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*)

Abstract

Bioerosion, involving the weakening and breakdown of calcareous coral reef structures, is due to the chemical and mechanical activities of numerous and diverse biotic agents. These range in size from minute, primarily intra-skeletal organisms, the microborers (e.g., algae, fungi, bacteria) to larger and often externally-visible macroboring invertebrate (e.g., sponges, polychaete worms, sipunculans, molluscs, crustaceans, echinoids) and fish (e.g., parrotfishes, acanthurids, pufferfishes) species. Constructive coral reef growth and destructive bioerosive processes are often in close balance. Dead corals are generally subject to higher rates of bioerosion than living corals, therefore, bioerosion and reef degradation can result from disturbances that cause coral mortality, such as sedimentation, eutrophication, pollution, temperature extremes, predation, and coral diseases. The effects of intensive coral reef bioerosion, involving El Niño-Southern Oscillation, *Acanthaster* predation, watershed alterations, and over-fishing, are re-examined after ~20 years (early 1990s–2010). We review the evidence showing that the biologically-mediated dissolution of calcium carbonate structures by endolithic algae and clionaid sponges will be accelerated with ocean acidification. The $CaCO_3$ budget dynamics of Caribbean and eastern tropical Pacific reefs is reviewed and provides sobering case studies on the current state of coral reefs and their future in a high-CO_2 world.

Keywords

Rates • Excavating • Degradation • Acidification • Microborer

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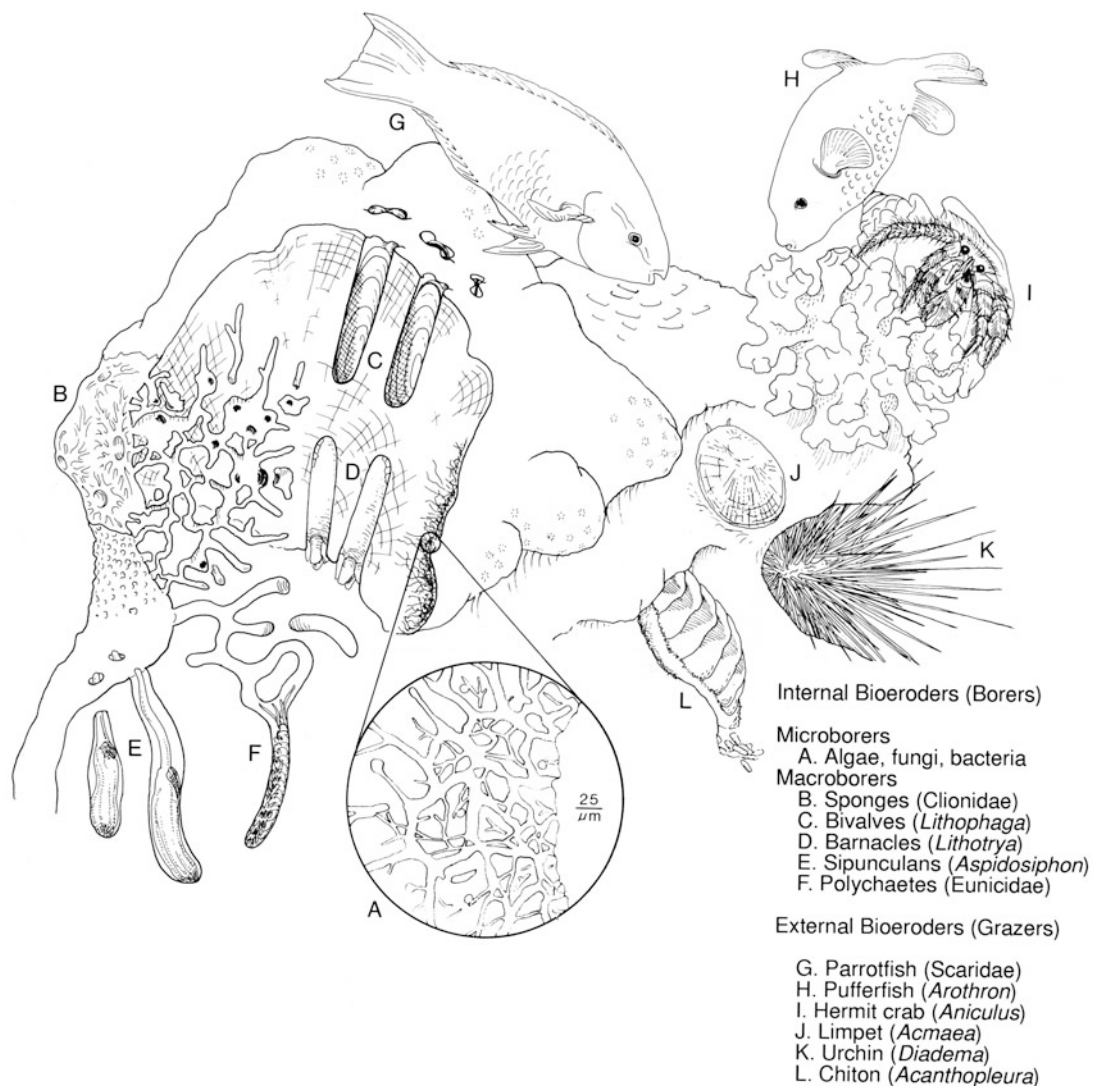e-mail: pglynn@rsmas.miami.edu

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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). Recent research supports this hypothesis (Enochs 2012). 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,

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*)

Fig. 4.1 Variety of external and internal bioeroders that commonly attack coral skeletons. A legend provides identification of the taxa illustrated

Fig. 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)
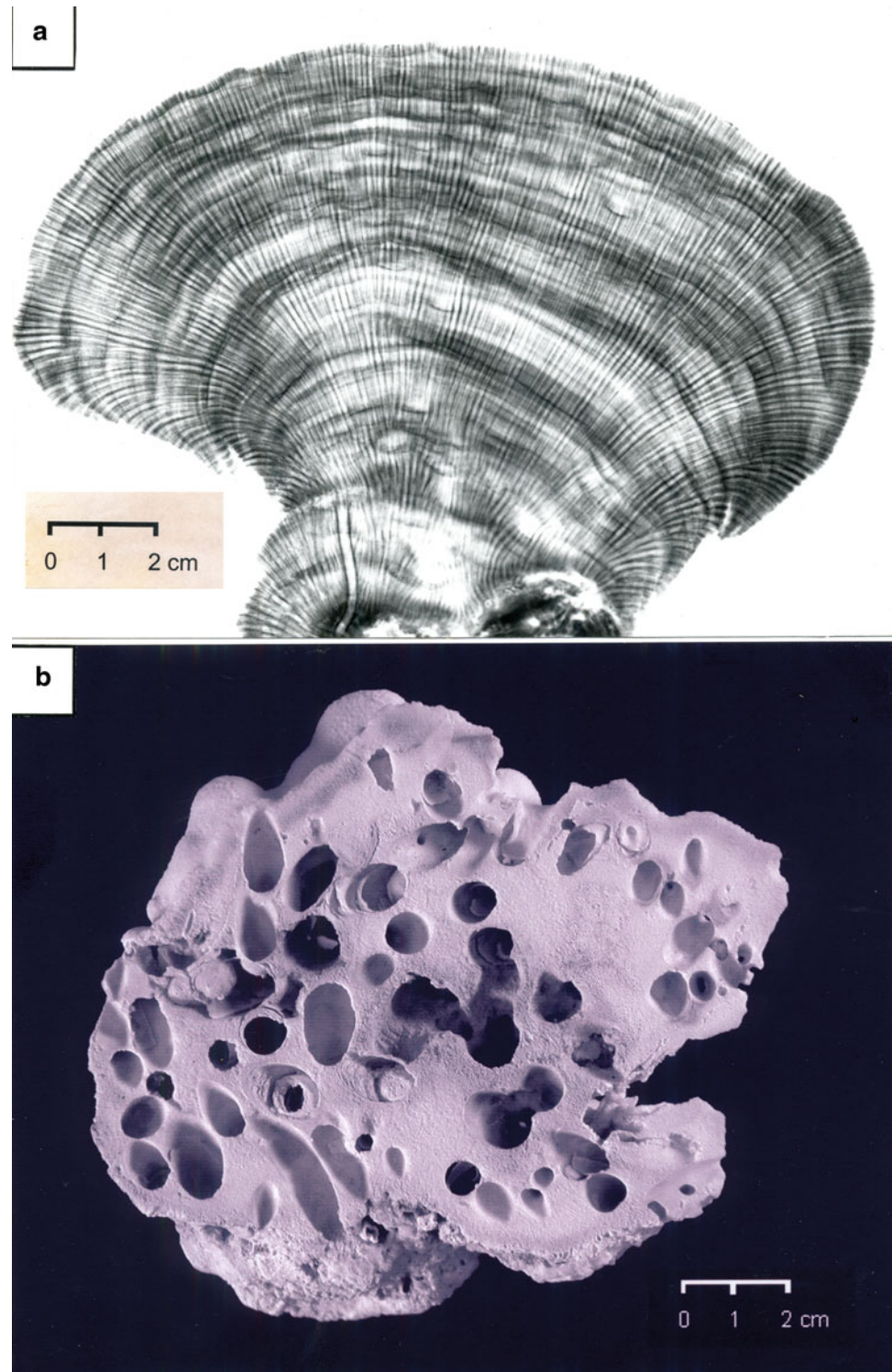
e.g. lithophagine bivalves, can severely damage and weaken the colony skeleton (Fig. 4.2b).

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
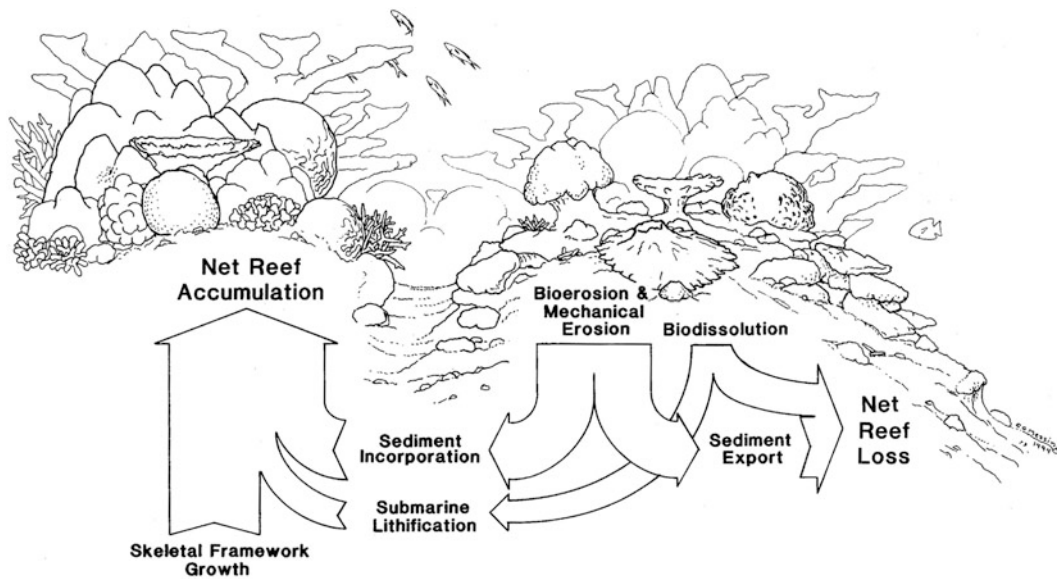
Fig. 4.3 A generalized scheme illustrating the principal components of coral-reef construction and destruction. In order for reef growth to occur, rates of bioerosion and mechanical erosion must not exceed the rate of net reef accumulation. The relative contribution of inorganic and biological dissolution (= biodissolution) to total reef dissolution is presently unknown. Both components are likely to increase with ocean acidification

decline abruptly, for example during a stressful thermal bleaching event, or over an extended period, such as years of increasing sedimentation or eutrophication, coral recruitment and growth decline or cease, limestone foundations are compromised 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. For example, the recovery of the Kān'eohe Bay *Porites* fringing reef, from 1993 to the present (2013), is examined. More recently attention has turned to ocean acidification and its effects on coral carbonate structures. This newly recognized factor, affecting calcification and cementation, can potentially exacerbate bioerosive processes and is also considered below.

In light of 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, 2005), Warme (1975, 1977), Risk and MacGeachy (1978), Trudgill (1983), Macintyre (1984), Hutchings (1986, 2011), Perry and Hepburn (2008), Tribollet (2008), and Tribollet and Golubic (2011). An online bibliographic review of the bioerosion literature is provided by Wilson (2008).

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 1983a). 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 features made up of calcareous particles that are generated in large measure by the activities of bioeroders (Sects. 2.2 and 3.4).

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 five to nine 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 are probably more intense now than at any time in the past (Steneck 1983b). 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 Hawai'i 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 m. Species of *Hyella*, *Plectonema*, *Mastigocoleus*, and *Entophysalis*, for example, have been found on limestone surfaces, inside cavities, and penetrating reef rock (Fig. 4.4a, 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 and 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 [1988] 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. 4.4c, d). Endolithic fungi growth can cause unique skeletal protuberances in living corals due to the localized deposition of dense skeletal material, perhaps as defensive barrier (Le Campion-Alsumard et al. 1995). Fungi have also been implicated in the etching of calcareous surfaces, the weakening and dissolution of calcareous

Fig. 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** = 40 μm, **c** = 5 μm, **d** = 25 μm, **e** = 200 μm, **f** = 100 μm (From May et al. 1982)
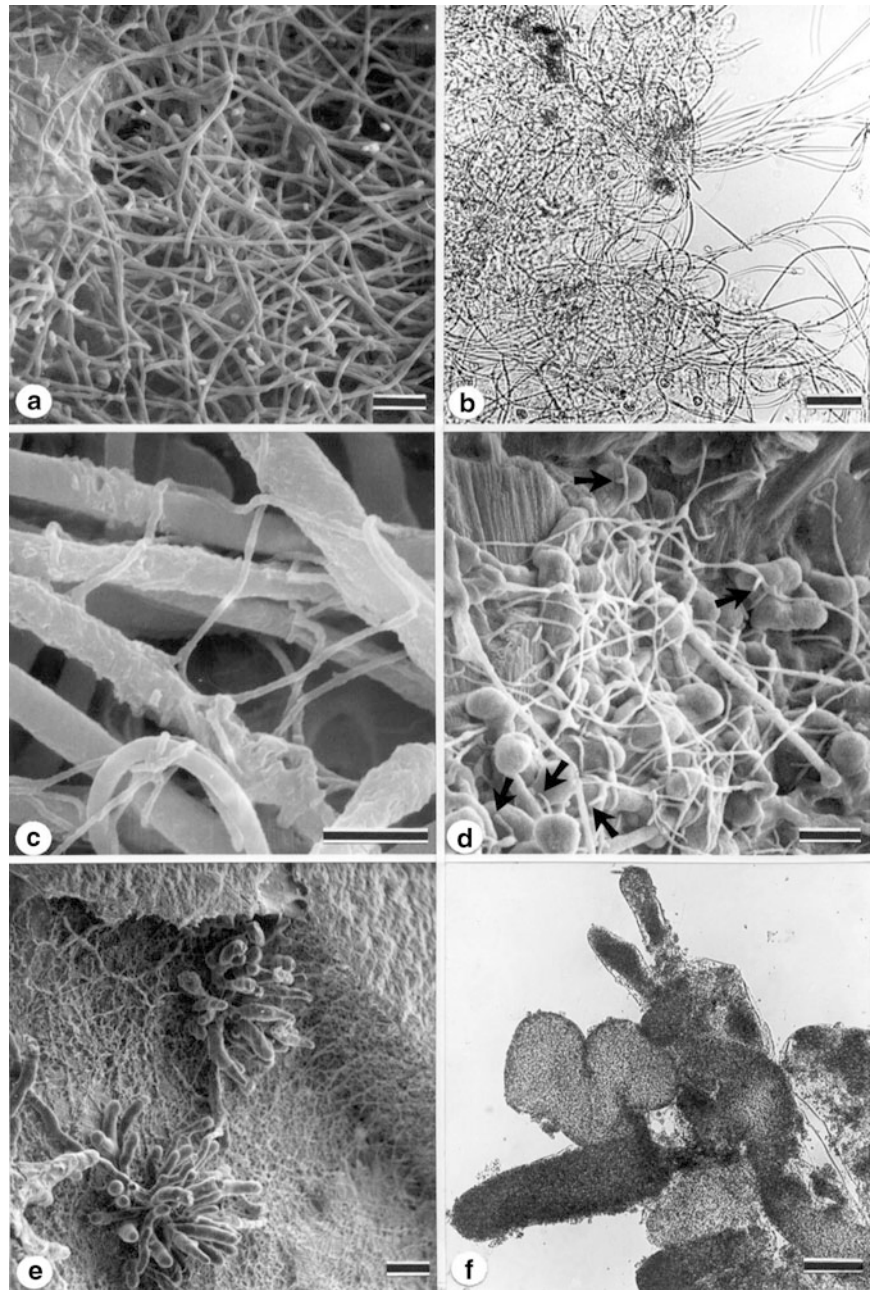
sediments as well as the calcareous tube linings of various endoliths. Because of the difficulty of distinguishing between fungal and algal borings, estimates of dissolution rates due to boring fungi alone are not yet available.

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. 4.4e, 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 (Sect. 1.1). Nonetheless, mixtures of internal bioeroder taxa – including green and red algae, bacteria, cyanobacteria, and fungi – can produce similar high-end erosion rates, ranging from 330 g $CaCO_3$ m^{-2} year^{-1} on a Caribbean coral reef at Bonaire to 470 g $CaCO_3$ m^{-2} year^{-1} on the Great Barrier Reef (Table 4.1).

Table 4.1 Rates of bioerosion by internal borers

Taxonomic group	Erosion rate (g CaCO$_3$/m^2/year)	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 (GBR), Australia	Tudhope and Risk (1985)
Cyanobacteria, algae, fungi	80	Chlorophyte and cyanobacteria predominant[a]	?	Inshore reef, eutrophic, turbid waters	Snapper Island, GBR	Tribollet and Golubic (2005)
	430			Offshore reef, oligotrophic, clear waters	Harrier Reef	
	470				Osprey Reef	
Cyanobacteria, chlorophytes, rhodophytes, fungi, bacteria	330 ± 50[b]	?	?	Leeward reef, high coral cover	Bonaire	Perry et al. (2012)
	290 ± 10[b]	?	?	Windward reef, low coral cover		
Porifera						
Clionaid sponges, *Pione lampa* Laubenfels predominant	23,000	Infested limestone substrates	30–80	Subtidal limestone notch, 1–3 m depth	Bermuda	Neumann (1966)
Cliona and *Siphonodictyon*	7000	Abundant in crustose coralline algae and in dead and live corals	30–80	Subtidal test blocks fringing reef	Bermuda	Rützler (1975)
	180[c]				Barbados	Scoffin et al. (1980)
Clionaid sponges	10 ± 2	*Cliona delitrix*	?	Leeward reefs, high coral cover	Bonaire	Perry et al. (2012)
	70 ± 20	*C. aprica*	?			
		C. caribbaea				
	2 ± 4	*Cliona delitrix*	?	Seaward reefs, low coral cover		
	5 ± 4					
Polychaeta						
Cirratulid, eunicid, sabellid, and spionid worms	690	13,000 ind. m^{-2}	10–30[d]	Forereef slope	Lizard Island, GBR	Davies and Hutchings (1983)
	840	24,000 ind. m^{-2}		Reef flat		
	1800	85,000 ind. m^{-2}		Lagoonal patch reef		
Crustacea						
Lithotrya ?dorsalis Sowerby	14[c]	Common	?	Fringing reef	Barbados	Scoffin et al. (1980)
	0.8 cm^3 ind^{-1} year^{-1}					
Lithotrya sp.		Common	2–4[e]	Intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)
Sipuncula						
Phascolosoma, 3 spp.		Uncommon in corals	<63	Fringing reef	Barbados	Scoffin et al. (1980)
Paraspidosiphon, 3 spp.	8[d]					
Lithacrosiphon gurjanovae Murina						
Mollusca						
Lithophaga nausta (Phillipi)	0.9 cm^3 ind^{-1} year^{-1}	Common	?	Intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)

(continued)

Table 4.1 (continued)

Taxonomic group	Erosion rate (g CaCO$_3$/m^2/year)	Borer abundance	Particle size (μm)	Habitat	Locality	Source
Lithophaga laevigata (Quoy and Gaimard)	9000	1,870 ind. m^{-2}	10–100	Largely dead patch reef, 6–10 m depth	Caño Island, Costa Rica	Scott et al. (1988)
Lithophaga aristata (Dillwyn)						
Invertebrata						
Sipunculans, Polychaete worms, Bivalve molluscs	50 ± 23[f]	All taxa present	?	Inshore reef, eutrophic,	Low Isles	Tribollet and Golubic (2005)
			?	Turbid waters	Snapper Island, GBR	
	280[g]	Increase in boring sponges	?	Inshore and offshore reefs	Snapper Island	
					Low Isles	
					Harrier Reef	
	80[g]	Worms predominant (sipunculans, polychaetes)	?	Offshore reefs, oligotrophic	Lizard Island	
					Ribbon Reef	
					Osprey Reef	

[a]Predominant taxa present on exposed surfaces

[b]Mean rate (±1SD), low confidence in data

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

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

[e]From Ahr and Stanton (1973)

[f]Mean rate (±1SD) for six sites, exposure time = 1 year

[g]Mean rate for three sites, exposure time = 3 years

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, molluscs, 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 formerly regarded single species of *Cliona* in the Caribbean consists of at least three distinct excavating sponge species. Upon splitting open infested corals, clionaid sponges are revealed as brown, yellow or orange patches lining the corroded interiors of the coral skeleton (Fig. 4.5a, 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,

Table 4.2 Rates of bioerosion by external grazers

Taxonomic group	Erosion rate (g CaCO$_3$ m^{-2} year^{-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	2–4	0.5–2.0	Lower seaward slope	Gulf of Chiriquí, Panama	Glynn (1988)
	3,470–10,400	50–150				
Diadema savignyi 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	0.09	?	Outer reef flat	La Saline reef, Reunion Island	Chazottes et al. (2002)
	4,300	14.0				
Echinothrix diadema (Linnaeus)	803	0.6	Sand	Reef lagoon	Moorea, French Polynesia	Bak (1990)
Eucidaris galapagensis Döderlein	3,320	4.6	0.05–3.0	Reef flat, pre-1982	Floreana Island, Galápagos Islands	Glynn (1988)
	22,300	30.8		Reef flat, post-1983		
Diadema antillarum	10 ± 10	*D. antillarum*	?	Leeward reefs	Bonaire	Perry et al. (2012)
Echinometra viridis	10 ± 20	Predominant grazer		High coral cover		
	0			Windward reefs		
				Low coral cover		
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)

Table 4.2 (continued)

Taxonomic group	Erosion rate (g CaCO$_3$ m^{-2} year^{-1})	Grazer abundance (ind. m^{-2})	Particle size (mm)	Habitat	Locality	Source
Scarus vetula (Bloch and Schneider)	140 ± 30[c]	0.08	Silt-sand?	Reef slope	Bonaire,	Bruggemann et al. (1996)
	2,420 ± 190			Shallow reef	Netherlands Antilles	
Grazing and browsing fishes	110	0.01	?	Patch reef	Bermuda	Bardach (1959, 1961)
Chlorurus microrhinos[d]	420–5,470	0.0007–0.009[e]	Fine sand	Fringing reef	Lizard Island	Bellwood (1995)
	1,010–3,280	0.002–0.005[f]	Fine sand	Fringing reef	Heron Island	Bellwood (1996)
	6,500	0.006		Shallow reef edge	Lizard Island, GBR	
Chlorurus sordidus (Forsskål)	110–500	0.02[e]	Fine sand	Fringing reef	Lizard Island	Bellwood (1995)
	260–980	0.011–0.12[f]		Fringing reef	Heron Island	
Parrotfishes (dominantly)	110–9,100	?	?	Reef flat, slope,	Llewellyn reef, Australia GBR	Kiene (1988)
	400–600	0.04–0.06	Fine sand-gravel	Lagoon habitats		
				patch reefs	Saipan, Mariana Islands	Cloud (1959)
Scaridae	7 ± 1	primary grazers	?	Inshore reefs, eutrophic, turbid waters	Snapper Island	Tribollet and Golubic (2005)
					Low Isles	
	320 ± 40	primary grazers	?	Offshore, oligotrophic, clear waters	GBR	
					Lizard Island	
	770 ± 220				Ribbon reef	
					GBR	
Sparisoma viride	2100 ± 1060	*S. viride* predominant	?	Leeward reefs	Bonaire	Perry et al. (2012)
	2750 ± 1390			High coral cover		
				Seaward reefs		
	950 ± 620			Low coral cover		
	1750 ± 810					
Pufferfish						
Arothron meleagris (Bloch and Schneider)	30	0.004	2–8	Pocilloporid reef	Pearl Islands, Panama	Glynn et al. (1972)

[a]Dominant echinoid affecting 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 *Chlorus 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)

Cliona sp. 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). In a comparative study in Bonaire, of leeward and seaward reefs with high and low coral cover respectively, Perry et al. (2012) reported significantly higher clionaid bioerosion rates on the former than the latter (Table 4.1).

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. 4.5e–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. Based on careful microscopic examination, Rützler and Rieger (1973) estimated that only about 2–3 % of coral skeletons are dissolved with the remainder dispersed as

Fig. 4.5 Boring sponges in limestone substrates. (**a**) Two oscula of *Pione* (formerly *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 *P. lampa*. (**g**) Group of chips etched from substratum by *P. lampa* but still in place. Magnification: **a**, **c**, **d** ×3; **b** ×140; **e**, **f** ×1,500; **g** ×600 (**a**–**d** from Rützler 1974; **e**, **f**, **g** from Rützler and Rieger 1973)
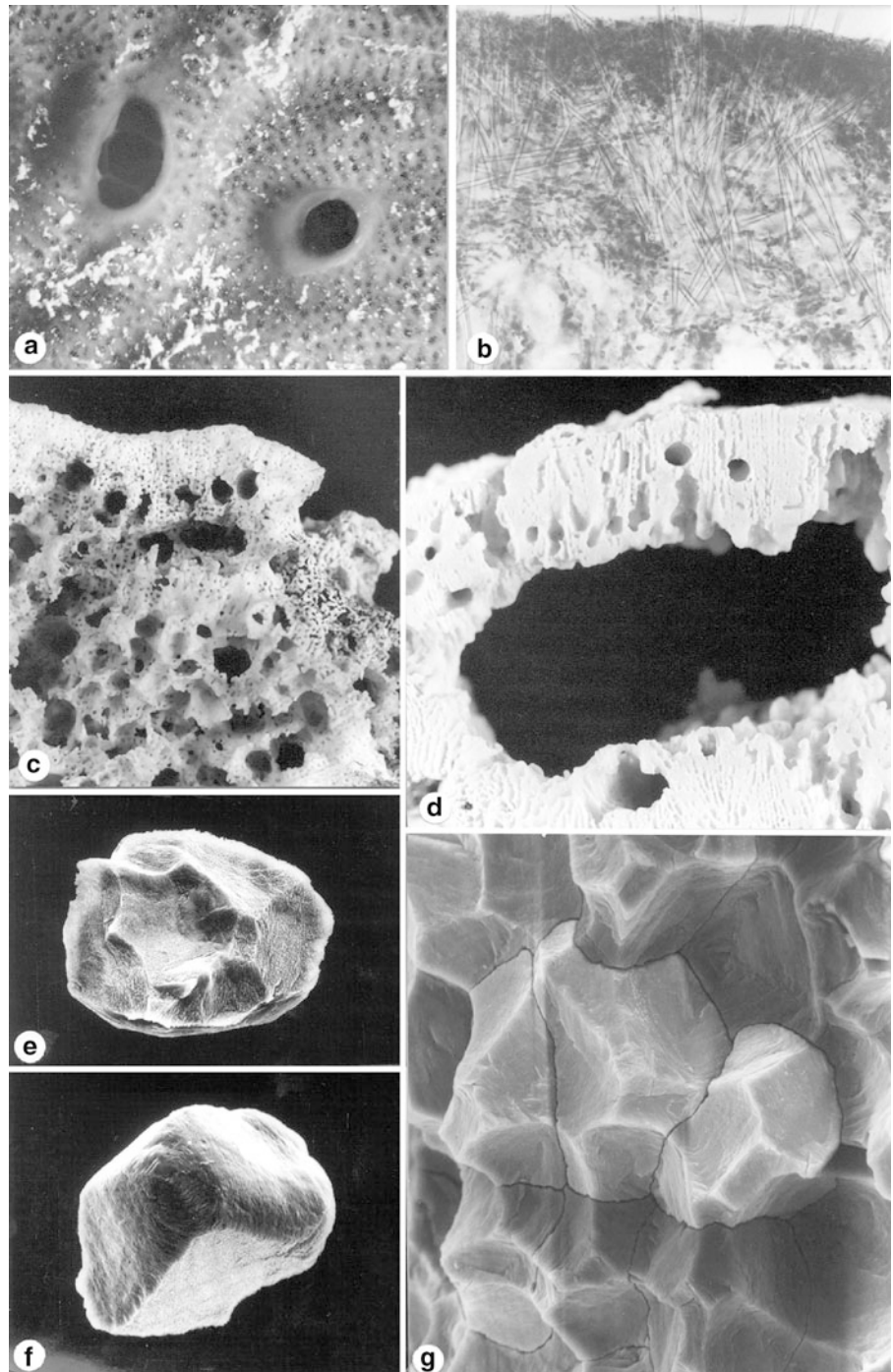
silt-sized chips. These oval-shaped, faceted chips are easily recognized in sediments and can contribute up to 30–40 % numerically to the fine silt fraction of sediments on Pacific and Caribbean reefs. However, a recent study that simultaneously measured chemical and mechanical (chip production) bioerosion found that the rate of chemical dissolution was three times greater than the amount of $CaCO_3$ eroded via chip production (Zundelevich et al. 2007).

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,

Fig. 4.6 A Caribbean boring sponge (*Cliona* cf *caribbea*) covering and eroding several square meters of reef substrate, San Blas, Panama, 3 m depth (30 June 1993). *Arrows* denote perimeter of sponge patch

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 chaetae (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).

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} year^{-1} on the reef front to 1.8 kg m^{-2} year^{-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 the 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*, members of the thoracican barnacle taxon, 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 ha^{-1} year^{-1} 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).
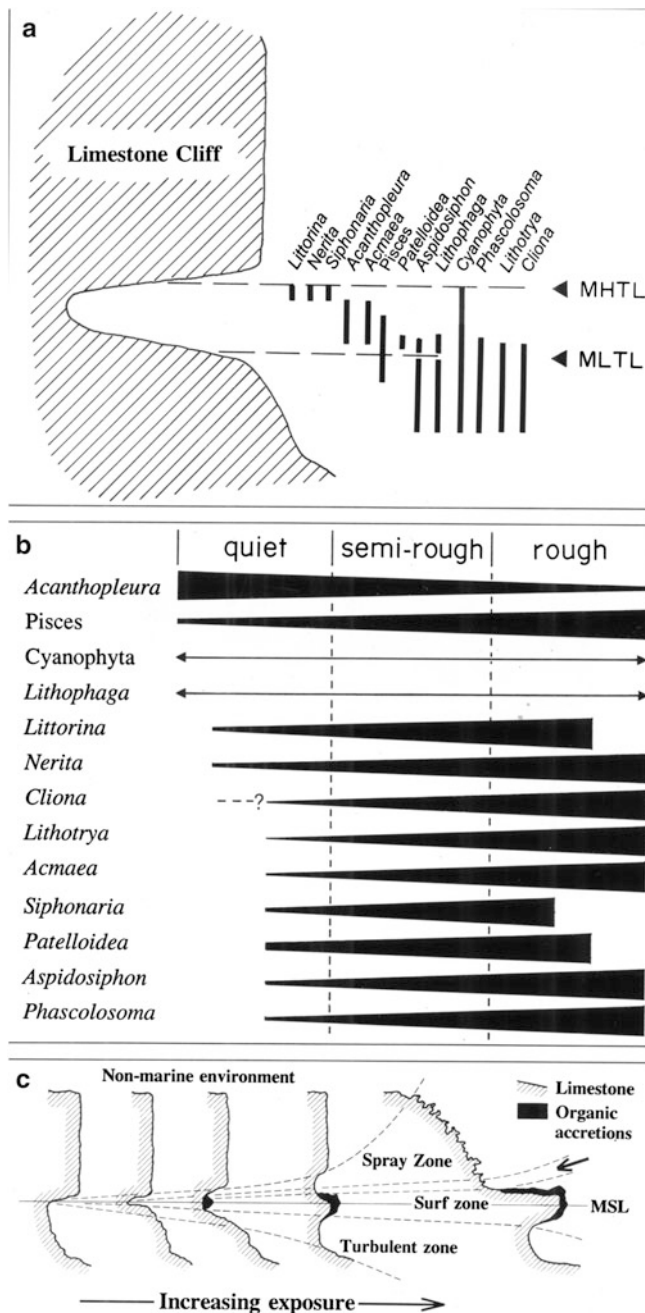
4.2.9 Mollusca

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 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$_3$O$_4$) 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).

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

which they feed (Table 4.2). Some gastropods (muricaceans, naticids) and cephalopods (notably *Octopus* spp.) employ the radula as a drilling tool, producing circular holes in thick shells to help expose the soft tissues of their gastropod and bivalve prey (Ekdale et al. 1984). The contribution of the fine grains thus produced to reef sedimentation rates has not been reported, but drilled mollusc shells are commonly observed in reef sediments.

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 (Figs. 4.1 and 4.2b). 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 to 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. In the Bonaire study by Perry et al. (2012), high echinoid bioerosion occurred on leeward reefs with high coral cover, but none was reported on windward reefs, similar to the habitat differences noted for clionaid sponges (Table 4.2). Sea urchins can cause substantial erosion at low and moderate population densities; at high densities, their destruction of reef substrata rivals clionaid sponge erosion and can lead to rapid framework loss.

Fig. 4.7 Vertical (**a**) and horizontal (**b**) distributions of bioeroding molluscs 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)

scrape rock surfaces. The radula of patellacean limpets is an especially effective excavating organ with opal ($SiO_2 \cdot nH_2O$) 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

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 1990a). 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. 4.2a). 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} year^{-1} on a Caribbean reef in Panamá with a high abundance of just under one 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} year^{-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 g m^{-2} year^{-1} (Table 4.2). Parrotfishes can exhibit interesting spatial differences vis-à-vis grazing activity and consequent erosion (Table 4.2). On the Great Barrier Reef, highest erosion was observed on offshore reefs in oligotrophic waters compared to inshore reefs in eutrophic environments (Tribollet and Golubic 2005). On reefs at Bonaire, parrotfish erosion rates were generally highest on leeward reefs with high coral cover compared to seaward reefs of low coral cover (Perry et al. 2012).

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} year^{-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 3,000–5,000 g $CaCO_3$ m^{-2} year^{-1} have been reported for many of the world's coral reefs (Kinsey 1983). Among the internal borers, clionaid 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.

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 (Sect. 4.5).

Aside from a few species that invade coral rock directly through living tissues (e.g., some boring sponges, bivalves and 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 dislodges and topples corals, sediment scour and burial, tidal exposures, sudden temperature changes, freshwater 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
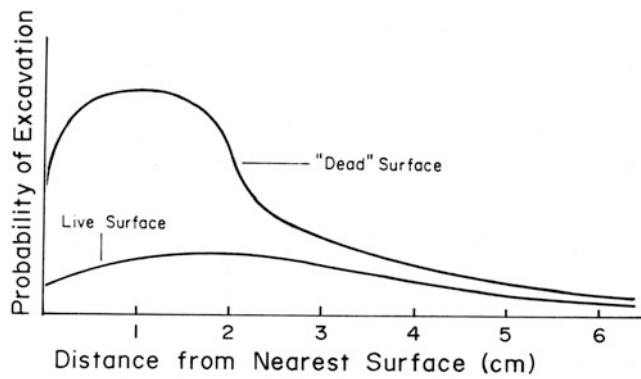
Fig. 4.8 Graphic model showing the probability of excavation of endolithic bioeroders as a function of distance from a coral's surface (Redrawn from Highsmith 1981a). *Curves* are illustrated for corals with dead and live surfaces

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. Rützler (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 parrotfishes and sea urchins (Glynn and Wellington 1983; Eakin 1993).

Coral tissue loss due to a variety of diseases can be substantial (Chap. 8; 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 elevated sea water temperature, 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 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.

Fig. 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
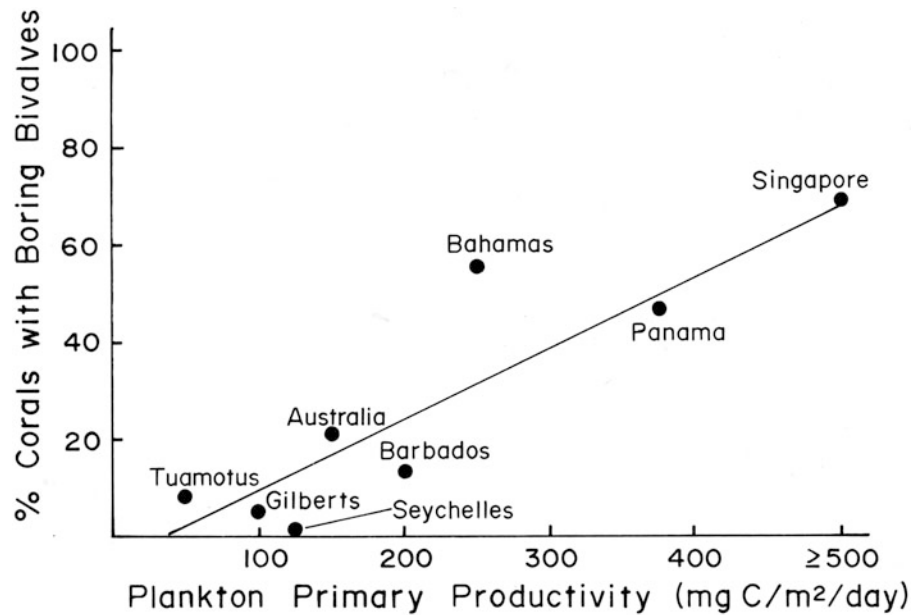

Overfishing can also promote increased bioerosion on reefs. If natural fish predators of some bioeroder populations are eliminated, e.g. triggerfishes that prey on sea urchins, then it is possible for grazing sea urchin populations to increase in size with a devastating effect on reef limestones. Overfishing of parrotfishes causes declines in bioerosion, given their role as important bioeroding agents on reefs. However, the long-term effect of parrotfish exploitation is a depression in the overall carbonate budget because the absence of parrotfishes leads to a decline in coral cover and carbonate production from increases in algal abundance due to reduced grazing (Kennedy et al. 2013). Angelfish predation exerts a strong control on the abundances of clionaid sponges (Hill and Hill 2002), thus overfishing of these species might lead to increases in boring sponge population size.

Climate change, owing to anthropogenic CO_2 emissions since the industrial revolution, is a leading threat to the survival of coral reef ecosystems over the twenty-first Century (Hoegh-Guldberg et al. 2007). Elevated and increasing CO_2 concentration in the Earth's atmosphere is associated with global warming and an increase in extreme weather events and patterns (IPCC 2007). Warm water bleaching events have increased in severity and spatial scale, particularly over the past 30 years (Baker et al. 2008). Bleaching events reduce $CaCO_3$ production by corals, but also can be followed by increases in bioeroder abundances (Glynn 1988). After ENSO-related bleaching and mortality in the eastern tropical Pacific (ETP), echinoid abundances increased greatly, in part due to the resultant increase of algal food sources on dead coral skeletons, and caused significant bioerosion of reef framework structures (Glynn 1988; Eakin 2001). Clionaid sponges have also been reported to increase after bleaching events, perhaps due to the increase in available substrates following coral mortality (Rützler 2002; Schoenberg and Ortiz 2009). This is not limited to warm water bleaching, as clionaid sponge populations also exhibited large increases after cold-water bleaching in the Florida Keys (Manzello, pers. obs.) that caused mass coral mortality (Lirman et al. 2011). An increase in the frequency, severity, and/or duration of warm and cold-water events with climate change negatively impact the $CaCO_3$ budget of coral reefs via reductions in coral calcification and increases in bioerosion.

Anthropogenic CO_2 emissions are not only changing the climate of the planet, but they are also altering the chemistry of the world's oceans. About one-third of all the CO_2 released into the atmosphere since the industrial revolution has been taken up by the oceans (Sabine et al. 2004). This process, termed ocean acidification (OA), has caused a decline in oceanic pH of 0.1, and will likely cause a further decline of 0.3–0.4 pH units by the end of the twenty-first century (IPCC 2007). The anthropogenic acidification of the oceans is occurring at a rate that is unprecedented over at least the past 55-300 million years (Hönisch et al. 2012). OA results in a decrease in seawater $[CO_3^{2-}]$ and, consequently, a decrease in the saturation state of carbonate minerals ($\Omega = [CO_3^{2-}]\ [Ca^{2+}]/K'sp$, where $K'sp$ is the solubility product for a carbonate mineral). Declines in aragonite saturation state (Ω_{arag}, aragonite is the crystalline form of $CaCO_3$ precipitated by scleractinian corals) lead to reduced rates of coral calcification (Langdon and Atkinson 2005). In this review, we have emphasized that the rate of $CaCO_3$ production only slightly exceeds its rate of loss on healthy coral reefs, therefore any disturbance forcing global-scale declines in calcification, such as OA, is alarming (Kleypas et al. 1999a).
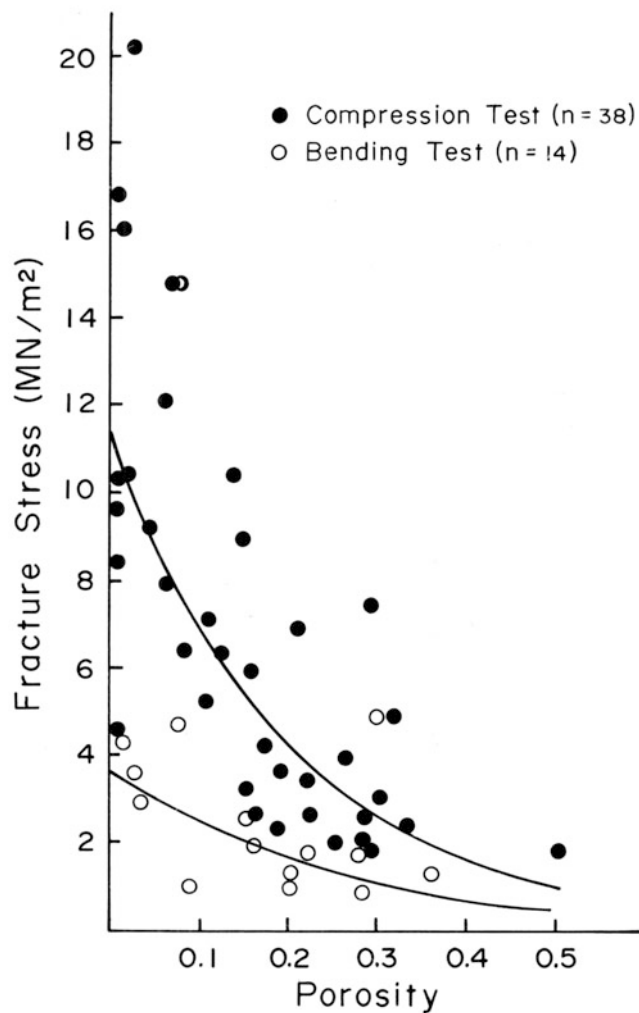
Fig. 4.10 Plot of coral strength to breaking versus amount of bioerosion by *Lithophaga* (Redrawn from Scott and Risk 1988). The compression and bending tests are two measures of a coral's strength. N = newton, a unit of force, MN 0.22481×10^6 lbf. Porosity indicates the percent of the skeleton removed

Recent experimental work has shown that high-CO_2 conditions lead to accelerated rates of bioerosion by endolithic algae and clionaid sponges. Tribollet et al. (2009) exposed coral blocks to 400 ppm and 750 ppm pCO_2 for three months following the recruitment of a natural epilithic and endolithic community over 8 months of field deployment in Hawai'i. The alga, *Ostreobium querkettii*, was the dominant agent of bioerosion and the depth to which its filaments penetrated the coral rock substrate increased significantly in the high-CO_2 treatment, leading to a 48 % increase in $CaCO_3$ dissolution. Reyes-Nivia et al. (2013) observed enhanced biologically-mediated dissolution associated with increases in endolith biomass and respiration during combined exposure to elevated CO_2 and temperature. These workers found a significant effect of substrate, as skeletons of the coral *Porites cylindrica* exhibited a higher

increase in endolith bioerosion when compared to the more dense *Isopora cuneata*, as well as an increase in the relative abundance of *O. querkettii* within the endolithic community. This is intriguing as previous authors have suggested that internal bioerosion is highest in more dense coral skeletons (Highsmith 1981b; Schönberg 2002), yet the response due to high temperature and high-CO_2 may follow a reverse pattern.

Bioerosion by clionaid sponges will also intensify in a high-CO_2 world (Wisshak et al. 2012; Fang et al. 2013a, b; Enochs et al. 2015). Biologically-mediated chemical dissolution by the common Caribbean boring sponge *Pione lampa* (formerly *Cliona lampa*) is predicted to increase 99 % by the end of the twenty-first century as a result of OA, which is nearly double the expected decline in coral calcification (Enochs et al. 2015). Fang et al. (2013a) examined the combination of high-CO_2 and high-temperature and reported increases in both sponge biomass and bioerosion rate by the zooxanthellate Pacific boring sponge *Cliona orientalis*. However, these workers found that *Symbiodinium* population abundances within *C. orientalis* decreased with increasing CO_2 and bleached in their experimental treatment, mimicking elevated temperatures and CO_2 concentration expected by the end of the century under a business-as-usual emissions scenario. In spite of this, bioerosion rates were still highest in the bleached sponges at the highest exposures of CO_2 and temperature, even though biomass was reduced by bleaching and peaked at a lower CO_2 scenario. In a complementary study, it was suggested that the stimulation of bioerosion at high-CO_2 in *C. orientalis* may be tempered by high temperatures due to bleaching, reductions in biomass, and an overall negative energy balance, as more carbon is consumed than produced at high temperature (Fang et al. 2013b). This suggests that bioerosion rate could increase up to some thermal threshold and then decline due to bleaching, and potentially cease, if mortality occurs.

Enochs et al. (2015) observed a similar parabolic or asymptotic response in *Pione lampa* to high-CO_2, however this was independent of bleaching, as this species is azooxanthellate, and temperature was held constant at 25 °C. Further work is necessary to better understand the mechanism of CO_2 stimulation of biologically mediated chemical dissolution in clionaid sponges to determine if this similarity is a coincidence or represents an optimal pH range for clionaid physiological function.

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 (Enochs and Manzello 2012a, b). 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

Fig. 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–e** illustrate seaward (*deep*) to shoreward (*shallow*) reef sections. The inset plan view shows the location of the panels (After Scoffin et al. 1980)
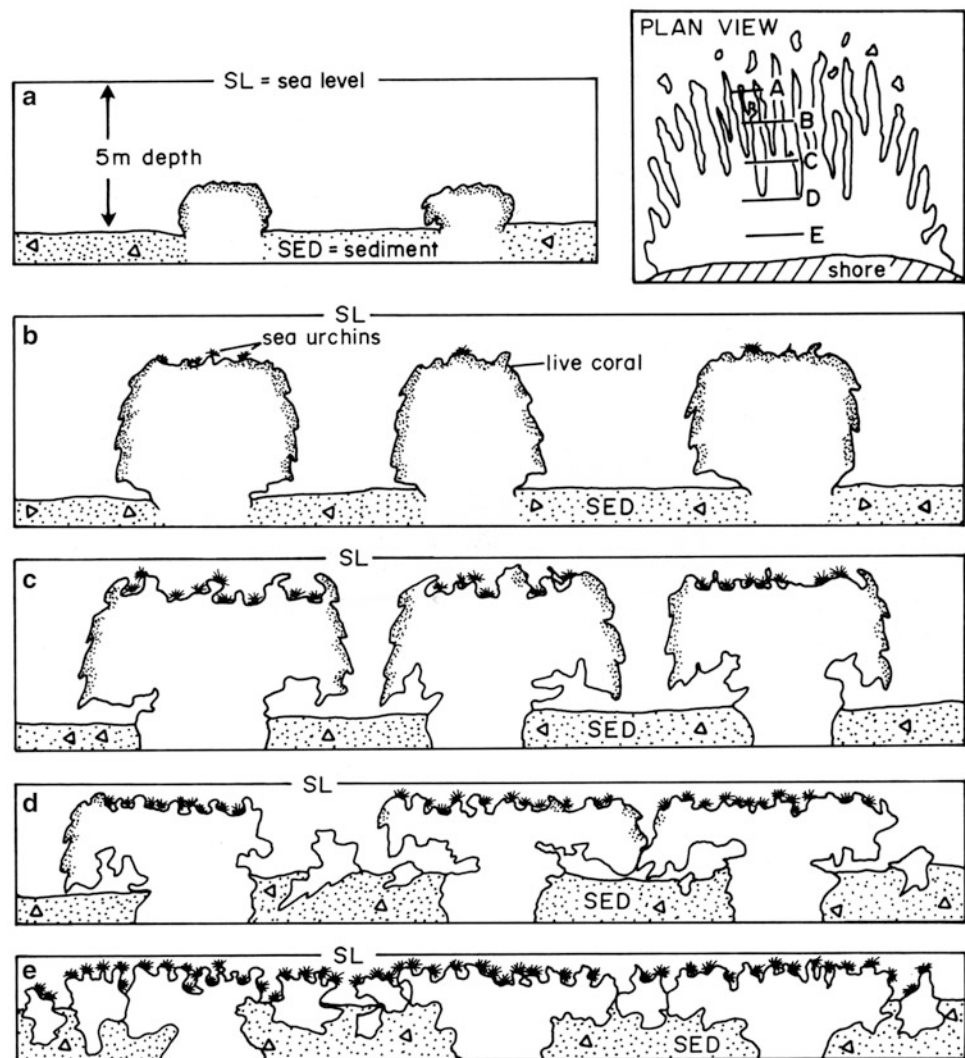
western Pacific that were subjected to intense predation by *Acanthaster* and then bioeroded, lost much of their three dimensional structure with the collapse of the *Acropora* canopies. The loss of these erect corals would eliminate important microhabitats for fishes. The topographic complexity of eastern 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 fine-grained sediments following high coral mortality and low recruitment, respectively, during and after the 1982–1983 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, plate-like 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).

4.5 Case Studies

Six documented cases of environmental alterations that have affected or threaten reef-building corals 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. In addition, we discuss how many Caribbean reefs are presently in a net erosional state and how they will further be affected by climate change. Lastly, we show how eastern tropical Pacific reefs represent a real-world climate change model, providing insight into how thermal stress and ocean acidification may affect coral reefs of the future.

4.5.1 El Niño-Southern Oscillation

Elevated seawater temperatures that accompanied the 1982–1983 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 many of 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 most monitored sites for periods of up to 20+ years (Wellington and Glynn 2007; Baker et al. 2008; Glynn et al. 2015).

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. Probably contributing to this post-El Niño sea urchin increase were the high mortality of lithophagine molluscs (Scott et al. 1988) and the resulting large numbers of vacant bore holes that became available in massive *Porites* colonies. Numerous juvenile *Eucidaris* (≤ 1 cm test diameter) recruited to these newly available shelter sites. 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 to 20 kg CaCO$_3$ m^{-2} year^{-1} in Panamá and from 20 to 40 kg CaCO$_3$ m^{-2} year^{-1} in the Galápagos Islands. Both of these rates exceed net carbonate production of ~10 kg CaCO$_3$ m^{-2} year^{-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.

Studies in the Galápagos Islands and Panamá to the year 2000, demonstrated virtually total reef frame loss in the central and southern islands (Glynn 1994; Reaka-Kudla et al. 1996; Glynn et al. 2001) and substantial calcium carbonate declines in the latter region (Eakin 2001). *Eucidaris* population densities have remained high in the central and southern Galápagos Islands through 2012 with continuing bioerosion of any remaining limestone structures. Eakin's modeling results, incorporating post 1997–1998 data, indicated that the Uva Island reef in Panamá was still in an erosional state in the year 2000, ranging from around −3,000 to −18,000 kg CaCO$_3$ year^{-1} net. A current assessment of coral recovery on the Uva reef in Panama, up until

2010, has revealed a steady increase in live coral cover of ~35 %, and no increase in populations of echinoid bioeroders (Glynn et al. 2014).

While the coral mortality noted above had been caused primarily by elevated sea temperature extremes during El Niño events, it is necessary to recognize that sudden declines in temperature during La Niña events can also result in widespread and significant coral mortality. A sudden transition from a moderate El Niño warm event to a strong La Niña cold condition in 2007, from 26–28 °C to 16 °C over just 6 days, resulted in island-wide coral bleaching in the Galápagos Islands (Banks et al. 2009). Little recovery was observed after one year, which likely increased the vulnerability of corals to bioerosive processes.

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 eight 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 Kāne'ohe Bay, Hawai'i coral reef ecosystem (Banner 1974; Smith et al. 1981; Jokiel et al. 1993). Because the mismanagement of the Kāne'ohe 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 stressors. 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 Kāne'ohe Bay coral reefs over two decades (1960–1978).

During the first half of the Twentieth century the coral reefs of Kāne'ohe 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 cavernosa*) 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) had remained favorable.

Another 16 years have passed without a major disturbance event affecting corals, however, notable changes in several reef-associated benthic species have occurred. Thanks to the monitoring efforts of P Jokiel, J Stimson, and N Sukhraj, the recent status of the Coconut Island (= Moku o Loe Island) fringing poritid reef can be briefly reviewed. Since 2006, *Dictyosphaera* has decreased in abundance, and several species of red algae have become closely associated with *Porites compressa*, in some instances attached to the peripheral branches of corals (Stimson and Conklin 2008; N Sukhraj pers comm). In addition, a non-boring invasive sponge, *Mycale grandis*, is sometimes present adhering to the sides of coral branches (Coles
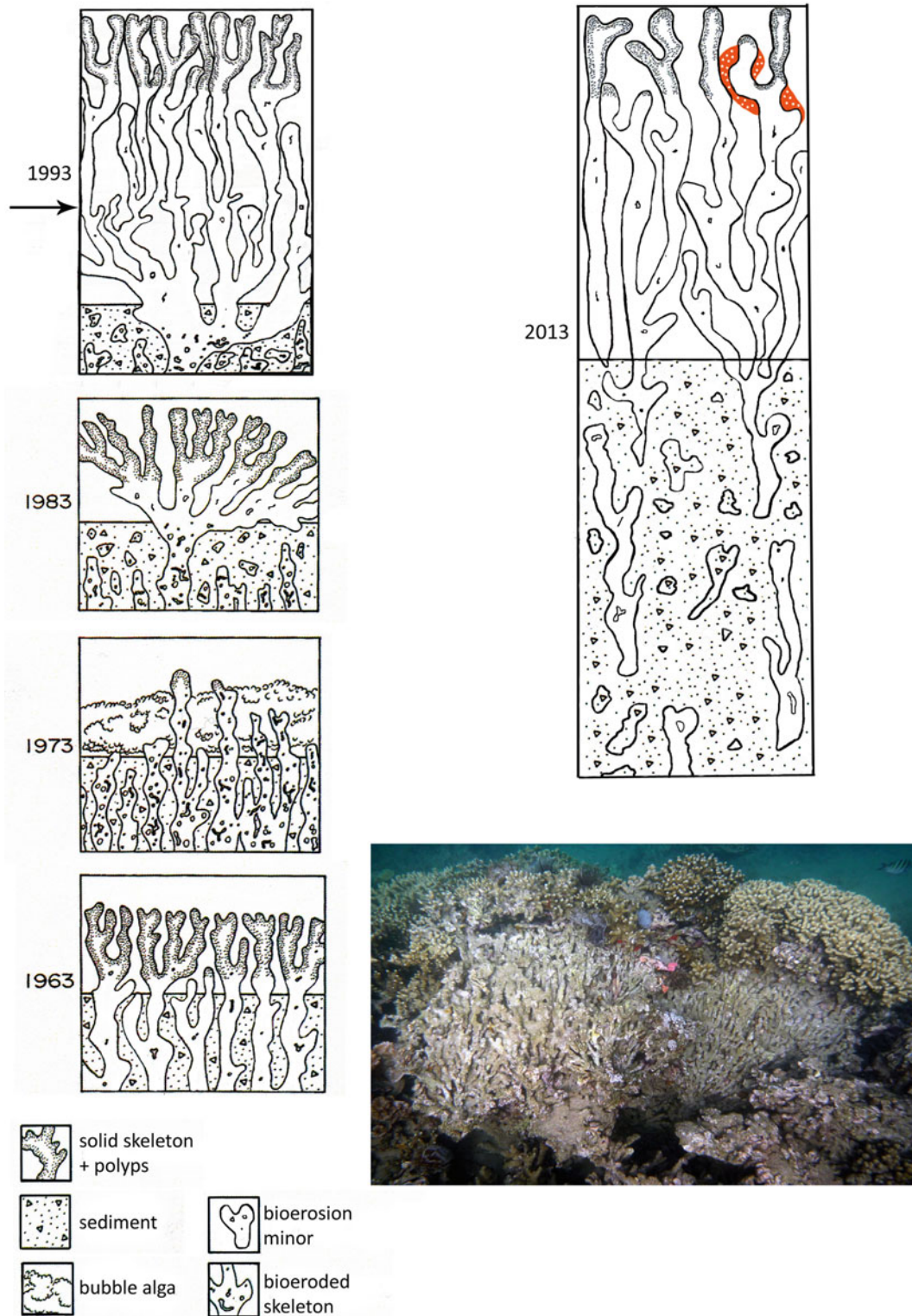
Fig. 4.12 Cross-section of *Porites compressa*, the predominant frame-building coral of the Coconut Island fringing reef. Prepollution (1963), pollution (1973), and postpollution (1983–2013). *Arrow* marks 1987 flooding event. Colored overgrowth denotes *Mycale grandis*

et al. 2007). It now appears that interphyletic competition is more prevalent, but rapid coral growth, with branch elongation rates of 2.4–3.5 cm year^{-1} in reef crest and slope zones (Jokiel 1986), is contributing to vigorous reef progradation.

Rapid vertical coral growth at shallow crest depths leads to framework instability, fracturing, and downslope block transport, extending reef foundations seaward. 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 have been documented in studies in 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 and Ogden 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.

A convincing case of the over-harvesting of sea urchin predators (lobsters, fishes) in the Galápagos Islands, leading to increased external bioerosion, exemplifies the potential for secondary additive effects that could impede coral and reef recovery (Edgar et al. 2010). Low abundances of *Eucidaris galapagensis* were present in marine protected areas or far from fishing ports, sites supporting high natural abundances of urchin predators. These areas also demonstrated higher levels of coral cover and less disturbance to coral communities recovering from ENSO mortality events.

4.5.5 Caribbean Reef CaCO$_3$ Budgets: Current Status and Future Trends

Coral reefs are in decline globally and the state of Caribbean reefs is arguably the most alarming. Caribbean reefs have experienced multiple interacting disturbances that have driven or exacerbated large-scale coral mortality. In no particular order of importance, the loss of acroporids due to white-band disease, the basin-wide ecological extinction of the keystone sea urchin herbivore *Diadema antillarum* due to an unidentified pathogen, overfishing, coral bleaching, and land-based sources of pollution have all been linked to the collapse of Caribbean coral reefs (Hughes 1994; Aronson and Precht 2001; Jackson et al. 2001; Eakin et al. 2010). Live coral cover has declined by about 80 % since the 1970s, reefs are losing architectural complexity, CaCO$_3$ production has declined to 50 % below historical averages, and more than a third of sites recently surveyed (37 %) were already net erosional (Gardner et al. 2003; Alvarez-Filip et al. 2009; Perry et al. 2013). Many Caribbean reefs are at or close to CaCO$_3$ budget neutral, termed "accretionary stasis," leading to the concern that the persistence of architecturally complex reef framework structures is in doubt (Perry et al. 2013).

Two recent studies have forecasted future Caribbean reef CaCO$_3$ budgets using different approaches, yet both yielded similarly negative prognoses. Enochs et al. (2015) used the *reef budget* methodology of Perry et al. (2012) to estimate present day and future CaCO$_3$ budgets for 37 reefs across the Florida Reef Tract when projected atmospheric CO$_2$ levels reach 750 ppm, a conservative estimate for end of the twenty-first century conditions. These workers assessed three differing scenarios: (1) no change in coral cover, no change in coral and coralline algae calcification with OA, increase in bioerosion with OA; (2) no change in coral cover relative to present-day, expected declines in coral and coralline algae calcification due to OA, increase in bioerosion; and (3) 50 % decline in coral cover with expected declines in

calcification and increases in bioerosion. The declines in calcification were estimated based on published rates, whereas changes in bioerosion were based on the rate of increase in chemical dissolution shown for the common Caribbean bioeroding sponge *P. lampa* with high-CO_2 (+99 %) in the same study, coupled with the predicted rate of dissolution increase by endolithic algae of 48 % (Tribollet et al. 2009). Under present-day conditions, 89 % of reefs on the Florida Reef Tract were already net erosional. For scenario 1, 92 % of reefs became net erosional, whereas all reefs considered were net erosional under scenarios 2 and 3. This modeling exercise illustrated the potential importance of endolithic algae bioerosion. Even though the rates of dissolution per area coverage and the expected stimulation of bioersoion at high-CO_2 are both lower than what is expected for *P. lampa*, the dominance of bare substrate as a result of very low coral cover leads to a domineering role for endolithic algae in the reef $CaCO_3$ budget in a high-CO_2 world. These projections stress the likely importance of local management to safeguard reef ecosystem function in an era of global change. Overfishing of those species that control clionaid populations, such as angelfishes, as well as coastal eutrophication should be controlled and not allowed to exacerbate the expected increase in bioerosion (Rose and Risk 1985; Hill and Hill 2002; Ward-Paige et al. 2005).

Kennedy et al. (2013) combined ecological models with carbonate budgets and assessed the dynamics of simulated Caribbean coral reefs based on the latest climate projections. This study assessed the interacting role of local management of fisheries and land-based sources of pollution. The same trend towards net erosion was apparent under all climate scenarios of increased temperature and CO_2, but local management of fisheries, specifically protection of grazing parrtofishes, was found to delay reef loss by a decade. However, positive $CaCO_3$ budgets were only generated when local action was combined with aggressive emission reductions that would limit global warming to less than 2 °C. Changes in coral calcification due to warming and acidification were most important in their $CaCO_3$ budget simulations for healthy, coral-dominated reefs. The controls on bioerosion, such as sea urchin population sizes, sponge boring rates, and nutrification became the dominant drivers of the carbonate budget at low coral cover.

4.5.6 Eastern Tropical Pacific Coral Reefs: A Real-World Climate Change Model

Coral reefs of the eastern tropical Pacific (ETP) provide a real-world example of reef growth, development, structure and function under high-CO_2, low-Ω_{arag} conditions that encompass the range of expected changes for the entire tropical surface ocean with a doubling and tripling of atmospheric CO_2 (Manzello et al. 2008; Manzello 2009, 2010a). The naturally high-CO_2 of the ETP causes reefs in this region to persist near the Ω_{arag} distributional threshold for coral reefs (Kleypas et al. 1999b). Reef structural development is highly limited in the marginal low-Ω_{arag} environment of the ETP and reef structures are ephemeral on geological timescales (Manzello 2009). Calcium carbonate cements, which bind reef frameworks and sediments, do not precipitate above trace levels in the ETP and rates of bioerosion are the highest measured anywhere in the world (Manzello et al. 2008).

Eastern tropical Pacific reef response to ENSO warming varies regionally as a function of CO_2, providing possible insight into reef persistence vis-à-vis warming in a high-CO_2 world. Galápagos coral reef communities experienced a greater thermal stress (+2 to 3 °C for several months) during the 1982–1983 ENSO when compared to Panamá (+1 to 2 °C for two months) (Podestá and Glynn 2001). As a result, coral bleaching mortality was higher in Galápagos (97–99 %) compared to Panamá (75–85 %; Glynn 1990b). Following this mass mortality, reef framework structures in the southern Galápagos Islands were rapidly bioeroded to rubble and sand and are now non-existent (Glynn 1994; Reaka-Kudla et al. 1996). Conversely, reef framework structures have persisted in Panamá despite net erosion and the additional severe 1997–1998 ENSO event (Eakin 2001). Intriguingly, only one reef has persisted in the northern Galápagos Islands, where pH and Ω_{arag} are regionally elevated (Manzello et al. 2014). The impact of high-CO_2, low-Ω_{arag} seawater on carbonate cement precipitation and its apparent inverse relationship to bioerosion rate in the ETP adds a key piece to the puzzle as to why reefs throughout the ETP are poorly developed and ephemeral on geologic time-scales (Manzello et al. 2008).

The observation that the highest bioerosion rates ever documented on coral reefs are coincident with very low-Ω_{arag} and bioerosion rates across the ETP are inversely related to Ω_{arag} and $CaCO_3$ cement abundance (Manzello et al. 2008) has been criticized by Tribollet and Golubic (2011). Three specific criticisms were stated: (1) correlations of bioerosion rate with cement abundance and Ω_{arag} were considered "erroneous" because they were not supported experimentally, (2) the presentation of differing types of bioerosion (total, internal, external) were said to be incomparable, and (3) the increase in substrate available for colonization after the 1982–1983 ENSO coral bleaching mortality event was argued to be a more "probable" explanation for the high rates of bioerosion reported by Reaka-Kudla et al. (1996); and they also suggested the rates of bioerosion during the time of study were likely different. Only ETP bioerosion rates were compared and plotted alongside the measured cement abundances in our study because (a) these are where the Ω_{arag} and cement data were

collected, and (b) these rates are in fact comparable. Bioerosion research in the ETP has a considerable history and was initiated more than 30 years ago by Glynn et al. (1979), who showed the characteristic very rapid rate of bioerosion by the echinoid *Eucidaris galapagensis* in the Galápagos Islands. The pioneering research by Glynn and colleagues was subsequently advanced by Scott et al. (1988) in Costa Rica, Eakin (1993, 2001) in Panamá and later by Reaka-Kudla et al. (1996) in the Galápagos Islands. The methodology employed by Glynn and Eakin was the same (Glynn et al. 1979; Glynn 1988; Eakin 1996). The work by Reaka-Kudla et al. (1996) did use different methods, but generated similar rates to those initially published by Glynn (1988). Rates of bioerosion were comparably high prior to the 1982–1983 ENSO (23.5 kg m^{-2} year^{-1}) in the southern Galápagos Islands (Glynn 1988) to the results reported nearly two decades later by Reaka-Kudla et al. (1996). The assertion that the rates reported by Reaka-Kudla et al. (1996) were most likely just an artifact of an increase in available substrate for colonization is uninformed. Three different studies have shown that bioerosion in the Galápagos is uncharacteristically high and this was known and published before the 1982–1983 ENSO bleaching/mortality disturbance (Glynn et al. 1979; Glynn 1988; Reaka-Kudla et al. 1996).

A comparison of published rates of bioerosion was explored by Manzello et al. (2008) because of the suggestion by pioneering coral reef geologist, Ian Macintyre, that submarine cementation is an important control on the construction and binding of reef framework structures (Macintyre 1997). With this in mind, and the finding that only trace amounts of cement precipitate in ETP reef structures, maximum published rates of bioerosion were compiled to determine if the rates of ETP bioerosion were unique. The ETP bioerosion rates mirrored coral reef cement abundances. The non-ETP maximum rates reported in the literature illustrate that ETP reefs are subject to unprecedented levels of rapid bioerosion, reconfirming that which was known for more than three decades (e.g., Glynn et al. 1979). Differing agents of bioerosion were indeed reported, but the chief objective was to show maximum mean recorded rates from the literature, regardless of bioerosion agent, to confirm the far greater magnitude of rates in the ETP. Bioerosion rates from outside the ETP were listed for qualitative comparison and were not used in the study.

This study was further misrepresented by Tribollet and Golubic (2011) when they claimed that the conclusion was drawn that bioerosion was negatively correlated with Ω_{arag} and cement abundance, when no such statistical test was conducted or reported. In fact, Manzello et al. (2008) solely stated "cement abundance was positively related to Ω_{arag}, but inversely related to bioerosion rate in the ETP." This

statement only reported an apparent trend. The lack of cement in the ETP is later hypothesized to be a factor in the high bioerosion rates of this region, referencing the other published rates to show just how high rates in the ETP are relative to other locations. The publication concludes, "In summary, this study suggests a link between Ω_{arag}, inorganic reef cementation, and coral reef development in the ETP...The ETP examples suggest that coral reefs of the future could be more susceptible to erosion." Tribollet and Golubic (2011) misinterpreted the hypotheses, unnecessarily attacking claims that were not stated.

Recent research on Galápagos reefs and calcification dynamics provide new insights into reef structure and function in a high-CO_2 world. As previously mentioned, only one coral reef persists today within the entire Galápagos archipelago and this reef is located at the remote, northern-most Darwin Island (Glynn et al. 2009, 2015), where pH and Ω_{arag} are regionally elevated (Manzello et al. 2014). Conversely, coral reefs in the southern islands disappeared where pH < 8.0 and $\Omega_{arag} \leq 3.0$, and have not recovered. We found that high nutrients in the upwelled waters of the southern Galápagos Islands may enhance coral calcification under high-CO_2, but ultimately increase reef ecosystem sensitivity to ocean acidification. The warming and acidification that caused the functional collapse of Galápagos reefs is expected to occur world-wide by mid-century for most reefs based on current CO_2 trajectories (Frieler et al. 2013; van Hooidonk et al. 2014).

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.

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 bioerosion 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.

The existence of coral reefs beyond this century is in jeopardy. The concern has progressed from the dramatic losses of live coral (Gardner et al. 2003), to the likelihood that the underlying framework of coral reefs will erode away (Hoegh-Guldberg et al. 2007; Manzello et al. 2008; Perry et al. 2013). Coral cover has declined across broad geographic scales (Gardner et al. 2003; De'ath et al. 2012), leading to declines in $CaCO_3$ production. Furthermore, declines in coral growth and calcification have been documented in the Indian, Pacific, and North Atlantic Oceans over the past 30 years (Edmunds 2007; Cooper et al. 2008; Bak et al. 2009; De'ath et al. 2009; Tanzil et al. 2009; Manzello 2010b). The production of $CaCO_3$ on coral reefs is depressed at a seemingly global scale. This suggests that the future impacts of OA on the negative side of the coral reef carbonate budget, namely via stimulation of biologically-mediated dissolution, may be more detrimental than the decline of coral calcification. Indeed, Kennedy et al. (2013) explicitly demonstrated that changes to coral calcification are only reflected in the $CaCO_3$ budget when coral cover is high. When coral cover is low, bioerosion of the reef framework becomes the dominant process.

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, freshwater 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.

It is now generally understood that bioerosion will be accelerated in a high-CO_2 world via stimulation of biologically-mediated chemical dissolution in endolithic algae and clionaid sponges. It has been suggested that a similar amplification of erosive ability may occur in all bioeroding organisms that utilize chemical dissolution to excavate reef substrates (Enochs et al. 2015). This includes lithophagine bivalves, cirripedes, and various polychaete worms. Many of these bioeroders have greater tolerances to environmental perturbation than corals. In fact, clionaid sponges appear to gain a competitive advantage during thermal stress and coral bleaching events (Rützler 2002; Schönberg and Ortiz 2009). There is much to be learned about coral reef bioerosion, but one thing seems clear – research on bioerosion will most certainly increase over this century because the importance of this fundamental process in coral reef dynamics will likely become increasingly difficult to ignore. Local-scale management of fisheries and watershed pollution would not only benefit corals, but should help limit the proliferation of bioeroders in a high-CO_2 world.

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.

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