Fish, Coral, and Sponge Assemblages Associated With Altiphotic and Mesophotic Reefs Along the Guánica Biosphere Reserve Continental Shelf Edge, Southwest Puerto Rico

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The benthic and fish communities of the central portion of the Guánica, Puerto Rico shelf edge were studied to determine species abundance, distributions and species overlap between two depth stratifications, 20 and 45 m, at eight sites. A total of 67 fish species belonging to 21 families were identified. Similar species richness estimates were observed between depths, though fish assemblage composition differed significantly, with observable changes in feeding guild contributions of herbivore and omnivore (20 m) to a deeper assemblage composed of piscivores and planktivores (45 m). Coral assemblages consisted of 31 species at 20 m and 11 species at 45 m, accounting for 17.0% (±1.76 SE) and 2.6% (±0.89 SE) benthic cover for the altiphotic and mesophotic surveys, respectively. The altiphotic and mesophotic coral reef communities support different scleractinian coral assemblages with minimal species overlap. Altiphotic surveys of sponges yielded a higher species richness than mesophotic, with 60 and 54 species respectively, and an overall total of 71 species identified from both depths, with 45 species overlapping (63.0%). The percent cover of sponges surveyed at altiphotic reefs accounted for 9.0% (±1.04 SE), while the percent cover of sponges surveyed at mesophotic reefs was 14.0% (±1.96 SE). Our data show fish, coral, and sponge assemblages are differentiated between 20 and 45 m along the Guánica shelf edge offshore of the Guánica Biosphere Reserve. This study represents the first observations for species distributions of adjacent altiphotic and mesophotic coral reef habitats along the Guánica shelf edge, as well as provides an annotated species list of the local sponge fauna. Combined, these results highlight the need for continued environmental stewardship and conservation in the area.

Keywords: MCE, biodiversity, conservation, ecology, management, Caribbean, coral reefs

INTRODUCTION

Mesophotic coral ecosystems (MCEs) are found on insular and continental slopes between 30–40 and 150 m in the tropics (Hinderstein et al., 2010; Locker et al., 2010; Slattery et al., 2011). They are characterized by low light, decreasing water temperatures, upwelling of nutrients, as well as providing unique ecological niches for benthic and mobile fauna (Lesser et al., 2009; Sherman et al., 2010). Research on MCEs has increased substantially over the past two decades (Kahng et al., 2010, 2014; Loya et al., 2016). This is largely due to the combination of increased ease of *in situ* data observations and collections through underwater technological advancements (i.e., SCUBA, closed circuit rebreathers, remotely operated vehicles, and submersibles) and the appraisal of MCEs as potential refuges for adjacent altiphotic (i.e., shallow reef habitats adjacent to upper mesophotic reefs; see Baldwin et al., 2018) coral reefs (Glynn, 1996; Lesser et al., 2009; Bongaerts et al., 2010; Hinderstein et al., 2010). As deep-water refuges, MCEs may provide a haven for scleractinian corals and commercially important fish (Lindfield et al., 2016), thereby replenishing adjacent impacted shallow water reefs with both coral (Bongaerts et al., 2017; Kahng et al., 2017) and fish larvae (Bejarano et al., 2014; Vaz et al., 2016), leading to the formation of the deep reef refuge hypothesis (Bongaerts et al., 2010).

Despite their depth (∼30–120 m), mesophotic reefs are not immune to stressors and can experience environmental degradation at levels comparable to nearby altiphotic coral reefs (Lesser and Slattery, 2011; Loya et al., 2016; Smith et al., 2016). For instance, mesophotic reefs in the Bahamas experienced drastic reductions in coral and sponge coverage associated with a lack of herbivorous fish, which was caused by predation from the invasive lionfish (Lesser and Slattery, 2011). The effect of this outbreak casts doubts on whether MCEs are more resilient than their altiphotic counterparts to the effects of invasive species (Lesser and Slattery, 2011). In addition, MCEs closer to shore, and especially near terrestrial outflows and coastal development, exhibit decreased coral coverage and smaller associated fish assemblages (Appeldoorn et al., 2016a; Baker et al., 2016; MacDonald et al., 2016). Thus, mesophotic reefs cannot be assumed to be buffered from natural and anthropogenic stressors solely because of their increased depth or distance from the coast (Smith et al., 2016; White et al., 2017).

Recently, more attention has been given to MCEs in the Atlantic and Caribbean region, including research off Puerto Rico (Galindo-Estronza et al., 2016; Veglia et al., 2018), the US Virgin Islands (Holstein et al., 2016; Weinstein et al., 2016), Curaçao (Hoeksema et al., 2016; Glasl et al., 2017), Bermuda (Goodbody-Gringley et al., 2015), Honduras (Laverick et al., 2017), Belize (Lesser and Slattery, 2013), the Bahamas (Slattery and Lesser, 2012; Slattery et al., 2016), Little Cayman (Brazeau et al., 2013), Colombia (Gonzalez-Zapata et al., 2018), and Mexico (Gress et al., 2017). In Puerto Rico, the primary focus of past (e.g., Starck and Colin, 1978; Nelson and Appeldoorn, 1985; Dennis et al., 2004) and more recent work (Sherman et al., 2010, 2013a,b) has been on MCEs located off the south coast of the island (see review by Appeldoorn et al., 2018). Along this coast, benthic coral coverage tends to increase east to west along the insular continental shelf edge; from Ponce, a major city and a maritime port, to La Parguera Natural Reserve (Appeldoorn et al., 2016b). In general, benthic coral coverage and tridimensional complexity are affected regionally by sediment transport levels and the slope degree of the insular shelf edge (Sherman et al., 2016), both of which change rapidly over small distances (Sherman et al., 2010, 2013a,b). The well documented nature of this area (García-Sais et al., 2017), combined with the influence of freshwater outflow from the nearby coastline (Whitall et al., 2013a), allows for comparisons between less affected MCEs to the west (La Parguera) and more affected MCEs to the east (Ponce) (Appeldoorn et al., 2016a).

Located centrally between Ponce and La Parguera, the Guánica Biosphere Reserve was created in 1981 to protect terrestrial, coastal, and marine (strictly within the insular shelf-break, <30 m) ecosystems (García-Sais et al., 2001). Detailed studies regarding Guánica's marine ecosystem have only begun taking place within the last 20 years (Sherman et al., 2010, 2013b, 2016). Several concerns persist for the area, such as the introduction of pollutants and terrigenous sediments flowing in through the Rio Loco system (Morelock et al., 1994; Sherman et al., 2013a). Further coastal development in the city of Ponce (García-Sais et al., 2005) is of concern as well due to the westerly currents created by the northeast-trade winds, which has the potential to significantly decrease water quality, affecting shallow and mesophotic coral reefs west of Ponce (**Figure 1**).

Though many studies in Puerto Rico have investigated both the physical conditions (e.g., bathymetry, sediment transport, prevailing hydrodynamic forces, etc.) (Lumsden et al., 2007; Hubbard et al., 2008; Locker et al., 2010; Armstrong and Singh, 2012; Sherman et al., 2013a,b; Whitall et al., 2013a; Appeldoorn et al., 2016a,b) and biological components (Armstrong et al., 2009, 2011; Bauer et al., 2013; Ballantine et al., 2016) of these deep coral reef habitats, few have attempted to compare the ecology between altiphotic and mesophotic reefs (García-Sais, 2010; Pittman et al., 2010; Bejarano et al., 2014; Lucas et al., 2016; Hammerman et al., 2017). In Puerto Rico, even less studies have explored the diversity, abundance, disease and biomass of altiphotic and mesophotic reef sponges (e.g., Vicente, 1990; Weil, 2005; Rivero-Calle, 2010). Within the Caribbean region, sponges are considered one of the most visually dominant and diverse taxa inhabiting shallow and deep coral reef ecosystems (Rützler, 2004; Wulff, 2012; Slattery et al., 2013). In Puerto Rico, one of the first studies regarding marine sponges were carried out by Wilson (1902) and de Laubenfels (1934). Wilson (1902) reported a total of 41 new sponges from Puerto Rico and the remainder of the Greater Antilles ecoregion. Three decades later, de Laubenfels (1934) analyzed a large collection of Puerto Rican deep water sponges which were collected during the First Johnson-Smithsonian Deep-Sea Expedition, identifying 27 species of sponges. In the late twentieth century, Vicente (1990) produced the first list of sponge species (35) associated with photosynthetic symbionts from shallow surveys off La Parguera Natural Reserve. Followed by Weil (2005), who produced an updated systematic list of marine invertebrates from Puerto Rico, emphasizing that no
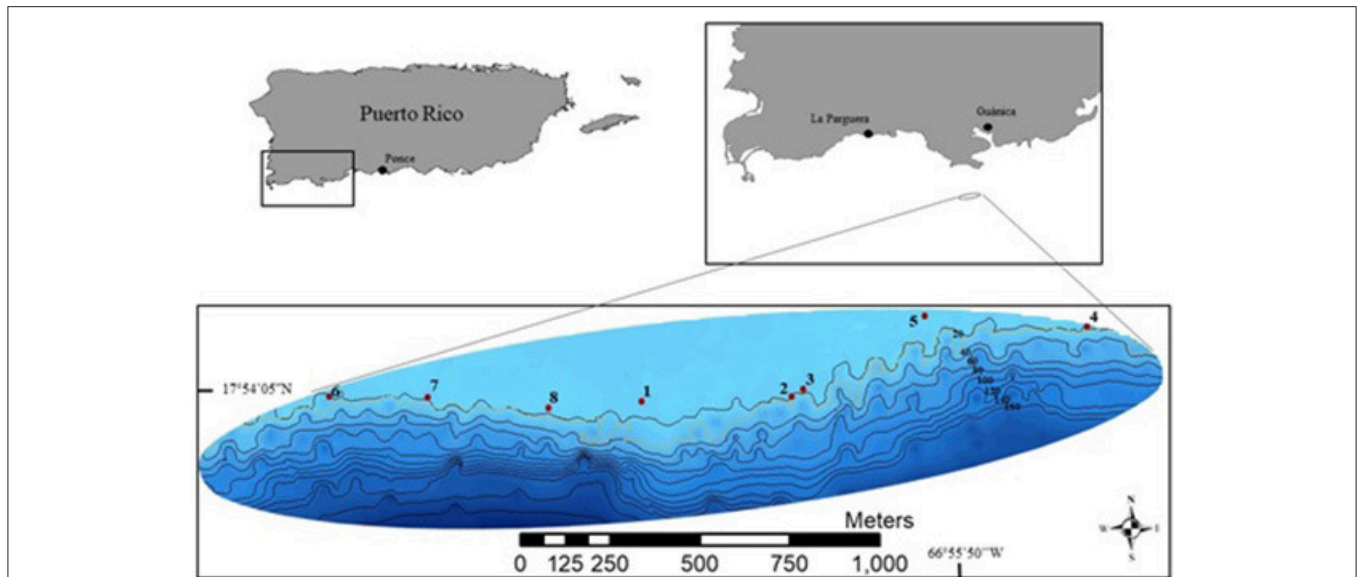
FIGURE 1 | Site map for the central portion of the Guánica shelf edge, Puerto Rico. Numbers one to eight represent each specific transect area for the shallow (20 m) surveys, with the mesophotic (45 m) surveys being done directly adjacent to the shallow surveys.

major taxonomic revisions of sponges have been done in the last 60 years.

Thus, the aim of this study is to characterize, describe and compare the biological composition along the Guánica shelf edge to: (1) rest if there is a difference in the presence, overlap, and abundance of coral, fish, and sponge species between altiphotic (20 m) and mesophotic (45 m) coral reefs, and (2) to provide an annotated list of sponges encountered within our surveys, since the true diversity of Puerto Rican sponges is currently not known. This comparison will give insight into the dynamics of the Guánica MCE, which is adjacent to the less impacted and better studied MCEs of La Parguera, and whether Guánica could act as a refuge for important coral, fish, and sponge species.

MATERIALS AND METHODS

Site Selection

Surveys were conducted in two depth stratifications, classified here as either altiphotic (20 m) or mesophotic (45 m) (**Figures 2A,B**). Eight altiphotic sites were chosen randomly along the central extension of the Guánica shelf edge using the program ARCGIS v. 10 (ESRI, 2011). The most direct downslope reef at 45 m respective to each altiphotic site was then selected for the mesophotic surveys (**Figures 1**, **2I–K**). The maximum distance between randomly selected altiphotic survey sites was roughly 1.5 km, and the minimum was at least 50 m apart.
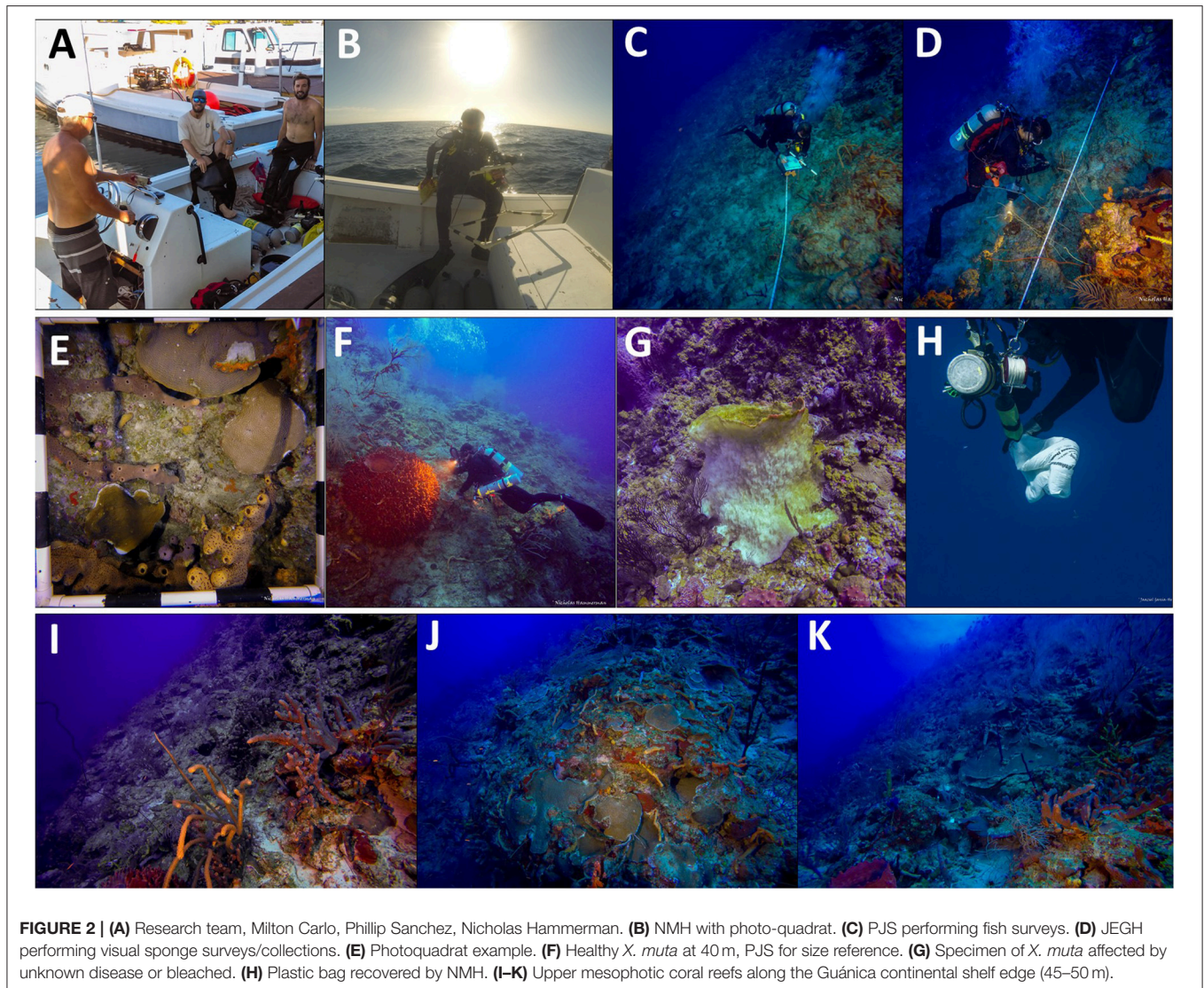
Fish Sampling

A 15 × 3 m belt transect survey, over a standardized 10-min duration, was conducted at each site on SCUBA (**Figure 2C**). Altiphotic transects (20 m) were run on top of the benthos, while mesophotic transects (45 m) were run alongside the slope. Skittish fish were documented at the onset of the survey due

to their likelihood of diver avoidance; common and cryptic species were targeted for the remainder of the survey along the transect. Fish were identified to species and lengths estimated within five cm bins up to 30 cm, after which they were classified as greater than 30 cm. While retrieving the transect tape, the point of highest rugosity (area of largest uninterrupted relief perpendicular to the surface of the benthos) was measured to the nearest cm using a 1 m long measuring stick, for each 1 m-length of the transect, extending 1.5 m to each side (1 × 3 m bin), resulting in 15 rugosity measurements per transect. A roving fish survey was conducted simultaneously with the transect survey and rugosity measurement collection to document the presence of meso-predators unlikely to be encountered within the limited spatial scale of the belt transect. In the roving survey, all meso-predators and lionfish observed were identified to species with lengths estimated to the nearest cm. No distance of fish to diver restrictions were placed on the roving surveys. The belt-transects and roving survey datasets were then combined into a single dataset for assemblage analysis. No length data was ultimately used in the analyses.

Fish Data Analysis

Species percent frequency (frequency of occurrence seen in transects) and density (ind./45 m^2) were calculated for the 20 and 45 m depth transects. Differences in fish abundance and richness between depths were analyzed using Welch's t-tests. Species were categorized into the following feeding guilds: herbivores, mobile invertivores, omnivores, piscivores, planktivores, and sessile invertivores. Classifications were based on a combination of Randall (1967), Bejarano et al. (2014), and fishbase.org.

A nonmetric multidimensional scaling (NMDS) ordination analysis was used to inspect the relationship between the species assemblages across sites coupled with a vector fit of the

FIGURE 2 | (A) Research team, Milton Carlo, Phillip Sanchez, Nicholas Hammerman. (B) NMH with photo-quadrat. (C) PJS performing fish surveys. (D) JEGH performing visual sponge surveys/collections. (E) Photoquadrat example. (F) Healthy *X. muta* at 40 m, PJS for size reference. (G) Specimen of *X. muta* affected by unknown disease or bleached. (H) Plastic bag recovered by NMH. (I–K) Upper mesophotic coral reefs along the Guánica continental shelf edge (45–50 m).

environmental variables depth, mean rugosity (per transect), and maximum rugosity (per transect). ANOSIMS were ran to analyze the effects of the environmental variables on fish assemblages and a multi-response permutation procedure (MRPP) was used to statistically analyze the effects of depth on differences of fish assemblages in R package "VEGAN" (Oksanen et al., 2017). Distances were calculated using the Bray-Curtis dissimilarity. The NMDS was inspected using a stress plot and goodness-of-fit test. Individual species contributions to assemblage differences between depths were analyzed using an indicator species analysis (ISA) in R-package "INDICSPECIES" (De Cáceres and Legendre, 2009).

Coral and Sponge Photographic Documentation

A total of 320 photo-transect images using a 0.50 m^2 quadrat, across 16 surveys (altiphotic and mesophotic), were acquired

and analyzed (**Figure 2B**). Quadrate photos were taken at one-meter increments along the first 10 m of the fish belt transect, one photo on each side of the tape. This resulted in 20 photos per transect, totaling a 10 m^2 image field per transect (**Figure 2E**). All photographs were then exported to CPCe for visualization and quantification (Kohler and Gill, 2006). The average percent cover and abundance of benthic groups, including corals and sponges, were calculated accordingly for further analysis. Within CPCe every coral's parameter was outlined to get a total percent cover per photoquadrat. Sponges were identified to lowest taxonomic identity using relevant identification guides (Zea et al., 2014) and morphological analysis to species that were uncertain.

Benthic Composition Analysis

Custom bash shell scripts were used to quantify average coral and sponge percent cover and abundance (**Supplementary Table 1**). Percent cover was calculated by averaging coral or sponge

TABLE 1 | Fish data for transect surveys along the central portion of the Guánica shelf edge.
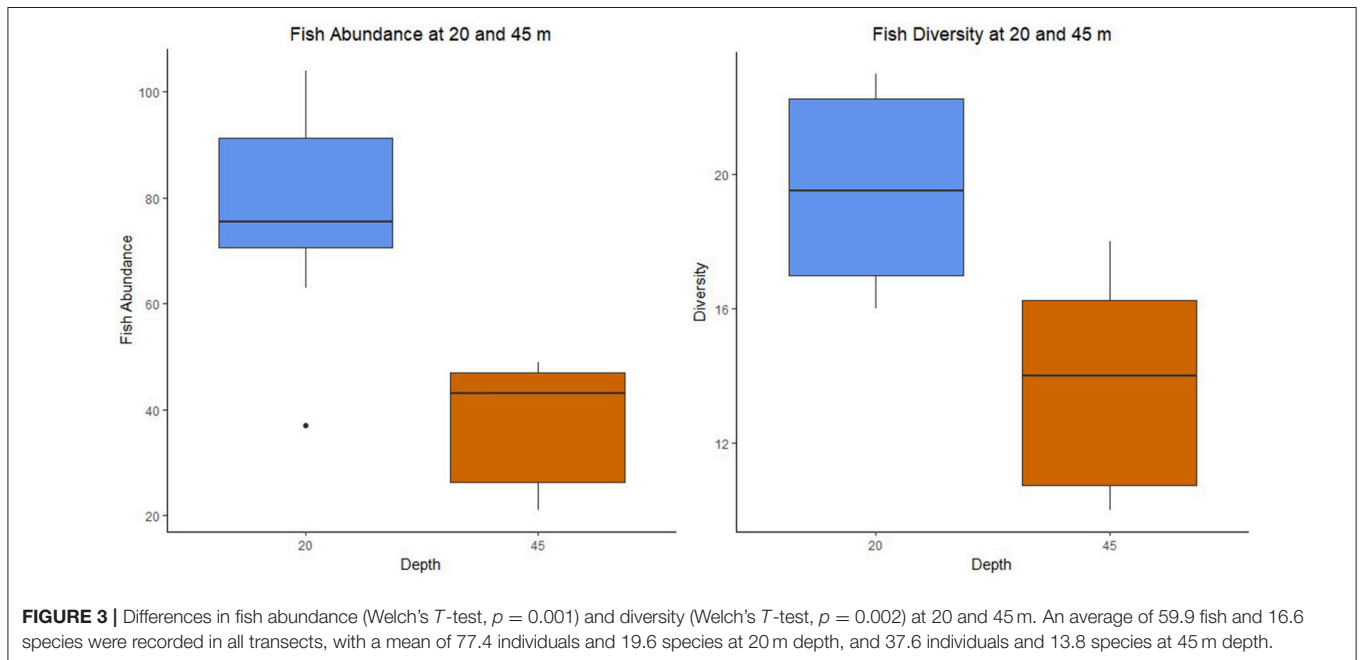
Species name	Common name	20 m			45 m		
		% F	MD	S.D.	% F	MD	S.D.
Abudefdus taurus	Night Sergeant	12.5	0.1	0.4	0.0	0.0	0.0
Acanthurus bahianus	Ocean Surgeonfish	100.0	2.3	1.8	37.5	1.3	2.6
Acanthurus chirurgus	Doctor fish	12.5	0.1	0.4	0.0	0.0	0.0
Acanthurus coeruleus	Blue Tang	25.0	0.4	0.7	12.5	0.1	0.3
Anisotremus surinamensis	Black Margate	0.0	0.0	0.0	25.0	0.3	0.4
Anisotremus virginicus	Porkfish	12.5	0.1	0.4	12.5	0.1	0.3
Aulostomus maculatus	Trumpetfish	25.0	0.3	0.5	0.0	0.0	0.0
Balistes vetula	Queen Triggerfish	0.0	0.0	0.0	25.0	0.3	0.4
Canthigaster rostrata	Sharpnose Pufferfish	37.5	0.5	0.8	25.0	0.3	0.4
Caranx bartholomei	Yellow Jack	12.5	0.3	0.7	0.0	0.0	0.0
Caranx ruber	Bar Jack	25.0	0.3	0.5	25.0	0.4	0.7
Centropyge argi	Cherubfish	0.0	0.0	0.0	12.5	0.6	1.7
Cephalopholis cruentatus	Graysby Grouper	50.0	1.5	1.9	75.0	1.8	1.9
Cephalopholis fulvus	Coney Grouper	25.0	0.4	0.7	12.5	0.1	0.3
Chaetodon capistratus	Foureye Butterflyfish	62.5	1.0	0.9	12.5	0.3	0.7
Chaetodon ocellatus	Spotfin Butterflyfish	25.0	0.4	0.7	12.5	0.3	0.7
Chaetodon striatus	Banded Butterflyfish	12.5	0.3	0.7	0.0	0.0	0.0
Chromis cyanea	Blue Chromis	100.0	15.1	12.0	100.0	4.8	3.0
Chromis insolata	Sunshine Chromis	0.0	0.0	0.0	75.0	5.4	5.4
Chromis multilineata	Brown Chromis	37.5	2.0	3.0	50.0	1.6	1.9
Clepticus parrae	Creole Wrasse	50.0	3.8	4.7	0.0	0.0	0.0
Coryphopterus personatus	Glass/Masked Goby	0.0	0.0	0.0	50.0	0.5	0.5
Epinephelus guttatus	Redhind	0.0	0.0	0.0	12.5	0.1	0.3
Gramma loreto	Fairy Basslet	0.0	0.0	0.0	25.0	1.3	2.4
Liopropoma mawbrayi	Cave Basslet	0.0	0.0	0.0	12.5	0.3	0.7
Gymnothorax funebris	Green Morey Eel	12.5	0.1	0.4	0.0	0.0	0.0
Haemulon aurolineatum	Tomtate	25.0	0.4	0.7	0.0	0.0	0.0
Haemulon chrysargyreum	Smallmouth Grunt	12.5	0.6	1.8	0.0	0.0	0.0
Haemulon flavolineatum	French Grunt	87.5	1.6	0.9	12.5	0.1	0.3
Haemulon sciurus	Bluestripe Grunt	25.0	0.3	0.5	12.5	0.1	0.3
Halichoeres garnoti	Yellowhead Wrasse	75.0	1.8	1.4	100.0	6.0	3.7
Holacanthus ciliaris	Queen Angelfish	37.5	0.5	0.8	12.5	0.3	0.7
Holacanthus tricolor	Rock Beauty	25.0	0.3	0.5	25.0	0.3	0.4
Holocentrus adscensionis	Squirrelfish	25.0	0.3	0.5	12.5	0.1	0.3
Holocentrus rufus	Longspine Squirrelfish	50.0	1.1	1.2	87.5	1.3	0.7
Hypoplectrus chlorurus	Yellowtail Hamlet	12.5	0.1	0.4	12.5	0.1	0.3
Hypoplectrus puella	Barred Hamlet	0.0	0.0	0.0	25.0	0.4	0.7
Lachnolaimus maximus	Hogfish	0.0	0.0	0.0	12.5	0.1	0.3
Lutjanus apodus	Schoolmaster	12.5	0.1	0.4	0.0	0.0	0.0
Lutjanus cyanopterus	Cubera Snapper	0.0	0.0	0.0	12.5	0.1	0.3
Lutjanus jocu	Dog Snapper	0.0	0.0	0.0	25.0	0.4	0.7
Melichthys niger	Black Durgon	50.0	4.5	6.2	0.0	0.0	0.0
Microspathodon chrysurus	Yellowtail Damselfish	37.5	0.5	0.8	0.0	0.0	0.0
Mulloidichthys martinicus	Yellow Goatfish	25.0	0.4	0.7	0.0	0.0	0.0
Myripristis jacobus	Barred Soldierfish	62.5	1.5	1.7	0.0	0.0	0.0
Neoniphon marianus	Longjaw Squirrelfish	0.0	0.0	0.0	62.5	0.8	0.7
Ocyurus chrysurus	Yellowtail Snapper	75.0	2.1	2.2	12.5	0.1	0.3
Paranthias furcifer	Creolefish	0.0	0.0	0.0	25.0	0.8	1.4
Pomacanthus arcuatus	Grey Angelfish	0.0	0.0	0.0	12.5	0.1	0.3

(Continued)

TABLE 1 | Continued

Species name	Common name	20 m			45 m		
		% F	MD	S.D.	% F	MD	S.D.
Pomacanthus paru	French Angelfish	25.0	0.4	0.7	0.0	0.0	0.0
Prognathodus aculeatus	Longsnout Butterflyfish	0.0	0.0	0.0	25.0	0.3	0.4
Pseudopeneus maculatus	Spotted Goatfish	12.5	0.1	0.4	0.0	0.0	0.0
Pterois volitans	Lionfish	37.5	0.5	0.8	50.0	1.1	1.3
Scarus iserti	Striped Parrotfish	87.5	3.0	3.6	12.5	0.1	0.3
Scarus taeniopterus	Princess Parrotfish	100.0	2.5	2.0	12.5	0.3	0.7
Serranus baldwini	Lantern Bass	0.0	0.0	0.0	12.5	0.1	0.3
Serranus tabacarius	Tobacco fish	0.0	0.0	0.0	12.5	0.8	2.0
Serranus tigrinus	Harlequin Bass	12.5	0.3	0.7	12.5	0.4	1.0
Sparisoma aurofrenatum	Redband Parrotfish	87.5	1.3	0.7	50.0	1.0	1.1
Sparisoma virides	Stoplight Parrotfish	62.5	0.6	0.5	0.0	0.0	0.0
Sphyraena barracuda	Barracuda	12.5	0.1	0.4	12.5	0.1	0.3
Stegastes leucostictus	Beaugregory	37.5	0.6	0.9	0.0	0.0	0.0
Stegastes partitus	Bicolor Damselfish	87.5	11.1	6.5	50.0	2.0	2.6
Stegastes planifrons	Threespot Damselfish	12.5	0.1	0.4	0.0	0.0	0.0
Stegastes variabilis	Cocoa Damselfish	12.5	0.1	0.4	0.0	0.0	0.0
Thalassoma bifasciatum	Bluehead Wrasse	100.0	11.9	6.8	12.5	0.5	1.3
Xanthichthys ringens	Sargassum Triggerfish	0.0	0.0	0.0	37.5	0.5	0.7

% F, Frequency; MD, Median Density and S.D., Standard Deviation.

FIGURE 3 | Differences in fish abundance (Welch's *T*-test, $p = 0.001$) and diversity (Welch's *T*-test, $p = 0.002$) at 20 and 45 m. An average of 59.9 fish and 16.6 species were recorded in all transects, with a mean of 77.4 individuals and 19.6 species at 20 m depth, and 37.6 individuals and 13.8 species at 45 m depth.

cover from all eight sites per depth and variance was shown with standard error (**Figures 6–8**). Order was depicted in **Figure 8**, since family level delineation created values too small to accurately or easily portray on a graph. Diversity indices were calculated per coral and sponge species respective to either solely the altiphotic or mesophotic transects (e.g., Species Richness, Simpson's Index, Simpson's Index of Diversity, Simpson's

Reciprocal Index, Shannon-Wiener Index and Evenness) (**Tables 4, 5**). Sorting of coral and sponge specimens resulted in a data matrix for numerical abundance of different taxa that were used to construct similarity matrices among transects using the Bray-Curtis index. Dissimilarity matrices were used to perform non-metric multivariate ordinations (NMDS) to illustrate patterns of spatial distribution of coral and sponge

TABLE 2 | The fifteen most common fish species for each depth.

20 m species	Total	45 m species	Total
Chromis cyanea	121	Halichoeres garnoti	48
Thalassoma bifasciatum*	95	Chromis insolata*	43
Stegastes partitus*	89	Chromis cyanea	38
Melichthys niger	36	Stegastes partitus	16
Clepticus parrae	30	Cephalopholis cruentatus	14
Scarus iseri*	24	Chromis multilineata	13
Scarus taeniopterus*	20	Acanthurus bahianus	10
Acanthurus bahianus	18	Gramma loreto	10
Ocyurus chrysurus*	17	Holocentrus rufus	10
Chromis multilineata	16	Pterois volitans	9
Halichoeres garnoti	14	Sparisoma aurofrenatum	8
Haemulon flavolineatum*	13	Neoniphon marianus*	6
Cephalopholis cruentatus	12	Paranthias furcifer	6
Myripristis jacobus*	12	Serranus tabacarius	6
Sparisoma aurofrenatum*	10	Centropyge argi	5

Stars indicate species identified as significant contributors to the differences in assemblages between depths.

assemblages associated with altiphotic and mesophotic transects. All analyses were done in RStudio (R version3.2.4) running the Vegan, MASS, and DPLYR Packages (R Core Team, 2016).

RESULTS

Fish Abundance and Diversity

A total of 67 species belonging to 21 families were recorded. Forty-eight species (19 families) were recorded at 20 m depth and 47 species (18 families) were recorded at 45 m depth. A total species list with both frequency of occurrence and density (ind./45 m^2) are given in **Table 1**. Though overall richness is comparable at 20 and 45 m, mean abundance and diversity per transect at the two depths are different (**Figure 3**). Fifteen of the twenty-one families have higher abundances at 20 m. Six families (Epinephelidae, Gobiidae, Gramatidae, Pomacanthidae, Scorpaenidae, and Serranidae) however, have higher abundances at 45 m. Pomacentridae (9 species) and Serranidae (7) were the most speciose families represented, but displayed opposite trends in abundance between the two depths. Pomacentridae abundance at 20 m is greater than at 45 m depth, while Serranidae abundance is higher at 45 m than 20 m. These fish families were followed in decreasing order by Haemulidae (6), Pomacanthidae (5), Chaetodontidae (4), Holocentridae (4), Labridae (4), Lutjanidae (4), and Scaridae (4).

Maximum and average rugosity were collinear (Pearson's, p-value < 0.01), and neither were found individually to be significant as a covariable with depth and so were removed from species assemblage comparisons (ANOSIM, p-values = 0.351 and 0.191, respectively). However, assemblages are significantly different between 20 and 45 m (MRPP, p = 0.002) (**Figure 5**). Ten species are significantly associated with the depth-related assemblage differences; eight species correlated with 20 m and an additional two species at 45 m

(Multilevel pattern analysis, p < 0.05). Five of the eight species (Ocyurus chrysurus, Scarus taeniopterus, Scarus iseri, Sparisoma virides, and Stegastes partitus) identified at 20 m are classified as herbivorous or omnivorous. On the other hand, Chromis insolata and Neoniphon marianus, identified at 45 m, are a planktivore and mobile invertivore, respectively (**Table 2**). Lionfish (Pterois volitans) were seen at both depths with regular frequency of occurrence (**Tables 1**, **2**).

Effects of depth on feeding guild composition changes were not statistically analyzed due to data limitations. The following description therefore does not reflect statistics results, but the trends found in the data play a potential role in assemblage divergences and are supported in the current body of literature. This is further addressed in the Discussion. Herbivores, planktivores, and mobile invertivores composed greater than 80% fish abundance at 20 m, accounting for 28.3, 27.0, and 25.7% of all individuals recorded, respectively (**Figure 4**; **Table 3**). However, at 45 m, the relative abundance of herbivores was half of that at 20 m, while the relative abundances of planktivores and mobile invertivores were higher at 45 m. The only guild with a higher overall abundance at the deeper sites was the piscivores (12.9%), compared to 4.5% at 20 m (**Figure 4**; **Table 3**).

Scleractinian Corals Abundance, Percent Cover, and Diversity

A total of 33 coral species were recorded in the 16 transect surveys. Thirty-one species (16 genera) of corals were recorded at 20 m, while eleven species (6 genera) were recorded at 45 m (**Table 4**). Of the 33 species of coral observed, nine species had overlapping distribution between altiphotic and mesophotic surveys. The most abundant genera within the altiphotic surveys were Orbicella and Porites. The most abundant species in the shallow surveys were Orbicella franksi (N = 185) and Porites astreoides (N = 117). In contrast, the most abundant genera within the mesophotic surveys were Madracis (N = 49) and Agaricia (N = 58), with the corals Madracis senaria and Agaricia grahamae solely encountered on the 45 m surveys.

The coral species with the greatest percent coverage for the 20 m surveys were O. franksi (6.9%) and O. faveolata (3.2%) followed by Montastraea cavernosa and P. astreoides (1.3%, for both). Agaricia lamarcki constituted the largest percent cover for the 45 m surveys at 1.6% (**Table 4**). Hard corals accounted for 17.0% (±1.76 SE) and 2.6% (±0.89 SE) benthic cover for the altiphotic and mesophotic surveys, respectively (**Figure 6**). The altiphotic and mesophotic coral communities support vastly different scleractinian assemblages with minimal species overlap, as represented with the nonmetric multidimensional scaling (NMDS) using Bray-Curtis similarities (**Figure 5**). This result was supported by PERMANOVA analysis, with a significant division between the depth stratifications (PERMANOVA: df = 1, r^2 = 0.560, P = 0.001). However, among sites per depth, coral assemblages were not significantly different (PERMANOVA: df = 7, r^2 = 0.239, P = 0.897).

Additional functional groups analyzed were algae and unconsolidated sediment, though were not the central theme of this investigation. Algae accounted for 19.0% (±2.20 SE)
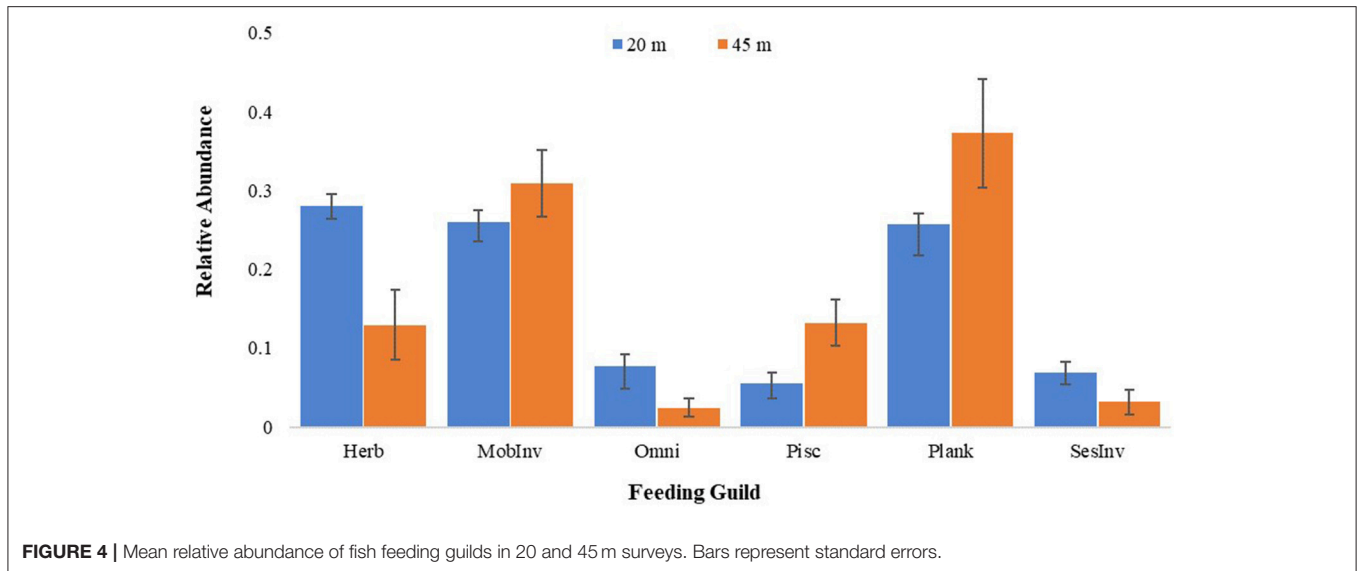
FIGURE 4 | Mean relative abundance of fish feeding guilds in 20 and 45 m surveys. Bars represent standard errors.

TABLE 3 | Total and relative abundances of fish feeding guilds at 20 and 45 m depth fish surveys.

	20 m			45 m		
	TA	RA (%)	St. Err RA	TA	RA (%)	St. Err RA
Herbivore	21.9	28.3	1.7	5.4	14.3	4.5
Mobile invertivore	19.9	25.7	2.5	11.4	30.2	4.2
Omnivore	5.9	7.6	2.9	0.8	2.0	1.2
Piscivore	3.5	4.5	1.9	4.9	13.0	2.9
Planktivore	20.9	27.0	3.9	14.0	37.2	6.9
Sessile invertivore	5.4	6.9	1.4	1.3	3.3	1.6
Total	77.4	100.0		37.6	100.0	

TA, Total Abundance; RA, Relative Abundance; St. Err RA, Standard Error Relative Abundance.

cover at 20 m, and 7.7% (±1.92 SE) cover at 45 m. Further identification of algal species was not performed (see Ballantine et al., 2016; van der Loos et al., 2017). Lastly, accumulation of hardground/unconsolidated sediments accounted for 52.0% (±1.76 SE) at 20 m and 75.0% (±3.41 SE) at 45 m (**Figure 7**).

Sponge Abundance, Percent Cover and Diversity

A total of 3,464 individual sponges were recorded, 1,163 throughout altiphotic reefs (20 m), and 2,301 for mesophotic reefs (45 m). Comparing both depth ranges, altiphotic surveys revealed a higher species richness than mesophotic, 60 and 54 species respectively (**Table 5**), with a total of 71 species found at both depths (63.0% species overlap). As for depth specific species, altiphotic surveys revealed a higher number of species ($N = 17$) compared to those found in mesophotic surveys ($N = 11$). The percent cover of sponges surveyed at altiphotic reefs was 9.0% (±1.04 SE), while percent cover of sponges surveyed at mesophotic reefs was 14.0% (±1.96 SE) (**Figure 8**; **Table 5**).

Within the total sponge percent cover calculated from altiphotic surveys, the sponges *Amphimedon compressa* (1.8%),

Agelas conifera (1.7%), *Cliona caribbaea* (1.6%), *Xestospongia muta* (0.9%), and *Agelas dispar* (0.4%) comprised the largest percent cover at this depth. With respect to total abundance, the sponges *A. compressa* ($N = 115$), *Agelas dispar* ($N = 70$), *A. conifera* ($N = 67$), *Cliona delitrix* ($N = 63$), and *Plakortis* sp. ($N = 55$) dominated the altiphotic reef substratum. In contrast, within the total percent sponge cover calculated from mesophotic reef sites, the sponges *Plakortis* sp. (2.2%), *Agelas sceptrum* (1.6%), *A. conifera* (1.5%), *Plakortis symbiotica* (1.0%), and *Oceanapia bartschi* (0.6%) comprised the largest percent cover at 45 m. With respect to total abundance, the sponges *Plakortis* sp. ($N = 340$), *A. sceptrum* ($N = 256$), *P. symbiotica* ($N = 87$), *Prosuberites laughlini* ($N = 52$), and *Niphates erecta* ($N = 49$), dominated the mesophotic reef substratum (**Table 5**). Overall, demosponges dominated numerically and visually both our altiphotic and mesophotic coral reef benthic surveys.

NMDS analysis showed two major clusters of sponges, suggesting that depth significantly influenced abundance and composition of sponge species (**Figure 5**) (PERMANOVA: $df = 1$, $r^2 = 0.591$, $P = 0.001$), however no significant difference was observed between sites per depth (PERMANOVA: $df = 7$, $r^2 = 0.027$, $P = 0.866$).

TABLE 4 | Scleractinian species identified in deep (45 m) and altiphotic (20 m) transect surveys from the central portion of Guánica shelf edge, southwest Puerto Rico; ~ 40 m^2 was surveyed per depth designation.
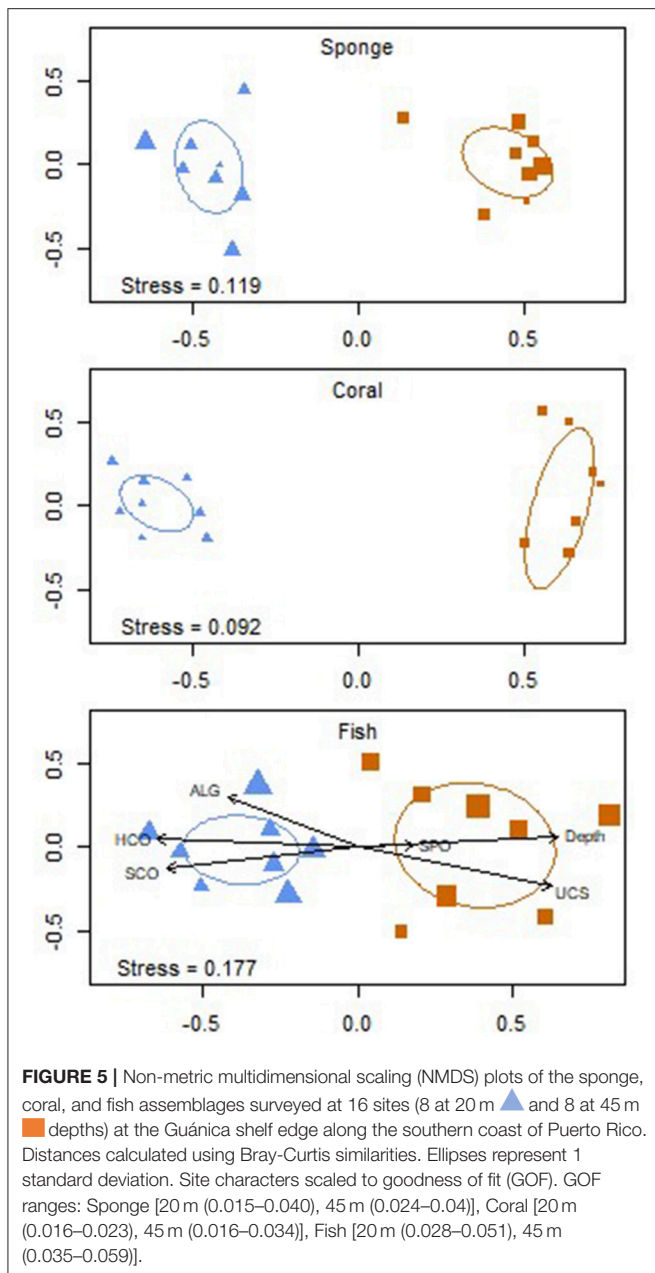
Species	Absolute % cover	N	Index	Value
20m depth - Hard Corals				
Acropora cervicornis	0.28	3	Species Richness (S)	31
Agaricia agaricites	1.03	59	Simpson's Index (D)	0.11
A. fragilis	0.0074	3	Simpson's index of diversity (1-D)	0.89
A. humilis	0.055	11	Simpson's reciprocal index (1/D)	8.7
A. lamarcki	0.028	2	Shannon-Wiener Index (H)	2.5
A. tenuifolia	0.092	2	Evenness (E)	0.73
Helioseris cucullata	0.055	3		
Agaricia sp.	0.035	16		
Colpophyllia natans	0.023	2		
Pseudodiploria strigosa	0.16	7		
Diploria labyrinthiformis	0.35	11		
Eusmilia fastigiata	0.016	1		
Favia fragum	0.0037	2		
Madracis carmabi	0.019	1		
Madracis decactis	0.014	5		
Madracis formosa	0.019	3		
Madracis sp.	0.063	15		
Meandrina meandrites	0.3	27		
Montastraea cavernosa	1.4	72		
Orbicella annularis	0.38	6		
O. faveolata	3.2	86		
O. franksi	6.9	185		
Orbicella sp.	0.44	56		
Mycetophyllia sp.	0.014	1		
Porites astreoides	1.3	117		
P. porites	0.071	4		
Porites sp.	0.0307	6		
Stephanocoenia intersepta	0.0602	3		
Scolymia cubensis	0.0037	1		
Siderastrea siderea	0.607	116		
Coral unknown	0.079	24		
Total	17.04	850		
45 m depth - Hard Corals				
Agaricia agaricites	0.14	6	Species Richness (S)	11
A. grahamae	0.38	13	Simpson's Index (D)	0.17
A. lamarcki	1.7	27	Simpson's index of diversity (1-D)	0.83
Agaricia sp.	0.086	12	Simpson's reciprocal index (1/D)	5.8
Coral unknown	0.029	17	Shannon-Wiener Index (H)	2.006
Madracis sp.	0.079	47	Evenness (E)	0.84
Madracis senaria	0.0053	2		
Montastraea cavernosa	0.015	6		
Stephanocoenia intersepta	0.037	4		
Scolymia cubensis	0.1006	1		
Siderastrea siderea	0.0068	14		
Total	2.58	149		

DISCUSSION

Fish Assemblage

The fish abundance and species richness per survey in Guánica decreased with increased depth, including a 51.4% decrease in mean fish abundance (**Figure 3**). The two depths, however, exhibit similar levels of overall richness (48 and 47 total number of species) and depth specialists, species unique to a single depth (18 and 17 species). Fifty-two percent of the recorded fish species are unique to either the 20 or 45 m surveys, suggesting a divergence in fish assemblages evident in **Figure 5**. In nearby La Parguera, a distinct MCE fish assemblage was found at similar depths, between 40 and 70 m (Bejarano et al., 2014). Similar trends with depth were found in fish assemblages from eastern

FIGURE 5 | Non-metric multidimensional scaling (NMDS) plots of the sponge, coral, and fish assemblages surveyed at 16 sites (8 at 20 m ▲ and 8 at 45 m ■ depths) at the Guánica shelf edge along the southern coast of Puerto Rico. Distances calculated using Bray-Curtis similarities. Ellipses represent 1 standard deviation. Site characters scaled to goodness of fit (GOF). GOF ranges: Sponge [20 m (0.015–0.040), 45 m (0.024–0.04)], Coral [20 m (0.016–0.023), 45 m (0.016–0.034)], Fish [20 m (0.028–0.051), 45 m (0.035–0.059)].

Australia, Hawaii, and Brazil (Pearson and Stevens, 2015; Pyle et al., 2016; Rosa et al., 2016), though the depth that a distinct MCE assemblage develops can vary with geographical location (Pinheiro et al., 2016).

Our data shows that fish assemblage differences include a potential beginning transition at shallow from herbivore and omnivore to a deeper assemblage composed of more piscivores and planktivores (**Figure 4**). Decreased light availability at mesophotic depths limits primary productivity potential for benthic autotrophs, and therefore food availability for grazers (Brokovich et al., 2010; Sherman et al., 2010). In our benthic surveys, coral percent cover decreased while sponge percent cover increased, supporting the likelihood of this light availability transition.

Terrigenous sediment outflow has also been shown to effect benthic community structure both locally (Torres, 2001; Sherman et al., 2010; Appeldoorn et al., 2016a) and along other coastal zones (MacDonald et al., 2016). However, neither light availability nor bay outflow data were collected in this study, therefore the observed changes in benthos and associated fish assemblages cannot be directly attributed to these physical parameters.
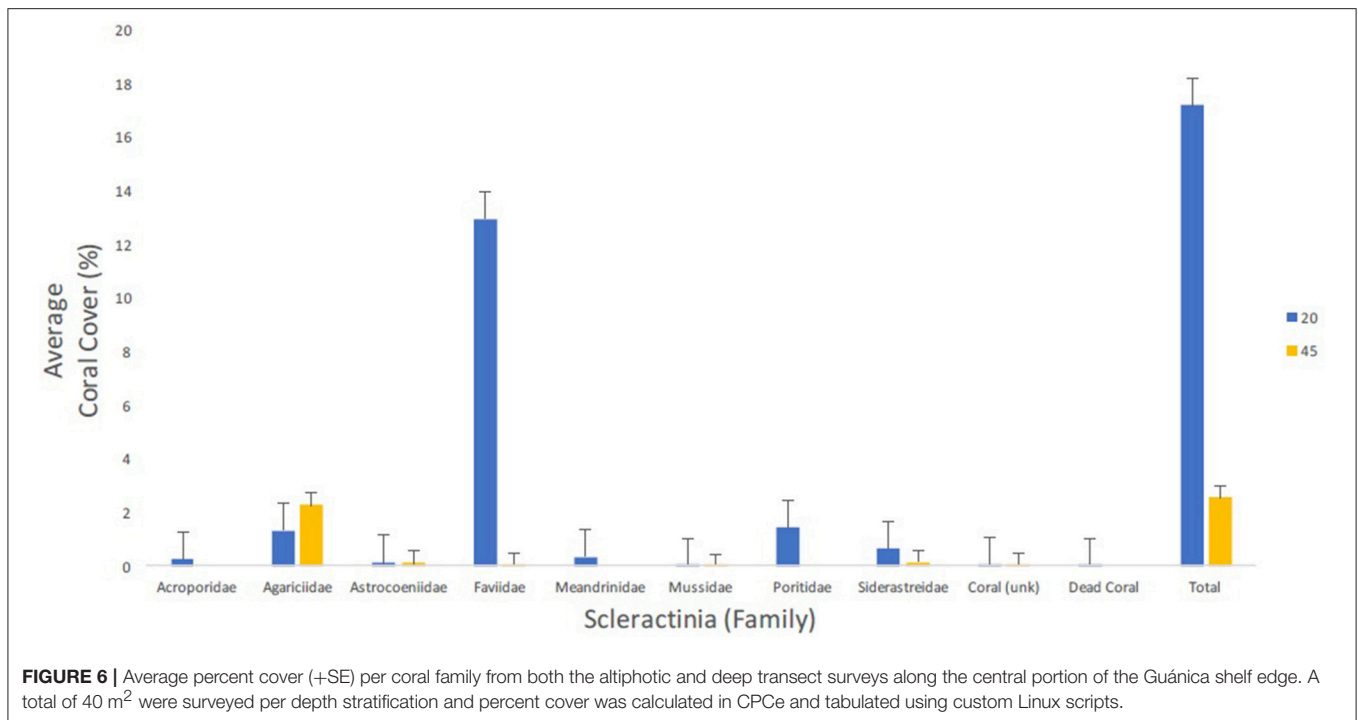
The increase in fish planktivore and mobile invertivore relative percentages at 45 m, combined with decreased herbivore concentration, is indicative of a transition toward a plankton-based trophic web between the two depths (Brokovich et al., 2008). The vertical geomorphology of the shelf slope provides access to deeper water through potential upwelling, and therefore higher concentrations of zooplankton, which support previous results from Puerto Rico (García-Sais et al., 2010a). However, schooling planktivorous fishes (e.g., *Ocyurus chrysurus*, *Clepticus parrae*, etc.) congregated in the water column just seaward from the top of the Guánica shelf edge (PJS pers. obs.). Therefore, the adjacent nature of the altiphotic survey sites to the vertical escarpment of the shelf edge could have minimized the magnitude of change for the observed feeding guild transition, which may become more evident with increased cross-shelf surveys.

The addition of an insular shelf sampling band (closer to shore) could clarify if assemblage changes increase even more moving along the shelf perpendicular to the shelf edge (e.g., MacDonald et al., 2016). Conversely, additional transects further down the shelf edge (>50 m) would allow us to determine if the fish assemblages continue to diverge from its shallow water counterpart (e.g., altiphotic vs. deep mesophotic) as is shown in the adjacent La Parguera (Bejarano et al., 2014).

Coral Assemblage

The central portion of the Guánica shelf edge had 31 and 11 coral species at 20 and 45 m, respectively, nine of which have distributional overlaps (**Figures 5**, **6**; **Table 4**). The geomorphology of MCEs in the area, as originally described by Sherman et al. (2010), could be a key factor in the lack of corals in the 45 m surveys, indicative of the predominate southeast facing walls surveyed. Here, sediment transport is amplified across open and low relief slopes, which may hinder coral recruitment by smothering newly settled juvenile corals (Sherman et al., 2013b). However, where sediments, light attenuation, and slope are not key factors in coral propagation, mesophotic reefs to the east at El Seco (Vieques, PR) had an astonishing 41.0% hard coral coverage (García-Sais et al., 2014, 2016), as well as MCEs in St. Thomas (USVI), which had a maximum coral cover of 70.0% between depths of 38–40 m (Armstrong et al., 2006).

In contrast, the spur and groove bathymetry which typified the 20 m surveys, afforded corals ample substrate to thrive and accounted for 17.0% (±1.76 SE) overall benthic coverage. A similar percentage of hard coral coverage was recorded in Guánica at 10–30 m (García-Sais et al., 2017). In our phototransects, *O. franksi* ($N = 185$) and *P. astreoides* ($N = 117$) were the most common species, while *O. franksi* and *O. faveolata* accounted for the highest individual coral coverage, 6.9 and
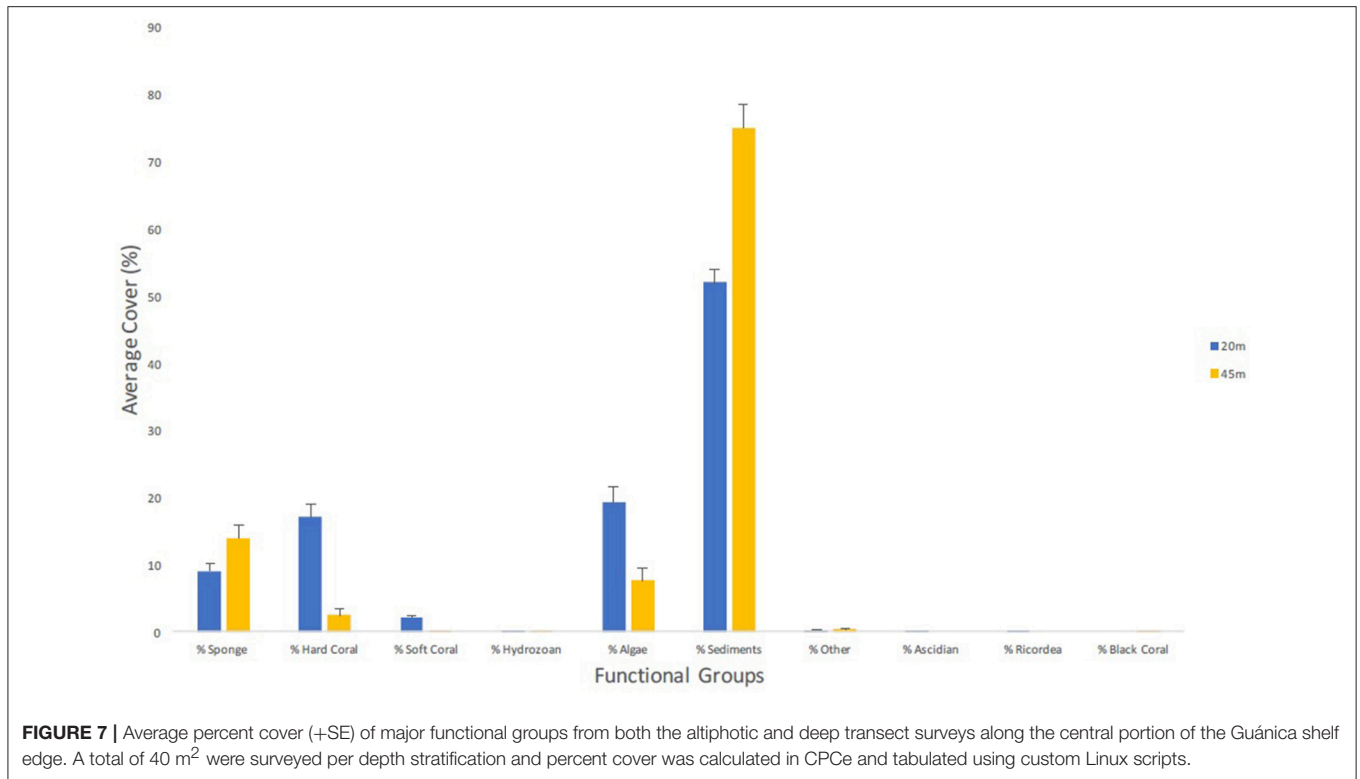
FIGURE 6 | Average percent cover (+SE) per coral family from both the altiphotic and deep transect surveys along the central portion of the Guánica shelf edge. A total of 40 m^2 were surveyed per depth stratification and percent cover was calculated in CPCe and tabulated using custom Linux scripts.

3.2%, respectively (**Figure 6**; **Table 4**). *Orbicella* and *Porites* are thought to be the most abundant genera in the Caribbean due to their variable genomic responses to thermal anomalies (Wegley et al., 2007; Dziedzic et al., 2017), advantageous morphologies for sediment removal and ability to broadcast spawn to increase dispersal potential (Miller and Mundy, 2003; Cowen and Sponaugle, 2009). Combined, these traits might predisposition these genera to recover in areas where coral mortality due to bleaching and disease is prevalent. For instance, in several deep reefs off the US Virgin Islands (∼40 m depth), the *O. annularis* complex dominated benthic composition accounting for roughly 16.0% of total coral coverage (Armstrong et al., 2006; Smith et al., 2010). This species complex is also the most important contributor to percent cover of reefs across the Puerto Rican basin, though since 2005, bleaching events have drastically diminished the presence of the species complex (García-Sais et al., 2017). The other most abundant coral species *P. astreoides*, is a highly adaptable species which can quickly alter zooxanthellae composition with changing environmental conditions and has thermo-tolerant bio-physiology (Wegley et al., 2007; Serrano et al., 2016). *Porites astreoides* dominated the coral composition at both 15 and 20 m depth within study sites at Isla Desecheo (west coast of Puerto Rico) and has increased its relative abundance in relation to other corals since the 2005 bleaching event in many reefs around Puerto Rico (García-Sais et al., 2017).

The *Agaricia* genus was found in both depths but often was difficult to differentiate species due to observed morphological convergence and phenotypic plasticity (Todd, 2008). *Agaricia* did account for the largest number of individuals and percent cover for the mesophotic surveys, with *A. lamarcki* being the most prevalent species (N = 27). A similar trend in prevalence

of *Agaricia* spp. was observed for mesophotic reefs at Desecheo, being the predominate coral to a depth of at least 60 m (García-Sais, 2010) and at 70–85 m in Curaçao (Hoeksema et al., 2016). The *Agaricia* genus has a wide morphological plasticity, including encrusting sheets, thick leaves, and flat plates, which allows them to attach to a wide range of substratum, including sponges (García-Hernández et al., 2017). However, the plate-like morphology of *Agaricia* makes them particularly susceptible to sedimentation, as was noticed on several colonies on the 45 m surveys (NMH per. obs.).

The *Madracis* genus is also moderately abundant across both depths, though identification to species was difficult for most individuals in the mesophotic surveys. Both the *Agaricia* and *Madracis* genera are thought to be primarily brooders. The release of competent planula larvae throughout the year gives these corals a higher reproductive potential in more hostile habitats such as sediment laden insular slopes (Bongaerts et al., 2017; Prasetia et al., 2017). However, their re-seeding capabilities are limited since brooded larvae typically settle within 50–100 m of the adult colony, making both horizontal and vertical dispersion more difficult (Bongaerts et al., 2010).

The altiphotic and mesophotic surveys showed nine species with distributional overlaps; the NMDS analysis showed clear divisions between altiphotic and mesophotic surveys (**Figure 5**). Compared to the 20 m surveys, most of the 45 m surveys had low scleractinian coral abundance, possibly due to the geomorphological constraints. The extent to which the shared species are interconnected is dependent upon vertical connectivity patterns and local adaptation of all components of the coral holobiont. For example, six of the nine shared corals are brooders and would be expected to have limited vertical dispersal, however caution should be used in asserting such claims without

FIGURE 7 | Average percent cover (+SE) of major functional groups from both the altiphotic and deep transect surveys along the central portion of the Guánica shelf edge. A total of 40 m^2 were surveyed per depth stratification and percent cover was calculated in CPCe and tabulated using custom Linux scripts.

the inclusion of genetic connectivity estimates, which often are species-specific (Foster et al., 2012; Hammerman et al., 2017; Rippe et al., 2017).

Several threatened coral species were observed on these surveys, these included *O. franksi, O. faveolata, O. annularis, M. cavernosa, Acropora cervicornis,* and *Mycetophyllia ferox.* The *Orbicella* genus was particularly abundant in the 20 m surveys, which is supported by previous studies in the Caribbean (Carpenter et al., 2008; García-Sais et al., 2014, 2016, 2017). The presence of many rare and threatened species makes this area particularly valuable for coral conservation and management (García-Sais et al., 2017). Conservation is especially important in Guánica, given regions to the east are affected by local dredging and continual watershed activities that have significantly smothered shelf edge reefs in both terrigenous and re-suspended sediments (Appeldoorn et al., 2016a). The prevailing northeast trade winds create a westward driven current, therefore sediment and watershed activities to the east of Guánica have the potential to negatively affect water clarity and quality (Capella and Laboy, 2003; Sherman et al., 2013b). Coupled with recent reports of organic and metal contamination in Guánica Bay, only three km north of the Guánica shelf edge, there exist many land-based threats (e.g., contamination, nutrient input, sedimentation, diseases, trash, plastics) that are negatively contributing to the health of Guánica coral ecosystems (Pait et al., 2008, 2009; Sherman et al., 2013b; Whitall et al., 2013b, 2014). The cumulative effect could hinder coral recovery after bleaching and disease events, which given anthropogenic perturbations, the periodicity of such events are expected to strengthen and increase with time (Hughes et al., 2018; **Figure 2H**).

Sponge Assemblage

Comparison of overall species richness along Guánica's altiphotic and mesophotic reefs remained relatively similar across both depths, with 60 species at 20 m, and 54 species at 45 m, accounting for 63.0% species overlap (**Figure 8**; **Table 5**). The total number of species (71) found across Guánica's altiphotic and mesophotic reefs reflects the general trend of sponge diversity within other regions in the Caribbean (e.g., van Soest, 1978; Hajdu and Rützler, 1998; Alcolado, 2002; Diaz and Rützler, 2009; Thacker et al., 2010; Valderrama and Zea, 2013; Villamizar et al., 2013; Loh and Pawlik, 2014; Pérez et al., 2017; Cóndor-Luján et al., 2018). However, additional detailed surveys and exploratory dives targeting specific groups, such as calcareans (Fontana et al., 2018; JEGH unpubl. data) and homoscleromorphs (Ruiz et al., 2017) are necessary, and will surely yield new species, especially those inhabiting cryptic and sciophilous environments (Rützler et al., 2014; Ribeiro et al., 2016). Within our surveys, *Agelas* spp., *A. compressa, Iotrochota birotulata, N. erecta,* and *X. muta* were the most abundant sponges and major component of the benthic substratum across both depths.

In contrast to species richness, our data shows an increase of percent sponge cover between altiphotic to mesophotic depths, 9.0% (±1.04 SE) and 14.0% (±1.96 SE), respectively (**Figure 8**). These data reflect similar results to what previous studies have reported along the southwest and west coasts of Puerto Rico (Armstrong et al., 2009; García-Sais, 2010; Rivero-Calle, 2010; Sherman et al., 2010; Appeldoorn et al., 2016a). Interestingly, sites surveyed to the east of the main

TABLE 5 | Marine species identified in altiphotic (20 m) and deep (45 m) transect surveys from the central portion of the Guánica shelf edge, $\sim$ 40 m^2 was surveyed per depth designation.

Species	Absolute % cover	N	Index	Value
20 m depth-Porifera				
Amphimedon compressa (TS)	1.7466	115	Species Richness (S)	60
Agelas dispar	0.3558	70	Simpson's Index (D)	0.0452
Agelas conifera	1.6552	67	Simpson's index of diversity (1-D)	0.95
Cliona delitrix	0.1047	63	Simpson's reciprocal index (1/D)	22.1
Plakortis sp.	0.1360	55	Shannon-Wiener Index (H)	3.41
Cliona caribbaea	1.5613	50	Evenness (E)	0.328
Iotrochota birotulata	0.1655	50		
Scopalina ruetzleri	0.0462	44		
Ectyoplasia ferox	0.1216	40		
Niphates caribica	0.0453	36		
Mycale laevis	0.0634	36		
Agelas sventres (TS)	0.0779	35		
Niphates amorpha	0.0236	27		
Neopetrosia proxima	0.1258	25		
Agelas citrina	0.0647	21		
Cliona sp.	0.0711	21		
Xestospongia muta (TS)	0.9398	21		
Aplysina cauliformis	0.0240	20		
Niphates erecta	0.0189	17		
Aiolochroia crassa (TS)	0.0801	17		
Agelas sp.	0.0394	16		
Ircinia strobilina	0.0949	12		
Agelas sceptrum	0.0702	11		
Agelas tubulata	0.0744	10		
Svenzea zeai	0.1365	10		
Smenospongia sp.	0.0146	9		
Niphates sp.	0.0057	9		
Verongula sp.	0.0503	8		
Ircinia felix	0.1023	7		
Ircinia sp.	0.1084	7		
Cliona tenuis	0.1312	6		
Monanchora arbuscula	0.0216	6		
Smenospongia conulosa	0.0845	5		
Niphates digitalis	0.0006	5		
Petrosia pellasarca (TS)	0.0424	5		
Aplysina fistularis	0.1245	5		
Spirastrella coccinea	0.0108	4		
Desmapsamma anchorata	0.0171	4		
Neofibularia nolitangere	0.0563	4		
Aplysina sp.	0.0071	4		
Smenospongia aurea (TS)	0.0114	3		
Prosuberites laughlini	0.0052	3		
Neopetrosia sp.	0.0303	3		
Cinachyrella sp.	0.0123	3		
Myrmekioderma sp	0.0070	2		
Callyspongia plicifera	0.0031	2		
Niphates alba	0.0028	2		
Oceanapia bartschi	0.0046	2		

(Continued)

TABLE 5 | Continued

Species	Absolute % cover	N	Index	Value
Erylus sp.	0.0074	1		
Geodia neptuni	0.0116	1		
Chondrilla sp.	0.0149	1		
Dragmacidon reticulatum	0.0010	1		
Cribrochalina vasculum	0.0516	1		
Niphates recondita	0.0003	1		
Petrosia weinbergi	0.0060	1		
Clathria echinata	0.0024	1		
Aplysina archeri	0.0034	1		
Aplysina lacunosa	0.0034	1		
Suberea sp.	0.0038	1		
Plakinastrella sp.	0.0060	1		
Sponge (unidentified)	0.2082	154		
Total	9.01	1,163		
45 m depth-Porifera				
Plakortis sp.	2.165	340	Species Richness (S)	54
Agelas sceptrum	1.550	256	Simpson's Index (D)	0.127
Plakortis symbiotica	1.117	87	Simpson's index of diversity (1-D)	0.873
Prosuberites laughlini	0.176	52	Simpson's reciprocal index (1/D)	7.87
Niphates erecta	0.127	49	Shannon-Wiener Index (H)	2.83
Scopalina ruetzleri	0.102	46	Evenness (E)	0.264
Axinella sp.	0.025	39		
Aiolochroia crassa (TS)	0.298	36		
Agelas conifera	1.519	35		
Agelas sventres (TS)	0.271	32		
Aplysina sp.	0.065	30		
Agelas citrina	0.239	25		
Ircinia sp.	0.398	22		
Aplysina cauliformis	0.049	22		
Plakinastrella sp.	0.174	22		
Amphimedon compressa (TS)	0.043	20		
Svenzea zeai	0.363	19		
Verongula sp.	0.118	17		
Oceanapia bartschi	0.577	16		
Niphates sp.	0.013	12		
Agelas sp.	0.021	11		
Agelas dispar	0.064	10		
Petrosia pellasarca (TS)	0.182	10		
Petrosia weinbergi	0.138	10		
Agelas clathrodes	0.216	9		
Spirastrella coccinea	0.039	9		
Xestospongia muta (TS)	0.569	9		
Ectyoplasia ferox	0.045	9		
Cinachyrella sp.	0.066	9		
Plakortis deweerdtaephila	0.110	7		
Ircinia felix	0.059	4		
Spirastrella hartmani	0.023	4		
Desmapsamma anchorata	0.011	4		
Iotrochota birotulata	0.005	4		
Agelas tubulata	0.023	3		

(Continued)

TABLE 5 | Continued

Species	Absolute % cover	N	Index	Value
Myrmekioderma sp.	0.018	3		
Callyspongia fallax	0.010	3		
Niphates amorpha	0.006	3		
Batzella sp.	0.006	3		
Monanchora arbuscula	0.016	3		
Placospherastra sp.	0.008	2		
Suberea sp.	0.191	2		
Agelas cervicornis	0.026	1		
Geodia neptuni	0.002	1		
Ircinia strobilina	0.024	1		
Smenospongia sp.	0.002	1		
Callyspongia plicifera	0.005	1		
Cribrochalina vasculum	0.011	1		
Niphates alba	0.003	1		
Niphates caribica	0.002	1		
Niphates digitalis	0.002	1		
Clathria echinata	0.001	1		
Verongula reiswigi	0.013	1		
Xestospongia deweerdtae	0.002	1		
Sponge (unidentified)	2.741	981		
Total	14.05	2,301		

TS, Trididemnum solidum overgrowing surface of sponge. Unidentified sponges were not taken into consideration for Diversity index calculations.
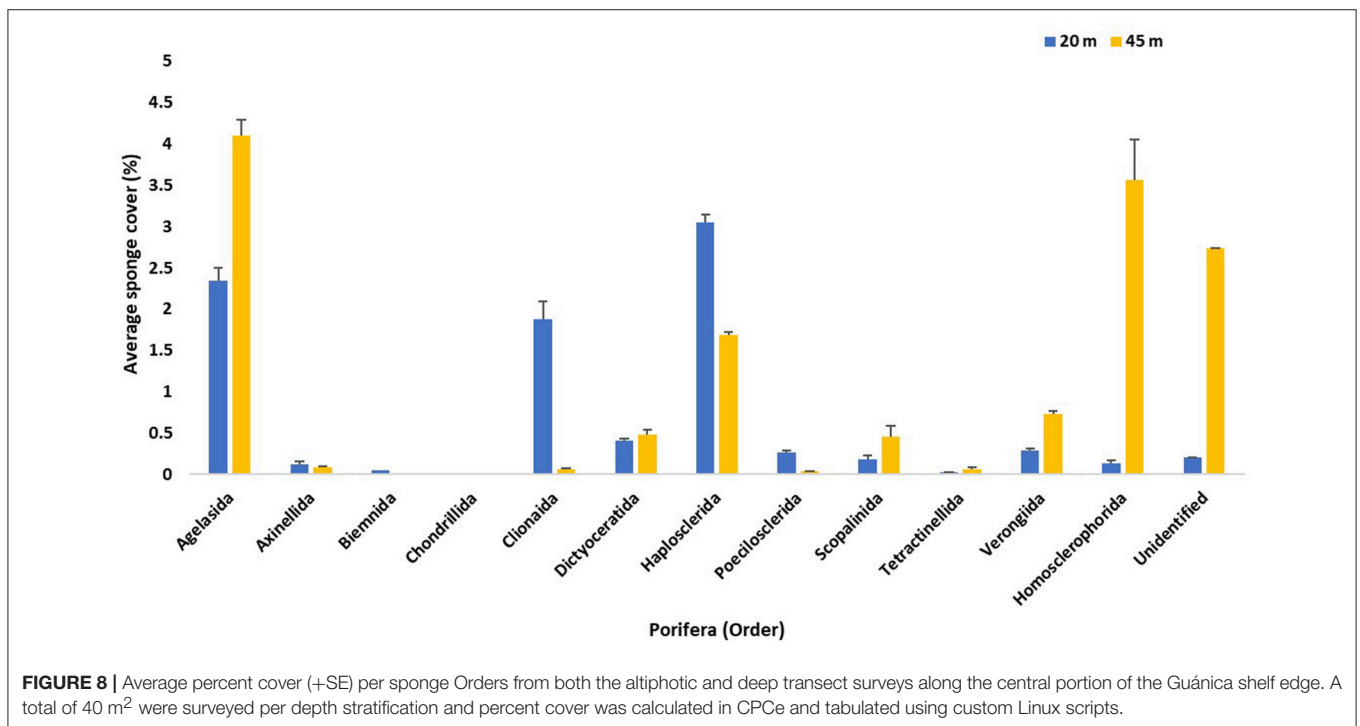
FIGURE 8 | Average percent cover (+SE) per sponge Orders from both the altiphotic and deep transect surveys along the central portion of the Guánica shelf edge. A total of 40 m^2 were surveyed per depth stratification and percent cover was calculated in CPCe and tabulated using custom Linux scripts.

island of Puerto Rico (i.e., Culebra, Fajardo, Vieques and the US Virgin Islands) show extremely low percent sponge coverage (1.0–4.0%) which can be attributed to the dominance of the scleractinian corals *O. annularis* (16.0%; Smith et al., 2010) and *O. franksi* (38.0%; García-Sais et al., 2016), leaving little substrate for other benthic invertebrates to colonize. Comparing our results to what has been reported from the La Parguera Natural Reserve shelf edge. Armstrong et al. (2009)

reported an average sponge cover of 13.0% at 25–35 m, while Appeldoorn et al. (2016a) reported sponge cover from two sites, Hole-in-the-Wall (17% and 16% from 50 m and 70 m, respectively), and El Hoyo (15% and 18% from 50 m and 70 m, respectively). Isolated and offshore sites to the west of Puerto Rico like Abrir La Sierra (García-Sais et al., 2010b), Isla Desecheo (García-Sais, 2010), Bajo de Sico (García-Sais et al., 2007), and Isla Mona (García-Sais et al., 2010a) have also reported high percent sponge cover at depths surveyed from 30–60 m.

Within Guánica's coral reef ecosystems, our total sponge cover data from 20 m (9.0% ± 1.04 SE) and 45 m (14.0% ± 1.96 SE) resemble those made by previous studies. García-Sais et al. (2014, 2015, 2017) reported an average sponge cover of 7.0% at 20 m from the Guánica insular shelf edge. Rivero-Calle (2010) analyzed phototransect surveys and compared benthic cover from two separate sampling years within Guánica's shelf edge. Rivero-Calle (2010) results show an apparent decrease of sponge cover across time and depth, with sponge cover at 30–40 m in 2004 (15.0%) decreasing to 10.0% in 2008, while sponge cover at 40–50 m in 2004 (11.0%) decreased to 7.7% in 2008, with similar decreases in sponge cover across 50–100 m depth intervals. Armstrong et al. (2009) also analyzed phototransects collected in 2004 across two depth stratifications, reporting overall similar results, with 25.0% cover at 25–35 m, and 38.0% cover at 36–50 m. Sponge cover, and to some extend diversity and abundance (154 unidentified specimens at 20 m, compared to 981 unidentified specimens at 45 m), seems to follow a similar trend at specific locations within the Caribbean, increasing with depth (García-Sais, 2010; Lesser and Slattery, 2013). However, care should be taken not generalize this trend until more studies (with a standardized method) take place across across multiple sites in the Caribbean (see Scott and Pawlik, 2018).

The incidence of unidentified sponge disease and bleaching affecting several species (*A. conifera*, *A. sceptrum*, *A. compressa*, *C. vaginalis*, *S. zeai*, *V. gigantea*, and *X. muta*) was opportunistically observed across both depths (i.e., Rützler, 1988; Olson et al., 2006, 2014; Angermeier et al., 2011, 2012; Deignan and Pawlik, 2016). However, since these observations occurred outside of our phototransect surveys, they were not considered for quantitative analysis. A potential disease of great concern (most likely orange band disease) was observed affecting the giant barrel sponge (*X. muta*) at both depths (**Figure 2G**) (JEGH pers. obs.), a species which acts as a bioengineer and provides habitat and structure for an array or organisms (McMurray et al., 2008; Hammerman and García-Hernández, 2017; Skinner, 2018; Swierts et al., 2018). Monitoring, recording and reporting sponge disease/bleaching outbreaks, subsequent die-offs and/or recovery events of large and morphologically diverse species (and their associates) is crucial to assess the overall health of the ecosystem in an ever-changing environment (Wulff, 2013; Deignan et al., 2018; Pita et al., 2018). For example, at Bajo de Sico seamount, an important Nassau and Black grouper aggregation site in Puerto Rico (Tuohy et al., 2015; Sanchez et al., 2017), occurrence of disease and bleaching was observed affecting several large specimens of *X. muta* at depths between 35 and 50 m (JEGH and

Tuohy pers. Obs.). In one occasion, the complete disintegration of a large specimen of *X. muta* occurred 3–5 days after initial monitoring (Cowart et al., 2006; McMurray et al., 2011).

Duffy et al. (2013) highlighted a devastating example of how the disappearance of important host sponge species from reefs in Belize and Jamaica served as the primary cause for the dramatic decline of two species of eusocial shrimps. Large sponges may also be serving as zoogeographical "stepping-stones" as suggested by Collette and Rützler (1977), as well as recruitment habitat for several species of fish and benthic invertebrates (Tyler and Böhlke, 1972; Colin and Clavijo, 1988; Rocha et al., 2000; Rocha, 2003; García-Sais et al., 2007, 2010b). Future benthic surveys of Puerto Rican altiphotic and mesophotic coral reefs should include sponges in their ecology assessments, especially the most common and large species (Wulff, 2001; Bell et al., 2017). These large sponges play a key role in the overall health of the coral reef ecosystem by providing ecological services (Diaz and Rützler, 2001; de Goeij et al., 2013), and in some instances, contribute to the preservation of associated fauna biodiversity (Thomas and Klebba, 2006; Hultgren et al., 2010; Padua et al., 2013; Rix et al., 2018). A collapse of large species of sponges in Guánica and nearby reefs, which provide structure and habitat, may be devastating to some species of fish, especially at mesophotic depths (**Figure 2F**).

Unconsolidated sediments (**Figure 7**) accounted for a large portion of percent cover and influence both sponge and hard coral cover (Lesser and Slattery, 2011; Slattery and Lesser, 2014; Appeldoorn et al., 2016a), by limiting availability of substrate for larvae to settle upon (Duckworth, 2016). Algal cover of mesophotic sites in the adjacent La Parguera (50–70 m depth) averaged 52% of the habitat followed by sponges and corals, highlighting the importance of these taxa in shaping the communities at those depths (Appeldoorn et al., 2016b). This contrasts with what we observed, where algae benthic cover at 20 m (19.0 ± 2.20 SE) was greater than that at 45 m (7.6 ± 1.92 SE) (**Figure 7**), thus making sponges the most abundant, dominant, and important taxa at upper mesophotic reefs in Guánica. Additional attention should be given to any local increase of biological threats to these deeper reefs, such as cyanobacterial mats, known to disrupt benthic community assemblages (de Bakker et al., 2017), opportunistic benthic algae blooms (Langston and Spalding, 2017; Sherman and Tuohy pers. obs.), and the aggressive overgrowing colonial ascidian (*Trididemnum solidum*) known to overgrow corals (e.g., Rodríguez-Martínez et al., 2012; JEGH pers. obs.) and sponges (**Table 4**; JEGH pers. obs.).

CONCLUSION

Our dataset increases the knowledge of southwest Puerto Rico's altiphotic and mesophotic fish, coral, and sponge assemblages. We highlight the need to continue monitoring this dynamic ecosystem and emphasize that it is crucial to perform long-term time series assessments of the general

area to fully assess any fluctuations in community structure (i.e., abundance, dominant species shift, disease, bleaching) (Wulff, 2001, 2006; Easson et al., 2015) and preservation of the overall marine biodiversity (Miloslavich et al., 2010; Jenkins and van Houtan, 2016; Hoeksema et al., 2017). This study demonstrates that altiphotic and mesophotic reefs across the Guánica continental shelf edge support different assemblages of corals, sponges and fish. These results provide preliminary data for the region supporting the arising hypothesis that mesophotic coral reefs should not be seen as refuge for shallower reefs, instead, they are actually different and unique ecosystems (i.e., Semmler et al., 2017; Rocha et al., 2018). Of the species which were present across both depths, only the inclusion of genetics can decisively determine gene flow and connectivity. Given the prevalence of anthropogenic vectors both directly adjacent to Guánica (e.g., Rio Loco System and Guánica Bay) and further east in Ponce (e.g., Ponce mega port and watershed activities), and the presence of a wide array of unique and ecologically important species, we propose increased monitoring from local, state, and federal agencies to protect and include mesophotic coral reef ecosystems within the Guánica Biosphere Reserve.

AUTHOR CONTRIBUTIONS

JG-H, PS, and NH contributed equally to the manuscript. JG-H, PS, NH, and NS conceived, designed, and drafted the article. JG-H served as the sponge specialist. PS served as the fish specialist. NH served as the coral specialist. NS served as the PI of the first three authors. All authors developed, implemented, and analyzed data, and contributed to the theory and interpretation of the data. All authors critically revised and approved the final version of the article.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2018.00303/full#supplementary-material

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