surveyed *I. palifera* colonies on the Heron Island reef flat (Fig. 1e). The median density of boreholes per cubic metre of coral was slightly lower than those recorded on previous surveys of date mussel density in massive *Porites* spp. (Rice et al. 2020; Rotjan and Lewis 2005). However, our method for approximating coral volume might be expected to overestimate the true volume of substrate available for macroboring. In the *I. palifera* branches inhabited by a macroboring bivalve, the microendolithic biomass was almost double that of adjacent, uninhabited branches from the same colony (Fig. 2a). Additionally, the concentrations of chlorophylls $a$ and $b$ were approximately 4 and 2-fold greater in the presence of a macroborer (Fig. 2b). Chlorophyll $b$ is the primary accessory pigment found in microendolithic green algae, such as *Ostreobium* spp., which commonly dominate the microboring communities of coral skeletons (del Campo et al. 2017; Marcelino and Verbruggen 2016; Pernice et al. 2019; Ricci et al. 2019). Our data therefore suggest that the increased microbial biomass was in part due to a higher abundance of green microalgae in the skeleton. The data also indicate the presence of chlorophyll $d$-containing cyanobacteria within our *I. palifera* samples. The only recorded genus of alga known to use chlorophyll $d$ is *Acaryochloris* (Larkum and Kühl 2005), which has been
identified previously from endolithic habitats under crustose coralline algae at this location (Behrendt et al. 2011).

We have found evidence of a positive association between the presence of a lithophagous bivalve macroborer and the biomass of endolithic microalgae, within an *I. palifera* coral host. Both Rotjan and Lewis (2005) and Rice et al. (2020) found that parrotfish bite frequency on a coral colony was correlated with the density of resident macroboring bivalves. All authors suggested that these relationships could reflect targeted feeding of parrotfish on nutrient-rich macroborers, as Rotjan and Lewis (2005) found no difference in the nutritional quality of overlying coral tissue. Rice et al. (2020) went on to hypothesise that it may also be partly mediated by microendolithic algae which live alongside the macroborer in the coral skeleton. Our results lend credence to this hypothesis. Higher microalgal biomass in the skeleton concomitant with macroborer infestation would increase the nutritional value of a particular patch of coral. This is especially true if the parrotfish species shows preferential feeding on microalgae (Bruggemann et al. 1994; Clements et al. 2017) and/or is omnivorous (Bellwood and Choat 1990). Similarly, the bivalve-microendolith association could help explain the results presented by Simon-Blecher et al. (1996). They recorded higher chlorophyll fluorescence in healthy coral tissue adjacent to a lithophagous borehole in the coral *Goniastrea* sp. compared to tissue without a borehole next to it. They suggest that this might reflect nitrogen-enrichment of coral tissue through bivalve excretion (Simon-Blecher et al. 1996). However Rotjan and Lewis (2005) found no difference in coral tissue nitrogen content whether next to or away from a borehole. Instead the stronger fluorescence signal may have been due to the microendolithic ‘halo’, as described here (Fig. 1), beneath the coral tissue. Fine et al. (2005) have previously shown that endolithic algae beneath the tissue of the coral *Oculina patagonica* can influence chlorophyll fluorescence measured in the coral tissue.
There are several possible mechanisms driving the association between macroboring bivalves and algal microendoliths inside the skeleton of *I. palifera*. First and foremost is the potential for fertilisation of the endolithic microhabitat by excretion of nitrogenous waste from the macroboring bivalve. This dynamic underlies the hypothetical mutualism between corals and boring bivalves (Mokady et al. 1998) and occurs in seagrass beds where infaunal blue mussels, *Mytilus edulis*, enhance the growth of *Zostera marina* by faecal biodeposition (Reusch et al. 1994). Additionally, artificial enriching the endolithic habitat with nitrogenous inorganic matter increases colonization and bioerosion by microendoliths in the shells of giant clams *Strombus gigas* (Carreiro-Silva et al. 2012; Carreiro-Silva et al. 2005; Carreiro-Silva et al. 2009). It is also possible that CO$_2$ produced by bivalve respiration diffuses into the skeleton and enhances daytime microbial photosynthesis. This could be coupled with oxygen produced by photosynthesis diffusing into the macroborer burrow; endolithic algae have been previously shown to cause skeletal porewater to become supersaturated with respect to oxygen (Kühl et al. 2008). Finally, there is evidence that photoassimilates produced by endolithic algae are a source of sugars for the coral host (Fine and Loya 2002; Sangsawang et al. 2017; Schlichter et al. 1995) and this may also be the case for lithophagaine bivalves. Taken together this is suggestive of metabolic exchange between endolithic bivalves and microalgae in the form of series of positive feedback loops (Fig. 3). The limited diffusion of metabolic waste products through the skeleton may also explain the shape of the green ‘halos’ around macroborer boreholes. This has important implications for the spatial extent of this association within a coral colony.

Bioerosion by microendolithic algae can promote colonization by macroborers such as polychaetes and sponges, by weakening substrates and thereby reducing the energetic cost of
macroborer colonization (Che et al. 1996; Schönberg et al. 2017). Equally the secretion of an acidic mucus by the macroborer, which is the primary form of chemical erosion in boring bivalves (Kleemann 1996), weakens skeletal matrices (Scott and Risk 1988) and so may reduce the energetic cost of boring for microendoliths. Additionally, the presence of an external opening on the coral surface may increase the endolithic light field and promote more settlement by microendoliths that colonise new substrates from the water column as opposed to from neighbouring substrates (Massé et al. 2018) (Fig. 3). Therefore both members of this association have the capacity to promote colonization and bioerosion by each other. In the freshwater bivalve *Lignopholas fluminalis*, cooperation with co-occurring microorganisms was found to promote the bioerosion of silicate siltstone (Daval et al. 2020). The association described in this study may therefore be maintained through metabolic exchange and/or by the combined weakening of the coral skeleton (Fig. 3). It is beyond the scope of this study to state how the relationship is first established. It is possible that the initial trigger is macroborer settlement which enhances growth in the already present microendolith community, which then serves to reduce the energetic cost of burrowing by the bivalve. In this vein, pre-existing microendolithic biomass (i.e. before infestation by a macroborer) might be an important factor affecting settlement success (i.e. recruitment) in bivalves.

The bivalve-microendolith association described here is comparable to the relationship between macroboring polychaetes and microendoliths, wherein each guild promotes bioerosion by the other (Che et al. 1996; Schönberg et al. 2017). These inter-guild relationships affect overall rates of bioerosion on a reef through the ‘bioerosion loop’ (Carreiro-Silva and McClanahan 2012; Schönberg et al. 2017). While it is not clear how this relationship between boring bivalves and microendoliths affects net bioerosion, it does have
some interesting implications for the health of the coral host. Both lithophagine bivalves and endolithic microalgae have been previously independently proposed as symbiotic to their host coral (del Campo et al. 2017; Mokady et al. 1998). Describing and understanding these multispecies interactions is a promising area for discovery and continues to be an important step in understanding the role of bioeroders on coral reefs.

Declaration of Competing Interest

The authors declare no competing interests.

Data availability

Data and R code is available on Github

(https://github.com/GusFordyce/MacroMicroAssociation)

Bibliography

Behrendt, L., A. W. Larkum, A. Norman, K. Qvortrup, M. Chen, P. Ralph, S. J. Sørensen et al. 2011. Endolithic chlorophyll d-containing phototrophs. The ISME journal 5:1072-1076.

Bellwood, D. R., and J. H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environmental Biology of Fishes 28:189-214.

Bruggemann, H., M. van Oppen, and A. M. Breeman. 1994. Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. Marine Ecology Progress Series 106:41-55.

Carreiro-Silva, M., W. Kiene, S. Golubic, and T. McClanahan. 2012. Phosphorus and nitrogen effects on microbial euendolithic communities and their bioerosion rates. Marine Pollution Bulletin 64:602-613.

Carreiro-Silva, M., and T. McClanahan. 2012. Macrobioerosion of dead branching Porites, 4 and 6 years after coral mass mortality. Marine Ecology Progress Series 458:103-122.

Carreiro-Silva, M., T. R. McClanahan, and W. E. Kiene. 2005. The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. Coral Reefs 24:214-221.

—. 2009. Effects of inorganic nutrients and organic matter on microbial euendolithic community composition and microbioerosion rates. Marine Ecology Progress Series 392:1-15.

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

Che, L. M., T. Le Campion-Alsumard, N. Boury-Esnault, C. Payri, S. Golubic, and C. Bézac. 1996. Biodegradation of shells of the black pearl oyster, *Pinctada margaritifera var. cumingii*, by microborers and sponges of French Polynesia. Marine Biology 126:509-519.

Clements, K. D., D. P. German, J. Piché, A. Tribollet, and J. H. Choat. 2017. Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biological Journal of the Linnean Society 120:729-751.
Coker, D. J., N. A. J. Graham, and M. S. Pratchett. 2012. Interactive effects of live coral and structural complexity on the recruitment of reef fishes. Coral Reefs 31:919-927.

Cook, R. D. 1977. Detection of influential observation in linear regression. Technometrics 19:15-18.

Daval, D., F. Guyot, I. N. Bolotov, I. V. Vikhrev, A. V. Kondakov, A. A. Lyubas, A. Y. Bychkov et al. 2020. Symbiotic cooperation between freshwater rock-boring bivalves and microorganisms promotes silicate bioerosion. Scientific Reports 10:1-10.

Davidson, T. M., A. H. Altieri, G. M. Ruiz, and M. E. Torchin. 2018. Bioerosion in a changing world: a conceptual framework. Ecology letters 21:422-438.

del Campo, J., J.-F. Pombert, J. Šlapeta, A. Larkum, and P. J. Keeling. 2017. The ‘other’ coral symbiont: Ostreobium diversity and distribution. The ISME Journal 11:296-299.

Fine, M., and Y. Loya. 2002. Endolithic algae: An alternative source of photoassimilates during coral bleaching. Proceedings of the Royal Society B 269:1205-1210.

Fine, M., E. Meroz-Fine, and O. Hoegh-Guldberg. 2005. Tolerance of endolithic algae to elevated temperature and light in the coral Montipora monasteriata from the southern Great Barrier Reef. Journal of Experimental Biology 208:75.

Glynn, P. W., and D. P. Manzello. 2015. Bioerosion and coral reef growth: a dynamic balance, Pages 67-97 in C. Birkeland, ed. Coral reefs in the Anthropocene. New York, Springer.

Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315-326.

Grinham, A. R., T. J. Carruthers, P. L. Fisher, J. W. Udy, and W. C. Dennison. 2007. Accurately measuring the abundance of benthic microalgae in spatially variable habitats. Limnology and Oceanography: Methods 5:119-125.

Jeffrey, S. t., and G. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen 167:191-194.

Jokiel, P. L. M., J. E. 1978. Coral growth: buoyant weight technique, Pages 529 - 542 in D. R. Stoddart, and R. E. Johannes, eds. Coral Reef Research Methods, UNESCO.

Kegler, P., H. F. Kegler, A. Gärdes, S. C. A. Ferse, M. Lukman, Y. R. Alfiansah, C. Hassenrück et al. 2017. Bacterial biofilm communities and coral larvae settlement at different levels of anthropogenic impact in the Spermonde Archipelago, Indonesia. Frontiers in Marine Science 4.

Kleemann, K. 1980. Boring bivalves and their host corals from the Great Barrier Reef. Journal of Molluscan Studies 46:13-54.

Kleemann, K. 1996. Biocorrosion by bivalves. Marine Ecology 17:145-158.

Kühl, M., G. Holst, A. W. Larkum, and P. J. Ralph. 2008. Imaging of oxygen dynamics within the endolithic algal community of the massive coral Porites lobata. Journal of Phycology 44:541-550.

Larkum, A. W., and M. Kühl. 2005. Chlorophyll d: the puzzle resolved. Trends in Plant Science 10:355-357.

Marcelino, V. R., and H. Verbruggen. 2016. Multi-marker metabarcoding of coral skeletons reveals a rich microbiome and diverse evolutionary origins of endolithic algae. Scientific Reports 6:35108.

Massé, A., I. Domart-Coulon, S. Golubic, D. Duché, and A. Tribollet. 2018. Early skeletal colonization of the coral holobiont by the microboring Ulvophyceae Ostreobium sp. Scientific reports 8:1-11.

Miyajima, T., M. Suzumura, Y. Umezawa, and I. Koike. 2001. Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. Marine Ecology Progress Series 217:273-286.

Mokady, O., Y. Loya, and B. Lazar. 1998. Ammonium contribution from boring bivalves to their coral host--a mutualistic symbiosis? Marine Ecology Progress Series 169:295-301.

Pernice, M., J.-B. Raina, N. Rädecker, A. Cárdenas, C. Rogoreutz, and C. R. Voolstra. 2019. Down to the bone: the role of overlooked endolithic microbiomes in reef coral health. The ISME journal:1-10.

Perry, C. T., G. N. Murphy, P. S. Kench, E. N. Edinger, S. G. Smithers, R. S. Steneck, and P. J. Mumby. 2014. Changing dynamics of Caribbean reef carbonate budgets: emergence of reef
bioeroders as critical controls on present and future reef growth potential. Proceedings of the Royal Society B 281:20142018.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reusch, T. B., A. R. Chapman, and J. P. Gröger. 1994. Blue mussels Mytilus edulis do not interfere with eelgrass Zostera marina but fertilize shoot growth through biodeposition. Marine Ecology Progress Series:265-282.

Reyes-Nivia, C., G. Díaz-Pulido, D. Kline, O. H. Guldberg, and S. Dove. 2013. Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. Global Change Biology 19:1919-1929.

Ricci, F., V. R. Marcelino, L. L. Blackall, M. Kühl, M. Medina, and H. Verbruggen. 2019. Beneath the surface: community assembly and functions of the coral skeleton microbiome. Microbiome 7:159.

Rice, M. M., R. L. Maher, A. M. S. Correa, H. V. Moeller, N. P. Lemoine, A. A. Shantz, D. E. Burkepile et al. 2020. Macroborer presence on corals increases with nutrient input and promotes parrotfish bioerosion. Coral Reefs 39:409-418.

Ritchie, R. 2008. Universal chlorophyll equations for estimating chlorophylls a, b, c, and d and total chlorophylls in natural assemblages of photosynthetic organisms using acetone, methanol, or ethanol solvents. Photosynthetica 46:115-126.

Roff, G., J. Joseph, and P. J. Mumby. 2019. Multi-decadal changes in structural complexity following mass coral mortality on a Caribbean reef. Biogeosciences Discussions:1-16.

Rotjan, R. D., and S. M. Lewis. 2005. Selective predation by parrotfishes on the reef coral Porites astreoides. Marine Ecology Progress Series 305:193-201.

Sangsawang, L., B. E. Casareto, H. Ohba, H. M. Vu, A. Meekaew, T. Suzuki, T. Yeemin et al. 2017. 13C and 15N assimilation and organic matter translocation by the endolithic community in the massive coral Porites lutea. Royal Society Open Science 4.

Santos, I. R., D. Erler, D. Tait, and B. D. Eyre. 2010. Breathing of a coral cay: Tracing tidally driven seawater recirculation in permeable coral reef sediments. Journal of Geophysical Research: Oceans 115.

Schlichter, D., B. Zscharnack, and H. Krisch. 1995. Transfer of photoassimilates from endolithic algae to coral tissue. Naturwissenschaften 82:561-564.

Schönberg, C. H., J. K. Fang, M. Carreiro-Silva, A. Tribollet, and M. Wisshak. 2017. Bioerosion: the other ocean acidification problem. ICES Journal of Marine Science 74:895-925.

Scott, P., and M. J. Risk. 1988. The effect of Lithophaga (Bivalvia: Mytilidae) boreholes on the strength of the coral Porites lobata. Coral Reefs 7:145-151.

Simon-Blecher, N., Y. Achituv, and Z. Malik. 1996. Effect of epibionts on the microdistribution of chlorophyll in corals and its detection by fluorescence spectral imaging. Marine Biology 126:757-763.

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

Vergés, A., M. A. Vanderklift, C. Doropoulos, and G. A. Hyndes. 2011. Spatial patterns in herbivory on a coral reef are influenced by structural complexity but not by algal traits. PLoS One 6:e17115.

Veron, J. E. N., and M. Stafford-Smith. 2000, Corals of the World. Queensland, Australia, Townsville MC.
Figure 1. A – External view of a borehole made by a lithophagine bivalve. Note the darker coral tissue pigmentation around the bore hole. B – Internal view of the same borehole. Note the thick green band surrounding the bore hole. C – A lithophagine mussel removed from the coral skeleton. D – Longitudinal cross-section of a coral skeleton with a lithophagine bore hole. E – Histogram of macrobore density defined as number of individuals per approximate cubic metre of coral skeleton ($n = 45$ colonies surveyed).
**Figure 2.** Results from analyses of branches with (green) or without (grey) a macroborer present. **A** – Barplot of ash-free dry weight microbial biomass of endolithic community. **B** – Barplots of concentrations of chlorophylls $a$ to $d$. Bars represent mean ± S.E. *, ** and *** denote significant differences of relative to α thresholds of 0.05, 0.01 and 0.001 respectively.

**Figure 3.** Conceptual diagram illustrating the hypothetical mechanisms driving the relationship described here. 1 – Biodeposition of nitrogenous compounds through bivalve excretion enhances microalgal growth. 2 – Exchange of the products of photosynthesis and
respiration for mutual benefit. 3 – Each bioeroder reduces the energetic cost of boring for its skeletal co-habitant. 4 – The open borehole increases irradiance for and promotes settlement of microalgal endoliths.

Data S1. Excel file with data on biomass, chlorophyll, macroborer density and buoyant weight used to normalise values to fragment volume.
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170x143mm (300 x 300 DPI)