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Abstract

The study of bioerosion, a widespread process greatly impacting reef biodiversity, structural complexity, and sediment production, has largely focused on shallow-water reefs with no review of this process in deeper environments. In this first synthesis of bioerosion literature for mesophotic reefs (subtropical and tropical ecosystems in low-light conditions at depths of ~30 to 150 m), we show that the distribution of key bioeroder taxa, their abundances, and overall bioerosion rates are considerably different on mesophotic reefs compared to their shallow-water counterparts. In particular, carbonate grazing and phototrophic microboring rates decline with depth from shallow to mesophotic reefs. In the absence of significant erosive action by grazers, sponges are hypothesized as the primary long-term bioeroders on lower mesophotic reefs (60–150 m) and possibly on some upper mesophotic reefs (30–60 m). Given these factors, we postulate that mesophotic reef substrates experience slower bioerosion rates and lose less carbonate than shallower reefs over the same timeframe. This likely stems from differences in photosynthetically active radiation and other factors such as temperature, sedimentation, bioeroder food abundance and quality, substrate characteristics, and exposure time for bioerosion. There is a critical need to document mesophotic bioeroders via taxonomic inventories, as well as quantify their bioerosion rates across mesophotic depths

in terms of specific bioeroder guilds using experimental substrates. These data will aid management efforts to maintain positive net carbonate budgets on mesophotic reefs, ensuring that sufficient three-dimensional structure is available to support biodiversity at mesophotic depths.

Keywords

Mesophotic coral ecosystems · Bioerosion · Grazing · Microboring · Reef accretion

43.1 Introduction

Bioerosion, the destruction of hard substrates by an organism (Neumann 1966), occurs in all reef systems. The dislodgement of calcium carbonate (CaCO_3) by bioeroders is a fundamental process impacting reef accretion, habitat and structural complexity, and preservation potential (Hutchings 2011; Glynn and Manzello 2015; Perry and Harborne 2016). Bioerosion has important ecological functions such as recycling material, creating cavities that can be used by diverse taxa, facilitating larval recruitment, and producing large amounts of sediment infill, which can consolidate and strengthen parts of the reef along with cementation and micritization (Tribollet and Golubic 2011; Glynn and Manzello 2015; Schönberg et al. 2017b). However, in stressed reefs such as those frequently experiencing coral bleaching or disease, bioerosion may exceed reef carbonate production and result in the loss of reef framework and structural complexity (Reaka-Kudla et al. 1996; Perry et al. 2014).

Three main functional groups/guilds facilitate bioerosion (Schönberg et al. 2017b): (1) microborers (<100 μm diameter traces; Golubic et al. 1975), (2) grazers, and (3) macroborers ($\geq 100 \mu\text{m}$ diameter traces). Microboring organisms include cyanobacteria, rhodophytes, chlorophytes, heterotrophic fungi, and bacteria (Golubic et al. 1975; Tribollet 2008; Wisshak 2012). Of the macroborers, boring sponges primarily remove the most CaCO_3 from frameworks (Perry and Harborne 2016; Schönberg et al. 2017a), with polychaetes, sipunculans,

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and molluscs strongly contributing, along with lesser mentioned bioeroding species of foraminifera, crustaceans, brachiopods, and bryozoans (Glynn and Manzello 2015). Microborers and macroborers that truly remove internal substrate are referred to as euendoliths (Schönberg et al. 2017b). CaCO_3 grazers are external bioeroders and engage in excavating and scraping of substrate. Of the grazers, fishes and echinoids are typically the main agents (Schönberg et al. 2017b), but molluscs and crustaceans also contribute (Glynn and Manzello 2015; Perry and Harborne 2016). Bioerosion rates and total substrate CaCO_3 removed by each functional guild are controlled by a variety of abiotic factors including temperature, depth, light, nutrients, water chemistry, sedimentation, and substrate density, type, and availability (both living and dead substrate) (Perry and Harborne 2016; Schönberg et al. 2017b). Controlling biotic factors include competition, predation, and succession (Hutchings 2011; Perry and Harborne 2016; Schönberg et al. 2017b). Reviews exist for bioeroder ecology and biology, their effects on local habitats, and their reactions to changing environmental conditions (e.g., Tribollet 2008; Hutchings 2011; Tribollet and Golubic 2011; Tribollet et al. 2011; Wisshak 2012; Glynn and Manzello 2015; Perry and Harborne 2016; Schönberg et al. 2017a, b).

Although marine bioeroders are found at all depths where reefs occur (see Fig. 43.1 for examples of bioeroders present at depths 30–60 m), the majority of bioerosion research has been conducted on shallow (<30 m) reefs. Relatively few studies have addressed bioerosion on mesophotic reefs, which we consider here as low-light communities dominated by zooxanthellate and azooxanthellate coral, macroalgae, sponges, and/or other invertebrates in subtropical to tropical waters typically at depths of ~30 to 150 m (modified from Hinderstein et al. 2010). Of these studies, most have been conducted on upper mesophotic reefs (30–60 m), with few from lower mesophotic reefs (60–150 m). Herein, we summarize what is currently known about bioerosion on mesophotic reefs, translate this into hypotheses regarding how and why bioerosion may differ between mesophotic and shallow-water reefs, and extrapolate how bioerosion may impact the structure of these deeper ecosystems. We focus on the bioerosion of tropical carbonate substrates, with some exceptions to reference depth-related trends. Finally, we offer several suggestions regarding how future research efforts can test the hypotheses presented and fill critical gaps in our knowledge of bioerosion on mesophotic reefs.

43.2 General Trends of Bioerosion Groups with Depth

When generalizing bioerosion trends from shallow to mesophotic depths (Fig. 43.2), bioerosion rates are hypothesized to decrease with depth (Hubbard 2009; Perry and

Harborne 2016), as indicated globally by most quantitative studies of bioerosion in temperate to tropical locations with measurements including sites at 20 m or deeper (Table 43.1 and Fig. 43.3). This trend follows two major observations: first, that autotrophic microborers are largely restricted to euphotic environments (Wisshak 2012) and that light is a major regulator of autotrophic microborer depth distribution (Tribollet et al. 2011), and second, that bioerosional grazing works in synergy with microborers (Tribollet and Golubic 2005; Schönberg et al. 2017b) and can be associated with the presence of epilithic turf and macroalgae (Bellwood and Choat 1990; Glynn and Manzello 2015). Herbivores usually concentrate on shallower reefs (<20 m) where primary producers are abundant (Ogden and Lobel 1978; Bruggemann et al. 1996). As a result, grazers often erode more carbonate at shallower sites (<30 m), at least initially (≤ 3 year), than macroborers (Kiene and Hutchings 1994; Chazottes et al. 1995; Reaka-Kudla et al. 1996; Hassan 1998; Tribollet and Golubic 2005; Weinstein et al. 2014). To provide context for total bioerosion patterns on mesophotic reefs (Fig. 43.2), we first examine each of the major bioeroding guilds separately and discuss how these guilds may inhibit or facilitate the action of another group, creating an interactive network or loop (Tribollet and Golubic 2011; Schönberg et al. 2017b).

43.2.1 Microboring

Studies investigating microbioerosion in tropical to temperate waters have found microborer abundance (Wisshak et al. 2011) and depth of penetration into carbonate substrate (Budd and Perkins 1980; Vogel et al. 2000; Wisshak et al. 2011) decreases with water depth. Trends from the Bahamas also indicate that microbioerosion rates generally decrease with depth; reported rates on mesophotic reefs ($0.002\text{--}0.123 \text{ kg m}^{-2} \text{ year}^{-1}$) were up to two orders of magnitude lower than at shallower depths ($0.208\text{--}0.237 \text{ kg m}^{-2} \text{ year}^{-1}$; Table 43.1; Hoskin et al. 1986; Vogel et al. 2000). Additionally, a greater microborer diversity (number of distinct ichnotaxa) is typically reported in shallow reefs compared to their deeper mesophotic counterparts (Günther 1990; Perry and Macdonald 2002; Gektidis et al. 2007; Wisshak et al. 2011). However, depth zonation studies suggest that some microborers are more common at mesophotic depths such as rhodophytes (red algae) and light-independent fungi and organotrophs (Perry 1999; Vogel et al. 2000; Perry and Macdonald 2002; Wisshak et al. 2011; Färber et al. 2015).

Phototrophic microboring species such as the chlorophyte *Ostreobium quekettii* Bornet and Flahault, 1889 and the cyanobacterium *Leptolyngbya terebrans* (Bornet and Flahault ex Gomont, 1892) (accepted as *Plectonema terebrans*) occupy a vertical range that can include mesophotic depths

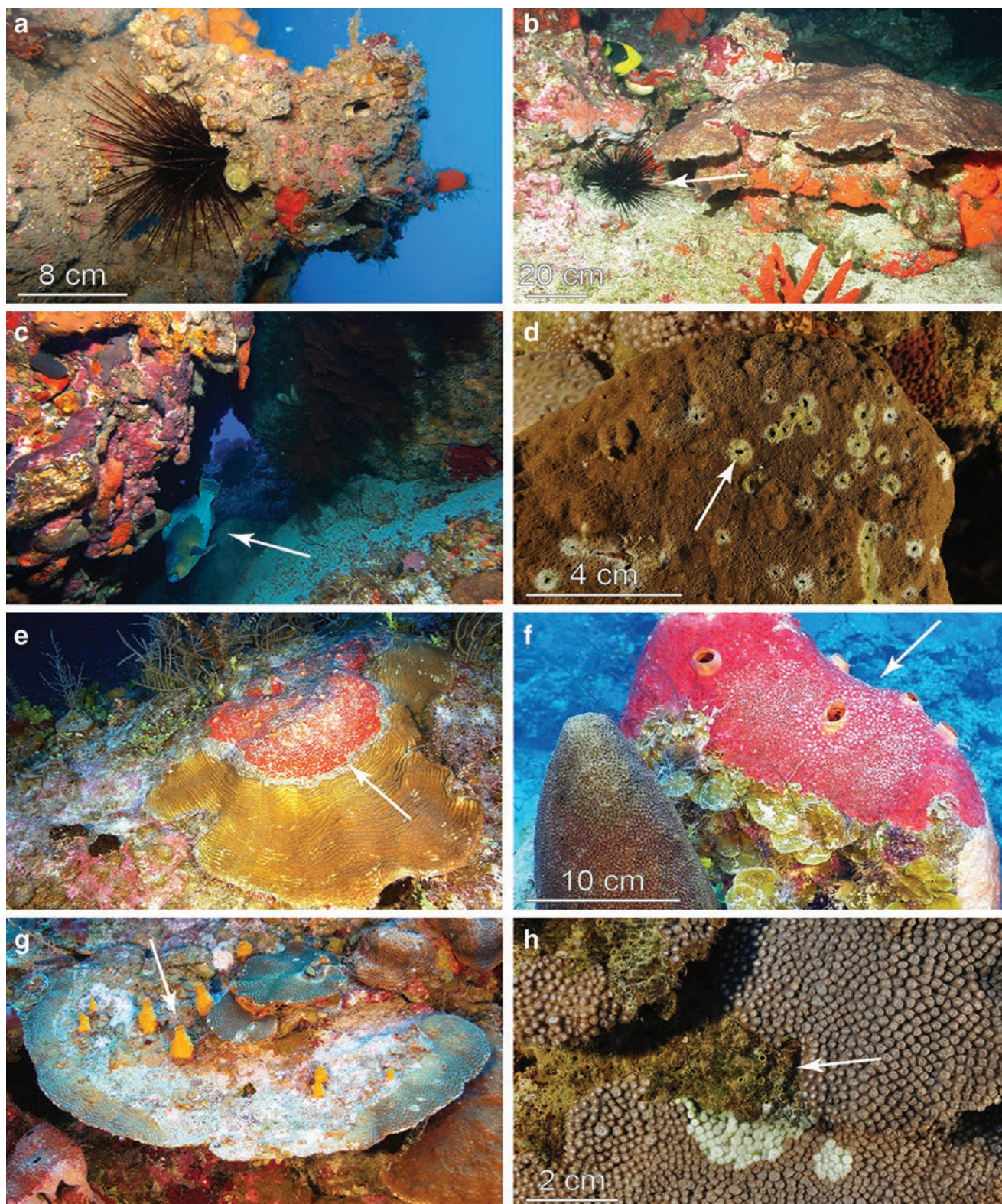


Fig. 43.1 Bioeroders present on upper mesophotic reefs and rocky outcrops. (a) *Centrostephanus* sp., a sea urchin known for bioerosion (Toro-Farmer et al. 2004), on a rocky reef at 47 m off Michmoret, Israel (Mediterranean Sea). (b) Sea urchin *Diadema* sp. (white arrow) at 47 m on McGrail Bank (Northwest Gulf of Mexico). (c) Scrapping parrotfish *Scarus guacamaia* Cuvier, 1829 (white arrow) at 44 m off Bajo de Sico, Puerto Rico. (d) Boreholes of the bivalve *Lithophaga* sp. (e.g., white arrow) in the coral *Montipora* sp. at 50 m off Eilat, Israel. (e) Boring sponge *Cliona delitrix* Pang, 1973 (white arrows) adjacent to the coral *Agaricia lamarki* Milne Edwards and Haime, 1851 at 40 m off Isla de la Juventud, southwest Cuba and (f) on substrate adjacent to the coral *Orbicella faveolata* (Ellis and Solander, 1786) at 45 m off Cuba's northwest coast. (g) Bioeroding sponge *Siphonodictyon coralliphagum* Rützler, 1971 (e.g., white arrow) on dead substrate of the coral *O. faveolata* at 45–50 m off west Cuba. (h) Boring sponge *Cliona* sp. (white arrow) adjacent to the coral *Plesiastrea versipora* (Lamarck, 1816) at 55 m off Eilat, Israel. Scale bars provided when available (Photo credits: (a, d, h) Gal Eyal; (b) FGBNMS/UNCW-UVP; (c) Michelle Schärer; and (e–g) the Voss Lab at FAU Harbor Branch)

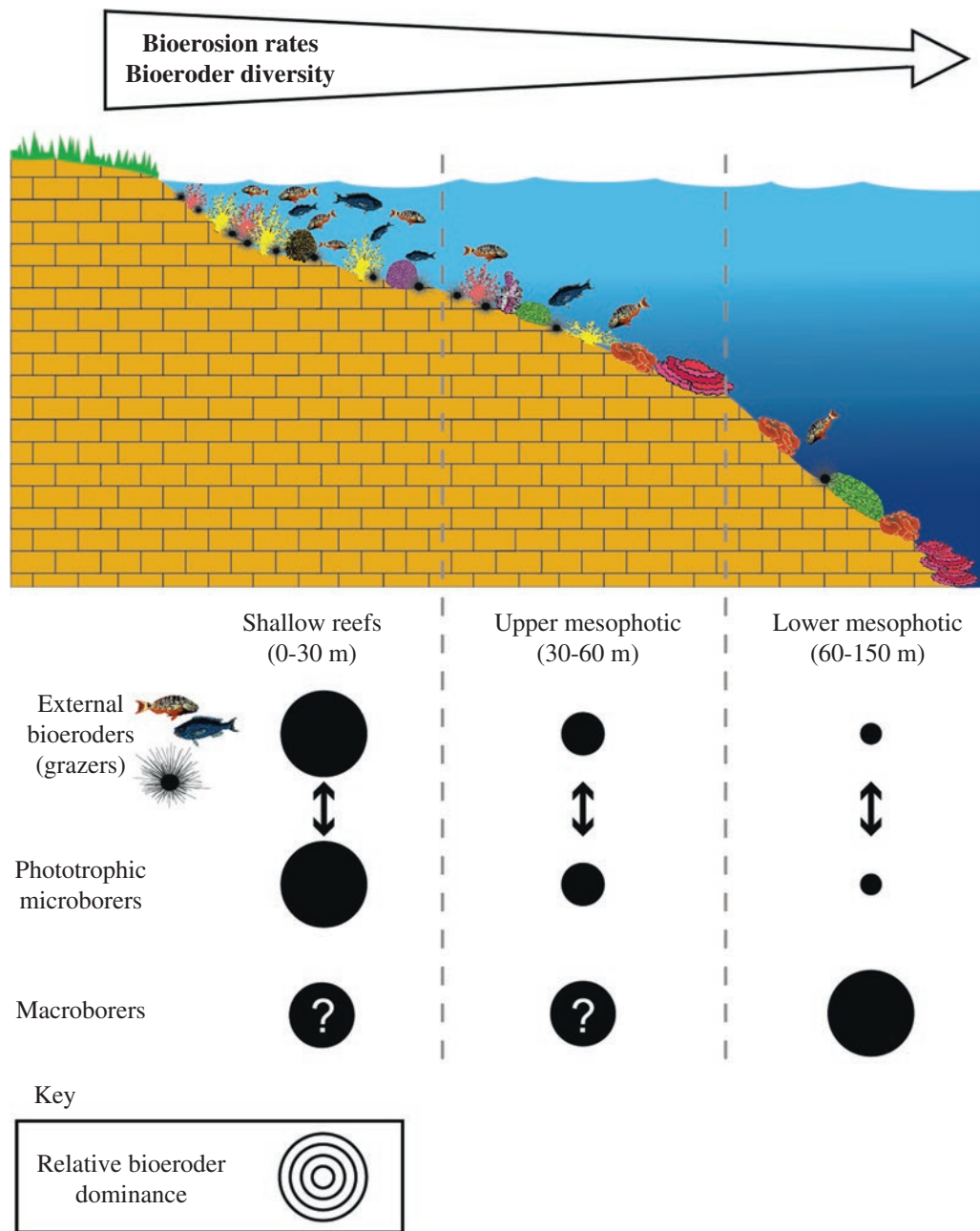


Fig. 43.2 Conceptual diagram indicating general, qualitative depth trends in bioerosion activity based on published literature referenced throughout the chapter. Overall bioerosion rates decrease with depth from shallow (<30 m) to mesophotic depths (30–150 m) at least initially (≤ 3 years), over the same given timeframe. Reported bioeroder diversity also decreases with depth. This may have a biological basis and/or result from the fact that available taxonomic inventories decrease with depth. The relative dominance of the major bioeroding groups (external grazers, phototrophic microborers, and macroborers) at shallow, upper, and lower mesophotic reefs are represented by black circles, where the relative importance of a bioeroding group (based on abundance and/or bioerosion rates) is scaled to circle size. Differences in circle size should not be interpreted quantitatively. As limited data are available for many bioeroders at mesophotic depths, this figure focuses on the best-studied members of each group, where appropriate. Light-independent microborers are not included. Relative abundances of parrotfishes and sea urchins (external grazers) are depicted in the diagram by representative images. Facilitative interactions between bioerosional grazers and phototrophic microborers that may cause their abundances to be correlated are represented by double-headed arrows. General trends in macroborer abundances and bioerosion rates with depth are currently inconclusive (Table 43.3); this uncertainty is represented for shallow and upper mesophotic reefs by a question mark. Still, sponges are hypothesized as the main long-term (>5–10 years) framework bioeroders on lower mesophotic reefs (as indicated by large black circle) and to be relatively less dominant than other bioeroder guides in shallower reefs (as indicated by medium black circle). Coral images in the diagram represent the general trend that branching and massive coral morphologies are more common on shallower reefs and platy coral morphologies are more common on mesophotic reefs

Table 43.1 Studies examining temperate to tropical bioerosion rates at depths ≥ 20 m, including the shallowest depth per study (shaded light gray) for comparison when available. By convention, rates are reported in units of G ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$) unless otherwise indicated. Rates should not be directly compared between study locations, as different methods were used. Not all sites are displayed per source, and the shallowest sites did not always harbor the fastest rates (e.g., Hassan 1998). Data, reported to significant figures provided in original text, were only presented if definitive depths could be ascertained. Estimates (~) indicate that only graphs were provided in the original source. “Unscaled” indicates that rates are based solely on experimental substrates and not applied to specific benthic measurements of the particular site. Dark gray shaded locations are from temperate regions. Blank areas indicate a lack of available data. *SD* standard deviation, *SE* standard error, *GBR* Great Barrier Reef (Australia)

Location	Method	~Exposure time/ Sampling interval	Depth (m)	Total bioerosion rate (G)	Grazing rate (G)	Macroboring rate (G)				Microboring (G)	Source	Figure 43.3 reference number
						Sponge	Worm	Bivalve	Total			
Lizard Island, GBR	<i>Porites lutea</i> experimental substrate blocks	5 years	3	~1.68	~1.53	~0.0845			~0.15 ^a		Kiene and Hutchings (1994)	1
			20	~0.42	~0.07	0.256			~0.35 ^a			
Lizard Island, GBR	<i>Porites lutea</i> experimental substrate blocks	7-9 years	3	2.21 \pm 0.53 SD	2.15 \pm 0.54 SD		0.02 \pm 0.01 SD		0.06 \pm 0.08 SD		Kiene and Hutchings (1993)	1
			20	0.59 \pm 0.25 SD	0.35 \pm 0.20 SD	0.14 \pm 0.10 SD	0.07 \pm 0.01 SD		0.24 \pm 0.14 SD			
Au'au Channel, Hawai'i	Living <i>Porites lobata</i> colony holdfasts	age of measured corals	50						$\geq 3.02 \pm 0.05$ SE mm yr ⁻¹ a,b		Grigg (2006)	2
Marine Science Station of Aqaba, Jordan, Red Sea	<i>Porites</i> sp. experimental substrate blocks	2 years ^c	5	1.249 \pm 0.248 SD ^d							Hassan (1998)	3
			40	0.354 \pm 0.321 SD								
Gulf of Aqaba, Red Sea	Gut content and abundance of bioeroding sea urchin <i>Diadema setosum</i>	not relevant	5		~1.17 ^e						Dullo et al. (1995)	3
			50		~0.73 ^e							
Zabargad Leeward, Red Sea	<i>Porites</i> sp. experimental substrate blocks	2 years ^c	5	0.562 \pm 0.225 SD							Hassan (1998)	4
			40	0.352 \pm 0.177 SD								
Zabargad Windward, Red Sea	<i>Porites</i> sp. experimental substrate blocks	2 years ^c	5	1.176 \pm 1.736 SD							Hassan (1998)	4
			40	0.425 \pm 0.180 SD								
Ski Slopes, Bahamas	Census-based carbonate budget (bioerosion rates scaled by benthic cover and rugosity)	not relevant	20	1.21 \pm 0.05 (average of 3 sites)							Perry et al. (2013)	5
Lee Stocking Island, Bahamas	Micritic limestone experimental blocks	1 year	2							0.208 \pm 0.039 SD	Vogel et al. (2000) (exact values provided by Kiene 2014, pers. comm.)	5
			30							0.123 \pm 0.019 SD		
			100							~0.01		
Black Rock, southwest Little Bahama Bank	Paleozoic biomicritic limestone cubes	1 year	2							0.237	Hoskin et al. (1986), as reported by Wisshak et al. (2010)	5
			32							0.040		
			79							0.002		

(continued)

Table 43.1 (continued)

Location	Method	~Exposure time/ Sampling interval	Depth (m)	Total bioerosion rate (G)	Grazing rate (G)	Macroboring rate (G)				Microboring (G)	Source	Figure 43.3 reference number
						Sponge	Worm	Bivalve	Total			
Bonaire, Netherlands Antilles	Fish surveys and direct behavior observations	not relevant	0–4		7.62 ± 0.47 SE ^f						Bruggemann et al. (1996)	6
			12–25		0.69 ± 0.10 SE ^f							
Curaçao, Netherlands Antilles	<i>Orbicella annularis</i> control experimental substrates ^g	1 year	3	3.1 ± 0.6 SD g yr ⁻¹							Bak (1976)	6
			25	3.2 ± 0.6 SD g yr ⁻¹								
Discovery Bay, Jamaica	Sponge chips in sediment traps ^h	58 days	15			1.860					Moore and Shedd (1977)	7
			40			0.223						
U.S. Virgin Islands, USA	<i>O. annularis</i> (2 m) experimental substrate disks (unscaled)	3 years	9	1.215 ± 0.162 SE	1.011 ± 0.190 SE	0.020 ± 0.015 SE	0.030 ± 0.005 SE	0.078 ± 0.017 SE	0.127 ± 0.026 SE	0.077 ± 0.007 SE ⁱ	Modified from Weinstein (2014)	8
			31	1.066 ± 0.102 SE	1.001 ± 0.097 SE	0.008 ± 0.003 SE	0.007 ± 0.003 SE	0.002 ± 0.000 SE	0.018 ± 0.007 SE	0.047 ± 0.002 SE ⁱ		
			45	0.403 ± 0.041 SE	0.339 ± 0.042 SE	0.001 ± 0.001 SE	0.005 ± 0.001 SE	0.001 ± 0.000 SE	0.007 ± 0.001 SE	0.057 ± 0.001 SE ⁱ		
Azores Archipelago (Faial Channel)	Limestone experimental plates	combined exposure times (2 years)	15	0.048							Wisshak et al. (2010)	9
			60	0.028								
			150	0.002								
Peloponnese Peninsula (Greece)	Limestone experimental plates ^j	1 year (400 days)	15	0.060 ± 0.031 SD							Färber et al. (2015)	10
			50	0.027 ± 0.010 SD								
			100	0.017 ± 0.004 SD								

^aMay indirectly include microborers or definition for “micro” differed from the definition used in this chapter, so all boring data was included as macroborers

^bValue based on growth rate of *P. lobata* at indicated depth

^cRates after second year were calculated by subtracting average of first year from value from the second year of exposure

^dValue reported differently in other sections of source (1.240)

^eRates based on weight of gut content divided by abundance per 5 m² of the bioeroding sea urchin *Diadema setosum*, calculated per day (Fig. 27 in source), but extrapolated to year and reported in units of G

^fResults based on direct measurements of two key bioeroding species, *Scarus vetula* and *Sparisoma viride*

^gSubstrates elevated to remove from sea urchin grazing but not necessarily other sources of grazing

^hSediments may have derived from other regions of the reef beyond the depth specified (Moore and Shedd 1977)

ⁱValues scaled (based on exposure time and substrate surface area) by rates obtained from Vogel et al. (2000) for similar depths

^jCalculated as the average of all down-facing and up-facing limestone plates (source supplemental) from the same depth, exposed for one year

(Budd and Perkins 1980; Vogel et al. 2000; Chazottes et al. 2009; Heindel et al. 2009; Weinstein et al. 2016). *O. quekettii*, which forms green mm-thick bands below the substrate surface (e.g., Weinstein et al. 2016), is considered one of the most widely distributed and active microborers (Tribollet 2008). Adapted to low-light levels (Budd and Perkins 1980), *O. quekettii* has been recorded to a depth of 300 m in clear oligotrophic tropical waters and was found to be the only abundant microborer algae between 100 and 300 m in the Bahamas (Vogel et al. 2000). However, some studies indicate that *O. quekettii* abundances decline on lower mesophotic reefs (Budd and Perkins 1980; Vogel et al. 2000).

The distribution of *O. quekettii* and other phototrophic microborers is likely controlled by site-specific variations in light intensity (Budd and Perkins 1980; Perry and Macdonald 2002). Perry and Macdonald (2002) defined microborer assemblages by light penetration (upper photic, lower photic, dysphotic). The influence of photosynthetically active radiation (PAR) is evident from observations that the morphology of microborings changes with depth. In shallow waters, borings are deep and perpendicular to the substrate surface, whereas borings at deeper depths (≥20 m) are shallow and in parallel alignment (Budd and Perkins 1980; Vogel et al. 2000), presumably to maximize harvest of available light at these

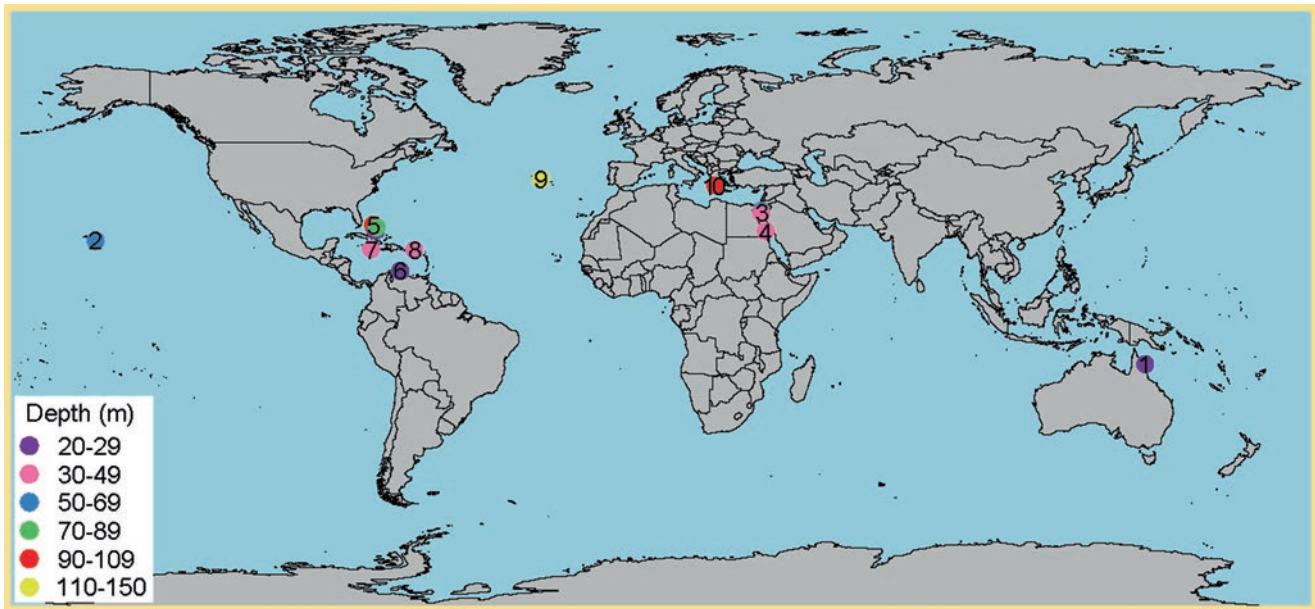


Fig. 43.3 Locations (dots) of studies that quantified temperate to tropical bioerosion rates at depths ≥ 20 m. Color of dot corresponds to the deepest depth (≤ 150 m) recorded for the particular study, and numbers in dots correspond to the regional reference number of the study listed in Table 43.1. Map generated using the package ggmap in RStudio 0.99.486 (Kahle and Wickham 2013)

depths. Despite the presence of microborers on mesophotic reefs, current data suggest that the reduction in PAR with depth (Baker et al. 2016) helps regulate microborer taxonomy and limits microborer diversity, abundances (Fig. 43.2), and carbonate removal by microbioerosion on mesophotic reefs (Budd and Perkins 1980; Perry and Macdonald 2002; Vogel et al. 2000; Heindel et al. 2009; Wisshak et al. 2011).

43.2.2 Grazing

External bioerosion trends on mesophotic reefs are mostly inferred from indirect estimates such as abundances of herbivores. It is critical to note that not all herbivores actually remove carbonate from reef substrate (Bellwood and Choat 1990). Thus, assumptions regarding bioerosion based on herbivore abundances, including those herein, may result in overestimates. The following depth-related discussion of grazers focuses on the organisms for which the most mesophotic data are currently available: herbivorous sea urchins and fishes.

43.2.2.1 Sea Urchins

Sea urchins are generally reported as rare (Fig. 43.1a, b) or absent at mesophotic depths (Liddell and Ohlhorst 1986; Brokovich et al. 2010; Lesser and Slattery 2011; Weinstein et al. 2014; Smith et al. 2015). Prior to the 1983/1984 Caribbean mortality event, population density and qualitative measurements of grazing by the bioeroding sea urchin *Diadema antillarum* Philippi, 1845 decreased with depth based on studies spanning 1–56 m (Bak 1976; Steneck 1983;

Liddell et al. 1984; Liddell and Ohlhorst 1986; Morrison 1988). Similarly, the number of individual *Diadema setosum* (Leske, 1778) observed in the Red Sea decreased with depth from ~ 20 individuals m^{-2} at 5 m to 1 individual m^{-2} at 50 m, as did the daily bioerosion rates of these individuals from ~ 3.2 g m^{-2} at 5 m to ~ 2.0 g m^{-2} at 50 m (Dullo et al. 1995). These results imply that sea urchin bioerosion rates generally decrease with depth and that these organisms are usually not major mesophotic reef substrate modifiers.

43.2.2.2 Fishes

Herbivorous fish (including bioeroders) biomass and/or abundances generally decrease with depth in shallow reefs (e.g., Lewis and Wainwright 1985; Bruggemann et al. 1996; Friedlander et al. 2010). Of studies that characterized shallow to mesophotic herbivorous fish communities, most indicated that their abundance, density, and/or biomass also decreased with depth (Thresher and Colin 1986; Brokovich et al. 2010; Smith et al. 2012; Andradi-Brown et al. 2016; Fukunaga et al. 2016; Asher et al. 2017, but see Lindfield et al. 2016; Muñoz et al. 2017). Parrotfishes dominate herbivorous fish biomass in many areas (Mumby 2009), and some species have been suggested to be the most important carbonate substratum bioeroders of all herbivorous fishes on shallow-water reefs (Woods 1999; Perry et al. 2012). Parrotfishes, including a few major bioeroding species, have also been reported on mesophotic reefs (Table 43.2 and Fig. 43.1c), although their abundances at these depths are usually relatively low. Brokovich et al. (2010) found that average parrotfish biomass was greatest on shallow reefs in the Gulf of Aqaba (Red Sea). Biomass of all recorded par-

Table 43.2 Representative list of studies documenting herbivorous fishes and specific parrotfish species (sometimes only most abundant fish were reported by sources). Bolded species names signify taxa specifically identified as major parrotfish bioeroders (i.e., species classified as excavators or large scrapers; Bruggemann et al. 1996; Cardoso et al. 2009; Bonaldo et al. 2014), although Perry et al. (2012) suggested that bioerosion rates of two major Caribbean species (*Scarus vetula* and *Sparisoma viride*) can be extrapolated within genera for bioerosion rates of other species. Names of other species suggested to remove relatively small amounts of carbonate (Alwany et al. 2009; Cardoso et al. 2009) were not bolded

Ocean basin	Location	Study depth range (m)	Method listed	Parrotfishes identified	Source
Caribbean/ Atlantic	Northwestern Brazil	35–70	Visual observations, collections, video recordings	<i>Cryptotomus roseus</i> , <i>Scarus trispinosus</i> , <i>Scarus zelindae</i> , <i>Sparisoma axillare</i> , <i>Sparisoma amplum</i> , <i>Sparisoma frondosum</i> ^a	Feitoza et al. (2005)
	Vitória-Trindade Seamount Chain, Brazil	0–120	Multiple methods (see source)	<i>Cryptotomus roseus</i> , <i>Scarus zelindae</i> , <i>Sparisoma amplum</i> , <i>Sparisoma axillare</i> , <i>Sparisoma frondosum</i> , <i>Sparisoma radians</i> , <i>Sparisoma rocha</i> , <i>Sparisoma tuiupiranga</i>	Pinheiro et al. (2015)
	St. Peter and St. Paul's Archipelago, Brazil	30–90	Video footage of circular area from remote-operated vehicles	None listed	Rosa et al. (2016)
	Curaçao and Bermuda	45–130	Visual census along transects	<i>Scarus iseri</i> , <i>Scarus taeniopterus</i> , <i>Scarus vetula</i> , <i>Sparisoma aurofrenatum</i> , <i>Sparisoma chrysopteron</i> , <i>Sparisoma juvenile</i> , <i>Sparisoma rubripinne</i> , <i>Sparisoma viride</i>	Pinheiro et al. (2016)
	Honduras	5–40	Diver-operated stereo-video system transects	<i>Scarus iseri</i> ^b , <i>Scarus taeniopterus</i> ^c , <i>Scarus vetula</i> , <i>Sparisoma aurofrenatum</i> ^c , <i>Sparisoma viride</i>	Andradi-Brown et al. (2016)
	Northwest Gulf of Mexico, USA	15–140	Visual transect observations (video)	<i>Scarus taeniopterus</i> ^d , <i>Scarus vetula</i> ^d , <i>Sparisoma atomarium</i> ^d , <i>Sparisoma aurofrenatum</i> ^d , <i>Sparisoma viride</i> ^d	Dennis and Bright (1988)
	Flower Garden Banks, USA	18–45	Visual transects	<i>Scarus iseri</i> , <i>Scarus taeniopterus</i> , <i>Scarus vetula</i> , <i>Sparisoma atomarium</i> , <i>Sparisoma aurofrenatum</i> , <i>Sparisoma radians</i> , <i>Sparisoma viride</i>	Muñoz et al. (2017)
	NW Puerto Rico, USA	15–50	Belt transects	<i>Scarus iseri</i> ^b , <i>Sparisoma atomarium</i> , <i>Sparisoma aurofrenatum</i>	García-Sais (2010)
	SW Puerto Rico, USA	30–70	Belt transects and roving surveys	<i>Scarus iseri</i> ^e , <i>Scarus taeniopterus</i> , <i>Sparisoma atomarium</i> , <i>Sparisoma aurofrenatum</i> , <i>Sparisoma viride</i> ^e	Bejarano et al. (2014)
	SW Puerto Rico, USA	50–70	Belt transects	<i>Scarus taeniopterus</i> , <i>Sparisoma atomarium</i> ^c	Appeldoorn et al. (2016)
	U.S. Virgin Islands, USA	9–45	Belt transects	<i>Scarus guacamaia</i> , <i>Scarus iseri</i> ^b , <i>Scarus taeniopterus</i> , <i>Scarus vetula</i> , <i>Sparisoma aurofrenatum</i> , <i>Sparisoma chrysopteron</i> , <i>Sparisoma rubripinne</i> , <i>Sparisoma viride</i>	Smith et al. (2012) and Weinstein et al. (2014)
Pacific	Main Hawaiian Islands, USA	0–100	Baited remote underwater stereo-video system	<i>Calotomus carolinus</i> , <i>Chlorurus perspicillatus</i> ^f , <i>Chlorurus sordidus</i> , <i>Scarinae sp.</i> , <i>Scarus dubius</i> ^f , <i>Scarus psittacus</i> , <i>Scarus rubroviolaceus</i>	Asher et al. (2017)
	Northwestern Hawaiian Islands (NWHI), USA	3–67	Belt transects ^g	None (from 2010 supplement dataset, 39–67 m)	Fukunaga et al. (2016)
	NWHI, USA	30–90	Belt transects and roving-diver searches	<i>Chlorurus perspicillatus</i> , <i>Scarus psittacus</i>	Kane et al. (2014)
	NWHI, USA and Pohnpei, Federated States of Micronesia (and Puerto Rico)	30–50	Belt transects	<i>Chlorurus perspicillatus</i> , <i>Chlorurus sordidus</i> , <i>Scarus dubius</i> , <i>Scarus guacamaia</i> ^h , <i>Scarus iseri</i> ^h , <i>Scarus psittacus</i> , <i>Scarus taeniopterus</i> ^h	Bridge et al. (2016)

(continued)

Table 43.2 (continued)

Ocean basin	Location	Study depth range (m)	Method listed	Parrotfishes identified	Source
	Mariana Islands, USA	9–91	Baited remote underwater stereo-video system	<i>Chlorurus microrhinos</i> , <i>Chlorurus spilurus</i> , <i>Scarus forsteni</i> , <i>Scarus psittacus</i> , <i>Scarus schlegeli</i>	Lindfield et al. (2016)
	Marshall Islands	30–300	Visual timed transect census	<i>Chlorurus sordidus</i> ⁱ , and “other scarids”	Thresher and Colins (1986)
Red Sea	Gulf of Aqaba, Jordan	1–40	Visual census along transects	<i>Chlorurus sordidus</i> ⁱ , <i>Scarus ferrugineus</i> , <i>Scarus niger</i> , <i>Scarus</i> sp.	Bouchon-Navaro and Harmelin-Vivien (1981)
	Gulf of Aqaba, Israel	1–65	Visual census along transects	<i>Calotomus viridescens</i> , <i>Cetoscarus bicolor</i> ^d , <i>Chlorurus genazonatus</i> ^d , <i>Chlorurus gibbus</i> ^e , <i>Chlorurus sordidus</i> ^f , <i>Scarus ferrugineus</i> , <i>Scarus fuscopurpureus</i> , <i>Scarus niger</i>	Brokovich et al. (2010)

^aListed as common, but all others from this study were listed as occasionally observed

^bReported as *Scarus iserti*

^cOnly observed once

^dNever observed >85 m, and only listed as “rare,” “occasional,” or “present” from 45 to 85 m in East and West Flower Garden Banks

^eNot observed at deepest (70 m) site

^fNot observed deeper than 30 m

^gCompared to previous data collected from stationary point counts in circular plots

^hFrom Puerto Rico (Caribbean/Atlantic) part of the source

ⁱReported as *Scarus sordidus*

rotfish species decreased with depth down to 45 m in the northern US Virgin Islands (USVI), but this relationship was less clear when scaling daily bioerosion rates by biomass of *Sparisoma viride* (Bonnaterre, 1788) and *Scarus vetula* Bloch and Schneider, 1801 (Fig. 43.4), as described by Weinstein et al. (2014). These two species, which are considered primary bioeroding parrotfishes in the Caribbean (Bruggemann et al. 1996; Cardoso et al. 2009), were also documented in low abundances at a depth of 40 m in Honduras (Andradi-Brown et al. 2016) and were either absent below 30 m (García-Sais 2010) or at a very low mean density (*S. viride* at 60 m only; Bejarano et al. 2014) in Puerto Rico (Table 43.2). Contradictory to most other studies, a relatively high biomass of parrotfishes (e.g., 330.5 g 60 m⁻² of *S. vetula*) was recorded from 45 to 80 m in Bermuda, although no parrotfishes were found from 85 to 130 m (Pinheiro et al. 2016). Pinheiro et al. (2016) suggested this could result from high light penetration facilitating the foraging of macroalgae below 100 m. Parrotfishes may also be important contributors to sediment production on mesophotic reefs. Weinstein et al. (2015) found a strong correlation between adjusted bioeroding parrotfish biomass and percent of coral-derived particles in upper mesophotic reef sediment. However, additional studies from other regions are necessary to determine whether this is a general trend for mesophotic reefs on low-angle slopes. The available literature supports the finding that, globally, parrotfish are more common in shallow-water reefs and most species found on mesophotic reefs are not substantial bioeroders (Table 43.2) or are at low abundances.

43.2.2.3 Experimental Substrate Case Studies

Experimental substrates, i.e., blocks and disks of unaltered solid calcium carbonate left in a reef environment and then retrieved and analyzed in terms of their boring communities and their loss of CaCO₃, can provide more direct estimates of herbivore grazing and bioerosion compared to visual census and bioassay methods. Although restricted to initial (<10 year) modification, experimental substrates can be directly compared in terms of bioerosion type at multiple locations without bias when using the same substrate type, study duration, and methodology for all locations (e.g., Kiene and Hutchings 1994; Tribollet and Golubic 2005). Still, caution is needed when extrapolating results from experimental substrates as rates from these methods are rarely homogeneous across space and time. Results from coral reef studies using experimental substrates indicated that bioerosion rates, primarily associated with grazing, were lower at deeper sites (20 m; Kiene and Hutchings 1993), including most of the upper mesophotic reef sites analyzed (Table 43.1; Hassan 1998; Weinstein 2014; Weinstein et al. 2014). Substrate weight change correlated with bioeroder-adjusted parrotfish biomass in the USVI, implying that parrotfishes were the most dominant substrate bioeroders down to 30–39 m (Weinstein et al. 2014; Smith et al. 2015). Based on their Great Barrier Reef study and other studies, Kiene and Hutchings (1993) proposed that “high grazing destruction” occurs from 1 to 20 m depth. These authors also found that grazing rates at 20 m (their deepest study site) were significantly lower than boring rates after 5 years (Kiene and Hutchings 1994). However, past experimental

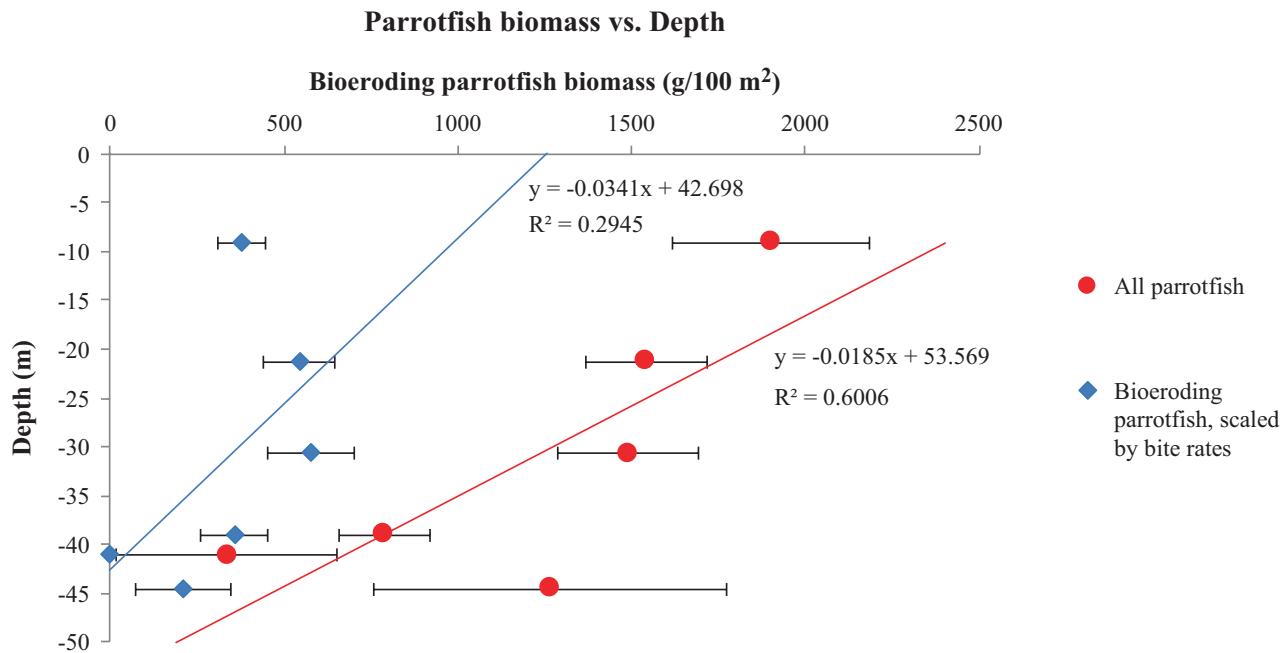


Fig. 43.4 Variation of parrotfish biomass with depth (Data from the US Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP) study, Nemeth et al. 2008; Smith et al. 2012). Biomass of all recorded parrotfish species (circles) and bioerosion-adjusted biomass (diamonds), calculated as the sum biomass of the primary Caribbean bioeroding parrotfish species *Sparisoma viride* and *Scarus vetula* (Bruggemann et al. 1996), with *S. vetula* biomass divided by 7 (Weinstein et al. 2014) to compensate for lower recorded daily bioerosive activity (Bruggemann et al. 1996)

substrate mesophotic studies that found grazers to be the most dominant bioeroding guild (Hassan 1998; Weinstein 2014; Weinstein et al. 2014) may not have allocated sufficient exposure time for the establishment of mature sponge bioerosion communities (e.g., Kiene 1985; Chazottes et al. 1995; Weinstein et al. 2014). The amount of time needed for the establishment of mature macroboring communities below 30 m is presently unknown and could be greater than that needed by grazers to degrade experimental substrates (Kiene and Hutchings 1993). Regardless, these experimental substrate studies, along with herbivory abundance patterns with depth, strongly indicate that the impact of grazing bioerosion is lower on mesophotic reefs than nearby shallower locations.

43.2.3 Macroboring

Although data are sparse, macroborer diversity appears to be lower on deeper (≥ 30 m) reefs compared to shallower reefs (Perry and Hepburn 2008; Weinstein et al. 2014; but see MacGeachy and Stearn 1976). Still, evidence indicates macrobores are important substrate modifiers on mesophotic reefs. For example, large boring bivalves can contribute locally to significantly weakening the holdfasts of corals such as *Porites lobata* Dana, 1846 on mesophotic reefs

(Grigg 2006). But of all macroborer organisms, sponges are often the most dominant and destructive in shallow-water reefs (Perry and Harborne 2016; Schönberg et al. 2017a). Considering this and the limited macroboring research available for mesophotic reefs, sponges are likely the main contributors to internal macrobioerosion on most deeper (15–50 m) reef fronts (Goreau and Hartman 1963; MacGeachy and Stearn 1976; Perry 1998; Grigg 2006; Weinstein et al. 2014; Perry and Harborne 2016). Furthermore, given the general decline of microboring and grazing bioerosion with depth (see Sects. 43.2.1 and 43.2.2, respectively), we hypothesize that sponges are the main long-term (>5–10 year) agents of bioerosion on lower mesophotic reefs. This is likely the case on most upper mesophotic reefs as well (Fig. 43.1e–h). However, since initial (≤ 3 year) grazing bioerosion rates exceeded macroboring rates of shallow coral experimental substrates on some upper mesophotic reefs (Hassan 1998; Weinstein 2014; Weinstein et al. 2014), there is a need for additional research with experimental substrates composed of mesophotic coral to test this hypothesis.

Based on the few quantitative studies available, other more specific consensus trends cannot be determined for macroborers or their bioerosion rates across a depth gradient to mesophotic reefs (Table 43.3). This may be due to the different metrics applied to document the cryptic infaunal lifestyle of most macroborers. For example, visual censuses

Table 43.3 Selected studies containing data for shallow and mesophotic reefs indicating various metrics of macroboring with depth. Trends with depth represent comparisons between shallow and deepest sites from the referenced studies and do not necessarily imply a linear relationship

Location	Depth range (m)	Metric/measurement (units)	Method/notes	Metric trend as depth increases	Source
Gulf of Aqaba, Red Sea	10–30	Species abundance of boring sponge <i>Pione cf. vastifica</i>	10 × 1 belt transects	↑	Zundeleovich et al. (2007)
		Number of individual sponges per area (individual m ⁻²)	Analysis from plan view		
Barbados	2–37	Volume of macroboring traces in <i>Orbicella annularis</i> coral heads	“Freshly collected coral heads” serially sectioned (7 mm thick) and X-rayed. Radiographs were used to estimate volume	↑	MacGeachy and Stearn (1976)
		Estimated volume of all borings divided by measured volume of sample (% bored)	Percent bored also significantly correlated with increasing age of samples		
Discovery Bay, Jamaica	15–40	Boring sponge silt accumulation	Sediment traps on stakes for 58–60 days	↓	Moore and Shedd (1977)
		Weight of silt per area of sediment trap per time (converted to g m ⁻² y ⁻¹)	Sediment might have derived from other regions of the reef beyond depth specified		
Discovery Bay, Jamaica	15–120	Benthic cover of “boring sponges”	Census along 10-m transects (at 15 & 30 m); photo transects with 0.14 m ² area from SCUBA (at 45 m) and submersible (53–120 m) at 1 m intervals per site	↓	Liddell and Ohlhorst (1988)
		Mean percent community composition out of all benthic categories (% cover of transect)	Analysis from plan view		
Discovery Bay, Jamaica	5–30	Macroboring trace identification in coral rubble slabs	“Recent mortality” coral rubble collection (54 samples) of multiple species types. Samples were slabbed and the amount of borings were quantified with point-count analysis	↑	Perry (1998)
		Area of collected coral rubble cross sections covered with macroboring traces (% surface area macrobored)	Trend (arrow) based only on fore-reef sites		
Flower Garden Banks, USA	20–38	<i>Lithotrya dorsalis</i> barnacle apertures on coral <i>Orbicella franksi</i>	Barnacle aperture counts and <i>O. franksi</i> surface area measurements from long-term monitoring photos	↓	Maher et al. (2018)
		Density of barnacles per m ² of <i>O. franksi</i> cover			
U.S. Virgin Islands, USA	7–38	<i>L. dorsalis</i> barnacle apertures on coral <i>O. franksi</i>	Barnacle aperture counts and <i>O. franksi</i> surface area measurements from long-term monitoring photos	↓	Maher et al. (2018)
		Density of barnacles per m ² of <i>O. franksi</i> cover			
U.S. Virgin Islands, USA	9–45	Macroboring rates (see Table 1)	<i>O. annularis</i> (2 m) experimental substrate disks exposed for 3 years	↓	Modified from Weinstein (2014)
		Product of percent of disk cross-sections macrobored and original disk weight, per 3D surface area of disk and time of exposure (kg CaCO ₃ m ⁻² year ⁻¹)	Macroboring accounted for less than 15% of total bioerosion at all sites		
U.S. Virgin Islands, USA	9–45	Macroboring trace identification in coral rubble slabs	“Opportunistic” coral rubble collection (44 samples) of multiple species types. Samples were slabbed approximately parallel to growth axis and amount of borings were quantified with point-count analysis	↑	Weinstein et al. (2014)
		Area of collected coral rubble cross sections covered with macroboring traces (% surface area macrobored)	Trend (arrow) when not including low coral cover deep patch site where most samples were protected by coralline algae		

applied by some studies only quantify organisms in plain view and would thus exclude macroboring organisms that can grow on the underside of coral plates, which are common in mesophotic reefs (e.g., Liddell and Ohlhorst 1988). Additionally, the cryptic nature of most macroborers implies that PAR is not a major influence controlling their distributions (Perry and Hepburn 2008). Regardless, observations suggest mesophotic coral substrates suffer from high levels of internal erosion (Goreau and Hartman 1963; MacGeachy 1977; Wilkinson 1983; Weinstein et al. 2014) and imply macroborers may have a greater relative impact on the structure of mesophotic reefs than on shallower reefs (Fig. 43.2).

43.3 Comparing Bioerosion on Mesophotic and Shallow Reefs

There are several important trends that distinguish bioerosion patterns on shallow versus mesophotic reefs. First, average bioerosion rates (Table 43.1) and the amount of substrate material removed by bioerosion are often lower on mesophotic reefs than on shallow reefs initially (≤ 3 year) (Hassan 1998; Weinstein 2014; Weinstein et al. 2014). This is because initially, over the same timeframe, microborer and grazer bioerosion rates (see Sects. 43.2.1 and 43.2.2 respectively) and abundances (Fig. 43.2) are often lower on mesophotic reefs than on shallower reefs. An implication of this is that grazers, in association with microborers, remove more CaCO_3 substrate than macroborers on shallow and some upper mesophotic reefs (see Sect. 43.2). Second, sponges are likely the most important bioeroders on lower and possibly upper mesophotic reefs (see Sect. 43.2.3), given the well-documented destructive effects of bioeroding sponges on shallow reefs and the diminished role of grazers and microborers in mesophotic habitats. However, direct comparisons between mesophotic and shallow-water reef studies, and bioerosion studies, remain difficult because different methods, units, and experimental time durations have been applied across studies. These and other sources of variability (e.g., temporal comparisons complicated by fluctuations in epizootics and mortality events, and fishing pressure; Perry and Harborne 2016) make generalizing bioerosion trends difficult and require data to be normalized. Regardless, we discuss several hypotheses regarding why differences may exist in bioerosion with depth and explore the implications for mesophotic reef development and restructuring.

43.3.1 Why Is Bioerosion Different on Mesophotic Reefs?

The contrasts in bioerosion guild dominance between mesophotic and shallow-water reefs (see Sect. 43.2) stem from the

variation of multiple factors. Reduced PAR on mesophotic reefs (Baker et al. 2016) is likely one of the most significant of these factors, triggering heterogeneous distributions in herbivorous fishes with depth based on preferred food availability and nutrition (Bonaldo et al. 2014). It may also have a similar impact on sea urchin distribution. External bioeroders often prefer grazing on substrates inhabited by endolithic algae (Bruggemann et al. 1996; Wisshak et al. 2010); parrotfishes specifically feed selectively on autotrophic microorganisms (Clements et al. 2016). Thus, declining PAR not only causes reduced microbioerosion rates and abundances of phototrophic microborers with depth (see Sect. 43.2.1), but the relative paucity of microboring autotrophs may indirectly explain lower bioeroding grazer abundances and bioerosion rates on mesophotic reefs (see Sect. 43.2.2). CaCO_3 removal by phototrophic microborers in lower mesophotic reefs may also be limited because there are fewer bioeroding grazers at these depths (Fig. 43.2) to facilitate the penetration of microborers into deeper recesses of carbonate substrate (Tribollet et al. 2011).

There is uncertainty regarding whether bioeroding parrotfishes specifically target endolithic algae or if the consumption of these microborers results from parrotfishes feeding on epilithic algal matrix (EAM), defined as epilithic algal communities (small communities forming low mats or turfs on coral reefs; Hatcher and Larkum 1983) plus detritus (non-living organics), microbial, and inorganic (sediment) components (Wilson and Bellwood 1997), and microalgae (Bonaldo et al. 2014). Not all parrotfishes have the same feeding method (Bellwood and Choat 1990), and Clements et al. (2016) suggested that the excavating feeding mode of some bioeroding parrotfishes seems incongruent with the hypothesis that these bioeroders are specifically targeting EAM. Yet, microscopic algae have been observed on, under, and in multiple substrates such as macroalgae, crustose coralline algae, sparse and dense algae turf, and living coral (Clements et al. 2016). Surveying for EAM presence and density in a variety of substrates along depth transects on shallow and mesophotic reefs constitutes a next logical step in understanding the role of EAM in the feeding behavior and distribution of bioeroding parrotfishes.

The abundance of EAM, which bioeroding sea urchins are also known to feed on to some degree (as turf and macroalgae; e.g., Chazottes et al. 2002; Glynn and Manzello 2015), may influence grazing bioerosion with depth or be influenced by herbivore abundance. Some mesophotic reef studies reported that turf and/or macroalgal cover, biomass, and relative productivity decrease with depth (Aponte and Ballantine 2001; Brokovich et al. 2010; Andradi-Brown et al. 2016). However, other studies did not find a similar decline with depth on mesophotic reefs for all algal types (van den Hoek et al. 1978; Liddell and Ohlhorst 1988; Morrison 1988; Bejarano et al. 2014), possibly related to a

decline in herbivorous organisms (including some bioeroders) with depth (van den Hoek et al. 1978; Liddell and Ohlhorst 1988; Morrison 1988). Additionally, Kahng et al. (2010) noted that low algal biomass has been linked to heavy grazing and suggested depleted herbivore abundance in mesophotic coral ecosystems may be related to low structural/habitat complexity. Beyond abundance, nutritional content of EAM is also greatest on shallower exposed reefs (Bonaldo et al. 2014). Algal food sources on mesophotic reefs may have a lower nutritional value, digestibility, and palatability (as suggested by Brokovich et al. 2010; Bejarano et al. 2014), leading to reduced grazer abundance. Further observations and experiments with regard to the effect of algal distribution patterns and nutritional context on bioerosion rates are needed on mesophotic reefs. Spatial distribution of parrotfishes and other epilithic bioeroders may also be driven by additional biotic factors beyond dietary preference, including shelter and predator abundance (Lewis and Wainwright 1985).

Other factors additionally spur differences in bioerosion between mesophotic and shallow reefs. Water temperature is typically lower on mesophotic reefs (Lesser et al. 2009; Baker et al. 2016), and colder temperatures have been linked to reduced grazing and macroboring rates of some species (Schönberg et al. 2017b). However, it is unknown whether grazers and/or macroborers on mesophotic reefs are acclimated to slightly colder conditions such that their rates of erosion would not be reduced like in experimental studies from colder temperatures (Schönberg et al. 2017b). As in shallow habitats, sedimentation, nutrient concentrations, and pH may additionally impact bioerosion. While these interactions are complex, increased ocean acidification (lower pH) and nutrients may boost bioerosion (Schönberg et al. 2017b), and sedimentation is detrimental to bioerosion and coral growth (Perry and Harborne 2016). Some studies have recorded elevated nutrient levels on mesophotic reefs compared to shallower reefs (Lesser et al. 2009), which along with reduced grazing, may help indicate why qualitative observations suggest macroborers dominate carbonate substrate erosion on lower mesophotic reefs (Fig. 43.2). However, sedimentation varies greatly among mesophotic reefs depending on geomorphology, geography, and local sources (Weinstein et al. 2015; Appeldoorn et al. 2016; Baker et al. 2016), and little data are available regarding pH variability between mesophotic and shallower reefs (Baker et al. 2016). Therefore, it is currently difficult to generalize how these factors and their interactions on local and global scales may result in bioerosion differences across shallow to mesophotic depth gradients.

Substrate characteristics including availability; type; gross and specific skeleton density, thickness, and porosity; coral growth rates; and reef carbonate production rates may also provide insight into bioerosion differences between

shallow and mesophotic reefs (Highsmith 1981; Bruggemann et al. 1996; Perry 1998; Vogel et al. 2000; Schönberg 2002; Hernández-Ballesteros et al. 2013). Some of these characteristics impact how easily bioeroders can remove CaCO_3 from reef structures. This has mostly been observed on mesophotic reefs for sponges (Goreau and Hartman 1963; MacGeachy and Stearn 1976; James and Ginsburg 1979; Wilkinson 1983; Weinstein et al. 2014). Bioeroding sponges, as well as other macroborers, have been suggested to remove more carbonate from denser substrates (Highsmith 1981; Rose and Risk 1985; Schönberg 2002; Hernández-Ballesteros et al. 2013; Schönberg et al. 2017a, but see Tribollet et al. 2002; Schönberg et al. 2017b). Coral growth and carbonate production rates are generally thought to decrease with depth (Baker and Weber 1975; MacGeachy 1977; Huston 1985; Perry and Harborne 2016; Watanabe et al. 2019). A review of coral growth band studies suggested that skeleton density increases with depth for massive corals with annual density banding (Lough and Cooper 2011). Although, this has only been demonstrated for a few coral species (Baker and Weber 1975; Hughes 1987). Other studies suggest skeleton density may decrease with depth depending on species and location (Watanabe et al. 2019). Regardless, the skeletal densities of many thin plate coral species such as *Pachyseris speciosa* (Dana, 1846) on mesophotic reefs have not been reported, but sponge boring of these species is possible (Fig. 43.5a). Additional research into the range of skeletal densities on mesophotic reefs and whether they change with depth will further reveal if bioeroders are likely to have differential activity on mesophotic reefs based on substrate density.

Age of substrate and length of exposure also greatly impact bioerosion rates, which have been shown to increase as boring communities mature (Chazottes et al. 1995; Tribollet and Golubic 2005; Hutchings 2011). Reduced sedimentation on low-slope mesophotic reefs (Weinstein et al. 2015), slow coral growth rates, lower frequency of stress and disturbance from warm-water bleaching and storms (Bongaerts et al. 2010; Baker et al. 2016), and reduced grazing (see Sect. 43.2.2) have all been documented or suggested on mesophotic reefs. Mesophotic reef framework is also below the direct physical influence of surface waves (Bongaerts et al. 2010). These attributes suggest mesophotic reef substrate, on average, may be older and exposed longer prior to burial than on shallower reefs (Greenstein and Pandolfi 2003; Grigg 2006; Perry and Hepburn 2008; Weinstein et al. 2014) and may be available for multiple cycles of substrate erosion (Perry and Hepburn 2008). Moreover, corals with plating morphologies are common on mesophotic reefs (Figs. 43.2 and 43.5; Baker et al. 2016). This offers CaCO_3 surface area on plate undersides that is unprotected by coral tissue, creating ideal conditions for additional euendolithic recruitment (e.g., Goreau and Hartman



Fig. 43.5 Macroborings in mesophotic platy coral rubble, viewed in cross section. (a) *Pachyseris* sp. (*speciosa* or *foliosa*) rubble collected in Okinawa, Japan, at 42 m (White et al. 2017). Yellow sponge tissue (e.g., white arrows) fills the small excavation chambers. (b) *Agaricia* sp. rubble collected in the USVI at 45 m (Weinstein et al. 2014) showing the porous and cavernous traces generated primarily by two or three different species of bioeroding sponges

1963; MacGeachy 1977; Wilkinson 1983; Perry 1999). Together, these multiple substrate qualities and physical conditions may explain much of why mesophotic reef substrate is heavily infested with internal borings (Fig. 43.5; Goreau and Hartman 1963; MacGeachy 1977; Wilkinson 1983) and why dead coral framework may remain in situ longer than on shallow reefs.

Lastly, the balance between coral calcification and bioerosion rates may also shift with depth such that there is more relative internal damage in mesophotic reefs (Goreau and Hartman 1963; MacGeachy 1977; Wilkinson 1983). The higher relative damage from bioerosion observed in substrates from mesophotic reefs (Goreau and Hartman 1963) may also result from slower coral and coralline algae growth at depth (Baker and Weber 1975; Hubbard and Scaturro 1985; Huston 1985; Weinstein et al. 2016). This allows mesophotic reef borers to remove relatively more CaCO_3 substrate compared to borers infesting faster-accreting substrates in shallower reefs. The role of internal bioerosion may become more important on “deeper” reefs as a result of relative differences between coral growth and bioerosion rates (Perry

and Harborne 2016), but it is still unknown if the relatively high amount of internal bioerosion on mesophotic reefs compares with the higher grazing rates commonly observed on shallower reefs.

43.3.2 Implications of Mesophotic Reef Bioerosion

Bioerosion is fundamental to our understanding of past mesophotic reefs (see references in Sherman et al. 2019) and the evolution of coral reef biodiversity (Weinstein et al. 2015). Weinstein et al. (2015) suggested that sedimentary facies, along with other clues from ancient deposits, could help to characterize past mesophotic reefs and interpret past ecological and geological conditions. Such factors, as well as bioeroder indicator traces, could be useful in identifying paleophotic zones in the carbonate record (Budd and Perkins 1980). Ichnogenera have especially been recognized as tools to study paleoenvironments in the geological record (Tribollet et al. 2011; Tapanila and Hutchings

2012). However, reefs must be preserved in the rock record for this to occur. Perry (1999) found low framework preservation and accretion potential on an upper mesophotic Jamaican reef (30 m fore-reef slope), implying that some mesophotic reefs may not be well represented in the fossil record.

Variability in bioerosion rates and bioeroder abundances on and between shallow and mesophotic reefs critically impacts various reef attributes such as habitat heterogeneity, net reef accretion, and framework integrity. Weinstein et al. (2014) hypothesized that bioerosion variability on USVI mesophotic reefs may exaggerate pronounced differences in reef-scale geomorphology and increase habitat heterogeneity. From a broader perspective, studying bioerosion in mesophotic reefs is important for understanding past and future shelf-wide reef accretion trends and the maintenance of habitat-forming structures through net positive CaCO_3 production. For example, through the analysis of 151 western Atlantic Holocene cores with coral samples at paleodepths less than 25 m, Hubbard (2009) provided evidence to refute previous reef accretion theory assumptions that net vertical reef accretion decreases with depth (Schlager 1981; Bosscher and Schlager 1992). Hubbard (2009) hypothesized that potential declining absolute rates of bioerosion with depth might be offset by decreases in carbonate production with depth, assuming the sediments produced by bioerosion would primarily be transported off the reef. But while grazing decreases with depth (see Sect. 43.2.2), is total bioerosion on upper mesophotic reefs slow enough such that rates of accretion at these depths are similar to rates of net accretion at shallower locations? Preliminary evidence seems to indicate this is possible. Carbonate budget-calculated accretion rate estimates from the USVI found contemporary accretion rates at upper mesophotic reefs (31–45 m) were slower than on a mid-patch reef (21 m), but faster than on a shallow (9 m) fringing patch reef (modified from Weinstein 2014). USVI estimated mesophotic accretion rates were also faster than carbonate budget-calculated accretion rate average estimates ($0.29 \text{ mm year}^{-1}$) on modern reefs throughout the Caribbean at depths of 10–20 m (Perry et al. 2013). These results also appear to contradict previous assumptions that net vertical reef accretion decreases with depth. However, analysis of reef short cores retrieved at ~50 m in Puerto Rico (Sherman 2017, pers. comm.) and carbonate budget analysis on upper mesophotic USVI reefs (modified from Weinstein 2014) both estimated modern mesophotic reef accretion to be at least an order of magnitude slower than Holocene accretion rates at paleowater depths of 10–20 m (2.9 mm year^{-1} ; Hubbard 2009). Therefore, it is likely that carbonate budgets in mesophotic reefs (and related bioerosion rates) have changed with time.

Regardless of how substrate erosion rates change with depth, we suggest bioerosion, and macroboring in particular,

is an important factor shaping mesophotic reefs. As overall coral growth often declines with depth (see Sect. 43.3.1), net carbonate budgets could shift toward erosional states (Perry et al. 2013) even if bioerosion rates remain constant on mesophotic reefs. Substrata below 50 m water depth in the Hawaiian Au‘au Channel were ^{14}C -dated by Grigg (2006) to be between 8000 and 9600 years old; substrata above 50 m were of modern age. Even though models predicted *P. lobata* should grow at depths of 80 m (Grigg 2006), the above results imply that reef growth significantly slowed or ceased below 50 m; *P. lobata* basal attachment growth rates were equal or slower than bioerosion rates of colony holdfasts at 50 m. Grigg (2006) suggested that, at least in Au‘au Channel, bioerosion was the limiting factor for accretion of attached coral on mesophotic reefs. Alternatively, unlike the shallowest study site in the USVI, all deep sites (30–45 m) experienced net accretion and thus implied that upper mesophotic reefs may retain sufficient structural sustainability to maintain complex habitats to harbor healthy reef systems (modified from Weinstein 2014). However, more studies are needed, including analyses of sediment distribution at mesophotic depths (Hubbard et al. 1990). The importance of monitoring bioerosion in mesophotic reefs is clear, particularly when considering that small changes may shift the carbonate balance from precarious positive net carbonate production (e.g., Weinstein 2014) to net erosion that could remove the foundational structures of these vital ecosystems. This is especially true as rapid global environmental changes increasingly affect mesophotic reefs (Baker et al. 2016), likely disrupting current patterns of mesophotic bioerosion as predicted in shallower reefs (Perry and Harborne 2016).

43.4 Conclusions

Overall, there are three main trends in terms of mesophotic reef bioerosion. First, bioerosion by phototroph microborers and grazers generally declines with depth down to mesophotic reefs. Second, due to reduced grazer densities, sponges appear to be the main substrate modifying group on lower (and possibly on some upper) mesophotic reefs, although on different time scales and with different outcomes than on shallower reefs. Third, mesophotic reef bioerosion rates may be slower than on shallower reefs. Challenges in comparing shallow and mesophotic reef systems arise from different substrate characteristics (i.e., age, density, growth rate, and amount exposed) and differences in methods applied between studies. There is a significant need for further research on mesophotic reef bioerosion, especially on lower mesophotic reefs. Such studies will provide more insight into how mesophotic reefs will change with time and how to manage them appropriately. One goal of future research should be to determine how bioerosion on meso-

photic reefs might impact structural sustainability, in terms of the overall reef carbonate budget, as oceanic conditions continue to respond to climatic changes. Several other works (Tribollet and Golubic 2011; Perry and Harborne 2016; Schönberg et al. 2017b) have provided insightful questions and research priorities for bioerosion on coral reefs; these are applicable to mesophotic reefs. In addition, we recommend the following research priorities for mesophotic reefs be conducted globally, including a full-depth range with shallow sites for comparison:

1. Generation of a detailed bioeroder taxonomic inventory in habitats at mesophotic depths, including analysis of easily attainable coral rubble.
2. Better documentation of the abundance of grazers and borers, quantification of bioerosion in relative proportions for the bioeroder guilds, and direct measurements of grazing with reference to depth (see Bruggemann et al. 1996).
3. Further evaluations of bioerosion rates using experimental substrates of similar material quality, as well as using substrates composed of the main framework type at each depth, and using microcomputed tomography (microCT) and scanning electron microscopy for subsamples with microboring to better quantify internal bioerosion. Given the extended time needed for macroborers to establish and reach mature community compositions, to the extent possible, we suggest that these studies be conducted on longer timeframes (5–10 years) using large substrates (e.g., blocks $>15 \times 15 \times 8$ cm or disks with diameters and heights >15 and 8 cm, respectively). We also recommend using grazer exclusion cages in these studies to tease out the importance of different bioerosion groups.
4. Additional data on mesophotic coral growth and calcification rates, coral density variation, substrate age and amounts of exposed substrate, and sediment composition analyses will help place mesophotic reef bioerosion in the context of overall reef accretion and will allow for more holistic comparisons to shallower reefs. Mesophotic reef carbonate budget studies and analysis of cores collected at these depths are also of critical importance.

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