ORIGINAL ARTICLE

Dissolution of Dead Corals by Euendolithic Microorganisms Across the Northern Great Barrier Reef (Australia)

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Abstract Spatial and temporal variabilities in species composition, abundance, distribution, and bioeroding activity of euendolithic microorganisms were investigated in experimental blocks of the massive coral *Porites* along an inshore–offshore transect across the northern Great Barrier Reef (Australia) over a 3-year period. Inshore reefs showed turbid and eutrophic waters, whereas the offshore reefs were characterized by oligotrophic waters. The euendolithic microorganisms and their ecological characteristics were studied using techniques of microscopy, petrographic sections, and image analysis. Results showed that euendolithic communities found in blocks of coral were mature. These communities were dominated by the chlorophyte *Ostreobium quekettii*, the cyanobacterium *Plectonema terebrans*, and fungi. *O. quekettii* was found to be the principal agent of microbioerosion, responsible for 70–90% of carbonate removal. In the offshore reefs, this oligophotic chlorophyte showed extensive systems of filaments that penetrated deep inside coral skeletons (up to 4.1 mm) eroding as much as 1 kg $CaCO_3$ eroded m^{-2} year^{-1}. The percentage of colonization by euendolithic filaments at the surface of blocks did not vary significantly among sites, while their depths of penetration, especially that of *O. quekettii* (0.6–4.1 mm), increased significantly and gradually with the distance from the shore. Rates of microbioerosion (0.1–1.4 kg m^{-2} after 1 year and 0.2–1.3 kg m^{-2} after 3 years of exposure) showed a pattern similar to the one found for the depth of penetration of *O. quekettii* filaments. Accordingly, oligotrophic reefs had the highest rates of microbioerosion of up to 1.3 kg m^{-2} year^{-1}, whereas the development of euendolithic communities in inshore reefs appeared to be limited by turbidity, high sedimentation rates, and low grazing pressure (rates <0.5 kg m^{-2} after 3 years). Those results suggest that boring microorganisms, including *O. quekettii*, have a significant impact on the overall calcium carbonate budget of coral reef ecosystems, which varies according to environmental conditions.

Introduction

Recent studies have emphasized the importance of studying simultaneously the activity of the different agents of bioerosion (boring microflora, macroborers, and grazers) and constructive forces (recruitment, growth, and calcification of corals and coralline algae) to assess the state of health of coral reef ecosystems and their carbonate balance [14, 57]. The importance of such studies increases as coral reef environment become increasingly affected by destructive anthropogenic activities and natural environmental threats such as overfishing, eutrophication, sedimentation, and rising sea surface temperature and atmospheric pCO$_2$ [14, 25, 32, 39, 54]. Those factors are currently contributing to coral mortality and an accelerated degradation of reef framework putting in jeopardy the survival of coastal and insular human populations [61]. The rise of coral mortality induces an increase in variety and surface area of substrates exposed to intensified bioerosion. Although bioerosion occurs in both live and dead carbonate substrates, its intensity in dead substrates is significantly higher [34, 55, 57].

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In comparison to constructive forces, bioerosion has received relatively less attention. Bioerosion studies have assessed, in particular, the taxonomic and ecological characteristics of macroborers and grazers (sponges, polychaetes, bivalves, gastropods, sea urchins, and fish) in natural settings or in experimental substrates (see [28, 29, 46, 57]). In contrast, there are a few studies that have focused on boring microorganisms—also called boring microflora—which comprise euendolithic cyanobacteria, algae, and fungi [23]. Euendoliths are ubiquitous in coastal environments including Mediterranean [33], Adriatic [20], Antarctic [12], and tropical environments [34, 45, 55]. They trigger food chains [7, 28, 44] that would otherwise not be present on coasts with hard and compact substrates such as volcanic rocks [50]. Garcia-Pichel [17] suggested that microboring organisms actively dissolve substrates, including carbonate substrates, excavating microscopic galleries during respiration, and using active calcium pumps. Most of studies on the boring microflora have focused on its taxonomy, biology, and physiology in diverse coastal ecosystems [5, 21, 33 and more recently 1, 2, 18, 24, 42, 58]. Others revealed its bathymetric distribution and role as a paleoecological indicator [9, 21, 37, 41, 42, 45, 60]. Recently, Tribollet and Golubic [57] showed that the boring microflora is one of the main agents in the long-term bioerosion process in dead carbonate substrates in tropical ecosystems (Great Barrier Reef, Australia). However, the role of each component/species of the microbial boring flora in bioerosion has never been studied. It is expected that rates of microbioerosion, and therefore, rates of bioerosion (= microbioerosion + macrobioerosion + grazing), vary depending on the species composition of the boring microflora.

In this study, I determined the species composition of euendolithic communities, which were allowed to colonize experimental coral substrates over a 3-year period under different environmental conditions (inshore–offshore transect across the northern GBR) and their ecological characteristics measuring the filament density, depth of penetration, and rate of microbioerosion of each euendolithic species. This work provides, for the first time, a detailed picture of the role played by each euendolithic microorganism in the process of microbioerosion in dead carbonate substrates at a large spatial and temporal scale.

Methods

Sites

Measurements were made at six sites located near either end of a 200-km-long inshore–offshore transect of the northern Great Barrier Reef (GBR; Fig. 1). Those sites were
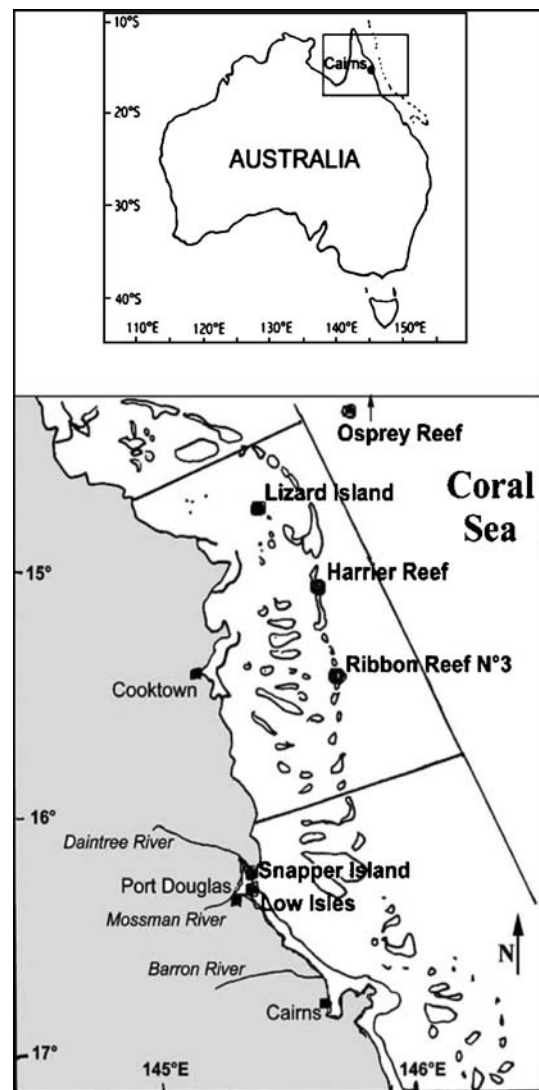
Figure 1 Studied sites located on an inshore–offshore profile along the northern Great Barrier Reef (map from Tribollet and Golubic 2005).

Snapper Island, Low Isles, Lizard Island, Ribbon Reef 3, Harrier Reef, and Osprey Reef. Snapper Island and Low Isles were considered inshore reefs and were surrounded by nutrient-enriched turbid waters [16]. In contrast, Lizard Island, Ribbon Reef 3, Harrier Reef, and Osprey Reef were considered offshore reefs and were surrounded by clear and oligotrophic waters [3, 16]. Detailed information on sites is given in Tribollet et al. [56].

Preparation of Experimental Blocks

Ninety-six experimental blocks (8×8×5 cm) were cut from the interior of live colonies of massive *Porites* sp. collected at Snapper Island and Lizard Island in shallow waters, using a band saw.

Blocks showing traces of previous macrobioerosion were discarded. Pieces of coral skeleton cut in the middle of live colonies were analyzed using SEM to verify that initial microbioerosion was negligible. Selected blocks for the experiment were soaked in fresh water, dried, and measured for their initial dimensions and volume. Coral skeleton density was determined by water displacement (see method [8]). Eight blocks, randomly chosen, were affixed at equidistance on a steel grid using stainless steel bolts and nuts through a hole that was previously drilled in the center of each block. In September 1996, two such grids were deployed on top of dead reef substrate, 3–5 m apart at 7–10 m depth at each site ($n=16$ blocks per site). Blocks were colonized by epilithic and endolithic autotrophs and heterotrophs during 1 and 3 years. Two blocks per grid were thus collected in 1997 and again in 1999 for analysis of the euendolithic microflora and its erosive activity. Thus, a total of 24 blocks were collected during each sampling period and preserved in buffered 7% solution of formaldehyde in seawater to be transported to the laboratory and preserved pending analysis.

Block Treatment

At the laboratory, colonized experimental blocks were cut in half using a band saw. For the purpose of this study, only one half-block per block was used. It was cut further perpendicular to the upper surface into four slices, each 7 mm thick, using a thin band saw (for details see Fig. 2 in [56]). The first slice was discarded because of the bolt trace (artificial erosion); so was the last slice because of its five exposed sides to colonization. Only the two slices with four exposed sides were studied. Then, two pieces of 1 cm^3 were randomly cut on the upper side of each studied slice (four pieces per block) for analysis.

To understand the role of the euendolithic microflora in the destruction of dead coral substrates, several variables were investigated: (a) specific composition of euendolithic communities, (b) diameter of euendolithic filaments, (c) distribution of each euendolithic species in the coral skeleton (depth of penetration), (d) percentage of substrate colonized by each species at the surface of blocks, and (e) rates of microbioerosion. Those variables were obtained using methods allowing the direct study of the euendolithic microflora inside carbonate skeleton (see description below).

Euendolithic Community Study

Several small fragments of substrate were taken randomly on each exposed side of the studied slices using a hammer and a chisel. They were dissolved by using HCL 5% to determine the specific composition of euendolithic communities. Species of euendoliths were identified using a

Leitz Orthoplan compound microscope with a ×40 power objective and according to Bornet and Flahault [5]. This identification was completed by observing resin casts (microborings) of euendoliths on petrographic thin sections using scanning electronic microscopy (SEM) (see Golubic et al.'s method [22]).

Measurement of Euendolithic Filament Diameters

After identification of the different species of euendoliths, diameters of their filaments were determined ($n=100$ filaments) using a drawing tube calibrated using an object
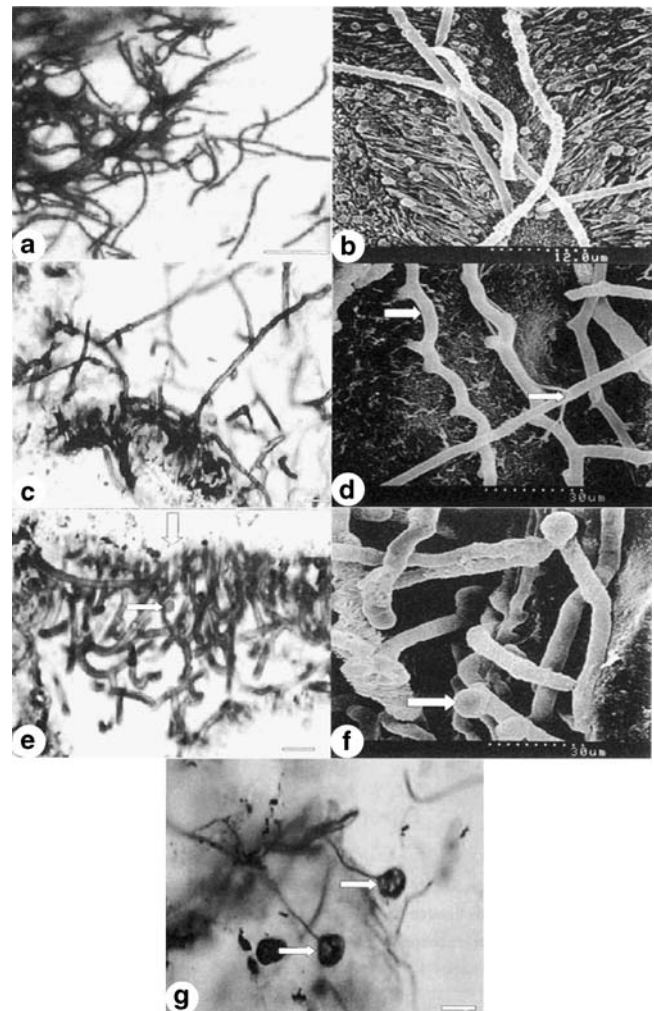
Figure 2 Species of the boring microflora observed in blocks of Porites lobata exposed more than a year to colonization. Filaments colored by Toluidine blue (scale of images=10 μm), as well as their corresponding borings (SEM pictures), are presented for each species. a Filaments of Plectonema tererbrans, b Borings of P. terebrans, c Filaments of Ostreobium quekettii, d Borings of O. quekettii (large arrow) and a parasitic fungi (narrow arrow), e Filaments of Mastigocoleus testarum; the large arrow indicates the upper surface of the block, while the short arrow shows a heterocyst. This picture also shows the depth of penetration of M. testarum filaments, f Borings of M. testarum with a heterocyst (arrow), g Filaments of fungi with reproductive organs (arrows).

micrometer slide and attached to the compound microscope. Based on the diameter of the euendolithic filaments, size classes of microborings were determined. When the diameter of filaments of two euendolithic species were too close to allow distinguishing microborings of one species to the other on SEM pictures, the two species were grouped. Then, one size class of microborings was attributed to this group of euendoliths.

Determination of Euendolith Distribution Inside Coral Skeletons

One of the pieces of coral skeleton cut per slice was used to make petrographic thin sections to measure the depth of penetration of euendolithic filaments per species (Dp). Millimeter thin slabs of substrate, perpendicular to the upper surface, were cut, dehydrated in an ethanol series, embedded in araldite, and then mounted on microscope slides (method described by Golubic *et al.* [22]). The mounted slabs were grounded to a thickness of 0.2–0.3 mm to the quality of petrographic thin sections. Selected sections were briefly etched by diluted HCL, rinsed carefully, and stained with 5% toluidine blue for a few seconds. The depth of penetration of euendolithic filaments per species was measured using the drawing tube attached to the compound microscope. Rare filaments (<5) of some species scattered deep inside the coral skeleton and were, therefore, not considered in the estimation of the averages depth of penetration.

Quantification of the Relative Abundance of Euendoliths

The other piece of coral skeleton cut per slice (≈1 cm^3) was used to quantify the relative abundance of the different species of euendoliths in communities and the surface area of CaCO$_3$ dissolved by the euendolithic microorganisms at the surface of blocks. Twenty pictures were randomly taken at the upper surface of each piece using a SEM (surface area of 20 pictures ≈0.45 cm^2) and were analyzed by image analysis using the software Visilog 5.1. (two pieces were analyzed per block; $n=40$ pictures per block). The number of pictures ($n=40$) taken per block necessary to represent the whole surface area of blocks was determined as part of a preliminary study (unpublished data) where the upper and lateral sides of blocks were studied. On each picture, the different traces of microbioerosion were visible. Those traces (microborings) were attributed to each identified species or group of euendoliths using the size classes of microborings determined previously.

The relative abundance of the species or group of euendoliths i (%) was calculated by dividing the number of borings of this species by the total number of microborings per picture (RA$_i$ in %).

The total surface area of substrate bioeroded by all euendolithic microorganisms (S_t) was measured using Visilog 5.1. To obtain the surface area of CaCO$_3$ dissolved by the species i (S_i in cm^2), RA$_i$ was multiply by S_t (cm^2); the diameter of microborings of the species i being taken into account in the calculation. That way, the role in the microbioerosion process of a species showing abundant but thin filaments was not overestimated, and the role of a species presenting a few but large filaments was not underestimated.

Then, the surface area bioeroded by each species obtained on the small pieces of coral was extrapolated to the whole surface area of the upper and lateral sides of each block (initial slice dimensions known). In this study, the bottom side of each slice was not considered because euendoliths on this side were exposed to different microenvironmental conditions (low light intensity, no sedimentation, no grazing pressure by fish, and sea urchins) than on the sides and top of blocks in situ.

Calculation of Microbioerosion Rates

Rate of microbioerosion for the euendolithic species i, per block, was obtained using the following equation:

Rate of microbioerosion

$$= \frac{S_i(\mathrm{cm}^2) \times Dp_i(\mathrm{cm}) \times d(g\,cm^{-3}) \times 10^{-3}}{S_{\mathrm{block}}(\mathrm{m}^2) \times \mathrm{time(either\ 1\ or\ 3\ years)}}$$

where d is the coral skeleton density and S_{block} is the surface area of the top and lateral sides of a block. Rates of microbioerosion were expressed in kg of CaCO$_3$ eroded per square meter of exposed surface area to colonization after 1 and 3 years of exposure. Total microbioerosion rates were calculated by adding the different rates of microbioerosion of each species.

Statistics

Data sets were tested for normality and homoscedasticity using frequency histograms and Cochran's test [49]. The following data sets were transformed by log $(x+0.01)$ to show a normal distribution [49]: coral skeleton densities, filament diameters, percentage of surface area bored by euendoliths at the surface of blocks (total and per species), and rates of microbioerosion (total and per species). A series of analysis of variance (ANOVA; one-way, two-way crossed and three-ways nested ANOVAs) with equal or unequal replication were performed on those different sets of data to test their variation among blocks of a grid, between grids within a site, among sites, and over time (after 1 and 3 years of exposure) [51]. Subsequently, multiple comparisons of means according to Student–Newman–Keuls (SNK) test [51]

Table 1 Diameter of filaments of the principal euendolithic species (μm)

Species/category	1 Year (μm)	3 Years (μm)
Mastigocoleus testarum	5.8±0.7	5.3±1.1
Ostreobium quekettii	4.3±1.0	4.5±1.1
Fungi	1.8±0.3	1.9±0.3
Plectonema terebrans	1.4±0.3	1.4±0.3

Means and standard deviation are indicated per species or category (*n*=100 filaments per species or category)

were used to determine which means was different from each other (α=0.05). A two-way crossed analysis of similarity (ANOSIM), testing sites and years (1997 and 1999), was conducted using PRIMER 5.2.9 [11] to determine if differences in species composition of euendolithic communities occurred among sites and between years.

The mean values and standard deviation (SD) of each variable for each block (or colony in the case of coral skeleton density) were calculated using the statistical packages Statview 5.0 [52] and Super ANOVA 1.11 [53].

Results

Euendolithic Communities

The euendolithic microflora in experimental blocks of *Porites* sp. consisted of an assemblage of several species (Fig. 2), principally the cyanobacteria *Plectonema terebrans* Bornet & Flahault and *Mastigocoleus testarum* Lagerheim, the chlorophyte *Ostreobium quekettii* Bornet & Flahault, and undetermined filaments of fungal hyphae. A few filaments of the chlorophyte *Phaeophila dendroides* Crouan et Crouan were also observed as well as rare unidentified filaments of chlorophytes.

Filaments of *P. terebrans* and *M. testarum* showed narrow size distribution expressed here as mean±SD (1.4±0.3 and 5.5±0.9 μm, respectively). In contrast, the diameter of *O. quekettii* filaments showed more variability ranging between 3 and 6 μm with an average of 4.4±1.1 μm. Filaments of fungi had an average diameter of 1.9±0.3 μm, and the unidentified chlorophytes showed always a diameter larger than 10 μm. Filament diameters of *O. quekettii*,

Figure 3 Relative abundance (%) of each species or group of microborers in the euendolithic communities after one (**a**) and three (**b**) years of exposure. *Others* Other chlorophytes than *Ostreobium quekettii*.
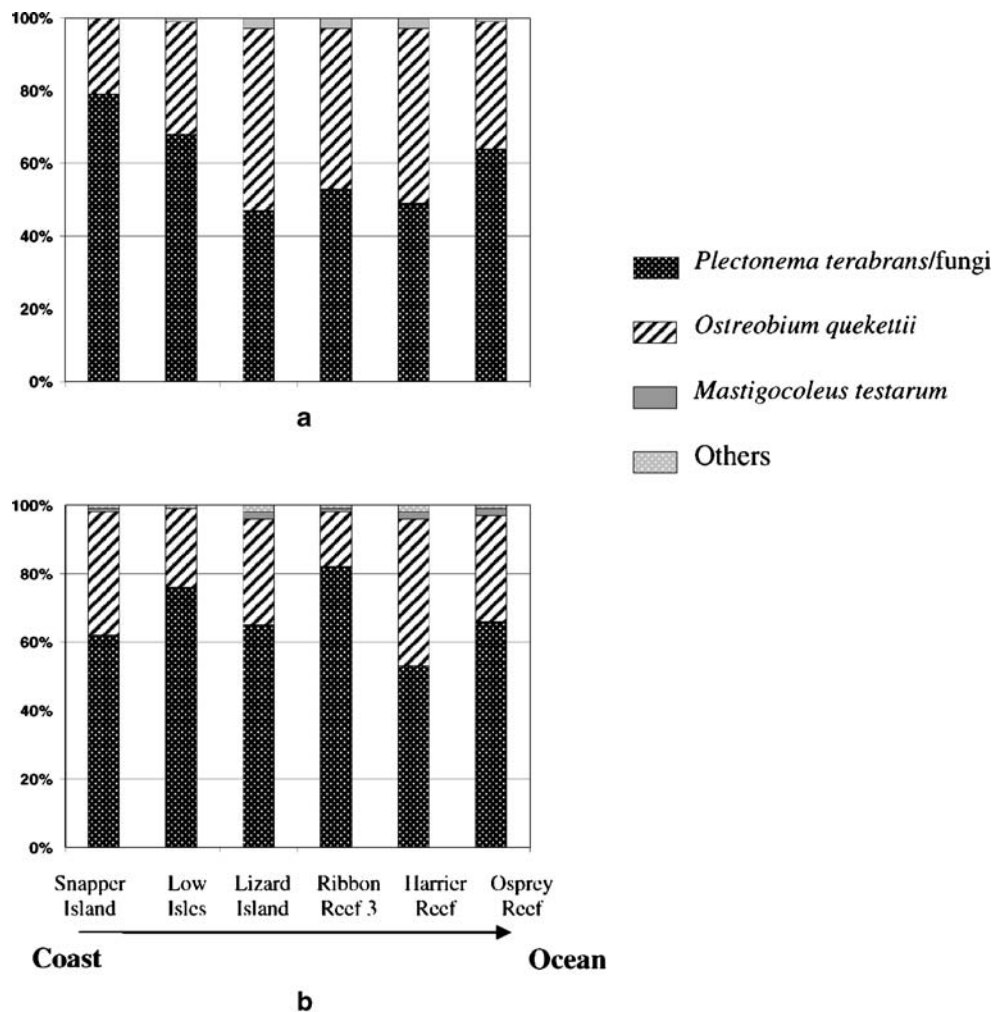
P. terebrans, *M. testarum*, and fungi were significantly different from each other (*p*<0.0001, Table 1). The size of microborings of *P. terebrans* and fungi were too similar to be easily distinguished on SEM images; therefore, they constituted a single class. Thus, a total of four size classes of microborings could be recognized and observed as resin casts using SEM (*O. quekettii*, *M. testarum*, *P. terebrans*/fungi, 'Others' comprising the unidentified chlorophytes).

The species composition of communities (i.e., the relative abundance of each species of euendolith in the community) did not vary significantly among sites and over time (ANOSIM *R*<0.14; Fig. 3). After 1 year of exposure, filaments of *P. terebrans* and fungi dominated euendolithic communities followed by *O. quekettii*. *M. testarum* was always a minor component in communities (1–3%), as well as the undetermined chlorophytes (<0.4%). After 3 years of exposure, a similar trend was observed with filaments of *P. terebrans* and fungi dominating euendolithic communities with 53% at Ribbon Reef 3 to 82% at Harrier Reef (Fig. 3).

Distribution of the Euendolithic Filaments Inside Coral Skeletons

Depths of penetration of euendolithic filaments varied significantly among species and sites (two-way ANOVA with cross-classification, *p*<0.0004; Fig. 4). After one year of exposure, filaments of *M. testarum* had the lowest depth of penetration (0.13±0.06 mm at Snapper Island to 0.81±0.74 mm at Osprey Reef), while filaments of *O. quekettii* had the highest (0.56±0.33 mm at Snapper Island to 4.14±1.47 mm at Osprey Reef). Filaments of fungi were encountered in most cases as deep in carbonate substrates as those of *O. queketti*. Depth of penetration increased from inshore reefs to offshore reefs and was especially pronounced at Osprey Reef (Fig. 4). After 3 years of exposure, the depth of penetration of filaments of *M. testarum* remained the lowest (0.55±0.27 mm) and that of *O. quekettii* and fungi, the highest (2.56±2 and 2.54±1.8 mm, respectively). The latter were not significantly different and averaged together 2.55±1.8 mm. The depth of penetration of *M. testarum* was similar at all sites (0.44±0.15 mm) except at Ribbon Reef 3 and Harrier Reef (SNK test) where it was higher (0.75±0.22 mm). The same trend was observed for *P. terebrans*. Depths of penetration of fungi and *O. quekettii* filaments were lower at the inshore reefs than at the offshore reefs (the four offshore sites were pooled together by the SNK test).

All depths of penetration increased significantly between the first and the third year of exposure (two-way ANOVA with cross-classification, *p*<0.0001) at all sites, except for those of *M. testarum* which did not change (*p*=0.62; Fig. 4).

Surface Area of Block Bioeroded by Euendoliths (%)

There were no significant differences in the surface area of blocks bioeroded by euendoliths among sites after 1 year (three-way nested ANOVA, *p*=0.13) and 3 years of exposure (three-way nested ANOVA, *p*=0.14). From 21.8±6.4% to 32.1±6.4% of the surface area of blocks was bioeroded by euendoliths after 1 year of exposure (27.8±7.6% on average) and between 25.6±8.6 and 39.7±6.1% after 3 years of exposure (32.7±8.1% on average) (Table 2). In contrast, the analyses of variance highlighted differences between grids of a site (*p*<0.01) and among blocks within a grid

Figure 4 Depth of penetration of filaments of each euendolithic species, after 1 year (**a**) and 3 years (**b**) of exposure.
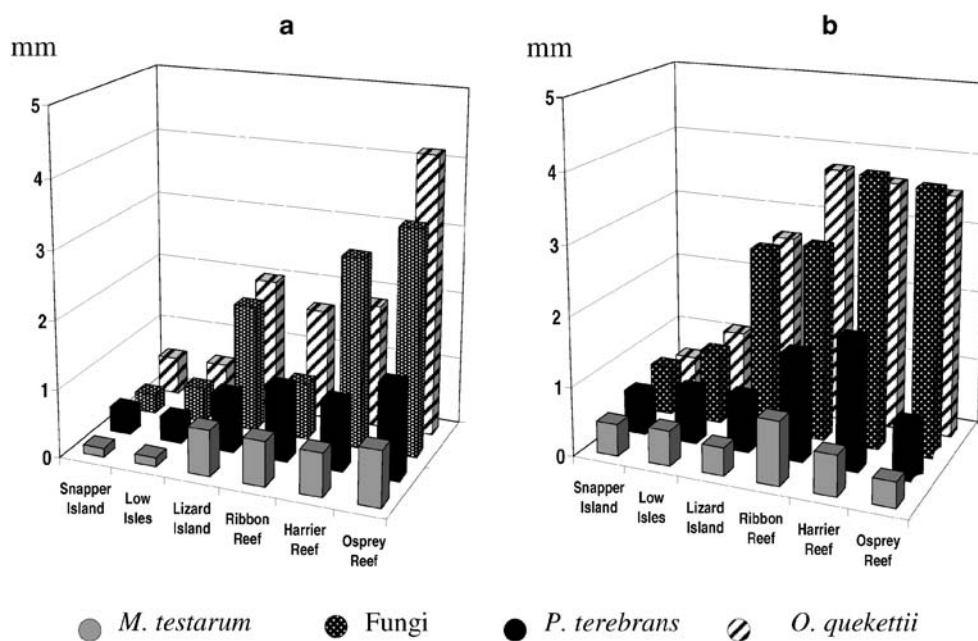
Table 2 Surface area of block bioeroded by euendoliths (%) after 1 and 3 years of exposure

Sites	1 Year (%)	3 Years (%)
Snapper Island	21.8±6.4	32.3±6.9
Low Isles	26.0±5.8	39.7±6.1
Lizard Island	32.1±6.4	31.6±5.5
Ribbon Reef 3	24.9±8.3	25.6±8.6
Harrier Reef	31.0±6.5	31.8±7.3
Osprey Reef	31.1±6.1	35.1±6.8

Means and standard deviations are given per site ($n=160$ pictures analyzed per site)

($p<0.002$). More than 65% of this small-scale heterogeneity was due to the variability of the surface area bioeroded by euendoliths within a block as recorded from SEM images (distribution patchiness).

There was a significant increase of the surface area bioeroded per block between 1997 and 1999 (two-way ANOVA with cross-classification, $p<0.0001$). The significant interaction between factors 'site' and 'length of exposure' ($p<0.0001$) and the associated SNK test highlighted that this increase was significant only at the inshore sites (Table 2); increase by a factor 1.5. At the other sites, the surface area bioeroded per block was constant over time (Table 2).

Rates of Microbioerosion

After 1 year of exposure, rates of microbioerosion due to *Plectonema terebrans*/fungi did not vary significantly among sites (three-way nested ANOVA, $p=0.29$; average rate of 0.1 ± 0.1 kg m^{-2} year^{-1}; Table 3) while those of *Ostreobium quekettii* and *Mastigocoleus testarum* did vary among sites ($p<0.001$; Fig. 5). However, rates of microbioerosion due to *M. testarum* were so low that the spatial variability among sites is negligible; rates varied between 0.00002 and 0.0003 kg CaCO$_3$ eroded m^{-2} year^{-1} at

Snapper Island and Harrier reef, respectively (Table 3). Microbioerosion by *O. quekettii* significantly increased from inshore reefs to offshore reefs (0.09 ± 0.1 kg m^{-2} year^{-1} at Snapper Island and 1.12 ± 0.53 kg m^{-2} year^{-1} at Osprey reef; Fig. 5). Variability of microbioerosion rates at small spatial scales (grids, blocks) was highlighted by three-way nested ANOVAs. More than 47% of this heterogeneity resulted from variability of rates measured from SEM images. Similarly to rates of microbioerosion due to *O. quekettii*, total microbioerosion rates varied significantly among sites ($p=0.004$) and among blocks within a grid ($p<0.0001$). The lowest rate was found at Snapper Island (0.13 ± 0.1 kg m^{-2} year^{-1} or 0.6% of the block volume eroded), while the highest rate was recorded at Osprey reef (1.35 ± 0.6 kg m^{-2} year^{-1} or 5.3% of the block volume eroded). The chlorophyte *O. quekettii* was responsible for 70 to 90% of the total microbioerosion (Fig. 5). In contrast, *M. testarum* contribution was negligible (less than 0.1%).

After 3 years of exposure, similar trends to those obtained after a year of exposure were found for rates of microbioerosion due to *P. terebrans*/fungi and all euendoliths (total microbioerosion). Rates of microbioerosion due to *O. quekettii* did not vary among sites ($p=0.05$), while those due to *M. testarum* varied among sites ($p<0.0001$). Although the *p*-value for rates of microbioerosion due to *O. quekettii* was close to the limit of significance ($\alpha=0.05$), rates increased slightly from 0.15 ± 0.1 at Snapper Island to 0.96 ± 0.54 kg m^{-2} year^{-1} at Osprey reef (Table 3; Fig. 5). Microbioerosion due to *M. testarum* was also low at Snapper Island and high at Osprey reef (Table 3). For all rates, the ANOVAs revealed a significant variability of microbioerosion at the small spatial scale (among blocks within a grid essentially). After 3 years of exposure, total microbioerosion was mostly due to the activity of *O. quekettii* (60 to 90%; Fig. 5). The contribution of *M. testarum* was still negligible (<2%).

All rates of microbioerosion varied among sites ($p<0.0001$) and increased between 1997 and 1999 ($p<0.0001$)

Table 3 Rates of microbioerosion (per species and total) after 1 and 3 years of exposure (kg CaCO$_3$ eroded m^{-2} after 1 and 3 years)

Sites	1 Year (kg m^{-2} year^{-1})				3 Years (kg m^{-2} 3 years^{-1})			
	M. t.	P.t./fungi	O.q.	Total	M. t.	P.t./fungi	O.q.	Total
Snapper Island	1E^{-05}±1E^{-05}	0.04±0.04	0.09±0.06	0.13±0.13	0.003±0.01	0.07±0.05	0.15±0.06	0.23±0.07
Low Isles	3E^{-05}±5E^{-05}	0.04±0.04	0.11±0.07	0.16±0.16	0.001±0.01	0.19±0.14	0.35±0.22	0.54±0.22
Lizard Island	2E^{-05}±3E^{-05}	0.06±0.06	0.64±0.36	0.70±0.70	0.01±0.02	0.20±0.17	0.67±0.33	0.89±0.29
Ribbon Reef 3	2E^{-05}±3E^{-05}	0.04±0.04	0.32±0.17	0.36±0.18	0.01±0.02	0.09±0.14	0.86±0.49	0.96±0.51
Harrier Reef	3E^{-05}±3E^{-05}	0.13±0.14	0.62±0.38	0.75±0.41	0.01±0.02	0.53±0.46	0.88±0.65	1.42±0.82
Osprey Reef	2E^{-05}±4E^{-05}	0.23±0.25	1.12±0.53	1.35±0.48	0.01±0.01	0.32±0.32	0.96±0.54	1.29±0.75

Means and standard deviations are given per site ($n=4$ blocks per site).
M.t. Mastigocoleus testarum, *P.t./fungi* Plectonema terebrans/fungi, *O.q.* Ostreobium quekettii, *Total* addition of microbioerosion rates due to the different euendoliths, E^{-05} 10^{-5}
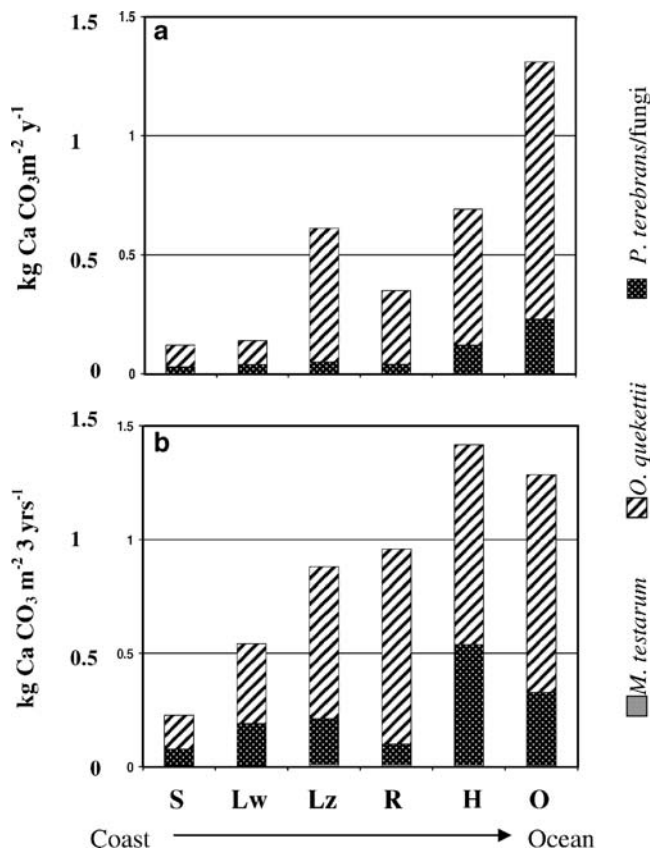
Figure 5 Rates of bioerosion for each species of microborers and rates of total microbioerosion after 1 year (**a**) and 3 years (**b**) of exposure. *S* Snapper Island, *Lw* Low Isles, *Lz* Lizard Island, *R* Ribbon Reef 3, *H* Harrier Reef, *O* Osprey Reef.

except at Osprey reef where they remained relatively constant. The analyses of variance revealed a significant interaction between the two factors ($p < 0.0001$). Therefore, the increase of microbioerosion rates was different, depending on the site studied. The contribution of each euendolithic species also changed over time and along the transect. The contribution of *Plectonema terebrans*/fungi to rates of total microbioerosion increased at all sites between 1997 and 1999. *Ostreobium* contribution was relatively constant over time. *Mastigocoleus'* contribution remained negligible.

Discussion

Characteristics of Euendolithic Microflora

The use of experimental blocks of cleaned coral skeletons of massive *Porites* to quantify rates and progression of microbioerosion provides a better approximation of processes occurring on dead corals and coral rubble than experimental substrates such as Iceland spar crystals [31]. Iceland spar crystals were used by Kobluk and Risk [31] to

avoid initial microbioerosion. In this study, experimental blocks cut in the middle of large live colonies of massive *Porites* showed negligible initial microbioerosion rates (only rare microborings were observed using SEM). Most of borings inside live coral colonies were probably cemented or filled with new aragonite resulting from processes of remineralization and diagenesis [43]. Massive *Porites* was used because it is generally abundant in Atlantic and Pacific reefs, especially on the Great Barrier Reef, and it is a natural habitat for euendolithic microorganisms. Extrapolations of the euendolithic community's characteristics (species composition, distribution, rates of erosion) studied for one specific substrate such as *Porites*, to coral reefs as a whole, have limitations. It has been shown indeed that bioerosion varies largely between carbonate substrates [38, 47, 55]. Several studies of bioerosion have been, however, carried out with massive *Porites*, thus, allowing for comparison of the results.

Cleaned and newly exposed substrates become colonized by microbial biofilms followed by a succession of epilithic and euendolithic microorganisms [19, 28]. After 1 year of exposure, the dominance of *P. terebrans*, *O. quekettii*, and fungal filaments in communities was established at all sites as it did not change after 3 years of exposure. Gektidis [19] and Tribollet and Golubic [57] showed that about a year is required for stabilization of the microbioeroding community. Gektidis [19] showed that one of the factors controlling colonization of carbonate substrates by euendoliths is light availability, which decreases when water depth increases and decreases over time (see [41]). After more than 6 months, epilithic organisms overgrow dead substrates, whereby shading the euendoliths [19, 57]. Then, euendolithic species which are able to grow under low light intensities (i.e., oligophotic species) such as *P. terebrans* and *O. quekettii*, become dominant in euendolithic communities. Our inshore sites were exposed to high rates of sedimentation so that the light reaching euendoliths inside coral skeleton was limited by a layer of sediments (2–3 mm thick) accumulated on the top of the blocks [56]. The presence of such layers of mud had a similar effect on euendolithic species composition as the epilithic algal layers overgrowing offshore blocks.

Microbial assemblages composed of *P. terebrans*, *O. quekettii*, and fungi are considered 'mature' according to Gektidis [19] and are commonly reported in tropical coastal environments [44, 45]. The euendolithic communities reported here were similar to those found at Lee Stocking Island (Bahamas) in micrite [60] and in French Polynesia in 6-month-old blocks of *Porites* [9], in dead colonies of *Porites* [34], in shells [38] and in encrusting coralline red algae [55] collected under diverse environmental conditions.

The cyanobacterium *Mastigocoleus testarum* was a minor component in euendolithic communities (less than

4%), especially at the inshore reefs (≤1%). This species is known as a pioneer species that is abundant in dead carbonate substrates only in early stages of bioerosion [9, 19]. Moreover, it is a species that requires considerable light intensities [33], and does not tolerate high variation in salinity [15]. Salinities at Snapper Island and Low Isles were subject to variation mostly due to run offs from Daintree River [6]. The presence of M. testarum in experimental blocks on offshore reefs may have been promoted by grazing activity [57]. Tribollet and Golubic [57] found indeed important grazing rates at the offshore reefs (0.53 kg m^{-2} after 1 year of exposure and 4.80 kg m^{-2} after 3 years of exposure vs 0.01–0.31 kg m^{-2} after 1 and 3 years, respectively, at the inshore reefs). Removal of the substrate surface by grazers, which feed on epiliths and euendoliths [7], frees new surface areas for euendolithic pioneers to colonize [28, 57], although excessive grazing pressure such as at Osprey Reef (0.68 kg m^{-2} after 1 year and 4.23 kg m^{-2} after 3 years of exposure; [57]) may inhibit the development of a pioneer euendolithic community dominated by cyanobacteria such as Mastigocoleus testarum [19]. Only mature euendolithic communities can keep up with excessive grazing as they are present deep inside coral skeletons and move like a front through the substrates until they reach their new depth of compensation (photosynthesis = respiration) [50].

In addition to its effects on the species composition of euendolithic communities, light controls the depth of penetration of filaments into carbonate substrates. At the same water depth (≈10 m), the depth of penetration of euendolithic filaments increased from the coast of Queensland to the Coral Sea following different patterns of penetration into coral skeletons depending on the euendolithic species. The oligophotic species, O. quekettii and P. terebrans, were able to penetrate down to 4 mm into carbonate substrates, while species requiring high light intensities such as M. testarum and the unidentified chlorophytes, were never observed at more than 0.81 mm deep inside substrates (Osprey Reef). Such patterns are comparable to bathymetric distribution of these organisms [41]. P. terebrans and O. quekettii have been observed at more than 300 m depth [30, 36], while M. testarum was found only in shallow waters [19, 33, 60]. The depth of penetration of M. testarum in blocks of this study corresponds well to that found in similar substrates in French Polynesia (0.77 mm; [9]). In contrast, it is higher than the ones measured in calcite (0.20 mm) in the Mediterranean Sea [33] and in bivalve shells (0.06 mm) in French Polynesia [38]. The depth of penetration of O. quekettii measured in our 3-year-old blocks (2.55 mm on average) is also similar to the one found in experimental blocks exposed 2 years to colonization in French Polynesia (2.73 mm; [8]). It is interesting to notice that fungal filaments

follow a similar pattern as filaments of O. quekettii. Fungi are heterotrophs, and thus, are independent to light. They depend on organic matter [24] and are often observed in association with O. quekettii. It has been suggested that euendolithic fungi use O. quekettii as a source of food [4, 34, 35, 55].

The gradient of depths of penetration observed, increasing from inshore reefs to offshore reefs, reflects the availability of light along transect on the northern Great Barrier Reef. Euendolithic filaments did not penetrate deep inside coral skeletons at Snapper Island and Low Isles because of turbid waters, a layer of mud deposited on top of blocks and a low grazing pressure [6, 57]. Russ [48] showed that grazing fish abundance is less important at inshore reefs than at offshore reefs on the Great Barrier Reef, which may account for the low grazing pressure at Snapper Island and Low Isles [57]. The gradient of depth of penetration was more pronounced for O. quekettii and P. terebrans than for M. testarum. The high light intensity specialist M. testarum reached more quickly its depth of compensation (<1 mm). Depths of penetration of euendoliths also varied over time. They increased between the first and the third year of exposure, especially that of O. quekettii. Such increase is due to changes in environmental conditions such as the increase of grazing pressure and abundance of large borings due to macroborers [57]; both allowing light to penetrate deeper into coral skeletons.

Microbioerosion Pattern

Microbioerosion rates in dead substrates depend on the depth of penetration of euendolithic filaments and their density in substrates; those parameters varying with the species composition of communities and the relative abundance of species. In this study, microbioerosion rates were probably underestimated for two reasons. First, the quantification of microbioerosion did not take into account the possible ramifications of euendolithic filaments inside substrates. Second, microbioerosion rates represent here a net or 'residual' microbioerosion, whereas the gross microbioerosion rates include the part of substrate which has been removed by grazers [9, 57]. Those rates can be, however, compared among sites and over time, and with rates found in the literature when similar protocols were used.

Microbioerosion increased with the distance from the coast, mainly because rates of microbioerosion due to O. quekettii dominated the process along transect. Filaments of O. quekettii contributed for 60 to 90% to microbioerosion. In this experiment where 'mature/stable' euendolithic communities were observed, the principal variable influencing rates of total microbioerosion was the depth of penetration of euendolithic filaments, especially that of O. quekettii, which varies with environmental conditions as

shown above (inshore–offshore gradient). The percentage of surface area bioeroded on top of blocks was constant among sites and compared well with those found by Chazottes *et al.* [9] in French Polynesia (31% after 2 years of exposure). This study confirms at a larger scale, Chazottes *et al.* [9] observations about the infestation of coral block surfaces by euendoliths, which becomes maximal within a year. At the early stages of bioerosion and in shallow waters where the cyanobacterium *Mastigocoleus testarum* and large chlorophytes such as *Phaeophila dendroides* dominate euendolithic communities [9, 34, 60], the pattern of microbioerosion is expected to depend on the most abundant euendoliths which show the largest diameter (i.e., *M. testarum* and *P. dendroides*).

In the present study, rates of microbioerosion quantified after 1 and 3 years of exposure were on average 3- to 25-fold higher than those found by Chazottes *et al.* [10] at La Reunion after 1 year of exposure (0.04 to 0.07 kg $CaCO_3$ m^{-2} $year^{-1}$) and by Chazottes *et al.* [9] in French Polynesia after 1 and 2 years of exposure (0.14 to 0.40 kg CaCO3 m^{-2}, respectively). Part of the discrepancy between results may be due to the use of different techniques for microbioerosion quantification. But most probably, the discrepancy results from the different types of grazing that blocks experience in both studies. At La Reunion and in French Polynesia, grazers are mostly echinoids, while they are fish at the six studied sites on the GBR [56]. Echinoids are known to be more efficient grazers than fishes [see 26]; at La Reunion and in French Polynesia rates reached more than 3.5 and 1.7 kg m^{-2} $year^{-1}$, respectively, while the highest grazing rate quantified at the offshore reefs on the Great Barrier Reef was 0.5 kg m^{-2} $year^{-1}$ on average [57]. Thus, residual microbioerosion rates at la Reunion and in French Polynesia were much lower than on the Great Barrier Reef. In this study, rates were also much higher than those found by Tudhope and Risk [59] in sediments at Davies Reef (0.35 kg m^{-2} $year^{-1}$), and by Vogel *et al.* [60] in various carbonate substrates including *Porites* skeletons at Lee Stocking Island and at One Tree Island (<0.6 kg m^{-2} $year^{-1}$). Those differences are due to the nature of substrates (see [40]), the water depth at which experiments were carried out, and the different techniques of quantification of microbioerosion. In addition, rates found by Vogel *et al.* [60] were obtained after 6 and 5 months of exposure, respectively, and were then extrapolated per year. Tribollet and Golubic [57] showed that rates of bioerosion (including microbioerosion) do not increase proportionally and linearly with length of exposure, and therefore, they should not be extrapolated per year. Based on rates expressed per year, Vogel *et al.* [60] concluded that microbioerosion did not increase over time at most of the studied sites, which is opposite to the trends obtained in the present study. After recalculation of microbioerosion rates found at Lee Stocking

Island (after 3 months, 6 months, 1 year, and 2 years), I found that microbioerosion did increase over time until it reached a stable state after more than 6 months of exposure. This increase was also not proportionally nor linearly; rates were cumulative over time. Those results show that a good estimation of microbioerosion rates (a) cannot be expressed per year unless rates are quantified in experimental substrates exposed to colonization during one year and (b) should take into account species composition of euendolithic communities, the relative abundance, and the depth of penetration of filaments of each species.

Until the recent study of Tribollet and Golubic [57], microbial euendolithic organisms were considered as a negligible agent of bioerosion except at the early stages of colonization of dead carbonate substrates [9, 10]. Tribollet and Golubic [57] showed that euendoliths are the main agents of bioerosion in synergy with grazers, over time, and especially in tropical clear waters. Important development of euendolithic communities supported high rates of grazing at offshore reefs, while a lower development of euendoliths accounted for a low grazing pressure on dead coral substrates at inshore reefs. Inversely, low grazing pressure limits, among other factors (see above), the development in depth of euenedolithic communities. Therefore, total bioerosion rates increased with distance from shore on the northern Great Barrier Reef. The present study strengthens results of Tribollet and Golubic [57] about microbioerosion pattern along the studied transect, and highlights for the first time, the importance of the euendolithic oligophotic chlorophyte *Ostreobium quekettii* in this long-term process. A similar role has been suggested for this microscopic chlorophyte in live corals, as it is the dominant euendolith in communities in those substrates [34]. Tudhope and Risk [59] suggested that a rate of microbioerosion of 0.35 kg m^{-2} $year^{-1}$ contributes 18–30% of the global flux of sediments in the lagoon of Davies Reef. Therefore, rates of microbioerosion and especially rates due to *O. quekettii* found in the 'pristine reefs' as represented by offshore reefs in this study, may contribute greatly to the flux of sediments and the export of carbonates from those reefs to the open ocean [13, 27]. I suggest that the boring microflora including *O. quekettii* has a significant impact on the overall calcium carbonate budget of coral reef ecosystems, and probably in coastal environments in general, due to its wide distribution and abundance in carbonate substrates.

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