The boring microflora in modern coral reef ecosystems: a review of its roles

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Abstract. Euendolithic microorganisms (boring microflora) – cyanobacteria, algae and fungi – colonize all carbonate substrates in modern coral reefs and are distributed worldwide. Recent studies showed that in dead carbonate, they are important primary producers and are fed upon by various excavating invertebrate and vertebrate grazers, contributing greatly to biodestruction processes (bioerosion) and sedimentation. Additionally, it has been shown that in some live calcifying organisms, they either inflict damages to live tissues or provide a benefit to the host, depending on the euendolithic community involved (parasitic or mutualistic relationships). Based on those recent studies, the following question is raised: Are euendoliths key organisms in the functioning and maintenance of coral reefs? Reviewed literature includes studies on (1) the mechanisms used by euendoliths to penetrate into carbonate substrates (production of acids or chelating fluids; use of the products of photosynthesis / respiration and / or calcium pumps), (2) their roles in reef bioerosion and sedimentation (major roles), (3) their metabolism (important rates of production), (4) their interactions with their live hosts (symbiosis, mutualism and / or parasitism) and (5) the effects of various environmental factors such as eutrophication, sedimentation and rising atmospheric pCO_2 on euendolith activities. The review concentrates on modern coral reef ecosystems.

Keywords. Boring microflora, bioerosion, environmental factors, euendoliths, modern coral reefs, production, symbiosis

Introduction

Boring autotrophic and heterotrophic microorganisms or euendoliths (boring microflora) actively penetrate (biochemical dissolution) into the interior of the hard substrates they inhabit (Golubic et al. 1981). In contrast, the chasmoendoliths colonize fissures and cracks in substrates while the cryptoendoliths colonize structural cavities within porous substrates, including spaces produced and vacated by euendoliths (Golubic et al. 1981). Some euendoliths can show an epilithic or chasmoendolithic stage in their life cycle (Golubic et al. 1975; Kobluk and Risk 1977; Jones and Goodbody 1982). The term 'endolith' includes the euendoliths, chasmoendoliths and cryptoendoliths.

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Euendoliths live in various substrates such as carbonates (Schneider and Torunski 1983; Mao Che et al. 1996; Tribollet and Payri 2001; Tribollet and Golubic 2005), glass (Jones and Goodbody 1982), apatite (Königshof and Glaub 2004) and granite (De Los Rios et al. 2005). They are observed in terrestrial (Friedmann et al. 1988; Ascaso et al. 1998; Golubic and Schneider 2003), freshwater (Schneider et al. 1983; Anagnostidis and Pantazidou 1988) and marine ecosystems including the Adriatic Sea (Ghirardelli 2002), the Mediterranean Sea (Le Campion-Alsumard 1979), cold-temperate coasts (Wisshak et al. 2005), Antarctic (De Los Rios et al. 2005) and tropical waters (Le Campion-Alsumard et al. 1995a; Radtke et al. 1997a; Perry 1998; Tribollet 2007). On marine limestone coasts, carbonate rock surfaces can be infested by more than half a million euendolithic filaments per square cm (Schneider and Le Campion-Alsumard 1999).

Euendoliths have long geological histories, having been identified within substrates from Mesoproterozoic (Zhang and Golubic 1987), Neoproterozoic (Knoll et al. 1986) and Paleozoic strata (Klement and Toomey 1967; Campbell 1980; Golubic et al. 1980; Königshof and Glaub 2004). The first record of euendolithic cyanobacteria was found in 1.5 billion year old stromatolite rocks in China (Zhang and Golubic 1987). As a result, they are believed to have played a major role in the production and destruction of carbonate, including reef framebuilders and sediments, over long periods of geological time. The well fossilized microborings of euendoliths are used as proxies in paleoecological and paleobathymetrical studies (Chazottes et al. 1995; Radtke et al. 1997b; Perry and MacDonald 2002; Glaub and Vogel 2004; Radtke and Golubic 2005) as their diversity, distribution and abundance depend on substrates and environmental conditions (Gektidis 1999; Radtke et al. 1997a; Vogel et al. 2000; Tribollet 2007). They are also used for ichnological and ichnotaxonomic determinations (Glaub and Vogel 2004; Chacón et al. 2006). Those studies are based on comparisons between modern and fossilized microborings. Thus, it is important to better understand euendolith ecological characteristics as well as their metabolism in modern environments in order to improve our knowledge on the past environmental conditions and to better predict the future.

Coral reefs are maintained when constructive forces (reef framebuilders growth and calcification) are balanced with destructive forces (mainly bioerosion including boring microflora, macroborers and grazers). These ecosystems are increasingly threatened by anthropogenic and natural stresses such as overfishing, sedimentation, eutrophication, rising seawater surface temperature and atmospheric pCO_2 (Edinger et al. 1998, 2000; Kleypas et al. 1999; Langdon et al. 2000; Szmant 2002; Hallock 2005). These factors increase coral bleaching events, the rate of coral mortality and can favor shifts from coral-dominated reefs to algal-dominated reefs (Mumby et al. 2001; Szmant 2002; Wilkinson 2004). More and more dead substrates are, therefore, available for colonization by euendoliths and other agents of bioerosion. When bioerosion rates exceed accretion rates, the degradation of reef framework is accelerated (Hutchings 1986; Sheppard et al. 2002). Reefs are then even more subject to damage by cyclones and storms (Harmelin-Vivien 1994) putting in jeopardy the survival of coastal and insular human populations.

Recently, a few studies showed the necessity of studying simultaneously constructive and destructive processes in coral reefs in order to estimate their state of health under different environmental conditions (Edinger et al. 2000; Risk et al. 2001; Tribollet and Golubic 2005; Harborne et al. 2006; Mallela and Perry 2007). Euendoliths play a role in those different processes but have received much less attention than other organisms involved, such as corals, macroborers and grazers. Boring microflora is well known to colonize live and dead carbonate substrates although colonization is more intense in dead ones (Le Campion-Alsumard et al. 1995a; Radtke et al. 1997a; Perry 1998; Tribollet and Payri 2001; Tribollet 2007). Through their activity, they are known to inflict damages to their live hosts or to provide benefits to them, to be important primary producers in dead substrates, to prepare substrates for macroborers, to attract excavating invertebrate and vertebrate grazers in a combined bioerosion activity, to enhance fine sediment production and to alter sediment grains (Kobluk and Risk 1977; Hutchings 1986; Bruggemann et al. 1994; Chazottes et al. 1995; Bentis et al. 2000; Perry 2000; Fine and Loya 2002; Tribollet et al. 2002; Tribollet and Golubic 2005; Chacón et al. 2006; Tribollet et al. 2006a). But what are the contributions of euendoliths in those processes at the reef scale and under various environmental conditions?

To my knowledge there is no review summarizing the different roles played by boring microflora in modern coral reef ecosystems. Hutchings (1986) published a review on bioerosion processes including the erosive activity of boring microflora, while Radtke et al. (1997b) provided a bibliographic overview of micro- and macrobioerosion. More recently Schneider and Le Campion-Alsumard (1999) provided a review on processes of construction and destruction of carbonates by aquatic cyanobacteria including marine euendolithic cyanobacteria. The purpose of the present paper is to highlight the main functions played by boring microflora in coral reefs and their consequences on the functioning of those ecosystems. The variability of euendolith activities in space and over time will also be discussed and perspectives will be suggested. The present contribution does not pretend to be exhaustive. It is based on 162 references and highlights the most recent studies on the topic.

Diversity of the boring microflora

Boring microflora comprises cyanobacteria, algae (chlorophytes, rhodophytes) and fungi. Their taxonomy has been studied for decades (Bornet and Flahault 1889; Lukas 1974; Le Campion-Alsumard 1979; see also literature review by Kobluk and Kahle 1977) but new species are still being discovered, especially since the emergence of molecular tools (Al-Thukair and Golubic 1991; Chacón et al. 2006). Recently, Komárek and Anagnostidis (1999, 2005) published a determination manual on cyanobacterial diversity (Oscillatoriales) including endolithic cyanobacteria. Kendrick et al. (1982), Porter and Lingle (1992), Bentis et al. (2000) and Golubic et al. (2005) provided information on euendolithic fungi but their taxonomy remains relatively unknown.

The most common genera of autotrophic euendoliths observed in coral reef substrates around the world are the chlorophytes *Ostreobium* Bornet and Flahault, 1889 and *Phaeophila* Hauck, 1876 (Fig. 1A, 1B), the rhodophyte *Porphyra* Agardh, 1824 (Conchocelis stage) and the cyanobacteria *Hyella* Bornet and Flahault, 1888, *Mastigocoleus* Lagerheim, 1886 (Fig. 1C), *Plectonema* Thuret in Gomont, 1892 (Fig. 1D) and *Solentia* Ercegovic, 1927 (Raghukumar et al. 1991; Chazottes et al. 1995; Le Campion-Alsumard et al. 1995a; Gektidis and Golubic 1996; Golubic et al. 1996; Radtke et al. 1997a; Perry 1998; Gektidis 1999; Vogel et al. 2000; Tribollet and Payri 2001; Tribollet 2007). Lukas (1973) has documented the ubiquitous nature of the siphonale *Ostreobium quekettii* Bornet and Flahault, 1889 infestation in corals, occurring at 100% frequency in Atlantic and Pacific corals. However, there might be more than one species of *Ostreobium* involved (Lukas 1974). The phylogeny of this chlorophyte (Bryopsidale) is poorly known (Woolcott et al. 2000) and seems to show different lineages (pers. comm. H. Verbruggen).

Species composition of euendolithic communities varies between live and dead substrates. In the skeleton of live corals and crustose coralline algae, the dominant euendoliths are *Ostreobium quekettii*, *Plectonema terebrans* Bornet and Flahault, 1889 and fungi (Lukas 1974; Le Campion-Alsumard et al. 1995a; Tribollet and Payri 2001). However, Conchocelis were found very abundant in some skeletons of live corals from Caribbean coral reefs (Laborel and Le Campion-Alsumard 1979). The species composition of microbial euendoliths in those live substrates is a result of a selection in favor of oligophotic, positively phototrophic, fast-growing taxa which can follow the accretion rate of skeletons. Such an infestation occurs at the early stage of the calcifying organism's growth, and starts from the substrate of fixation. Following the death and denudation of corals and crustose coralline algae, a new colonization by euendoliths occurs at the surface of skeletons. Thus, the species composition of communities changes dramatically and a succession of communities is observed over time (Gektidis 1999). Short-lived opportunistic pioneer species such as *Mastigocoleus testarum* Lagerheim, 1886 and *Phaeophila dendroides* Crouan (Batters, 1902) are observed in substrates within a few days (Hutchings 1986; Le Campion-Alsumard et al. 1995a; Gektidis 1999). Then after 6 to 12 months, euendolithic communities become dominated by the low-light specialists (sciaphile species), *O. quekettii* and *P. terebrans,* as well as by heterotrophic fungi (Chazottes et al. 1995; Le Campion-Alsumard et al. 1995a; Gektidis 1999; Tribollet and Golubic 2005; Tribollet 2007). Those communities are called 'mature communities' (Le Campion-Alsumard et al. 1995a; Gektidis 1999; Tribollet 2007). Changes in species composition of euendolithic assemblages in dead substrates is primarily due to light availability which varies with depth (bathymetry) and over time due to the growth of epilithic organisms providing shade to euendoliths (Gektidis 1999; Tribollet 2007). Chazottes et al. (2002) showed that *M. testarum* is particularly abundant in dead *Porites lobata* Dana, 1846 under turf algae while the assemblage of *P. terebrans*, *M. testarum* and *O. quekettii* prevails under crustose coralline algae and phaeophytes (*Lobophora* Agardh (Womersley, 1987)).

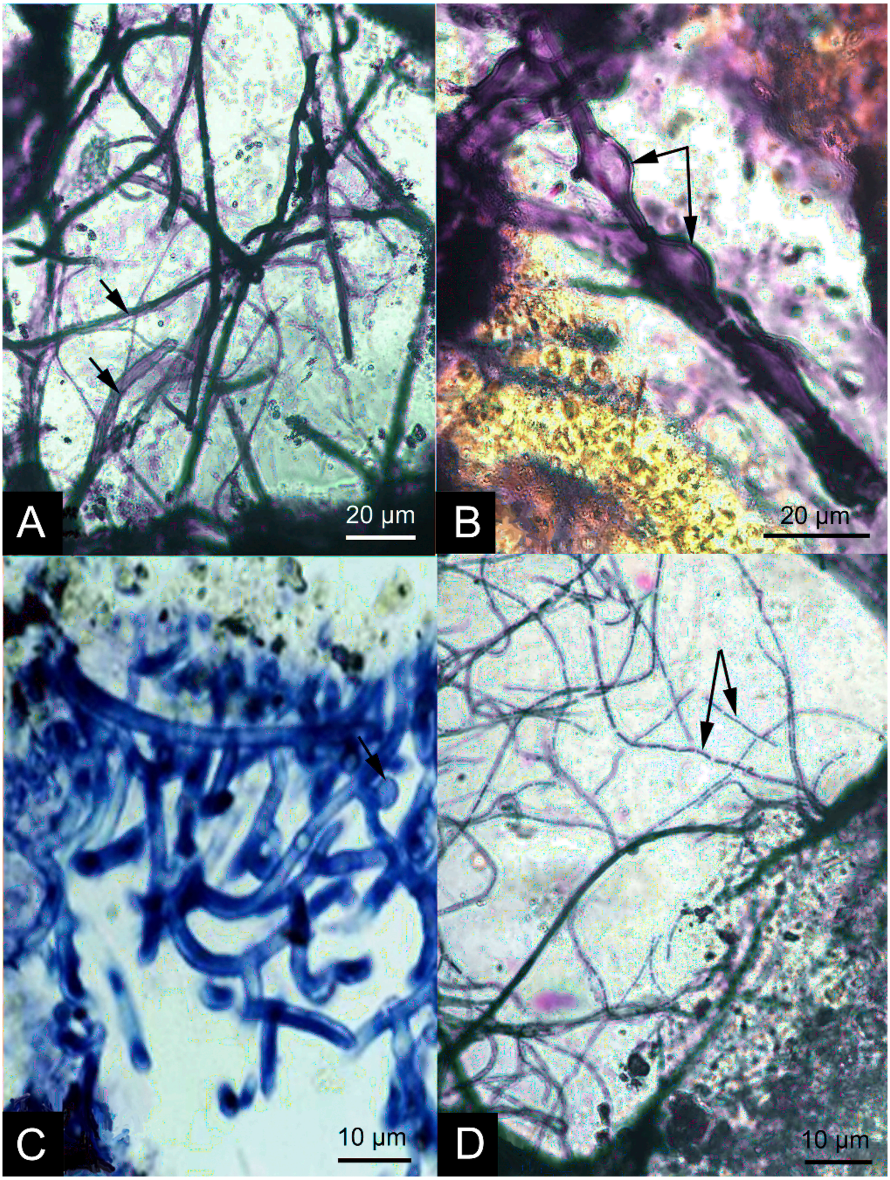

Fig. 1 Different species of euendoliths stained with Toluidine blue and determined on petrographic thin sections of the dead coral *Porites lobata*. **A** Filaments of the chlorophyte *Ostreobium quekettii* (black arrows). Thin filaments penetrating into filaments of the chlorophyte are fungal hyphae. **B** Filaments of the chlorophyte *Phaeophila dendroides* (arrows show cells). **C** Filaments of the cyanobacterium *Mastigocoleus testarum* (arrow shows a heterocyste). **D** Filaments of the cyanobacterium *Plectonema terebrans* (arrows show cells)

Differences in community species composition may result from the effects of grazing pressure. Grazers remove the surface of substrates, more or less intensively, creating new surfaces available for colonization by pioneer euendoliths and allowing light to penetrate deeper inside substrates. Crustose coralline algae and phaeophytes are less palatable than turf algae for grazers (Bruggemann et al. 1994; Chazottes et al. 2002), therefore substrates covered by those epilithic organisms are less grazed, which limits the colonization by pioneer species such as *M. testarum*. When grazing is too intense, immature assemblages of euendoliths do not develop and only mature communities are observed penetrating deeper inside coral skeletons (Schneider and Torunski 1983; Tribollet 2007). The effects of environmental factors such as eutrophication and freshwater inputs on species composition of euendolith communities are, however, relatively unknown. Ercegovic (1930) observed that *Mastigocoleus testarum* does not tolerate high variation in salinity. The effects of those factors as well as the interactions between grazers, epilithic organisms and euendolithic assemblages need to be more studied in order to better understand the spatial and temporal variability of the boring microflora activities (erosion and production).

Process of penetration into substrates

It is not clear why euendoliths evolved to live inside hard substrates. Paleontologists cannot answer clearly this question but the same hypothesis implied for decades is: unoccupied ecological niche providing protection against sunlight, grazers and desiccation (Schneider and Le Campion-Alsumard 1999).

Euendolithic autotrophs penetrate rapidly into new available substrate by dissolving chemically its crystals (Tudhope and Risk 1985; Fig. 2A). They leave

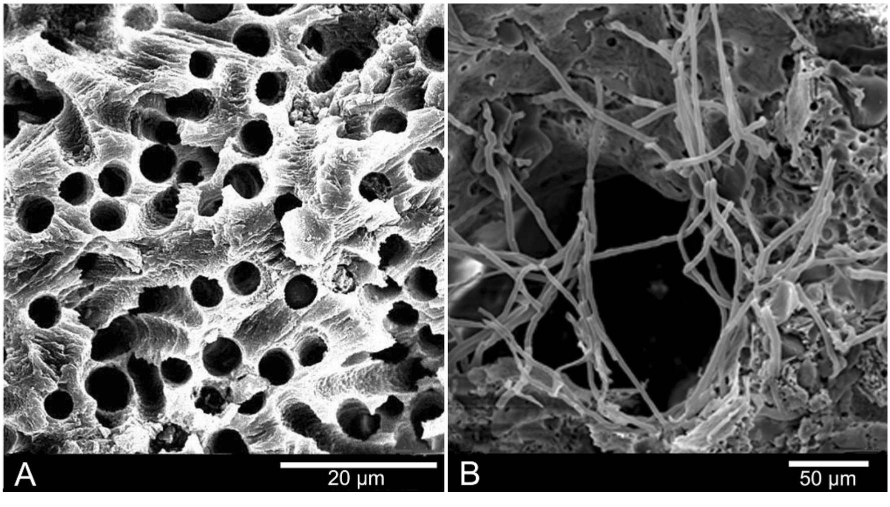

Fig. 2 Pictures of the surface of dead corals taken by SEM, showing: **A** Traces of microbioerosion due to filaments of *Ostreobium quekettii*. **B** Filaments of *Ostreobium quekettii* penetrating into coral skeleton

microborings (1-100 μm in diameter) which conform to the shape of their thalli (Fig. 2B). Crystals of substrates show a specific arrangement around microborings suggesting a precisely controlled excavating process (Alexandersson 1975; Golubic et al. 1975; Le Campion-Alsumard 1975, 1979). This process is poorly understood. It has often been suggested that substrate dissolution results from the production of acid or chelating fluids at the apical cell of euendolithic filaments (Le Campion-Alsumard 1975; Golubic et al. 1984), and even involves organelles (Alexandersson 1975). The dissolution process in coral reefs occurs in waters saturated or supersaturated with respect to aragonite and calcite, and is thermodynamically unfavorable. Excavation must thus be performed at the cost of cellular energy.

Recently, Garcia-Pichel (2006) suggested other mechanisms to explain dissolution of carbonate substrates by euendolithic cyanobacteria. Those mechanisms are (1) a temporal separation of photosynthetic and boring activities during the daily cycle (dissolution due to the CO_2 produced during respiration at night), (2) a spatial separation of photosynthetic and boring activities, and (3) the use of calcium pumps. A combination of those mechanisms is possible but the use of calcium pumps seems the most probable mechanism. Garcia-Pichel (2006) showed that an active transport of Ca^{2+} from the apical cell of euendolithic filaments to their trailing end would make dissolution thermodynamically favorable around the apical cell while interstitial pH is high due to photosynthesis. This is consistent with the known range of bored substrates including aragonite, calcite, granite and hydroxylapatite, and with precipitation of micrite and brucite observed around euendolithic filaments at the surface of dead substrates. Kobluk and Risk (1977) showed that micrite is precipitated inside and around dead filaments of *Ostreobium quekettii* after they protruded at the surface of dead carbonate substrates (filaments partially epilithic). Those authors could not explain the process involved in the micrite precipitation but suggested that *'something peculiar in the composition of Ostreobium filaments and probably of some others, facilitates precipitation'*. If euendolithic chlorophytes possess Ca^{2+} pumps like euendolithic cyanobacteria, the Ca^{2+} pumped at the apical cell and released at the other extremity of filaments (i.e., at the surface of carbonate substrates) may create the conditions necessary to induce precipitation of carbonates (micrite) at ambient pH. Le Campion-Alsumard (1978) found higher calcium contents in euendolithic cyanobacterial filaments as compared with epilithic forms. Moreover, Nothdurft et al. (2005) suggested that euendoliths allow precipitation of brucite in scleractinian corals while ambient seawater of coral reefs is undersaturated in brucite. The model proposed by those authors to explain such a precipitation follows: (1) semiconfined intracorallum spaces contain dead organic matter and live filaments of cyanobacteria, algae and fungi, (2) photosynthetic removal of CO_2 lowers the pCO_2 and increases the pH, leading to aragonite precipitation on organic matter or synthaxially on exposed skeletal aragonite, (3) aragonite precipitation lowers Ca^{2+} activity, thereby increasing the local Mg / Ca ratio, (4) increased pH due to degradation of organic matter (possibly by bacteria or fungi) produces excess of OH^-, leading to localized brucite precipitation. The increase of Mg / Ca ratio may in fact result from the decrease of Ca^{2+} in the boring microenvironment due to calcium pumps, thus creating favorable conditions for brucite precipitation under high pH. Elevated pH (>9) has been measured inside coral heads by Risk and Kramer (1981) during the day while lower pH was quantified under dark conditions by Risk and Muller (1983) due to endoliths respiration. Nevertheless, it is possible that other mechanisms are involved in substrate dissolution by euendoliths. In Antarctic desertic sandstones (arkosic / feldspar), euendoliths (in lichen: *Plectonema*) seem to penetrate by secreting oxalic acids, which require the mobilization of inorganic nutrients such as iron and potassium (Edwards et al. 1997; Russell et al. 1998). Euendolithic fungi, which are heterotrophic, penetrate both mineral substrates but also organic matter using digestive enzymes (Golubic et al. 2005). Processes involved in substrate dissolution by euendoliths as a whole may vary depending on taxa and species, the type of substrate and environmental conditions.

Distribution of the boring microflora

Type of substrates

Euendoliths penetrate all kinds of reef carbonate substrates such as live and dead corals (Le Campion-Alsumard et al. 1995a, 1995b; Tribollet 2007), crustose coralline algae (Tribollet and Payri 2001), calcifying macroalgae such as *Halimeda* Lamouroux, 1812 (Perry 2000), foraminifera (Golubic et al. 1984; Perry 1998), shells (Radtke 1993; Mao Che et al. 1996; Radtke and Golubic 2005), sediments (Tudhope and Risk 1985) and limestone (Le Campion-Alsumard 1979; Reaka-Kudla et al. 1996; Vogel et al. 2000). Infestation of dead substrates is always higher than in their live counterparts due to the new colonization of their surface by euendoliths (Le Campion-Alsumard et al. 1995a; Tribollet and Payri 2001). Moreover, Perry (1998) showed that coral sediments are more infested than those of molluscs, foraminifera, *Halimeda*, crustose coralline algae and echinoids. The structure, porosity and skeletal mineralogy of calcifying organisms influence euendolith infestation (Perry 1998; Chacón et al. 2006).

Depth of penetration in substrates – light dependence

In live and accreting reef framebuilders, such as corals and coralline algae, phototrophic as well as heterotrophic euendoliths are located beneath the layer of live tissue and keep up with the calcification rates of their hosts. For example, the chlorophyte *Ostreobium quekettii* usually forms mm-thick green colored bands beneath the surface of massive coral skeletons (Le Campion-Alsumard et al. 1995a), and some filaments have been observed in contact with polyps (Kanwisher and Wainwright 1967; Schlichter et al. 1995). Heterotrophic fungi maintain their presence close to the polyps, as they attack both algae and the polyps (Le Campion-Alsumard et al. 1995b; Bentis et al. 2000; Priess et al. 2000).

In dead corals, the depth of penetration of euendolithic filaments varies depending on the species. Species requiring high light intensities such as *Mastigocoleus testarum* do not penetrate deep into substrates (<1 mm in dead *Porites lobata*;

Chazottes et al. 1995; Tribollet 2007). In contrast, oligophotic species such as *Plectonema terebrans* and *Ostreobium quekettii* show a depth of compensation of 2 to 4 mm in dead *Porites lobata* (Chazottes et al. 1995; Tribollet 2007). Heterotrophic fungal filaments are independent of light and use the euendolithic chlorophytes and the residual organic matter in coral skeletons as a source of food (Bentis et al. 2000; Golubic et al. 2005; Tribollet 2007). The depth of penetration of euendolithic filaments in dead substrates correspond to their bathymetric distribution. Euendoliths are found from the intertidal and wave spray zones of marine environments to abyssal depths (see Golubic et al. 1984, 2005), yet individual species are restricted to special environments and water depths due to their light requirements. *M. testarum* is always found in shallow waters (Gektidis 1999; Vogel et al. 2000) while *O. quekettii* and *P. terebrans* can be observed at more than 300 m depth (Lukas 1978; Kiene et al. 1995). Diversity of euendoliths is higher in shallow waters than at depth (Perry 1998, 2000; Gektidis 1999). In general, the bathymetric distribution of euendolithic assemblages in coral reefs has been well documented and will not be detailed here (see Golubic et al. 1975; Kiene et al. 1995; Radtke et al. 1996; Radtke et al. 1997a; Gektidis 1999; Hoffmann 1999; Vogel et al. 2000).

Factors affecting the depth of penetration of euendolithic filaments in substrates

Depth of penetration of euendolithic filaments varies from species to species but also with the nature of the substrate and environmental conditions. For example, in shallow waters, depths of penetration are lower in bivalve shells than in coral skeletons (<0.1 mm; Mao Che et al. 1996; Perry 1998). This probably results from the difference in substrate architecture, porosity and respective translucency of the substrate. It was shown that at 10 m depth, the depth of penetration of euendoliths in experimental blocks of *Porites lobata* increased from inshore to offshore reefs on the northern Great Barrier Reef (GBR); inshore reefs showed turbid and eutrophic waters and a low grazing pressure. This gradient was particularly evident for *O. quekettii* (0.6 to 4.1 mm with distance from shore; Tribollet 2007). Development of euendolithic communities at inshore reefs was probably limited by the entrapment of sediments within epilithic turf algal filaments, thus restricting the light availability. Depths of penetration of euendoliths also increased over a three year period due to the increase of grazing pressure (see Schneider and Torunski 1983) and the presence of larger holes made by macroborers (they increased the amount of light penetrating deep inside substrates). This trend was less pronounced for *M. testarum*, which reaches its depth of compensation (photosynthesis = respiration) more rapidly than the oligophotic euendoliths (after one year). Tribollet (2007) showed that the depth of penetration of euendolithic filaments is the main variable affecting rates of microbioerosion in dead substrates exposed more than one year to bioerosion; the level of infestation at the surface of substrates being stable. This first study implies the necessity of studying more the effects of biotic and abiotic factors on the euendolith vertical distribution inside substrates over long periods of time to better understand the spatial and temporal variability of microbioerosion.

Boring microflora: roles in processes of bioerosion and sedimentation

Microbioerosion and sedimentation

By dissolving calcium carbonate (microbiocorrosion), the boring microflora recycles ions of calcium and carbonate which are used by calcifying organisms for their growth and calcification. Euendoliths also disintegrate the substratum into smaller particles which are then more susceptible to dissolution and abrasion (Schneider and Le Campion-Alsumard 1999). The pattern of boring is not random and determines the size of sediments produced by grazers or physical erosion (Schneider and Torunski 1983). Fine-grain sediments are usually produced with a size below 125 µm (most of the material falls into the 20-63 µm class). Part of the new sediment produced by bioerosion contributes to the sandy areas of the seafloor whereas another part is entrapped and cemented into the coral reef structure (Perry 2000). The rest is exported into the open ocean. About half of the sediment produced in shallow areas may be exported (Hubbard et al. 1981; Eakin 1996).

Sediment grains on the sea floor of shallow marine environments are colonized by euendolithic communities (Perry 1998), which contribute to their destruction by dissolving calcium carbonate (Kobluk and Risk 1977; Schneider and Le Campion-Alsumard 1999; Perry 2000). Euendoliths participate greatly to early diagenesis of sediments (Perry 1998, 2000). Tudhope and Risk (1985) estimated microbioerosion rates of 0.35 kg $CaCO_3$ dissolved per m^{-2} y^{-1} in sediments at Davies Reef (Australia). Similar rates were found in dead coral skeletons of *Porites lobata* on an oligotrophic reef at Moorea in French Polynesia (0.14 kg m^{-2} y^{-1}; Chazottes et al. 1995). But rates found in this substrate vary greatly depending on grazing pressure and other factors. Microbioerosion rates quantified by Chazottes et al. (2002) at different reefs of La Reunion Island after one year of exposure were lower than 0.07 kg m^{-2} y^{-1} because of intense grazing by echinoids on substrates (3.5 kg m^{-2} y^{-1}). Those estimated on the northern Great Barrier Reef were much higher (0.13 kg m^{-2} y^{-1} at inshore turbid reefs to 1.3 kg m^{-2} y^{-1} at offshore oligotrophic reefs), with grazing primarily by fish (0.5 kg m^{-2} y^{-1}; Tribollet and Golubic 2005; Tribollet 2007). Echinoids are known to be more efficient grazers than fishes (Hutchings 1986; Reaka-Kudla et al. 1996; Harborne et al. 2006).

Rates of microbioerosion measured in dead carbonate substrates using microscopy techniques and image analysis (see Chazottes et al. 1995; Tribollet and Golubic 2005) are ‘residual’ rates (underestimated rates), i.e., the difference measured after the removal of euendolith-affected layers by grazers. Since the carbonate loosened by microbial euendoliths and removed by grazers cannot be quantified, the observed rates are underestimated relative to the total rates of microbial bioerosion. Interactions between grazers and euendoliths have been described by several authors (see Schneider and Torunski 1983; Chazottes et al. 1995; Tribollet and Golubic 2005). The latter authors showed a positive correlation between grazing and microbioerosion rates at a large spatial scale (inshore-offshore transect along 200 km of the GBR). Phototrophic euendoliths provide a renewable food source for grazers (e.g., gastropods, echinoids and fishes). They make substrates attractive for grazers and by weakening the surface of substrates they facilitate grazing rates. On the other hand, by constantly removing the surface of substrates, grazers extend the depth to which the light can penetrate in substrates and therefore, the depth of compensation of euendoliths (Schneider and Torunski 1983). But low rates of 'residual' microbioerosion prevail when grazing pressure is too intense and catches up with microbioerosion. However, such conditions have a regulatory effect by requiring re-colonization and re-establishing of a primary trophic level for grazers. On the other hand, low rates of microbioerosion were quantified at inshore reefs on the northern Great Barrier Reef because waters at those reefs were turbid (Tribollet and Golubic 2005). Lots of particles in suspension and a thin layer of mud (2-3 mm) deposited at the surface of the studied blocks of *Porites lobata*, limited the development of euendolithic communities while it allowed the important development of macroborers which were mostly filter feeders. Grazing rates were also low at those reefs, with population of fishes (Russ 1984) and their food source (epilithic and endolithic flora) being less abundant (Tribollet and Golubic 2005). Rates of microbioerosion vary also among substrates because infestation by euendoliths depends on this factor as seen earlier (see also Vogel et al. 2000; Zubia and Peyrot-Clausade 2001; Carreiro-Silva et al. 2005; Tribollet and Golubic 2005). In mussel shells, infestation by euendoliths can be so intense that it causes sub-lethal or lethal effects on mussel populations inducing changes in growth and reproduction output (see example of *Perna perna* on the coast of South Africa: Kaehler and McQuaid 1999).

Finally, rates of microbioerosion increase over time but not linearly nor proportionally – they are cumulative over time – as shown by Chazottes et al. (1995) and Tribollet and Golubic (2005) in experiments carried out over two to three years. In higher latitudes there are probable significant seasonal differences in bioerosion rates which need to be assessed in more detail. In order to create a model of microbioerosion, and more generally a model of bioerosion (= macrobioerosion + microbioerosion + grazing), carbonate destruction by agents of bioerosion has to be studied under different environmental conditions and over long time periods.

Effects of eutrophication on microbioerosion rates

A few attempts were made to study the effects of eutrophication (high concentration of nutrients) on microbioerosion but results are controversial. Kiene (1997) and Vogel et al. (2000) reported inconclusive results on the effect of eutrophication on microbioerosion of five month-old dead substrates in microatolls on the Great Barrier Reef (ENCORE experiment). Kiene (1997) suggested that boring microflora were already saturated in nutrients. But, this may also have resulted from the design of the experiment, the residence time of seawater charged with nutrients inside microatolls being very low (microatolls were flushed at each tide), as well as to grazing pressure (data were lacking). In contrast, Chazottes et al. (2002) found an increase of microbioerosion under eutrophic conditions at La Reunion Island but again the direct effect of this factor was not evident. Under eutrophic conditions, substrates were covered by macroalgae such as *Lobophora variegata* Lamouroux in Oliveira (Womersley, 1987) and encrusting coralline algae. Those algae are less attractive to grazers. Thus, high rates of microbioerosion may be due to low grazing pressure and protection from epilithic algae. Inversely, Zubia and Peyrot-Clausade (2001) found higher rates of microbioerosion in dead skeletons of acroporids under eutrophic conditions outside damselfish territories than inside damselfish territories. In this study, the time of exposure to bioerosion was unknown and could have influenced rates of microbioerosion; branches of coral may have been exposed longer to bioerosion outside damselfish territories than those inside territories.

Other studies attempted to show that eutrophication affects microbioerosion but only the biomass of euendoliths mixed with epiliths was studied (Le Bris et al. 1998; Pari et al. 1998, 2002). Microbioerosion rates are due to the accumulation of borings of euendoliths over time. Measuring the biomass of boring microflora at one particular time gives an idea of the euendolithic community present in substrates at that specific time and not of the succession of different communities over time. Moreover, measurements of boring microflora biomass are not accurate as they include the biomass of the coral residual organic matter and of small heterotrophic organisms.

Only Carreiro-Silva et al. (2005) really showed that microbioerosion increases under high concentrations of nutrients (Glovers Reef, Belize) on a short period of time (49 days), and that this effect varies with grazing intensity. Inorganic nutrients were the strongest factors increasing microbioerosion by a factor of 10 in the absence of macrograzers (0.06 kg m^{-2} $CaCO_3$ eroded after 49 days under fertilized conditions versus 0.0007 kg m^{-2} after 49 days under unfertilized conditions). Microbioerosion rates were of course lower as they were residual when macrograzers had access to substrates (shells). In this experiment, nutrients were released slowly underneath substrates and not in the water column as in the ENCORE experiment on the Great Barrier Reef (Kiene 1997). This suggests that boring microflora may respond only to nutrient inputs in their close environments and are probably not influenced by nutrient pulses in the water column (problem of the boundary layer at the surface of substrates, dilution in the water column and water residence time). Further studies should be carried out to better understand the impact of eutrophication on microbioerosion rates. How are euendolithic communities affected by eutrophication (changes of community species composition and metabolism)? Are there any thresholds of nutrient concentrations? Is the increase of microbioerosion rates under eutrophic conditions maintained over time?

Effects of other factors on microbioerosion rates

Eutrophication is a major issue in conservation of coral reefs but it is not the only one. One important question being increasingly asked by coral reef scientists is how the rise of atmospheric partial pressure of CO_2 will affect coral reefs? By 2065-2100, the atmospheric pCO_2 should be doubled according to the forecast by the Intergovernmental Panel on Climate Change (Houghton et al. 1996). Several studies showed that calcification rates of reef framebuilders will decrease by 30-40% on average by 2065 due to the decrease in the aragonite saturation state (Borowitzka 1981; Kleypas et al. 1999; Hallock 2005; Tribollet et al. 2006b). Kleypas et al. (2001) concluded that a shift in saturation state projected for 2065 *'will shift many reefs from a net carbonate accumulation to net carbonate loss'*. Halley et al. (2005) showed that sediment dissolution increases under elevated concentration of CO_2. They suggested that this may result from the activity of boring microflora colonizing sediments but no direct proof has been provided. The question is: do euendoliths have the potential to buffer coral reef seawater under elevated pCO_2? Langdon et al. (2000) suggested that dissolution of carbonates would not compensate the acidification of coral reef seawater but considered only a maximal rate of dissolution measured by night. Anderson et al. (2003) suggested similarly that dissolution will not be enough to buffer waters of shallow environments including reefs. But those authors used a simplified model with only two major domains: surface-water and pore-water sediment domains. First of all, euendoliths probably dissolve carbonate by day and by night using different mechanisms as seen earlier (Ca^{2+} pumps by day and products of respiration by night). Secondly, boring microflora dissolve all carbonate substrates in coral reefs and not just sediments. It has been shown recently that those microorganisms are one of the main agents of bioerosion in coral reefs. Chazottes et al. (1995) showed that they are the main agents at the early stage of the bioerosion process (≤1 year) studying simultaneously all agents, i.e., microborers, macroborers and grazers at the reef of Tiahura (Moorea, French Polyensia). Tribollet et al. (2002) and Tribollet and Golubic (2005) confirmed this result at a larger scale on the northern Great Barrier Reef and showed that the important role of boring microflora is maintained over time. After a 3 years experiment, euendoliths are still contributing between 20% and 40% to total bioerosion (total bioerosion of more than 6 kg m^{-2} after three years at oligotrophic reefs). Tribollet (2007) found that the chlorophyte *Ostreobium quekettii* was the main agent of microbioerosion in blocks of *Porites lobata* exposed more than a year to bioerosion on the northern GBR, dissolving more than 1 kg of $CaCO_3$ m^{-2} y^{-1}. A similar role for this euendolith was suggested before by Le Campion-Alsumard et al. (1995a) in live colonies of *Porites lobata* as it is the most abundant euendolith. At the scale of coral reefs, *Ostreobium quekettii* is probably the most important agent of microbioerosion and therefore, plays a crucial role in reefal carbonate dissolution as a whole as it is ubiquitous in all kinds of carbonate substrates, in shallow and deep waters, and all around the world. This role may be even greater in the near future as the number of substrates available for colonization increases as a consequence of the rise of reef framebuilder mortality rate, due to diseases (coral and crustose coralline diseases), predators (e.g., Crown-of-Thorns starfish), sedimentation, rising sea surface temperature and many other factors (Goreau et al. 1998; Wilkinson 2004; Hallock 2005; Voss and Richardson 2006). The effects of elevated atmospheric pCO_2 and other factors such as rising sea surface temperature and UV on euendolith activities should receive more attention in the next few years if the overall effect of those factors on coral reef functioning is to be understood. Such research is a prime topic with biological and geological implications.

Boring microflora: important primary producers?

In 1955, Odum and Odum were the first to suggest that euendolithic oxygenic phototrophs are one of the main primary producers in coral reefs. Their assumption was based on endolithic biomass (including euendolithic biomass) and chlorophyll a concentration quantified in live corals (endolith biomass represented 81% of the total biomass of live corals on average). Their conclusion when extrapolated to the reef scale assumes a 100% cover by healthy growing corals, which is rarely the case. In contrast, Kanwisher and Wainwright (1967), Shibata and Haxo (1969) and Shashar and Stambler (1992) suggested a rather limited contribution of euendoliths in live corals to primary production amounts to less than 4% of the total activity of live corals (see also Schlichter et al. 1997). These authors measured the oxygen production of euendoliths in live coral colonies maintained in tanks or chambers, the absorption spectra of those phototrophs and the spectral distribution using various sensors. In order to assess the metabolism of euendoliths in the interior of coral skeleton, it is essential to measure the available light.

Light intensity inside substrates

To date, measurements of light intensity inside substrates were only carried out in live corals. In those substrates, the amount of light reaching euendoliths is limited by (i) the absorption of incidental light by zooxanthellae in the coral tissue, (ii) internal architecture of the coral skeleton and (iii) water depth. Enriquez et al. (2005) showed that coral endosymbionts (zooxanthellae) of *Porites branneri* Rathbun, 1887 are able to collect more than 85% of solar radiation with one order magnitude less pigment density than terrestrial leaves. This is due to multiple scattering by the skeleton which enhances the local light field (absorption increased). This would leave less than 15% of light for euendoliths. Only 1% of the Photosynthetically Active Radiation (PAR) was estimated to reach the layer of euendoliths within the skeleton of the coral *Favia pallida* Dana, 1846 in Australia by Halldal (1968) and Shibata and Haxo (1969); 0.1% of light between 340 nm and 680 nm penetrates into coral skeleton, as well as 1% and 2% at 700 nm and 720 nm, respectively. Schlichter et al. (1997) estimated that 3.9% of white, 3.8% of blue, 3.6% of green, and 6.4% of red light penetrate skeletons of deep corals in the Gulf of Aqaba. But in this case, light absorption by live coral tissues only was measured (skeleton of samples was removed), which may introduce an error in the calculation of the amount of light reaching euendoliths. Direct measurements of light intensity and wavelengths reaching the layer of euendoliths, and in general endoliths, in skeletons of live and dead corals, and other live and dead carbonate substrates, for different water depths are lacking. However, the information thus far available shows that euendoliths live in extremely shaded environments.

Euendoliths are adapted to low light intensities

To be able to live inside carbonate substrates, euendoliths present a certain number of adaptations. They have specific cellular ultrastructures such as complex and thick sheaths, well developed thylakoids and abundant cytoplasmic storage substances

(Le Campion-Alsumard 1976, 1979) and are able to absorb red and far red (peak at 730 nm) wave lengths using different forms of chlorophyll. Fork and Larkum (1989) and Koehne et al. (1999) showed that the genus *Ostreobium* including *O. quekettii,* possesses red-shifted chlorophylls. The antenna size is approximately 340 chlorophyll molecules (chlorophyll a and b) per PS II reaction center, which is significantly larger than in higher plants (~240). Additionally, euendoliths have high carbonic anhydrase and catalase activities (Shashar and Stambler 1992). The first enzyme transforms HCO_3^- into CO_2 (Weis et al. 1989) which is used by the RUBISCO for photosynthesis. During the day, euendoliths produce large amounts of O_2 (210% inside the skeleton of *Porites compressa* Dana, 1846 versus ambient seawater) which turns into H_2O_2 (Shashar and Stambler 1992). This hydrogen peroxide may inhibit CO_2 fixation (H_2O_2 is easily fixed by RUBISCO), destroy algal cellular membranes, damage their DNA and generate even more reactive oxygen species via metalcatalyzed reactions. The catalase catalyzes the reduction of H_2O_2 into H_2O and O_2. Such a catalase activity is a protecting mechanism for euendolithic filaments against reactive oxygen species; mechanisms which are also found in corals and their endosymbionts (Lesser and Shick 1989).

Those mechanisms and cellular ultrastructures change with environmental conditions. Koehne et al. (1999) showed that red-shifted chlorophylls (chlorophylls absorbing wavelengths >700 nm) are more abundant in euendolithic thalli deep inside skeletons than close to the white light at the surface of substrates. Shashar and Stambler (1992) and Schlichter et al. (1997) showed that concentration of pigments in *Ostreobium* vary depending on the illumination of the habitat (shaded versus lighted) and depth. With increasing depth, the ratio of chlorophyll b to chlorophyll a increases indicating improvement of light harvesting under low light conditions (Schlichter et al. 1997). Concentration of chlorophyll a can also vary with the type of substrate and species of coral. Endolithic chlorophyll a is much more abundant in dead corals (59 µg cm^2 which convert to 12 µg mL^{-1} of substrate; Tribollet et al. 2006a) than in healthy or bleached corals (4.6 µg cm^2 and 15 µg cm^2, respectively; Fine and Loya 2002) but less abundant than in bivalve shells (20 µg mL^{-1} of substrate; Raghukumar et al. 1991).

Euendolithic phototrophs seem to saturate at low light intensities which is another adaptation to their extreme environment. Shashar and Stambler (1992) suggested that euendoliths in live *Porites compressa* collected in 1-2 m depth are saturated at less than 160 µE m^{-2} s^{-1} external light, which corresponds to 1 µE m^{-2} s^{-1} inside skeleton (Shibata and Haxo 1969). Schlichter et al. (1997) suggested a light compensation of 10 µE m^{-2} s^{-1} for *O. quekettii* within skeletons of deep corals and a light saturation of 35-40 µE m^{-2} s^{-1}. In *Oculina patagonica* De Angelis d'Ossat, 1908 from shallow shaded waters along the coast of Israel, Fine et al. (2004) suggested that euendoliths saturate at 50 µE m^{-2} s^{-1} in healthy colonies (coral tissues + zooxanthellae) while they saturate at around 200 µE m^{-2} s^{-1} in bleached colonies (bleaching >40% of the colony), and no photoinhibition was observed at 850 µE m^{-2} s^{-1}. Those authors found that euendoliths photoacclimate to increased irradiance during a coral bleaching event. Fine et al. (2006) also showed euendolith photoacclimation in bare skeletons after corals were attack by the white syndrome (disease). However, in the case of a rapid bleaching event, euendoliths are photoinhibited by combined high light intensities and temperatures (Fine et al. 2005). This delays the recovery process of those phototrophs (Fine et al. 2005). The outcome of euendoliths in bleached coral seems to depend on two major parameters: (1) the microhabitat the coral lives in (back reef, reef crest, etc.) and (2) the response time of the coral host and its endosymbionts to the stress and recovery. Finally, Vooren (1981) found that endoliths, including *O. quekettii* and *P. terebrans*, were saturated at an external irradiance of 200 µE m^{-2} s^{-1} in dead corals. All those studies – while different techniques and substrates were used – show the same pattern: euendoliths are light saturated at low light intensities and are able to optimize the absorption of wavelengths available inside coral skeletons.

Production rates of endoliths (including euendoliths)

Although absorption spectra and spectral distribution of endolithic phototrophs in various substrates and under different environmental conditions need more investigation, there are a few indications that endoliths may be one of the main primary producers in coral reef environments. First of all, Bruggemann et al. (1994) showed that grazing fish feed preferentially on epilithic turf and endolithic algae. Endoliths are one of the main sources of food for grazers so they must be highly productive (Schneider and Torunski 1983; Hutchings 1986; Bruggemann et al. 1994; Chazottes et al. 1995; Tribollet and Golubic 2005). Schlichter et al. (1995) and Fine and Loya (2002) also showed that euendolithic communities can cover up to 30% of coral when bleached, which suggest that they are highly productive under those conditions. In the live hydrozoan *Millepora* (1-20 m depth), Bellamy and Risk (1982) found large volumes of oxygen trapped inside skeletons (69% of oxygen, 31% of molecular nitrogen and race CO_2) and attributed this production to euendolithic phototrophs. They compared volumes of O_2 in the morning and in the afternoon and found that there was net community photosynthesis (excess of O_2 produced over 24h). In dead substrates, Wanders (1977) determined that endoliths are the most important primary producers within the sparse vegetation on dead coral limestone. Wanders (1977) suggested that it might be *'an important feature in coral reefs that boring algae are present everywhere in the limestone substrate and whenever a primary producer disappears, its task as a primary producer is replaced by the boring algae which are present in the limestone beneath it'*. Vooren (1981) found similar results in natural substrates colonized by *Ostreobium* from Curaçao at 10-25 m depth (net photosynthesis ranging between 0.4-0.8 g C m^{-2} d^{-1}). Recently, Tribollet et al. (2006a) quantified that endoliths contribute at least 40% of the overall productivity of experimental blocks of the coral *Porites lobata* in shallow waters at Kaneohe Bay, Hawaii (3 m depth), with rates of net photosynthesis averaging 2.3 g C m^{-2} d^{-1}. Casareto et al. (2004) found the same participation (40%) in natural coral rubble in shallow waters at Bora Reef (Japan). Those values are probably underestimated as epilithic organisms such as encrusting coralline algae and bivalves, which are also colonized by endoliths, have been scraped off to quantify endolithic metabolism in dead substrates. The metabolism of endoliths quantified by Casareto et al. (2004) and Tribollet et al. (2006a) is comparable to that of turf algae and live corals (Kinsey

1985; Adey 1998). It is interesting to note that reef community production rates estimated in very diverse coral reef environments always fall within the same range (2-10 g C m^{-2} d^{-1} on average; Kinsey 1985). Endolithic metabolism might be one of the factors creating certain homogeneity in coral reef production, as they are ubiquitous, and show similar rates of production as corals and turf algae.

Spatial and temporal variability of production rates

The significance of the role played by endoliths in coral reef productivity may increase as coral bleaching events and the rate of coral mortality increase. But what are the effects of environmental factors such as rising sea surface temperature, rising atmospheric pCO_2, eutrophication and terrestrial inputs on boring microfloral metabolism? So far, rare studies investigated the effects of environmental factors on the endolithic metabolism.

Tribollet et al. (2006a) showed that production of endoliths varied along an inshore-offshore transect in Kaneohe Bay; the inshore and intermediate reefs showing low wave energy, more eutrophic and turbid waters than the offshore reef (high water motion, oligotrophic and clear water). Dead substrates from the offshore reef were covered mostly by encrusting coralline algae while inshore substrates were covered by turf algae and bivalves. Hydrodynamic energy is one major factor controlling the epilithic algal cover on dead substrates (Adey 1998) and influences the thickness of the boundary layer at the surface of substrates (Williams and Carpenter 1998). Those factors could explain why endolithic production was higher at the offshore reef. Moreover, endolithic productivity in dead corals and coral rubble is probably enhanced by eutrophication because Carreiro-Silva et al. (2005) showed that locally rates of microbioerosion in those substrates increase under such conditions. Microbioerosion or dissolution of calcium carbonate increases as a result of the rise of euendolithic filament growth. Studies of the direct effects of different concentrations of nutrients on euendolithic metabolism in live and dead carbonate substrates have to be carried out over time if the variability in space and time of total bioerosion rates is to be understood.

Tribollet et al. (2006b) also studied the effects of elevated atmospheric pCO_2 (750 ppm) on endolithic metabolism which included euendolithic metabolism. No effect was highlighted under controlled conditions over a three month period. Tribollet et al. (2006b) hypothesized that endoliths as a whole, under such conditions, may have been already at saturation or limited by nutrients in tanks. Further experiments are needed to determine precisely the effects of this factor on euendolithic metabolism separately and therefore, on rates of dissolution of carbonate substrates.

Fine and Loya (2002) and Fine et al. (2004) showed that euendolithic metabolism increases with irradiance when corals experience bleaching. However, when bleaching is too rapid, euendolithic filaments are photoinhibited. Their metabolism is reduced by 80% due to an elevated temperature combined with high light intensities. Euendolithic communities are more diverse, abundant and efficient in in dead substrates, thus it would be interesting to determine the effects of those combined factors on their metabolism in dead substrates and over time.

Interactions between euendoliths and their live hosts

Mutualistic relationship

One of the most intriguing questions being asked increasingly by coral reef researchers is why some coral species, mostly massive and encrusting forms, survive bleaching events, while others do not. Coral bleaching corresponds to the disruption of the symbiotic relationship between the coral host and its algal symbionts (zooxanthellae) following in general an increase of the sea surface temperature (Hoegh-Guldberg 1999). As a consequence, corals loose their main source of energy putting at risk their main biological functions (e.g., reduced proteins and lipids, lowered growth rate, lower calcification and repair capabilities, and termination of gametogenesis; see Fine and Loya 2002). There may be more than one reason why some corals survive bleaching and others do not, but one has been given recently involving boring microflora (Fine and Loya 2002). The boring microflora and live corals may have a mutualistic relationship, helping corals survive better during bleaching events. Back in 1955, Odum and Odum suggested for the first time a symbiotic relationship between phototrophic euendoliths and live corals (ectosymbiosis). Those authors hypothesized that nutrients of coral metabolism readily diffuse through the porous skeleton to euendoliths, and polyps provide to them a protection against competitors, browsing and intense sunlight. From phototrophic euendoliths, corals would benefit in return from diffusion of organic substances, but no evidence of that was provided by Odum and Odum (1955). Later works carried out on this topic since confirmed or contradicted the hypothesis proposed by Odum and Odum and are presented below.

Shashar et al. (1997) stated that it is an advantage for phototrophic euendoliths to live inside skeletons of live corals as the latter provide mycosporine-like amino-acids (MAAs) which absorb most of UV-A and UV-B. Those authors were unable to find MAAs in euendolithic filaments suggesting that either: (a) those compounds are not synthesized by euendoliths because they are not induced by environmental conditions or (b) they do not have the ability to produce them, which forces euendoliths to live in protected niches such as coral skeletons. They also suggested that live corals provide a protection for euendoliths against predation by grazers because grazing fishes feed rarely on live corals (Rojtan and Lewis 2005). It is also plausible that euendoliths use nutrients derived from coral metabolism and degradation of residual organic matter within the skeleton. Such a short circuit of nutrient supply schemes have been shown in other closed environments such as microbial mats (Paerl and Pinckney 2005).

Schlichter et al. (1995) carried out the first study showing a transfer of photoassimilats produced by phototrophic euendoliths (*O. quekettii*) to coral tissues of the azooxanthellate coral *Tubastrea micranthus* Ehrenberg, 1834 in a shallow reef of the Red Sea, using ^{14}C incubations. Fixation of ^{14}C was light dependent. Those authors showed that euendolithic filaments are in contact with coral tissues and that within 24h-48h algal precursors are integrated into coral lipids. An ‘ectosymbiotic relationship’ was suggested with an intracolonial recycling of nutrients. Risk and Muller (1983) quantified high concentrations of nutrients in live colonies of *P. lobata* from the Great Barrier Reef and attributed those concentrations to euendolith metabolism. Ferrer and Szmant (1988) estimated that euendoliths may satisfy 55% to 65% of N required by live corals for balanced growth. Pore-waters extracted from skeletons of *Montastrea annularis* Ellis and Solander, 1786 showed concentrations of 9 µM, 0.3 µM, and 0.4 µM of NH_4^+, NO_3^-, and PO_4^{3-}, respectively, over ambient seawater concentrations. Shashar et al. (1994) and Casareto et al. (2004) also showed that the uptake of N_2 by endolithic communities is very high. The mutualistic relationship between boring microflora, especially *Ostreobium quekettii*, and azooxanthellate corals may support their distribution into deeper waters.

Recently, Fine and Loya (2002) highlighted an ectosymbiotic relationship between phototrophic euendoliths and the zooxanthellate coral *Oculina patagonica* from the oriental Mediterranean Sea. They found that euendoliths bloom in bleached corals (increase of biomass and pigments concentration) within 2 weeks and transfer photoassimilats to coral tissues. This is an alternative source of energy for live coral tissues which could explain the low mortality rate of *O. patagonica* following bleaching events. Such external symbiosis may be advantageous to the coral over endosymbiosis with zooxanthellae during periods of environmental changes (e.g., elevated seawater temperature). This source of energy is however insufficient for reproduction (Fine et al. 2001) but may help bleached coral to better survive and to recover from stress. In zooxanthellate corals from the Great Barrier Reef, Fine et al. (2005) observed a similar bloom of phototrophic euendoliths after bleaching events. These euendoliths photoacclimated well to their new conditions except when they were exposed too quickly to high temperature and light intensities. This study suggests that the role of phototrophic euendoliths in the resilience of corals when exposed to stresses such as bleaching (and associated rise of sea surface temperature) may vary greatly with environmental conditions and over time. This has to be investigated more.

Parasitic relationship

While phototrophic euendoliths seem to be beneficial for their live hosts, heterotrophic euendoliths often have a parasitic relationship with their hosts (Bentis et al. 2000; Golubic et al. 2005), or are associated with coral diseases (Alker et al. 2001). In live corals such as *Porites lobata*, euendolithic fungi are observed in newly deposited skeletal spines (pali), demonstrating that they are able to keep up with coral skeleton accretion (Le Campion-Alsumard et al. 1995b). Also, fungi were observed penetrating into live coral tissues of different coral species (Pacific and Atlantic oceans; Bentis et al. 2000; Golubic et al. 2005). The damage to corals caused by fungal penetration remains unknown but to defend themselves, coral tissues form pearl-like deposits of carbonate (or ‘cones’) around fungal hyphae to prevent further penetration (Le Campion-Alsumard et al. 1995b; Bentis et al. 2000). But as polyps respond by producing cones, fungal hyphae continue to penetrate along the axis of the defence structure (Bentis et al. 2000). Recently, Domart-Coulon et al. (2004) showed that fungal infestation extends coral cell survival of

Pocillopora damicornis (Linnaeus, 1758) up to 2 days, by producing a transient cytoprotective effect, selectively enhancing the survival of skeletogenic cell types. This may result from the activation of cell metabolism or inhibition of death. Such a result supports previous observations of cone repair production around hyphae. Additionally, euendolithic fungi may be involved in the formation of skeletal growth tissue anomalies in *Porites compressa* in Kaneohe Bay (Domart-Coulon et al. 2006). Fungi engaged in lichenization with phototrophic euendoliths may have mutually beneficial effect (Le Campion-Alsumard et al. 1995b; Golubic et al. 2005).

Factors that directly or indirectly impair skeletogenesis in corals – such as elevated sea surface temperature (Hoegh-Guldberg and Salvat 1995), coastal eutrophication (Marubini and Davies 1996) and increased atmospheric CO_2 (Kleypas et al. 1999) – could compromise the ability of corals to defend themselves against euendolithic fungal attacks. Bentis et al. (2000) suggested that coral's inability to deposit enough repair aragonite, in conjunction with factors that may increase the frequency of coral-fungal interactions, could increase the regularity with which hyphae are successful in reaching the skeletal surface of actively growing corallites. Domart-Coulon et al. (2004) also suggested that the contact of fungal hyphae with coral soft tissue may cause tissue sloughing. All those effects are likely to be deleterious to the host coral's health. This may be even more dramatic because corals may not be able to defend themselves against other pathogens (Kushmaro et al. 1997) or to invest energy in other processes such as tissue regeneration or recovery from bleaching (Meesters and Bak 1995). In regard to the increased concern over the health of coral reefs and coral diseases, with an attempt to diagnose and to identify their causative agents, more attention needs to be paid to euendolithic fungi.

Conclusions

In order to better understand the functioning of coral reef ecosystems and how they will respond to global change and anthropogenic activities in the near future, it appears critical to study rapidly the different roles played by the boring microorganisms at various spatial and temporal scales, as they had biological and geological implications for millions of years. This review summarizes evidence that they are key organisms in coral reef functioning and maintenance. The preliminary studies reported here, all tend to show that boring microflora are major primary producers and agents of bioerosion dissolving large quantities of calcium carbonate with a potential in buffering seawater, recycling nutrients and producing metabolites allowing survival of corals when bleached. High productivity of microbial euendoliths in live coral is in support of a balance between constructive and destructive processes, and appears to be beneficial to the health of the reef as a whole, whereas the high productivity of euendoliths on coral rubble may feed the grazers that destroy the reef in the process. Additionally, a few studies show that some euendoliths may be involved in coral diseases and may weaken coral health, rendering them more susceptible to death. Those studies opened new questions, especially on the effects of environmental factors such as eutrophication, rising sea surface temperature, UV and atmospheric CO_2 on euendolith metabolism.

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