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Demersal fish assemblages on seamounts and other rugged features in the northeastern Caribbean

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ABSTRACT

Recent investigations of demersal fish communities in deepwater (> 50 m) habitats have considerably increased our knowledge of the factors that influence the assemblage structure of fishes across mesophotic to deep-sea depths. While different habitat types influence deepwater fish distribution, whether different types of rugged seafloor features provide functionally equivalent habitat for fishes is poorly understood. In the northeastern Caribbean, different types of rugged features (e.g., seamounts, banks, canyons) punctuate insular margins, and thus create a remarkable setting in which to compare demersal fish communities across various features. Concurrently, several water masses are vertically layered in the water column, creating strong stratification layers corresponding to specific abiotic conditions. In this study, we examined differences among fish assemblages across different features (e.g., seamount, canyon, bank/ridge) and water masses at depths ranging from 98 to 4060 m in the northeastern Caribbean. We conducted 26 remotely operated vehicle dives across 18 sites, identifying 156 species of which 42% of had not been previously recorded from particular depths or localities in the region. While rarefaction curves indicated fewer species at seamounts than at other features in the NE Caribbean, assemblage structure was similar among the different types of features. Thus, similar to seamount studies in other regions, seamounts in the Anegada Passage do not harbor distinct communities from other types of rugged features. Species assemblages, however, differed among depths, with zonation generally corresponding to water mass boundaries in the region. High species turnover occurred at depths < 1200 m, and may be driven by changes in water mass characteristics including temperature (4.8–24.4 °C) and dissolved oxygen (2.2–9.5 mg per l). Our study suggests the importance of water masses in influencing community structure of benthic fauna, while considerably adding to the knowledge of mesophotic and deep-sea fish biogeography.

1. Introduction

Investigations of deepwater (> 50 m) habitats over the past few decades have considerably increased our knowledge of the factors that influence the distribution and assembly of demersal fish communities. A large contributing factor to these discoveries has been targeted investigations in deepwater habitats combined with dramatic increases in sampling and observation technologies, including high-resolution imagery and remotely operated vehicles (ROVs). Exploration in rugged habitats with deep submergence vehicles has consistently yielded novel insights into the biogeography and ecology of deep-sea and mesophotic reef fishes (e.g., Auster et al., 2005; Quattrini and Ross, 2006; De Leo et al., 2012; Ross et al., 2015). The importance of various abiotic environmental variables (e.g., temperature, dissolved oxygen, light levels, substrate) in influencing community structure has been suggested in numerous investigations of deepwater fish communities. Substrate type, in particular, has been shown to influence the distribution of fishes in the deep sea. Many deepwater fish species have affinities to hard substrates (i.e., biogenic coral mounds of the scleractinian coral *Lophelia pertusa,* boulder fields, rock outcrops), while others are associated with softer substrates including mud and sand (Auster et al., 1995, 2005; Quattrini and Ross, 2006; Ross and Quattrini, 2007; Milligan et al., 2016). Variation in fish assemblages has also been found among

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larger-scale, seafloor features, such as submarine canyons, cold seeps, seamounts, and open slope regions, particularly in productive regions such as the northeastern U.S. continental margin (Quattrini et al., 2015; Ross et al., 2015).

Fish assemblages are also known to vary substantially with depth, with zonation often corresponding with overlying vertical distribution of water masses (Menezes et al., 2006, 2009, 2015; Quattrini et al., 2015). Because water masses have specific characteristics of temperature, dissolved oxygen, salinity, and density, these environmental properties can influence distribution and community structure of fishes in deep waters (Koslow, 1994; Clark et al., 2010a; Menezes et al., 2003, 2009; Tracey et al., 2012). Water masses also play an important role in dispersal, by either aiding larval dispersal across large distances or preventing dispersal by creating a physiological or physical barrier (e.g., Norcross and Shaw, 1984; Richards et al., 1993; Grothues and Cowen, 1999; Galarza et al., 2009). Thus, characteristics of water masses can serve as basic proxies for defining the realized ecological niche of a fish species. Clark et al. (2010a), however, noted that the distribution across depth of deep-sea fishes does not simply correspond to water mass distribution. Complex interactions among water masses, food supply, and habitat heterogeneity likely work in concert to shape community structure patterns of deep-sea fishes. Whether we can generalize or predict how such large-scale factors of water mass and seafloor features will impact deepwater fish communities requires surveying over large spatial scales and depth gradients in different regions.

One region in which deepwater fishes has been poorly investigated is the Caribbean Sea. Although shallow-water, coral -reef fish communities in the Caribbean have been well studied for decades, the mesophotic (> 50 m) and deep-sea (> 200 m) fish assemblages remain less understood due to the various challenges associated with surveying complex topographies in deeper waters. Surveys of deepwater fishes throughout the Caribbean have been limited (Miloslavich et al., 2010; Bejarano et al., 2014), although there are a few exceptions (e.g., Colin, 1974; Thresher and Colin, 1986; Nelson and Appeldoorn, 1985; Baldwin and Robertson, 2014, Bejarano et al., 2014). Rugged seafloor features (i.e., seamounts, submarine canyons, ridges) have been particularly difficult to investigate in deep waters, as they cannot be adequately surveyed using surface deployed gears such as traps, benthic sleds, and bottom trawls. ROVs and submersibles provide an effective way to survey demersal fishes on rugged features across a broad depth range.

The NE Caribbean (Fig. 1) hosts numerous types of rugged seafloor features that increase habitat heterogeneity in deep waters. In the area encompassing Puerto Rico and the Virgin Islands, insular margins are incised with submarine canyons (Trumbull and Garrison, 1973; Gardner et al., 1980; Scanlon and Masson, 1996), escarpments line deep trenches (ten Brink et al., 2004; Grindlay et al., 2005; Bruña et al., 2009; Chaytor and ten Brink, 2014), ridges and banks rise off the seafloor (Chaytor and ten Brink, 2010; Chaytor and ten Brink, 2015) and vertical walls border deep basins (Jany et al., 1990; Mondziel et al., 2010; Chaytor and ten Brink, 2015). Seamounts (isolated features rising at least 1000 m from the surrounding seafloor) are also prominent features in the Caribbean, punctuating insular margins and deep passageways (Bouysse et al., 1985; Jany et al., 1990). Although features such as these can increase local biodiversity in the deep sea (Samadi et al., 2006; De Leo et al., 2012), it remains poorly known whether these different features are equivalent in harboring similar fish assemblages and/or levels of diversity. In fact it has remained a challenge to examine these community attributes among different features without adding confounding factors such as depth (but see O'Hara (2007), Howell et al. (2010), Rowden et al. (2010)). Thus, the NE Caribbean provides a remarkable setting to examine whether different types of rugged features serve as functionally equivalent fish habitats over similar depths.

Seamounts, in particular, have been suggested to be biodiversity hotspots (Santillo and Johnston, 2005; Samadi et al., 2006; Morato et al., 2010). Seamounts encompass a large depth range and they contain a diversity of macrohabitats (i.e., hard bottom, soft substrate, sessile invertebrate communities). Thus, demersal fish community structure can differ along flanks and summits of seamounts and between seamounts (Lundsten et al., 2009; Menezes et al., 2009) and often differ from communities on the adjacent seabed (Tracey et al., 2004). Seamounts that rise into the euphotic zone can support large aggregations of fishes (Koslow, 1997; Clark et al., 2010b). Pelagic fish diversity can be enhanced at summits of seamounts when compared to the adjacent seabed (Morato et al., 2008; Morato et al., 2010). As such, deepwater commercial fisheries often heavily target seamounts (e.g., Koslow, 1997; Morato and Clark, 2007; Clark et al., 2007, 2010b). Although limited commercial fishing activity occurs on deep seamounts in the Caribbean due to the high costs (e.g., fuel, deepwater fishing gear) and challenges of fishing in deep waters, the Western Central Atlantic Fishery Commission noted that some fishers are expanding into depths > 200 m, and this could lead to the further development of fisheries in the deep Caribbean (FAO, 2015). Thus, the vulnerability of seamount communities to future fishing and mineral extraction is a matter of concern, particularly as technological advances are enabling expansion into deeper depths (Morato et al., 2006; Clark et al., 2010b; Ramirez-Llodra et al., 2011; Watling and Auster, 2017). In order to preserve and effectively manage deepwater fish populations, it is important to understand whether seamounts serve as isolated features that harbor distinct communities or whether they are similar to other rugged features in the deep sea. It is necessary, therefore, to compare fish composition, diversity, and abundance within similar depths to help explain the community differences or similarities at seafloor features of equivalent topographic complexity.

In our study, ROVs were used to survey demersal fish communities across a variety of rugged seafloor features and depths in the NE Caribbean. Our objectives were to: 1) determine whether fish assemblages differ between seamounts and other rugged features, 2) examine if assemblage change with depth corresponds to vertical water mass structure in the region, and 3) examine what abiotic factors (temperature, salinity, oxygen, feature, location) influence regional variation in fish assemblages. This study also provided the opportunity to add important biogeographical information, including depth and range extensions, for numerous fish species in the region.

2. Material and methods

2.1. ROV surveys

Three expeditions using ROVs were conducted to survey deep waters in the northeastern Caribbean region (Fig. 1, Table S1). The ROV *Hercules* was tethered to the camera sled *Argus* and deployed from the E/V *Nautilus* in October 2013 (9 dives, 98–2987 m depth) and September 2014 (7 dives, 165–2206 m depth). The ROV *Deep Discoverer* (*D2*) was tethered to the camera sled *Seirios* and deployed from the NOAA Ship *Okeanos Explorer* in April 2015 (10 dives, 300–4060 m depth). Both ROVs were equipped with high definition cameras and paired lasers positioned 10 cm apart. ROV *Hercules* was equipped with a Sea-bird FastCAT 49 conductivity-temperature-depth (CTD) logger and an Aanderaa oxygen optode to measure dissolved oxygen (DO). ROV *D2* was equipped with a Sea-bird 911+ logger with a DO sensor. Environmental data were logged at ≥1 scan per second intervals.

Multibeam bathymetry (Andrews et al. (2013) and additional data collected during *Okeanos Explorer* Cruises EX1502L1-L3 and E/V *Nautilus Cruise* NA052) was used to guide dive selection. Dive sites and directions were chosen based on high slope angles (> 40°) and potential for hardbottom relief. The ROVs were deployed to a maximum target depth on the feature and generally moved to shallower depths. The ships followed the vehicles using dynamic positioning and tracked vehicle position relative to the ship with an ultra-short baseline