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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 different structural characteristics ideal for studying the relationship between habitat variability and sedimentary facies. Textural, compositional, and geochemical analyses of surface sediments were used to identify mesophotic reef subfacies associated with distinct benthic communities and structural habitats. Sediment grain composition and bulk geochemistry were found to broadly record the distribution and abundance of coral and macroalgae communities, foundational mesophotic reef benthic organisms. Overall, sediment composition was found to be a good indicator of specific reef environments in low-angle mesophotic reef habitats. Sedimentological analyses indicate that hydrodynamic forces do not transport a significant amount of allochthonous sediment or potentially harmful terrigenous material to USVI mesophotic reefs. Episodic, maximum current velocities prevented deposition of most silt-size grains and smaller, but biological processes were found to have a greater influence on subfacies partitioning than hydrodynamic processes. Results provide a new analog for studies of ancient mesophotic coral ecosystem geological history and document the relationship between mesophotic reef subfacies, structural complexity, and habitat heterogeneity. They also demonstrate how mesophotic reefs along the same shelf system do not always share similar sedimentary characteristics and thus record a diverse set of ecological and environmental conditions.

1. Introduction

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

In shallow reef environments, biodiversity is promoted by ecologically diverse habitats fostered by a spectrum of tidal and wave energy conditions and by habitat modifying species that increase structural complexity, alter hydrodynamics, and increase overall habitat surface area (Connell, 1978; Roberts and Ormond, 1987; Bruno and Bertness, 2001). Structural complexity increases biodiversity and habitat heterogeneity by providing areas with reduced environmental stress needed

Abbreviations: MCE, mesophotic coral ecosystem; USVI, United States Virgin Islands; ADCPs, Acoustic Doppler Current Profilers; ANOVA, one-way analysis of variance; HSD, Honestly Significant Difference; TCRMP, US Virgin Islands Territorial Coral Reef Monitoring Program; NMDS, non-metric multidimensional scaling.

Study site abbreviations: D1, Hillock Basin; D2, Deep Patch; D3, Primary Bank; D4, Secondary Bank; M5, Mid-shelf Patch; S6, Fringing Patch.

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for other organisms to thrive (Thompson et al., 1996) and by improving propagule retention (Eckman et al., 1989). Direct correlations between habitat heterogeneity, fish diversity, and shallow-water reef structural complexity (Roberts and Ormond, 1987; Dustan et al., 2013) and the negative affect global warming is projected to have on reef rugosity (Bozec et al., 2014) emphasize the importance of protecting reef architectural complexity (Dryden et al., 2012). However, little is known about the role of habitat heterogeneity and structural complexity in mesophotic reefs, including their relationship to sedimentary processes and the extent that depositional processes can identify distinct habitats.

The mesophotic reefs of the northern U.S. Virgin Islands (USVI) developed on a low-angle reefal margin that provides space for differing architectural features. Here we present a detailed characterization and interpretation of sediment found within distinct mesophotic reef habitats. Our objectives were to: (1) resolve if low gradient shelf mesophotic reef systems produce recognizable sedimentary facies that reflect structurally distinct reef habitats; and (2) determine the significance of these potential facies differences in terms of biological and hydrodynamic processes. The ability to identify causes and indicators of habitat heterogeneity and structural complexity in modern MCEs 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, but approximately 66.8% of the Red Hind Marine Conservation District was composed of adjacent mesophotic coral reefs shallower than 50 m in 2007 (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 study 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. Eastward 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. Benthic cover (protocol after Smith et al., 2008, 2010) and rugosity (3 m chains; Luckhurst and Luckhurst, 1978) were obtained from the United States Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP). Table 1 displays site average benthic coverage and rugosity measurements from 2012, except for benthic cover at D1 and D2 (recorded in 2007 and 2013, respectively), and rugosity at D3 and M5 (recorded in 2011). The maximum number of transects conducted per site (monthly or episodically, depending on monitoring protocol) during the indicated year were used to calculate the most representative average benthic coverages.

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 and dried prior to analysis. Representative living framework samples of *Orbicella* spp. were taken near three of the mesophotic reef sites (D1, D3, D4) for isotopic comparison to bulk sediments. Sediment samples from sites D2, D3, and D4 were collected in the vicinity of Nortek Aquadopp Acoustic Doppler Current Profilers

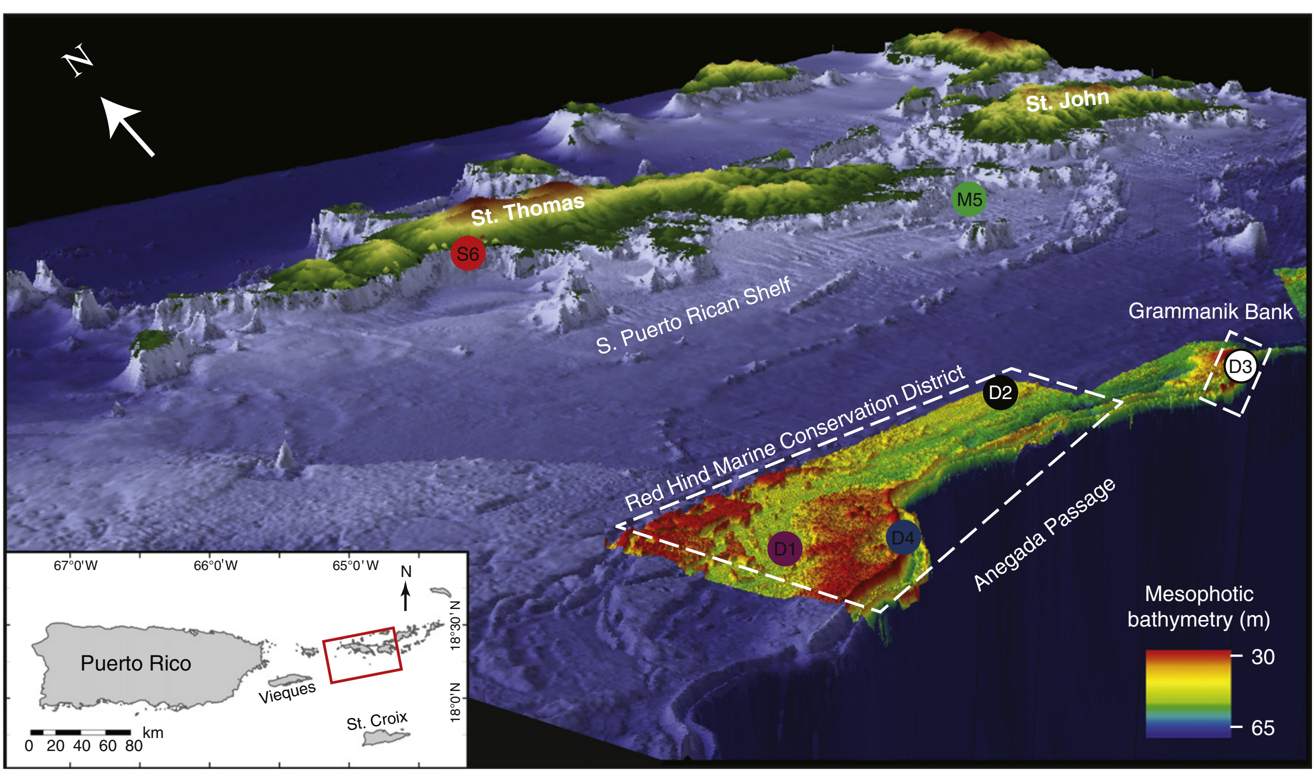

Fig. 1. South Puerto Rican Shelf, with inset marking study location. Multi-beam bathymetry 1 m resolution (20× vertical exaggeration). Study sites include: Hillock Basin (D1); Deep Patch (D2); Primary Bank (D3); Secondary Bank (D4); Mid-shelf Patch (M5); shallow Fringing Patch (S6). 'D' = Mesophotic "deep", 'M' = Mid-shelf, and 'S' = Shallow.