

MICROBIAL ASSEMBLAGES INVOLVED IN TROPICAL COASTAL BIOEROSION:  
AN ATLANTIC-PACIFIC COMPARISON

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ABSTRACT

Bioerosion on tropical limestone coasts consists of interaction between microbial endoliths and invertebrate grazers. Distribution of both is correlated with the frequency of wetting and water retention on the habitat. A steep gradient in water availability across the intertidal ranges causes a general zonal distribution of organisms, modified by bio-karstic microtopography. Several zones of characteristic color can be distinguished, as they are dominated by particular assemblages of organisms each with its own pigmentation. From the subtidal level upward, the zones are dominated by: 1 - the chlorophyte *Ostreobium quekettii*; 2 - *Conchocelis*-stages of bangiacean rhodophytes; 3 - cyanobacteria *Mastigocoleus testarum* and *Plectonema terebrans*; 4 - cyanobacteria *Herpyzonema intermedium*, *Scytonema endolithicum* and *Hormathonema luteo-brunneum*. The dominant grazers are sea urchins, followed by polyplacophores and gastropods. Maximum bioerosive effect is in the mid-intertidal ranges, where a combined and interdependent microbor-ing-grazing activity results in formation of a deep bioerosive coastal notch. Such notches occur on carbonate coasts of all warmer seas, however, their development is most accentuated in soft calcarenitic limestone in protected lagoonal waters. Good preservation potential of microbial endoliths permits assessment of coastal paleo-environments and determination of the position of ancient sea levels.

INTRODUCTION

Marine bioerosion has been recognized as a complex of biogeochemical interactions which are able to significantly modify marine benthic environments and shape carbonate coasts. The balance between bio-constructive and bio-destructive agents is of particular importance in tropical oceans, including coral reefs, where the highest activity rates are encountered. Most attention thus far has been given to carbonate removal rates by grazing animals (reviewed by Hutchings 1986; Bak 1990) although the subject is increasingly being addressed in its full ecological complexity (Chazottes et al. 1994; Schuhmacher et al. 1995). Vertical distribution of microbial euendoliths and microborings have environmental and paleoenvironmental relevance and may serve for paleobathymetric indication (Golubic et al. 1975). Microbial bioerosion in subtidal ranges comparing euendoliths attacking live and dead coral skeletons has been studied in French Polynesia (Le Campion-Alsumard et al. 1995a, b). Diversity and vertical distribution of microbial euendoliths across coastal profiles has been studied in the Mediterranean region (Ercegovic 1932, Le Campion-Alsumard 1979) Bermuda (Hoffman 1984) and Florida (Lukas 1979). Rates of carbonate removal by microbial endoliths alone have been measured by Tudhope and Risk (1985). However, these rates become significantly enhanced in the presence of grazers (Schneider 1976). The relationship between microbial epiliths and endoliths, as the primary producers of the bioerosional community, and their grazers represents a synergistic mechanism: grazing removes the stabilizing effect of light limitation so that the bioerosional process becomes progressive (Torunski 1979; Schneider and Torunski 1983). Schneider and Torunski (1983) have also established the link between coastal bioerosion of compact carbonate substrates and biogenic production of fine sediment fraction.

Microbial endoliths and their grazers are distributed in zones, which are wide and variable in the subtidal ranges, becoming narrower, more distinct, and biologically well defined toward the intertidal and supratidal ranges (see Golubic et al. 1975, fig.12.2). Along tropical limestone coasts, the vertical coastal profiles reflect the intensity of combined bioerosion rates from zone to zone, resulting in the formation of a characteristic horizontal groove - the coastal notch (Radtke et al. 1996). This conspicuous geomorphological feature (Viles and Spencer 1986; Spencer 1988) has been used as a marker in reconstructions of past sea level changes (Neumann and Moore 1975). The present paper compares the distribution of microbial euendolithic assemblages and their principal grazers along coastal profiles of the tropical Atlantic (Lee Stocking Island, Bahamas) and Pacific oceans (Moorea, French Polynesia).

MATERIALS AND METHODS

Small chips of carbonate substrate (ca 5mm across) containing endoliths were removed from the rock by hammer and chisel and fixed in a buffered 2-3% formaldehyde solution in sea water. Carbonate substrate was removed with Perenyi solution (0.5% chromic acid: 10% nitric acid: 70-90% alcohol in relations 3:4:3). The extracted endoliths were mounted on slides and observed by light microscopy. The microborings were cast in Durcupan Araldite following fixation in 2.5% glutaraldehyde in seawater, postfixation with 2% osmium tetroxide in seawater (for 2 hrs) and gradual dehydration in an alcohol series. The borehole casts were observed with a Scanning Electron Microscope (SEM) following dissolution of carbonate substrate using dilute HCl. The effect on the substrate was studied in partially etched preparations by SEM after treatment with concentrated sodium hypochlorite to remove the organic matter. Following fixation, dehydration and embedding, microorganisms were studied in growth position in oriented petrographic thin sections.

RESULTS

Environmental settings

The present research compares coastal bioerosion in two geographically remote locations: The barrier reef of the high Polynesian island Moorea, Société Archipelago, French Polynesia, in the Pacific Ocean (17°30'S, 149° 50' W) and Lee Stocking Island, Exuma Archipelago, Bahamas in the Atlantic ocean (23°46'N, 76°06'W). Lee Stocking Island is positioned on the edge of a large carbonate platform. Like other islands of the Bahamas it is comprised of elevated fossil beaches, ooid shoals and coral reefs of Pleistocene age. The coasts show a sharp contrast between the windward side, open to surf from the deep Exuma sound waters and the protected leeward side turned toward shallow warm waters of higher salinity on the carbonate platform.

Moorea is a typical high volcanic island surrounded by a fringing reef and a barrier reef. Elevated portions of the ancient coral reef (locally called 'coral conglomerate') form an extensive carbonate coastline, interrupted by larger and smaller lagoons and rock pools. The degree of elevation of the ancient reef varies, reaching upward into the wave spray supratidal zone toward the reef's outer edge and into the freshwater range toward the inner side of the lagoon.

Thus the zonal distribution of microbial endoliths and their grazers is stretched horizontally, emphasizing the importance of relief-dependent micro-environments over the absolute elevation above the mean water levels.

Both compared sites are characterized by carbonate rocks of considerable structural porosity, which enables capillary water transport and water retention, and provides interstitial microbial habitats. Zonal distribution of organisms is more pronounced along the steep profiles of the Bahamian island coast than along flat profiles of the Pacific coral reefs. The coastal notch was also best expressed on protected coasts and on rock pools of Lee Stocking Island (Fig. 1), whereas in Moorea it was most clearly visible on the margins of rock pools.

**Table 1:** Vertical distribution of principal phototrophic microbial euendoliths in percent dominance from the lower intertidal zone (1) upward to the supratidal wave spray zone (4) on calcarenite coasts of Lee Stocking Island, Bahamas.

		ZONES			
		1	2	3	4
SPECIES					
1	<i>Hormathonema luteo-brunneum</i>	0	0	15	35
2	<i>Hormathonema violaceo-nigrum</i>	0	0	10	25
3	<i>Scytonema endolithicum</i>	0	0	20	20
4	<i>Herpyzonema intermedium</i>	0	0	10	5
5	<i>Solentia</i> spp.	0	10	25	10
6	<i>Hyella caespitosa</i>	0	5	10	5
7	<i>Mastigocoleus testarum</i>	5	35	5	0
8	<i>Plectonema terebrans</i>	10	15	0	0
9	<i>Conchocelis</i> stages	65	25	5	0
10	<i>Ostreobium quekettii</i>	20	10	0	0

#### Microbial euendolith distribution.

Euendolith distribution has been analyzed zone by zone starting with the subtidal ranges, where the highest biological diversity and interspecific competition is encountered, toward the zones of increased air-exposure, accompanied by lowering of species diversity. Each zone harbors a number of microenvironments identifiable by microtopography and by color. These microenvironments were sampled and microscopically analyzed. The general distribution of microbial euendoliths by zones is summarized in tables 1 and 2, for each of the compared geographic locations. Three short profiles were sampled at the Lee Stocking Island, Bahamas: a 2m long profile at the cave entrance on the Norman's Pond island, a 3m long profile at a small islet called Tugboat with particularly deep erosional notch, and a 20m long profile on the northeastern windward coast of Lee Stocking Island.

The coral reef buildup around the Pacific island of Moorea expands the coastal euendolithic habitats horizontally, extending accordingly the water supply, and stretching the euendolithic zonation. Accordingly, a larger number of biologically characterized zones could be distinguished in the Pacific than in the Atlantic setting. However, the boundaries between these zones are less clear on Pacific coral reefs than on the steeper coastlines of the emergent carbonate platform islands in the Bahamas. On the horizontally spreading reef settings, the species composition and dominance depends more on microenvironmental differences, so that the microbial assemblages have a more patchy, mosaical distribution.

In both compared locations, the microbial euendoliths cluster in two ecologically distinct assemblages. One assemblage is predominantly subtidal in origin, gradually losing more sensitive members with the increased intertidal exposure. The other assemblage is specialized to survive extreme ecological fluctuations of the periodically desiccating upper intertidal ranges, where it dominates. Individual species, however, frequently cross the boundaries between these two zones or are interspersed within them in a mosaical fashion.

In both locations the predominant coloration of the subtidal ranges is a dark red, stemming from the dominance of crustose rhodophytes. In this zone the constructive and protective role of coralline red algae predominates over microbial and invertebrate bioerosion. Microbial endoliths occur beneath the coralline crust and on denuded surfaces. The dominant early settlers on denuded surfaces are euendolithic septate chlorophytes, such as *Phaeophila* and *Eugomontia*. These pioneer settlers spread horizontally by shallow tunnels maintaining repeated connections to the substrate surface. The tops of the cells in *Phaeophila dendroides* often protrude from shallow tunnels and grooves sending wavy tubular bristles into the water column above. Their life cycle appears to be on the order of a few weeks to months, so that most substrates contain only empty borings (Kiene et al. 1995). *Phaeophila*-like chlorophytes were rarely observed on Moorea profile, they were common, however, in freshly attacked pearl oyster shells (*Pinctada margaritifera*). The long term dominance in subtidal and lowermost intertidal ranges, both on the Atlantic and in the Pacific sites is taken by *Ostreobium*. In addition to *Ostreobium quekettii* which also dominates the interior of coral skeletons, two other forms of *Ostreobium* were encountered in the current study, possibly representing separate species. Within the same range, euendolithic *Conchocelis*-stages of unidentified bangiacean rhodophytes dominate locally, producing macroscopically recognizable areas of light pink coloration. Both *Ostreobium* and *Conchocelis*-stages dominate in shaded places and on the underside of rocks. Largest contiguous area under *Conchocelis* have been observed on rock debris of the collapsed notch roofs on the exposed coasts of the Lee Stocking Island, Bahamas.

**Table 2:** Vertical and horizontal distribution of phototrophic microbial euendoliths in percent dominance per zone (+ indicates rare occurrences) from the outer (1) to the inner (9) edge of the exposed reef surface on the Pacific Moorea Island (French Polynesia).

		ZONES								
		1	2	3	4	5	6	7	8	9
SPECIES										
1	<i>Hormathonema luteo-brunneum</i>	0	0	0	0	0	0	0	5	15
2	<i>Hormathonema violaceo-nigrum</i>	0	0	0	0	0	0	0	5	15
3	<i>Scytonema endolithicum</i>	0	0	0	0	0	0	0	10	60
4	<i>Herpyzonema intermedium</i>	0	0	0	0	0	0	15	70	10
5	<i>Solentia</i> spp.	0	0	0	0	0	+	75	10	0
6	<i>Hyella caespitosa</i>	5	5	5	15	50	100	10	0	0
7	<i>Mastigocoleus testarum</i>	+	40	60	75	45	0	0	0	0
8	<i>Plectonema terebrans</i>	5	10	5	5	5	0	0	0	0
9	<i>Conchocelis</i> stages	10	15	20	5	0	0	0	0	0
10	<i>Ostreobium quekettii</i>	80	30	10	0	0	0	0	0	0

The lower intertidal zone is conspicuous by its bright olive-brown coloration. This zone is characterized by a diverse endolith assemblage usually dominated by *Mastigocoleus testarum*. This dominance was more pronounced on Moorea where it included two to three distinct forms of *Mastigocoleus*. On Lee Stocking Island this range was frequently occupied by *Conchocelis* stages of Bangiacean rhodophytes, which expanded successfully upward into the lower intertidal ranges.

*Plectonema terebrans*, a small filamentous cyanobacterium is widely distributed with local dominance but, because of its small size, it constitutes a minor proportion of endolith biomass and of the carbonate removed. A similarly wide distribution shows the coccoidal cyanobacterium *Hyella caespitosa*. It dominates locally forming radiating bush-like boring clusters in the subtidal ranges, and it occurs less commonly in the intertidal ranges, interspersed between other endoliths. *H. caespitosa* requires constant water supply, but tolerates wide fluctuations in salinity. In Moorea, this organism takes absolute dominance in larger upper intertidal rock pools, where the salinity reaches saturation levels with respect to sea salt.

*Solentia* is another genus of euendolithic coccoid cyanobacteria with several species covering a wide range of occurrences across the coastal profiles of both, Atlantic and Pacific sites. *S. achromatica* dominates subtidal and lower intertidal ranges. When illuminated, its exopolysaccharide envelopes are stained yellow by the light-protecting extracellular pigment scytonemin. The envelopes of *Solentia* expand into long colorless stalks that penetrate deep into the rock. In upper intertidal rock pools this species becomes replaced by *S. foveolarum*, characterized by bluish black gloeocapsin-stained envelopes, which turn red when treated with acids. Small, bluish-gray colored depressions in the well drained upper intertidal ranges are dominated by *S. paulocellulare*. This taxon shows longer stalks in the Pacific sites studied, while it appears more stunted on the Atlantic and Mediterranean coasts (Fig. 2).

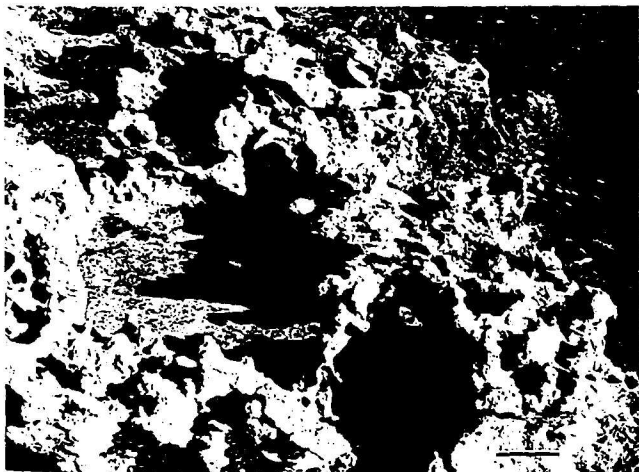


Fig. 1: Small rock pools in the upper intertidal ranges of the Lee Stocking Island, Exuma Archipelago, Bahamas. Interaction of selective microbial boring and invertebrate grazing results in flat-bottom pans with overhang margins. Each rock pool forms its own 'coastal notch'. Scale bar is 20cm long.

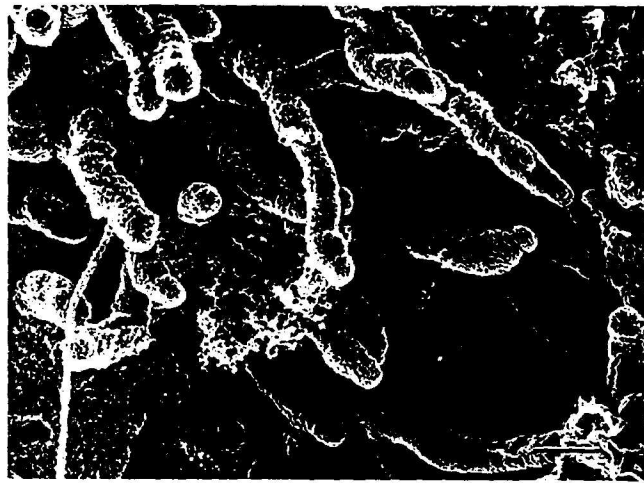


Fig. 2: Resin casts of microbial borings of *Solentia achromatica* in the intertidal rock pool on the tropical coral limestone coast of Moorea Island, French Polynesia. Partial etching preparation. Scale bar is 20µm long.

In the uppermost intertidal and supratidal ranges (rock pools excluded), the predominant color shades that the endoliths render to the rocks are bluish black to dark brown. The supratidal ranges which receive water only by wave spray and rain can be subdivided in three biologically characterized zones: A zone of *Herpyzonema intermedium* is conspicuous in shaded, concave, grayish green depressions in the rock. In higher and dryer habitats it becomes coated and finally replaced by a dark brown endolithic felt of *Scytonema endolithicum*. The latter species also colonizes loose sand grains on beaches of Pacific atolls at a corresponding level with respect to the mean water mark. The uppermost well drained peaks of the karstified coastal limestones of both sites are coated by semi-endolithic coccoid cyanobacteria *Hormathonema luteo-brunneum* and *H. violaceo-nigrum*. Both taxa are protected from excessive solar illumination by extracellular pigments, scytonemin and gloeocapsin, respectively. All ranges under study show the presence of fungal hyphae, which increase in abundance in the more frequently wetted lower intertidal ranges. These euendolithic heterotrophs are commonly following algae and cyanobacteria, sending haustoria into their cells. A high abundance of heterotrophic bacteria is also frequently observed, some of them seem to be specific degraders of cyanobacterial polysaccharide sheaths.

Cyanobacteria which dominate the euendolithic community of the emergent coastal ranges are present both on Atlantic and Pacific islands and seem to be pantropical in distribution. Slight differences in dominance of particular taxa and variance in composition of the assemblages were observed, possibly indicating an ongoing speciation of this ancient group of prokaryotes providing a distinction at a subspecies level. Eukaryotic euendoliths also appear similar in their morphology and distribution. Regional taxonomic differences among them could not be ascertained based on field observations alone because of high morphological variability of their euendolithic growth. A large presence and diversity of *Conchocelis*-stages is in sharp contrast to the paucity of epilithic stages of bangiacean rhodophytes in both compared regions.

#### Invertebrate grazers

Invertebrate grazers dominate the intertidal and supratidal ranges, while the vertebrates, specifically scarid fish are restricted to the subtidal, paying only occasional visits to the upper coastal ranges during high tide. Sea urchins are important grazers in the subtidal ranges and in larger permanent rock pools. *Diadema antillarum* is the most conspicuous echinoid of the submersed regions in the Bahamas. *Echinometra lacuntra* makes and occupies deep holes in the lowermost intertidal ranges and is particularly common on wave exposed coasts of the Lee Stocking Island. On the Pacific islands, the sea urchin grazing by *Diadema setosum*, *Echinothrix calamaris* and *Echinometra mathaei* is dominant in shallow lagoons and large interconnected rockpools on top of the reefs.

The most important bioeroding invertebrates of the intertidal and supratidal ranges are polyplacophores (chitons) and gastropods. Their grazing activity is also distributed in zones, however, populations of these grazers move up and down with the tides. Chitons and limpets forage radially around a home position to which they return. On the Atlantic Lee Stocking Island the most common chitons are *Chiton tuberculatus* and *C. marmoratus*. The most common limpet is *Acmaea leucopleura*. The lower zones are grazed by the large gastropod *Cittarium pica*, while smaller grazing snails include *Merita versicolor* on the leeward, and *N. peloronta* and *N. tessellata* on the windward side of the island. Numerous small grazers include *Littorina ziczac*, *L. meleagris*, *L. nebulosa* and *L. mespillum*. The upper ranges are grazed by snails that spend extended periods of time in a dormant state: the dark brown *Echininus nodulosus* and whitish-gray *Tectarius muricatus*.

Gastropods grazing emerging portions of the Pacific coral reefs include: *Patella flexuosa* and *Turbo setosus*, in seaward ranges which are frequently wetted by tides and waves. *Merita plicata*, *Littorina coccinea* and *Tectarius grandinatus* are grazing in landward ranges. Loose sediments trapped in rock pools support *Cerithium alveolus*.

#### DISCUSSION

Sharp zonation of microbial euendoliths 'telescopically' compressed along coastal profiles from the subtidal toward supratidal ranges is determined by worsening of ecological conditions (Golubic et al. 1975). It is paralleled by similarly sharp zonation of sessile invertebrates with skeletons that serve as substrate to microbial euendoliths (e.g. barnacles, spirorbids), as well as of the vagile invertebrate grazers supported by microbial euendoliths. Settlement along a gradient of diminishing seawater supply requires physiological adaptations and ability to survive desiccation in a latent stage, properties that assured an absolute dominance of cyanobacteria as primary producers. Several euendolithic zones are defined by dominance of particular specialized euendolithic cyanobacteria (Ercegovic 1932, Le Campion-Alsumard 1979, Lukas 1979). The extent of these zones observed on the Mediterranean coasts depends on water supply through wave exposure (Ercegovic 1934). However, this general picture is complicated by the elaborate karstic microtopography of coastal limestone, which offers microenvironments with various capacities of water retention. A patchy, mosaical distribution is particularly conspicuous in porous rocks, such as the soft calcarenite of the Bahamas and coral limestone of the Polynesian reefs.

In addition, combined bioerosion by microbial euendoliths and their grazers has a positive reinforcement effect on karstic microtopography, deepening the shaded and moist depressions and generally

increasing the surface-to-volume ratio of the available substrate (Schneider and Torunski 1983) further increasing water retention. Additional bioerosion may be caused by bacterial decay of the organic matter produced by phototrophic microbial euendoliths. Thus, biological activities are directly involved in microenvironmental diversification of this coastal habitat. The outcome of natural selection and final dominance of euendolithic taxa depends on the relationship between wetting frequency, water retention and drainage, and on fluctuations in physico-chemical conditions that depend on this relationship.

Colonization of freshly denuded substrates does not restore the previously dominant euendolithic microflora. Rather, there is a succession of colonizers starting with pioneer species and ending with slower growing persistent assemblage characteristic of each microbial zone. For the lower intertidal and subtidal ranges colonization sequence starts with *Phaeophila* and ends with *Ostreobium* (Kiene et al. 1995). Colonization sequence of the upper intertidal ranges has been established for the Mediterranean limestone coasts (Le Campion-Alsumard 1970), but has not been included in the present report.

The taxonomic composition of microbial euendolithic assemblages in the two tropical sites under study documents an increase in species diversity when compared with similar environments in higher latitudes. This is expressed both in terms of the number of taxa, and in equitability of their distribution. This finding is in contrast with past generalizations assuming extremely low diversity, cosmopolitan distribution and ecological insensitivity of cyanobacteria (e.g. Fogg et al. 1973). Our findings are consistent with the increased cyanobacterial diversity encountered among tropical euendoliths in subtidal sands grains (Al-Thukair and Golubic 1991a, b; Al-Thukair et al. 1994), and with the findings of high diversity of microbial molecular signatures in environmental nucleotide sequence analyses in tropical marine environments (Giovannoni et al. 1990).

#### ACKNOWLEDGEMENTS

This work is a part of the research Project on Bioerosion supported by the Deutsche Forschungsgemeinschaft, DFG-Vo. 90/14: "Controls of biogenic sedimentation: Reef Evolution" to K. Vogel. The Grant INSU/ORSTOM (AIP Récifes coraliens) supported the work in French Polynesia and the NOAA grant CMRC-94-24 to W.E. Kiene supported the work in the Bahamas. The international cooperation was made possible by the National Associate Professor Program of the University of Aix-Marseille 2, for the Centre d'Océanologie de Marseille. We thank K Vogel, WE Kiene, M Gektidis, K Hofmann and CE Payri for their support. The staff of the French Polynesian University and of the Caribbean Marine Research Center (CMRC) offered generous help in the field work.

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