Mesophotic bioerosion: Variability and structural impact on U.S. Virgin Island deep reefs

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Abstract

Mesophotic reef corals, found 30–150 m below sea level, build complex structures that provide habitats for diverse ecosystems. Whereas bioerosion is known to impact the development and persistence of shallow reef structures, little is known regarding the extent of mesophotic bioerosion or how it might affect deeper reef geomorphology and carbonate accretion. Originally pristine experimental coral substrates and collected coral rubble were both used to investigate the variation and significance of mesophotic coral reef bioerosion south of St. Thomas, U.S. Virgin Islands. Bioerosion rates were calculated from experimental coral substrates exposed as framework for 1 and 2 years at four structurally distinct mesophotic coral reef habitats (between 30 and 45 m) as well as at a mid-shelf patch reef (21 m) and a shallow fringing patch reef (9 m). The long-term effects of macroboring were assessed by examining coral rubble collected at all sites. Overall, differences in bioerosional processes were found between shallow and mesophotic reefs. Increases in bioerosion on experimental substrates (amount of weight lost) were related to both decreasing seawater depth and increasing biomass of bioeroding parrotfish. Significant differences in coral skeleton bioerosion rates were also found between the transitional mesophotic reef zone (30–35 m) and the upper mesophotic reef zone (35–50 m) after 2 years of exposure, ranging from —19.6 to 3.7 g/year. Total coral rubble macroboring was greater at most deep sites compared to shallower sites. Bioerosional grazing was found to dominate initial substrate modification in reefs 30.7 m and shallower, but sponges are believed to act as the main time-averaged long-term substrate bioerosors in reefs between 35 and 50 m. Although initial substrate bioerosion rates of a uniform substrate were relatively homogeneous in the 35–50 m depth zone, comparison of site composition suggests that mesophotic bioerosion will vary depending on the amount, location, and type of available substrate, and the duration both coral rubble and in situ coral framework are exposed on the seafloor. These variations may exaggerate pronounced structural differences in mesophotic reef habitats that experience few other methods of erosion.

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1. Introduction

Mesophotic coral ecosystems (MCEs), defined as living in waters 30–150 m deep, receive only a small percentage (0.07–5.84%) of surface photosynthetically active radiation (Kahng et al., 2010), and can experience seawater temperatures more than 5 °C cooler than the surface (Lesser et al., 2009). Given the attenuation of wave motion with depth, these environments also experience less wave energy compared to shallow water reefs. MCEs are dominated by both zooxanthellate and azooanthellate scleractinian corals, sponges, and macroalgae (Lesser et al., 2009), and are thought to have large ecologic and economic value (Puglise et al., 2009). Vast areas of undiscovered mesophotic reefs have been predicted (Ginsburg and Reed, 2008; Puglise et al., 2009), with an estimated 182,000 km² of potential MCEs in the US Gulf of Mexico, Florida, and U.S. Caribbean alone (Locker et al., 2010). Yet MCEs are still considered among the least studied of all reef ecosystems (Kahng et al., 2010). One area of emerging interest is the connectivity of mesophotic reefs to shallow reefs and the importance of MCEs to the persistence of tropical reef biodiversity (Riegl and Piller, 2003; Bongaerts et al., 2010; Slattery et al., 2011). Unlike isolated lower mesophotic reefs (60–150 m), which contain many endemic species (Reed and Pompioni, 1997; Lesser and Slattery, 2011), upper mesophotic reefs (30–60 m) are inhabited by numerous shallow reef organisms (Bak et al., 2005; Bongaerts et al., 2010). These reefs potentially provide sources of larvae (Hughes et al., 2003; Lesser et al., 2009) or serve as refugia for shallow reef species threatened by local and global stressors (Glynn, 1996; Riegl and Piller, 2003; Bak et al., 2005; Bongaerts et al., 2010; Slattery et al., 2011).

Despite a number of recent physiological (Lesser et al., 2010; Bongaerts et al., 2011; Cooper et al., 2011; Morsilli et al., 2012) and
ecological MCE studies (Dustan, 1982; Bak et al., 2005; Menza et al., 2007; Rooney et al., 2010; Smith et al., 2010; Bridge et al., 2011, 2012; Lesser and Slattery, 2011), many crucial research and resource management needs outlined in The Mesophotic Coral Ecosystems Research Strategy remain unaddressed (Puglise et al., 2009). Among the central MCE research needs is an understanding of the basic sedimentary processes that construct, maintain, and modify mesophotic reef framework, and ultimately influence shelf-wide reef accretion.

Reef accretion patterns are not only influenced by calcification rates but also by cementation, encrustation, and bioerosion (Stearn and the architectural integrity of a reef (Hubbard, 2009) and plays an important role in the formation and maintenance of reef relief and structural complexity through the production, modification, and transport of the main sedimentary elements of a reef (Scoffin et al., 1980; Hutchings, 1986; Glynn, 1988, 1997; Kiene and Hutchings, 1994). Studies of carbonate budgets assess the impact of bioerosion on reef geomorphology (Glynn, 1997; Edinger et al., 2000; Perry et al., 2008, 2012), but direct observations of bioerosional modification to reef geomorphology are rare. In one example, large coral skeleton bioerosion rates compared to lower rates of carbonate formation at Champion Island, Galapagos were believed to be responsible for observed rapid structural destruction (Reaka-Kudla et al., 1996). Increased bioerosion rates responsible for destroying structural framework were hypothesized to result from environmental changes induced by the 1982–1983 El Nino Southern Oscillation (ENSO). Reaka-Kudla et al. (1996) suggested that these changes led to increased benthic algal cover and the availability of cryptic habitat, facilitating a biomass increase of the bioeroding sea urchin Eucidaris thouarsii.

Previous studies suggest that bioerosion on deeper reef-fronts (15–50 m) is dominated by boring organisms (Goreau and Hartman, 1963; Perry, 1998; Greenstein and Pandolfi, 2003) and that bioerosion group diversity is lower in deeper reefs (Perry and Hepburn, 2008). Grazing bioerosion is also thought to decrease with depth (Kiene and Hutchings, 1994; Bruggemann et al., 1996; Brokovich et al., 2010). Most modern data used to infer patterns of deep reef bioerosion were obtained on shallow reefs, with occasional sampling of one site along the reef slope deeper than 30 m. No studies have comprehensively or quantitatively analyzed how bioerosional induced framework modification changes along a depth gradient to mesophotic reefs (Hubbard, 2009), or between structurally distinct mesophotic habitats.

The purpose of our study was to determine how bioerosion rates and bioeroding organism distributions vary between MCE habitats of different geomorphology and with shallow-water reef counterparts. This paper describes a two-pronged approach for studying mesophotic bioerosion in mesophotic reefs with varying geomorphology by: (1) comparing time-averaged macroboring of coral rubble; and (2) calculating bioerosion rates of experimental coral substrates exposed for 1 and 2 years.

2. Study area

Although the majority of MCE research has focused on wall and slope habitats (Goreau and Goreau, 1973; James and Ginsburg, 1979; Hubbard, 1989; Grammer and Ginsburg, 1992; Bak et al., 2005), mesophotic reefs also form a variety of distinct geomorphic habitats on deep, nearly horizontal banks, implying the potential for high levels of complexity, diversity, and functionality (Armstrong, 2007; Smith et al., 2010). For the present study, mesophotic bioerosional processes were investigated within distinct geomorphic habitats south of St. Thomas in the northern U.S. Virgin Islands (Fig. 1). The region is part of the broader Puerto Rican Shelf, which contains Puerto Rico, the British Virgin Islands, and the northern U.S. Virgin Islands. The north–south width of the shelf across St. Thomas is approximately 45 km. Adjacent to the southern coast of St. Thomas is an array of shallow patch reefs surrounded by seagrass beds (Smith et al., 2008). As water depths deepen to the south, mid-shelf linear and patch reefs (15–20 m deep) periodically occur within more extensive seagrass habitats. Below 30 m approximately 10 km south of St. Thomas, mesophotic coral growth becomes more prolific, but is surrounded by rhodolith deposits, barren sand, or pavement (Fig. 1). The southern extent of the Puerto Rican shelf is marked by the Anegada Passage, with a maximum depth greater than 2.6 km (Holmes and Kindinger, 1985).

Mesophotic reefs in the Virgin Island region are best developed within the Red Hind Marine Conservation District (MCD) and the Grammanik Bank (Smith et al., 2010). Outlined below are the six sites chosen for the present study. Within the MCD and Grammanik Banks, sites 1–4 consist of structurally distinct MCE habitats identified based on bathymetric geomorphic classifications and biological differences (Smith et al., 2010). We reclassify the water depths of these sites into a transitional mesophotic zone (TMZ), 30–35 m deep, and an upper mesophotic zone (UMZ), 36–50 m deep. Sites 5 and 6 are shallower reefs chosen for comparison. Data from 2007 linear transect surveys (Smith et al., 2007) providing coral cover and amount of exposed consolidated substrate (dead coral, rubble, boulders, pavement, and surfaces covered by macroalgae) are found in Table 1.

Site 1 The primary high bank (Fig. 1b) is best observed along the shelf edge of Grammanik Bank and represents the southernmost mesophotic habitat of the study. It is a narrow width bank with >5 m relief that parallels the margin of the Anegada Passage for over 1 km. Coral cover in 2007 was dominated by living stony coral within the Orbicella annularis species complex (Smith et al., 2007).

Site 2 The secondary high bank (M1 supplementary video), separated by a deep narrow sand channel, parallels the primary bank and exhibits a more continuous trend and broader sloping northern edge than the primary high bank. Maximum relief is over 5 m above the surrounding shelf. Coral cover in 2007 was also dominated by coral within the O. annularis species complex (Smith et al., 2007). The northern edge of the secondary high bank transitions to a flat region (24.5% of the total MCD area) consisting of the hillock and flat basin.

Site 3 The hillock basin (Fig. 1c and M2 supplementary video) is composed of more than 10,000 coral covered semi-conical hills and knolls standing 2–10 m above surrounding sand flats and sparse live coral, extending more than 1 km² on a flat expanse.

Site 4 The deep patch reefs, identified through bathymetry, are located in the northeastern MCD and are each isolated by unconsolidated sandy substrates with occasional algae. The patches have topographic relief less than 5 m and are characterized with high macroalgae cover and low live coral cover compared to the other mesophotic sites, a composition common in other Caribbean MCEs (Fricke and Meischner, 1985; Reed, 1985; Phillips et al., 1990; García-Sais et al., 2008). The coral found at the deep patch randomly selected for our study (Fig. 1d and M3 supplementary video) had a relatively high abundance of Porites and Agaricia, and Manicina areolata. The coral community appeared to be ephemeral opportunists unable to form large colonies as they attach to loose rubble substrate. Additionally, approximately 75% of rubble samples collected from the deep patch were rhodoliths with no identifiable internal coral skeleton.

Site 5 The mid-shelf patch reef selected for our study is located 1 km from the protruding southeastern most part of St. Thomas. Separated from adjacent reefs by at least 1 km of unconsolidated sand and rhodolith beds, this isolated patch reef is 18–24 m below sea level. The coral reefs rises about 7 m above a surrounding sand apron and consists of a diverse coral community dominated by the O. annularis species complex.

Site 6 The shallow fringing patch reef selected for our study is partially-isolated, just offshore in Perseverance Bay, west of Black Point.
The reef consists of a sparse coral community dominated by *Siderastrea siderea*, *S. radians*, and *Porites astreoides*.

Antecedent platform theory suggests that any bank, located within the circum-equatorial coral reef zone at a proper depth, is a potential site for coral reef development (Hoffmeister and Ladd, 1944). Hubbard et al. (2008) suggested an absence of late Pleistocene reef buildups in the Virgin Island region due to rapid sea-level rise and high southerly off-shelf sediment transport, but the necessary seismic surveys and coring studies have not yet been done to determine the relationship between potential antecedent topography and the modern mesophotic reefs south of St. Thomas. This does not preclude the possibility that the modern mesophotic reefs of St. Thomas are built up on earlier (10,000–7000 yr. BP) shallow-water Holocene reef deposits.

3. Material and methods

3.1. Macroboring of coral rubble

In August 2010, technical research divers utilizing decompression and tri-mix techniques conducted an opportunistic collection of exposed random-sized rubble (3–30 cm in diameter), south of St. Thomas, USVI (Fig. 1). Rubble was defined as hard substrate unattached to the underlying reef framework (Rasser and Riegl, 2002). After collection, each sample was soaked overnight in a dilute bleach solution (~1:3 bleach to water), rinsed in fresh water, and dried in the sun for 2 days. Dried coral rubble was cut into slices parallel to the primary growth axis and identified to species. After being cut, samples identified entirely as coralline algae rhodoliths (primarily from the deep patch site) were not included in any subsequent analyses. From the six reef sites, 44 useable coral rubble samples were analyzed (4–8 samples/site).

Digital photographs were taken of each cut surface, from which spatial coverage and abundances of macroborings were determined by point-count analysis (Perry, 1998; Macdonald and Perry, 2003). For each sample, three randomly selected non-adjacent surfaces were evaluated using Coral Point Count with Excel Extensions V3.6 (Kohler and Gill, 2006). Results from each of the three slices were averaged. The excavations produced by endolithic boring organisms were identified using published descriptions (Pang, 1973; Rützler, 1974; Bromley, 1978; Rice and Macdonald, 1982; Scott and Risk, 1988; Macdonald and Perry, 2003). Classification was restricted to the categorical groups of sponges, worms (polychaete and sipunculan), bivalves, other (boring
The experimental design used to determine bioerosion rates was modified from Kiene (1988). By-product cores drilled through healthy colonies of Orbicella annularis 2 m deep in the Florida Keys (Hudson, 1977) were used to create experimental coral substrates (Fig. 3) that all share similar material properties. Following a visual inspection to eliminate previously eroded substrates, cylindrical cores of pristine coral skeleton 9.4 cm in diameter were cut into disks approximately 2 cm thick. After drilling a hole through the center, the disks were washed, dried in an oven for 2 days at 55 °C, assigned a sample number, and photographed. A total of 216 pristine coral substrates, simulating newly available bare coral framework, were deployed. Sets of 12 randomly selected disks were mounted with nylon nuts on top and spacers below to one of 18 PVC quadrats (Fig. 3a). In August 2010, divers used reinforced steel to anchor three quadrats, with the coral disks parallel to seafloor, at each site. The first quadrat at each habitat was semi-randomly installed based on where divers first dropped onto the reef. The other two quadrats were attached to the seafloor approximately 10 m apart in random directions from each other. Three randomly pre-selected disks from each quadrat were scheduled for collection once a year for 3 years (Fig. 3b,c), with a final collection scheduled 10 years after deployment.

The first and second substrate disk collections occurred in August 2011 and May 2012 (Fig. 3b,c). Collected substrate samples were soaked in a weak bleach solution for up to 2 days before being air-dried. Prior to weighing, samples were oven dried at 55 °C for an additional 2 days. A small number of samples were eliminated from analysis due to damage during transport, or incorrect documentation (Table 1). Differences in mean weight change of substrate disks (Fig. 3d–f) were compared with a nested two-way factorial ANOVA conducted in JMP 10.0 (SAS Institute Inc., 2012) with year of collection and site as crossed factors and quadrat nested within the site factor. Data were transformed with a natural logarithm to meet assumptions of homogeneity of variances. Significant site differences among substrate weight change means within factors were tested with a Tukey's post-hoc HSD test. The relationship between substrate weight change and other explanatory variables was tested in R Version 2.15.0 (R Core Development Team, 2009) with a Pearson correlation and linear regression.

4. Results

4.1. Coral rubble

Site average amount of macroboring excavation (Fig. 4) was highest in coral rubble collected from the mesophotic sites closest to the Anegada Passage (43.0–46.1%) and lowest at the deep patch site (18.7%), where many samples were encased by coralline algae (Fig. 2b). A one-way analysis of variance (ANOVA) indicated significant differences in the average percentage of rubble excavated by macroboring collectively between all sites ($F_{5,43} = 6.248, P < 0.0003$), with Tukey's pairwise indicating macroboring significant differences (between sites 1, 2 and 3 with 6, and 1, 2 and 3 with 4). Sponge borings, which showed significant differences between the sites ($F_{5,43} = 3.465, P = 0.012$), were the most abundant macroboring group at all sites, ranging from 88.5% at the primary high bank to 47.0% at the shallow fringing patch site (Fig. 4). Worms were the next most common macroboring at all sites except the deep patch site. Overall, the shallow fringing patch reef had the most diverse macroboring assemblage (sponges, worms, bivalves), and the largest contribution of gastropod
4.2. Parrotfish and Diadema antillarum abundance

Transect surveys showed the site-average biomass of the bioeroding parrotfish S. vetula and S. virde ranged from 0 g/100 m² at the deep patch site to 578.17 g/100 m² at the secondary high bank site (Fig. 6). Excavating parrotfish biomass was significantly different between study sites (Kruskal–Wallis, $df = 5, X^2 = 15.23, P < 0.0094$). There were no detectable significant differences between means with Tukey’s HSD post hoc comparison; however, there was a trend of increasing biomass at the shallow sites and the deep secondary bank. *Diadema antillarum* only occurred at three of the study sites, and mean densities never surpassed 2 per 100 m² (Smith et al. 2012; shallow fringing patch = 1.15 ± 0.74 SE, $n = 61$; mid-shelf patch = 0, $n = 75$; deep primary bank = 0, $n = 75$; deep secondary bank = 0, $n = 72$; deep hillock basin = 0, $n = 6$; deep patch = 0, $n = 4$).

4.3. Substrate bioerosion

The weight change of coral substrates provides a proxy for framework carbonate modification through bioerosion and encrustation. To directly compare bioerosion at different locations, we used uniform substrate with similar material properties and subsequently eliminated differential substrate composition as a variable. However, these also induced limitations, as the substrates were not composed of a dominating mesophotic coral but a shallow form with material properties different than that of coral naturally found at the mesophotic sites. Therefore, all conclusions from the resultant data must be considered specific for the particular substrate used.

Analysis showed significant differences in substrate weight change between sites (Fig. 7) among various factors ($df = 23, F = 7.30, p < 0.0001$). Comparison of means showed that the site, year, and nested quadrat factors were all significantly different among groups, whereas year and the year × site interaction were not significant (Table 2). This indicated that weight change was not consistent across sites and that the rate of weight change increased from year 1 to year 2, except at the deep patch. The significant nested quadrat factor also indicated that experimental quadrats behaved differently within the sites, suggesting inter-site differences in bioerosion potential. Experimental substrates at the two shallower sites and the shallowest mesophotic site had negative rates of average substrate weight change (weight loss) not significantly different from each other. In contrast, the primary bank, deep patch, and hillock basin sites initially experienced small weight gains that were not significantly different from one another, but were significantly different from the shallower sites.

Inspection of sliced experimental substrates revealed few macroborings in the first year and only slightly more in the second year, with bivalves and worms primarily responsible for the macroborings observed at all sites. There was also significantly more colonization of bio-accreting calcareous organisms on experimental substrates collected from the reefs in the UMZ compared to substrate disks from the shallower sites. A full quantitative analysis of macroboring abundance and bioaccretion will be conducted following the third year of sample collection.

To better understand patterns of substrate modification, the average weight change at each site was compared to: (1) water depth; (2) coral rubble macroboring; and (3) grazer biomass. A strong correlation was found between average substrate weight change and water depth ($n = 6, r = −0.866, p = 0.026$) after 1 year of exposure (Fig. 8). The relationship becomes less obvious after 2 years of exposure ($n = 6, r = −0.744, p = 0.090$); however, removing the secondary high bank samples (Fig. 8) greatly increased the correlation ($n = 5, r = −0.966, p = 0.008$). Despite no significant correlation between the rate of average experimental substrate weight change and average coral rubble macroboring per site (year 1: $n = 6, r = 0.055, p = 0.918$; year 2: $n = 6, r = −0.137, p = 0.796$), a linear regression relationship between the rate of experimental substrate weight change and average measured bioeroding parrotfish biomass per site (Fig. 9) was nearly significant after 1 year of exposure ($n = 6, R^2 = 0.832, p = 0.059$).
Fig. 4. Schematic cross section of Southern Puerto Rican Shelf, indicating the location of each study site and corresponding values of averaged percent of total macroboring and percent abundances of macroboring groups per site (lower). Error bars equal ±1 standard error. Values displayed on each bar provide number of coral rubble samples used to obtain site average.

Fig. 5. Relationship between water depth and site average percent coral rubble excavated by macroborings. Error bars equal ±1 standard error.

Fig. 6. Average biomass of bioeroding parrotfish Sparisoma viride and Scarus vetula per site. Values displayed on each bar provide number of transects used to calculate site mean. Error bars equal ±1 standard error.
and significant after 2 years of exposure, with the measured bioeroding parrotfish biomass explaining a moderately high amount of weight change variability ($n = 6, R^2 = 0.674, p = 0.045$).

5. Discussion

5.1. Grazing

Two years of substrate weight change (Fig. 7) clearly indicate a major bioerosional difference between mesophotic reefs and that initial bioerosion generally decreases with depth, results consistent with previous studies (Stearn and Scoffin, 1977; Kiene, 1988; Chazottes et al., 1995; Tribollet et al., 2002). The limited number of macroborings observed in all substrate disks suggests that virtually all weight change was a result of substrate grazing and bioaccretion. Due to the minimal occurrence of $D. antillarum$ within our study area and the moderate relationship between excavating parrotfish biomass and substrate weight loss (Fig. 9), we conclude that parrotfish grazing is the dominate initial bioeroder of coral reefs down to the TMZ in the USVI and that reduction of fish biomass explaining a moderately high amount of weight change variability ($n = 6, R^2 = 0.674, p = 0.045$).

5.2. Macroboring

Macroboring requires a minimum exposure time of 2–5 years before site differences are observed (Hutchings et al., 1992; Kiene and Hutchings, 1993, 1994; Chazottes et al., 1995; Pari et al., 2002; Tribollet et al., 2002). Therefore, coral rubble offers the best record of long-term macroboring modification within a reef. However, the taphonomic effects of exposure time and sample age, initial framework bioerosion, rubble transport, and collection randomness can skew interpretations, constituting a fundamental “coral rubble problem” that must be addressed. A random sampling of mesophotic coral rubble in reefs with similar coral distributions (except the deep patch) ensured that on average, the same types of coral species were sampled. We can classify the collected mesophotic coral rubble from the USVI as a longer-term time-averaged inventory of macroboring activity experienced at the particular collection site for multiple reasons. Although rubble exposure time is unknown, the average amount of macroborings in collected mesophotic rubble is significantly greater than in all experimental substrates, increasing the rubble potential time-average span. Trends in sedimentation, sediment transport, and bathymetry also imply longer exposure times and the likelihood of collection from the original taphonomic “active” zone (not buried then re-exposed). With MCD sedimentation rates of 0.316 mg cm$^{-3}$ day$^{-1}$, almost 50 times lower than near-shore rates (Rothenberger et al., 2008), and located on bathymetric highs along a very gradual slope over 10 km from shore, the mesophotic sites are unlikely to harbor allochthonous downslope transported rubble or experience significant burial. It has been suggested that slower growth rates of deeper corals lead to lower sedimentation rates. Pandolfi and Greenstein (1997) corroborate our arguments, suggesting the potential for long-term mesophotic coral rubble exposure.

Coral rubble analysis in the USVI showed that the average percent of exposed rubble carbonate removed by macroborers usually increases in dense mesophotic corals, potentially because bioerosion is thought to increase with longer exposure time (Scoffin et al., 1980). These results

![Figure 7](image)

**Fig. 7.** Weight change of experimental substrates with time. Error bars equal ±1 standard error of the average from each quadrat. Slope of the lines provide rates of bioerosion between 0–1 year and 1–2 years.

| Table 2 |
|--------------|------------|-------------|-----------------|--------------|-----------|--------------|-----------|-------|
| Factor     | df | $F$ value | $P$ value | Secondary bank | Fringing/patch | Mid-shelf patch | Primary bank | Hillock basin | Deep patch |
| Apricot | 12 | 3.48 | <0.0004 | A | A | A | B | B | B |
| Year | 1 | 9.54 | 0 | A | A | A | B | B | B |
| Site | 5 | 21.27 | <0.0001 | A | A | A | B | B | B |
| Year × site | 5 | 1.81 | 0.12 | A | A | A | B | B | B |

Statistical results of a nested two-way factorial ANOVA comparing the weight change with collection year and site factors and quadrat nested within site factor. Post-hoc results are given for the site factor. Sites with different letters were significantly different.
do not contradict the statement that total initial bioerosion decreases with depth, as several studies show grazing initially removes much more carbonate than macroboring (Kiene and Hutchings, 1994; Chazottes et al., 1995; Reaka-Kudla et al., 1996; Perry et al., 2012). Using dead coral framework and coral rubble, studies in Jamaica found macroboring infestation highest in the deeper fore-reefs compared to shallow fore-reefs (Perry, 1998; Macdonald and Perry, 2003), and other non-experimental substrate studies documented higher macroboring in deeper reef-fronts than shallow fronts (Goreau and Hartman, 1963; Greenstein and Pandolfi, 2003).

Grazing intensity has also been suggested to partially regulate macroboring community succession by creating new available substrate for macroborer recruitment (Kiene and Hutchings, 1994); however, it is uncertain if this is more beneficial for recruitment of coral or bioeroders. Regardless, Sammarco et al. (1987) found that different levels of grazer accessibility alter the composition of bioerosional communities. Macroboring communities mature with increasing substrate age, starting as immature communities of small, short-lived worms, followed by longer-lived larger worms, sipunculans, mollusks, and finally mature boring sponge communities (Hutchings et al., 1992; Kiene and Hutchings, 1994; Hutchings, 2008). With higher sedimentation rates, faster coral growth rates, and more storm disturbances and branching coral, the time-average age of shallow reef coral rubble is likely to be much younger than deep rubble (Perry and Hepburn, 2008). Results from our study indicate that the coral rubble macroboring community is primarily mature at the mesophotic reef sites, intermediate at the mid-shelf patch, and immature at the shallow site, where rapid substrate grazing, along with a suggested shorter exposure time probably limits the time needed to establish mature bioerosional communities. This explanation is more complex when considering the secondary high bank, where coral rubble macroboring is similar to other mesophotic sites but still harbors the highest biomass of parrotfish and has the greatest experimental substrate weight loss. We speculate that processes differentiating shallow and mesophotic bioerosion are less defined at this location, where the deepest shallow water conditions meet the very shallowest mesophotic depths. The high parrotfish biomass is likely due to the fact that this site is a marine protected area and experiences fast bottom currents, facilitating high productivity attractive for parrotfish (Smith et al., 2012).

Although parrotfish grazing appears to be the primary initial bio-modifier of reef framework down to the TMZ, data suggest that macroboring is the main process responsible for most reef framework long-term modification in the UMZ. This trend is reasonable when considering the lack of grazing disturbance and longer rubble exposure time in the UMZ, along with the likely assumption that mesophotic reefs usually sustain low impact from wind-generated waves (Goldberg, 1983). Pacific experimental substrate studies found no boring sponges for up to 1.5 or 3 years (Davies and Hutchings, 1983; Kiene, 1988; Chazottes et al., 1995). However, they predicted that longer exposure times would allow for boring sponge recruitment, given extensive sponge excavation in nearby coral heads. With similar coral rubble observations in our study (Fig. 2), we assume that sponge erosion in mesophotic experimental substrates will increase with time. This assumption and results from our study and others implicating sponges as the most common and destructive coral macroborer group (Goreau and Hartman, 1963; Hein and Risk, 1975; Highsmith et al., 1983; Risk et al., 1995; Glynn, 1997; Holmes, 1997; Perry, 1998) lead us to suggest that sponges are likely the chief macroborers responsible for long-term substrate modification in and below the UMZ, despite the short 2 year exposure time that allowed for minimal immature bioerosional community development and no sponge borings. Whereas the same outcome would initially be true for coral rubble, sufficient time eventually passed so that the dominant endolithic boring group could infiltrate and allow multiple episodes of sponge bioerosion to erase nearly all traces of the initial immature community (Focke and Gebelein, 1978; James and Ginsburg, 1979). This may also explain why our results show that coral rubble macroboring group-diversity decreases with depth (Perry and Hepburn, 2008).

![Fig. 8.](image) Relationship between mean bioerosion parrotfish biomass and rates of substrate weight change at each site after 1 year (diamonds) and year 2 (circles). Numbers in shapes distinguishes sites. Vertical and horizontal error bars equal ±1 standard error.

![Fig. 9.](image) Comparison between mean bioerosion parrotfish biomass and rates of substrate weight change at each site after 1 year (diamonds) and year 2 (circles). Numbers in shapes distinguishes sites. Vertical and horizontal error bars equal ±1 standard error.
5.3. Bioerosion variability between mesophotic habitats

When utilizing coral rubble of comparable composition, and homogeneous experimental substrates, our results show similar mesophotic long-term coral rubble macroboring patterns and similar initial UMZ bioerosion rates, regardless of depth or structural habitat. Yet, despite significant initial substrate bioerosion rate differences between the TMZ and the UMZ, there is no evidence to suggest that these differences either result from or cause variability in mesophotic geomorphology. Homogeneous experimental substrates were used to limit variables and focus primarily on bioerosion. But composition and amount of available substrate are not always similar for nearby mesophotic reefs, as best observed at the rhodolith-rich deep patch site sparsely covered with live coral. The only non-rhodolith skeletal rubble samples retrieved after multiple collections were of *M. areolata* and *Mycetophyllia aliciae*, coral with skeletal densities much lower than the coral rubble collected at other mesophotic sites. This skewed the deep patch rubble results towards low levels of macro boring, as endolithic sponges are able to remove more carbonate from denser coral than from less dense, more porous coral (Highsmith, 1981; Highsmith et al., 1983; Schönberg, 2002). Additionally, deep patch coral rubble was often encased in coralline algae (Fig. 2b), creating a protective coating believed to block endolithic surface access holes and limit macroboring infiltration beyond the algal layers into the coral (Bromley, 1978; Peyrot-Clausade and Bruno, 1990).

Although the distinct structure of mesophotic habitats may not be due to differences in bioerosion directly, we propose that the mesophotic bioerosion impact on maintaining or at least exaggerating differences in habitat geomorphology will depend on how the interaction of similar bioerosional conditions change for habitats that vary in composition and other parameters. Reef differences in position and exposure time of available substrate, and in benthic recruitment patterns change the amount of coral rubble and *in situ* coral framework available for bioerosion and new coral colonization (Perry and Hepburn, 2008).

The amount of available substrate for erosion and colonization can vary between mesophotic sites (Table 1) and can be influenced by disturbances, potentially impacting the overall effect of bioerosion (Pang, 1973; Highsmith et al., 1983; Kiene, 1988).

For example, coral skeleton examined from the hillock basin verified a history of multiple die-off events, probably related to intercotsal mortality syndrome, an abiotic extreme disease event documented as preferentially occurring at the hillock basin compared with other mesophotic sites (Smith et al., 2010). Surveys after the outbreak showed significantly more substrate available in the hillock basin than even the shallowest reef sites. Therefore, a possible scenario for hillock development could entail that disease events produced new available substrate that may promote coral colonization and episodic vertical hillock accretion while lower initial bioerosion rates and slow water currents (Smith et al., 2010) may prevent rubble from breaking off the hillocks into the surrounding sand. Formation of a more homogeneous reef geomorphology may become more difficult without these new areas for coral colonization between the hillocks. An alternative scenario for lateral homogenous mesophotic reef extension may partially depend on if bioerosion helps create new coral rubble without eroding it away completely. Faster currents recorded at the primary and secondary high banks (Smith et al., 2010) and similar amounts of available substrate (Table 1) may partially explain the maintenance of similar trending lateral bank geomorphology. If currents are strong enough to dislodge framework weakened through bioerosion, they may be colonized in an orientation following the local water currents that carry coral larvae. However, more mesophotic data on the regulation of factors such as recruitment patterns, rubble production, and habitat composition, as well as longer rates of mesophotic sponge bioerosion are needed to fully assess the impact bioerosion may have on the long-term structural sustainability of mesophotic reefs.

6. Conclusion

Like shallow reefs, mesophotic coral ecosystems are three-dimensional structures built up from the skeletons of marine organisms. This paper presents one of the first comprehensive mesophotic reef bioerosional studies, specifically comparing bioerosion variability between multiple mesophotic reefs with distinctive geomorphologies and with adjacent shallow reefs south of St. Thomas, USVI. Results suggest differences in both initial bioerosion and long-term coral rubble macroboring between mesophotic reef habitats, and also with their shallow-water counterparts. The general pattern of increasing coral rubble macroboring and lower macroborer community diversity with depth is attributed to relationships between substrate grazing patterns, bioerosional community succession, and lengthy substrate exposure time. Despite this general pattern, initial USVI bioerosion rates are generally believed to decrease with depth partially as a result of decreasing bioeroding parrotfish biomass. We suggest that substrate modification in UMZ reefs is fundamentally different from that in shallower reefs, with macroboring sponges believed to be the main long-term UMZ substrate modifiers. Variability in mesophotic bioerosion rates may be more related to varying distributions and amounts of available substrate, dependent on localized environmental conditions and disturbances. Bioerosion likely exaggerates the effects of variable substrate distribution and availability, thus continuing to increase structural diversity between reefs. Our study extends the knowledge of initial carbonate substrate modification to mesophotic reef depths. However, mesophotic sponge bioerosion rates are needed to compare to mesophotic coral growth rates, and more data are needed to determine the relationships between bioerosion, substrate type, availability, distribution, and colonization patterns to better understand mesophotic reef structural modification and how it influences overall ecosystem development.

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Appendix A. Supplementary data

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References
