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 ºC) 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.

Key Words
Mesophotic; Deep Sea; Seamount; Water Mass; Community Structure; Habitat Associations; Vertical Distribution

Highlights

- Seamounts do not harbor distinct communities from other rugged seafloor features
- Depth zonation of demersal fishes corresponds with water mass stratification
- Strong species turnover at depths shallower than 1200 m
- New depth and/or locality information for 42% of demersal fishes
- Increased knowledge of the biogeography of mesophotic and deep-sea fishes

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; Auster et al., 2005; Quattrini and Ross, 2006; Ross and Quattrini, 2007; Milligan et al., 2016). Variation in fish assemblages has also been found among 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 feature 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, 1974; Nelson and Appeldoorn, 1985; Baldwin and Robertson, 2014, Bejerano 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

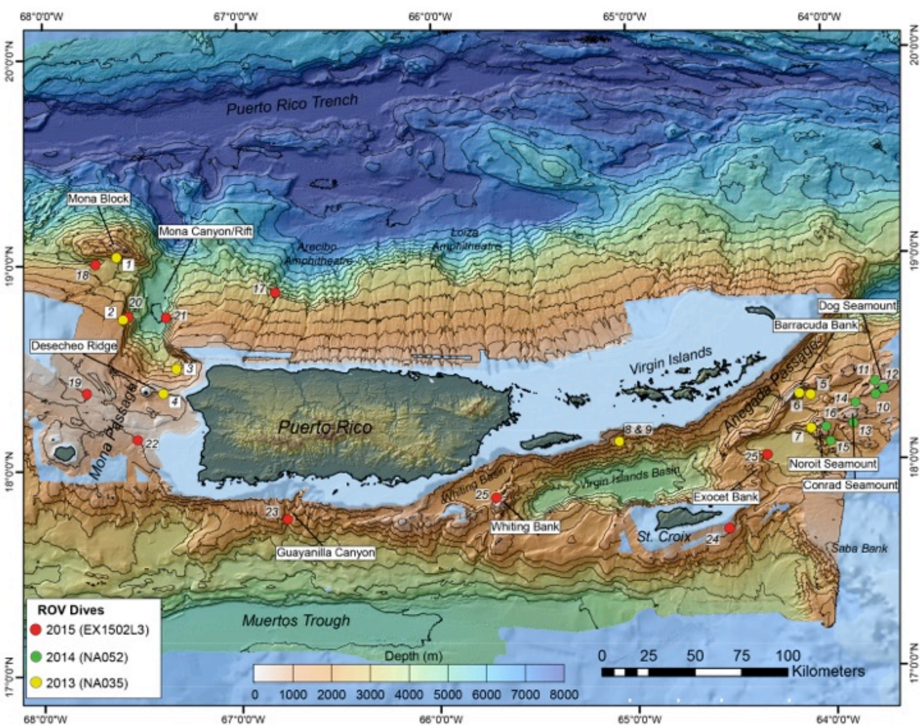

Figure 1. Map of the NE Caribbean region from Mona Passage to Anegada Passage. Circles denote ROV dives (numbered 1-26), which were conducted in 2013-2015 (color coded by year).

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., 2008; 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 1,000 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 et al., 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., 2010). As such, deepwater commercial fisheries often heavily target seamounts (e.g., Koslow 1997; Morato and Clark, 2007; Clark et al., 2007; Clark et al., 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.

Material and Methods

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., 2014 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 deg) 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 tracking system. The ROVs continuously traversed the seafloor as near to the bottom as practical at a slow speed (0.05-0.1 m per s); however, transects were occasionally interrupted by stopping the ROV for sampling purposes. During dives, the forward-facing cameras were set on wide-angle view, but frequent snap-zooms (up to 20 sec) were conducted to aid in species identification. In 2015, numerous zooms of longer durations (up to 5 min) were conducted to obtain detailed imagery of habitats and species during the *Okeanos Explorer* expedition.

Video Analyses

Video data that were of poor quality (i.e., out of focus, too high off the bottom, clouded by sediment) were removed from analyses. All individuals were enumerated and identified to the lowest possible taxon using the high-quality video collected from the forward-facing video cameras. Some individuals could not be identified either due to inadequate camera zooms and angles or fast swimming speeds of fishes. Mesopelagic fishes were not adequately surveyed with the ROVs, thus they were left out of community analysis (but counts are included in Table S2 and results). Identifications were made using taxonomic keys (e.g., Carpenter et al., 2002; Cohen et al., 1990), but images were also sent to additional taxonomic experts as needed. In addition, biological reference specimens and data from the Florida Museum were used to aid in the identification of some fishes that were not easily identifiable from keys or literature. Both unidentified individuals and mesopelagic species were counted, but removed from all community analyses.

Each dive was categorized into one of six rugged seafloor feature types (Table S1): 1) seamount (an isolated feature rising from the seafloor, > 1000 m height, and of limited extent across the summit), 2) submarine ridge or bank (an elongated steep-sided elevation off the seafloor, with rugged or smooth topography, and often which constitutes a natural prolongation of land territory, 3) submarine canyon (a steep valley cut into the insular slope), 4) basin wall (a steep margin of an enclosed or semi-enclosed depositional environment regardless of size that is otherwise not associated with another discrete feature class), 5) platform (top or the flanks of the carbonate platform that rims Puerto Rico and the Virgin Islands) and 6) mound (an isolated feature of limited extent across the summit, rising from the seafloor <1000 m in height). Each dive on mound, canyon, platform, basin, and ridge/bank features were also categorized into an “other” feature category.

Water Mass Analyses

CTD data were used to determine water mass structure over each site. Downcast CTD data collected during the deployment of the ROV were input into Ocean Data View v4.7. Water masses occupying particular depth zones in the region were then determined following Morrison and Nowlin, 1982; Molinari et al., 1992; Pickart, 1992; Fine et al., 2002; Metcalf, 1976; Fine and Molinari, 1988; Corredor and Morell, 2001 (see Table 1). Water masses for the Greater-Lesser Antilles Region along with their depth and temperature ranges and defining oceanographic features (salinity, oxygen, etc) are summarized in Table 1. Supplemental Figure 1 includes CTD plots representative of each general area surveyed during the study period [Arecibo Escarpment (North of Puerto Rico), Mona Canyon (Mona Passage), Whiting Bank, (South of Puerto Rico), and Noroît and Conrad Seamount (Anegada Passage)].

Table 1. Water masses found in the NE Caribbean. Depth range, temperature range, and defining oceanographic feature are included along with abbreviations used throughout the text.

Water Mass	Abbrev.	Approx. Depth Range (m)	Approx. Temp. Range (°C)	Defining Feature
Caribbean Surface Water	CSW	0-100	25-29	Salinity Min.
Subtropical Underwater	SUW	100-200	20-27	Salinity Max.
18 °C Sargasso Sea Water	SSW	200-400	14-20	Oxygen Max.
Tropical Atlantic Central Water	TACW	400-700	8-14	Oxygen Min.
Antarctic Intermediate Water	AAIW	700-1200	5-8	Salinity Min.
Upper North Atlantic Deep Water	UNADW	1200-1600	4-5	Salinity Max.
Lower North Atlantic Deep Water/Labrador Sea Water	LNADW/ LSW	1600-2300	3-4	Decreasing Salinity
Lower North Atlantic Deep Water/ Iceland Scotland Overflow Water	LNADW/ IOW	>2300-3200	2.5-3	--
Lower North Atlantic Deep Water/Denmark Straits Overflow Water	LNADW/ DOW	>3200	<2.5	--

References: Morrison and Nowlin, 1982; Molinari et al., 1992, 1998; Pickart, 1992; Fine and Molinari, 1988; Metcalf, 1976; Fine and Molinari, 1988; Corredor and Morell, 2001; Fine et al., 2002

Community Analyses

Rarefaction curves were constructed to examine how well the regional demersal species pool was surveyed. These curves were used to determine whether species richness differed between seamounts and other features as well as among water masses. Sample-based rarefaction curves (S_{est}) with corresponding 95% confidence intervals were constructed (100 randomizations, EstimateS v9, Colwell et al., 2004, 2012; Chao et al., 2005) using data from: 1) all 26 dives, 2) seamounts only (9 dives), 3) other features (17 dives), and 4) other features in comparable depths (13 dives) to seamounts. We also created rarefaction curves using the Chao 1 and Michaelis-Menten estimators (Chao 1984; Raaijmakers 1987; Colwell et al. 2004). Rarefaction curves were also calculated for each water mass. Each dive was divided into 100 m depth intervals (164 samples) and matched to the corresponding water mass present in that depth range, resulting in the following number of samples per water mass: SUW: 3 samples, SSW: 13 samples, TACW: 27 samples, AAIW: 35 samples, UNADW: 21 samples, LNADW/LSW: 35 samples, LNADW/IOW: 15 samples, LNADW/DOW: 15 samples. An analysis of covariance (ANCOVA) on log-transformed data was used to determine whether species richness differed between seamounts and other rugged features and among water masses (performed in R, R Core Team 2015).

Multivariate analyses were used to determine whether rugged features and/or water mass influenced fish assemblages (Primer v6, following Clarke and Warwick, 2001; Clarke and Gorley, 2006). Each 100-m depth interval (164 samples) per dive represented a sample with species counts and corresponding environmental data including water mass type. Species' counts per sample were standardized to relative abundance. Standardized abundances were fourth-root transformed to downweight the abundant species relative to the rare species. To test whether fish assemblages differed between seamounts and other rugged features in the region, we calculated similarities in fish assemblages between all pairs of samples using a Bray-Curtis similarity index. We then performed two-way crossed ANOSIMs using all 164 samples to test whether assemblages were significantly dissimilar between seamounts and other features while controlling for the effect of the 100 m depth intervals and of water masses. We performed a third two-way ANOSIM to test whether assemblages differed among water masses while controlling for the effect of feature. Non-metric multidimensional scaling (MDS) ordination plots were then constructed. To reduce noise (see Clarke and Gorley, 2006), species counts were averaged within similar 100-m depth intervals across seamounts (n=57) and across other features (n=107 samples). The MDS plot was then created based on Bray-Curtis similarities calculated on these averaged, standardized fourth-root transformed abundances. We also ran a SIMPROF test to determine if the significantly dissimilar clusters of samples corresponded to known water mass boundaries. Finally, SIMPER analyses were used to determine which species contributed to dissimilarity among assemblages.

We further examined what abiotic factors were important in explaining variation in fish assemblages in the region. Each sample (n=164) was linked to corresponding environmental variables in that depth range. Continuous environmental data (temperature, salinity, dissolved oxygen) were log transformed. Six rugged features (seamount, canyon, ridge/bank, platform, mound, basin) and four general locations (Caribbean Sea, Subtropical Atlantic, Anegada Passage, Mona Passage, see Fig. 1) were coded as binary variables. Distance-based linear modeling (DISTLM) combined with redundancy analyses was performed using PERMANOVA (Anderson et al., 2005). The BEST model was used in conjunction with the Akaike Information Criterion (AIC, Akaike, 1973) to determine which factors combined explained the variation in the model.

Depth range was plotted for a subset of species using the average depth and range of depth occupied. For these analyses, we chose each top discriminating species per 100-m depth zone identified by SIMPER and the most abundant species observed across the study region.

Results

ROV Surveys

Twenty-six ROV dives were conducted across six types of rugged seafloor features, resulting in 297 hours of bottom time and 60 km of seafloor traversed over depths of 98 to 4060 m (Table S1). Nine dives were conducted at seamounts (165-2987 m, 149 hr) and 17 dives (98-4060 m, 148 hr) were conducted across other rugged features including: basin walls (8 dives, 882-406 m, 61 hr), ridges/banks (5 dives, 98-2895 m, 51 hr), platforms (2 dives, 305-610 m, 19 hr), canyons (1 dive, 1687-2138 m, 10 hr) and mounds (1 dive, 825-922 m, 8 hr) (Fig. 1, Table S1). Bottom temperatures ranged from 2.29-24.28 °C with corresponding salinities of 34.54-36.75 and dissolved oxygen values of 2.2-9.9 mg per l. Dissolved oxygen changed rapidly throughout the water column down to depths of ~1200 m, with the oxygen minimum zone found at approximately 400-700 m corresponding to the TACW mass (Fig. S1, Fig. 2). During one dive on the platform site in the Mona Passage, we noted a current direction change with a drop in dissolved oxygen at a depth of ~300-400 m. We note that DO measurements were lower at similar depths in April of 2015 than in September of 2013 and 2014 (Table S1, Fig. S1, Suppl. Fig. 2).

Community Analyses

A total of 3736 individuals were observed at depths of 101-3890 m during the ROV surveys. Of these, 3326 represented at least 156 demersal species from 60 families (Table S2). The rarefaction curve that included all 26 dives indicated that we adequately surveyed the regional species pool of demersal

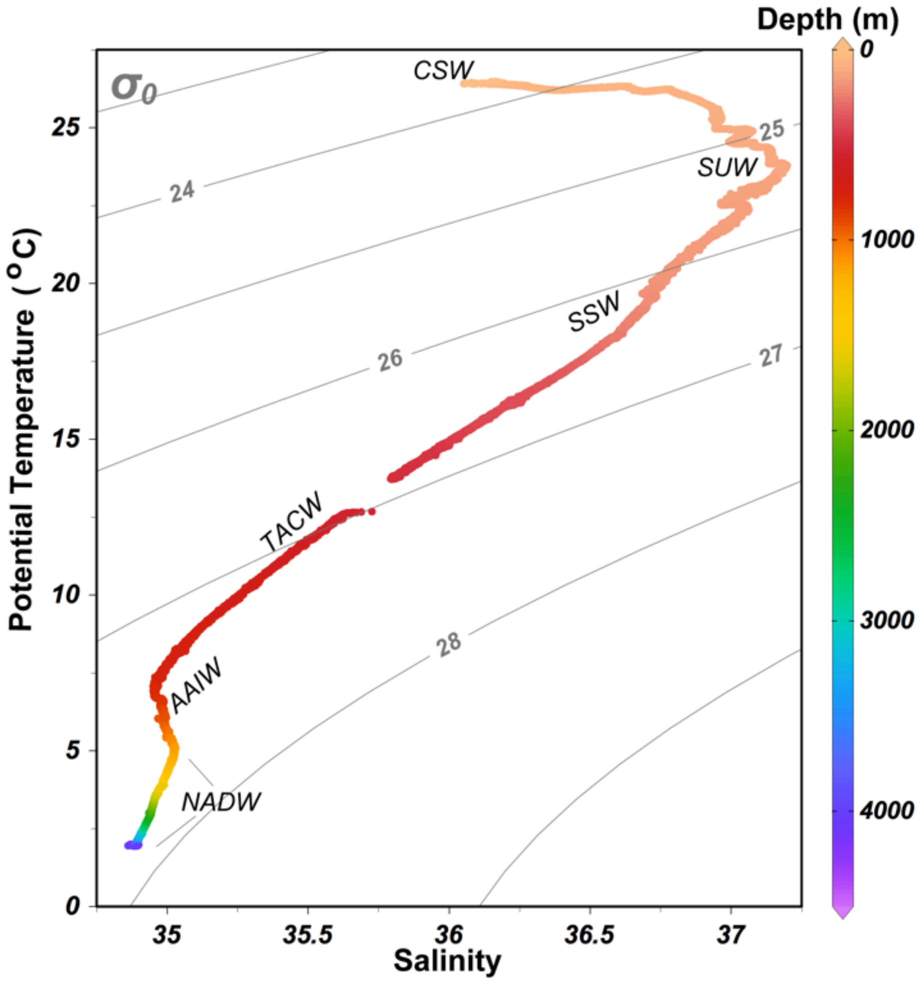

Figure 2. Temperature-salinity data collected with a Sea-bird CTD from the deepest station sampled at the Arecibo Escarpment. Isopycnals and a depth color gradient are included. CSW=Caribbean Surface Water, SUW=Subtropical Underwater, SSW=Sargasso Sea Water, TACW=Tropical Atlantic Central Water, AAIW=Antarctic Intermediate Water. NADW=North Atlantic Deep water (including all upper and lower portions).

fishes; however, additional species will likely be found with further exploration (Fig. 3). The most frequently observed species included deepwater cardinalfishes, *Epigonus* cf. *occidentalis* (17.7%) and *Epigonus* sp. 1 (5%), the halosaurs *Aldrovandia* spp. (10%), and the anthiines, including unidentified species (4.9%) and *Pronotogrammus martinicensis* (3.7%). The majority of species (136 spp.), however, were comparatively uncommon with relative abundances of <1% across the entire study region. Approximately 8% of all fishes could not be identified to species. An additional 410 individuals (11% of all observations) representing 11 species from 10 families of meso- and bathypelagic species were observed near the bottom (Table S2).

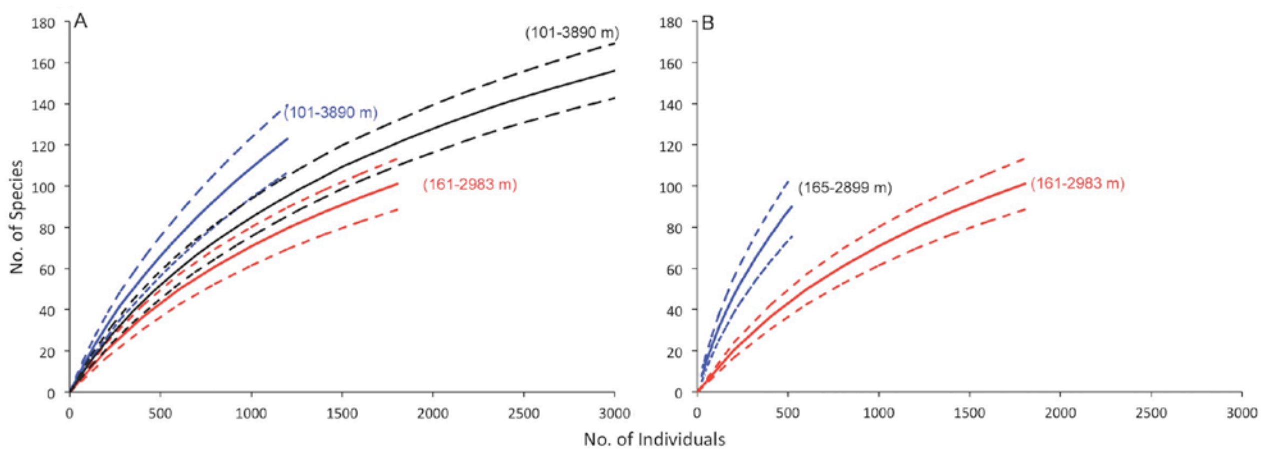

Figure 3. Rarefaction curves of species richness (S_{est}, with 95% CI) (A) across all sites (black, n=26 dives), seamounts only (red, n=9 dives), and other features (blue, n=17 dives) and (B) across seamounts (red, n=9 dives) and other features (blue, n=13 dives) in comparable depths. Depth ranges (m) of fish observations are noted.

We further examined the extent to which demersal fish assemblages differed between seamounts and other rugged seafloor features. Rarefaction curves were significantly different (ANCOVA, F-value=653, p<0.001), with seamounts containing fewer numbers (101 spp., 161-2983 m) of species compared with other features (123 spp., 101-3980 m, Fig 3a). Results using Chao 1 and Michaelis-Menten richness estimators are similar to results using S_{est} (Supp. Fig. 3). Restricting the analysis to a subset of data to include species in comparable depths (~160-3000 m) between seamounts and other features also indicated significantly higher numbers of species at other features compared to seamounts (ANCOVA, F-value=1233 p<0.001, Fig 3b). Rarefaction curves also indicated that many more species would likely be found with additional surveys on other rugged features (Fig 3). Despite the difference in species richness, multivariate analyses indicated that assemblages were similar between seamounts and other features across similar depths (two-way ANOSIM, R=-0.02, p=0.62) and water masses (two-way ANOSIM, Global R=0.004, p=0.41) (Fig. 4A).

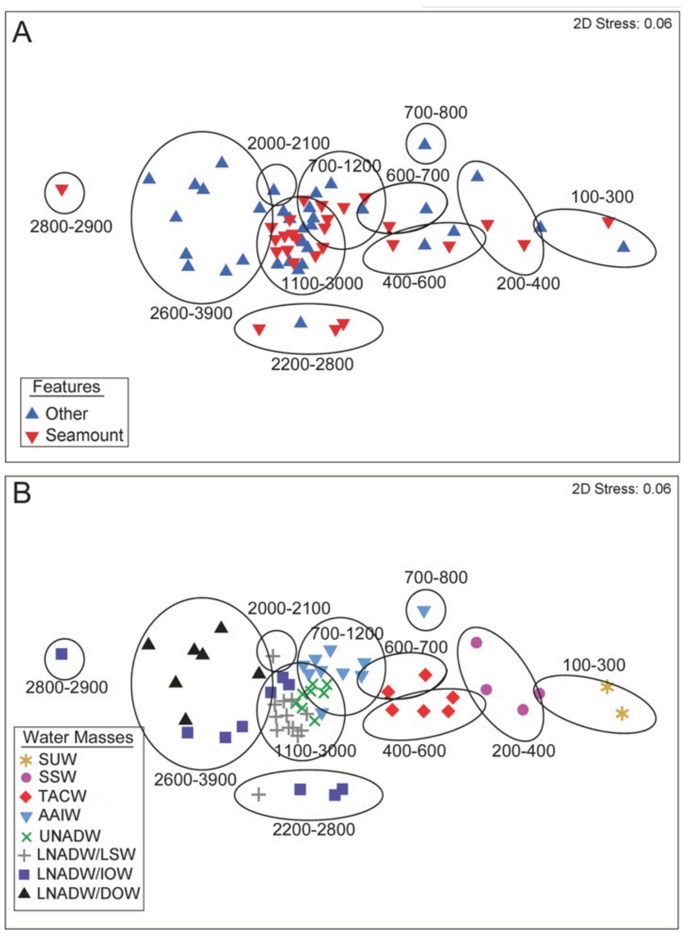

Figure 4. Non-metric multidimensional scaling ordination based on Bray Curtis similarities calculated on fourth-root, transformed relative, averaged abundances. Significant similarity clusters are included (SIMPROF, p<0.05) with corresponding depth ranges (m). A) Symbols=seamounts and other rugged features, B) Symbols=water mass types.

Demersal fish species richness differed among water masses. Rarefaction curves were significantly different among water masses (ANCOVA, F-value=212, p<0.001), with more species in AAIW (700-1200 m) and TACW (400-700 m) water masses compared to others; however, more surveys are needed to adequately document fishes in each water mass as the curves did not reach asymptotes (Fig. 5). Results using Chao 1 and Michaelis-Menten richness estimators are similar to results using S_{est} (Supp. Fig. 3).

Assemblage structure was also significantly different among water masses (two-way ANOSIM, Global R=0.37, p=0.001, Fig. 4B, Table 2), with strong dissimilarities among assemblages occurring in water masses at shallower depths (100-700 m) compared with those at deeper depths (>700 m). Results from the SIMPROF test also indicated 11 clusters (p<0.05) of fish assemblages, which corresponded to the approximate depth boundaries between water masses (Fig. 4B, Suppl. Fig. 2). A few outliers were evident on the MDS plot (see Fig. 4B), and these were due to low alpha diversity at these sites compared to sites in similar water masses (1-4 spp. per sample).

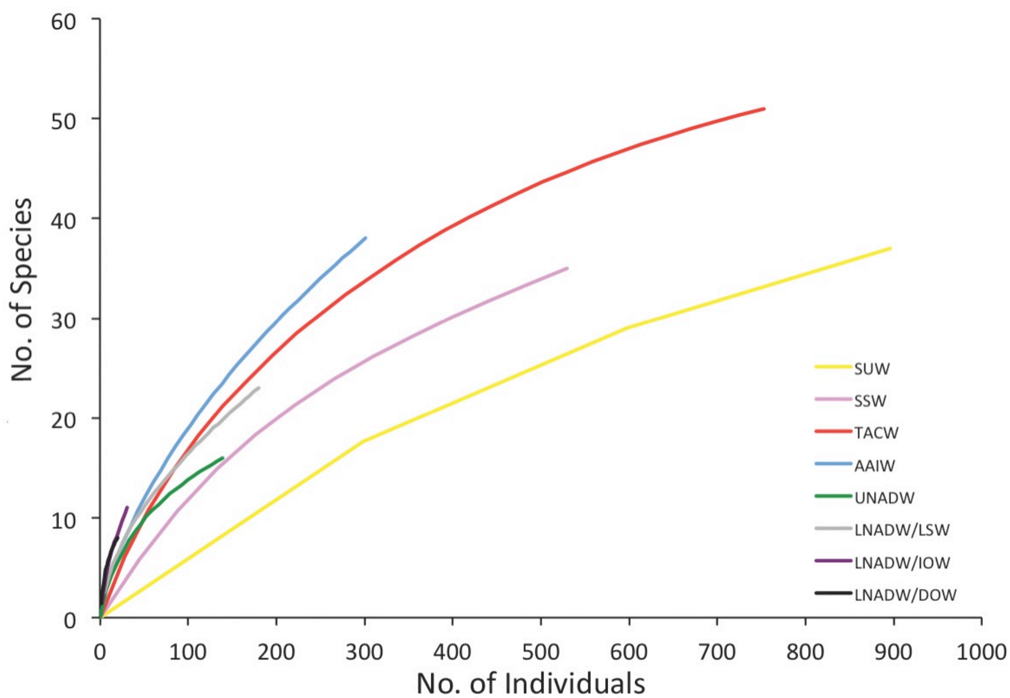

Figure 5. Rarefaction curves of species richness (S_{est}, with 95% CI) across different water masses. (SUW: 3 samples, SSW: 13 samples, TACW: 27 samples, AAIW: 35 samples, UNADW: 21 samples, LNADW/LSW: 35 samples, LNADW/IOW: 15 samples, LNADW/DOW: 15 samples).

We also examined community dissimilarities between water masses occupying adjacent depth zones. Assemblages were significantly different (70-75% average dissimilarity) between TACW (400-700 m) with the adjacent water masses AAIW (700-1200 m) (R=0.5, p=0.001) and SSW (200-400 m) (R=0.3, p=0.001, Table 2). Assemblage structure was also significantly different between LNADW/LSW and LNADW/IOW (R=0.3, p=0.001, Table 2), but these differences were moderate with 48% average dissimilarity between the water masses. LNADW/IOW and LNADW/DOW were also significantly dissimilar (63% average) from one another, although the R-value was low (R=0.1, p=0.01, Table 2). Assemblages found in SSW and SUW water masses were highly dissimilar (83% average dissimilarity) and the R-value was moderate (0.3), but these assemblages were not significantly different from one another (p=0.18). Assemblages were also not significantly different between AAIW (700-1200 m) and UNADW (1200-1600 m) (R=-0.01, p=0.48; 69% dissimilar) and LNADW/LSW and UNADW (R=0.01, p=0.43; 48% average dissimilarity, Table 2).

Table 2. Results from the two-way ANOSIM test on demersal fish assemblages in different water masses. Values in bold are significantly different (p<0.01). R-values closer to 1 indicate stronger dissimilarities between assemblages.

	SUW	SSW	TACW	AAIW	UNADW	LNADW/LSW	LNADW/IOW
SUW (100-200 m)							
SSW (200-400 m)	0.28						
TACW (400-700 m)	**0.61**	**0.64**					
AAIW (700-1200 m)	**0.64**	**0.66**	**0.51**				
UNADW (1200-1600 m)	**0.78**	**0.77**	**0.57**	-0.01			
LNADW/LSW (1600-2300 m)	**0.67**	**0.67**	**0.59**	**0.17**	0.01		
LNADW/IOW	**0.23**	**0.37**	**0.49**	**0.36**	**0.30**	**0.29**	

(2300-3200 m)							
LNADW/DOW (>3200 m)	**0.24**	**0.22**	**0.35**	**0.38**	**0.30**	**0.46**	**0.13**

Differences among assemblages were driven by the relative abundances of certain species in particular water masses (SIMPER). Planktivores, including anthiines spp., *P. martinicensis*, *C. scotti*, and *C. insolata*, and the piscivore *P. volitans* were important discriminating species for the shallowest assemblage in SUW (100-2000 m). The benthivore *Ostichthys trachypoma*, planktivore *E.* cf. *occidentalis*, and the piscivore *Lutjanus vivanus* distinguished the SSW (200-400 m) assemblage. The planktivore *Epigonus* sp. 1, the benthivores *Chlorophthalmus agassizi* and *Polymixia* spp., the micronektonivore *Gephyroberyx darwinii*, and the planktivore cf. *Benthocometes robustus* distinguished the assemblage in TACW (400-700 m). The benthivores *Aldrovandia* spp., *Bathypterois phenax*, and *B. viridensis*, and the micronektonivore *Monomitopus* sp. 1 were important distinguishing species in AAIW (700-1200 m) and UNADW (1200-1600 m) assemblages. The benthivores *Aldrovandia* spp., *Ipnops murrayi*, and *B. phenax* and *A. armatus* were important discriminating species in LNADW/LSW (1600-2300 m). *Aldrovandia* spp. and *I. murrayi* were also relatively abundant in LNADW/IOW (2300-3200 m) whereas the micronektonivore *Bassozetus* spp., and the opportunistic scavengers *C. armatus*, and *Coryphaenoides* sp. 1 distinguished the deepest assemblages in LNADW/DOW (>3200 m).

The BEST model from the DISTLM analyses indicated that depth, feature, temperature, salinity and dissolved oxygen were important factors influencing demersal fish assemblages in the region (DISTLM, BEST Model, AIC=1330). These factors, however, explained only 27% of the variation in demersal fish assemblage structure (R^2=0.27, Fig. 6). The first two dbRDA axes explained 68% of the fitted variation and 18% of the total variation in assemblage structure (Fig.

6). Variables strongly associated with dbRDA axis 1 included temperature (r=0.74) and dissolved oxygen (r=-0.49) (Fig. 6), with positive values indicative of communities occurring in warmer temperatures and lower levels of DO. Depth (r=-0.60) and salinity (r=-0.59) were strongly correlated with dbRDA axis 2 (Fig. 6), with positive values indicating communities at mid/shallow depths and higher salinities. Of all the rugged features, basin (r=-0.32) and seamount (r=0.28) features were the most strongly correlated with dbRDA axis 2 (Fig. 6). Location (Caribbean Sea, Anegada Passage, Mona Passage, Subtropical Atlantic) was not an important factor in the model.

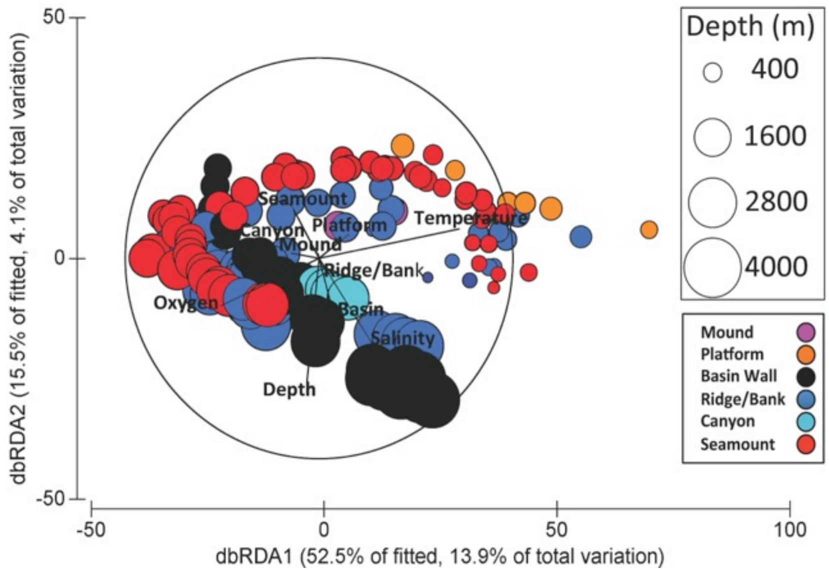

Figure 6. Distance-based redundancy analysis based on Bray Curtis similarities calculated on fourth-root transformed relative abundances in 100-m depth intervals (n=164 samples). Circle size=depth (m); Colors=rugged features.

Depth ranges of numerous species observed in this study were quite narrow for those species occupying depths <1000 m (Table S2, Fig. 7). Depth distributions broadened for those species inhabiting depths >1000 m; except *Coryphaenoides armatus* and *Coryphaenoides* sp. 1 were observed over a relatively narrow depth range >3200 m, corresponding to the LNADW/DOW (Fig. 2, Fig. 7). Although *Aldrovandia* spp. was observed across a broad depth range (536-3568 m), individuals likely represent multiple species, as they could not be identified to species on video. Of note, several closely related species displayed depth divergence, having minimal overlap in their depth distributions (Fig. 7, Table 2). For example, *Bathypterois bigelowi* was observed at 642-882 m, *B. viridensis* was observed at 716-1390 m, and *B. phenax* was observed at 1214-2622 m. *Bathypterois grallator* overlapped (1996-3232 m) with *B. phenax*, but *B. grallator* was observed at the deepest depths surveyed down to 3232 m. *Bathysaurus ferox* and *B. mollis* also diverged in depth ranges, with *B. ferox* found at shallower depths (1349-1647 m) than *B. mollis* (1914-3683 m). The trachichthyids *G. darwinii* and *H. occidentalis* also overlapped minimally in depth with *G. darwinii* found at depths of 294 to 566 m and *H. occidentalis* found at depths of 528-823 m. Three species of chaunacids also diverged in depth, with observations of *Chaunax pictus* at 454-620 m, *C. suttkusi* at 757 m, and *Chaunacops roseus* at 1816-2691 m. In contrast, three species of *Chromis* had similar depth distributions in shallow waters and co-occurred at the same sites: *C. scotti* (114-172 m), *C.* aff. *enchrysura* (116-172 m), and *C. insolata* (112-135 m).

Noteworthy Records and Observations

Numerous depth and geographic range extensions were noted from video observations in this study (Table S2, Figs. 8-10) Thirty-five species were observed deeper than previously reported, including many common reef species (e.g., Chaetodontidae, Holocentridae, Pomacanthidae, Pomacentridae, Serranidae) and the lionfish, *P. volitans* (Table S2). In addition, new locality records for Puerto Rico and the Virgin Islands are documented for 20 species, including at least eight species that have not been previously reported from the Caribbean Sea or subtropical Western North Atlantic (Table S2). Below, we further detail these eight new range extensions.

One *Deania profundorum* (Smith & Radcliffe, 1912), the Arrowhead Dogfish (Fig. 8A), was observed on Conrad Seamount (Dive H1375) at a depth of 583 m. This centrophorid shark is known from the Atlantic, Indian and Pacific Oceans at depths of 205 to 1800 m (Kiraly et al., 2003; Castro, 2011). In the Pacific, *D. profundorum* has been reported from the Philippine Sea (Smith, 1912). This species has also been reported in the eastern North Atlantic off Africa

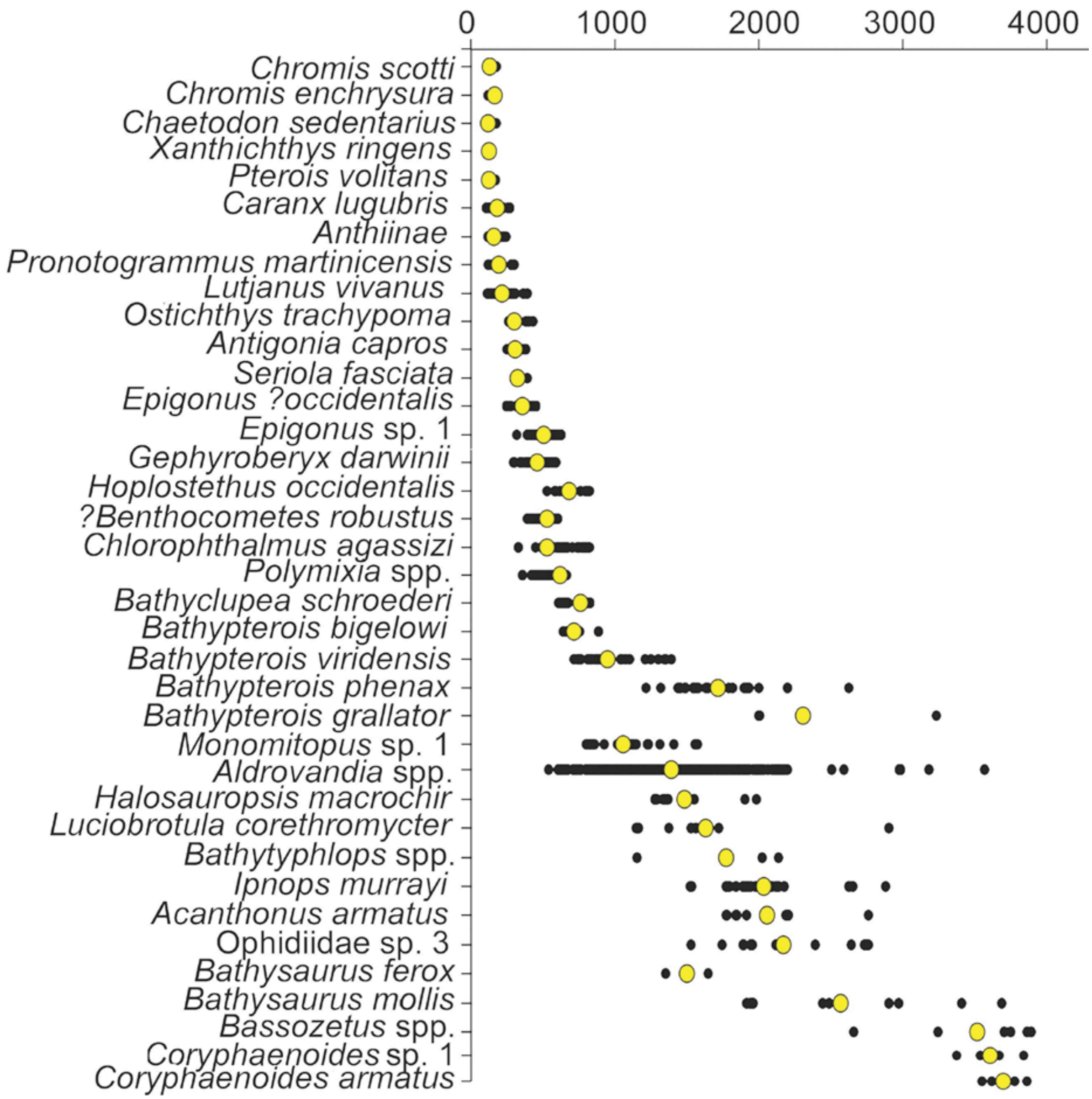

Figure 7. Depth of occurrence (m) of dominant and selected taxa. Yellow circle=average depth.

(Gilchrist, 1922; Cadenat, 1960; Bass et al., 1976) and in the western North Atlantic off North Carolina (Springer, 1959). Our records significantly extend the known geographic range of *D. profundorum,* although there are unpublished records of specimens collected off the Lesser Antilles and in the Gulf of Mexico (G. Burgess pers. comm.). Visual identification was based on the presence of a long, broad flattened snout, a higher second dorsal fin with edge slightly concave (vs. straight), and a subcaudal keel (confirmed by G. Burgess).

Two specimens of *Coryphaenoides leptolepis* Günther, 1877 (Fig. 8B), the ghostly grenadier (Family Macrouridae), were observed; one in Mona Block (H1298) and one along the Arecibo escarpment (EX1502L3-Dive 1) at depths of 2888 to 3690 m. This rattail is known from the Atlantic and North Pacific at depths of 610 to 4000 m (Whitehead et al., 1986). This species was previously recorded in the eastern North Atlantic from off northwestern Ireland south to Mauritania, Azores and the Mid-Atlantic Ridge (Whitehead et al., 1986; Geistdoerfer, 1990; Carneiro et al., 2014; Iwamoto, 2015). In the western Atlantic, *C. leptolepis* is known from the continental slope and rise off Canada and the U.S. (Iwamoto, 2015), off the Bahamas (Sulak, 1982) and off Brazil (Melo et al., 2010). Our observations represent a new locality record for the western North Atlantic off the Greater Antilles. Visual identification was based on the distinct pale coloration becoming dusky towards the tail and dark lips. Fins were transparent with a black first dorsal spine, and elongated first rays of pelvic fins. Sensory pores were extremely large and prominent on the head.

One *Haplomacrourus nudirostris* Trunov, 1980 the naked snout rattail (Family Macrouridae), was observed at Conrad Seamount (H1376) at a depth of 1708 m (Fig. 8C). This observation extends both its geographic and depth ranges and represents a new record for the Caribbean. This species was previously collected from the eastern North Atlantic off Morocco at

1336 m depth (Sobrino et al., 2012) and in the western Atlantic off Brazil (Melo et al., 2010). The majority of records, however, have been from the eastern South Atlantic (Iwamoto and Anderson, 1994), Indian Ocean (Iwamoto et al., 2004), and in the Pacific off Australia and New Zealand (Iwamoto and Merrett, 1997; Merrett and Iwamoto, 2000; Iwamoto and Graham, 2001; McMillan and Iwamoto, 2015) at depths of 690-1600 m. The most noticeable features to identify this species are the laterally compressed head and protruding snout (confirmed by T. Iwamoto).

One *Odontomacrurus murrayi* Norman, 1939, the roundhead grenadier (Family Macrouridae), was observed at Whiting Ridge (EX1502L3-Dive 12) at a depth of 1011 m (Fig. 8D). Our record significantly extends the geographical range in the western Atlantic and represents a new locality record for the Caribbean Sea. This meso- to bathypelagic species is known from north of the Azores to South Africa (Geistdoerfer, 1990; Santos et al., 1997; Porteiro et al., 1999) and off Brazil (Menezes et al., 2003). This species has also been reported to occur in the Indian Ocean (Endo, 1997; Iwamoto et al., 2004) and in the western Pacific (Iwamoto and Graham, 2001; Frickle et al., 2011; McMillan and Iwamoto, 2015; Nakayama et al., 2015; Roberts et al. 2015). Characters used for visual identification included: steeply rounded head profile, terminal, large mouth, upper jaw reaching well beyond a relatively small eye, and a dark, brown body coloration. The bathypelagic species was observed near the bottom moving through rocks.

One *Lepidion* Swainson, 1838 sp. was observed at Barracuda Bank (H1305) at a depth of 1104 m (Fig. 8E). This record substantially extends the geographic and depth ranges of the genus *Lepidion* (Family Moridae) in the western Atlantic Ocean and represents a new record for the Caribbean. The genus, with nine valid species, ranges from the western North Atlantic (Cohen et al., 1990; Quattrini et al., 2015), eastern North Atlantic (Cohen et al., 1990), South Atlantic (Bianchi et al., 1999; Cohen et al., 1990), western Indian Ocean (Cohen, 1986), Southern Ocean

(Duhamel, 2005), and the Pacific Ocean (Masuda et al., 1984; Paulin and Roberts, 1997; Mundy, 2005). Visual identification at the genus level was based on a combination of characters: presence of chin barbel, anal fin notably indented at mid-length, longest ray in first dorsal fin longer than head length and pelvic fin with at least two elongated rays (confirmed by T. Iwamoto).

One snailfish, *Paraliparis* Collett, 1879 sp. (Fig. 8F), was observed in Guayanilla Canyon (EX1502L3-Dive 7) at a depth of 1890 m. This genus of *Paraliparis* (Family Liparidae) is circumglobal at depths of 150 to 1207 m in the Atlantic Ocean (Musick et al., 1975; Wenner, 1979; Scott and Scott, 1988) and depths exceeding 3000 m in the Pacific Ocean (Stein and Drazen, 2014). According to Moore et al. (2003) there are four species from the western North Atlantic: *P. calidus, P. copei, P. garmani,* and *P. liparina*. Our records represent a new locality record for the Caribbean Sea. Visual identification was based on the absence of a ventral sucking disk and the presence of notched pectoral fins (Stein, 2012). Unfortunately, identification to species was impossible from the available views.

Two specimens of the sea toad, *Chaunacops roseus* (Barbour, 1941), were observed (Fig. 8G) at depths ranging from 1816-2961 m. One individual was observed at Mona Block, north of the Mona Passage at 2961 m (H1298), and another individual was observed at Barracuda Bank in the Caribbean at 1816 m (H1304). The holotype (MCZ35380) of this species was collected once before in the Greater Antilles region (Caruso et al., 1989), but the location is a bit ambiguous as it was collected by trawl south of Cuba and the coordinates are unknown (MCZ35380 record). Scattered records of *C. roseus* are also known from the western North Atlantic off Florida and Bermuda (Caruso et al., 1989), the northeastern U.S. coast (Moore et al., 2003) and the New England Seamount Chain (Quattrini et al., 2015). Visual identification of this species was based on neuromast counts (confirmed by J. Caruso).

Three specimens of the North Atlantic Slope Dragonet, *Centrodraco acanthopoma* (Regan, 1904) (Fig. 8H), were observed at Platform (EX1502L3-Dive 6) and Desecheo Ridge (H1302) at depths of 446 to 508 m. This draconettid is known from the eastern and western North Atlantic Ocean at depths of 170 to 594 m (Fricke 1992). In the western North Atlantic, this species was previously recorded from Florida to Georgia (Fricke, 1986). In the eastern North Atlantic it is known from Portugal, Meteor Bank, Josephine Bank, Madeira and off Morocco (Fricke, 1986). Our records represent a new locality record for the Caribbean. Visual identification was based on the lack of prominent longitudinal stripes, with the second dorsal-fin spine appearing to be the longest (confirmed by R. Robertson).

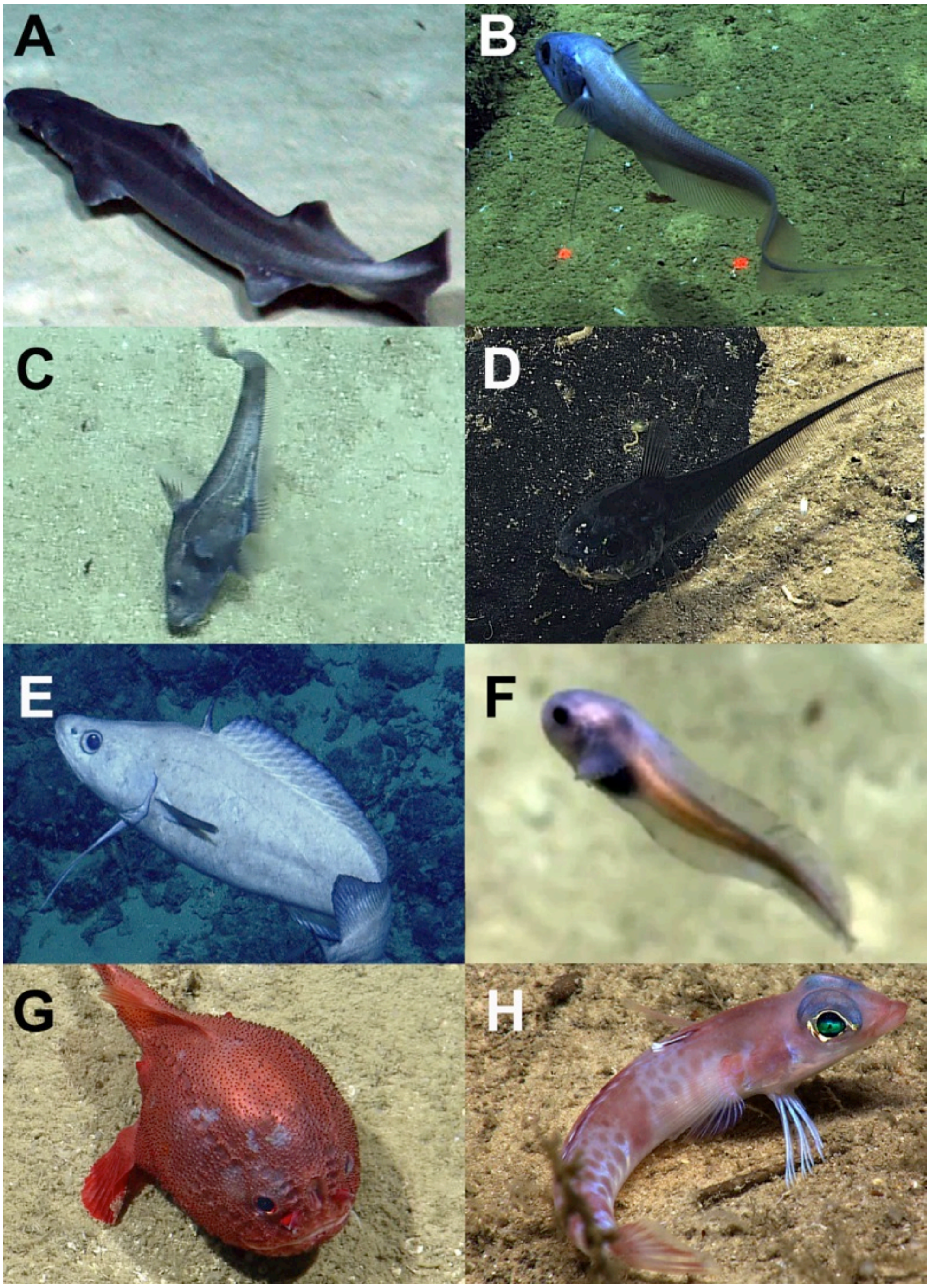

Figure 8. New records for the Caribbean Sea and/or tropical western North Atlantic. (A) *Deania profundorum*, 583 m, H1375 (Conrad Seamount); (B) *Coryphaenoides leptolepis*, 3690 m, EX1502L3-Dive 1 (Arecibo Escarpment); (C) *Haplomacrourus nudirostris*, 1078 m, H1376 (Conrad Seamount); (D) *Odontomacrurus murrayi*, 1011 m, EX1502L3-Dive 12 (Whiting Seamount); (E) *Lepidion* sp., 1104 m, H1305 (Noroit Seamount); (F) *Paraliparis sp.*, 1890 m, EX1502L3-Dive 7 (Guayanilla Canyon); (G) *Chaunacops roseus*, 2691 m, H1298 (Mona Block); (H) *Centrodraco acanthopoma*, 508m, EX1502L3-Dive 6 (Platform). Image credits: Ocean Exploration Trust and NOAA Okeanos Explorer Program.

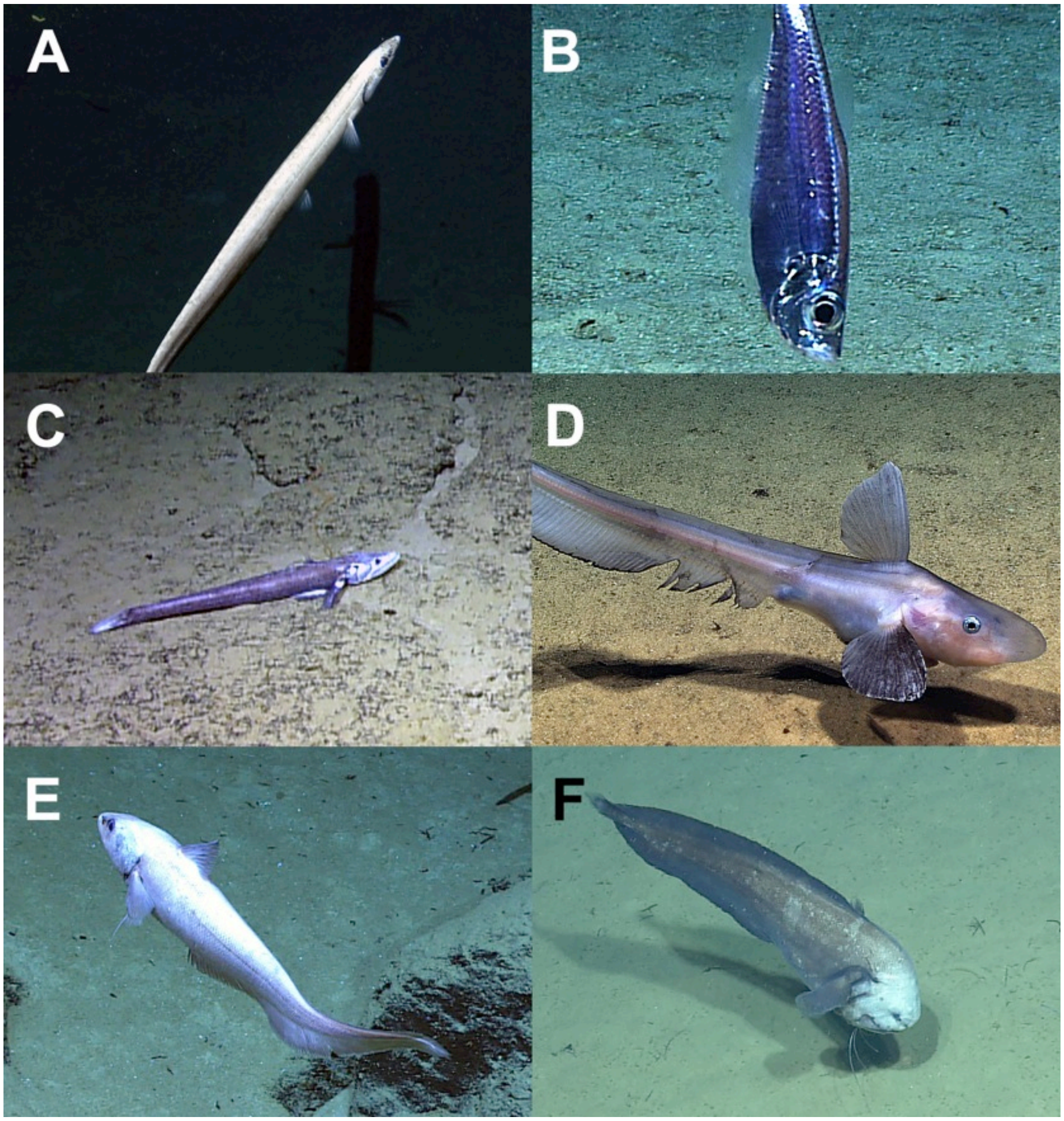

Figure 9. New records for the U.S. Virgin Islands and Puerto Rico. (A) *Polycanthonotus merretti*, 1994 m, H1301(Mona Slide); (B) *Bathyclupea schroederi*, 823m, EX1502L3-Dive 12 (Whiting Seamount); (C) *Bathysaurus ferox*, 1349 m, H1298 (Mona Block); (D) *Ijimaia cf. antillarum*, 546 m, EX1502L3-Dive 12 (Whiting Seamount); (E) *Coryphaenoides armatus*, 3583 m, EX1502L3_Dive 1 (Arecibo Escarpment); (F) *Xyelacyba myersi*, 1888m, H1301 (Mona Slide). Image credits: Ocean Exploration Trust and NOAA Okeanos Explorer Program.

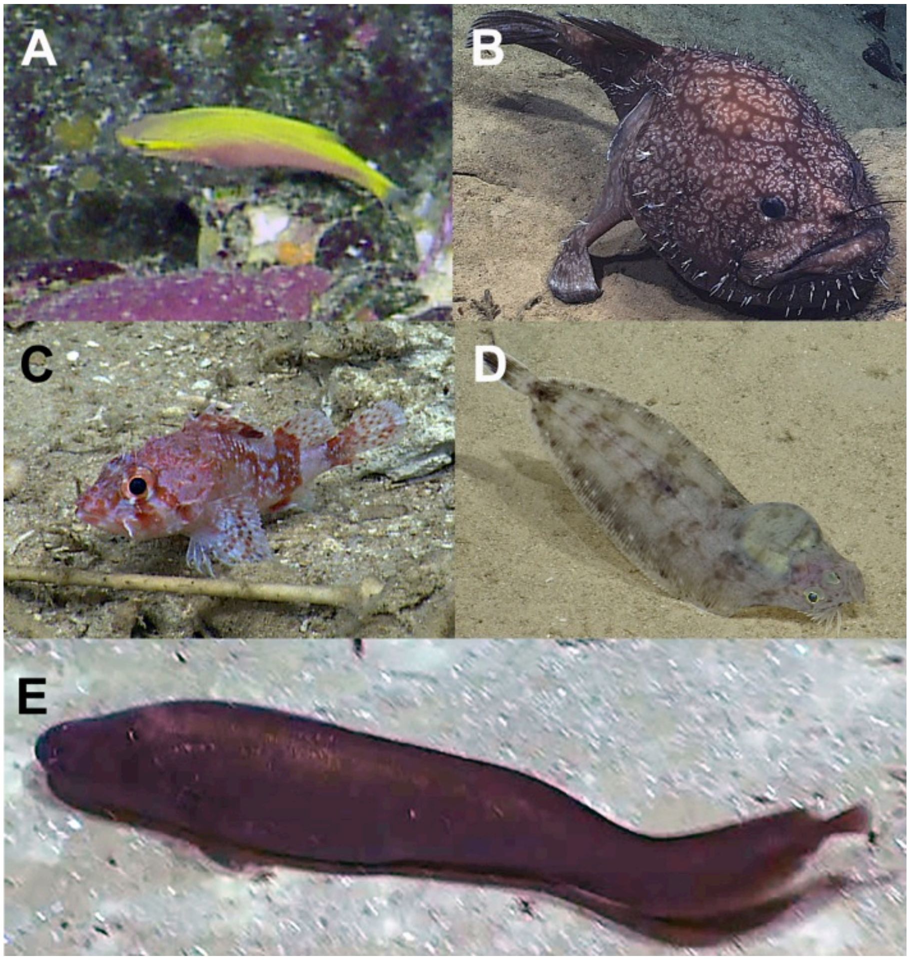

Figure 10. New records for the U.S. Virgin Islands and Puerto Rico. (A) *Liopropoma aberrans*, 172 m, H1375, (Conrad Seamount); (B) *Sladenia shaefersi*, 1009 m, EX1502L3-Dive 12 (Whiting Seamount); (C) *Phenacoscorpius nebris*, 606m, EX1502L3-Dive 3 (Pichincho); (D) *Chascanopsetta danae*, 504 m, H1375, (Conrad Seamount); (E) *Luciobrotula corethromycter*, 2899m, EX1502L3-Dive 11 (Exocet Seamount). Image credits: Ocean Exploration Trust and NOAA Okeanos Explorer Program.

In addition to the new records, we observed at least one, and possibly two new species in the region. Four individuals of a possible un-described species (K. Soares, pers. comm.) of catshark, *Scyliorhinus* Blainville, 1816 sp., (Family Scyliorhinidae) were observed at depths of 508 to 574 m at the Platform (EX1502L3-Dive 6) site in Mona Passage (Fig. 11A). This species resembles *S. torrei;* however, it differs in size and coloration. The individuals observed during the present study had both white and dark spots, well-defined saddles, and were much larger (>40 cm TL) than reported sizes of *S. torrei (*maximum reported size of 32 cm TL, Compagno, 2002). We recognize that collections are required to corroborate whether or not this is a new species of *Scyliorhinus*, but these observations warrant further study.

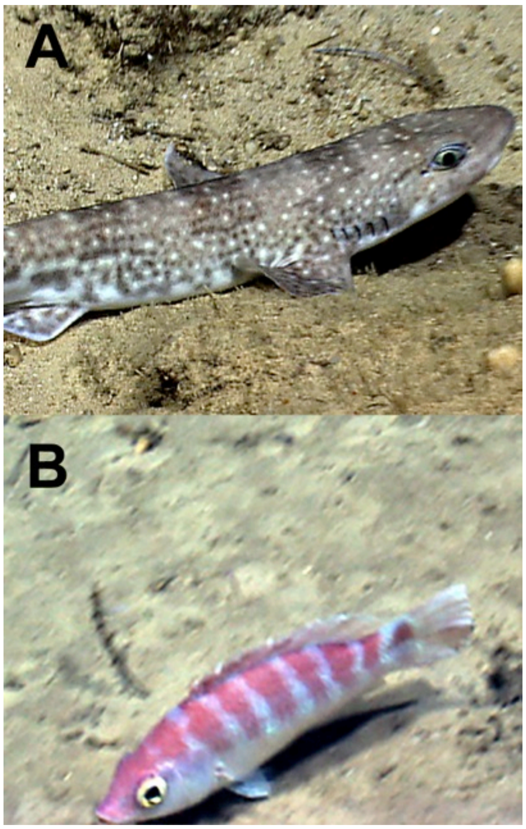

Figure 11. Potential new species identified from ROV video. (A) *Scyliorhinus* sp., 574m, EX1502L3-Dive 6 (Platform); (B) *Polylepion* sp. A, 363 m, EX1502L3-Dive 3 (Pichincho). Image credits: NOAA Okeanos Explorer Program.

Four individuals of the red-band wrasse *Polylepion* Gomon, 1977 sp. A (Family Labridae) were observed at depths of 240 to 457 m (Fig. 11B). This species was observed in the Anegada Passage at Noroît (H1305) and Conrad (H1375) seamounts and in the Mona Passage at Platform (EX1502L3-Dive 6) and Pichincho (EX1502L3-Dive 3) sites. This species was previously collected in the Caribbean Sea off Curaçao, and is in the process of being described (C. Baldwin and R. Robertson, pers. comm.). Visual identification of this wrasse was based on the presence of six distinct red bands and a dark spot in the caudal region (confirmed by C. Baldwin and R. Robertson).

Discussion

Our study highlights that abiotic variables are linked to the assembly of demersal fish communities in deep waters of the NE Caribbean. Water masses, with distinct temperature, salinity, and dissolved oxygen signatures, generally corresponded with the vertical zonation of fishes at deep, rugged seafloor features. In particular, strong species turnover occurred in the upper ~1200 m depth range, and may be driven by changes in water mass characteristics including temperature (~20ºC temperature change) and dissolved oxygen (~7 mg per l DO change). Our study also indicated that species composition was similar between seamounts and other rugged features across comparable depths. Therefore, similar to seamount studies in other regions (Lundsten et al., 2009; Howell et al., 2010; Rowden et al., 2010), seamounts in the Anegada Passage do not harbor distinct communities from other rugged features along insular margins in the Caribbean. Also, they do not appear to be biodiversity hotspots, at least when compared to features of equivalent topographic complexity. With 35 new depth records, 20 new locality records for the U.S. EEZ, eight range extensions for the tropical Atlantic and/or Caribbean Sea, and two possible new species, our study adds considerably to the knowledge of mesophotic and deep-sea fish biogeography. These observations can also serve as important baseline data for assessing future range shifts caused by warming ocean temperatures.

Patterns in Community Structure

Comparisons of fish faunas between seamounts and other rugged seafloor features at similar depths indicated that seamounts in the Anegada Passage do not harbor distinct communities. Overall, a consensus has emerged that seamounts may be functionally equivalent to other rugged features. Other studies have also indicated that communities are highly similar between seamounts and other features (i.e., canyons, banks, ridges) of equivalent complexity and substratum types (i.e., hard substrate). For example, epibenthic (Howell et al., 2010), ophiuroid (O'Hara et al., 2007), fish (Tracey et al., 2004) and squat lobster (Rowden et al., 2010) communities at seamounts were shown to be similar to nearby non-seamount communities at comparable depths. Communities between different types of rugged features may be exceptionally similar in areas like the Caribbean, where various rugged features exist in close proximity to one another (50-100 km apart).

Our results also indicated that seamounts in the Anegada Passage do not appear to be biodiversity hotspots. Rarefaction curves indicated fewer species at seamounts compared to other rugged seafloor features in comparable depths. Tracey et al. (2004) also found lower species richness of fishes at seamounts off New Zealand compared to the surrounding slope, and suggested that seamounts may not be suitable habitats for all species. For example, species that feed in the soft sediment benthos would be absent or rare from seamounts dominated by hard substrate. Howell et al. (2010) also found lower levels of epibenthic faunal diversity at seamounts compared to nearby banks. Although Howell et al. (2010) attributed diversity differences to overall depth range covered by surveys, the authors also suggested that lower species diversity on seamounts may be related to a species-area effect as seamounts may have overall less area than other features that are more contiguous at comparable depths. Because we also analyzed data only from comparable depths, our results suggested that overall depth range covered was not a factor in our study and thus a species-area effect warrants further investigation. It is possible that the other features combined (i.e., canyons, banks/ridges, basin walls, and mounds) encompassed an overall higher habitat heterogeneity, which could lead to higher overall species diversity at other rugged features compared to seamounts. Thus, comparisons among individual features are warranted. Nevertheless, a consensus has emerged (Tracey et al., 2004; O'Hara et al., 2007; Schlacher et al., 2007; Howell et al., 2010): seamounts do not appear to be biodiversity hotspots when compared to features of equivalent substratum types in comparable depths.

Depth zonation of fish assemblages is a common theme in deep waters worldwide (see Carney 2005). In general, demersal fish assemblages found at different depths in the NE Caribbean corresponded with the vertical stratification of local water masses. Depth zonation patterns matching water mass distribution have been noted for deep-water fishes in the eastern Atlantic off the Azores, Cape Verde, and Madeira (Menezes et al., 2006, 2009, 2015), around the rim of the North Atlantic (Koslow, 1993; Bergstad et al., 2012), in the temperate western North Atlantic (Quattrini et al., 2015), and off Australia (Williams et al., 2001). Likewise, results from two different methods (SIMPROF, ANOSIM) in our study indicated that the vertical patterns in the NE Caribbean fish fauna generally corresponded to boundaries between water masses, suggesting the importance of local water mass characteristics influencing the distribution of deep-water demersal fishes in the NE Caribbean.

We found strong species turnover in the upper 1200 m of the depth range surveyed. Fish assemblages were highly dissimilar between adjacent water masses at depths < 1200 m (SUW, SSW, TACW, AAIW). Both a strong thermocline and halocline occur at these depths (Suppl. Fig. 1), and as indicated in the multivariate analyses, influence variation in fish assemblages. The strongest differences were between fish assemblages in depth ranges overlain with TACW (400-

700 m) compared to adjacent water masses AAIW (700-1200 m) and SSW (200-400 m). Not only do temperature and salinity change in this depth zone, an oxygen minimum layer is also associated with the TACW water mass. Although dissolved oxygen in this depth zone (2-4 mg per l) is higher than oxygen minimum zones around the globe (0.5 ml per l, Levin, 2003), the low oxygen combined with strong temperature and salinity changes associated with the TACW may influence variation in fish assemblages over a bathymetric gradient. It appears that TACW could serve as a strong physiological barrier to species invading either shallower or deeper depths.

Fish assemblages became more similar between adjacent water masses in deeper waters, suggesting a more gradual change among fish assemblages in deeper waters instead of a strong turnover in species composition as seen in shallower depths. Fish assemblages at sites overlain with AAIW (700-1200 m) and UNADW (1200-1600 m) and at sites overlain with UNADW (1200-1600 m) and LNADW/LSW (1600-2300 m) were similar. We also found only moderate differences in assemblages between LNADW/LSW (1600-2300 m) and LNADW/IOW (2300-3200 m) and LNADW/IOW (2300-3200 m) and LNADW/DOW (>3200 m). Although there were a few species unique to each depth zone, many species (e.g., *Aldrovandia* spp., *Bathypterois* spp.) at depths >1000 m had broad depth distributions and occupied different water mass types. We note that *Aldrovandia* spp. includes multiple species that could not be consistently identified using video alone. *Aldrovandia affinis, A. gracilis, A. oleosa, A. phalacara,* and *A. rostrata* have been recorded from either the sub-tropical Atlantic (Bahamas, Sulak, 1982), or the Caribbean Sea (Anderson et al., 1985) and also occur across broad depth ranges at depths >1000 m. The presence of numerous species with broader depth distributions at deeper depths agrees with the accepted trend of deeper species occupying larger areas due to the uniformity of environmental conditions (Gage and Tyler, 1991; Merrett and Haedrich, 1997). Deep-sea fishes tend to have more widespread distributions than shallower species due to the overall homogeneity and stability of environmental conditions (Menezes et al., 2006; Clark et al., 2010a). Our study indicated little change in temperature, salinity, and dissolved oxygen at depths >1200 m throughout the NE Caribbean (Suppl. Fig. 1, Suppl. Table 1). The relative homogeneity in environmental characteristics at deeper depths corresponds to the presence of NADW; there were only slight changes in abiotic characteristics (e.g., ~ 2 ºC temperature change) between the upper and lower portions of NADW.

Although the abiotic factors associated with water masses explained a substantial (~20%) proportion of the variation in fish assemblages in the NE Caribbean, several environmental factors were missing from our analyses (e.g., nutrients, particulate organic matter, light intensity, hydrostatic pressure, coral abundance). In addition, biotic factors have rarely been considered (e.g., competition, food web linkages, parasitism) in deep-sea fish community ecology studies. In our study not only did species assemblages change, but the diversity or dominance of particular feeding guilds (at least for the SIMPER discriminating species) changed as well. At the shallowest depths, small planktivores (pomacentrids, anthiines) and piscivores (i.e., lionfish) were important discriminating species. Small planktivores are not only capitalizing on the increased productivity in shallower depths, they are able to tolerate higher temperatures (see Brown and Thatje, 2013). At deeper depths, there was a switch to a dominance of benthivores (or hyperbenthic crustacean feeders, following Drazen and Sutton, 2016). These included ipnopids (*I. murrayi, Bathypterois* spp.) and the halosaurs *Aldrovandia* spp. Opportunistic scavengers, including *Coryphaenoides* spp. (Drazen and Sutton, 2016), dominated the deepest depths, perhaps to capitalize on limited and ephemeral food resources present. Thus, food availability and light intensity are important factors structuring fish assemblages that could not be directly addressed in the present study, but need to be investigated in conjunction with functional diversity to provide more thorough insights into ecosystem functioning across a bathymetric gradient.

Our study also indicated that numerous closely related species exhibit depth divergence in the NE Caribbean. We observed depth divergence in several bathyal and abyssal genera, including *Bathypterois* spp., *Bathysaurus* spp. and the Chaunacidae and Trachichthyidae families. This depth divergence is likely driven by the factors that co-vary with depth, such as water mass characteristics (temperature, salinity, dissolved oxygen) and hydrostatic pressure, as these factors influence the ecology, physiology, and biology of fishes. Menezes et al. (2006) suggested that the influence of water mass characteristics on fish distributions must be established over evolutionary time if water masses are to shape consistent patterns in assemblage structure and depth zonation. In addition, a recent study by Gaither et al. (2016) indicated that depth was important in the evolution of the genus *Coryphaenoides*, with abyssal species arising only once and then subsequently diversifying in deep water. Likewise, Baldwin and Robertson (2014) noted that species in the genus *Liopropoma* overlap minimally in depth distributions, and suggested depth-mediated speciation may have been important in the evolution of this genus. Depth and the co-factors that vary with it (i.e., water masses) are important in the evolution of deepwater taxonomic groups, and leads to distinct zonation of fish assemblages.

Insights into Biogeography

Surveys across rugged seafloor features continually yield new data in poorly known mesophotic and deep-sea ecosystems. The use of ROVs and submersibles on rugged features, which are conventionally difficult to sample using surface deployed gear (e.g., trawls and traps), provide valuable data on distributions, behavior, and live colorations of species that have been rarely seen *in situ*. Based on 26 dives completed across the NE Caribbean, 42% of all species observed in this study had not been previously recorded from particular depths or general localities in the region. Recent submersible surveys in deep waters in other regions of the Caribbean (i.e., Curaçao) have also documented range and depth extensions and species new to science (see Baldwin and Robertson, 2014, 2015; Baldwin et al., 2016). Our study combined with these recent efforts suggests that further investigations across mesophotic to deep-sea depths are essential to fully document species' distributions and unveil patterns in biodiversity across the globe.

A total of 22% of the observed species were seen deeper than what was previously recorded in the literature. These included several reef-associated species, including chaetodontids, holocentrids, pomacentrids, pomacanthids, and serranids, which are known to be common inhabitants of shallow-water Caribbean reefs (see http://biogeodb.stri.si.edu/caribbean, R. Robertson). Fully documenting depth distributions is important to help determine whether deep reefs can serve as refugia by re-populating shallow-water coral reefs in the face of global ocean change (Glynn et al., 1996). In addition, we documented 28 individuals of the invasive lionfish *P. volitans* at depths of 101-167 m. To our knowledge, these represent the deepest documented records of this species in the Caribbean.

We also note that chondrichthyans were absent beyond 2000 m in the NE Caribbean; the deepest observation was of an unknown skate (family Rajidae) at a depth of 1715 m. This lends support to the premise that chondrichthyans are uncommon deeper than 2000 m, which may be due to their high energy demands created by near-constant swimming and an oil-rich liver for buoyancy (see Musick and Cotton 2015).

As noted by Miloslavich et al. (2010), fish inventories for the Caribbean are incomplete and new species and range extensions of known species are expected. In particular, fishes inhabiting insular slopes along deepwater reefs from mesophotic depths down to ~500 m throughout the Caribbean are poorly known (Colin, 1974; Bunkley-Williams and Williams, 2004). Our observations added 20 new locality records for Puerto Rico and the Virgin Islands and eight new records for the Caribbean Sea and/or sub-tropical western North Atlantic waters. These species have likely remained undiscovered in sub-tropical and Caribbean waters due to association with complex habitats that precluded their prior detection. All species new to the region have broad distributions in the temperate, western and eastern North Atlantic. We acknowledge that collections are needed to confirm these species identifications as cryptic species are highly likely; recent DNA-based methods have documented many cryptic species from both mesophotic reefs (e.g., Baldwin and Robertson, 2015) and the deep sea (Roa-Varon, unpubl. data). Regardless, our data suggest many more discoveries remain in deep regions of the Caribbean.

The abyssal fish fauna from the Caribbean region may be more similar to other areas of the North Atlantic than previously suggested. Based on 35 species collected by trawl at depths of ~2000-6800 m throughout the Caribbean, Anderson et al. (1985) suggested that the Caribbean abyssal fauna differed strikingly from temperate latitudes of the North Atlantic. Although we only documented ~35% of the fishes (identified to lowest possible taxon) reported by Anderson et al. (1985), we documented 15 abyssal species, including at least 13 taxa known from the temperate North Atlantic (Musick et al. 1975; Sulak, 1982; Haedrich and Merrett, 1988; Moore et al. 2003). We also added four records to the abyssal fish inventory for the region, including *C. roseus*, *C. leptolepis*, *C. armatus*, and *H. macrochir*; species documented previously from the temperate N. Atlantic (Moore et al. 2003, Quattrini et al. 2015). The absence of certain North Atlantic abyssal species in the Anderson et al. (1985) study is likely due to the trawling methods used and lack of sampling in steep, rugged and rocky terrain. The absence of certain species in our study that

Anderson et al. (1985) reported could either be due to species' associations with soft substrates or to our inability to identify some individuals (e.g., ophidiiformes) to species. It is also possible that the ROV did not document some species that either avoid submergence vehicles (Lorrance and Trenkel 2006) or are too small and cryptic to be observed with the ROV. Regardless, the abyssal fish fauna may be more similar throughout the greater North Atlantic (e.g., Musick et al. 1975; Sulak, 1982; Haedrich and Merrett, 1988; Moore et al., 2003), than suggested by Anderson et al. (1985).

Future Research and Conclusions

Our study improved our understanding of the deepwater fish fauna inhabiting the NE Caribbean. The high-definition video collected during these expeditions is invaluable, capturing images of many fishes never or rarely seen in situ. Although future collections are warranted to confirm some species identifications, describe new species and provide more information on feeding ecology, the imagery collected can provide further information on behavior (e.g., locomotion) and habitat associations of fishes. Our results indicated the importance of water mass characteristics in influencing the vertical distribution patterns of the demersal fish fauna. Changes to temperature regimes from ocean warming will impact species not only by shifting geographic distributions, but also by shifting vertical distributions. However, more work is necessary to examine the importance of biotic factors and other abiotic factors (i.e., substratum heterogeneity, productivity) that are also driving variation in fish communities in the NE Caribbean. Our results also suggested that seamounts are functionally equivalent to other rugged seafloor features; however, we suggest a need to compare different features individually, as certain features (e.g., submarine canyons) may contain higher biomass than others (e.g., banks). Finally, further work is critical to understand the role that the Anegada seamounts play as stepping-stones in linking deepwater communities from the Atlantic to the Caribbean Sea.

Acknowledgements

Funding was provided by NOAA-OER for the 2014 E/V Nautilus cruise and by the USGS Environments and Hazards Program and Ocean Exploration Trust for the 2013 E/V Nautilus cruise. The NOAA Okeanos Explorer Program supported and funded the 2015 cruise. This research used data provided by the *Nautilus* Exploration Program, Cruise NA052 and NA035. Thanks to the ship crews of the E/V Nautilus and E/V Okeanos Explorer and the expedition coordinators K. Croff Bell, N. Raineault, B. Kennedy, and K. Cantwell. We also thank the crews of both *ROV* Hercules and *ROV* Deep Discoverer and the onshore science team for the Okeanos Explorer, particularly M. Scharer and G. Garcia-Moliner. Particular thanks to R. Robertson for helpful discussions and J. McClain-Counts for data management. We also thank the following ichthyologists for confirming species identifications: B. Andrews, C. Baldwin, G. Burgess, J. Caruso, T. Iwamoto, B. Mundy, T. Munroe, J. Nielsen, P. Moller, J. Moore, S. Poss, R. Robins, R. Robertson, S. Ross, D. Smith, K. Soares, and K. Sulak. We thank D. Tracey, M. Randall, and two anonymous reviewers for their helpful edits and suggestions. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author Contributions: AMQ and AWJD conceived and designed the research. AMQ identified fishes, conducted analyses and wrote the article with significant contributions from AWJD. RS and ARV identified a portion of the fish observations; both researched and provided text on noteworthy observations. JDC provided information on habitat types and created the map. All authors edited the text and approved the final version of the manuscript.

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