4

Bioerosion and Coral Reef Growth:
A Dynamic Balance

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> The question at once arises, how is it that even the stoutest corals, resting with broad base upon the ground, and doubly secure from their spreading proportions, become so easily a prey to the action of the same sea which they met shortly before with such effectual resistance? The solution of this enigma is to be found in the mode of growth of the corals themselves. Living in communities, death begins first at the base or centre of the group, while the surface or tips still continue to grow, so that it resembles a dying centennial tree, rotten at the heart, but still apparently green and flourishing without, till the first heavy gale of wind snaps the hollow trunk, and betrays its decay. Again, innumerable boring animals establish themselves in the lifeless stem, piercing holes in all directions into its interior, like so many augurs, dissolving its solid connexion with the ground, and even penetrating far into the living portion of these compact communities.
>
> —L. Agassiz, 1852

4.1 INTRODUCTION

Coral reefs are among the Earth's most biologically diverse ecosystems, and many of the organisms contributing to the high species diversity of reefs normally weaken them and convert massive reef structures to rubble, sand and silt. The various activities of those reef species that cause coral and coralline algal erosion are collectively termed **bioerosion**, a name coined by Neumann (1966). A **bioeroder** is any organism that, through its assorted activities, erodes and weakens the calcareous skeletons of reef-building species. Although an extensive terminology has been adopted only during the past three decades, bioerosion has been recognized as an important process in reef development and maturation for more than a century (e.g., Darwin, 1842; Agassiz, 1852). Traces of biologically-induced erosion in ancient reef structures indicate that bioerosion has probably had some effect on reef carbonate budgets since Precambrian and Cambrian times (Vogel, 1993).

Most bioeroder species are both small in size and secretive in living habits. Although the majority of bioeroders and other cryptic organisms are not visible on coral reefs, it has been suggested that their numbers and combined mass equal or exceed that of the surface biota (Grassle, 1973; Ginsburg, 1983). Ginsburg has coined the term **coelobite** to refer to the profusion of organisms inhabiting cavities on reefs. For convenience, bioeroders that are usually present and visible on reef surfaces are termed **external bioeroders** and those living within calcareous skeletons are termed **internal bioeroders** (Fig. 4-1A). The feeding scars produced by an external bioeroding pufferfish (*Arothron*) can become permanently incorporated in the skeleton of a massive coral (Fig. 4-2A). A heavily infested coral by internal bioeroders, e.g. lithophagine bivalves, can severely damage and weaken the colony skeleton (Fig. 4-2B).
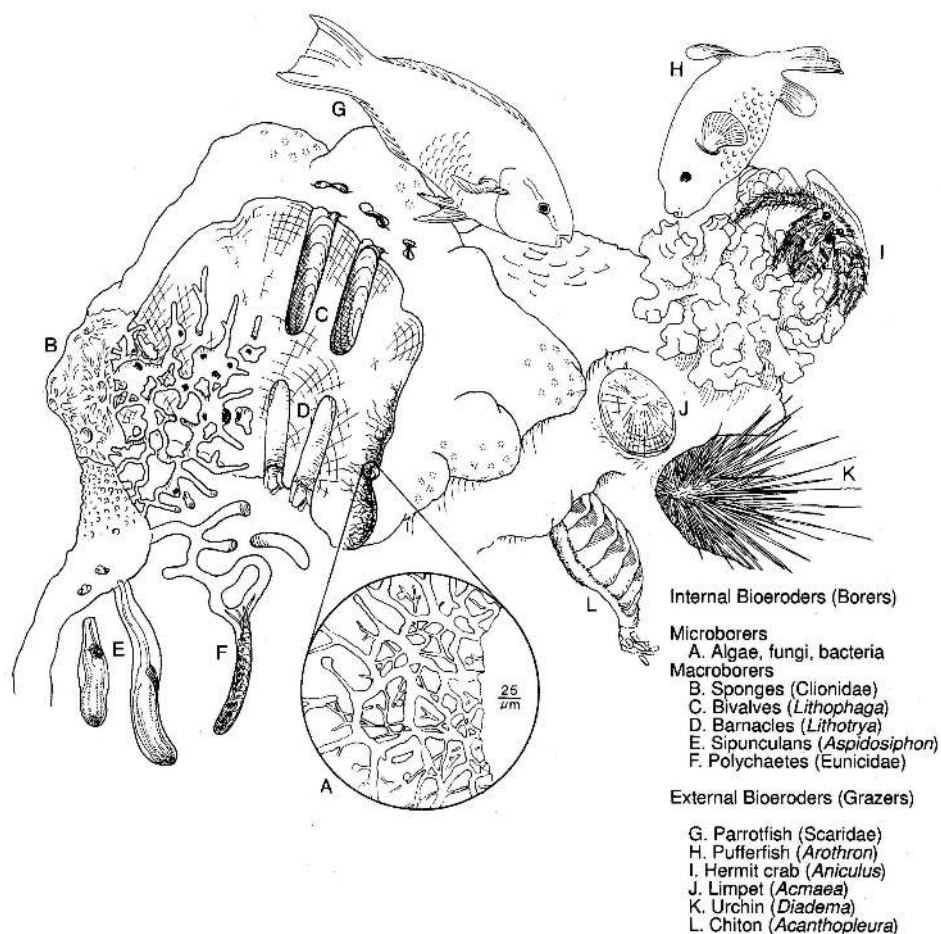

Internal Bioeroders (Borers)

Microborers
  A. Algae, fungi, bacteria
Macroborers
  B. Sponges (Clionidae)
  C. Bivalves (*Lithophaga*)
  D. Barnacles (*Lithotrya*)
  E. Sipunculans (*Aspidosiphon*)
  F. Polychaetes (Eunicidae)

External Bioeroders (Grazers)

  G. Parrotfish (Scaridae)
  H. Pufferfish (*Arothron*)
  I. Hermit crab (*Aniculus*)
  J. Limpet (*Acmaea*)
  K. Urchin (*Diadema*)
  L. Chiton (*Acanthopleura*)

Figure 4-1. Variety of external and internal bioeroders that commonly attack coral skeletons. A legend provides identification of the taxa illustrated.
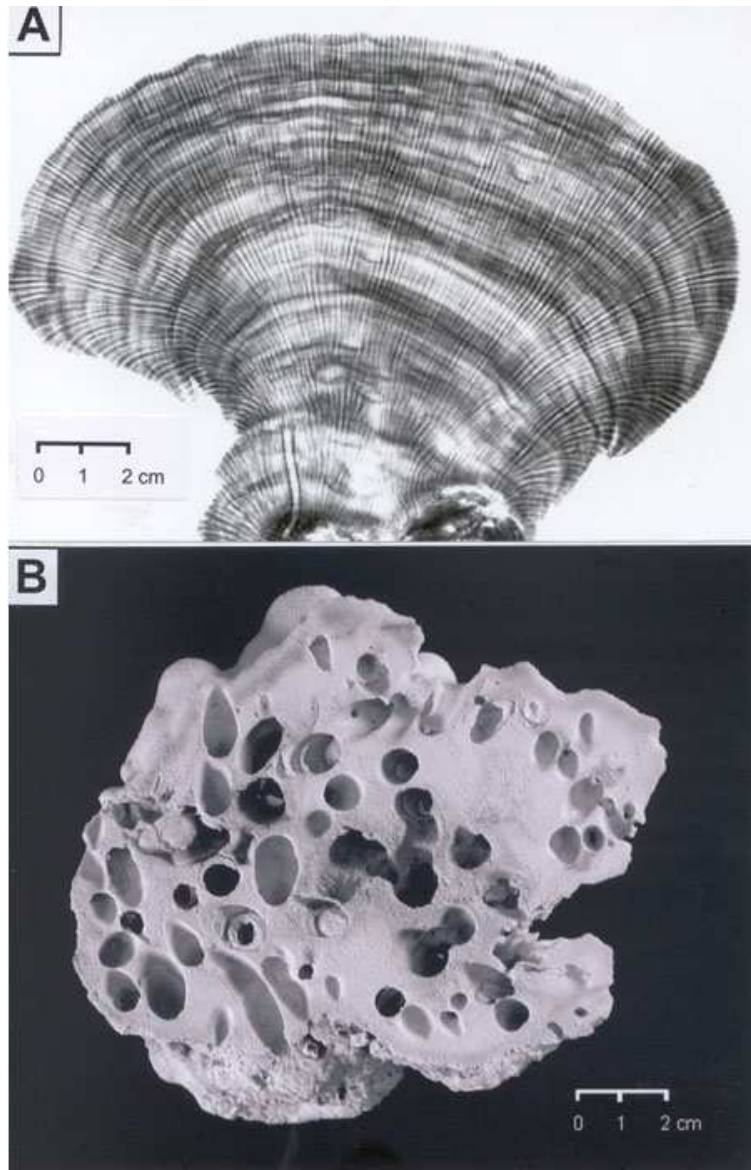
Figure 4-2. A – X-ray photograph of *Porites lobata* slab cut parallel to the skeletal growth axis. Lunate pufferfish feeding scars, produced externally, are now permanently embedded in the skeleton (6-8 m depth, Clipperton Atoll). B – Cross section of *Porites panamensis* extensively bored by lithophagine bivalves (5 m depth, Pearl Islands, Panama).
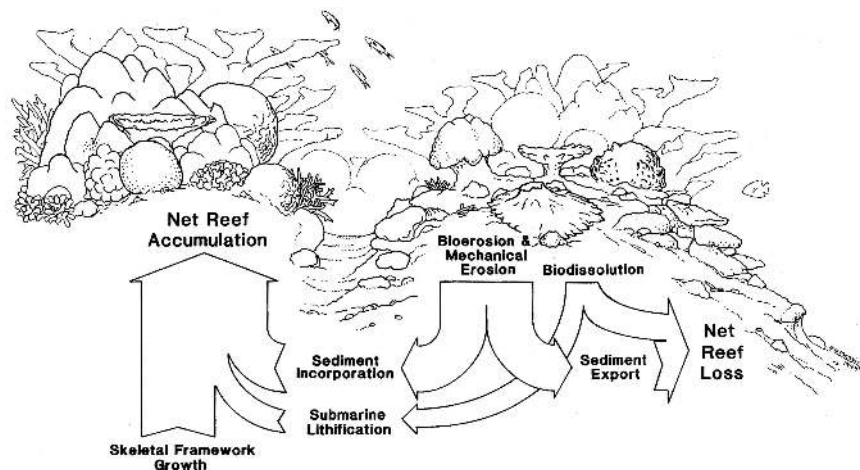
Figure 4-3. A generalized scheme illustrating the principal components of coral-reef construction and destruction. In order for reef growth to occur, rates of bioerosion and mechanical erosion must not exceed the rate of net reef accumulation.

Several studies have shown that bioeroders are important in sculpting coral reef growth and in producing the sediments (rubble, sand, silt and clay) that characterize coral reef environments. Indeed, carbonate budget studies have demonstrated that constructive and destructive processes are closely balanced on many reefs with net reef accumulation barely ahead of net reef loss (Scoffin et al., 1980; Glynn, 1988; Fig. 4-3). Bioerosion proceeds at high rates in certain zones which have high living coral cover and high rates of accretion (Kiene, 1988). Sometimes, however, an imbalance develops with erosional processes gaining the upper hand. When environmental conditions decline over an extended period reef growth ceases, reef foundations are destroyed and reef death ensues.

The aim of this chapter is to (a) illustrate the diversity of bioeroders on coral reefs, (b) identify the most destructive bioeroder groups, (c) describe the more prevalent modes of limestone destruction, and (d) highlight some case studies of intensified bioerosion on particular reef systems. In this updated review, with reference to the diversity of bioeroding taxa (a), protistan foraminiferans are now included as agents of reef carbonate breakdown although it is not yet possible to assess their overall importance. Under case studies (d), the effects of continuing, global-scale disturbances that impact coral communities and accelerate bioerosion, namely ENSO warming events and eutrophication, are re-examined in the light of recent findings. Considering the many well documented studies of accelerating coral reef decline during the past decade, it is now all the more critical to understand the conditions that promote bioerosion, a pivotal process affecting the growth potential of coral reefs. For more technical information on this subject, the reader may consult the articles in Carriker et al. (1969) and Barnes (1983), and the reviews by Golubic et al. (1975), Warme (1975,

1977), Risk and MacGeachy (1978), Trudgill (1983), Macintyre (1984) and Hutchings (1986).

4.2 BIOERODER DIVERSITY

Bioeroders are abundant and diverse members of coral reef communities, belonging to four of the five kingdoms of life on earth, and to most animal phyla. Why have so many taxa become bioeroders? By far, the bioeroders hidden within coral skeletons, the **cryptic biota**, have the greatest taxonomic diversity. It is probable that intense competition and predation have led to the selection and evolution of cryptic life styles. Many of these secretive species are without toxins, armature, spines and thick shells, traits that are so common to their congeners living on reef surfaces and exposed to predators.

Depending upon their location on calcareous substrata, bioeroders can be classified as epiliths, chasmoliths and endoliths (Golubic et al., 1975). **Epilithic species** live on exposed surfaces, **chasmoliths** occupy cracks and holes, and **endoliths** are present within skeletons. Assignment to these categories is not always clear, however, for some bioeroders may belong to more than one microhabitat or change microhabitats during feeding, reproduction and development.

Bioeroders breakdown calcareous substrata in a variety of ways. The majority of epilithic bioeroders are herbivorous grazers that scrape and erode limestone rock while feeding on associated algae. In terms of eroding capabilities, grazers range from non-denuding and denuding herbivores that remove mainly algae and cause little or no damage to substrata to excavating species that remove relatively large amounts of algae, including calcareous algae, and the underlying limestone substrata (Steneck, 1983). Most endoliths are borers that erode limestone mechanically, chemically or by a combination of these processes. The important role of bioeroders can be appreciated when one realizes that coral reefs are predominantly sedimentary environments made up of calcareous particles that are generated in large measure by the activities of bioeroders (**Chapter 2**).

Many species that bioerode calcareous skeletons are minute, requiring microscopical methods for study, and are referred to as **microborers** or endolithic microorganisms (Golubic et al., 1975; Macintyre, 1984). To this group belong three kingdoms, namely bacteria and cyanobacteria (PROKARYOTAE), FUNGI, and eukaryotic microorganisms such as protozoans and algae (PROTOCTISTA). The **macroborers** are generally more conspicuous on coral reefs, and include numerous invertebrate and vertebrate taxa in the kingdom ANIMALIA. Most endolithic invertebrates are suspension feeders, gathering their food passively or actively from the water column.

Endolithic microborers, possibly Cyanobacteria, are among the first recognizable bioeroders in the fossil record, having left minute borings in late Precambrian ooids of Upper Riphean/Vendian age, 570-700 Myr (Campbell, 1982). While endolithic borers increased steadily during the Paleozoic era, from 5 to 9 classes, they comprised only a small part of hard-ground communities and penetrated structures superficially, i.e., to maximum depths of 2-3 cm (Vermeij, 1987). A notable increase in endolithic taxa

occurred during the Mesozoic era with the appearance of deep borers, such as pelecypods, gastropods and lithotryid barnacles, capable of penetrating substrates to depths of 15 cm. Excavating bioeroders, comprising mobile epifaunal invertebrates and herbivorous fishes, made their first appearance during the Late Mesozoic and Early Cenozoic (70-60 Myr) and have persisted until today. These animals – chitons, limpets and other gastropods, sea urchins and parrotfishes – are dominantly herbivores whose feeding activities incidentally produce large quantities of sediment. Herbivory and bioerosion by these groups is probably more intense now than at any time in the past (Steneck, 1983). Vermeij (1987) has argued that this Mesozoic increase in the size and extent of excavation among vagile bioeroders can be interpreted as an evolutionary response to escalating predation and competition on open rock surfaces.

4.2.1. *Bacteria*

Although our knowledge of the bioeroding potential of bacteria and the various taxa involved is very limited, preliminary observations suggest that these organisms may be important under certain conditions. A pilot study in Hawaii indicated that brownish areas inside the skeletons of massive corals contained from 10^4 to 10^5 bacteria per gram dry weight (DiSalvo, 1969). Boring sponges also were closely associated with bacteria, which could possibly have assisted the sponges' penetration into the coral. Different workers have shown that bacteria can etch the surface of limestone crystals and dissolve the organic matrix of coral skeletons, causing internal bioerosion (DiSalvo, 1969; Risk and MacGeachy, 1978).

Several species of Cyanobacteria, formerly known as blue-green algae, are capable of eroding reef rock from the splash zone to depths of at least 75 meters. Species of *Hyella, Plectonema*, *Mastigocoleus*, and *Entophysalis*, for example, have been found on limestone surfaces, inside cavities, and penetrating reef rock (Fig. 4-4 a, b). A close relative of *Hyella* has been found in Precambrian algal reefs that existed 1.7 billion years ago (Vogel, 1993). The boring is a dissolution process accomplished by the terminal cells of specialized filaments. Cyanobacteria have been implicated in the erosion of lagoon floor sediments on the Great Barrier Reef, amounting to the dissolution of between 18-30% of the sediment influx rate (Tudhope and Risk, 1985) (Table 4-1). (It should be stressed that most of the rates of erosion listed in Tables 4-1 and 4-2 were obtained with different methods and therefore should be compared with due caution. See Kiene [1989] for an assessment of the strengths of the methods and some problems with the intercomparisons.)

4.2.2. *Fungi*

Boring fungi have been found in modern corals in the Caribbean, French Polynesia and on the Great Barrier Reef (Australia). Twelve genera belonging to the Deuteromycota or Fungi Imperfecti have been isolated from a variety of scleractinian corals and a hydrocoral (Kendrick et al., 1982). Fungi are capable of deep penetration into coral skeletons by chemical dissolution. The hyphae produce narrow borings and penetrate the deepest recesses of coral skeletons, probably because of their ability to utilize the organic matrix of coral skeletons (Fig. 4-4 c, d). Fungi have also been implicated in the etching of calcareous surfaces, the weakening and dissolution of

calcareous sediments as well as the calcareous tube linings of various endoliths. Because of the difficulty of distinguishing between fungal and algal borings, estimates of dissolution rates due to boring fungi alone are not yet available.

4.2.3. *Algae*
Green (Chlorophyta) and red (Rhodophyta) algae have been implicated in the erosion of coral rock under various reef settings. Green and red algae occur on limestone surfaces, in cavities and within coral skeletons (Fig. 4-4 e, f). Freshly fractured corals often reveal layers of green banding a few cm beneath the live coral surface. The green color is due to the presence of chlorophyll pigments, which intercept light passing through the coral's tissues and skeleton. This greenish layer is often referred to as the "*Ostreobium* band", named after a green alga that is commonly present in coral skeletons. However, the green band may also contain a variety of different kinds of algae, e.g., species of *Codiolum, Entocladia, Eugomontia*, and *Phaeophila*. The importance of boring algae as bioeroders is controversial; some workers claim that they are among the most destructive agents of reef erosion whereas others maintain that they cause only minimal damage.

4.2.4. *Foraminifera*
Some 20 species of bioeroding foraminiferans, belonging to 11 families, have been reported mainly from turbulent, tropical waters (Vénec-Peyré, 1996). The majority of these mostly endolithic species occur in coral reef environments and have been found to excavate a variety of substrates, e.g. coralline algae, foraminifers, corals, bryozoans, mollusks, crustacean carapaces, wood and rocks. Only a single species from the Red Sea, *Cymbaloporella tabellaeformis* (Brady), has been reported to excavate coral skeletons. Most workers hypothesize that foraminifers penetrate hard substrates by chemical dissolution. Only a few quantitative studies on the abundances of bioeroding foraminifers are available. One such survey estimated population densities of between 150,000 and 250,000 individuals/m^2 in bioclasts present in sedimentary biotopes on a coral reef at Moorea, French Polynesia. No information is presently available on the rates of bioerosion by foraminiferans. In addition to the erosion caused directly by these protists, it is likely that the minute depressions excavated on substrates may also facilitate the recruitment of other bioeroding taxa. Clearly, much remains to be learned about the destructive capacity of these organisms.

4.2.5.   Sponges
The most important genera of siliceous sponges known to bore into calcareous substrata are *Cliona, Anthosigmella* and *Spheciospongia*, order Hadromerida, and Siphonodictyon, order Haplosclerida (Wilkinson, 1983). Clionaid sponges (Family Clionaidae) are among the most common and destructive endolithic borers on coral reefs worldwide. Zea and Weil (2003) have revealed that a *Cliona* in the Caribbean consisting of at least three distinct excavating sponges. *Upon* splitting open infested corals, clionaid sponges are revealed as brown, yellow or orange patches lining the corroded interiors of the coral skeleton (Fig. 4-5 a, d). Most boring sponges form 5-15 mm   diameter   chambers   with   smaller   galleries   branching   off   the
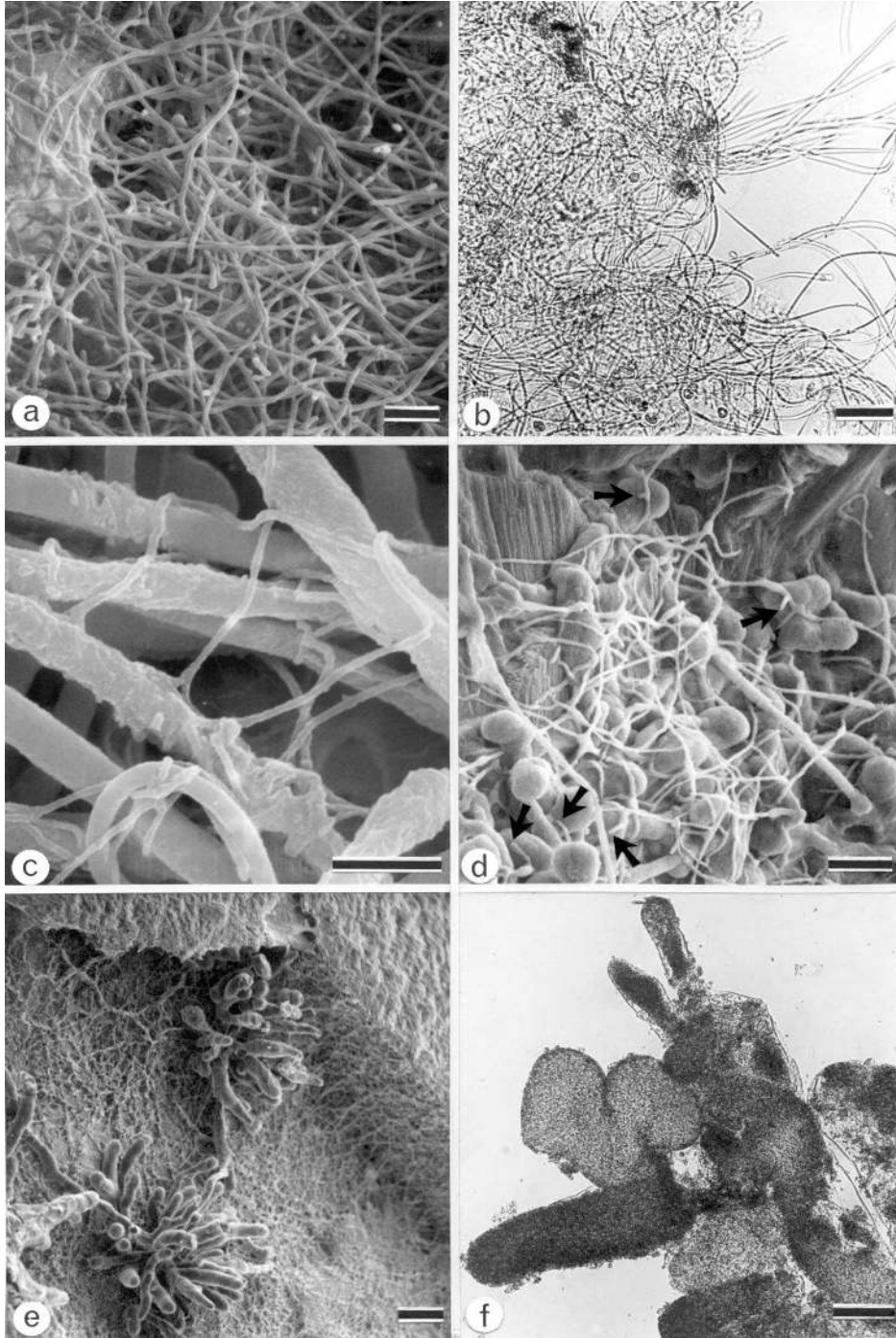
main chambers. Their depth of penetration into the coral skeleton is usually no greater than about 2 cm. Some sponges (*Siphonodictyon*), however, can form chambers up to 100 mm in diameter that penetrate to 12 cm into coral colonies. Subsurface excavation by clionaid sponges removes the skeletal support of coral calyces, thus causing the collapse and death of polyps. In highly infested colonies, some boring sponges emerge from the skeleton, grow over and even kill live coral tissues on reef surfaces. On western Atlantic reefs, *Cliona caribbaea* is sometimes very abundant, forming dark brown patches several meters in extent that kill or overgrow dead surfaces and erode all calcifying organisms (Fig. 4-6).

Sponge boring is accomplished by amoebocytes that etch and chip minute calcareous fragments from limestone substrata (Rützler and Rieger, 1973; Pomponi, 1979). The ends of etching amoebocytes flatten against the calcareous substratum and extend fine pseudopodial (filopodia) sheets into the limestone at the cell's periphery. The filopodia coalesce centrally, cutting out a hemispherical carbonate chip (Fig. 4-5 e-g). This cutting is accomplished by enzymes that simultaneously dissolve calcium carbonate and the organic matter matrix of skeletons. At the end of this process, both the chip and the etching cell are transported away from the site of erosion and are expelled from the sponge. Only about 2-3% of coral skeletons are dissolved with the remainder dispersed as silt-sized chips. These oval-shaped (faceted) chips are easily recognized in sediments and have been found to contribute up to 30-40% numerically to the fine silt fraction of sediments on Pacific and Caribbean reefs.

4.2.6. *Polychaete Worms*

Polychaete worms that bore into reef rock are enormously abundant in certain environments, prompting some workers to conclude that they are among the most important endolithic borers on coral reefs (Davies and Hutchings, 1983). Various species in the following families typically form circular holes 0.5-2 mm in diameter that penetrate up to 10 cm into the interiors of coral skeletons: Cirratulidae, Eunicidae, Sabellidae and Spionidae. Eunicid holes often form a sinuous and anastomosing network (Fig. 4-1). The mechanism of boring has been reported for a few polychaete species. Some eunicids employ their mandibles to excavate. Spionids bore mainly by chemical dissolution with some removal probably due to mechanical abrasion by setae (Haigler, 1969). Cirratulid and eunicid species are predominantly deposit-feeders whereas sabellids and spionids are mainly filter-feeders. The close physical association of eunicids and spionids with endolithic algae also has suggested the utilization of boring algae as a food source (Risk and MacGeachy, 1978).

◄*Figure 4-4.* Photomicrographs of endolithic microborers in limestone substrates. Cyanobacteria: **(a)** *Plectonema terebrans* Bornet and Flahault, scanning electron micrograph (SEM) of plastic casts of filaments in an acid-etched shell; **(b)** *P. terebrans*, transmitted light micrograph (TLM) of filaments isolated by dissolution. Fungi: **(c)** SEM of plastic casts of fine fungal hyphae intertwined with the larger filaments of *P. terebrans*; **(d)** SEM of fungal borings covering and possibly feeding (arrows) on the underlying cyanobacterium. Chlorophyta: **(e)** *Ostreobium brabantium* Weber Van-Bosse, SEM of plastic cast of large radiating growth form in an acid-etched shell fragment; **(f)** *O. brabantium*, TLM of filaments isolated by dissolution.

Scale bars: **a** = 50 μm, **b** = 40μm, **c** = 5μm, **d** = 25 μm, **e** = 200μm, **f** = 100μm (from May et al., 1982)

Table 4-1. Rates of Bioerosion by Internal Borers

Taxonomic Group	Erosion Rate (g CaCO₃/m²/yr)	Borer Abundance	Particle Size (μm)	Habitat	Locality	Source
Cyanobacteria						
mostly cyanobacteria with some fungi	350	microborings permeated sediment grains	2-6	lagoon-floor carbonate sediments	Davies Reef, Great Barrier Reef, Australia	Tudhope and Risk (1985)
Porifera						
clionid sponges, *Cliona lampa* Laubenfels predominant	23,000	infested limestone substrates	30-80	subtidal limestone notch, 1-3 m depth	Bermuda	Neumann (1966)
Cliona and *Siphonodictyon*	7,000 180[a]	infested limestone substrates abundant in crustose coralline algae and in dead and live corals	30-80	subtidal test blocks fringing reef	Bermuda Barbados	Rützler (1975) Scoffin et al. (1980)
Polychaeta						
cirratulid, eunicid, sabellid, and spionid worms	690 840 1,800	13,000 ind. m⁻² 24,000 ind. m⁻² 85,000 ind. m⁻²	10-30[b]	forereef slope feef flat lagoonal patch reef	Lizard Island, Great Barrier Reef, Australia	Davies and Hutchings (1983)
Crustacea						
Lithotrya ?dorsalis Sowerby	14[a]	common	?	fringing reef	Barbados	Scoffin et al. (1980)
Lithotrya sp.	0.8 cm³ ind⁻¹ yr⁻¹	common	2-4[c]	intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)
Sipuncula						
Phascolosoma, 3 spp. *Paraspidosiphon,* 3 spp. *Lithacrosiphon gurjanovae* Murina	8[a]	uncommon in corals	<63	fringing reef	Barbados	Scoffin et al. (1980)
Mollusca						
Lithophaga nasuta (Phillipi)	0.9 cm³ ind⁻¹ yr⁻¹	common	?	intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)
Lithophaga laevigata (Quoy and Gaimard) *Lithophaga aristata* (Dillwyn)	9,000	1,870 ind. m⁻²	10-100	largely dead patch reef, 6-10 m depth	Caño Island, Costa Rica	Scott et al. (1988)

[a]Calculated from an overall borer bioerosion rate of 200 g m⁻² yr⁻¹, and assuming that sponges were responsible for 89%, barnacles for 7%, and sipunculans for 4% of the total bioerosion (Scoffin et al., 1980).

[b]For an eunicid (Ebbs, 1966), and from information supplied by P. Hutchings (pers. Comm).

[c]From Ahr and Stanton (1973).

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A quantitative study of boring polychaetes conducted at Lizard Island, Great Barrier Reef provides numerical abundances and bioerosion rates of a pioneer polychaete community. At various times during the study it was not uncommon to find between 27,000 and 80,000 boring polychaetes per m^2 in experimental coral blocks set out in three different reef environments (Davies and Hutchings, 1983). These worms caused erosional losses of from 0.7 kg m^{-2} yr^{-1} on the reef front to 1.8 kg m^{-2} yr^{-1} on a leeward patch reef (Table 4-1).

4.2.7. *Crustacea*

Barnacles, shrimp, hermit crabs and other kinds of crustaceans can erode reef rock (Warme, 1975). Barnacles and shrimp are endolithic borers, producing cylindrical chambers whereas hermit crabs are external bioeroders that abrade live coral surfaces.

Three groups of barnacles contain species that reside in skeletons of dead corals, namely thoracicans, acrothoracicans and ascothoracicans. Members of the latter two taxa occupy small, mm-sized cavities that keep pace with the host coral's growth, i.e., they become embedded within the coral skeleton without causing extensive erosion. Species of *Lithotrya*, thoracican barnacles, erode 2-10 cm long oval-shaped cavities on the undersides of reef rock and beach rock in shallow, agitated waters (Fig. 4-1). The barnacle's basal plate is attached at the inner-most end of the cavity and the body hangs downward toward the opening with cirri exposed to food-bearing currents. The cavities are formed apparently by mechanical abrasion effected by calcified plates that cover the barnacle's body. Unlike other invertebrate endoliths, such as polychaete worms and gastropods, adjacent tubes of boring *Lithotrya* are commonly interconnected, and heavily infested limestones are thoroughly honeycombed and subject to frequent breakage. An average of one boring per cm^2 was observed on beach rock in Puerto Rico, and up to 30% of the substratum had been removed from some of the samples examined (Ahr and Stanton, 1973). Overall, however, results from studies in the Caribbean and Indian Ocean indicate that boring barnacles cause relatively little erosion compared with other internal borers (Table 4-1).

Alpheus simus Guerin-Meneville, a pistol shrimp, bores into coral rock on Caribbean reefs and causes considerable erosion on some Costa Rican reefs (Cortés, 1985). Male/female pairs excavate 10-15 mm diameter chambers that penetrate as deep as 15 cm into dead coral rock. Microscopical study of the chamber walls suggests that this shrimp bores mainly by chemical means. Seven pairs of shrimp were found in one 1,500 cm^2 block, and each pair occupied an average chamber volume of 20 cm^3. This is equivalent to the removal of about 950 cm^3 of calcium carbonate m^{-2}. The life span of the shrimp is about 2 years, but since succeeding generations of shrimp probably occupy the same chambers it is not possible to calculate annual erosion rates.

Two species of hermit crabs that feed on live coral produce large amounts of calcareous sediment when they scrape corals to remove soft tissues (Fig. 4-1). The average mass of coral abraded by a small hermit crab [*Trizopagurus magnificus* (Bouvier)] was about 10 mg ind^{-1} day^{-1}, and for a large hermit crab (*Aniculus elegans* Stimpson) about 1 g ind^{-1} day^{-1}(Glynn et al., 1972). Relating hermit crab population
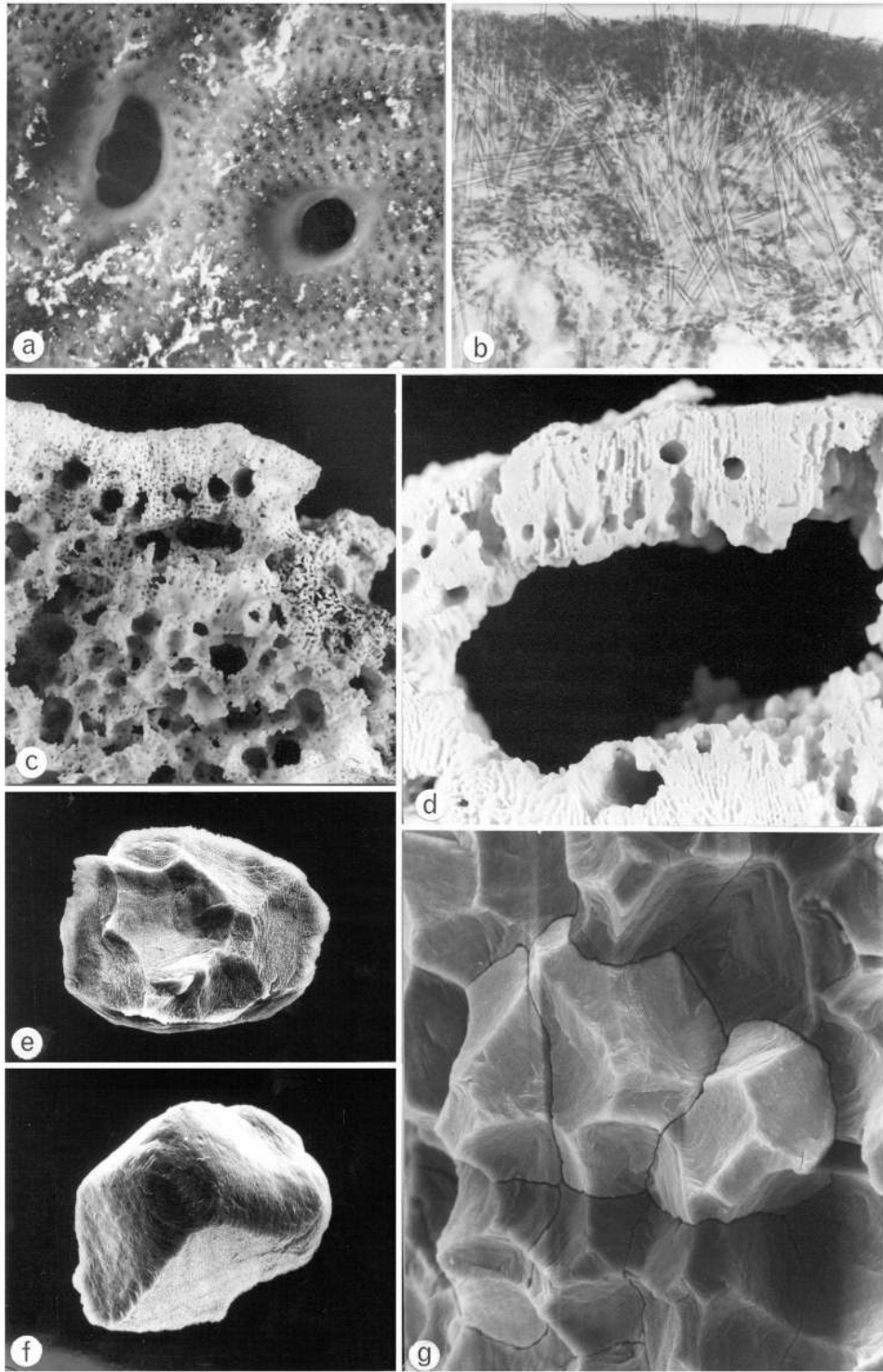
densities and erosion rates, it was found that *Trizopagurus* and *Aniculus* respectively were responsible for the generation of about 1 and 0.1 metric tons of coral sediment per ha per yr on a fringing reef in Panamá (Table 4-2). Since this rate of coral abrasion by hermit crabs has not been reported elsewhere, it is possible that these high levels of erosion are unique to the eastern Pacific.

4.2.8. *Sipuncula*

Although it is well known that species in several genera of sipunculans (peanut worms) penetrate coral skeletons, there is no general agreement on the overall importance of this group in the bioerosion of coral reefs. Perhaps this is due to their great variation in abundance from reef to reef and across reef zones (Macintyre, 1984).

Sipunculan borings are cylindrical and pencil-sized or slightly smaller, ranging from straight to sinuous and from near-surface to several cm deep in coral skeletons, depending on the species (Fig. 4-1). Sipunculans are abundant on some reefs: nearly 800 inds m^{-2} were present in reef crest substrata, and 1,200 inds m^{-2} in *Porites* coral skeletons in Belize (Rice and Macintyre, 1982). Even at 30 m depth, 40 inds m^{-2} were found. While feeding, sipunculans extended their introverts outside of their cavities and appear to ingest debris, sand and algae. The exact manner of boring is not known, but may involve both chemical dissolution and mechanical abrasion (Rice and Macintyre, 1972). An estimated sipunculan erosion rate on a Barbados reef indicated only minor carbonate loss (Table 4-1).

4.2.9. *Mollusca*

Most bioeroding molluscs are external grazers that abrade reef rock while feeding on algae and associated organisms residing on and within limestone substrata. The eroding capacity of surface enmeshed and endolithic algae, important components of the diet of grazing molluscs, also weakens the substratum and thus facilitates erosion during feeding. A group of mussel-like endolithic borers also is prominent on many reefs worldwide.

Molluscan bioeroders are generally most abundant in the intertidal zone with some species extending their ranges into supratidal and subtidal habitats (Fig. 4-7a). Species abundances also change horizontally with chitons often most plentiful in areas protected from strong wave assault and limpets, certain snails, and echinoids more common in wave swept habitats (Fig. 4-7b). Under quiet to rough water conditions, grazing molluscs are largely responsible for producing the notches and nicks on tropical limestone shores. Most early workers surmised that intertidal notches were formed through strictly physico-chemical processes (e.g. the localized lowering of pH and

◄*Figure 4-5.* Boring sponges in limestone substrates. **(a)** Two oscula of *Cliona lampa* (Laubenfels) visible on the surface of a massive coral (*Diploria).* **(b)** Vertical section through peripheral region of *Spheciospongia othella* Laubenfels revealing abundant spicules. **(c)** Chambers of *Cliona dioryssa* (Laubenfels) in porous coral rock. **(d)** A large tunnel running below the surface of coral rock excavated by *S. othella*. **(e)** Upper scalloped and **(f)** lower convex surfaces of isolated limestone chips discharged through the osculum of *Cliona lampa*. **(g)** Group of chips etched from substratum by *Cliona lampa* but still in place. Magnification: **a, c, d** x 3; **b** x 140; **e, f** x 1,500; **g** x 1,500; **g** x 600 (**a-d** from Rützler, 1984; **e, f, g** from Rützler and Rieger, 1973).

Table 4-2. Rates of Bioerosion by External Grazers

Taxonomic Group	Erosion Rate (g CaCO$_3$ m^{-2} yr^{-1})	Grazer Abundance (ind. m^{-2})	Particle Size (mm)	Habitat	Locality	Source
Crustacea (hermit crabs)						
Trizopagurus magnificus (Bouvier)	103	27.5	0.12-0.5	pocilloporid patch reef	Pearl Islands, Panama	Glynn et al. (1972)
Aniculus elegans Stimpson	8.5	0.02	0.25-3.0			
Mollusca						
Polyplacophora (chitons)						
Acanthopleura granulata Gmelin	227	5.5	0.03-1.0	intertidal limestone rock	San Salvador Island, Bahamas	Rassmussen and Frankenberg (1990)
Chiton tuberculatus Linné	394	22	?	lower intertidal coral rubble	La Parguera, Puerto Rico	Glynn (1970)
Gastropoda						
Acmaea sp.	19.2	8	0.03-1.0	intertidal limestone rock	Andros Island, Bahamas	Donn and Boardman (1988)
Nerita tessellata Potiez and Michaud	154	220	0.03-1.0	intertidal limestone rock	Andros Island, Bahamas	McLean (1967)
Echinodermata (sea urchins)						
Diadema antillarum Phillipi	4,600	9	?	patch reef	St. Croix, U.S. Virgin Islands	Ogden (1977)
Diadema antillarum	5,300	23	0.05-0.5	fringing reef	Barbados	Scoffin et al. (1980)
Diadema mexicanum A. Agassiz	139-277 3,470-10,400	2-4 50-150	0.5-2.0	lower seaward slope	Gulf of Chiriquí, Panama	Glynn (1988)
Diadema savingnyi Michelin	3,400	4.8	sand	reef lagoon	Moorea, French Polynesia	Bak (1990)
Echinometra lucunter (Linnaeus)	3,900	100	?	algal ridge	St. Croix, U.S. Virgin Islands	Ogden (1977)
Echinometra mathaei (Blainville)	70-260	2-7	?	limestone rock	Enewetak Atoll	Russo (1980)
Echinometra mathaei[a]	1,600 4,300	0.09 14.0	?	outer reef flat	La Saline Reef, Reunion Island	Chazottes et al. (2002)
Echinothix diadema (Linnaeus)	803	0.6	sand	reef lagoon	Moorea, French Polynesia	Bak (1990)
Eucidaris galapagensis Döderlein	3,320 22,300	4.6 30.8	0.05-3.0	reef flat, pre-1982 reef flat, post-1983	Floreana Island, Galápagos Islands	Glynn (1988)

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Table 4-2. Continued

Taxonomic Group	Erosion Rate (g CaCO$_3$ m^{-2} yr^{-1})	Grazer Abundance (ind. m^{-2})	Particle Size (mm)	Habitat	Locality	Source
Pisces						
Scarus iserti (Bloch)[b]	490	0.6	0.015-0.25	patch reef	Panama	Ogden (1977)
Sparisoma viride (Bonnaterre)	61	0.01	silt-sand	fringing reef	Barbados	Frydl and Stearn (1978)
Scarus vetula (Bloch and Schneider)	140±30[c] 2,420±190	0.08	silt-sand?	reef slope shallow reef	Bonaire, Netherlands Antilles	Bruggemann et al. (1996)
Grazing and browsing fishes	110	0.01	?	patch reef	Bermuda	Bardach (1959, 1961)
Chlorurus microrhinos[d]	420-5,470 1,010-3,280 6,500	0.0007-0.009[e] 0.002-0.005[f] 0.006	fine sand fine sand	fringing reef fringing reef shallow reef edge	Lizard Island Heron Island Lizard, Island, GBR	Bellwood (1995) Bellwood (1996)
Chlorurus sordidus (Forsskål)	110-500 260-980	0.02-0.005[e] 0.011-0.12[f]	fine sand	fringing reef fringing reef	Lizard Island Heron Island	Bellwood (1995)
Parrotfishes (dominantly)	110-9,100	?	?	reef flat, slope, lagoon habitats	Llewellyn Reef, Australia GBR	Kiene (1988)
	400-600	0.04-0.06	fine sand-gravel	patch reefs	Saipan, Mariana Islands	Cloud (1959)
Arothron meleagris (Bloch and Schneider)	30	0.004	2-8	pocilloporid reef	Pearl Islands, Panama	Glynn et al. (1972)

a. Dominant echinoid effecting erosion; represented overall between 80 and 100% of total sea urchin abundances.

b. A senior synonym of *Scarus croicensis*.

c. Mean ± standard deviation.

d. Formerly confused with *Chlorurus gibbus* Rüppell, a closely related Red Sea species.

e. Abundance data are from Choat and Bellwood (1985).

f. Abundance data are from Choat and Robertson (1975).

accompanying carbonate dissolution), which resulted in the erosion of the underlying rock. Under extremely rough conditions, many bioeroders either disappear or their activities are greatly reduced. Calcifying taxa, such as coralline algae and vermetid molluscs, increase in abundance with increasing exposure, probably because of ecologic requirements for high energy habitats and a lower abundance of fish consumers in rough water areas (Fig. 4-7c). Vermetid/coralline algal buildups help protect the underlying limestone, thus limiting bioerosion and the development of intertidal notches and nicks in such areas (Focke, 1978).

Several species of chitons (Class Polyplacophora), e.g. members of *Acanthopleura* and *Chiton*, erode chiefly intertidal limestone substrata while grazing on algae. The grazing is achieved with a magnetite (Fe_3O_4) or other mineral-enriched radula, a tooth-bearing strap of chitinous material, that effectively abrades the substratum (Lowenstam and Weiner, 1989). Some erosion also occurs at homing sites, rock depressions that are occupied by chitons when not foraging. As many as 50-100 sausage-shaped, 1-3 mm long fecal pellets are voided daily by individual chitons (Rasmussen and Frankenberg, 1990). Erosion rates vary greatly among sites as they are influenced by local differences in rock type and condition, and ecological factors affecting chiton abundances and feeding activities (Table 4-2).

Figure 4-6. A Caribbean boring sponge (*Cliona caribbea*) covering and eroding several square meters of reef substrate, San Blas, Panama, 3 meters depth (30 June 1993). Arrows denote perimeter of sponge patch.
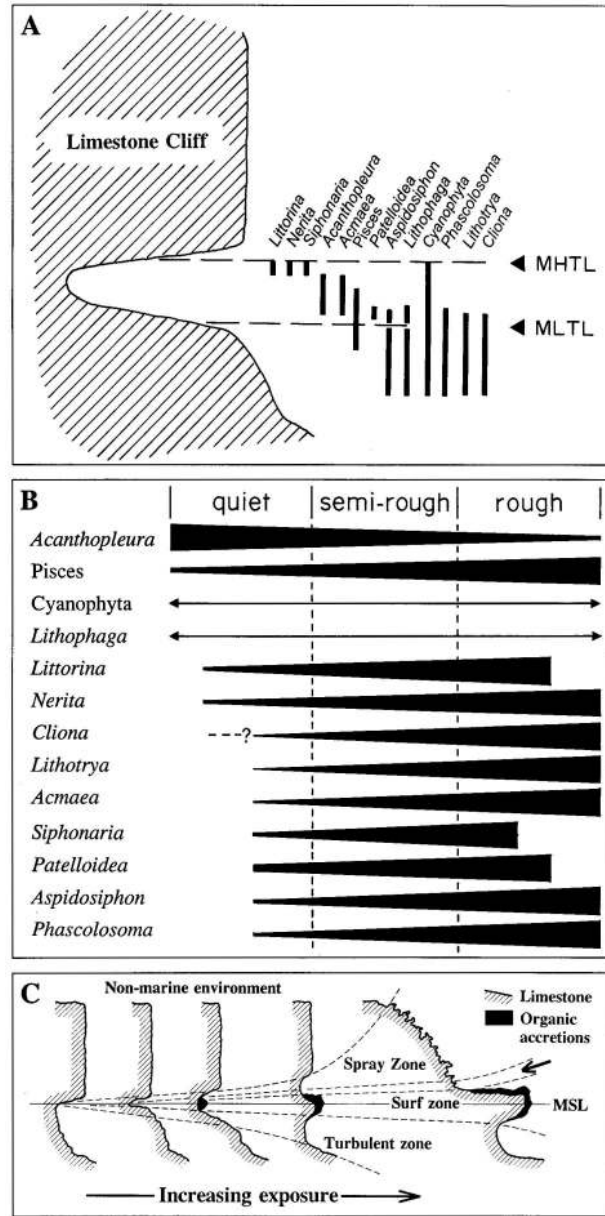
Figure 4-7. Vertical **(A)** and horizontal **(B)** distributions of bioeroding mollusks and other bioeroder taxa on a limestone shore at Palau, Caroline Islands. Theoretical relationship **(C)** of coastal profile morphology to water turbulence at Curaçao, Netherlands Antilles. An arrow locates a "transition zone" between the "spray" and "surf zones" (**A** and **B** after Lowenstam, 1974; **C** after Focke, 1978).

Limpets and snails (Class Gastropoda) often occur with chitons on intertidal carbonate substrata. *Acmaea, Cellana* and *Patelloida* are common limpet genera, and *Cittarium, Littorina, Nerita* and *Nodilittorina* are some common snail genera. Like chitons, limpets and snails utilize a radula to scrape rock surfaces. The radula of patellacean limpets is an especially effective excavating organ with opal ($SiO_2.nH_2O$) or goethite ($HFeO_2$)-sheathed radular teeth (Lowenstam and Weiner, 1989). The radula of snails contains proteinaceous teeth, but these grazers are still capable of erosion because of the often weakened condition of the rock substratum upon which they feed (Table 4-2).

Species of *Lithophaga* and *Gastrochaena* (Class Pelecypoda) bore into dead and live corals, and are most abundant subtidally, with some of these bivalves attacking reef corals to their lower depth limits. *Fungiacava* spp. penetrate live mushroom corals, but their activities are relatively minor. The siphonal openings of *Lithophaga* typically have a keyhole-like appearance on coral surfaces and the circular holes penetrate vertically into the skeleton, from 1 to 10 cm deep depending upon the species (Fig. 4-1**,** Fig. 4-2 B). The lithophagines are deposit and suspension feeders, often most abundant in areas of high productivity. The mantle glands of *Lithophaga* secrete acid that dissolves and weakens the limestone substratum. The vertical and rotational movements of the shell also assist in boring, resulting in the production of silt/sand-sized sediment. Population densities in productive equatorial eastern Pacific waters range from 500-10,000 inds m^{-2} (Scott et al., 1988), which can lead to rapid reef erosion (Table 4-1).

4.2.10. *Echinoidea*

Sea urchins (Echinoidea) are the only echinoderms capable of significant bioerosion. Several species in the following genera abrade large amounts of reef rock while feeding and excavating burrows: *Diadema, Echinometra, Echinostrephus*, and *Eucidaris*. Sea urchins possess a highly evolved jaw apparatus (Aristotle's lantern), a flexible and protrusible mastigatory organ consisting of five radially arranged, calcified teeth. The teeth are mineralized, and must be harder than the corroded surfaces they scrape. Sea urchin spines also assist in bioerosion when they are employed in the enlargement of burrows. Sea urchins graze on algae growing on dead coral substrata, but in some areas also attack live coral. On seaward reef platforms where water flow is vigorous, sea urchins usually remain in their burrows and feed predominantly on drift algae. Sea urchins can cause substantial erosion at low and moderate population densities (Table 4-2); at high densities, their destruction of reef substrata rivals clionid sponge erosion and can lead to rapid framework loss.

4.2.11. *Fishes*

Numerous fish species erode reef substrata while grazing on algae, and also fragment colonies while feeding on live coral tissues or when extracting invertebrates from coral colonies (Randall, 1974). Surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) are the principal grazing groups with some fishes in the latter family capable of scraping and extensive excavation. On western Pacific reefs, excavating parrotfishes primarily bite convex surfaces, thus reducing the topographic complexity of reefs (Bellwood and

Choat, 1990). Some Atlantic and Pacific parrotfishes occasionally scrape and ingest live coral tissues (Bellwood and Choat, 1990; Glynn, 1990). Triggerfishes (Balistidae), filefishes (Monacanthidae) and puffers (Tetraodontidae, Canthigasteridae) are largely carnivorous in feeding habits and are responsible for fragmenting or grazing on live coral colonies (Fig. 4-2 A). The jaw muscles and tooth armature are well developed in all of these families. Parrotfishes also have a pharyngeal mill, a gizzard-like organ that further reduces the size of ingested sediment. Fish teeth are composed of dahllite $[Ca_5(PO_4CO_3)_3(OH)]$ or francolite (the fluorinated form), both apatite minerals that are harder than $CaCO_3$ (Lowenstam and Weiner, 1989).

   Parrotfish grazers can produce large amounts of sediment on reefs, especially when their population densities are high. For example, *Scarus iserti* generated nearly 0.5 kg $CaCO_3$ $m^{-2}yr^{-1}$ on a Caribbean reef in Panamá with a high abundance of just under 1 fish per m^2. Entire grazing fish communities, comprised dominantly of parrotfishes, typically erode large amounts of reef substrata. One of the highest erosion rates reported for fishes, 9.1 kg $CaCO_3$ m^{-2} yr^{-1}, occurred in the lagoon of an Australian reef (Table 4-2). It should be recognized, however, that relatively few scarid species in any given fish community are capable of excavating significant amounts of carbonate substrata. For example, Bellwood and Wainwright (2002) noted that only one of 18 scarid species at a Lizard Island site (Great Barrier Reef) effected high rates of erosion. Additionally, at a Red Sea site, three of ten scarids contributed importantly to bioerosion, and at a Caribbean site (Carrie Bow Cay, Belize) only one of six scarids excavated reef substrata. In this regional comparison, the highest rate of bioerosion was effected by the Australian scarid *Chlorurus microrhinos,* which excavated 6,500 gm $m^{-2}yr^{-1}$ (Table 4-2). While carnivorous fishes can cause substantial damage locally, their reef-wide effects seem to be relatively minor. For example, a pufferfish (*Arothron*) that erodes about 20 g of coral per day results in a total reef loss of only 30 g $CaCO_3$ m^{-2} yr^{-1} (Glynn et al., 1972) because of a relatively low population size of 40 individuals per hectare (Table 4-2).

   Several other bioeroders known to produce traces or otherwise damage reef rock, e.g. foraminifers, zoanthids, bryozoans and brachiopods (Warme, 1975), may contribute to reef degradation under special conditions. To assess the relative importance of the various bioeroders considered in this survey, one may compare their rates of reef destruction with known carbonate production rates. Net carbonate production rates vary greatly among reefs and between reef zones, but 3,000 to 5,000 g $CaCO_3$ m^{-2} yr^{-1} have been reported for many of the world's coral reefs (Kinsey, 1983). Among the internal borers, clionid sponges and lithophagine bivalves can cause a comparable level of bioerosion, and of the external grazers sea urchins are equally destructive. Reef frameworks are generally reduced to silt and fine sand by internal borers and to fine and coarse sand by external grazers. The combined effects of other bioeroders may also contribute importantly to reef erosion in particular areas or zones and at different times.
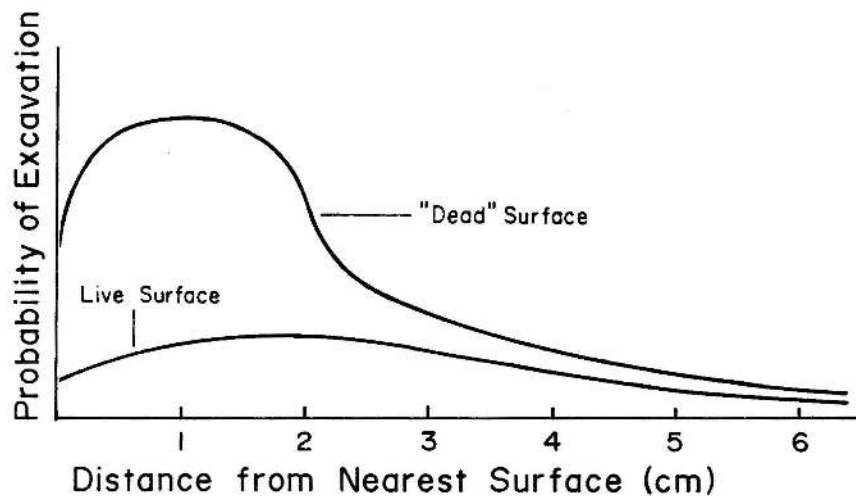
Figure 4-8. Graphic model showing the probability of excavation of endolithic bioeroders as a function of distance from a coral's surface (redrawn from Highsmith, 1981). Curves are illustrated for corals with dead and live surfaces.

4.3 CONDITIONS FAVORING BIOEROSION

Bioerosion increases under a variety of circumstances that can be classified according to (a) conditions causing coral tissue death and (b) conditions that provide a growth advantage to bioeroder compared with calcifying species' populations. Some of the more important situations that can alter the course of bioerosion are noted here in general terms. Specific examples are considered below in the examination of case studies (**4.5**).

Aside from a few species that invade coral rock directly through living tissues (e.g., some boring sponges, bivalves and possibly barnacles), the great majority of endolithic borers attack dead skeletons (Fig. 4-8). In general, any condition that causes coral tissue death will increase the probability of invasion by borers and grazers. Thus, any natural or anthropogenic disturbances that lead to the loss of live coral tissues will ultimately increase the chances of bioeroder invasion and higher rates of limestone loss. Many disturbances leading to tissue loss are obvious, including storm-generated surge that uproots and topples corals, sediment scour and burial, tidal exposures, sudden temperature changes, fresh-water dilution, sewage and eutrophication, predation, and disease outbreaks (Endean, 1976; Pearson, 1981; Grigg and Dollar, 1990).

While violent tropical storms are natural events that are known to seriously affect coral reefs, storm damage certainly must be exacerbated on reefs that have been heavily bioeroded beforehand. Sudden chilling episodes are also natural disturbances that can have devastating effects on tidally exposed or shallow coral assemblages, especially on high latitude reefs. Numerous incidences of coral bleaching (loss of zooxanthellae and/or pigmentation) and mortality were observed world-wide in the 1980s and 1990s,

and many of these events occurred during periods of elevated sea temperatures coincident with El Niño-Southern Oscillation activity. Corals that were damaged or killed during these bleaching events have been subject to further damage by bioerosion. Rutzler (2002) noted examples of accelerated boring sponge erosion on bleached Caribbean corals stressed by temperature extremes and other suboptimal conditions in recent years. In some parts of the eastern Pacific where coral mortality was high and community recovery slow, extensive damage by both internal and external bioeroders has been observed.

Increases in nutrient loading often cause coral tissue mortality, lowered reproductive success and lower rates of coral settlement and recruitment. Besides such direct negative effects on reef-building corals, nutrient inputs can also cause changes in the community structure of epilithic algae. On a La Saline Reef (Reunion Island), increased nutrification has been found to favor the replacement of algal turfs by encrusting calcareous algae and macroalgae (Chazottes et al., 2002). On the one hand, this qualitative change in algal cover can result in reduced bioerosion by external bioeroders and macroborers, but on the other hand it can elevate rates of bioerosion by microendolitic borers. External bioeroders (sea urchins and fishes) may feed less on calcareous algae and macroalgae than on turfs. This reduced grazing in turn allows the proliferation of endolithic borers, whose growth would otherwise be limited under intense grazing pressure. It is cautioned that this sequence of events is not invariant due to other factors that often accompany elevated nutrient conditions (see below).

Predator outbreaks leading to high coral mortality, such as by seastar (*Acanthaster*) and snail (*Drupella*) corallivores reported from various areas of the Indo-Pacific, can set the stage for rapid bioerosion. Territorial damselfish that colonize dead reef surfaces can cause complex responses that both increase and decrease bioerosion. Damselfish that invade dead coral patches typically kill nearby corals while enlarging their territories. Studies in Australia have shown that the algal turf communities maintained by damselfish favor the proliferation of internal bioeroders (Risk and Sammarco, 1982). However, the territorial defensive behavior of damselfish also limits the bioerosive activities of external grazers such as parrotfish and sea urchins (Glynn and Wellington, 1983; Eakin, 1993).

Coral tissue loss due to a variety of diseases can be substantial (**Chapter 6**; Peters, 1984). For example, "black line disease" or "black band disease", the result of a cyanobacterial infection (Rützler et al., 1983), may consume one-half of the living tissues of a coral during a single warm season infestation. All live tissues may be sloughed from corals by "white band disease", "shut-down-reaction" or "stress-related-necrosis". Though the causative agents of such diseases often remain elusive, their occurrence seems to be influenced by increased sedimentation and turbidity.

Since the majority of endolith bioeroders are suspension or filter feeders in contrast to calcifying species, which are dominantly autotrophic, generally increases in nutrients, organic matter and plankton biomass tend to favor increases in bioeroder compared with calcifier populations (Fig. 4-9). Because land runoff usually augments siltation and nutrient loading simultaneously (and sometimes pollutant levels), it is
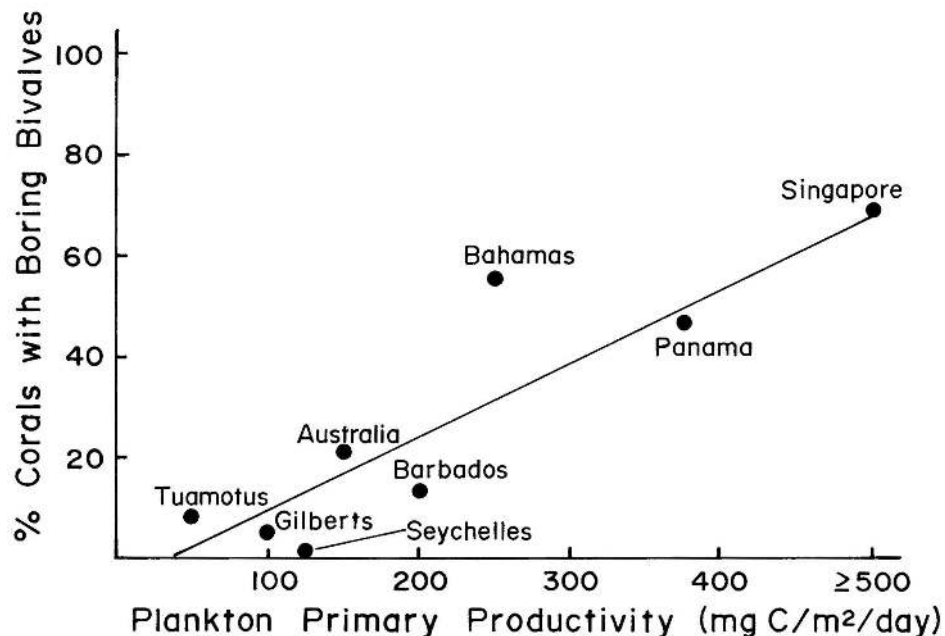
Figure 4-9. Relationship between the percentage of massive corals infested with boring bivalves and levels of phytoplankton productivity at several geographic locations (redrawn from Highsmith, 1980). Selected areas with values close to the plotted means are indicated. Each mean consists of various sampling areas and colony numbers, respectively, as follows: Tuamotu Islands—6, 212; Gilbert Islands—2, 58; Seychelle Islands—2, 12; Australia—7, 135; Barbados—7, 55; Bahama Islands—2, 64; Panama—4, 70; Singapore—5, 144.

often difficult to distinguish between these effects. Unlike La Saline Reef, Pari et al. (1998) found that a polluted reef in Tahiti (at Faaa) is subject to intense grazing by sea urchins. But this south Pacific site is influenced by elevated nutrients, and additionally by terrigenous sediments and chemical pollutants. Moreover, the Pacific reef also exhibits different algal assemblages. Thus, even though both reefs are subject to high nutrient regimes, it is not possible to predict changes in the rates of bioerosion because of potentially numerous confounding influences.

There are at least two ways in which bioerosion is self-reinforcing. The first of these is the weakening effect of bioeroders on reef structures and the skeletons of calcifying organisms. For example, as bioerosion increases the volume of internal spaces (porosity) of coral skeletons, less mechanical force is required for breakage, toppling and overturning (Fig. 4-10). Thus, heavily bioeroded reefs are more susceptible to damage by strong surge and projectiles accompanying violent storms. The second kind of positive feedback results from increasing levels of sediment production by bioeroders and its deleterious effects on calcifying populations.
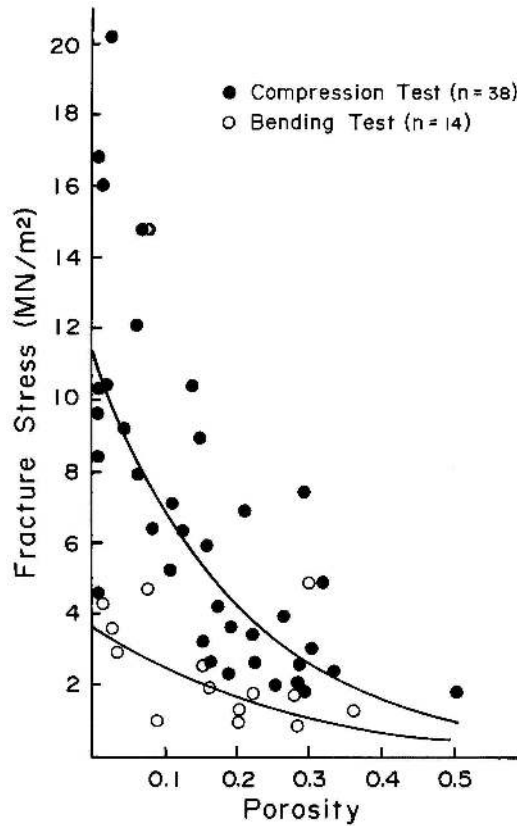
Figure 4-10. Plot of coral strength to breaking versus amount of bioerosion by *Lithophaga* (redrawn from Scott and Risk, 1988). The compression and bending tests are two measures of a coral's strength. n = Newton, a unit of force; MN = 0.22481 x 10^6 kg m s^{-2}. Porosity indicates the percent of the skeleton removed.

Overfishing can also promote increased bioerosion on reefs. If natural fish predators of some bioeroder populations are eliminated, e.g. triggerfishes that prey on sea urchins, then it is possible for grazing sea urchin populations to increase in size with a devastating effect on reef limestones (**4.5**).

4.4 VARIETY OF EFFECTS

The chief effect of bioerosion emphasized thus far is the mass of calcium carbonate that is reduced to sediments or is dissolved from reef substrata. The weakening of reef substrata by bioeroders that remove relatively little carbonate, but attack critical supporting structures, can be just as important in promoting reef erosion. Large massive corals may be easily toppled or overturned after their supporting bases have been weakened by endolithic borers such as *Cliona, Lithotrya* and *Lithophaga* or by

grazers that attack bases and hollow out the interiors of colonies such as *Diadema* and *Eucidaris*. Many of the displaced corals on reefs, e.g., those making up emergent, rubble ramparts or deep, forereef talus accumulations, owe their new locations in large measure to bioerosion. Large stands of *Acropora* corals that collapsed after *Acanthaster* predation on reefs in Japan, Palau and Australia were presumably destabilized as a result of the weakening of dead skeletons by intensified bioerosion (Moran, 1986; Birkeland and Lucas, 1990).

Aside from weakening reef substrata, the cavities produced by bioeroders increase habitat complexity and thus the variety and biomass of reef associated organisms. Numerous reef species live permanently attached to cavity walls, pass particular stages of development in cavities, and reside in cavities by day or night. Reef cavities tend to collect sediments that are produced locally or are transported to reefs from more distant sources. The microenvironmental settings of cavities promote internal cementation and the strengthening of reef substrata. Cycles of internal bioerosion, infilling of cavities and cementation may be repeated so that eventually the reef rock appears quite different from its original condition.

The sediments generated by bioeroders accumulate around reefs and eventually infill and bury frame-building species (Fig. 4-11). This effect leads to the shoaling of reef waters and influences the development of reef zonation. Under moderate regimes of bioerosion, sediment accumulation does not overwhelm reef framework growth, however, excessive bioerosion can lead to premature burial and widespread coral death.

When bioerosion is excessive it can reduce the topographic complexity of reefs. The reefs noted above in the western Pacific that were subjected to intense predation by *Acanthaster* and then bioeroded, lost much of their three dimensional structure with the collapse of the *Acropora* canopies. The loss of these erect corals would eliminate important microhabitats for fishes. The topographic complexity of eastern Pacific reefs can also be reduced by echinoid bioerosion following El Niño disturbances. Coral reefs in the eastern Pacific, particularly in the Galápagos Islands, have been bioeroded to rubble and sediment following high coral mortality and low recruitment, respectively, during and after the 1982-83 El Niño event (Glynn, 1994; Reaka-Kudla et al., 1996). Erect, branching coral frameworks have collapsed and massive corals have detached from the substratum and fragmented. Coral recruitment is now generally severely limited with macrobenthic communities composed dominantly of turf algae, gastropods, sea urchins and sea cucumbers.

Like many kinds of plants that spread from cuttings, it seems that some corals may actually benefit from increased breakage facilitated by bioerosion. A common mode of reproduction in many branching coral species is by asexual fragmentation (Tunnicliffe, 1979; Highsmith, 1982). It has been argued that propagation by this means, which usually results in local rather than distant dispersal, is advantageous to populations that are well adapted to particular environmental settings. Asexual reproduction occurs most commonly among branching, platey and other such colonies of delicate morphology with bioerosion aiding breakage by mechanical and biotic agents. Large clones of corals that dominate certain reef zones have arisen by this means (Highsmith, 1982).
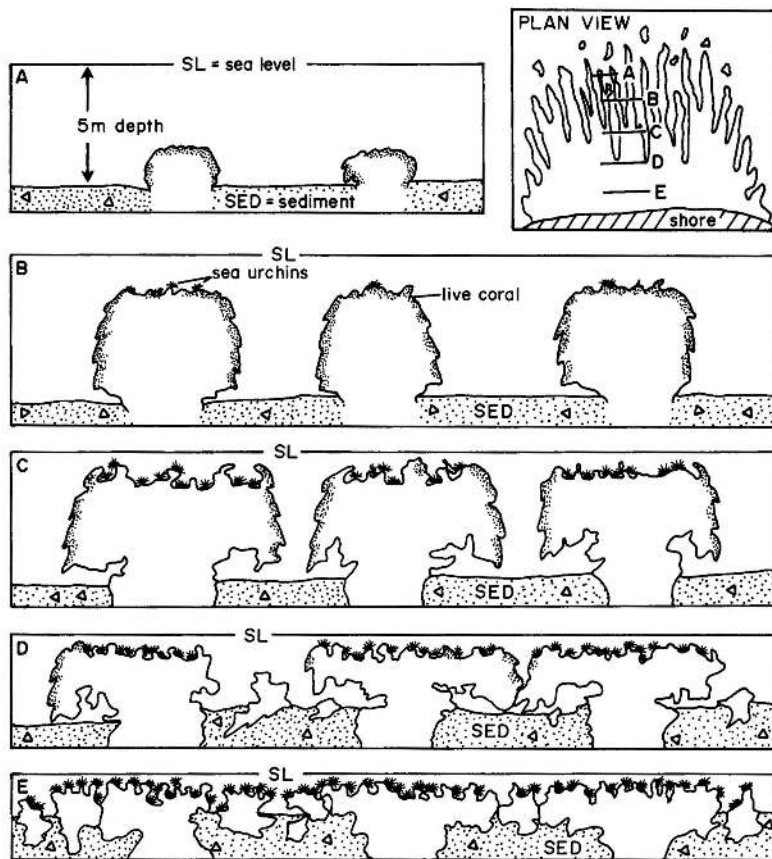
Figure 4-11. Cross-section views of a fringing reef off the west coast of Barbados showing coral framework growth, bioerosion, and infilling by bioeroded sediments. Panels **A** to **E** illustrate seaward (deep) to shoreward (shallow) reef sections. The inset plan view shows the location of the panels (after Scoffin et al., 1980).

4.5 CASE STUDIES

Four documented cases of environmental alterations that have affected reef-building corals and led to extensive bioerosion are now examined. The first two examples, disturbances caused by El Niño-Southern Oscillation and predator outbreaks, are ostensibly natural events. Runoff and overfishing effects are then examined, representing two examples caused by humankind.

4.5.1. *El Niño-Southern Oscillation*

Elevated seawater temperatures that accompanied the 1982-83 El Niño-Southern Oscillation **(ENSO)** caused high coral mortality on reefs in the equatorial eastern

Pacific. Mortality ranged from 50 to 99%, resulting in the virtual elimination of coral cover on many reefs. Coral recruitment has been low to non-existent on the affected reefs, which had shown little signs of recovery after 10 years. A more recent analysis of coral reef recovery in the eastern tropical Pacific, including effects of both the 1982-1983 and 1997-1998 ENSO events, revealed no recovery at 8 of 12 sites for periods of up to 20+ years (Wellington and Glynn, in press).

Sea urchin abundances have increased dramatically on dead reef patches. In Panamá, *Diadema* population densities have increased from 3 inds m^{-2} before 1983 to 80 inds m^{-2} after 1983 (Glynn, 1988). Similarly, in the Galápagos Islands *Eucidaris* population densities increased from 5 to 30 inds m^{-2} from before to after 1983. The grazing activities of these sea urchins are very destructive (Table 4-2) and their sudden increases in population size, combined with low coral recruitment, have resulted in severe bioerosion of coral reef frameworks. Post El Niño bioerosion rates for *Diadema* in Panamá amounted to 10-30 g dry wt $CaCO_3$ m^{-2} day^{-1}, and for *Eucidaris* in the Galápagos 50-100 g dry wt $CaCO_3$ m^{-2} day^{-1}. Carbonate breakdown caused by other external and internal bioeroders was about equal to that caused by sea urchins in Panamá, but only about one-fifth of the erosion caused by sea urchins in the Galápagos Islands. Total bioerosion ranged from 10-20 kg $CaCO_3$ m^{-2} yr^{-1} in Panamá and from 20-40 kg $CaCO_3$ m^{-2} yr^{-1} in the Galápagos Islands. Both of these rates exceed net carbonate production of [~10 kg $CaCO_3$ m^{-2} yr^{-1}], estimated for reefs in these areas before 1983. If bioerosion continues at this pace, without an increase in coral recruitment, it is highly likely that many reef formations in the eastern Pacific will disappear.

Continuing studies in the Galápagos Islands and Panamá, to the year 2000, demonstrate virtually total reef frame loss in the former region (Glynn, 1994; Reaka-Kudla et al., 1996; Glynn et al., 2001) and substantial calcium carbonate declines in the latter (Eakin, 2001). Eakin's modeling results, incorporating post 1997-98 data, indicate that the Uva Island reef in Panamá is still in an erosional state, ranging from around –3,000 to –18,000 kg $CaCO_3$ yr^{-1} net.

4.5.2. *Crown-of-thorns Seastar (Acanthaster)*

This example is instructive because it reveals some of the long-term consequences of coral death and bioerosion at the community level. Between 1981 and 1982, the corallivore *Acanthaster planci* increased greatly in abundance at Iriomote Island, southern Japan, and by the end of 1982 it had killed virtually all the corals on a large study reef (Sano et al., 1987). This sudden loss of live coral precipitated major changes in the physical and biological character of the coral reef.

About two years following the *Acanthaster* outbreak, most of the erect coral (*Acropora*) canopy had collapsed, a result of bioerosion and water movement. Compared with the live reef, the dead reef exhibited low structural complexity. By 1986 all of the corals were broken apart and the reef formation had been converted into a flat plain of unstructured coral rubble. The degradation of the reef was correlated with marked changes in the fish community. As the topographic complexity of the reef decreased, the numbers of associated fish species and their abundances also declined. Fishes that fed exclusively on live coral tissues disappeared completely from the dead

reefs. The declines in fishes with other diets, e.g. planktivores, herbivores and omnivores, were believed due in large measure to the loss of living space and to overall declines in prey on the degraded reef.

More recent studies of large-scale coral predation by *Acanthaster*, followed by intense bioerosion with reductions in reef fish abundances and diversity, have followed in broad outline the course of events at the Iriomote reef described above. A follow-up study of the degraded Iriomote reef demonstrated rapid recovery under conditions of high coral recruitment and survivorship (Sano, 2000). Arborescent *Acropora* spp. began recruiting in 1989, and by 1995 and following years coral cover had reached about 100%, closely matching pre-*Acanthaster* live coral cover values. This buildup in coral cover was accompanied by increases in the species richness and density of adult fish assemblages, to predisturbance levels. It will be instructive to compare this example of rapid recovery, occurring over a period of only 8 years, with data from other coral reef areas as they become available.

4.5.3. *Runoff (Eutrophication, Sedimentation, Freshwater and Pollutants)*

One of the best examples of reef degradation caused by runoff is that reported for the Kaneohe Bay, Hawaii coral reef ecosystem (Smith et al., 1981; Jokiel et al., 1993). Because man's mismanagement of the Kaneohe Bay water shed has led to multiple effects, e.g., sewage pollution, agricultural runoff, increased sedimentation and freshwater dilution, it is not always possible to identify individual or combined stressor effects. However, the occurrence of coral reef mass mortalities during storm floods and a general decline in coral cover during a period of increasing sewage stress implicates these stressors in the degradation of Kaneohe Bay coral reefs over the past several decades.

During the first half of this century the coral reefs of Kaneohe Bay were in a healthy state, supporting a local artisanal fisheries and offering one of the best underwater vistas of "coral gardens" in the Hawaiian Islands. In 1963, a large sewage outfall was installed in the bay, which had an increasing effect on corals until 1978 when the outfall was moved to the deep ocean outside the bay. The eutrophication caused by increasing sewage loads favored the growth of a bubble alga (*Dictyosphaeria*) and suspension feeding and bioeroding species that combined to degrade the reef communities over a 15 year period (Fig. 4-12). Following the sewage diversion, clear signs of renewed coral growth, reduced bioerosion and reef community recovery were evident by 1983. Severe storm flooding in 1987 caused extensive coral mortality, but surviving corals quickly resumed rapid growth and the condition of reef communities (as of 1993) has remained favorable. Another 10 years have passed without a major disturbance event (P. Jokiel, J. Stimson, pers. comm.). Therefore, it is likely that the restricted branch-growth areas resulting from the 1987 flooding event are now located at lower horizons on colonies due to the uninterrupted vertical skeletal growth over the past 16 years. This case history illustrates a degree of resiliency to a disturbance that might have led to reef community collapse in a sewage-stressed environment.

As the human population continues to increase along tropical and subtropical coastal areas, it should be no surprise that reports of associated pollution stress are also

on the rise. Indeed, numerous recent studies have documented the deterioration of coral reefs worldwide with eutrophication, related to urbanization (sewage pollution), inappropriate agricultural practices and industrial pollution sources, being the root cause of this decline. It is cautioned that the entry of polluted freshwater into coastal zone communities is not always obvious as sources can include large volumes of groundwater discharge as well as surface effluents. Representative examples of coral reef bioerosion and deterioration under nutrient-rich conditions are noted for the Indian Ocean (Risk et al., 1993; Chazottes et al., 2002), Indonesia (Tomascik et al., 1997; Holmes et al., 2000), the Great Barrier Reef, Australia (Risk et al., 1995) and at several other Pacific Ocean sites (Hutchings, 1994), off Brazil (Leão et al., 1993) and at several localities in the Caribbean Sea (Smith et al., 1993).

4.5.4. *Overfishing*

Several studies in the Caribbean and off the Kenyan coast in the Indian Ocean have presented evidence suggesting that sea urchin abundances are controlled by finfish predators. When fish predators of sea urchins are abundant, urchin abundances tend to be low, but when fishing pressure is high, leading to the disappearance of urchin predators, then urchins can become exceedingly abundant. A study of protected (non-fished) and overfished Kenyan coral reef lagoons indicates that the removal of top, invertebrate-eating, fish carnivores can have cascading effects on coral reef community structure and function (McClanahan and Shafir, 1990).

Triggerfish predators of sea urchins were relatively abundant in protected coral reef lagoons, but rare in comparable unprotected environments. The removal of the natural predators of sea urchins by overfishing resulted in several direct effects on the urchin prey and several indirect effects on the condition of the coral reef community. Overfished reefs demonstrated high sea urchin abundances, high urchin survival, and high urchin diversity compared with non-fished reefs. Correlated with the dominance of sea urchins on overfished reefs were declines in (a) live coral cover, (b) calcareous and coralline algal cover, (c) substratum diversity, and (d) topographic complexity. These changes were caused by increased substratum bioerosion, especially by *Echinometra mathaei* (de Blainville), the competitively dominant sea urchin in unprotected Kenyan reef lagoons. The end result of overfishing is accelerated bioerosion, a reef surface dominated by algal turf, and likely a decline in the reef's fisheries productivity.

4.6 CONCLUSIONS

The fossil record demonstrates that bioerosion and reef growth have always been inseparable. Moderate levels of bioerosion may benefit coral reefs in at least four ways, by (1) creating sedimentary substrata that provide lebensraum for hosts of associated reef species, (2) providing cavities and contributing toward topographic complexity that serve to increase the biodiversity, biomass and productivity of reef communities, (3) structuring reef morphology and growth, and (4) promoting the regeneration and rejuvenation of senescent reef-building organisms.
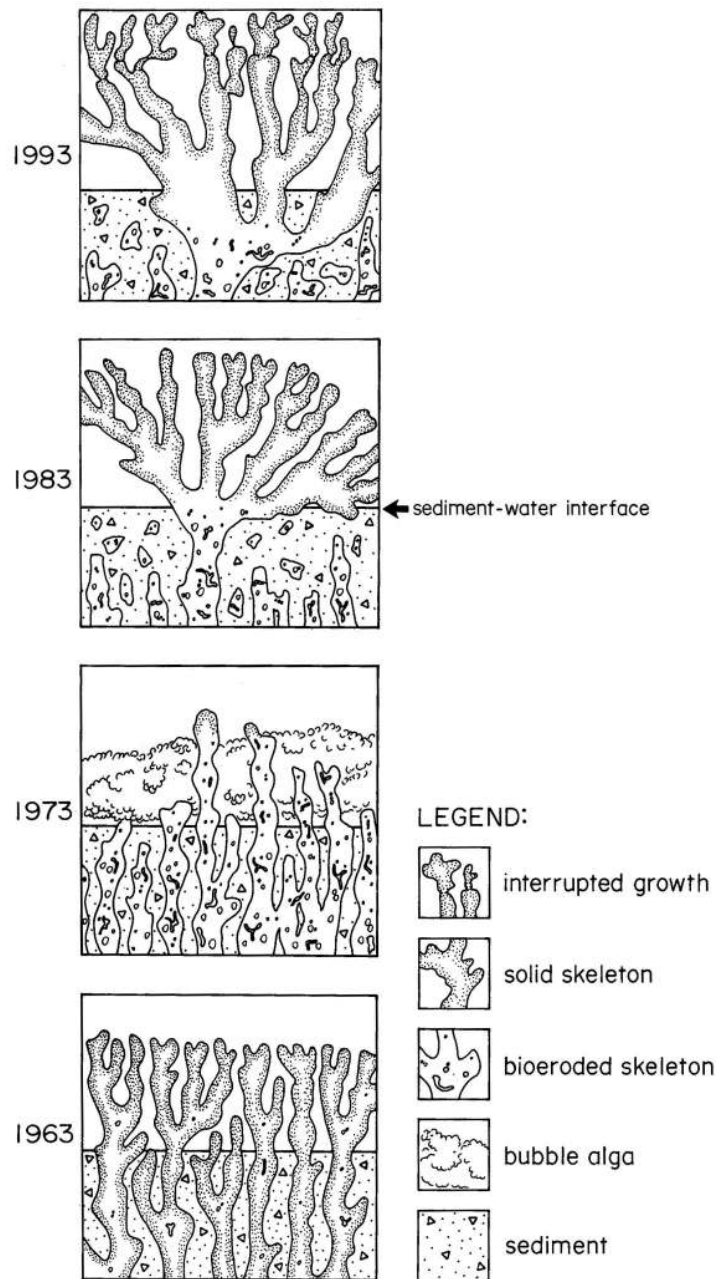
Figure 4-12. Cross-section of *Porites compressa*, the predominant frame-building coral of the Coconut Island fringing reef. Prepollution (1963), pollution (1973), and postpollution (1983 and 1993) periods are shown (modified after Jokiel, 1986).

Except for obvious reef destruction by large populations of sea urchins, bioerosion per se as a possible threat to coral reefs is seldom considered explicitly. This is probably because of the large amount of 'cryptic' bioerosion caused by endoliths and the often delayed effects of bioerosion on coral reef communities. For example, descriptions of reef damage caused by violent storms are numerous in the literature, but the contributory effects of bioersoion are seldom mentioned. The prior weakening of reef structures by bioerosion or the accumulation of sediments causing scour and burial during a storm are effects that may have been initiated years before an acute disturbance event resulting in reef devastation.

What are some of the measures that can be taken to limit bioerosion? The most obvious is to reduce coral mortality because numerous bioeroders increase their activities and abundances on dead reef substrata. Direct damage to calcifying organisms can be reduced significantly by several practices already adopted within protected coral reef parks. For example, the use of mooring buoys, navigational markers, the prohibition of destructive fishing techniques, and the banning of coral collecting or touching live corals have all alleviated damage to coral reefs in many areas. The possibility of indirect effects, such as overfishing causing increases in bioerosion, should also be considered in coral reef management plans.

Another method of limiting coral mortality after severe physical damage, e.g. by a ship grounding, involves restoration techniques to stabilize damaged corals and reef substrata (Hudson and Diaz, 1988). Hard and soft corals may be transplanted and cemented to stable reef substrata, fractured frameworks may be secured, and the rebuilding of reef topography accomplished by replacing and cementing dislodged corals and sections of framework.

Numerous effects that can accelerate bioerosion are often far-removed from coral reefs and therefore sometimes difficult to link with reef decline. Deforestation, land-clearing and mining activities lead to increased sedimentation, fresh-water dilution and nutrient loading around reefs that may be situated hundreds of kilometers from the affected sites. These sorts of activities may alter reef environments such that certain types of bioeroders could increase in number and possibly accelerate destructive processes. The potential damage of such anthropogenic stresses to coral reefs also may be augmented by natural disturbances such as violent storms, extreme temperature changes, diseases and predator outbreaks. For example, most corals may tolerate low salinities for a few hours or days, but salinity stress in combination with a pathogen could precipitate high coral mortality. Many kinds of runoff include combinations of several pollutants, e.g. sewage, detergents, heavy metals, fertilizers, pesticides, and oil, that may act synergistically to reduce live coral cover.

In summary, the dynamic balance between reef growth and bioerosion depends on the vitality of numerous calcifying species. If humankind's activities can be limited to non-intrusive pursuits such as observing and filming reef organisms, and if reef water quality and natural circulation patterns can be safeguarded, then one of the world's most exquisite ecosystems can be enjoyed by posterity.