Habitat heterogeneity reflected in mesophotic reef sediments

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Abstract

Modern reef sediments reflect the physical and chemical characteristics of the environment as well as the local reef fauna. Analysis of sedimentary reef facies can thus provide a powerful tool in interpreting ancient reef deposits. However, few studies have attempted to differentiate sedimentary facies in mesophotic coral ecosystems, low light habitats defined as residing 30-150 m below sea level. The low-angle shelf mesophotic coral ecosystem south of the northern U.S. Virgin Islands (USVI) consists of reefs with

24 different structural characteristics ideal for studying the relationship between habitat
25 complexity and sedimentary facies. Textural, compositional, and geochemical analysis of
26 surface sediment were used to identify mesophotic reef subfacies associated with distinct
27 benthic communities and structural habitats. Sediment grain composition and bulk
28 geochemistry were found to broadly record the distribution and abundance of coral and
29 green algae communities, foundational mesophotic reef benthic organisms.
30 Sedimentological analyses indicates that hydrodynamic forces do not transport a
31 significant amount of allochthonous sediment or potentially harmful terrigenous material
32 to USVI mesophotic reefs. Episodic, maximum current velocities prevented deposition of
33 most silt-size grains and smaller, but biological processes were found to have a greater
34 influence on subfacies partitioning than hydrodynamics processes. Results provide a new
35 analogue for studies of ancient mesophotic coral ecosystem geological history and
36 document the relationship between mesophotic reef subfacies, structural complexity, and
37 habitat heterogeneity. They also demonstrate how mesophotic reefs along the same shelf
38 system do not always share similar sedimentary characteristics and thus record a diverse
39 set of ecological and environmental conditions.

40

41 **Keywords:** mesophotic coral reefs, sedimentary facies, U.S. Virgin Islands, bioerosion,
42 stable isotopic analysis

43

44 **Abbreviations**

45 MCE: mesophotic coral ecosystem

46 USVI: United States Virgin Islands

47 ADCP: Acoustic Doppler Current Profilers

48 ANOVA: one-way analysis of variance test

49 HSD: Honestly Significant Difference

50 TCRMP: US Virgin Islands Territorial Coral Reef Monitoring Program

51 NMDS: non-metric multidimensional scaling

52

53 **Study site abbreviations**

54 D1: Hillock Basin

55 D2: Deep Patch

56 D3: Primary Bank

57 D4: Secondary Bank

58 M5: Mid-shelf Patch

59 S6: Fringing Patch

60

61 **1. Introduction**

62   Studies documenting the taxonomic richness of mesophotic coral ecosystems
63 (MCEs) suggest that biodiversity is a major ecosystem attribute (Cerrano et al., 2010;
64 Lesser et al., 2010; Bridge et al., 2012). Along with macroalgae and sponges, the benthic
65 coverage of mesophotic reefs (30-150 m deep) is dominated by light-dependent
66 scleractinian corals (Lesser et al., 2009). As a photo-adaptation to reduced illumination,
67 mesophotic corals commonly display an overall platy morphology (Fricke et al., 1987;
68 Lesser et al., 2010) similar to what has been found throughout the scleractinian fossil
69 record in environments interpreted as calm and deep (Rosen et al., 2000). The plasticity
70 of modern coral for altering algal symbiosis reliance (Baker et al., 2004) may have
71 evolved early in scleractinian history (Stanley and Fautin, 2001) and affected their ability
72 to survive major extinction events (Veron, 1995). Sedimentary facies analyses have been
73 conducted on a number of ancient mesophotic reef systems (Mesolella et al., 1970;
74 Insalaco, 1996; Dill et al., 2012; Mateu-Vicens et al., 2012; Abbey et al., 2013; Novak et
75 al., 2013; Mihaljević et al., 2014). However, few detailed modern analog studies exist to
76 improve interpretations of ancient MCE reef deposits, and no study has analyzed

77 sediment from multiple mesophotic reef habitats on a low-angle carbonate platform. This
78 limits our knowledge of mesophotic reef evolutionary history and the origins of reef
79 biodiversity.

80   In shallow reef environments, biodiversity is promoted by ecologically diverse
81 habitats fostered by a spectrum of tidal and wave energy conditions and by habitat
82 modifying species that increase structural complexity, alter hydrodynamics, and increase
83 overall habitat surface area (Connell, 1978; Roberts and Ormond, 1987; Bruno and
84 Bertness, 2001). Structural complexity increases biodiversity and habitat heterogeneity
85 by providing areas with reduced environmental stress needed for other organisms to
86 thrive (Thompson et al., 1996) and by improving propagule retention (Eckman et al.,
87 1989). Direct correlations between habitat heterogeneity, fish diversity, and shallow-
88 water reef structural complexity (Roberts and Ormond, 1987; Dustan et al., 2013) and the
89 negative affect global warming is projected to have on reef rugosity (Bozec et al., 2014)
90 emphasize the importance of protecting reef architectural complexity (Dryden et al.,
91 2012). However, little is known about the role of habitat heterogeneity and structural
92 complexity in mesophotic reefs, including their relationship to sedimentary processes and
93 the extent that depositional processes can identify distinct habitats.

94   The mesophotic reefs of the U.S. Virgin Islands (USVI) developed on a low-
95 angle reefal margin that provides space for differing architectural features. Here we
96 present a detailed characterization and interpretation of sediment found within distinct
97 mesophotic reef habitats. Our objectives were to: (1) resolve if low gradient shelf
98 mesophotic reef systems produce recognizable sedimentary facies that reflect structurally
99 distinct reef habitats; and (2) determine the significance of these potential facies
100 differences in terms of biological and hydrodynamic processes. The ability to identify
101 causes and indicators of habitat heterogeneity and structural complexity in modern MCEs
102 is a critical first step in understanding the evolution, development, and maintenance of

these attributes in ancient reef systems and the origins of modern biodiversity patterns (Flügel and Flügel-Kahler, 1992; Renema et al., 2008; Morsilli et al., 2012).

2. Materials and methods

2.1. Study Sites

Four upper mesophotic (30-60 m) reef habitats (sites D1-D4) with different geomorphology and biological characteristics (described by Smith et al., 2010) were sampled from the Red Hind Marine Conservation District and Grammanik Bank, located on the Puerto Rican shelf, 9.9-15.2 km south of St. Thomas, USVIs (Fig. 1). Two additional reefs (sites M5 and S6) were sampled for shallow-water comparison. Coral cover varied depending on habitat in 2007, but approximately 66.8% of the Red Hind Marine Conservation District was composed of adjacent coral reefs shallower than 50 m (Smith et al., 2010). *Orbicella* spp. was the dominant coral type in the Red Hind Marine Conservation District with a relative coral cover greater than 90%, although Smith et al. (2010) still found high hard coral species richness (37 scleractinian coral and hydrocoral species). The sites at the narrow (<0.5 km) Primary Bank (D3) and the wider (>1.5 km) Secondary Bank (D4) are the shallowest mesophotic reef sites (39.0 m and 30.7 m respectively), have the highest coral cover (>30%), and are geographically closest to the Anegada Passage. The site at the Hillock Basin (D1), north of the Secondary Bank, is located on a deeper (44.5 m) flat expanse, partially composed of thousands of semi-conical knolls. Westward from the hillocks are a series of low-relief “patches” with low coral cover and abundant rhodolith growth, one of which hosts the selected Deep Patch site (D2) at 41.1 m. The sites at the Mid-shelf Patch (M5) and the Fringing Patch (S6) are closer to shore than their deep-reef counterparts (.08-1.1 km) and reside at depths of 21.0 m and 9.0 m respectively.

In August 2011, technical divers collected 3-6 replicate samples from the top 3 cm of sediment at each study site (n=28). All samples were washed with distilled water

129 and dried prior to analysis. Representative living framework samples of *Orbicella* spp.
130 were taken near three of the mesophotic sites (D1, D3, D4) for isotopic comparison to
131 bulk sediments. Sediment samples from sites D2, D3 and D4, were collected in the
132 vicinity of Nortek Aquadop Acoustic Doppler Current Profilers (ADCPs), which recorded
133 hourly current velocities 1.5-2.5 m above the seafloor. ADCP measurements from a
134 nearby (1.36 km) site (Hind Bank from Smith et al., 2010) were used as a proxy for the
135 Deep Patch (D2) site. The average of each spring-neap tidal cycle current velocity mean
136 and maximum were calculated from 1 February 2008 to 31 January 2009 for sites D1-D3
137 (Table 1), and subdivided to distinguish summer (May-November) and winter
138 (December–April) trends (Electronic Supplementary Material, ESM Table 1). Secondary
139 Bank (D4) current data were only available from 20 May to 26 September 2014 (Table
140 1). Assuming a bed roughness length (z_0) of 0.3 mm (Soulsby, 1997), the von Karman-
141 Prandtl law-of-wall equation (with $\kappa = 0.4$) was used to calculate shear velocity (u_*) for
142 each hourly recorded current velocity. The equation was then used to recalculate the site
143 average spring-neap tidal cycle current velocity maximums to account for boundary layer
144 conditions $z = 25$ mm above the seafloor.

145 2.2. *Sediment Composition*

146 To quantify sediment composition, three sediment samples per site were passed
147 through a 2 mm mesh sieve, impregnated with resin, and thin-sectioned. Standard point-
148 count analysis was conducted on a minimum of 300 points per thin section using the
149 JmicroVision program (Roduit, 2008). Grain classifications were based on literature
150 descriptions (Ginsburg, 1956; Pusey, 1975; Scholle, 1978; Adams et al., 1984). Data
151 were corrected with the arcsin transformation, and one-way analysis of variance
152 (ANOVA) tests were conducted to determine significant univariate differences per site.
153 Specific pair-wise differences were identified using Tukey's Honestly Significant
154 Difference (HSD) multiple comparison test. Pearson's correlations were used to compare
155 sediment types with depth. Benthic coverage data lacked a normal distribution so

156 Spearman's correlations were used to compare the relative sample (3 per site) percentage
157 of coral, green algae, and red algae grains with the grain-equivalent average benthic cover
158 (coral and algae) at the sample collection sites (samples from the same sites were
159 compared to the same site average benthic cover values). Spearman's correlation was
160 also used to compare the relative sample percent of coral mesophotic sediment with
161 adjusted bioeroding parrotfish biomass, which lacks a normal distribution (from
162 Weinstein et al., 2014). Average benthic cover (protocol after Smith et al., 2008 and
163 Smith et al., 2010) and rugosity measurements (3 m chains; Luckhurst and Luckhurst,
164 1978) were obtained from the United States Virgin Islands Territorial Coral Reef
165 Monitoring Program (TCRMP; Table 1) in 2012, except for benthic cover at D1 (obtained
166 in 2007), and rugosity at D3 and M5 (obtained in 2011). Statistical testing was conducted
167 using the program R version 3.0.3 (R Core Team, 2014). Overall site differences were
168 visually assessed by non-metric multidimensional scaling (NMDS) of the Bray-Curtis
169 dissimilarity index using the PAST statistical software package (Hammer et al., 2001).

170 *2.3. Stable Carbon and Oxygen Isotopes*

171 Sediments from 26 samples that passed through a 2 mm mesh sieve were ground
172 in preparation for analysis. The bulk stable oxygen and carbon isotope ratios of both
173 sediment and coral samples were determined by the common acid bath method (Swart et
174 al., 1991). Phosphoric acid dissolution of ground samples (~0.5-1 mg) produced gas
175 analyzed with a Finnigan-MAT 251 mass spectrometer at the University of Miami Stable
176 Isotope Laboratory. Results were corrected for isobaric interferences (Craig, 1957) and
177 reported relative to the standard Vienna Pee Dee Belemnite. Replicate error analysis of
178 inorganic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ standards produced a standard deviation <0.1‰. Significant
179 univariant site differences were tested using one-way ANOVA and Tukey's HSD tests.
180 Pearson's correlations were used to compare $\delta^{18}\text{O}$ with $\delta^{13}\text{C}$, and also to compare isotope
181 concentrations with axis 1 of the grain composition NMDS ordination. Linear regression
182 was used to compare surface sediment bulk isotopic composition directly with the percent

183 of coral grains in corresponding sediments. The program R version 3.0.3 (R Core Team,
184 2014) was used for all isotope statistical analysis.

185 2.4. Grain Size Analysis

186 Standard wet sieving techniques (mesh sizes 4, 2, 1, 0.5, 0.25, 0.125, and 0.63
187 mm) for grain size analyses (Folk, 1974) were used on ~5-20 g of all samples (n=28).
188 Standard textural parameters (mean grain size, sorting, skewness, and kurtosis) were
189 obtained using the program GRADISTAT (Blott and Pye, 2001). One-way ANOVA and
190 Tukey's HSD tests were used to assess site variance with R version 3.0.3 (R Core Team,
191 2014).

192 To investigate allochthonous sediment deposition potential, settling velocities
193 (w_s) of unconsolidated suspended sediment grains were modeled using the empirically
194 derived formula of Soulsby (1997):

195

$$196 \quad w_s = \frac{v}{d} \left[\left(10.362 + 1.049 * \left[\frac{g(\frac{\rho_s}{\rho_f} - 1)}{v^2} \right]^3 \right)^{\frac{1}{2}} - 10.36 \right], \text{ where}$$

197

198 dynamic viscosity (μ) = 1.08 poises

199 fluid density (ρ_f) = 1.023 g/cm³ (Millero et al., 1980)

200 grain (sphere) density (ρ_s) = 1.850 g/cm³ (from Kench et al., 1998)

201 acceleration due to gravity (g) = 9.81 m/sec²

202 kinematic viscosity of water $v = \frac{\mu}{\rho_f}$

203

204 As all sample grain sizes were relatively small, modeling could be simplified by
205 applying equations derived for regular quartz grains (Prager et al., 1996).

206 Constants were calculated using a representative depth, temperature, and salinity of 40.5

207 m, 27.9 °C, and 35.577 ppt. The calculated w_s for unconsolidated fine sand (125 μm),
208 very fine sand (104.4 μm), and sponge chips (mean diameter of 40 μm , Rützler, 1975)
209 were 0.677 cm/s, 0.477 cm/s, and 0.072 cm/s, respectively. Settling velocities were
210 divided by u_* to determine the percent of time that currents were slow enough to permit
211 the fall of suspended particles (when $w_s/u_* \geq 1.25$; Cheng and Chiew, 1999), assuming
212 minimal baffling for depths ≤ 2.5 m above the seafloor.

213 2.5. *Currents of Removal*

214 Sieve-based grain size analysis was used to provide better comparisons with
215 ancient reefal deposit analyses. Application of carbonate sediment sieve analysis is
216 questionable, however, when interpreting hydrodynamic processes (see Kench and
217 McLean, 1997). Therefore a “currents of removal” approach (Kench, 1998) for
218 determining potential mobility was used to examine surface sediment erosion and
219 transport. To comply with potential mobility analysis assumptions, the sieve sizes were
220 converted to equivalent spherical quartz settling velocities (Gibbs et al., 1971). Assuming
221 an average grain density of $\rho_s = 1.850 \text{ g/cm}^3$ (Kench and McLean, 1996), equivalent w_s
222 values were multiplied by a corrective factor ($R_D = 0.98$; Komar, 1981), and converted to
223 the standard settling velocity chi (χ) parameter (May, 1981). Original weights associated
224 with the equivalent sieve settling velocities were plotted as mean cumulative settling
225 velocity distribution curves for each site.

226 When defining threshold velocity as the average velocity recorded 25 mm above
227 a flume bottom needed to move 50% of a heterogeneous reefal sediment fraction, Kench
228 and McLean (1996) suggested sediment fraction mobility could be characterized by a
229 mean settling velocity. The threshold curve derived by Kench and McLean (1996) was
230 assumed to be an accurate proxy because USVI sediment had similar compositional
231 characteristics to the sediment used to develop the threshold curve. Recalculated average
232 spring-neap tidal cycle current velocity maximum values (25 mm above the seafloor)

were plotted as the independent variable of an asymptotic convex regression equation fitted to the threshold curve from Kench and McLean (1996). The resultant dependent variable approximates the largest mean particle settling velocity (representing a particular heterogeneous sediment fraction) that can be entrained at the average spring-neap tidal cycle current velocity maximum. The largest mean settling velocity (in χ) was plotted vertically on the cumulative settling velocity distribution curve from the same site so that the line and curve intercepted. The percent of settling distribution fractions above the intercept is defined as the site surface sediment potential mobility at the site average spring-neap tidal cycle current velocity maximum. This procedure assumes all recalculated current velocities are as unobstructed by surrounding topography as the original measurements, minus bed roughness.

3. Results

3.1. Grain Composition

Twelve sediment-type categories were identified (Fig. 2a, ESM Table 2): coral; micritic grains; composite micritic grains; mollusk; foraminifera; green algae (primarily *Halimeda*), red algae; echinoderm; bryozoan; terrigenous; carbonate mud/silt; and other (spicules, fecal pellets, worm tubes, unattached cements, and unidentifiable). Classifications were intended to describe the dominant grain type each point resided on, despite the presence of intraskeletal cements or attached intragranular cements. Coral was the most common category in all but the Deep Patch samples. Terrigenous material was not found at any mesophotic sites, but constituted $\geq 10\%$ of the sediment from the shallow Fringing Patch site and a trace amount from the Mid-shelf Patch site.

Echinoderm, bryozoan, micritic cement, and carbonate mud/silt were $< 5\%$ of all samples.

Analysis of variance indicated statistically significant differences when comparing all sites and when just comparing mesophotic sites respectively for: coral ($F_{5,12} = 15.88, p < 0.001$; $F_{3,8} = 47.49, p < 0.001$); micritic grains ($F_{5,12} = 7.92, p = 0.002$;

259 $F_{3,8} = 14.67, p = 0.001$); foraminifera ($F_{5,12} = 16.68, p < 0.001$; $F_{3,8} = 30.59, p < 0.001$); and
 260 green algae ($F_{5,12} = 10.50, p < 0.001$; $F_{3,8} = 29.38, p < 0.001$). Significant differences were
 261 also found in the relative abundance of red algae between mesophotic sites ($F_{3,8} = 4.06, p$
 262 $= 0.050$). Pair-wise comparison results are displayed in Table 2. NMDS ordination of
 263 the Bray-Curtis dissimilarity matrix visually indicated differences in grain composition
 264 among the study sites (Fig. 2b) and was supported statistically by one-way analysis of
 265 similarity ($r = 0.7004, p = 0.0001$). Axis 1 of the NMDS ordination showed an overall
 266 gradient from sites with sediment composition dominated by coral grains (D3, D4, M5,
 267 and S6) to sites with sediment composition dominated by foraminifera, green algae, and
 268 micritic grains (D1 and D2). Fringing Patch sediment was distinguishable from other
 269 sites by an abundance of terrigenous material and greater amounts of mud/silt. Deep
 270 Patch sediment was distinguishable by a greater abundance of green algae and
 271 foraminifera-derived grains and fewer coral-derived grains.

272 Of all grain types, only foraminifera grain abundance was found to have a
 273 significant linear relationship with water depth (strong negative correlation; $n = 18, r = -$
 274 $0.86, p < 0.001$). Among mesophotic sites, strong significant correlations were found
 275 between abundance of coral sediment grains and benthic coral cover ($n = 12, \rho = 0.972, p$
 276 < 0.001) and between abundance of green algal sediment grains and green algae benthic
 277 cover (Fig. 2c) ($n = 12, \rho = 0.607, p = 0.036$). Strong, significant correlations were also
 278 found between the abundance of coral sediment grains and parrotfish biomass (Fig. 2d) (n
 279 $= 12, \rho = 0.972, p < 0.001$).

280 3.2. $\delta^{13}C$ and $\delta^{18}O$ Isotopic Composition

281 Bulk surface sediment stable isotope values (ESM Table 3) ranged from -2.22‰
 282 to -0.54‰ for oxygen ($\delta^{18}O$) and from 0.93‰ to 3.62‰ for carbon ($\delta^{13}C$). Both showed
 283 statistically significant differences between site means ($\delta^{18}O$: $F_{5,20} = 30.99, p < 0.001$;
 284 $\delta^{13}C$: $F_{5,20} = 44.28, p < 0.001$). Specific pair-wise differences are displayed in Table 2. A
 285 significant positive correlation was found between $\delta^{18}O$ and $\delta^{13}C$ (Fig. 3a) ($n = 26, r =$

0.829, $p < 0.001$). Furthermore, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values were generally related to depth, with more negative values found at shallow sites and positive values at deeper sites. To investigate potential relationships between bulk sediment stable isotope composition and sediment type, axis 1 from NMDS ordination analysis (primarily representing relative composition of coral, foraminifera, green algae, and micritic grains) was plotted versus sample bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Axis 1 showed a significant negative correlation with both $\delta^{13}\text{C}$ ($n = 18$, $r = -0.874$, $p < 0.001$) and $\delta^{18}\text{O}$ ($n = 18$, $r = -0.790$, $p < 0.001$). Additionally, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of collected bulk mesophotic reef sediments both had significant linear relationships (Fig. 2d) with the percent of coral grains in corresponding sediments ($\delta^{13}\text{C}$: $n = 11$, $R^2 = 0.961$, $p < 0.001$; $\delta^{18}\text{O}$: $n = 11$, $R^2 = 0.890$, $p < 0.001$). The projected isotopic composition of bulk mesophotic reef sediment with 100% coral composition is consistent with measured isotopic values of the dominant USVI mesophotic corals (Fig. 3b).

3.3. Grain Size and Hydrodynamics Analyses

The site average grain size distributions and site average of each main standard textural parameter are shown in Figure 4 (see ESM Table 4 for grain size distribution per sample). Standard textural parameters did not have any clear linear relationships with collection depth. Site average mean grain size was largest at the Deep Patch site and smallest at the Hillock Basin site (Fig. 4b). All 28 samples were primarily composed of sand size particles and gravel, with trace amounts of mud (Fig. 4c). On average, all mesophotic reef surface sediments contained <5% mud.

Site average grain size distributions were unimodal at the Deep Patch and Hillock Basin sites, bimodal at the Mid-shelf Patch and the Primary and Secondary Bank sites, and trimodal at the Fringing Patch site (Fig. 4a). The primary grain size mode was 0.5-0.3 mm for all sites except the Fringing Patch and Deep Patch sites (1-0.25 mm and 6-3 mm, respectively). The Deep Patch site primary grain size mode was similar to the secondary grain size mode of all other sites with bimodal and trimodal grain size distributions (D3, D4, M5, and S6). The ternary grain size mode of the shallow Fringing

Patch site was 40-20 μm . Site mean comparisons indicated statistically significant differences between each standard sediment textural parameter (grain size: $F_{5,22} = 5.01$, $p = 0.003$; sorting: $F_{5,22} = 4.73$, $p = 0.004$; skewness: $F_{5,22} = 7.48$, $p < 0.001$; and kurtosis: $F_{5,22} = 3.36$, $p = 0.021$). When comparing only mesophotic sites, significant differences between sites were found for mean grain size and sorting ($F_{3,17} = 9.93$, $p < 0.001$; $F_{3,17} = 4.68$, $p = 0.015$, respectively). Mesophotic reef sediment skewness and kurtosis did not meet assumptions for ANOVA. Specific pair-wise site differences for tested textural parameters are shown in Table 2.

Fine sand grains (diameter = 125 μm) could potentially deposit at the Hillock Basin and Deep Patch sites for 58.58% and 44.95% of all hours in the measured time span, respectively (Table 3). However, less than 1.3% of all hourly current measurements were conducive for unconsolidated sponge chip deposition. Site average spring-neap tidal cycle current velocity means were rarely strong enough to entrain unconsolidated reef surface sediment at any of the sites (potential mobility $< 4\%$) but high potential entrainment was possible in response to site average spring-neap tidal cycle current velocity maximums, especially at the Hillock Basin site (Table 3). Conditions necessary to entrain at least half of unconsolidated surface sediment (50% potential mobility) where most frequent at the Hillock Basin site but occurred $< 3\%$ of the hours in the sampled year (Fig. 5). Comparatively, 2.5% potential mobility frequency of unconsolidated surface sediment at the Hillock Basin was more than four times greater than at the Deep Patch.

3.4. *Sedimentary Subfacies*

The reef surface sediment samples collected in the USVI could all be broadly characterized as a carbonate bioclastic sand. Given their pre-lithified state, the surface samples were further classified into subfacies based on textural and compositional properties. Classification was restricted to two main properties per subfacies. To include all samples, average site composition values were used for samples where thin section analysis was not available. Subfacies descriptions (table 4) primarily group collected

340 samples into the six different habitat types analyzed in this study. Three of the subfacies
341 included one sample from a different habitat type, and only one sample was absent from
342 its associated main subfacies habitat group.

343 **4. Discussion and Conclusions**

344 Significant differences in sediment parameters (Table 2) indicate distinct
345 associations between mesophotic reef habitats with architecturally different
346 characteristics in the U.S. Virgin Islands and sedimentary subfacies. The type, size, and
347 chemical composition of reef sediment is controlled through a combination of
348 independent and interacting biological and physical processes. Isolating the effects and
349 interactions of these processes is an important step in using reef sediments as a means to
350 identify and interpret MCE habitat heterogeneity both in modern and ancient reef
351 environments.

352 *4.1. Biological Controls*

353 Overall, the mesophotic reef habitats in the USVI experience local sediment
354 production and deposition primarily controlled by biological processes. Mesophotic reef
355 sediment composition broadly records the abundance of two major habitat forming
356 benthic species. This record is indicated by significant correlations between sediment
357 grain types (coral and algae) and the living benthic cover, as well as by bulk isotopic
358 composition trends (coral generally has the most negative isotopic values and calcareous
359 algae has the most positive isotopic values of reefal skeletal sediment; Gischler et al.,
360 2009). For example, the Deep Patch and the Hillock Basin sites have the lowest
361 mesophotic coral cover and coral sediment percentages but the highest mesophotic green
362 algae cover and green algae sediment percentages. These two sites also have the heaviest
363 stable isotope compositions of analyzed surface sediments. Our conclusion supports the
364 general understanding that carbonate sand composition is largely controlled by the
365 relative abundance of skeletal producers (Basan, 1973) and is similar to results from deep

366 Jamaican fore-reefs (Boss and Liddell, 1987a; Perry, 1996). Contrastingly, high coral-
367 grain percentages (>30%) in Florida reefs have been interpreted as resulting from great
368 amounts of dead substrate accessible for bioerosion and imply the reef is in rapid decline
369 (Lidz and Hallock, 2000). However, long predicted framework exposure times
370 (Weinstein et al., 2014) and observations of USVI mesophotic reefs suggest an ample
371 supply of accessible, erodible substrate beneath the living platy coral veneer.

372 Poor sorting of all collected samples may also indicate that study site grain sizes
373 are primarily controlled by biological processes (Scoffin and Tudhope, 1985). Reef
374 sediments often split into discrete size intervals (Folk and Robles, 1964; Basan, 1973;
375 Flood and Scoffin, 1978). The main grain size interval from the USVI mesophotic sites
376 corresponds with coral grit (0.5 – .25 mm), a dominant fraction identified in other reefal
377 deposits (Folk and Robles, 1964; Garrett et al., 1971). The high coral grit to coarser coral
378 grain size ratio implies longer seafloor exposure (Scoffin, 1992). The primary grain size
379 mode at the Deep Patch is similar to whole *Halimeda* segments (8-4 mm; Folk and
380 Robles, 1964). This follows expectations given that the Deep Patch has a high relative
381 proportion of green algae-derived surface sediment compared to the other sites.

382 Biological processes also control reef sediment textural properties through
383 bioerosion, a dominant reef mechanism for sediment formation and framework alteration
384 (see review by Hutchings, 1986). Parrotfish typically produce sand-sized (0.5-0.125 mm)
385 fecal carbonate sediment (Gygi, 1969; Garrett et al., 1971) similar to grain size modes
386 common in USVI reefs (Fig. 4a). Parrotfish activity may also be the cause of the second
387 most common grain size mode (6-3 mm) at the shallowest four study sites (D3, D4, M5,
388 and S6) by detachment of coral framework not actually ingested. The relative absence of
389 gravel-sized grains at the Hillock Basin likely reflects the lower biomass of bioeroding
390 parrotfish recorded (Fig. 2d) compared to the higher coral cover mesophotic bank
391 habitats. Coarser grains, a relatively flat bathymetric profile, and low structural

392 complexity (Table 1) are reflected in the significant negative skewness of Mid-shelf Patch
393 sediment (Jordan, 1973).

394 4.2. *Hydrodynamic Controls*

395 Low-angle shelf mesophotic reef hydrodynamic processes appear to be less of a
396 factor in sediment deposition when compared to shallower-water reef systems (Randazzo
397 and Baisley, 1995; Orpin et al., 1999; Storlazzi et al., 2004). Significant terrigenous
398 material, easily distinguished from reef carbonates, was found exclusively at the
399 shallowest sites. This suggests that some portion of the land-based siliciclastic input
400 often associated with and transported as terrigenous sediment may still be affecting the
401 near-shore reef system (Gray et al., 2008), but is not likely to have a direct effect on
402 mesophotic sites.

403 Sand-sized sediments at mesophotic reef habitats in the USVI do not experience
404 significant transport between sites. This is observed by comparing models of suspended
405 particles to sediment trap deposits. Though almost never depositing at any mesophotic
406 reef sites during average spring-neap tidal cycle current velocity mean conditions,
407 suspended particles with diameters $\geq 104.4 \mu\text{m}$ (mean grain diameter collected in
408 sediment traps near D2; Smith et al., 2008) had potential to deposit at the Deep Patch site
409 during 25.72% of the measured hours, provided the grains were in the water column.
410 However, sedimentation trap rates near the Deep Patch were seven times lower than at the
411 Fringing Patch (D2: $0.315 \text{ mg/cm}^2/\text{day}$ SE = 0.037, S6: $2.315 \text{ mg/cm}^2/\text{day}$ SE = 0.327;
412 Smith et al., 2008). Therefore, particles with diameters $\geq 104.4 \mu\text{m}$ were either scarce at
413 neighboring sources (though not the case for neighboring mesophotic reefs, Fig. 2a), or
414 current energy was not sufficient to sustain transport of these grain sizes from other
415 sources to the Deep Patch. Assuming similar external sediment sources, sedimentation
416 rates at the other mesophotic reefs would be comparable to those recorded near the Deep
417 Patch and imply that sand-sized sediment at all analyzed mesophotic reef sites have
418 predominately localized origins.

419   Biological processes appear to be the primary control of sediment characteristics
420 at USVI mesophotic reefs. However, entrainment potential for fine sand grains and
421 smaller allow for some interpretation of hydrodynamic conditions in the mesophotic reef
422 sedimentary record. Mesophotic reef sediments have different potential for entrainment
423 per habitat when responding to average spring-neap tidal cycle current velocity
424 maximum; potential mobility generally increases with higher speeds. Grain size analysis,
425 low sedimentation rates and potential mobility analysis indicates that in 1 year,
426 production/deposition of fine sand grains and smaller (≤ 0.194 mm) was less frequent at
427 the Deep Patch than the 30 hours of the year (0.35%) in which conditions would be able
428 to cause at least 10% potential mobility to remove most fine grains (Fig. 5). However,
429 this hydrodynamic activity was not high enough to physically break down calcareous
430 green algae, the most abundant grain type in the surface sediments at the Deep Patch (Fig.
431 2) and one of the quickest reef skeletal grain types to disassociate (Ford and Kench,
432 2012).

433   The low proportion of mud and fine-grained sand in MCE reef sediments,
434 especially equivalent in size to average sponge chips (Fig. 4c), also indicates
435 hydrodynamic conditions have some influence on USVI mesophotic reef sedimentology.
436 The absence is not intuitive because sponge bioerosion is considered the primary long-
437 term modifier of substrate below ~35 m (Weinstein et al., 2014). USVI mesophotic coral
438 sponge bioerosion is either cryptic or primarily on the underside of platy coral heads.
439 Expelled chips from less-cryptic sponges must fall before autochthonous deposition.
440 However, energy levels were almost never low enough ($< 1.30\%$ of measured hours,
441 Table 3) for deposition, assuming fall heights ≥ 25 mm, or for long-term residence on the
442 surface. A greater abundance of sponge chips is expected in cryptic spaces, but these
443 may not mix into surrounding surface sediment. Therefore, although sponge chips can
444 constitute a high percent of reef sediment in low energy habitats (such as lagoons,
445 Fütterer, 1974), there is little potential for sponge chip accumulation on low-angle shelf

446 MCEs due to moderately strong episodic hydrodynamic forces. Further interpretation of
447 hydrodynamic impacts on sediment characteristics in the USVI are not possible. This
448 results from the observation that average spring-neap tidal cycle current velocity means
449 are relatively similar (Table 1) and that different sites can appear to experience greater
450 current depending on the interval of time measured (Smith et al., 2010).

451 A byproduct of hydrodynamic removal of sponge chips from USVI mesophotic
452 reefs is the high probability that most all other generation of coral-based sediment occurs
453 through parrotfish grazing. Therefore, another implication from this study is that
454 sediment analysis in shallower mesophotic depth range along long-angle slopes can be
455 used to infer past grazing bioerosional productivity. This is important considering
456 macroboring analysis in fossil reefs is possible but no method exists for estimating
457 grazing contributions to total bioerosion in the same deposits.

458 *4.3. Implications for Comparative Analysis*

459 Low diversity in grain producers has been suggested to result in reduced
460 sedimentary facies variability in reefs at mesophotic depth ranges compared to their
461 shallow-water reef counterparts (Purkis et al., 2014). However, our findings indicate
462 distinct associations between deep reef habitats with architecturally different
463 characteristics and sedimentary subfacies (Table 2). Results imply reservoir models of
464 carbonate deposits from ancient mesophotic reef settings could be refined to better reflect
465 heterogeneity of sediment properties. The present study suggests mesophotic reef habitat
466 heterogeneity in the USVI can be distinguished based on sedimentological data. This is
467 critical for future comparative studies of mesophotic reef paleoenvironments, especially
468 considering that mesophotic reef systems like those examined in the USVI may often be
469 dominated by one major taxonomic coral group. Although many studies have use key
470 species, growth forms, or ecological zonation to interpret reef paleoenvironments
471 (Mesolella et al., 1970; Chappell, 1974; Lighty et al., 1982), there is a risk of circular

472 reasoning error when relying on these sole factors to both interpret paleoenvironmental
473 conditions and paleoecology from the same samples (Pandolfi et al., 1999).

474   The subfacies identified allow for a more comprehensive interpretation of benthic
475 ecology and hydrological conditions experienced at mesophotic reefs with different
476 geomorphological habitats. They can also help determine the degree of habitat
477 heterogeneity in the particular reef system, different reef environments, and the lateral
478 extent of different reef habit types. Regardless, consideration is still needed when
479 interpreting ancient mesophotic reef deposits. Based on mean grain sizes, the classical
480 fluid sediment transport theory (smaller grains identify areas of reduced energy and larger
481 grains identify areas of greater energy, Purdy, 1963) would lead, incorrectly, to the
482 interpretation that the Deep Patch is a higher energy environment than the Hillock Basin.
483 Identifying high abundance of very fine grain reef sediment in ancient mesophotic reef
484 deposits should not be the only observation used to imply a Hillock Basin-type
485 environment. Interpreting other factors (such as bedding structures, syndepositional
486 cement, bioturbation, and amount of allochthonous material) is necessary before
487 subfacies equivalence can be inferred. These additional indicators, as well as the grain
488 composition, would help identify if smaller size grains resulted from low energy, or if
489 higher relative average spring-neap tidal cycle current velocity maximum conditions were
490 possible such, as those experienced at the Hillock Basin. At the least, we suggest that
491 similar paleomesophotic subfacies delineations to those in the USVI reefs would indicate
492 a high probability of mesophotic depth shelf-wide habitat heterogeneity that may
493 otherwise have been overlooked. Results from this study provide a new analog for
494 studying mesophotic reef systems in the geologic past and overall coral reef evolution.

495

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710

711 **Figure Legends**

712 **Fig. 1** South Puerto Rican Shelf, with inset marking study location. Multi-beam
 713 bathymetry 1 m resolution (20x vertical exaggeration). Study sites include: Hillock
 714 Basin (D1); Deep Patch (D2); Primary Bank (D3); Secondary Bank (D4); Mid-shelf
 715 Patch (M5); shallow Fringing Patch (S6). ‘D’ = Mesophotic “deep”, ‘M’ = Mid-shelf,
 716 and ‘S’ = Shallow.

717 **Fig. 2** Surface sediment composition. (a) Average percent of constitute sediment type
 718 per site, with error bars equal to one standard error. Mic = micritic, Forarm. =
 719 Foraminifera, Gr. = Green, R. = Red, Echino. = Echinoderm. (b) Non-metric
 720 multidimensional scaling (NMDS) ordination. Arrow length indicates correlation of
 721 sediment type to sample ordination. (c) Correlation between percent of carbonate
 722 sediment grain type (coral, green algae, and red algae) and corresponding average site
 723 benthic cover, as given in table 1. Clear circles on symbols indicate that a second nearly

724 identical data point is located at the same position. (d) Correlation between percent of
725 coral grains in bulk mesophotic sediment and adjusted bioeroding parrotfish biomass, as
726 defined by Weinstein et al., 2014. Key at bottom indicates habitats for all figures.

727 **Fig. 3** Bulk sediment isotopic composition. (a) Relationship between bulk sediment
728 stable carbon and oxygen isotopic composition. (b) Relationship between the percent of
729 coral grains in collected mesophotic reef bulk sediment and the corresponding bulk
730 sediment stable isotopic composition of oxygen (squares) and carbon (diamonds). Grey
731 vertical lines indicate the average isotopic ranges (with middle line showing mean)
732 obtained from representative living framework *Orbicella* spp. samples. Key at bottom
733 indicates habitats for all figures.

734 **Fig. 4** Grain size analysis. (a) Graph of average grain size distribution per site, with grey
735 area indicating distribution estimates after last sieve bin (63 μm). (b) Average textural
736 parameters per site, ± 1 standard error. (c) Classification of sediments as a ternary
737 diagram. Left side of (b) indicates habitats for figures.

738 **Fig. 5** Percent of hours measured in a year (or all hours measured at D4) for different
739 potential mobility fractions for the site mean settling velocity. Pie chart delineates hour
740 proportions per season (light gray = summer, dark gray = winter). Parentheses indicate
741 the maximum equivalent grain size diameter (mm) that could be entrained for the
742 corresponding potential mobility fraction. No 50% potential mobility graph is presented
743 for the Deep Patch site because conditions were never met. Secondary Bank data only
744 available during summer 2014.

745 **Table 1** Bathymetry, benthic coverage, rugosity, current velocity, and general
746 description of study sites. Benthic coverage and rugosity from 2012 surveys. Site
747 average maximum current velocity ($\overline{CV}_{\text{max}}$) and mean current velocity ($\overline{CV}_{\text{mean}}$) per
748 spring-neap cycle, from 1 February 2008 to 31 January 2009. Values are reported with
749 ± 1 SE. VR = vertical relief. N/A = unavailable data.

750 **Table 2** Surface sediment pair-wise analysis results of Tukey's Honestly Significant
751 Difference test, comparing sediment attributes between sites. Values were included when
752 significant ($p < 0.05$). Parentheses indicate test results for which only mesophotic sites
753 were considered. Foram. = Foraminifera.

754 **Table 3** Potential deposition and potential mobility. Percentage of hours measured in
755 which unconsolidated grains (three representative diameter sizes) would deposit from
756 suspension if initially present 25 mm above the seafloor. Potential mobility analysis is
757 applied to the site average grain size distribution. N/A = unavailable data.

758 **Table 4** Sedimentary subfacies classifications of USVI surface reef sediments. Bold text
759 indicates samples for which site average grain composition abundances were used for
760 classification purposes. Underlined text indicate samples classified in 2 subfacies.
761 Italicized text indicates samples from a different habitat than the associated geomorphic
762 site. Grey box indicates not all samples from the associated geomorphic site are included
763 in the subfacies. Sample ID numbers began with site abbreviation code. M_z = sample
764 mean grain size diameter (mm). Sk_1 = sample grain size distribution skewness.

765

Figure 1. color

Figure 1 B/W

Figure 2 color

Figure 2 grey

Figure 3 color

a

b

Figure 3 grey

Figure 4 color

Figure 4 grey

Figure 5

Table 1 Bathymetry, benthic coverage, rugosity, current velocity, and general description of study sites.

Benthic coverage and rugosity from 2012 surveys. Site average maximum current velocity ($\overline{CV}_{\max}$) and mean current velocity ($\overline{CV}_{\text{mean}}$) per spring-neap cycle, from 1 February 2008 to 31 January 2009. Values are reported with ± 1 SE. VR = vertical relief. N/A = unavailable data.

Geomorphic site/ depth (m)	Rugosity	% cover		# of transects	Annual tidal cycle (cm/s) $\overline{CV}_{\max}$ $\overline{CV}_{\text{mean}}$	Site description
		Live coral	G. algae R. algae			
Hillock Basin (D1) 44.5	1.84 $\pm$ 0.44	12.99 $\pm$ 4.17 ^a	45.42 $\pm$ 1.74 ^a 15.10 $\pm$ 2.22 ^a	3 ^a	34.84 $\pm$ 4.04 7.07 $\pm$ 0.75	Flat sand and sparse coral expanse 2.3 km ² with over 10,000 coral "hillock" semi-conical knolls ~5-20 m diameter with 2-10 m of VR.
Deep Patch (D2) 41.1	1.13 $\pm$ 0.02	1.79 $\pm$ 0.81	54.01 $\pm$ 6.56 12.36 $\pm$ 3.20	3	18.83 $\pm$ 0.97 6.92 $\pm$ 0.32	Semi-conical (>0.5 km diameter), <5 m of VR. High rhodolith cover and low cover of ephemeral coral opportunists. Near other isolated patches.
Primary Bank (D3) 39.0	2.62 $\pm$ 0.63	32.20 $\pm$ 2.59	34.28 $\pm$ 1.40 5.89 $\pm$ 0.93	6	19.53 $\pm$ 1.45 7.22 $\pm$ 0.38	Southernmost semi-continuous mesophotic reef parallel and adjacent to Anegada Passage for >1 km. Narrow (<0.5 km) width bank with >5 m of VR.
Secondary Bank (D4) 30.7	1.55 $\pm$ 0.14	33.73 $\pm$ 2.54	36.80 $\pm$ 1.64 8.94 $\pm$ 1.03	6	24.24 $\pm$ 3.31 ^b 7.57 $\pm$ 0.20 ^b	North, more continuous, wider (>1.5 km), and parallel to Primary Bank for >1 km, with a broader sloping northern edge and >5 m of VR.
Mid-shelf Patch (M5) 21.0	1.18 $\pm$ 0.04	18.26 $\pm$ 0.60	54.20 $\pm$ 2.68 2.04 $\pm$ 0.36	42	N/A	Large mid-shelf isolated flat-topped patch surrounded by rhodoliths and sand.
Fringing Patch (S6) 9.0	1.24 $\pm$ 0.01	3.19 $\pm$ 0.76	37.04 $\pm$ 3.71 0.34 $\pm$ 0.34	3	N/A	Isolated fringing patch ~30 m offshore in Perseverance Bay. Sparse coral community impacted by terrestrial runoff.

^adata from (Smith et al. 2007), ^bbased on data obtained from 20 May to 26 September 2014

Table 2

Table 2 Surface sediment pair-wise analysis results of Tukey's Honestly Significant Difference test, comparing sediment attributes between sites. Values were included when significant ($p < 0.05$).

Parentheses indicate test results for which only mesophotic sites were considered. Foram. = Foraminifera.

Site differences		Grain composition				Stable isotopes		Grain size analysis		
		Coral	Micritic grains	Foram.	Green Algae	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	Mean	Sorting	Skewness
Mesophotic	Primary Bank: Secondary Bank	(0.045)		(0.063)	(0.030)	<0.001 (<0.001)	0.038 (0.004)			
	Deep Patch: Secondary Bank	<0.001 (<0.001)	0.001 (0.002)	0.003 (<0.001)	<0.001 (<0.001)	<0.001 (<0.001)	<0.001 (<0.001)	(0.024)	(0.030)	0.003
	Hillock Basin: Secondary Bank	0.015 (0.002)		(0.002)	0.037 (0.007)	<0.001 (<0.001)	<0.001 (<0.001)			
	Deep Patch: Primary Bank	0.001 (<0.001)	0.002 (0.002)	0.047 (0.001)	0.009 (0.002)	<0.001 (<0.001)	<0.001 (<0.001)			0.009
	Hillock Basin: Deep Patch	0.016 (0.002)	(0.035)	(0.025)	0.038 (0.007)	<0.001 (<0.001)	0.047 (0.005)	0.001 (<0.001)	(0.036)	0.008
	Hillock Basin: Primary Bank					(0.016)	(0.034)			
Mesophotic / shallow	Secondary Bank: Fringing Patch								0.018	
	Primary Bank: Fringing Patch			0.005		<0.001	<0.001			
	Deep Patch: Fringing Patch	0.001	0.014	<0.001	0.006	<0.001	<0.001			
	Hillock Basin: Fringing Patch			0.001		<0.001	<0.001		0.021	
	Mid-shelf Patch: Secondary Bank					0.003				
	Mid-shelf Patch: Primary Bank						0.002			
	Mid-shelf Patch: Hillock Basin			0.023			<0.001			
	Mid-shelf Patch: Deep Patch	<0.001	0.027	0.001	0.012	<0.001	<0.001			<0.001
Shallow	Mid-shelf Patch: Fringing Patch					0.045				0.011

Table 3

Table 3 Potential deposition and potential mobility (PM). Percentage of hours measured in which unconsolidated grains (three representative diameter sizes) would deposit from suspension if initially present 25 mm above the seafloor. Potential mobility analysis is applied to the site average grain size distribution. N/A = unavailable data.

	Geomorphic habitats	Grains (µm)	Annual	Summer	Winter
% (hours in a year) of potential deposition	Hillock Basin (D1)	125	58.58%	31.71%	26.87%
		104.4	36.66%	20.24%	16.41%
		40	1.27%	0.64%	0.63%
	Deep Patch (D2)	125	44.95%	15.60%	29.36%
		104.4	25.72%	8.22%	17.50%
		40	0.84%	0.25%	0.59%
	Primary Bank (D3)	125	38.57%	20.76%	17.81%
		104.4	21.67%	11.01%	10.65%
		40	0.50%	0.18%	0.32%
	Secondary Bank (D4)	125	N/A	38.75%	N/A
		104.4		21.90%	
		40		0.71%	
PM (%)	Hillock Basin (D1)	Complete grain size distribution	88.8	95.1	49.0
	Deep Patch (D2)		8.1	14.1	0.1
	Primary Bank (D3)		10.8	10.9	10.8
	Secondary Bank (D4)		N/A	36.0	N/A

Table 4

Table 4 Sedimentary subfacies classifications of USVI surface reef sediments. Bold text indicates samples for which site average grain composition abundances were used for classification purposes. Underlined text indicate samples classified in 2 subfacies. Italicized text indicates samples from a different habitat than the associated geomorphic site. Grey box indicates not all samples from the associated geomorphic site are included in the subfacies. Sample ID numbers began with site abbreviation code. M_z = sample mean grain size diameter (mm). Sk_1 = sample grain size distribution skewness.

Sedimentary facies	Subfacies	Defining characteristics	Sample ID numbers	Associated Geomorphic site/ depth (m)
Carbonate bioclastic sand	Moderate coral rich, medium grained sand	<40% coral, $M_z < 0.70$	D1.1 , D1.2, D1.3 , D1.4 , D1.5, D1.6, <u>S6.4</u>	Hillock Basin (D1) 44.5
	Green algae rich coarse grained sand	>15% green algae, $M_z > 0.70$	D2.1, D2.2, D2.3, D2.4	Deep Patch (D2) 41.1
	Coral rich, foraminifera rich sand	>40% coral, >10% foraminifera	D3.1, D3.2, D3.3 , D3.4, D3.5 , <u>M5.1</u>	Primary Bank (D3) 39.0
	Coral rich, green algae poor sand	>40% coral, <1% green algae	D4.1 , D4.2 , D4.3 , D4.4, D4.5, D4.6, M5.3	Secondary Bank (D4) 30.7
	Coarsely skewed, terrestrial present sand	coarse to very coarsely skewed ($Sk_1 < -0.1$), >0% terrigenous	<u>M5.1</u> , M5.2	Mid-shelf Patch (M5) 21.3
	Terrestrial rich, muddy sand	>10% terrigenous, >2% mud content	S6.1, S6.2, S6.3 , <u>S6.4</u>	Fringing Patch (S6) 9.1