

Juan José Alvarado, Benjamin Grassian, Jaime Ricardo Cantera-Kintz,
José Luis Carballo, and Edgardo Londoño-Cruz

In loving memory of our colleague Ana Cecilia Fonseca Escalante (1970–2013)

Dreaming about boring a tunnel to escape from prison?

Dreaming about boring a reef and discover its formation history?

Dreaming about boring a being to possess it?

Dreaming about boring an oil pit that attaches us to money? Or

Dreaming about boring a skeleton to keep enclosed?

It is finally just dreaming about “boring to cope with boredom.”

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Abstract

Bioerosion, the weakening and erosion of hard substrates by boring, etching, and grazing organisms, is a major structuring force on coral reefs of the Eastern Tropical Pacific (ETP). Bioerosional processes are the main source of reef erosion, and facilitate recycling of reefal carbonate. In healthy reefs, a dynamic balance exists between destructive (i.e. bioerosion) and constructive (i.e. bioaccretion) processes, allowing for maintenance and growth of reef frameworks. In changing environments, however, bioerosion rates can exceed those of coral calcification, leading to reduced reef development and the destruction of reef frameworks. In the ETP, high rates of bioerosion are promoted by nutrient-rich upwelling and high primary productivity conditions, recurrent coral bleaching and mortality events, and a chemical environment characterized by high-pCO₂ and low aragonite saturation state. Here we examine bioerosion in ETP coral habitats and the variable roles of reef-dwelling bioeroder taxa: microbial euendoliths (microendoliths), sponges, polychaetes, sipunculans, crustaceans, molluscs, echinoids, and reef fishes. Among these agents of bioerosion, sponges, sipunculans, bivalves, and echinoderms have been relatively well studied in this

J.J. Alvarado (✉)
Centro de Investigación en Ciencias del Mar y Limnología,
Escuela de Biología, Universidad de Costa Rica, 2060-1000 San
José, Costa Rica
e-mail: juan.alvarado@ucr.ac.cr

B. Grassian
Rosenstiel School of Marine and Atmospheric Science, Marine
Biology and Ecology, University of Miami, 4600 Rickenbacker
Causeway, Miami, FL 33149, USA
e-mail: bgrassian@gmail.com

B. Grassian
Graduate School of Oceanography, University of Rhode Island,
215 S Ferry Rd, Narragansett, RI 02882, USA

J.R. Cantera-Kintz · E. Londoño-Cruz
Departamento de Biología, Universidad del Valle, Calle 100,
no 13-00, Cali, Colombia
e-mail: jaime.cantera@correounivalle.edu.co

E. Londoño-Cruz
e-mail: edgardo.londono@correounivalle.edu.co

J.L. Carballo
Instituto de Ciencias del Mar y Limnología (estación Mazatlán),
Universidad Nacional Autónoma de México, Mazatlán, México
e-mail: jlcarballo@ola.icmyl.unam.mx

region, while information is currently lacking or limited for microendolith assemblages, polychaetes and reef fishes. The frequency of coral invasion by clionaid sponges (e.g., *Cliona vermifera* and *Thoosa mismalolli*) is variable between ETP coral habitats. Dense boring sponge assemblages can lead to high rates of carbonate losses exceeding those of bioaccretion. Boring bivalves (i.e., species of *Lithophaga* and *Gastrochaena*) are very abundant on many actively accreting reefs and are generally more prominent contributors to reef erosion in the ETP than in other regions. Sea urchins are by far the most destructive grazers of coral substrates in habitats where abundant. Following ENSO-associated coral mortality events, intense bioerosion by sea urchins has impeded coral recovery and compromised reef health at many eastern Pacific sites. This chapter reviews factors important in ETP bioerosion, and current knowledge of bioeroder populations in the region.

Keywords

Carbonate degradation • Echinoids • Boring bivalves • Bioeroder diversity • Grazing and boring

12.1 Introduction

Coral reefs are ecologic and geomorphic formations constructed by calcifying organisms. The biological origin of these ecosystems presents a unique scenario, in that biotic processes not only drive ecological functioning but also the geological construction of these habitats. The degradation of coral habitats is predominantly of a biological derivation as well. Coral reefs are so often introduced as the ocean's "rainforests"—marine ecosystems supporting enormous biodiversity and biological activity. Among this biodiversity, many reef-dwelling organisms are bioeroders responsible for the erosion of coral structures. The occurrence and prevalence of reefal bioerosion may appear outwardly as an unsustainable ecological feedback. Bioerosional processes, however, are natural phenomena intrinsic to the functioning of these ecosystems, present on healthy reefs at rates approaching carbonate production (Hutchings 1986, 2011; Glynn 1997). The development of coral habitats relies on the maintenance of a dynamic equilibrium between destructive and constructive modifications of reefal carbonate. In scenarios where destructive processes gain favor over constructive ones, bioerosion can threaten coral reef structures and ecological functioning.

Currently, global climate change and increasing anthropogenic activities are testing the resilience of reef ecosystems. In response to shifting environmental conditions and heightened coral mortality, it is becoming progressively evident that on impacted habitats enhanced bioerosional processes can outperform constructive ones. Bioerosion appears to be playing important roles in the transformation of impacted reef habitats away from coral-dominated states (Perry et al. 2008). For effective conservation of coral reefs, a comprehensive understanding of bioerosional processes

must be established; and to understand these processes is to better grasp the biotic and ecological dynamics driving reefal carbonate budgets, and how these dynamics change on impacted reef environments.

Bioerosion is the removal and breakdown of geological materials by the actions of living organisms (Neumann 1966; Hutchings 1986; Tribollet et al. 2011). Depending on the organisms involved, bioerosion is performed through chemical means (e.g., etching), mechanical means (e.g., abrasion), or by a combination of both mechanisms (Neumann 1966; Warne 1975; Spencer 1992; Glynn 1997). For some organisms, the mechanisms of bioerosion are still not fully understood (Hutchings 2011). The agents of reef bioerosion can be broadly classified into either those performing internal or external erosion of substrates—endoliths and epiliths respectively. Endoliths (i.e., algae and microendoliths, sponges, polychaete worms, sipunculan worms, acrothoracican crustaceans, and molluscs) are cryptic organisms that excavate carbonate substrates internally and often become permanent residents within coral skeletons. Epilithic bioeroders (i.e., crustaceans, echinoids and fishes) are external grazers that erode coral structures via foraging behavior. Among and between these populations, numerous functional interactions provide feedback that drive the pace and pattern of the overall bioerosion process (Chazottes et al. 1995; Tribollet et al. 2002, 2005). Bioerosion is a dynamic and collectively complex process, varying across reef zones, among coral habitats, and over time (Eakin 2001; Perry et al. 2008; Hutchings 2011).

The impacts of bioeroder activities on corals and coral reefs are functionally diverse. Carbonate excavation by bioeroding organisms creates and elaborates upon the three-dimensional habitat used by a wide range of reefal organisms. Nestling invertebrates constitute a large

component of reef communities, and these cryptic populations (chasmoliths) occupy habitats provisioned by bioerosional activities. Sediments generated by bioerosional processes contribute to reef cementation, produce lagoonal sediments, and facilitate the recycling of carbonate materials (Hutchings 2011). The weakening and fragmentation of coral skeletons by bioerosion promotes asexual dispersal of coral colonies (Tunncliffe 1979; Highsmith 1982; Guzman and López 1991). Herbivorous grazing by epilithic bioeroders, while destructive, can limit algal competition (Tribollet et al. 2011). Bioerosion is inherently a destructive process, however, and when not balanced by reef accretion impedes the development, maintenance, and functioning of coral ecosystems. Bioerosional processes can compromise the structural integrity of reef frameworks and, when extreme, reduce the topographic complexity of coral habitats or can engender their destruction altogether (Tunncliffe 1979; Scoffin et al. 1980; Glynn 1997; Enochs and Manzello 2012).

This chapter will review environmental and ecological conditions influencing bioerosional processes in the ETP, followed by a summary of bioeroder populations in coral habitats, emphasizing current trends in their occurrence and contributions to reef erosion. Bioerosional dynamics in the ETP are assessed focally within this regional scope, and discussed in a global context to establish relevant comparisons. Among the agents of bioerosion: microendoliths, sponges, polychaetes, sipunculans, crustaceans, bivalve molluscs, echinoids, and fishes; not all groups have been well studied in ETP coral habitats (i.e., microendolith, polychaete, and fish bioerosion currently lack or have limited investigation). The scope of these taxa-specific discussions reflects current knowledge of the agents of bioerosion in coral habitats as well as the apparent significance of their contributions to ETP bioerosional processes.

12.2 Bioerosion in the Eastern Tropical Pacific

Bioeroder activities exert enormous influence on coral habitats in the ETP, perhaps uniquely so. For example, reefal bioerosion rates in the Galápagos Islands and Panama are among the highest reported worldwide to date (Glynn 1988; Eakin 1996; Reaka-Kudla et al. 1996; Glynn et al. 2015). In the ETP, bioerosional processes are promoted by a suite of environmental conditions that impede reef development and are responsible for the relatively ephemeral existence of this region's reefs over geological time (Colgan 1990; Toth et al. 2012): productive waters and seasonal upwelling; a shallow and fluctuating thermocline; surface waters characterized by elevated $p\text{CO}_2$, relatively low pH and low aragonite saturation state (Ω); poor reef cementation; and the considerable

influence of ENSO thermal shock events. Intense bioerosion regimes promoted by these conditions may, in turn, contribute to the poor development of coral reefs in the ETP.

In general, bioerosional processes are promoted by conditions (1) causing coral death and thereby enlarging opportunity for bioeroder recruitment, or (2) conditions providing growth advantage to bioeroders over calcifying organisms (Glynn and Manzello in press). The eastern Pacific environment is replete with conditions stimulating bioeroder activities by these means. Nutrient-loading of ETP surface waters, promoting bioeroder food chains, may be principal among these influences. Predominant bioeroders (i.e., boring bivalves and sponges) are suspension-feeders and a direct correlation between primary productivity, the abundance of these taxa, and bioerosion rates has been well-demonstrated globally (Highsmith 1980; Hallock 1988; Hutchings et al. 2005). Coinciding with this trend, boring bivalves occur in higher densities in the ETP and are responsible for more carbonate excavation than found in regions elsewhere (Highsmith 1980; Scott and Risk 1988; Kleemann 1990). Eutrophic conditions in the ETP increase the ecological competitiveness of algae and macroborers relative to hermatypic corals, thereby increasing bioerosion rate (Highsmith 1980; Hallock 1988).

Corals in the ETP are often subjected to severe episodic bleaching and mortality events associated with ENSO thermal perturbation. Coral communities impacted by these events are susceptible to increased bioerosion regimes, and enhanced bioeroder recruitment and bioerosion rates often accompany scenarios where there is a sudden reduction in live coral cover (Glynn 1984, 1990; Eakin 1992). ENSO-induced coral mortality events help drive bioeroder abundances and biogeographic trends in the ETP. Current distributions of boring sponges in Mexican reefs largely coincide with variable impact of ENSO events from reef to reef (Carballo et al. 2013). The rapid degradation of reef frameworks by echinoids in Panama and the Galápagos Islands after the severe 1982–83 El Niño event is a well-documented phenomenon (Glynn 1988, 1990, 1994; Eakin 1992, 1996; Wellington and Glynn 2007) and demonstrates the potential for rapid shifts in reef states via sudden promotion of bioerosional processes (Perry et al. 2008). Changes in coral reef community structure can also lead to or prolong outbreaks of high bioeroder population densities. Trophic-cascades triggered by over-harvesting of sea urchin predators (e.g., lobsters, fishes) in the Galápagos Islands has been proposed as a link to high echinoid abundance and bioerosion rate currently persisting on certain coral communities impacted by ENSO events years prior (Sonnenholzer et al. 2009, 2011; Edgar et al. 2011; Glynn et al. 2015).

The effects of ocean acidification and accelerating oceanic uptake of atmospheric CO_2 on coral reef maintenance and growth are key issues for the future of these ecosystems. Demonstration of low pH and low Ω waters acting as

physiochemical impediment to reef deposition is becoming increasingly robust (Orr et al. 2005; Kleypas et al. 2006; Kroecker et al. 2010; Manzello 2010a). Ocean acidification and lowered Ω enhance bioerosion phenomena as well via thermodynamic facilitation of chemical erosion mechanisms employed by predominant bioeroders, e.g. microbial euendoliths, sponges, and bivalve molluscs (Lazar and Loya 1991; Tribollet et al. 2009; Wisshak et al. 2012, 2013), while simultaneously impairing calcifying processes (Manzello et al. 2010b; Wisshak et al. 2012; DeCarlo et al. 2015). Upwelling of high $p\text{CO}_2$ subthermocline waters in the ETP creates low pH and low Ω surface waters throughout most of the region (Millero 2007; Manzello et al. 2008; Manzello 2010b). Although the direct interaction between ocean acidification and bioerosion phenomena is only recently becoming elucidated, ETP reefs provide a contemporary model for the interface between these processes. A high- CO_2 physical environment contributes to poor reef development and cementation in the ETP (Manzello et al. 2008, 2010a, b), and also increases bioerosion rates (Tribollet et al. 2009; Wisshak et al. 2012, 2013; DeCarlo et al. 2015). Coupling of high- CO_2 conditions with elevated nutrients in the ETP appears to accelerate synergistically reefal bioerosion (DeCarlo et al. 2015).

While it is becoming increasingly important to assess the threats bioerosional processes impose on impacted coral reefs, these activities also incite ecological benefits for coral communities. The weakening and fragmentation of coral skeletons by bioeroders stimulate propagation of coral colonies and are important initiators of asexual coral reproduction (Highsmith 1982). In the ETP, characterized by ephemeral reefs (Glynn and Macintyre 1977; Colgan 1990; Cortés 1997; Toth et al. 2012), rapid recycling of carbonate materials, and the predominance of fast-growing pocilloporid corals that reproduce chiefly through asexual means (Glynn and Macintyre 1977; Richmond 1985, 1987; Glynn et al. 1991), the dispersal of corals by bioerosion-induced colony fragmentation may contribute to the persistence of ETP corals in unfavorable environments (Scott et al. 1988; Scott and Risk 1988). In particular, the high abundance of boring bivalves that by their activities lower coral skeleton breaking stability (Scott and Risk 1988), and persistent excavation by reef fishes (e.g., tetraodontids and balistids) appear to be significant initiators of coral reproduction in the ETP (Guzman 1988; Guzman and López 1991; Palacios et al. 2014; see Chap. 15, Glynn et al.). In this way, the strong influence of bioerosional processes in ETP coral habitats likely helps to define both the transience and persistence of these structures over geological time—contributing to their rapid destruction and continuous rebuilding.

12.3 Microendolith Communities

A diverse assemblage of endolithic microorganisms inhabits skeletons of live and dead coral colonies. Certain cyanobacteria, chlorophyte and rhodophyte algae, fungi, and foraminifera are endolithic bioeroders of coral, chemically dissolving carbonate substratum as they invade within. Microendoliths are among the first recognized bioeroders in the fossil record, with microendolith borings identified in ooid grains of the late Precambrian, 570–700 million year (Campbell 1982). There is a relative paucity of research addressing microendoliths in comparison to studies of macroborers and grazers, and the role of micro-organismal populations in bioerosion of modern corals is less clear (Tribollet 2008). Reports suggest microendolith boring accelerates the overall bioerosion processes by structural weakening of the carbonate substratum. In some reef environments these assemblages perform high rates of carbonate erosion themselves (Tudhope and Risk 1985). In the ETP, there has not yet been an assessment of microendolith bioerosion rates or taxonomy. A brief inclusion is made here to outline functional interactions between microendolith bioerosion and other bioerosional agents demonstrated in coral habitats outside the ETP (e.g., French Polynesia, Great Barrier Reef)—these broad roles are more than likely to be conserved in eastern Pacific reef environments.

Microendoliths are present in both living and dead corals, but pioneer assemblages that recruit following coral mortality are taxonomically dissimilar from those that colonize and keep pace with live, calcifying corals (Hutchings 2011). Chlorophytes of the genus *Ostreobium* are reported to be ubiquitous in the skeletons of live scleractinian corals (Bentis et al. 2000; Gutner-Hoch and Fine 2011), with certain cyanobacteria (i.e. *Plectonema* spp.) and heterotrophic fungi being cosmopolitan as well.

Microendoliths can be highly abundant in dead coral skeletons (Le Campion-Alsumard et al. 1995). Microendoliths colonize dead coral substrata well before macroborer taxa and pioneer epibenthic communities can be established within days of coral death (Tribollet and Golubic 2005). Initial surface invasion by pioneer macroborers is followed by a distinct succession of microendolith assemblages that bore deeper into the limestone substrate. Mature communities taxonomically similar to assemblages found in live corals are established at roughly six months after substrate exposure in tropical waters, and are dominated by low-light specialists and heterotrophic fungi (Hutchings 2011; Tribollet and Golubic 2011). Most notably, there is a suggestion that rapid post-mortem invasion by microendoliths may condition newly available reef rock and render it suitable for recruitment of the larger bioeroding community (Hutchings 1986, 2011).

Several studies have demonstrated a salient functional interconnectedness between microendolith and grazer activities (Chazotte et al. 1995; Zubia et al. 2001; Tribollet and Golubic 2005). Initially, colonization of dead corals by microendolith assemblages attracts grazers, (many of which forage on algal mats), and thereby mediates high rates of epilithic bioerosion. The larger-scale excavation by grazers in turn accommodates for the progression of microendolith invasion, a process that otherwise would be self-stabilizing. As grazers remove epilithic material and continuously reduce shading, phototrophic microendoliths that have light-limited distributions are able to penetrate deeper into coral rock. In this way, reinforcing interactions between microendolith and grazer activity provide a synergistic expansion of the bioeroder-substrate interface and the overall bioerosion process (Chazotte et al. 1995).

It is well known that grazing species (i.e., sea urchins) are among the most destructive bioeroders in ETP reefs (Glynn 1988; Eakin 1996). Given our current understanding of interaction between microendolith assemblages and epilithic agents, ETP microendolith assemblages are near-assured to have substantial involvement in bioerosional processes. It therefore becomes necessary for microendoliths to be assessed by future studies attempting to explain the organismal and functional dynamics driving ETP bioerosion processes.

12.4 Excavating Sponges

Sponges are the most common macroendolith present in reef ecosystems worldwide and are responsible for the highest rates of internal coral destruction than any other endolithic borer (Goreau and Hartman 1963; MacGeachy 1977; Perry 1998; Schönberg and Ortiz 2008; Carballo et al. 2010a). Boring sponges are generally cryptic in nature and have great taxonomic and ecological complexity, thereby exacerbating difficulties in sampling and identification. This has led to frequent omission of boring sponges in community-level reef assessments, despite their well-established importance to reefal bioerosion (Schönberg 2008).

Sponge assemblages have been relatively well-studied in the ETP, especially in the Mexican Pacific region (e.g., Carballo et al. 2004, 2008; Nava and Carballo 2013). Assessment of boring sponges is robust on Mexican reefs, both ecologically and geographically. Sponge diversity, abundance, and prevalence within corals have been quantified at several of the most prominent reef sites in Mexico: Huatulco, Guerrero, Bahía Banderas, Baja California, and islands such as Isabel, Marietas, Marías and Socorro (Carballo et al. 2013). Reef-dwelling sponges were assessed earlier in Costa Rica (Guzman 1988; Scott et al. 1988) and Panama (Wulff 1997), and provide variable degrees of

additional ecological and biological insight (see Chap. 5 for site locations).

The early surveys of sponges in Panama established an initial characterization of ETP sponges by drawing a comparison with sponge assemblages inhabiting Caribbean reefs (Wulff 1997). In contrast to Caribbean species, sponges in the ETP are most often small, cryptic and, except for a few massive, exposed species (Cruz-Barraza and Carballo 2008; Fig. 12.1a, b), principally coral endoliths. These findings were later corroborated by studies on Mexican reefs, as a high abundance and diversity of boring sponges compared to encrusting (Fig. 12.1c–e) and non-boring massive sponges (Fig. 12.1f) are consistently reported (Carballo et al. 2004, 2008). This characterization is relatively unique to the ETP and should be seen as having much relevance for understanding biological and environmental factors influencing sponges in this region. While massive sponges do not contribute directly to bioerosion, these species establish spatial competition with corals and can induce coral mortality as a result.

The high proportion of cryptic azoanthellate sponges on ETP reefs is thought to be caused by environmentally-induced selectivity in larval recruitment (Wulff 1997). Sponge larvae, and the larvae of sessile macrofauna in general, demonstrate a strong preference for recruitment to cryptic, aphotic reef surfaces in the ETP (Zea 1993). Birkeland (1977) hypothesized that the enhanced accumulation of epibenthic biomass, resulting from high nutrient loading in ETP waters, promotes selective recruitment to cryptic spaces by decreasing survival of larvae settling on exposed substrates. In addition, grazing pressure by opportunistic predators may further restrict ETP sponges to cryptic spaces. Reef fishes abundant in the ETP, such as *Arothron hispidus*, are observed to readily consume cryptic sponges that become exposed and lack inherent defenses against predation (Wulff 1997).

A high diversity of cryptic boring sponges is found within coral bases and reef frameworks on ETP reefs. Twenty-two species have been described in the region to date, a majority belonging to the genus *Cliona* (Carballo et al. 2010a) (Table 12.1). Among ETP sponges, clionaid species are dominant, both in incidence and impact. *Cliona vermifera*, specifically, is the most abundant coral-excavating sponge in the ETP, and the prevailing significance of *C. vermifera* is conserved among all assessments from Mexican and Costa Rican reefs (Guzman 1988; Carballo et al. 2008; Bautista-Guerrero et al. 2014). *Cliona vermifera* is a highly adaptable species that demonstrates considerable resilience to environmental stress and an ability to thrive in a wide range of microhabitats (Bautista-Guerrero et al. 2014). *Thoosa mismalolli* is also found in high and consistent abundance in Mexico (Carballo et al. 2004, 2008), and is common on Costa Rican reefs as well (Pacheco-Solano

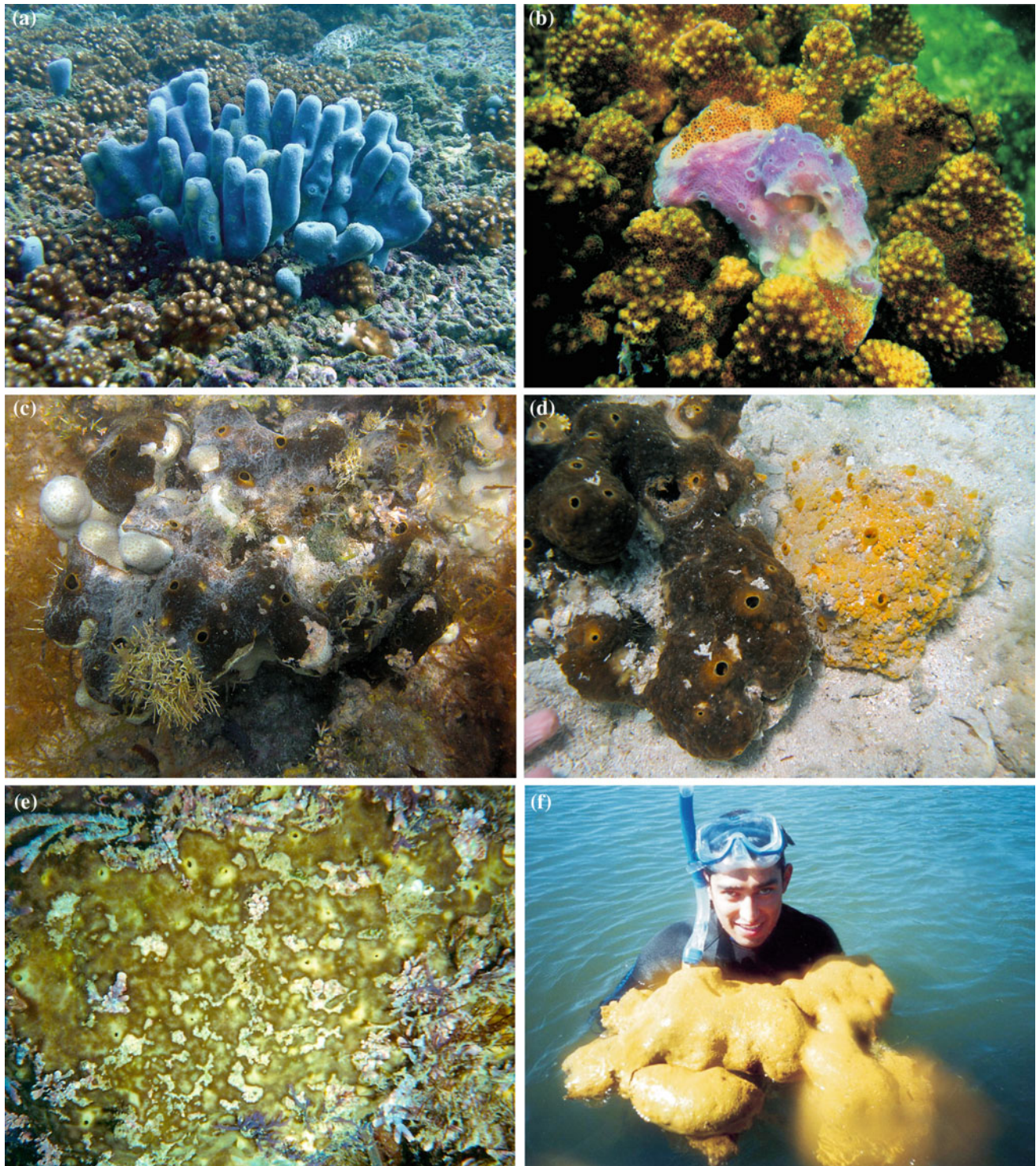


Fig. 12.1 ETP boring sponges. **a** *Amphimedon texotli* living between colonies of pocilloporid corals. **b** *Chalinula nematifera*, an encrusting sponge able to overgrow live corals of the genus *Pocillopora*. **c** *Cliona raromicrosclera* overgrowing corals of the genus *Porites*. **d** *Cliona*

raromicrosclera to left, and *Cliona californiana* to right, both encrusting (beta) growth forms. **e** *Cliona vallartense* in beta stage growing on dead coral. **f** Large, massive (gamma stage) specimen of *C. californiana*. All photographs from J.L. Carballo except c and d by E. Avila

2011). Both *C. vermifera* and *T. mismalolli* are known to be highly destructive coral-excavating sponges and are capable of producing large galleries in coral skeletons, especially those of branching *Pocillopora* spp. (Nava and Carballo 2008; Carballo et al. 2013; Bautista-Guerrero et al. 2014).

Endolithic sponges excavate distinct systems of chambers and branching galleries within coral skeletons (Fig. 12.2a–h). The boring process occurs at a cellular level by the combined chemical and mechanical actions of amebocytic etching cells (Rützler and Rieger 1973; Pomponi 1977). Along the internal substrate interface, etching cells are flattened against the substratum and pseudopodial structures are extended into the surrounding limestone. The penetrating filopodia then ramify and coalesce forming “pseudopodial baskets,” thereby cutting small, lenticular chips (15–100 μm in diameter) from the substrate. Cutting by filopodia is accomplished by enzymatic dissolution of both the inorganic calcium carbonate and the organic matrix of the coral skeleton. Once this dissolution occurs, the etching cells and calcareous chips are transported away from the substrate interface and expelled through the sponge’s aquiferous system (Rützler and Rieger 1973; Pomponi 1977).

This boring action can perform high rates of sediment production, and excavating sponge activities are known to contribute up to 30–40 % of the total sediment deposited on some Caribbean reefs (Goreau and Hartman 1963; Neumann 1966; Fütterer 1974). On reefs of the Mexican Pacific, calcareous chips characteristic of the sponge boring mechanism can comprise up to 15 % of the fine sediments present (Ovalle 2011). Until recently, it has been estimated that dissolved substrate represents only a small fraction (2–3 %) of the total skeletal material eroded by sponge boring (Rützler and Rieger 1973; Rützler 1975). Recent estimates, however, report a much larger fraction of material removed by chemical erosion than previously realized (Nava and Carballo 2008), with one study finding chemical dissolution by *Pione* cf. *vastifica* removes three times more carbonate than is produced as sediment (Zundeleovich et al. 2007).

There is only one study that has quantified bioerosion and sediment production rates for boring sponges in the ETP (Nava and Carballo 2008). Rates for both chemical and mechanical bioerosion of living *Pocillopora verrucosa* by the boring sponges *Cliona vermifera* and *Cliona flavifodina* were determined at Isla Isabel, Mexico. Chemical dissolution accounted for a significantly larger fraction of eroded skeletal material than the 2–3 % initially proposed and mean rates of dissolution were 1.2 and 0.5 $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ for *C. vermifera* and *C. flavifodina* respectively. The highest reported carbonate dissolution rate for *C. vermifera* was 2.4 $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. Sediment production rates were higher than those of dissolution, with means of 3.3 and 4.6 $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ calculated for *C. vermifera* and *C. flavifodina* respectively. Hence, a summation of chemical

dissolution and sediment production gives mean bioerosion rates of 4.5 for *C. vermifera* and 5.1 $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ for *C. flavifodina* (Nava and Carballo 2008), among the highest recorded for ETP endoliths. These bioerosion rates are within the range of those calculated for clionoids of the Caribbean, the Indian Ocean and Red Sea on coral substrates, though well below the highest reported rates—i.e. *Pione lampa* in the Caribbean (Rützler 1975), and *Cliona albimarginata* in the eastern Indian Ocean (Calcinai et al. 2007; see Fig. 12.3).

Of the 22 boring sponge species observed on ETP reefs, none has demonstrated a capacity to penetrate corals through soft tissue (Carballo et al. 2013). Boring sponges invade the skeletons of dead corals (Carballo et al. 2013; Nava and Carballo 2013) and live coral colonies having surfaces that lack soft tissues (Highsmith 1980, 1983; Nava and Carballo 2008). This dead skeletal requirement provides an explanation for why, on Mexican reefs, higher densities of boring sponges are found in corals on reef margins and structural depressions than densities found on reef platforms with high live cover (Carballo et al. 2008). It is on reef margins and depressions where boring sponge recruits can access the bases of coral colonies and other structures not covered by living tissue.

A recent study undertaken on two reefs from the Mexican Pacific found high sedimentation rates to restrict boring sponge distributions (Nava and Carballo 2013). Sediment movement associated with water flow causes abrasion or clogging impeding physiological functions, and accumulated sediments can also prevent larval settlement as has been reported for free-living sponges (Hutchings et al. 2005). Boring sponges such as *Cliona carteri* and *Cliona viridis* exhibit their lowest abundance near sites with high sedimentation (Muricy 1991). On some Oaxacan coral reefs on the Mexican Pacific coast, the highest abundance of boring sponges was recorded on reefs with a low sedimentation rate ($<0.2 \text{ kg m}^{-2} \text{ days}^{-1}$) (Carballo et al. 2008). *Cliona vermifera*, one of the most abundant and widely distributed boring sponges on eastern Pacific coral reefs, is considered to have a low tolerance to sediment deposition that restricts the species’ distribution (Carballo et al. 1994, 2008). In the ETP, only *Siphonodictyon* and *Sphaciospongia* species are considered tolerant of high sedimentation, since their aquiferous system is not easily overloaded (Rützler 1971). The abundance of *Siphonodictyon crypticum* on Mexican coral reefs under high sedimentation supports this relationship (Carballo et al. 2007, 2008).

Substantial increases in sponge abundance have been repeatedly reported for reefs having undergone bleaching events or reductions in live coral cover (Rützler 2002; Schönberg and Ortiz 2009), and this correlation is well documented in the ETP (Carballo et al. 2013; Nava and Carballo 2013). Reefs in the Mexican Pacific that have been

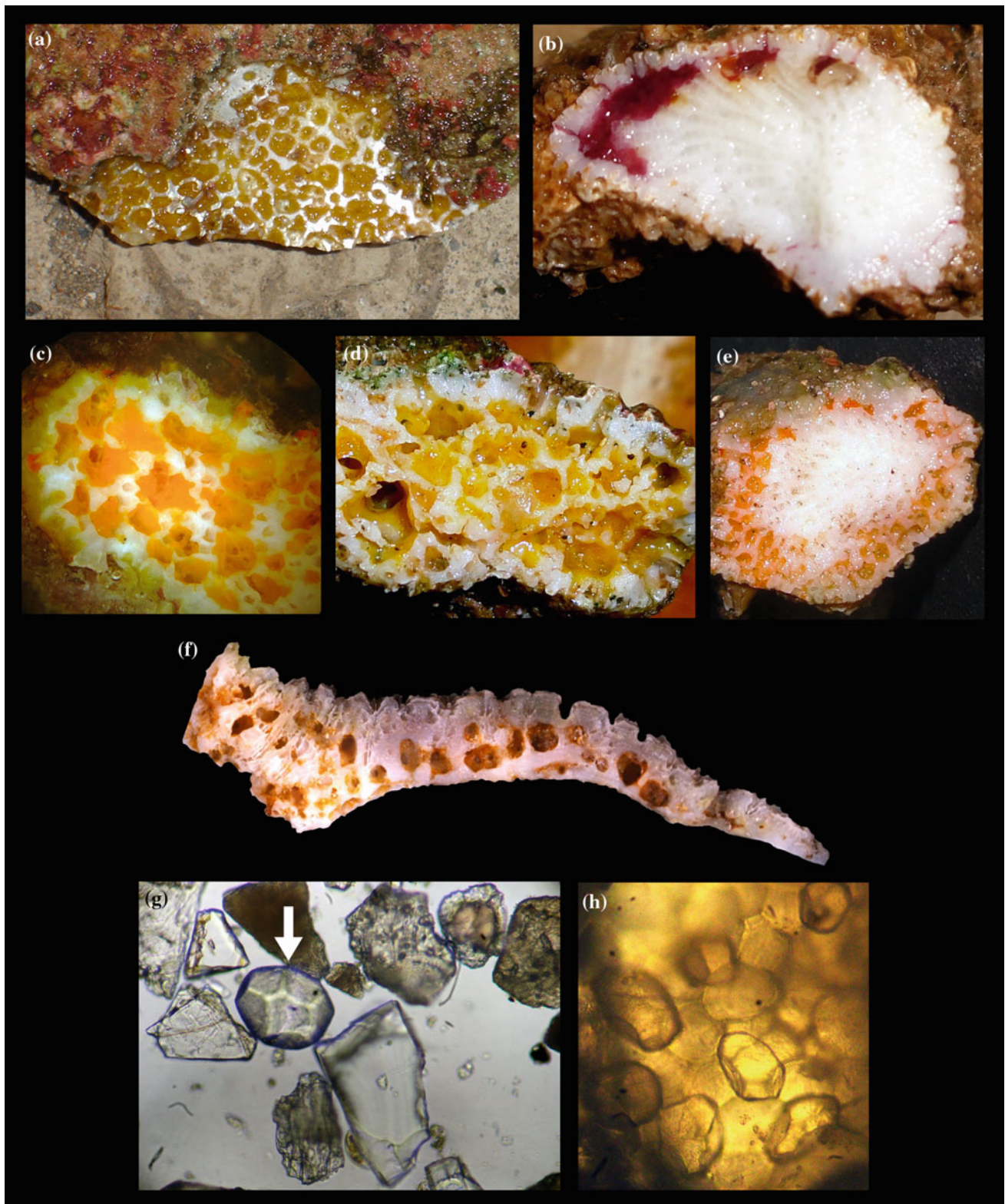


Fig. 12.2 Sponge excavation. **a** Chambers excavated by *Cliona californiana* in a bivalve shell after removing superficial layer. Cross-sections of coral skeletons showing chambers formed by **b** *Thoosa purpurea*; **c** *Pione carpenteri*; **d** *Cliona tropicalis*; **e** *Cliona mucronata*; and **f** *Cliona vermifera* (the latter boring into the coral *Pavona gigantea*). **g** Sediment sample containing a sponge chip (arrow) with characteristically faceted surface. **h** Sponge chips inside tissue before being expelled from oscula. Photographs by J.L. Carballo

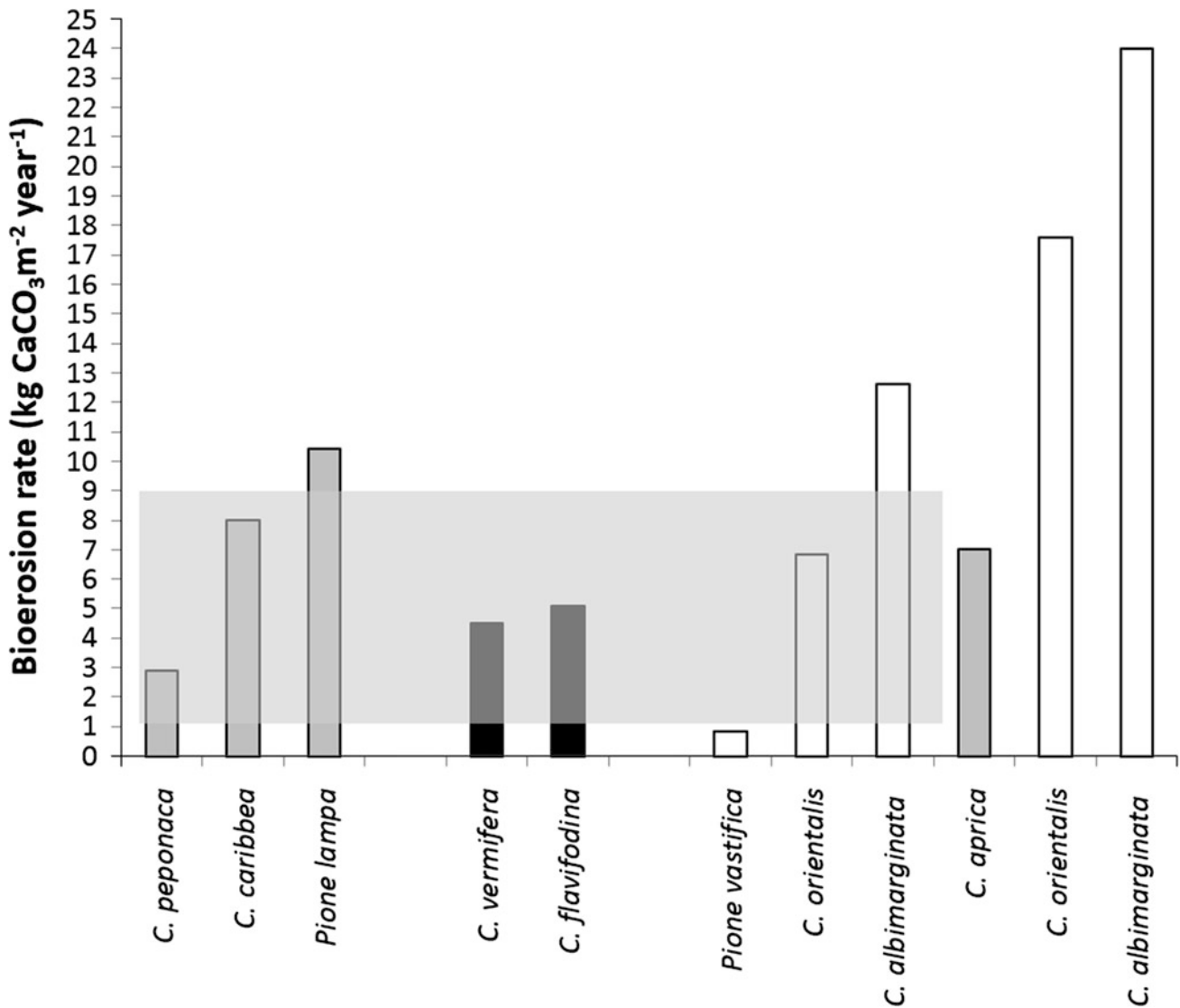


Fig. 12.3 Bioerosion rates ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$) of boring sponges of the genera *Cliona* and *Pione* in different oceans: grey bars represent sponge bioerosion rates from the Caribbean, black bars from the east Pacific Ocean, and white bars from the Indian Ocean and Red Sea. Shaded rectangular area inside plot represents calcification rates in coral communities, which have been estimated between 1.1 and 9 $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Stearn et al. 1977; Kinsey 1985; Silverman et al. 2007). Bars inside shadowed area represent bioerosion rates on coral

substrata; bars outside represent rates on mollusc shells in coral reef environments. Sources *C. peponaca* from Bak (1976), *C. caribbea* from Acker and Risk (1985), *C. orientalis* from Schönberg (2002), *C. vermifera* and *C. flavifodina* from Nava and Carballo (2008), *C. aprica* and *P. lampa* from Rützler (1975), *C. albimarginata* from Calcinai et al. (2007); *Pione* cf. *vastifica* from Zundelevich et al. (2007). Information on *P. lampa* from Neumann (1996) is not included (see text)

impacted by ENSO-associated bleaching events are currently heavily infested by boring sponges (Carballo et al. 2013). Forty six percent of coral samples on Mexican reefs are invaded by boring sponges, and reef frameworks are especially infested (56 % mean invasion in sampled frameworks). Furthermore, boring sponge abundances and assemblage diversity are highest at sites where coral communities have been most affected by ENSO bleaching events, such as: Carayeros, San Juanitas, and Islas Mariás reefs in Nayarit, Cabo Pulmo in the Gulf of California, and La Entrega in Oaxaca (Table 12.2; see Chap. 5 for site locations).

Certain clionaid sponges are highly resilient to anomalous temperature shifts (Shirley and Rützler 2010; Duckworth and Peterson 2013; Bautista-Guerrero et al. 2014), especially when compared to tolerance thresholds found for corals (Glynn et al. 2001; Hueerkamp et al. 2001). *Cliona celata* explants exposed to high water temperatures of up to 31 °C, demonstrated near unaltered growth, survival, and boring rates (Duckworth and Peterson 2013). In another study, *C. celata* explants were found to undergo no significant loss of sponge pigment in response to thermal and salinity stress (Shirley and Rützler 2010). Particularly relevant, a study of

Table 12.1 General characteristics and distribution of coral boring sponges from the Mexican Pacific Ocean

Species	Form ^a	Substrate	Live color	Distribution
<i>Cliona amplicavata</i> (Rützler, 1974)	α stage	Corals and mollusc shells	Bright yellow	Mediterranean, Caribbean, Pacific
<i>C. californiana</i> (de Laubenfels, 1930)	α, β, γ stage	Different carbonate substrates	Golden yellow, light pink, reddish brown	east Pacific
<i>C. euryphylla</i> (Topsent, 1887)	α stage	Different carbonate substrates	From yellow to light orange	Atlantic, Pacific
<i>C. flavifodina</i> (Rützler, 1974)	α, β stage	Different carbonate substrates	Bright yellow, purple brown	Caribbean, east Pacific
<i>C. medinae</i> (Cruz-Barraza et al., 2011)	α stage	Corals	Yellow-orange	Mexican Pacific
<i>C. mucronata</i> (Sollas, 1878)	α stage	Corals	Red to red-orange	Indian Ocean, Pacific
<i>C. pocillopora</i> (Bautista-Guerrero et al., 2006)	α stage	Corals	Light brown	Mexican Pacific
<i>C. raromicrosclera</i> (Dickinson, 1945)	α, β stage	Different carbonate substrates	Orange, brown	Mexican Pacific
<i>C. tropicalis</i> Cruz (Barraza et al., 2011)	α stage	Corals	Bright yellow	Mexican Pacific
<i>C. vallartense</i> (Carballo et al., 2004)	α, β stage	Corals	Olive green to pale yellow	Mexican Pacific
<i>C. vermifera</i> (Hancock, 1867)	α stage	Different carbonate substrates	Orange	Mediterranean, Atlantic, Pacific
<i>Cliothisa tylostrongylata</i> (Cruz-Barraza et al., 2011)	α stage	Corals and mollusc shells	Orange	Mexican Pacific
<i>Pione carpenteri</i> (Hancock, 1867)	α stage	Corals and mollusc shells	Light orange	Indian Ocean, Pacific
<i>P. mazatlanensis</i> (Hancock, 1867)	α stage	Different carbonate substrates	Red	Mexican Pacific
<i>Spheciospongia incrustans</i> (Carballo et al., 2004)	Encrusting	Corals and calcareous rocks	Purplish	Mexican Pacific
<i>Thoosa calpulli</i> (Carballo et al., 2004)	α stage	Corals	Light brown	Mexican Pacific
<i>T. mismalolli</i> (Carballo et al., 2004)	α stage	Corals and mollusc shells	Light brown	Mexican Pacific
<i>T. purpurea</i> (Cruz Barraza et al., 2011)	α stage	Corals	Bright purple	Mexican Pacific
<i>Siphonodictyum crypticum</i> (Carballo et al., 2007)	Fistulae	Corals	Whitish, translucent	Mexican Pacific

^aα, β, and γ stages represent cryptic, encrusting, and massive growth forms respectively

Cliona vermifera at Isabel Island, Mexico over a four-year period reported anomalous temperature rises that were detrimental to corals had no negative effect on *C. vermifera* abundances or reproduction in the same study area (Bautista-Guerrero et al. 2014). In fact, reproductive potential and developmental rates increased with water temperature, being highest during the warmest months and during periods of anomalous temperature elevation.

The resilience demonstrated by boring sponge species abundant in the ETP to thermal shock supports ecological projections that sponges will become an increasing threat to coral and coral reef health. The studies available so far suggest that boring sponges are competitively superior to corals in stressful environments that render corals beyond their survival threshold (Rützler 2002). In the ETP, corals are repeatedly affected by episodes of ENSO-associated thermal stress, persistently compromising coral health and

recovery on many reefs (Glynn et al. 2001; Baker et al. 2008). It is these reefs impacted by coral bleaching and mortality events that are most vulnerable to invasion by boring sponges. More generally, coral reef calcification rates at community level have been estimated between 1.1 and 9 kg CaCO₃ m⁻² year⁻¹ globally (Stearn et al. 1977; Kinsey 1985; Silverman et al. 2007). Bioerosion rates recorded for a single sponge species can reach similar values (Fig. 12.3). The current degradation of eastern Pacific reefs is likely to increase with the progression of temperature rise and ocean acidification (Glynn et al. 2001; Cortés and Jiménez 2003; Manzello et al. 2008; Carballo et al. 2013). It is suggested, concurrently, that sponge bioerosion will increase as coral health declines and the availability of reef substrates for bioeroders expands (Schönberg and Ortiz 2009; Carballo et al. 2010b). Thus, sponge bioerosion is, and will remain, a key issue for the future health of coral reef ecosystems.

Table 12.2 Variation of coral cover and boring sponge abundance on Mexican coral reefs (with respect to ENSO events)

State	Site	Coral coverage ^a						Framework extension (ha)	Frequency of sponge invasion (%)		No Species
		1991	1998	2001	2003	2005	2010		2005–2006	2009–2010	
Oaxaca	La Entraga		76		41			7.5	50	55	5
	Isla Cacaluta		90		61			1.7	41	*	9
	San Agustín		73		64			2.5	31	47	7
Manzanillo	Isla Ixtapa						24	6.9	*	14	6
	Playa Manzanillo						36	0.5	*	15	6
	Playa Blanca					13	12		38	41	13
Nayarit	Careyeros	44	22	3	1	0	0	83	77	**	12
	Antiguo Corral del Risco	38	33	3		7.5	6.5	0.001	41	52	12
	Guayabitos					0	0		55	57	7
	Bahía Tiburones				8.6	6.7	6.5	0.2	47	55	12
	Maria Cleofas					49			*	60	13
	San Juanito		40	42					*	63	8
	Maria Madre Sur		45	40					*	61	10
Baja	San Lorenzo		40			47		0.3	32	52	12
	San Gabriel					99	80		22	28	10
California	Cabo Pulmo	30	29	30	12		18	150	56	58	11
	Caleritas						74		37	32	8

Adapted from Carballo et al. (2013), see original publication for references on coral coverage data

^aLittle information exists for coral habitats prior to the 1997/98 coral bleaching event. Mean frequency of sponge invasion represents average percent invasion in 450 coral samples per site, comprised of coral rubble, small fragments of coral reef framework, and complete branches of live coral colonies in equal proportions (150 samples per category per site)

*Not sampled

**Sampled, but not in coral substrate

12.5 Polychaete Worms

Polychaete worms that bore into reef rock are regarded as dominant macroborers during initial stages of bioerosion, and are important bioeroders in various reef environments worldwide (Hutchings 1981, 2008; Davies and Hutchings 1983). On coral reefs of Australia and French Polynesia, boring polychaetes are found in enormously high densities and their contribution to reef erosion is considerable (Kiene and Hutchings 1994; Hutchings and Peyrot-Clausade 1989, 2002; Hutchings 2008). To date, there are few ETP studies that describe the abundance or distribution of polychaete borers and fewer that address their significance as agents of reef bioerosion. Assessments of bioeroding communities in the ETP that include polychaete borers have generally found their contributions to reef erosion marginal, especially in comparison to other macroborer taxa (i.e., bivalves and sponges). High densities of boring polychaetes have not been reported in

ETP corals. However, colonization of reef frameworks by polychaetes and other boring organisms is highly variable in time and space (Hutchings 1981; Kiene and Hutchings 1994). It is thus likely that existing assessments of boring polychaetes in the ETP are collectively inadequate to understand their roles as bioeroders in the region.

Species belonging to six polychaete families recognized as endolithic bioeroders are reported in the ETP: Eunicidae, Flabelligeridae, Sabellidae, Cirratulidae, Spionidae, and Dorvilleidae (Fauchald 1977; Blake 1991; Hutchings et al. 1992; Fonseca et al. 2006). The various boring species belonging to these families penetrate up to 10 cm into the interiors of carbonate substrates, excavating circular galleries from 0.5 to 2 mm in diameter (Glynn 1997). While there have been no studies describing boring mechanisms employed by polychaetes in the ETP, some authors (Haigler 1969; Hein and Risk 1975; Hutchings 2008) have described the mechanisms for eunicid and spionid borers elsewhere.

Eunicids excavate sinuous, anastomosing passages in carbonate substrates mechanically via the chewing action of a spade-like lower mandible. Spionid borers produce “U-shaped” burrows of constant diameter (0.3–0.5 mm) excavated by chemical dissolution, with abrasion by chaetae likely contributing minimally to substrate removal (Haigler 1969; Hein and Risk 1975).

A survey of infaunal associates and macroborers of *Pocillopora damicornis* colonies at Playa Blanca, Gorgona Island (see Chap. 5 for site location) identified fifteen polychaete species, of which five were suspected borers belonging to the families Eunicidae, Spionidae, and Flabelligeridae (Cantera et al. 2003). *Eunice* spp. and *Flabelligera* spp. were the most abundant boring polychaetes on the reef, accounting for 5.5 and 5.7 % of the total cryptofauna respectively. *Eunice* spp. occurred mainly on the reef platform and crest within the bases of dead *P. damicornis* colonies. This was characteristic of the overall distribution of polychaete borers on the reef—concentrated in dead coral colonies in the reef zone having the highest coral cover. *Flabelligera* spp. were more evenly distributed across reef zones than other boring species, and inhabited both live and dead coral colonies. Relative to other cryptofauna (i.e., bivalves and sipunculans), the impact of boring polychaete infauna was minimal at Gorgona Island (Cantera et al. 2003).

A subsequent study of polychaete macroborer assemblages in *Porites lobata*-dominated reefs of Costa Rica found similar trends in their distributions and relative abundance (Fonseca et al. 2006). Among the six families of polychaete borers identified, eunicid species were again found dominant. Higher polychaete densities were reported in coral colonies with 50–100 % tissue mortality compared to polychaete densities found in less degraded colonies (combined mean polychaete densities of 34.4 and 5.0 ind cm⁻² for the high and low coral mortality levels respectively). While this trend was statistically nonsignificant, a qualitative assessment demonstrates higher polychaete abundances in more degraded coral colonies across all three reefs surveyed. As was observed at Gorgona Island, boring polychaete abundances were a fraction of those recorded for other macroborer taxa, with endolithic bivalve and sipunculan populations dominating on the three surveyed reefs.

A few additional studies provide brief insight into ETP polychaete bioeroders. An assessment of cryptofaunal assemblages in Panama (Enochs 2012) found polychaetes to comprise a fraction percent of total infauna biomass, and were more abundant on dead rather than live coral colonies. A study of coral bioerosion in the Galápagos Islands (Reaka-Kudla et al. 1996) reported polychaetes and bivalves as the most abundant infaunal borers present in experimental blocks of *Porites lobata*. The contribution of endolithic agents to total carbonate loss, however, was again marginal, with rates of internal bioerosion approaching an order of

magnitude below rates calculated for external bioerosion (2.4 and 21.3 kg m⁻² respectively) by sea urchin grazers. The observation of high boring polychaete abundances on experimental carbonate blocks may support the importance placed on these bioeroders as opportunistic colonizers of newly available substrates, as is observed in French Polynesia and on the Great Barrier Reef (Osorno et al. 2005; Hutchings 1981, 2008). Given that there are no data on in situ macroborer abundances or recruitment patterns in the Galápagos for comparison, it is possible that the relative dominance of polychaete assemblages on newly exposed substrates also occurs in Galápagos coral habitats.

12.6 Crustaceans

There are three groups of crustaceans that erode coral skeletons and have relevance to ETP reef bioerosion: hermit crabs, ghost shrimps, and barnacles. Crustacean bioeroders have received little attention and are generally considered a fringe, inconsequential group. To assign no importance to crustacean bioeroders may be a premature conclusion, however, with certain ETP species, (specifically pagurid crabs), exhibiting a capacity for coral damage that is not insignificant in early studies. These findings should be provided contemporary inquiry and expansion.

12.6.1 Pagurid Crabs

There are two known species of coral-associated hermit crabs that abrade and remove skeletal material when foraging on live coral colonies. *Trizopagurus magnificus* and *Aniculus elegans* are found on reefs throughout the ETP often sheltering among branching pocilloporid corals and are especially common on *Pocillopora damicornis* (Gilchrist 1985). These pagurid crabs produce large amounts of fine and coarse-grained calcareous sediments when foraging on soft tissues of coral prey (Glynn et al. 1972).

Feeding rates and fractional mass components of targeted *Pocillopora* colonies were assessed experimentally in the 1970s using *Trizopagurus magnificus* and *Aniculus elegans* in Panama (Glynn et al. 1972). Inorganic skeletal material represented more than 90 % of the total coral mass abraded by pagurid foraging, and mean sediment production rates of 9.6 and 1160 mg dry wt day⁻¹ of carbonate were removed per individual for *T. magnificus* and *A. elegans* respectively. Given these rates, corallivorous predation by hermit crabs may have greater implications for bioerosion processes than for trophically-driven removal of coral tissues. A subsequent experiment in Panama reported an average of 3.6 cm² coral area damaged by individual *T. magnificus* every two days (Gilchrist 1985). Furthermore, crabs from Pacific waters are

persistent coral inhabitants compared to transient coral occupation by Caribbean species. As a result, non-feeding damage to corals by Pacific crabs is greater, with sustained contact and shell movement causing further surface abrasion and local polyp death (Gilchrist 1985).

12.6.2 Burrowing Shrimps

Burrowing thalassinidean shrimps in the genus *Pomatogebia* (formerly included in *Upogebia*) are specialized for boring into scleractinian coral skeletons. Two species are found in the ETP, *Pomatogebia rugosa* and *Pomatogebia cocosia* (Williams and Ngoc-Ho 1990). Male/female pairs excavate complex, ramifying burrows in massive corals. *Pomatogebia rugosa* tunnels are roughly 2.5 mm in diameter (Fonseca and Cortés 1998). With the exception of *Alpheus simus* infestation in some Caribbean reefs (Cortés 1985), boring shrimps are found to be minimal contributors to reef erosion. Sampling of thalassinidean shrimps in ETP reefs commonly report them absent or at very low densities, and excavating reef rock at near negligible rates—though reports of thalassinidean invasion on Costa Rican reefs are highly variable (Cortés 1991; Fonseca and Cortés 1998; Fonseca et al. 2006).

12.6.3 Acrothoracican Barnacles

Burrowing acrothoracican barnacles infest a wide variety of skeletal materials including carbonate reef rock (Warne 1975). Acrothoracican excavation is accomplished largely by mechanical abrasion via the action of chitinous teeth along the carapace. The initial penetration of carbonate substrates by acrothoracican recruits is thought to be performed by chemical dissolution, as suggested by experimental observations and the absence of abrading structures in larvae (Tomlinson 1969). Reports of acrothoracicans on reef substrates are rare (Zullo 1991), with sampling difficulties likely contributing to this paucity. Reef-dwelling barnacles in the ETP are poorly understood and little is known about this group's significance to reef bioerosion. At Gorgona Island, barnacles were early colonizers of experimental units of *Pocillopora* substrates and highly abundant during initial exposure periods (Londño-Cruz et al. 2003). Pioneer borings by acrothoracicans may be important for facilitating subsequent macroborer recruitment. Barnacles belonging to the Family Lithotryidae perform very high bioerosion rates in certain shallow, near-shore reef environments (Scoffin et al. 1980), but lithotryid species are not reported in ETP coral habitats (Tomlinson 1969; Zullo 1991).

12.7 Sipuncula

Species in several Sipuncula (peanut worms) genera bore into coral skeletons. As endolithic bioeroders, sipunculan worms share a few apparent characteristics with boring polychaetes. Both 'worm' taxa are exceptionally common marine cryptofauna, but occur in highly variable densities and distributions that shift across a broad range of spatial-temporal scales. As a result, there is no general agreement on the overall significance of sipunculans as bioeroders and, as is the case with polychaetes, it is more necessary to assess regional impacts or roles within coral habitats. Additionally, both sipunculans and polychaetes are known to have distinct roles within bioeroder community succession, and temporal trends of substrate colonization have been foci in the study of both groups. While polychaetes are well-recognized as early colonizers of newly available coral substrates, longer-lived sipunculan borers are predominant in the latter stages of the bioerosion process (Hutchings et al. 1992). Despite the morphological and ecological similarities between these endolithic worms, these assemblages demonstrate contrasting requirements for coral invasion and the role sipunculans play in bioerosional processes is generally less well understood.

Sipunculan burrows are found in dead corals or in the dead parts of live colonies (Williams and Margolis 1974). Sipunculan recruits excavate a single flask-shaped burrow that is inhabited individually and permanently. Sipunculan burrows are highly variable and species-specific, ranging from straight to sinuous, narrow to broad, and from near surface to penetrating centimeters deep into the coral skeleton (Glynn 1997). There is substantial evidence that sipunculan boring is accomplished by chemical and mechanical means in combination, though the exact manner is not known. It is likely that acidic or chelating fluids secreted by epidermal glands soften and dissolve the substrate, while cuticular papillae and a calcareous shield on the posterior trunk abrade concurrently (Rice 1969; Rice and Macintyre 1972; Williams and Margolis 1974). Sipunculan species reported on ETP corals are small (Fonseca and Cortés 1998; Londño-Cruz et al. 2003), limiting their contribution to reefal bioerosion.

In Costa Rica, there has been considerable effort to describe sipunculan diversity since the early 1990s, and more than 20 species have been described to date (Cutler et al. 1992; Dean et al. 2010). Sipunculans that excavate calcareous substrata belong to the families Aspidosiphonidae and Phascolosomatidae (Cutler 1994). Of these families, aspidosiphonid species are larger contributors to coral erosion in the eastern Pacific, with sipunculans in the genus *Aspidosiphon* being particularly abundant (Cantera et al. 2003; Fonseca et al. 2006). Coral-excavating sipunculans are

highly abundant on certain Costa Rican reefs. In Golfo Dulce, 92 and 83 % of *Porites lobata* colonies were infested by the sipunculan *Aspidosiphon elegans* at the Sándalo and Punta Islotes reefs respectively (see Chap. 5 for site locations), and *A. elegans* densities reached up to 300 ind m⁻³ (Fonseca and Cortés 1998). A subsequent study found sipunculan infauna to comprise more than 50 % of non-colonial macroborers surveyed at Platanillo (Caño Island) and Golfo Dulce, and were reported to have a mean density of 131.4 ind m⁻² across sites—sipunculan densities were more than three-fold higher than those found for bivalves, the second most abundant borers (Fonseca et al. 2006).

In the same study, reefal abundance of sipunculan infauna was suggested as a potential bio-indicator of overall reef health (Fonseca et al. 2006). Sipunculan distributions, specifically those of aspidosiphonids, demonstrated apparent and contrasting relationships with both overall reef health and individual coral colony mortality. Mean sipunculan densities were inversely related to the intensity of site degradation, with sipunculans being more abundant at reefs having higher coral cover (coral cover was highest at Platanillo, lowest at Sándalo and mean sipunculan densities were 131.2, 52.6, and 28.6 ind m⁻² at Platanillo, Punta Islotes and Sándalo respectively) (see Chap. 5 for site locations). With respect to individual host corals, however, sipunculan densities were significantly higher in corals having more than 50 % tissue mortality (Fonseca et al. 2006). Distributional separation between live and dead host coral was more pronounced in healthier reefs where sipunculan densities and relative abundance were highest (i.e. at Platanillo, mean sipunculan densities were 261.4 and 1.1 ind m⁻² in corals with greater and less than 50 % tissue mortality respectively). These findings support the notion that sipunculans are dead coral borers abundant in healthy reefs. In extensively degraded reef sites sipunculan populations are diminished and other macroborers (i.e. bivalves) dominate.

At Gorgona Island Colombia, sipunculan borers are reported to have a small impact on reefal bioerosion compared to populations observed on Costa Rican reefs (Cantera et al. 2003). Assessment of internal bioerosion at Gorgona found sipunculans to be among the least important macroborers of experimental units of *Pocillopora* branches, with small-sized individuals recruited in low abundances (Londoño-Cruz et al. 2003). While temporal patterns in bioeroder recruitment reported in this study were not consistent with findings elsewhere (Hutchings et al. 1992), there was apparent increase in sipunculan abundance over time in the majority of experimental units. These findings, however, were not considered supportive of sipunculans as late invaders, due to recruits being observed after only 6 months of exposure (Londoño-Cruz et al. 2003). The rate of total

internal bioerosion, however, increased over time more rapidly than is typical for non-ETP reefs (Davies and Hutchings 1983; Kiene and Hutchings 1994). It is possible that the nutrient-rich ETP environment accommodates for more rapid substrate conditioning as a result of bioerosion processes operating more quickly, thereby establishing unique or condensed temporal patterns in macroborer recruitment (Highsmith 1980; Reaka-Kudla et al. 1996).

At the Playa Blanca fringing reef off the southern coast of Gorgona Island, six sipunculan species were identified in a survey of *Pocillopora damicornis* cryptofauna (Cantera et al. 2003). *Aspidosiphon steenstrupii*, the most abundant sipunculan species, occurred in relatively moderate numbers among the infaunal community. Sipunculan distributions exhibited strong zonal preferences and *A. steenstrupii* occurred almost exclusively in the reef flat crest and reef front where coral cover was highest. More sipunculans were found in dead *P. damicornis* than in live colonies at the reef flat-crest (45 and 9 individuals extracted respectively), while sipunculans were found to be evenly distributed among dead and live corals at the reef front where coral cover was lower (44 and 56 individuals in dead and live coral respectively). These trends coincide with distributions reported for sipunculan populations in Costa Rican habitats by Fonseca et al. (2006).

12.8 Bivalve Molluscs

In the ETP, boring bivalves are often the most abundant and destructive endolithic bioeroders of coral skeletons. While gastropod and polyplacophoran molluscs can be important epilithic bioeroders in regions elsewhere (see Table 4-2 in Glynn 1997), these taxa do not directly or substantially contribute to carbonate excavation in ETP coral habitats. Bivalve assemblages in the ETP, however, demonstrate a much greater capacity for coral erosion than is found for taxonomically similar assemblages in regions elsewhere (Kleemann 1986, 1990, 2013; Scott et al. 1988). Endolithic bivalves, *Lithophaga* spp. in particular, often reach unusually high abundances on eastern Pacific reefs and densities of several hundred boring bivalves per m² of coral surface area are commonly reported (Table 12.3). Assessments of bioeroder communities at sites throughout the ETP frequently report bivalve excavating activity to have the most significant impact on coral erosion, and bivalve molluscs consistently dominate macroborer communities (Cantera et al. 2003; Londoño-Cruz et al. 2003; Fonseca et al. 2006).

The high abundance, growth potential, and capacity for carbonate erosion demonstrated by ETP bivalve assemblages are environmentally conditioned, with genetic or biological distinctions appearing less influential (Kleemann 1990). Nutrient loading and high primary productivity in ETP

Table 12.3 Bivalve densities reported in the eastern Pacific

Site	Host coral	Total	Density (ind m ⁻²)		Reference
			Live host	Dead host	
Panama	All genera		3060	76 ^a	Scott et al. (1988)
	<i>Porites</i>	35.2	18.7 (14.0) ^b	16.5 (21.2)	Highsmith (1980) ^c
	<i>Pavona</i>	20.9	5.1 (4.4)	15.8 (16.5)	Highsmith (1980)
Galápagos	All genera		480	381	Scott et al. (1988)
	<i>Porites</i>	13.8	12.3	1.5	Highsmith (1980)
	<i>Pavona</i>	31	4.9 (4.6)	26.1 (26.4)	Highsmith (1980)
Costa Rica	All genera		4810	3920	Fonseca et al. (2006) ^{d,e}
Caño Island			1870	2021	Fonseca et al. (2006)
		2529	2110	2920	Scott et al. (1988)
Punta Islotes		4350	5580	3120	Fonseca et al. (2006)
Sándalo		6220	6730	5710	Fonseca et al. (2006)

^aValues represent ind kg⁻¹

^bValues represent mean number of bivalves per coral colony

^cValues in parentheses are adjusted to show individuals encircled by coral growth after settlement and moved from live to dead category

^dValue converted from ind 100 cm⁻²

^eLive versus dead substrate category reflects coral colonies with 0–50 % and 50–100 % tissue mortality respectively

waters endow considerable growth advantage to bivalve endoliths (Highsmith 1982; Kleemann 1986, 1990). The abundance of filter-feeding bivalves in reef environments worldwide corresponds with a relative gradient in primary production, peaking in the ETP (Highsmith 1980). Nevertheless, the ecological success and dominance of bivalves among ETP macroborers may not be conditioned by trophic factors alone, with reefal (e.g., live cover, zonation, disturbance) and taxonomic composition (i.e., bivalves and coral substrate species) likely having additional influence.

Two groups of boring bivalves are found in ETP coral skeletons: bivalves belonging to the genus *Gastrochaena* in the family Gastrochaenidae and species in the genus *Lithophaga* (*Leiosolenus*) belonging to the family Mytilidae. Lithophagid bivalves are well-established as being the most important infaunal coral borers in the ETP in regards to both abundance and boring rates (Scott et al. 1988; Reaka-Kudla et al. 1996). The borings performed by less abundant and smaller-sized gastrochaenid bivalves are reported to have a large impact on pocilloporid corals at certain sites, however (Cantera et al. 2003; Londoño-Cruz et al. 2003).

Lithophaginid and gastrochaenid bivalves reside exclusively in calcareous substrates, with the possible exception of at least one lithophagid species (i.e., *Lithophaga plumula*) observed boring into mudstone and quartzose sandstone by Warne (1975), substrates that are largely non-calcareous in composition. Boring bivalves that inhabit coral skeletons gain shelter from predators while retaining ability to filter-feed via an apical siphonal opening. Endolithic bivalves are prominently invaders of dead coral colonies (Kleemann 1986; Enochs 2012). Within the lithophaginids,

however, there are a few species, i.e. *Lithophaga laevigata*, whose larvae can penetrate soft coral tissues and invade live corals (Kleemann 1977, 1980; Hutchings 1986; Guzman 1988). Boring bivalves are generally found to have strict requirements with respect to host coral species (Kleemann 1980, 1986, 1992, 1995, 2008; Kleeman and Hoeksema 2002). In the eastern Pacific, however, boring bivalves are atypically abundant in live coral skeletons (Kleeman 2013), and species considered to invade exclusively dead coral colonies (i.e., *Lithophaga aristata* and *Lithophaga attenuata*) are occasionally reported to inhabit live coral colonies as well (Highsmith 1980; Scott et al. 1988; Cantera et al. 2003; Kleemann 2013)—though such reports may owe in part to lateral overgrowth of coral tissues around borehole openings following invasion (Highsmith 1980; Kleemann, personal communication). *L. laevigata* is reported to be an obligate associate of live *Porites* and *Pavona* massive corals, not found in dead coral colonies, and declining in abundance with mortality of coral tissue (Guzman 1988). Trends reported for bivalve species invading dead versus live coral colonies are complex and demonstrate highly variable preferences with respect to bivalve species and reef zone (Table 12.4).

It is generally understood that the recruitment of bivalve larvae and subsequent invasion of carbonate rock occurs only after long periods of substrate exposure and preconditioning by pioneer boring assemblages (mainly microendoliths and polychaete worms), as is observed in many reefs outside the ETP (Kiene and Hutchings 1994; Chazottes et al. 1995; Hutchings 2011). Numerous studies of bioeroder community succession in a wide range of reef environments

Table 12.4 Abundance of infaunal bivalves sampled in three live and three dead *Pocillopora damicornis* colonies at major reef zones, Playa Blanca fringing reef, Gorgona Island, Colombia

Species	Backreef		Reef flat crest		Reef front		Outer slope		Totals		
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	All
<i>Lithophaga aristata</i>	0	3 (100)	10 (19)	43 (81)	4 (20)	16 (80)	3 (10)	27 (90)	17 (16)	89 (83)	106
<i>L. plumula</i>	2 (33)	6 (67)	12 (29)	29 (71)	8 (57)	6 (43)	3 (43)	4 (57)	25 (36)	45 (64)	70
<i>L. hancocki</i>	2 (22)	7 (78)	17 (7)	243 (93)	53 (82)	12 (18)	2 (2)	99 (98)	74 (17)	361 (83)	435
<i>L. calyculata</i>	4 (24)	13 (76)	21 (14)	125 (86)	50 (65)	27 (35)	9 (23)	30 (77)	84 (30)	195 (70)	279
<i>L. hastasia</i>	0	0	2 (100)	0	0	0	0	0	2 (100)	0	2
<i>Gastrochaena ovata</i>	2 (40)	3 (60)	7 (10)	61 (90)	21 (64)	12 (36)	4 (17)	19 (83)	34 (26)	95 (74)	129
All species	10 (30)	32 (70)	69 (12)	501 (88)	136 (65)	73 (35)	21 (10)	179 (90)	236 (23)	785 (77)	1021

Values in parentheses represent percent abundance in live or dead coral. Adapted from Cantera et al. (2003)

support the later-stage settlement of bivalve assemblages: boring bivalves were absent for the first 1–4 years of substrate exposure on the Great Barrier Reef (Kiene and Hutchings 1994; Tribollet et al. 2002; Osorno et al. 2005), and after two years at Moorea, French Polynesia and Aqaba, Red Sea (Chazottes et al. 1995; Hassan 1988). In the eastern Pacific, however, the settlement of bivalves on newly available substrates is much faster and can occur within days of coral death (Kleemann 2013). Macroborer community succession occurs more rapidly in the ETP, with temporal and successional trends deviating from trends demonstrated in reef habitats elsewhere (Kiene and Hutchings 1994; Londoño-Cruz 2001; Londoño-Cruz et al. 2003). In coral habitats in the Galápagos Islands, the profusion of vacant lithophage borings may have aided recruitment of *Euclidaris* and a massive increase in echinoid abundance following the 1982–83 El Niño event (Reaka-Kudla et al. 1996; Glynn et al. 2015; see Sect. 12.9.2.1).

Carbonate excavation by bivalves has historically been regarded as a predominantly mechanical process which, within the Mytilacea, may be assisted chemically (Yonge 1955; Ansel and Nair 1969; Hutchings 1986; Morton 1990). All other boring bivalves were considered to use exclusively mechanical means, i.e. abrasion (Ansel and Nair 1969; Pojeta and Palmer 1976). The controversial view that bivalves can bore by chemical means (corrosion) found little support in the literature despite many early studies dealing with boring bivalves in general (Cailliaud 1850; Deshayes 1850) and *Gastrochaena* in particular (Cailliaud 1843). It is now known that chelating agents secreted from pallial glands soften and dissolve calcium carbonate, initiating the boring process (Jaccarini et al. 1968; Morton and Scott 1980). Loosened small calcareous fragments are then removed by ciliary action of the mantle and exhalent siphon, producing fine-grain sediment (Kleemann 1973, 1974). Mechanical abrasion contributes to boring in some gastrochaenids, i.e. *Spengleria* spp. (Carter 1978; Hutchings 1986; Kleemann 1996). Coral excavation by lithophagid and gastrochaenid

species produces vase-shaped cavities penetrating 1 to >15 cm into the coral skeleton (Glynn 1997). Characteristically, lithophagid borehole openings usually resemble old-fashioned keyholes marking the surface of invaded host corals (Fig. 12.4b). Bivalves that invade dead corals may prevent lateral overgrowth of this siphonal opening by the secretion of chelating agents during the boring process (Morton and Scott 1980; Kleemann 2013).

In coral reefs at Costa Rica, Panama, and the Galápagos Islands, heavy infestation by associated lithophagids [i.e., *Lithophaga (Leiosolenus) laevigata*] is exceptionally common in massive *Porites lobata* corals (Fig. 12.4a–c), a predominant reef-building species (Kleemann 1982, 2013; Scott et al. 1988). Structurally, *Porites lobata* has the lowest compressive and bending strength of tested coral species (Scott and Risk 1988). The strongest un-bored *P. lobata* skeleton demonstrates bending strength an order of magnitude below that of un-bored *Acropora cervicornis* skeleton of approximately the same diameter. The high skeletal porosity and arrangement of septa and theca are thought to most affect the unusually low strength of *P. lobata* skeletons. Boring by lithophagid bivalves greatly reduces the breaking stability of reef-building *P. lobata* (Scott and Risk 1988) and corals in general.

Coral breakage generated or so predisposed by bivalve excavation promotes asexual dispersal and the recruitment of remnant coral colonies following major disturbances, such as mortality events that accompany ENSO phenomena (Scott et al. 1988). Endolithic bivalves also mediate coral colony fragmentation indirectly by attracting grazing predators (Guzman 1986; Scott and Risk 1988; see Chaps. 10 and 15, Enochs and Glynn, and Glynn et al. respectively). Triggerfishes (e.g. *Pseudobalistes naufragium*) in particular break apart large portions of *Porites lobata* in their foraging activities. After accessing bivalve prey, triggerfish leave behind uningested coral fragments, and a significant proportion of these coral fragments survive (Guzman 1986). Thus, a paradoxical couplet of destructive and propagating

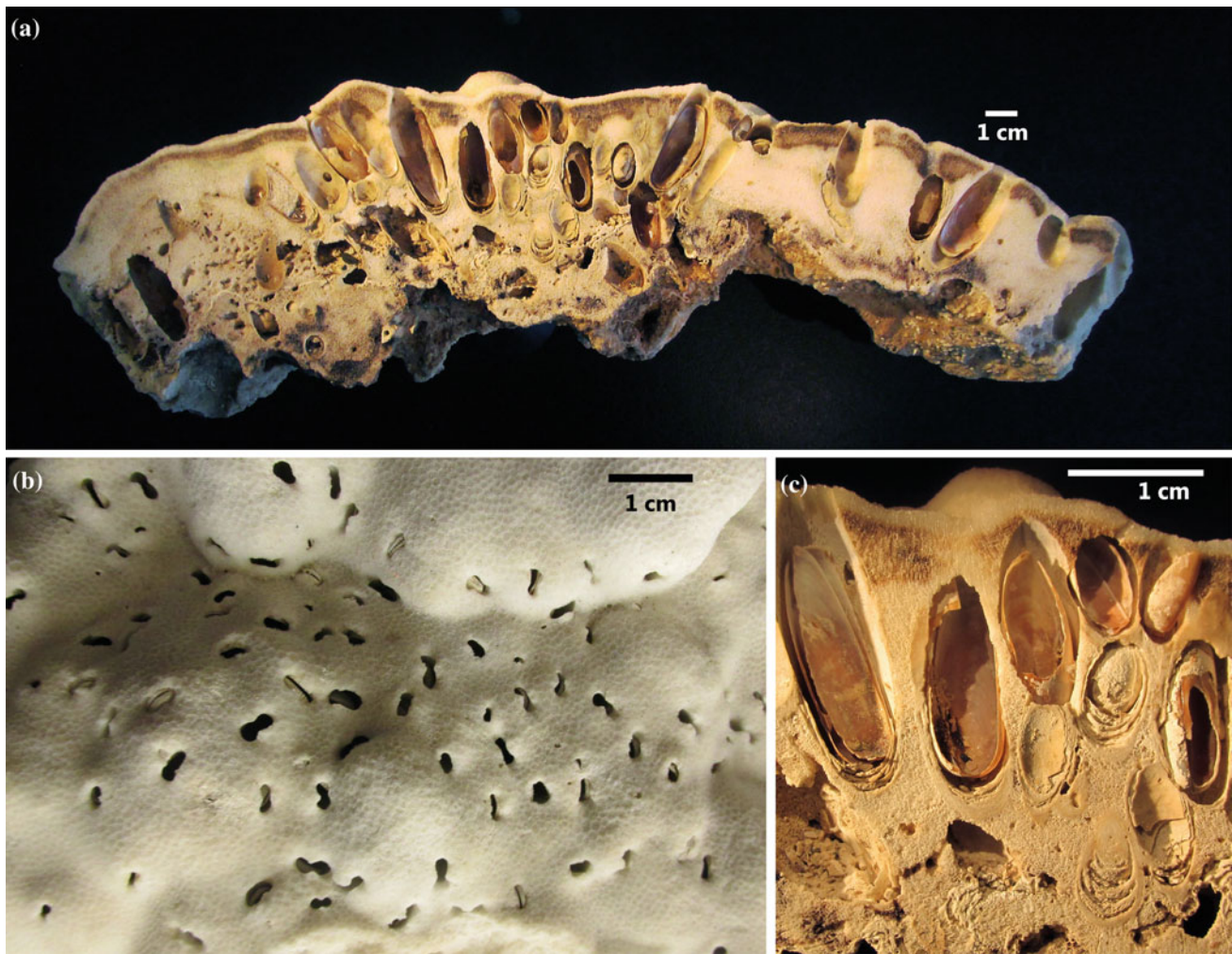


Fig. 12.4 *Lithophaga laevigata* excavations in live *Porites lobata*. **a** Boring bivalves revealed in a cross-section of coral skeleton, **b** coral surface with characteristic *L. laevigata* siphonal apertures, **c** magnified cross-section. Photographs by B. Grassian

reefal processes is driven by the activities of boring bivalves and their predators. Although boring bivalves perform extensive coral erosion, they also may play an important role in establishing coral populations in unfavorable ETP environments, and promote reef recovery after ENSO-associated mortality events (Scott and Risk 1988; Scott et al. 1988).

Boring bivalve assemblages have been assessed in most ETP coral environments, including: Panama, Galápagos Islands, Costa Rica, and Gorgona Island, Colombia (Kleemann 1986, 1990; Scott et al. 1988; Cortés 1991; Cantera et al. 2003; Londoño-Cruz et al. 2003; Fonseca et al. 2006). In all of these assessments, bivalve assemblages are highly abundant and large contributors to bioerosional processes (Table 12.3). Boring bivalves typically dominate macroborer communities and have been reported in extraordinarily high densities on ETP reefs. As example, one study reports *Lithophaga* population densities reaching upwards of 10,000 ind m⁻², with means of 3060 and 1870 ind m⁻² in Panama and Costa Rica, respectively (Scott et al. 1988).

These high densities are supported by subsequent surveys (Fonseca et al. 2006). An assessment of macroborer communities at Gorgona Island, Colombia reports boring bivalves to comprise 67.3 % of total macroborer abundance (Cantera et al. 2003). The importance of lithophagid bivalves in bioeroder communities throughout the ETP has been demonstrated with both definite consistency and significance.

Of ETP gastrochaenid bivalves, *Gastrochaena ovata* is found in highest abundance and is common in the dead bases of *Pocillopora damicornis* corals at Gorgona Island, Colombia (Cantera et al. 2001, 2003; Londoño-Cruz 2001). *Gastrochaena ovata* is observed less frequently in tissue-covered parts of branching corals as well, and is not reported to inhabit massive coral species (Cantera et al. 2001, 2003). Burrows excavated by *G. ovata* are cylindrical, deep and typically much larger than the bivalve occupant (Londoño-Cruz et al. 2003; Kleemann 2008). Boring rates for *G. ovata* are unknown but Guzman and Cortés (1993)

reported a rate for Costa Rican *Gastrochaena rugulosa* of $0.5 \text{ g CaCO}_3 \text{ m}^{-2} \text{ days}^{-1}$ on experimental plates of *Porites lobata*. (The calculation for this rate, based on percent of skeletal removal, was not explicitly noted.)

Several studies have calculated lithophagid boring rates on ETP reefs, though most provide a combined rate for macroborer communities dominated by bivalve assemblages. A study investigating bioerosional processes on reefs impacted by the 1982–83 El Niño event reported $9 \text{ kg m}^{-2} \text{ year}^{-1}$ of carbonate removed by infaunal bioeroders (Scott et al. 1988). The authors attribute a majority of sediment production to *Lithophaga* boring, corroborated by the preponderance of very fine to silt-sized grains resembling sediments produced by *Lithophaga* in laboratory experiments (Scott et al. 1988). At Gorgona Island, Colombia, mean rates of total internal bioerosion on experimental units of dead pocilloporid branches ranged from 0.69 ± 0.03 (SEM) to 2.58 ± 0.59 (SEM) $\text{kg m}^{-2} \text{ year}^{-1}$. These rates include the entire endolithic guild, but *Lithophaga* spp. again dominated and were responsible for a large majority of the observed carbonate removal (Londoño-Cruz et al. 2003).

A comparative assessment between functionally similar ETP and Caribbean bivalve species, as well as observations of bivalve transplants demonstrates considerable enhancement in bivalve growth rates and boring potential conditioned in eastern Pacific waters (Kleemann 1990, 2013). This study finds: Pacific *Lithophaga attenuata* bores twice as fast and grows two and a half times faster than similar-sized Caribbean *Lithophaga corrugata*; Pacific *Lithophaga plumula* bores twice as fast and has four-fold higher growth rates than similar-sized Caribbean *Lithophaga teres*; Pacific *Lithophaga aristata* bores three times faster and has four-fold higher growth rates than Caribbean *Lithophaga malaccana* (Kleemann 1990). Furthermore, Caribbean bivalve species transplanted to Urabá Island, Panama demonstrate substantially increased boring and growth rates approaching those observed for similar ETP species (rates for Caribbean transplants were only 10–20 % less than similar Pacific species). Although the transplanting of non-native species would no longer be practiced in field-based experiments today, these early findings are quite important and establish a strong linkage between the marine environment and bioerosion potential of bivalve macroborers (Highsmith 1980; Hallock 1988; Kleemann 1990).

12.9 Echinoderms

Among the echinoderms, echinoids are the only group that performs reefal bioerosion, although *Acanthaster* predation sets the stage for bioerosion by other organisms (Glynn 1973; Glynn and Manzello, in press). In certain regions (e.g., ETP, Caribbean, and French Polynesia), sea urchins are

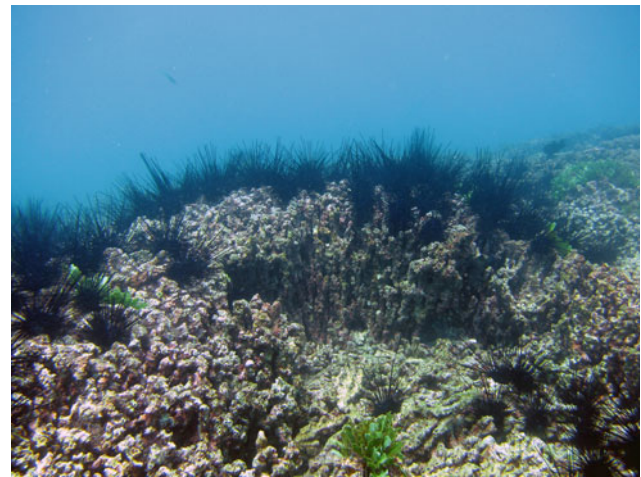


Fig. 12.5 *Pocillopora* framework impacted by bioerosion activity of *Diadema mexicanum* in Bahía Culebra, Costa Rica (see Alvarado et al. 2012)

common, conspicuous inhabitants of coral reefs, and can be responsible for considerable carbonate erosion (Scoffin et al. 1980; Reaka-Kudla et al. 1996; Pari et al. 1998). In the ETP specifically, abrupt increases in sea urchin population densities have led to large-scale modification of reef structure and functioning at certain sites—phenomena often initiated by sudden declines in reef condition (Birkeland 1989). Following ENSO thermal shock events, echinoid populations have rapidly expanded in eastern Pacific coral habitats affected by mass bleaching and coral mortality, establishing intense regimes of bioerosion and framework degradation (Fig. 12.5). The recovery of impacted coral habitats can be significantly influenced by attendant changes in sea urchin abundance (Glynn 1988; Eakin 1996; Glynn et al. 2015).

Sea urchins possess a highly developed jaw apparatus, the Aristotle's lantern; a flexible and protractile masticatory organ consisting of five radially arranged calcified teeth, which are harder than the surfaces they scrape (Glynn 1997). When feeding, sea urchins employ Aristotle's lantern to graze on epilithic algae, including those on the exposed skeletons of dead corals. During the foraging process, small chips of coral are scraped off and ingested with the primary algal food source. The carbonate material is then transformed into a paste from which the ruptured algal cells and sap are absorbed. Fecal pellets consist almost entirely of triturated calcium carbonate, which is deposited back on the reef (Hutchings 2011).

Grazing typically occurs at night when the echinoids leave their shelters to feed on exposed surfaces. Foraging is primarily on dead corals, though echinoids occasionally attack live corals as well (Bak and van Eys 1975; Glynn et al. 1979). Echinoid populations can perform substantial bioerosion at low to moderate densities ($0.5\text{--}5 \text{ ind m}^{-2}$), but at high densities ($>5 \text{ ind m}^{-2}$) degradation of reef substrata rivals that of

the most destructive endolith assemblages (Hutchings 1986; Glynn 1997). Where abundant, sea urchins are the most destructive grazers on coral reefs (Hutchings 1986), and are responsible for 80 % of total bioerosion at certain sites (Scoffin et al. 1980). The magnitude of echinoid bioerosion depends on species, mean test size, and population density (Bak 1994)—factors concurrently influenced by overall reef health, the availability of coral substrates, and oceanographic conditions affecting larval recruitment and growth.

12.9.1 Echinoid Bioerosion World-Wide

Sea urchins are extremely abundant on certain reefs: the highest population densities reported are on degraded reefs in French Polynesia (210 ± 60 SD ind m^{-2}) and the Galápagos Islands (60 ± 5 SEM ind m^{-2}) (Glynn et al. 1979; Reaka-Kudla et al. 1996; Pari et al. 1998). In these cases, coral reef frameworks can be altogether destroyed by sea urchin bioerosion. This situation commonly occurs on highly fished or over-fished reefs (Glynn 1988; Reaka-Kudla et al. 1996; Peyrot-Clausade et al. 2000; Tribollet and Golubic 2011), where echinoid populations are unfettered ostensibly by predation pressure (Sonnenholzner et al. 2009, 2011; Edgar et al. 2011), and execute unusually high bioerosion rates (McClanahan et al. 1994). It is hypothesized that on reefs where fishes maintain abundance, sea urchin populations are biologically controlled and usually do not threaten reef condition. Large increases in echinoid abundance can act as an alert signal to stakeholders and/or managers, indicating that either significant over-fishing may be occurring or changing environmental conditions (e.g., water quality and terrestrial run-off) are leading to declining coral health, and remedial action should be taken (Sonnenholzner et al. 2009, 2011; Hutchings 2011).

Damselfish populations also effect echinoid distributions and bioerosion rates, however not by predation (Eakin 1988). Damselfishes deter and clear benthic grazers from small, well-defined patches on the reef. The territorial behavior of damselfishes causes substantial localized reduction in sea urchin densities within defended algal lawns (Eakin 1987, 1988, 1991; Glynn 1988). In this way, spatial competition by damselfishes protects exposed coral substrates from echinoid bioerosion.

12.9.2 Echinoid Bioerosion in the ETP

The first reference to sea urchin erosion in the ETP was noted by E.W. Craig for *Echinometra vanbrunti* and *Eucidaris thouarsii* in Guaymas, Mexico (Fewkes 1890). More recent studies have shown that *Eucidaris galapagensis*, *Eucidaris thouarsii*, *Centrostephanus coronatus* and *Diadema*

mexicanum are the main external bioeroders in the ETP (Glynn et al. 1979; Eakin 1988; Glynn 1988; Colgan 1990; Guzman and Cortés 1992, 2007; Reaka-Kudla et al. 1996; Reyes-Bonilla and Calderón-Aguilar 1999; Toro-Farmer et al. 2004; Herrera-Escalante et al. 2005). The occurrence, relative abundance, and role of these ETP species vary across smaller, local scales. The impact of echinoid bioerosion on coral reef carbonate dynamics is greater in the ETP than on reefs elsewhere (Ogden 1977; Eakin 1996; Glynn et al. 2015; Table 12.5). The intensity of sea urchin bioerosion is generally responsive to that of ENSO-associated coral mortality events, and these phenomena together establish an erratic regime of reef degradation varying in severity across relatively small spatio-temporal scales. The following sections assess, within the ETP region, variable relationships between echinoid bioerosion and ENSO-associated reef disturbance (see Chap. 5 for site locations).

12.9.2.1 Galápagos Islands

Glynn et al. (1979) demonstrated that bioerosion by the sea urchin *Eucidaris galapagensis* in the Galápagos Islands prevented establishment of reef frameworks, composed mainly of pocilloporid corals. Intensive grazing by *E. galapagensis* on reef-building *Pocillopora damicornis*, *Pocillopora elegans*, and *Pocillopora capitata* corals, resulted in zero net carbonate production when coral cover was equal to or less than 30 %. The impact of echinoid bioerosion on Galápagos reefs increased following the dramatic 1982–83 El Niño event. Among ETP coral habitats, those in the Galápagos Islands experienced the largest decrease in coral cover as a result of the 1982–83 El Niño, with a mean coral mortality of 97 % estimated from 14 surveyed reefs (Glynn 1988). Following coral mortality, the high numbers of *E. galapagensis* that were mainly found on reef margins aggregated on the dead coral framework, resulting in a rapid loss of reef structure (Table 12.5; Fig. 12.6).

A decade later, Reaka-Kudla et al. (1996) showed that *Eucidaris galapagensis* abundance and bioerosion rates remained high at Champion Island in the southern Galápagos, with *E. galapagensis* responsible for 67–75 % of total reefal bioerosion. High echinoid population densities still persist in most coral communities in the central and southern Galápagos Islands, continuing for more than two decades after the initial population expansion (i.e., mean *Eucidaris galapagensis* population densities of 43.4 ind m^{-2} at Champion Island between 1985 and 2009). The indirect release of predation pressure via over-exploitation of piscine (i.e., the hogfish *Bodianus diplotaenia*) and crustacean predators of echinoids (i.e., *Panulirus* spp. and *Scyllarides astori* lobsters) is strongly implicated as being causal to the maintenance of high echinoid densities on these reefs (Ruttenberg 2001; Okey et al. 2004; Sonnenholzner et al. 2009; Edgar et al. 2011). Additionally, nutrient-rich

Table 12.5 Bioerosion rates of different sea urchin species at coral reef localities around the world

Species	Locality	Density (ind m ⁻²)	Test diam (cm)	Bioerosion rate (kg m ⁻² year ⁻¹)	Source	
<i>Eucidaris galapagensis</i>	Galápagos	10–50	4.9–5.5	20–40	Glynn (1988)	
		10–60	–	22.8	Reaka-Kudla et al. (1996)	
<i>Eucidaris thoursii</i>	Mexico	0.2	4.3	0.7	Reyes-Bonilla and Calderón-Aguilera (1999)	
<i>Diadema antillarum</i>	Barbados	–	–	9.7	Hunter (1977)	
		23	0.5–6.0	9.0	Stearn et al. 1977	
		23	1.0–6.0	9.7	Scoffin et al. (1980)	
	St. Croix, US Virgin Islands	9	6.0	4.6	Ogden (1977)	
	Venezuela	4	–	6.0	Weil 1980 in Griffin et al. (2003)	
		3		5.9		
		2.6		3.8		
	Curaçao	12	–	2.9	Bak et al. (1984)	
	<i>Diadema mexicanum</i>	Uva Is, Panama	3–150	1.8–2.7	5.0–20.0	Glynn (1988)
			1.78	–	0.1	Eakin (1996)
0.06			–	0.0		
18.76			–	1.0		
48.26			–	4.4		
Saboga Is, Panama		27.2	3.4–3.5	13–17	Glynn (1988)	
Huatulco, Mexico		1.0	4.0	0.9	Herrera-Escalante et al. (2005)	
		1.3	3.4	0.9		
		2.9	3.0	2.0		
		6.8	2.9	3.3		
		0.26	4.72	0.3	Benítez-Villalobos et al. (2008)	
		0.36	4.83	0.4		
		0.48	4.41	0.4		
		4.17	4.71	4.0		
<i>Diadema savignyi</i>		French Polynesia	4.87	5.5–5.9	3.9	Bak (1990)
	Kenya	0–0.1	5.7–8.3	0.1–1.2	Carreiro-Silva and McClanahan (2001)	
<i>Diadema setosum</i>	Gulf of Eilat	0.1–6.4	3.0	0.0–0.7	Mokady et al. (1996)	
	Kenya	0.01–0.4	5.3–7.8	0.65	Carreiro-Silva and McClanahan (2001)	
	Thailand	0.4–11.8	2.0–7.0	1.64–5.5	Ruengsawang and Yeemin (2000)	
<i>Echinothrix diadema</i>	French Polynesia	0.65	8.8	0.80	Bak (1990)	
	Kenya	0.02–0.07	9.1–12.0	2.00	Carreiro-Silva and McClanahan (2001)	
<i>Centrostephanus coronatus</i>	Colombia	6.86	0.91–2.58	0.2	Toro-Farmer et al. (2004)	
<i>Echinostrephus aciculatus</i>	Marshall Islands	0.50	2.4	0.1	Russo (1980)	
		1.05	1.8	0.06		
		0.66	1.68	0.03		

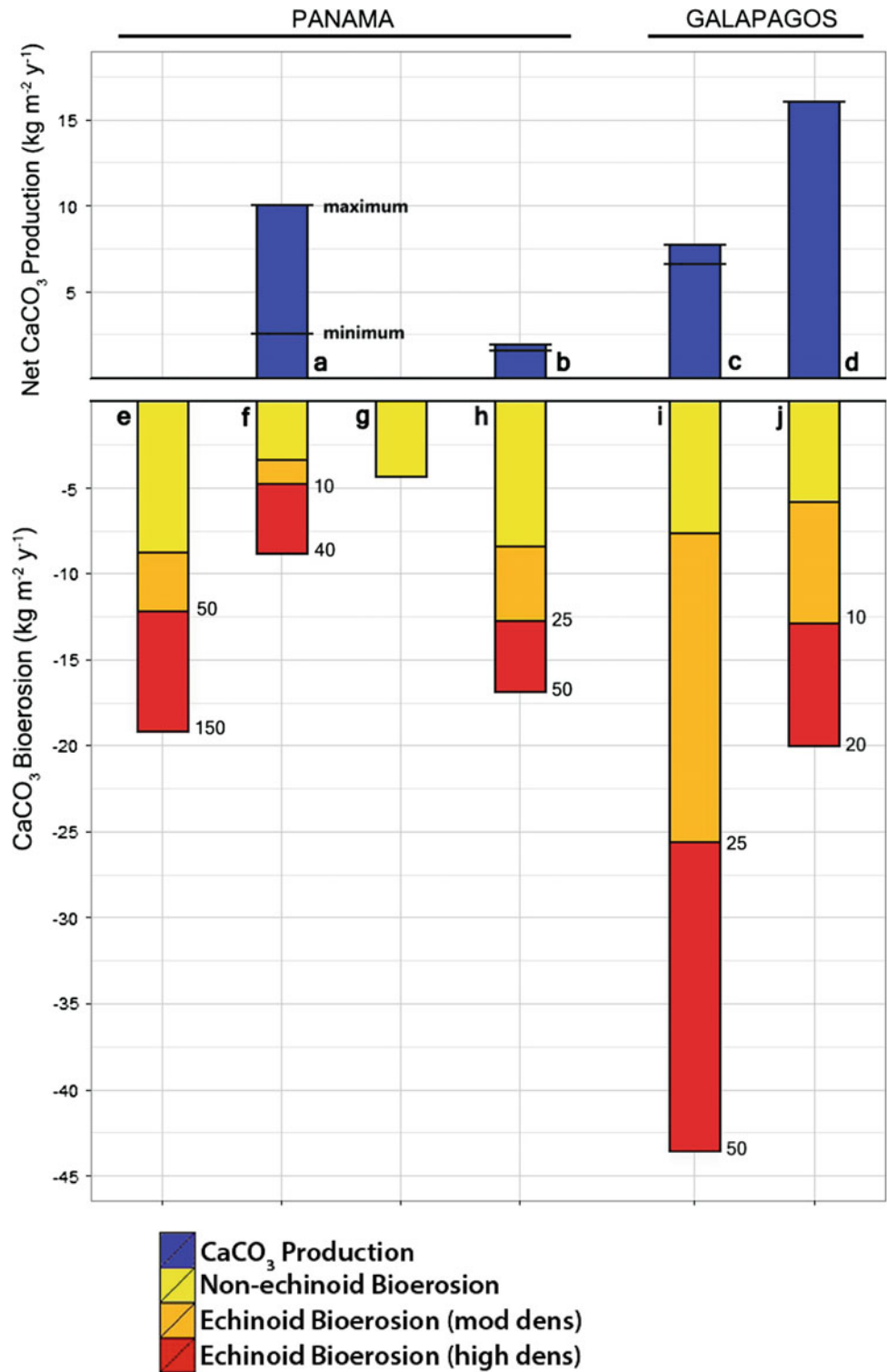
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Table 12.5 (continued)

Species	Locality	Density (ind m ⁻²)	Test diam (cm)	Bioerosion rate (kg m ⁻² year ⁻¹)	Source	
<i>Echinometra</i> sp. A	Fiji	1.08	38	0.04	Appana and Vuki (2006)	
		0.62	37	0.03		
		0.39	39	0.03		
		0.36	41	0.04		
<i>Echinometra mathaei</i>	Marshall Islands	0.16	2.2	0.01	Russo (1980)	
		6.50	1.9	0.26		
		1.75	1.95	0.07		
	La Réunion	49.1	–	8.3	Conand et al. (1997)	
		12.4		2.9		
		2.5		0.4		
		3.8–73.6	–	0.4–8.3		Peyrot-Clausade et al. (2000)
	French Polynesia	7.38	1.5–1.9	0.372	Bak (1990)	
			2–2.4			
			2.5–2.9			
		4.8	–	0.89		Pari et al. (1998)
		210	–	6.87		
		8	–	0.63		
	Kenya	1.7–14.2	3.8	0.4–3.6	McClanahan and Muthiga (1988)	
0.03–5.6		2.6–4.9	0.15	Carreiro-Silva and McClanahan (2001)		
Okinawa, Japan	10	–	0.2	Hibino and van Woesik (2000)		
Gulf of Eilat	3.7–10.5	2.3	0.6–1.6	Mokady et al. (1996)		
Kuwait	30	3.7	0.33	Downing and El-Zahr (1987)		
<i>Echinometra lucunter</i>	St. Croix, US Virgin Islands	100	–	3.9	Ogden (1977)	
	Bermuda	25	–	7.0	Hunt 1969 in Russo (1980)	
<i>Echinometra viridis</i>	Puerto Rico	0.8–62.6	2–2.5	1.1–4.1	Griffin et al. (2003)	
<i>Toxopneustes roseus</i>	Panama	–	5.1–7.5	–	Glynn (1988)	
Several species	Belize ^a	17.6	2.75	1.2	Brown-Saracino et al. (2007)	
		6.5	2.87	0.6		
		0.8	3.41	0.2		
		12.5	2.44	0.8		
		17.3	2.86	1.4		
		32.8	2.37	1.2		
		30	2.11	1.1		
		25	2.56	1.3		
		17.8	1.64	0.3		
		31.6	1.40	0.3		
		40.0	1.33	0.3		
	French Polynesia ^b	7.12–10.0	–	0.6–7.5	Peyrot-Clausade et al. (2000)	

^a*Echinometra viridis*, *Echinometra lucunter*, *Diadema antillarum*, *Euclidaris tribuloides*, *Lytechinus variegatus*, *Lytechinus williamsi*^b*Echinometra* types A and B, *Echinometra diadema*, *Echinothrix calamaris*, *Diadema savignyi*

Fig. 12.6 Net carbonate production pre-1982 (*above*) and carbonate bioerosion post-1983 (*below*) on coral reefs in Panama and the Galápagos Islands. Letters denote geographic areas and habitat conditions, and numbers densities (ind m⁻²) of sea urchins. Production (a–d): **a**—Gulf of Chiriquí, Uva Island; **b**—Gulf of Panama, Saboga Island; **c**—Floreana Island, Onslow Island reef, 70 % coral cover, maximum and minimum production levels at *Eucidaris* densities of 3 and 34 ind m⁻² respectively; **d**—Fernandina Island, *Eucidaris* absent; horizontal lines mark ranges of production values (after Glynn 1988). Bioerosion (e–j): **e–g** Gulf of Chiriquí, Uva Island; **e**—lower seaward slope, damselfish absent; **f**—lower seaward slope, damselfish present; **g**—upper seaward slope, live pocilloporid substratum; **h**—Gulf of Panama, Saboga Island, lower seaward slope; **i, j** Floreana Island, Onslow Island reef; **i**—damselfish absent; **j**—damselfish present



upwelling and high primary production in the southern Galápagos provisions a larger food source for echinoid recruits and adults. Coral habitats in the central and southern Galápagos Islands have undergone little or no coral recovery due to intense and persistent bioerosion by *Eucidaris galapagensis* (Glynn et al. 2015).

In comparison, coral habitats of the northern Galápagos Islands (i.e., the Wellington Reef at Darwin Island and Wenman Island coral community), have demonstrated periods of robust coral recovery since the 1982–83 El Niño, in spite of subsequent ENSO thermal shock events (Glynn et al. 2015). The Darwin and Wenman coral communities are

remote and protected habitats where minimal near-shore fishing pressure is exerted, and sea urchin abundances remain low at these sites. It then appears that large differences in the recovery of Galápagos coral reefs, occurring across a small latitudinal scale, results from differences in local echinoid abundances which in turn are controlled by nutrient upwelling and possibly fishing-induced trophic cascades (Glynn et al. 2015).

12.9.2.2 Gorgona Island, Colombia

At Gorgona Island, Colombia, Toro-Farmer et al. (2004) calculated the bioerosional impacts of the sea urchin *Centrostephanus coronatus* at Playa Blanca fringing reef, reporting small bioerosion rates compared to those calculated for *Eucidaris* and *Diadema* populations at ETP sites elsewhere. Significant statistical differences in *C. coronatus* bioerosion rates with both test size and reef zone were demonstrated: mean bioerosion rates were highest in the crest-platform ($0.103 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$), medium in the back reef ($0.071 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$), and lowest in the reef front ($0.052 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$). Using coral cover, growth rate and skeletal density data for *Pocillopora*, a carbonate accretion rate of $5.02 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ was calculated for the Playa Blanca reef. Thus, with respect to the overall carbonate budget, *C. coronatus* demonstrated only minor effects. Nevertheless, this study provides estimates for a single echinoid species. *Diadema mexicanum* present at higher densities (14 ind m^{-2}) than *C. coronatus* on Colombian reefs, likely effects greater bioerosion rates (Toro-Farmer 1998). Further complicating these findings, *D. mexicanum* juveniles are easily confused with *C. coronatus*, and therefore some individuals identified as *C. coronatus* may have actually been juvenile *D. mexicanum*.

12.9.2.3 Uva Reef, Panama

In the Pacific of Panama, mass coral bleaching and mortality caused by the severe 1982–83 El Niño event precipitated a rapid increase in *Diadema mexicanum* densities and bioerosion rates. The 1982–83 El Niño was responsible for a 50 % reduction in live coral cover at reefs in the Gulf of Chiriquí (Glynn 1985). Within years, the opportunistic expansion of *D. mexicanum* populations led to bioerosion rates that exceeded reefal calcification and rendered the overall carbonate budget in deficit. Glynn (1988) pointed out that the continuing recruitment success of echinoid larvae onto the Uva Island reef contributed to high *D. mexicanum* densities being maintained for years following the initial El Niño disturbance. The exposure of dead coral substratum also had the compounding effect of promoting an increase in algal biomass, expanding the echinoid food source. It is interesting to note that no significant fishing pressure had been exerted in near-shore Panamanian waters since the early 1970s, and stable populations of fish predators were well-established at

the Uva reef during the period of study. These observations suggest that echinoid abundances increased in response to ENSO-associated coral mortality and oceanographic conditions that favored a strong settlement pulse of *Diadema*, and not changes in predator-prey dynamics (Glynn 1988).

Prior to the 1982–83 El Niño, *Diadema mexicanum* population densities on the lower reef slope were between 2 and 5 ind m^{-2} at Uva reef (Glynn 1988). These densities persisted on deep reef areas with high coral cover from 1978 through 1983. By mid-1984, *D. mexicanum* densities had already approximately doubled, and from 1985 to early 1989 *D. mexicanum* densities fluctuated between 60 and 100 ind m^{-2} —enormously elevated from years prior to El Niño (Glynn 1988, 1990). The occurrence of these high echinoid densities over dead coral substrates was spatially heterogeneous, however, and damselfish lawns induced patchy echinoid distributions (Eakin 1987, 1988, 1991; Glynn 1990). At the Uva reef, vertical coral framework erosion was more than three-fold lower in defended damselfish lawns ($0.63 \text{ cm year}^{-1}$) than in non-lawn substrates (2.2 cm year^{-1}) (Eakin 1992). Eakin (1992) noted that without the protective influence of the damselfish algal lawn symbiosis, the carbonate budget of Uva reef would be more easily shifted towards deficit—especially during periods when reefs are rendered vulnerable to increased bioerosional processes via extensive coral mortality, i.e. following ENSO thermal shock events. Prior to 1982–83, damselfish protected, in total, less than $800 \text{ kg CaCO}_3 \text{ year}^{-1}$ from being eroded, whereas after the El Niño event this value rose to $2000 \text{ kg CaCO}_3 \text{ year}^{-1}$.

Grazing by *Diadema mexicanum* on Panamanian reefs contributed 78 % or >10 (to 20) $\text{kg m}^{-2} \text{ year}^{-1}$ of local bioerosion (Glynn 1988; Eakin 1991), more than doubling the total impact of non-echinoid grazers (Fig. 12.6). Eakin (1996) developed a box model for estimating CaCO_3 fluxes at Uva Island after the 1982–83 El Niño disturbance. Based on budget calculations, the 2.5 ha reef underwent a net loss of CaCO_3 structures due to intense bioerosion at the reef base, where *D. mexicanum* densities were highest (mean density of 48.3 ind m^{-2}). El Niño had shifted the carbonate budget at Uva Reef from a net deposition of $8600 \text{ kg CaCO}_3 \text{ year}^{-1}$ before 1982 to a net loss of $4800 \text{ kg CaCO}_3 \text{ year}^{-1}$ after the event (Eakin 2001). Echinoid bioerosion of the reef base was estimated at $4.4 \text{ kg m}^{-2} \text{ CaCO}_3 \text{ year}^{-1}$ —higher than accretion rates calculated in the most actively developing reef zones. The Eakin model implied that most material eroded by echinoids is defecated directly onto the reef framework, with roughly 43 % retention of echinoid produced sediments (Eakin 2001).

Perry et al. (2008) developed a ternary approach to assess temporal linkages between ecological and carbonate production states (as dictated by corals and secondary carbonate producers) and the geomorphic dynamics of reef landforms. Shift in the Uva Reef carbonate budget and ecological status

after the 1982–83 El Niño was used by Perry et al. (2008) to illustrate the potential for substantial changeover in reef states following major disturbance and that such phase-shifts can occur during ecological timescales. The lasting impacts of rapid erosion of reef structures over geological timescales are not certain (Perry et al. 2008).

Since Eakin's (1996) model, several changes have occurred at Uva Island, including minor bleaching events during the 1990s and a widespread El Niño event in 1997–98. High densities of *Diadema mexicanum* at the reef base and forereef persisted until the mid-1990s (~40–60 ind m⁻²) when they began to decline to near 1974 levels in the year 2000 (~10 ind m⁻²). The increase of *D. mexicanum* density during the 1980s and 1990s is attributed to both habitat expansion via coral mortality, and increased sea urchin recruitment owing to high oceanic productivity during the subsequent La Niña period (Glynn 1988; Eakin 1996, 2001). Declines in *D. mexicanum* densities coincided with declining topographic complexity of the reef habitat, suggesting a sea urchin population collapse regulated by their increased bioerosional activities (Eakin 2001). Reduced shelter availability may have rendered *D. mexicanum* vulnerable to predators such as pufferfishes, wrasses and balistids, possibly leading to the population collapse by 2000. No other causes of the *D. mexicanum* population collapse (e.g., disease) were evident (Eakin 2001).

12.9.2.4 Costa Rica

The impact of the 1982–83 El Niño event varied among the three most prominent Costa Rican reef sites: coral mortality was highest at Cocos Island, moderate at Caño Island, and lowest in Culebra Bay. Increases in *Diadema mexicanum* populations at these sites correlated with coral mortality intensity, i.e. greatest at oceanic Cocos Island and least in Culebra Bay (Alvarado et al. 2012). At Caño Island, Costa Rica, Guzman (1988) found low densities of *D. mexicanum* eroding the bases of massive corals. At Isla del Coco, however, *D. mexicanum* grazing activities caused high levels of bioerosion and reduced coral recruitment (Guzman and Cortés 1992). After the 1982–83 El Niño event, Guzman and Cortés (1992) predicted that coral recovery at Cocos Island would take centuries due to high bioeroder densities, and low coral cover and reproduction. Guzman and Cortés (1992, 2007) indicated that part of the erosion of reef structures at Isla del Coco was due to the bioerosive action of *D. mexicanum*. In 2002, there was a five-fold increase of coral cover and a large reduction in sea urchin abundance, and *D. mexicanum* was no longer playing an important role in reefal bioerosion (Guzman and Cortés 2007). At these lower densities, echinoids reduce spatial competition by algae and assist coral recruitment, as has been observed on Caribbean reefs (Sammarco et al. 1974; Sammarco 1980, 1982a, b; Mumby et al. 2006). The impact of *D. mexicanum*

at Cocos Island transitioned from impeding reef recovery via high bioerosion intensity from 1987 to 2002, to promoting reef recovery by performing a key herbivorous role at low densities from 2002 to 2009 (Alvarado et al. 2012).

The recovery from an erosional reef state at Isla del Coco following the 1982–83 El Niño took roughly 25 years. Conservation practices, aided by the distance of Cocos Island from mainland (500 km) Costa Rica, prevented further reef decline and allowed for fish populations to recover by 2002. Sea urchin abundances were then reduced and buffered by fish predators (Alvarado et al. 2012). In contrast, at Culebra Bay, on the Costa Rican mainland, *D. mexicanum* bioerosion rates have increased several orders of magnitude since 2009, in step with coral cover declines (Fig. 12.5).

12.9.2.5 Mexico

Coral reefs in the Gulf of California, Mexico were generally less impacted by the 1982–83 El Niño and subsequent ENSO events than were reefs closer to the equator (e.g., Galápagos Islands and Panama). Assessments of Mexican reefs since the early 1990s have generally reported small echinoid populations that result in much lower rates of carbonate removal than echinoids at highly impacted reef sites. Between 1991 and 1992, Reyes-Bonilla and Calderón-Aguilera (1999) surveyed *Eucidaris thouarsii* populations at the Cabo Pulmo reef in the Gulf of California, Mexico, reporting a low mean population density (0.67 ind m⁻²). Bioerosional activities by *E. thouarsii* demonstrated a minimal impact on coral carbonates, resulting in a mean bioerosion rate roughly twenty times lower than rates reported for *Eucidaris galapagensis* in the Galápagos Islands (Table 12.3). Together with *Arothron meleagris*, *E. thouarsii* reduced the coral standing crop at Cabo Pulmo by <4 % (performing a combined bioerosion rate of 0.002 kg CaCO₃ m⁻² year⁻¹), and had little influence on scleractinian coral abundance (Reyes-Bonilla and Calderón-Aguilera 1999).

Herrera-Escalante et al. (2005) assessed carbonate removal resulting from *Diadema mexicanum* foraging and spine abrasion at Bahías de Huatulco, Oaxaca, Mexico. Reefs at Huatulco are well-developed with high coral cover persisting through ENSO events. As was the case with *Eucidaris thouarsii* at Cabo Pulmo, *D. mexicanum* populations did not demonstrate a large overall impact on corals and coral reef structures at Oaxaca. *Diadema mexicanum* abundance and bioerosion rates varied among reef sites, however, and was responsible for carbonate losses ranging from 5 to 27 % of local carbonate production. Higher densities and bioerosion rates were reported at La Entrega (6.8 ind m⁻² and 3.3 kg CaCO₃ m⁻² year⁻¹ respectively) compared with the other reefs at Bahías de Huatulco. The coral reef at La Entrega has been more affected by ENSO events than reefs at neighboring sites. The 1987 ENSO event

caused coral mortality in deep reef areas of La Entrega, where *D. mexicanum* was found in highest abundance. The high abundances of *D. mexicanum* on La Entrega reef was atypical for coral habitats in the Gulf of California, where most reefs had been well protected from ENSO-associated disturbances. These findings further demonstrate the variable response of echinoid populations to ENSO thermal shock events across relatively small spatial scales.

Benitez-Villalobos et al. (2008) reevaluated echinoid populations on the Huatulco reefs and found a further reduction in the bioerosion intensity at all sites sampled previously by Herrera-Escalante et al. (2005). This later study reported a large reduction in *D. mexicanum* densities and bioerosion rates. A slight increase in mean test size at all sites was found as well, demonstrating population size to be a larger driver of echinoid bioerosion intensity than is the mean size of individuals.

12.9.3 Global Comparison of Echinoid Bioerosion Rates

Comparing echinoid bioerosion rates in reef provinces around the world, the highest values are found in the ETP and far surpass the highest rates reported in the Caribbean or Indo-Pacific (Table 12.5). Within the ETP, sea urchin densities and bioerosion rates are highest in the Galápagos Islands and Panama, and lowest in the Gulf of California, Mexico. Coral communities in the Galápagos Islands and Panama have been severely impacted by ENSO thermal shock events that have led to extensive coral cover losses from echinoids not observed in Mexican habitats (Glynn 1990; Reyes-Bonilla 2003). Records of *Eucidaris galapagensis* and *Diadema mexicanum* bioerosion in the Galápagos Islands and Panama demonstrate bioerosional regimes unmatched in intensity worldwide.

parrotfishes can cause extensive reef erosion and produce large amounts of fine sediments, though relatively few species possess the capacity to do so (Bellwood and Choat 1990). On ETP reefs, the common scarid species (e.g., *Scarus ghobban* and *Scarus rubroviolaceus*) scrape and abrade coral skeletons while foraging, which is generally less destructive than excavating mechanisms. According to Bellwood and Choat (1990), *S. ghobban* does not consistently produce feeding scars and only exceptionally large individuals do so, though scarring does become more common on internally eroded or soft substrates. Bioerosion by scraping species can be important on certain protected reefs, however, where there is minimal fishing pressure and high scarid densities (Bruggemann et al. 1996; Jiménez 1999; Peyrot-Clausade et al. 2000).

On coral reefs at Gorgona Island, Colombia, both *Scarus ghobban* and *Scarus rubroviolaceus* are dominant herbivorous fishes (Zapata and Morales 1997). A large *S. ghobban* population (1544 ind ha^{-1}) was responsible for losses of 1.59 ± 0.76 (SEM) $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ at Gorgona Island, a relatively high bioerosion rate on the reef, and compared with rates calculated for substrate scrapers elsewhere (Jiménez 1999; Cantera et al. 2001). *Scarus ghobban* bioerosion rates varied among reef zones, correlating with their abundance and distance from the shoreline: highest on the reef flat, but otherwise decreasing progressively from the backreef to reef slope (Jiménez 1999). Across reef zones, *Scarus ghobban* foraged mainly on coral rubble, but on the reef flat foraged equally on dead branching corals and rubble substrates. When feeding on coral colonies, parrotfishes will break off branches and convert intact substrates to rubble. If coral branches are ingested, the pharyngeal mill, a triturating structure unique to parrotfishes, further reduces coral skeletons into sediments (Glynn 1997). When foraging on rubble substrates, the change in substrate composition is much less severe (Jiménez 1999).

12.10 Fishes

Three fish guilds erode or break coral substrates as a result of foraging activities: (1) herbivorous fishes that abrade and remove substrate, (2) fish corallivores that denude and fragment corals, and (3) fish invertivores that break coral skeletons when searching for associated infauna.

12.10.1 Herbivorous Fishes: Family Scaridae

Parrotfishes are key herbivores and occasional corallivores that cause bioerosion while scraping or biting into coral skeletons with strong dental plates adapted for substrate excavation. When population densities are high, grazing

12.10.2 Fish Corallivores: Family Tetraodontidae

Pufferfishes (Family Tetraodontidae) are dominant corallivores in the ETP that prey upon branching corals, and massive species to a lesser extent (Glynn and Wellington 1983). Pufferfishes scrape into and bite off the tips of coral branches, removing coral skeleton and leaving small areas denuded and exposed. In spite of persistent grazing pressure, ETP pocilloporid communities are largely resilient to tissue loss and skeletal erosion inflicted by pufferfish corallivory. Following *Arothron meleagris* foraging, pocilloporid corals can regenerate tissues quickly (approximately two weeks, and two months for superficial damage and deeper lesions respectively), limiting opportunity for bioeroder recruitment (Neudecker 1979; Palacios et al. 2014).

While pufferfishes can perform considerable damage to individual coral colonies, their reef-wide impact on bioerosional processes appears to be minor (Glynn 1997). An early study in Panama reported a small *Arothron meleagris* population (40 ind ha⁻¹) that removed only 34 g of coral mass (soft tissue and skeleton) m⁻² year⁻¹ (Glynn et al. 1972). At Cabo Pulmo, Mexico, *A. meleagris* populations have a low impact on coral health and reef bioerosion, in total removing 16.4 g CaCO₃ m⁻² year⁻¹ (Reyes-Bonilla and Calderón-Aguilera 1999). *Arothron meleagris* is not abundant at Cabo Pulmo reefs (mean densities are 39 ind ha⁻¹) and coral tissues were found to be a small component of these fish's diets—11.8 and 4.8 % for *Pocillopora* spp. and *Porites* spp. respectively (Reyes-Bonilla and Calderón-Aguilera 1999; Moreno et al. 2009).

At Gorgona Island, Colombia, an early study reported that corallivorous foraging by pufferfishes did not adversely affect overall coral health and was ecologically beneficial; *Arothron meleagris*-mediated coral colony fragmentation may be aiding reef recovery and coral colony dispersal at this site (Guzman and López 1991). Pocilloporid corals often reproduce asexually (Glynn et al. 1991; see Chap. 15, Glynn et al.) and, as applies to all bioerosional processes inducing coral fragmentation, pufferfish foraging may enhance coral propagation in the ETP. Observations on a Panamanian reef demonstrated that more than 50 % of the coral mass lost due to pufferfish grazing represents fragments broken away from colonies and not ingested (Glynn et al. 1972). While pufferfishes mainly remove the tips of coral branches, the large number of fragments generated likely offsets the lowered survival probability attributable to their typically small-size (≤ 1 cm).

More recently, relatively high *Arothron meleagris* bioerosion rates have been reported at Gorgona Island, on La Azufrada reef. A large *A. meleagris* population (172 ind ha⁻¹) exerts a standing bite density of 366.2 ± 329.7 (SD) bites m⁻², and removes 0.89 kg CaCO₃ m⁻² year⁻¹ (Palacios et al. 2014). This carbonate 'removal' rate may be misleading, however, due to a novel finding: coral nubbins eroded by *A. meleagris* demonstrated similar rates of mass growth as found for nubbins protected from pufferfish foraging. Bioerosional pufferfish foraging stimulates skeletal deposition that compensates for carbonate losses. By way of this enhanced accretion, pufferfish (i.e., *Arothron meleagris*) also alter the morphology of pocilloporid colonies via reorienting corallum growth (Palacios et al. 2014). Pufferfish bioerosion reduces linear growth rates of pocilloporid nubbins and induces girth-wise carbonate deposition. Pocilloporid nubbins thus become shorter and thicker than nubbins protected from pufferfish corallivory (Fig. 12.7). The bioerosional activities of pufferfish thereby can change topographies of coral habitats, and engender variation among pocilloporid colonies locally (Palacios et al. 2014).

The electivity of pufferfish for coral prey, and subsequently bioerosional impact, is however variable. Guzman and Robertson (1989) investigated the relationship between *Arothron meleagris* diet composition and changes in coral cover. After a red tide-induced coral mortality event at Caño Island, Costa Rica, *A. meleagris* fed mainly on coralline algae and *Psammocora* corals (40.6 and 23.7 % of diet composition respectively). Two years after this event, *A. meleagris* electivity was appreciably altered, with *Porites lobata* representing 53.7 % of the diet composition. *Arothron meleagris* coral electivities also varied among ETP reef sites: on the Uva Island reef (Panama), pocilloporid corals comprised 96.8–100 % of pufferfish diets, but only 63.3 % of the live coral cover, while at Caño Island (Costa Rica) *P. lobata* comprised the large majority (75.3 %) of *A. meleagris* diet composition at ~90 % live coral substrate cover (Guzman and Robertson 1989). Feeding preferences of *A. meleagris* are flexible and variable across ETP reef sites, but do not consistently relate to the relative availability of potential coral species prey (Guzman and Robertson 1989). These findings illustrate pufferfish as opportunistic predators and bioeroders of live corals, having complex feeding habits. Consequently, the impacts of pufferfish bioerosion are probably highly variable from reef to reef, although it appears unlikely these populations typically play large roles in reefal carbonate budget losses—especially provided recent evidence that pufferfish predation stimulates skeletal deposition and asexual propagation in pocilloporid corals (Palacios et al. 2014). The ability for recovery and maintenance of carbonate production in branching corals may also help explain why pufferfish predation demonstrates negligible impact on ETP reef development and accretion, despite their dominance among the region's corallivores and negative impacts observed for corallivores on other tropical reefs (Guzman and Robertson 1989; Rotjan and Lewis 2008; see Chap. 10, Enochs and Glynn et al.).

12.10.3 Fish Invertivores and Other Predators

Predators of coral-associated invertebrates (e.g., bivalves, gastropods, echinoids, and crustaceans) can cause extensive damage to coral skeletons while foraging. Among fish invertivores in the ETP, triggerfishes (Family Balistidae) are frequent contributors to reef bioerosion. While extracting invertebrates from coral skeletons, mainly lithophagid bivalves, triggerfishes excavate carbonate material and expel sediments through the gill chambers, as well as causing coral breakage (Francisco 2000; Cantera et al. 2001). Thus, feedback exists whereby coral endoliths attract predators that perform further carbonate erosion. Bivalve distributions dictate which live and dead coral colonies are targets of triggerfish bioerosion, predominantly dead pocilloporid and

live massive corals such as *Porites* spp. and *Pavona* spp. (Glynn et al. 1972; Francisco 2000; Cantera et al. 2001). Alternatively, endolith abundances are reduced and limited by triggerfish predation.

On reefs at Gorgona Island, Colombia, the balistids *Sufflamen verres* and *Pseudobalistes naufragium* forage predominantly on dead pocilloporid corals and coral debris (Cantera et al. 2001). *Pseudobalistes naufragium* performs considerable damage to live massive corals when searching for associated lithophagid bivalves, as has been reported on reefs in Panama and at Gorgona Island (Glynn et al. 1972; Francisco 2000), and many balistid feeding scars are often apparent on the surfaces of live *Pavona varians*, *Gardineroseris planulata* and *Porites lobata* colonies. Live coral patches damaged by triggerfishes are readily colonized by algae and diverse endolith taxa (i.e., sipunculans, polychaetes, acrothoracican cirripeds, and bivalves) and are then vulnerable to further bioerosion by epilithic grazers (Cantera et al. 2001).

Triggerfish bioerosion rates have been calculated at the Playa Blanca reef at Gorgona Island, and rates among species correspond to their local abundance. The most abundant triggerfish, *Sufflamen verres* (270 ± 351 [SD] ind ha⁻¹), removes up to 1.13 kg CaCO₃ m⁻² year⁻¹; a moderately abundant *P. naufragium* population (30 ± 47 [SD] ind ha⁻¹) erodes 0.62 kg CaCO₃ m⁻² year⁻¹; and infrequently encountered *Balistes polylepis* was thought to perform minimal bioerosion, and was not assessed (Francisco 2000; Cantera et al. 2001). There are currently no additional data on triggerfish bioerosion from reefs elsewhere in the ETP for comparison.

White-tip reef sharks, *Triaenodon obesus* (Family Carcharhinidae) at times cause extensive damage to coral colonies when pursuing balistids and other fishes (Jiménez 1996–1997; Glynn 2008). At Coiba Island, Panama, white-tip sharks forage aggressively in pocilloporid recesses while chasing reef fishes, detaching and fragmenting coral colonies in the process (Jiménez 1996–1997). In an hour-long observation of three *T. obesus* hunting two *Sufflamen verres* juveniles sheltering among pocilloporid colonies, the sharks produced more than 60 coral fragments. Coral fragments resulting from this event were large (mean size 11.2 ± 4.6 [SD] cm) and their expected survival rate was estimated at >90 % (Guzman 1991; Jiménez 1996–1997). On ETP reefs, sea turtles also perform similarly-derived coral destruction while foraging (Glynn 2004, 2008). These periodic bioerosion events performed by large reef predators perhaps contribute more importantly to coral propagation than to the conversion of coral substrates into sediments. Furthermore, coral colony fragmentation mediated by triggerfishes also strongly promotes asexual propagation of coral colonies (see Chaps. 10 and 15, Enochs and Glynn, and Glynn et al. respectively).

12.11 Summary and Conclusions

Bioerosion is a highly diverse and complex process that affects the development of coral formations and exerts great influence on coral habitats of the ETP. The ETP physical environment is enormously conducive to bioerosion processes. Eutrophic conditions throughout most of the ETP enhance the ecological competitiveness of macroborers and increase overall bioerosion rates (Highsmith 1980; DeCarlo et al. 2015). A high-CO₂, low Ω physical environment not only contributes to marginal reef development and cementation in the ETP (Manzello et al. 2008), but also magnifies bioerosion rates (Tribollet et al. 2009; Wisshak et al. 2012; DeCarlo et al. 2015). Persistent interannual ENSO-induced coral mortality events are major drivers of ETP bioerosional dynamics and can bring about intense bioerosion regimes (Scott et al. 1988; Eakin 2001). ENSO thermal shock events promote and help shape bioeroder abundances and bioerosion rates. While heightened bioerosion has impeded the recovery of impacted coral habitats (Glynn et al. 2015), such activities are an important initiator of coral colony dispersal and may be responsible for the high occurrence of asexually derived coral communities, and enhance coral reef resistance to ENSO disturbances in the ETP (Highsmith 1982; Scott and Risk 1988; Scott et al. 1988; Guzman and López 1991).

Echinoid populations in particular have performed extensive bioerosion in many eastern Pacific coral habitats. The recovery of coral reefs affected by El Niño events can be significantly influenced by attendant changes in sea urchin abundances (Glynn 1988; Eakin 1996; Alvarado et al. 2012; Glynn et al. 2015). Destructive grazing by sea urchins has led to large-scale modification of reef structure and functioning at certain sites (Birkeland 1989). Coral communities of the Galápagos Islands and Panama have been especially affected by echinoid bioerosion (Eakin 2001; Glynn et al. 2015). This situation is likely exacerbated by cascading effects from over-fishing (Glynn 1988; Reaka-Kudla et al. 1996; Peyrot-Clausade et al. 2000; Tribollet and Golubic 2011), causing echinoid population densities to be unfettered by predation pressure (Sonnenholzer et al. 2009; Edgar et al. 2011; Glynn et al. 2015).

There has not yet been assessment of carbonate erosion by microendolith assemblages in the ETP. The activities of microendolith assemblages function in tandem with those of epilithic grazers (Chazotte et al. 1995; Zubia et al. 2001; Tribollet and Golubic 2005). It therefore is necessary to investigate microendolith bioerosion to better understand the ecological dynamics driving bioerosional activities of echinoids and fishes. However, irrespective of microendolith studies, bioerosion by fishes—parrotfishes, pufferfishes, and triggerfishes—has received relatively poor study to date in respect to their likely contributions. Scarids are reported to perform high bioerosion rates on protected reefs where

populations are abundant (Jiménez 1999; Cantera et al. 2001). Recent studies have demonstrated the persistent influence of pufferfish bioerosion on Colombian reefs (Jiménez 1999), and an induction of developmental and morphological changes in coral colonies resulting from their activities (Palacios et al. 2014). Triggerfishes perform significant carbonate excavation while foraging on endolithic prey (e.g., bivalves) and promote coral colony dispersal through asexual fragmentation (Francisco 2000; Cantera et al. 2001). Triggerfishes as prey further generate bioerosion and coral colony fragmentation via periodic highly destructive foraging performed by shark predators (Jiménez 1996–1997).

The high abundance and diversity of endolithic sponges compared to encrusting and non-boring massive sponges are a

strong characteristic of sponge assemblages in ETP coral habitats (Carballo et al. 2004, 2008), and may be due to eutrophic conditions causing selection for larval recruitment to cryptic aphotic spaces, as well as strong grazing pressure exerted by opportunistic fishes (e.g., *Arothron hispidus*; Birkeland 1977; Wulff 1997). Sponge assemblages have variable biogeographic importance in the ETP, and high sedimentation restricts the distribution of dominant clionaid species (Hutchings et al. 2005; Carballo et al. 2008; Nava and Carballo 2013). Many ETP boring sponges, however, demonstrate exceptional resiliency to temperature perturbation (Shirley and Rützler 2010; Duckworth and Peterson 2013; Bautista-Guerrero et al. 2014). This adaptive physiology renders boring sponges a threat to reefs having undergone

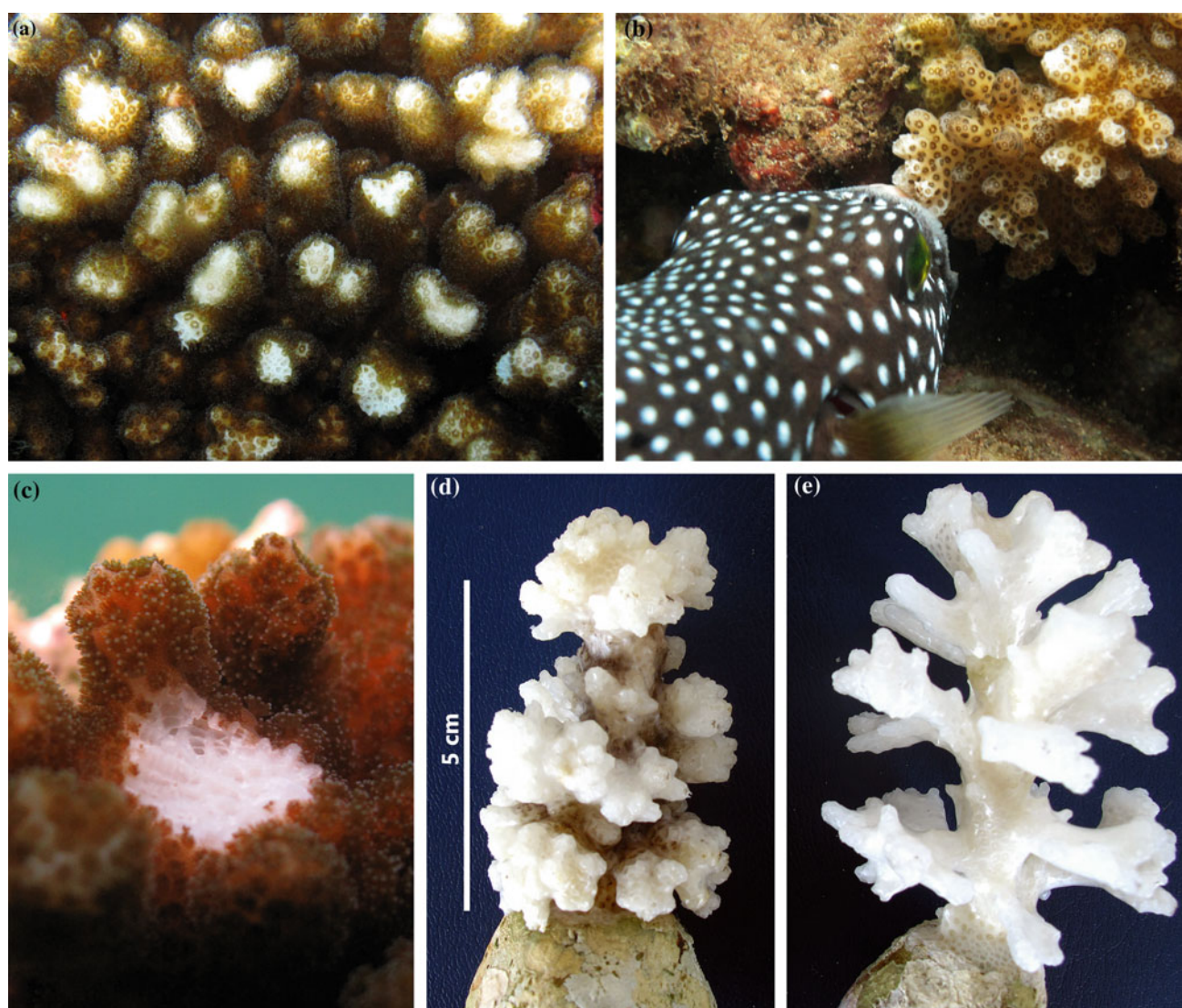


Fig. 12.7 *Arothron meleagris* bioerosion and induction of morphological change in pocilloporid corals at Gorgona Island, Colombia, adapted from Palacios et al. (2014). **a** Pufferfish bite marks on a *Pocillopora* sp. colony; **b** *Arothron meleagris* feeding on *Pocillopora*

sp.; **c** excavation of a *Pocillopora* sp. skeletal protuberance by *A. meleagris*; **d** corallum morphology of pocilloporid branch exposed to pufferfish corallivory; **e** corallum morphology of pocilloporid branch protected from fish corallivory

coral bleaching and mortality due to environmental stressors such as ENSO thermal shock (Carballo et al. 2013).

The profusion and predominance of lithophagine bivalves in dead coral colonies and live massive corals is an important characteristic of ETP reef bioerosion. Boring bivalve populations reach exceptionally high densities in the ETP not found in other regions (Scott et al. 1988). Lithophagine bivalves are dominant endolithic bioeroders throughout the ETP that weaken coral skeletons and are responsible for substantial carbonate losses (Scott and Risk 1988; Scott et al. 1988). The predominance of lithophagids among ETP endolith assemblages may engender a more limited contribution by other co-occurring coral borers (Scott et al. 1988; Reaka-Kudla et al. 1996; Londoño-Cruz et al. 2003).

The role polychaetes play in ETP coral bioerosion has not yet been made clear. Given current assessments, polychaete populations appear to be less abundant and less significant members of ETP bioeroder communities compared to the importance of their activities in coral habitats elsewhere (Hutchings 2008). Polychaete populations can be locally abundant (Reaka-Kudla et al. 1996), and resolving their contribution to bioerosion processes requires further study. Sipunculan worms can be found in very high densities locally and are dominant coral endoliths on Costa Rican reefs, though appear to be less significant bioeroders on Colombian reefs. Both sipunculan and polychaete assemblages demonstrate highly variable abundances and strong zonal preferences (Cantera et al. 2003; Fonseca et al. 2006). Measurements of bioerosion rates for either assemblage where abundant have yet to be performed.

Functional interaction among bioeroder recruits and temporal trends in bioeroder community succession have not been fully described for ETP coral habitats. It does appear characteristics of bioeroder community succession in the ETP deviates from regions elsewhere, and there is a strong indication that bioeroder recruitment, substrate conditioning, and community succession are especially rapid (Londoño-Cruz et al. 2003). Rapid and massive lithophagine bivalve recruitment on newly exposed substrates has been well-illustrated (Kleemann 2013), and the pace of boring bivalve activities likely helps to shape endolith community maturation. Sipunculan borers, also thought to be late-stage invaders, are present in ETP coral skeletons soon after exposure. Conditioning of newly exposed substrates by polychaetes may be less important for the maturation of bioerosion processes in the ETP, while acrothoracican crustaceans' pioneering behavior may play larger roles (Londoño-Cruz et al. 2003). There is thus considerable evidence that temporal and functional patterns of bioeroder community succession in ETP coral habitats deviate from

generalities well-described elsewhere, but these trends have not yet been resolved.

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