



# Depth and structure as environmental drivers of fish communities across a shallow to mesophotic gradient in the northern US Virgin Islands

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## Advances in Ecosystem-Scale Coral Reef Visual Surveys

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**ABSTRACT.**—The factors that drive fish communities on coral reefs are varied, complex, and often location specific. In the northern United States Virgin Islands, the large areas of mesophotic coral ecosystems across an insular shelf provide a multitude of gradients along which fish communities form. Using a stratified-random visual fish census, we collected comprehensive data on fish communities across a seascape scale. Fish density and diversity showed responses to depth and hard relief, with these factors occasionally interacting in ways that are species specific. Analysis of trophic groups showed that densities of all groups were positively associated with relief, but while herbivores and invertivores decreased with depth, planktivores and piscivores increased, and piscivores additionally showed an interaction. Some commercially important species occurred more frequently and in larger sizes on deeper reefs, suggesting that mesophotic reefs shelter more fisheries resources, although they are less commonly sampled in visual census programs. Understanding how fish communities change across the seascape informs patterns of ecosystem function, such as identifying areas of resilience and vulnerability. This dataset is a valuable contribution to more completely understanding the ecology and conservation of fishes in the western Atlantic.

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Tropical reef fish communities are varied and complex, with a multitude of biological and environmental drivers determining diversity and relative dominance of species. Broad-scale drivers of fish abundance and diversity on and around coral reefs include depth (e.g., Asher et al. 2017, Costello and Chaudhary 2017, Stefanoudis

et al. 2019), distance to shelf edge (e.g., Williams and Hatcher 1983, Cheal et al. 2012, Sanchez et al. 2022), and habitat (e.g., Grober-Dunsmore et al. 2008, Abesamis et al. 2018, Roff et al. 2019). On a finer scale, factors such as height of hard structure (e.g., Gratwicke and Speight 2005, Wilson et al. 2007, Asher et al. 2017) or the risk of predation or competition (e.g., Hensel et al. 2019, Lester et al. 2021) may come into play. These factors change in strength of association depending on the diet and trophic position of a species (e.g., Garner et al. 2019, Carrington et al. 2021, Scott et al. 2022). Determining the factors that drive fish communities on coral reefs around the world is an active area of research, and results are often location specific.

In the United States Virgin Islands (USVI), coral reef ecosystems are patchily distributed around the three large main islands and several smaller surrounding islands. The northern islands of St. Thomas and St. John have a southern insular shelf with extensive *Orbicella* reef development (Smith et al. 2019), which drops off steeply at a well-defined edge into the Anegada-Jungfern Passage (Fratantoni et al. 1997), creating an ecological separation of the northern islands from the island of St. Croix. Reefs around St. Thomas and St. John are generally found in fringing, patch, or spur and groove formations (Jeffrey et al. 2005), and reef fish communities have been documented in the area since the 1960s (e.g., Randall 1967). Invertivores and herbivores are common, while sharks and large-bodied groupers are extremely rare (Friedlander et al. 2013). The reefs have undergone major benthic habitat changes over the past few decades, including mass-bleaching events in 1998 (Rogers and Beets 2001) and 2005 (Smith et al. 2013), and the more recent 2019 outbreak of Stony Coral Tissue Loss Disease (Brandt et al. 2021). Other indirect threats facing coral reefs in the USVI include boating impacts (Rogers and Beets 2001), major storms, and coral diseases (Beets and Rogers 2000). There are additional less-well-documented effects such as coastal development, runoff, pollution, and tourism and recreation (Jeffrey et al. 2005).

In addition to nearshore shallow coral reefs, there are large areas of mesophotic coral ecosystems (MCEs) in the USVI that may be the most developed in the Eastern Caribbean, covering almost three times the extent of nearby shallow reefs (Smith et al. 2019). MCEs around the world are widespread and diverse, but largely unexplored and not often considered in conservation planning (Baker et al. 2016). Connectivity between shallow and upper mesophotic reefs is species- and location-specific (Kahng et al. 2014). Many studies of fish across a shallow to mesophotic depth gradient have occurred on steep slopes or seamounts (e.g., Garcia-Sais 2010, Pinheiro et al. 2015, Kane and Tissot 2017), but even across a short horizontal distance, communities are structured by depth (Kahng et al. 2010). Previous work on USVI MCEs have indicated diverse fish communities with high biomass, including many piscivores and planktivores (Smith et al. 2019).

Fish communities in the USVI and Puerto Rico have experienced detrimental effects from the fishing industry since the 1960s (e.g., Appeldoorn et al. 1992), even before major benthic habitat changes began. The USVI has a cultural history in the fishing industry. Local fishers target mostly multi-species reef fish, and the number of fishers has stayed constant over the last century (Kojis and Quinn 2006), however, intensity of fishing may have increased with technology. Highly valued commercial fish, such as snappers and groupers, have shown the most notable declines over time, in part due to their vulnerability to overexploitation (Kadison et al. 2017). This is of particular concern for several large-bodied species that reproduce at seasonal spawning aggregations on MCEs in the USVI (Kadison et al. 2010, Biggs and Nemeth 2016).

There are several marine protected areas (MPAs) across the northern USVI, including the territorial St. Thomas East End Reserves, as well as the federal Hind Bank Marine Conservation District (MCD), the seasonal Grammanik Bank closure, the Virgin Islands Coral Reef National Monument, and the Virgin Islands National Park. Previous studies of the VI National Park showed no major differences in fish assemblages across its boundaries (Rogers and Beets 2001, Friedlander and Beets 2008), and the VI Coral Reef National Monument was placed without consideration of critical habitats, so is unlikely to be effective (Monaco et al. 2007). On the other hand, at a spawning aggregation inside the MCD, *Epinephelus guttatus* have increased in size and number since protection began (Nemeth 2005).

There are a few existing coral reef monitoring efforts in the region, but at a limited scale. There has been monitoring of the La Parguera region of Puerto Rico that has produced comprehensive characterization of fish and benthic habitats, but studies have been limited to less than 30 meters water depth (e.g., Pittman et al. 2010) or more than 30 meters water depth (e.g., Bejarano et al. 2014), or have sampled only a small area (e.g., Garcia-Sais 2010). The USVI Territorial Coral Reef Monitoring Program takes an annual comprehensive snapshot of coral and fish community health at permanent monitoring sites across a depth gradient (e.g., Ennis et al. 2020), but these sites are not fully representative of the diversity of hardbottom habitats around the territory. There has yet to be a spatially randomized comprehensive study of fish communities at a broad spatial scale, including highly abundant mesophotic habitat, in the USVI.

This study describes fish communities in the northern US Virgin Islands and how they relate to environmental drivers such as depth and hard relief, which vary across the vast insular shelf. We focus on: (1) overall patterns in density and diversity of fish communities across sites, (2) the occurrence and density of the most abundant fish species in each trophic group, and (3) ecologically significant patterns of commercially important species in the USVI, which are most relevant to fisheries and ecosystem management objectives.

## METHODS

Seascape-scale reef visual census surveys were conducted in the northern USVI islands of St. Thomas and St. John between 2017 and 2022 (Fig. 1). Observations occurred from May to December, excluding the winter/spring spawning aggregation periods when large-bodied groupers and many snappers are potentially absent from their resident reefs, and present in anomalous numbers at deep MCE spawning sites. Surveys used National Coral Reef Monitoring Program (NCRMP) methods that target hardbottom habitats (i.e., aggregate reef, patch reef, and pavement) and occurred in two separate sampling efforts of independent design using the same protocols: (1) routine, biennial NCRMP sampling (0–≤30 m depth); and, (2) new, annual Deep Coral Reef Monitoring Program sampling (DCRMP, >30–50 m depth; Online Fig. S1). A full description of the sampling methodologies is described in NOAA (2021) and in a companion paper on the management implications of DCRMP sampling in the USVI by Grove et al. (In Press).

These fisheries-independent sampling efforts relied on a predefined 50 × 50 m gridded sample frame of hardbottom habitats from 0 to 50 m depth and a stratified-random sampling design to select fish survey sites (NOAA NCCOS 2018). Sites were

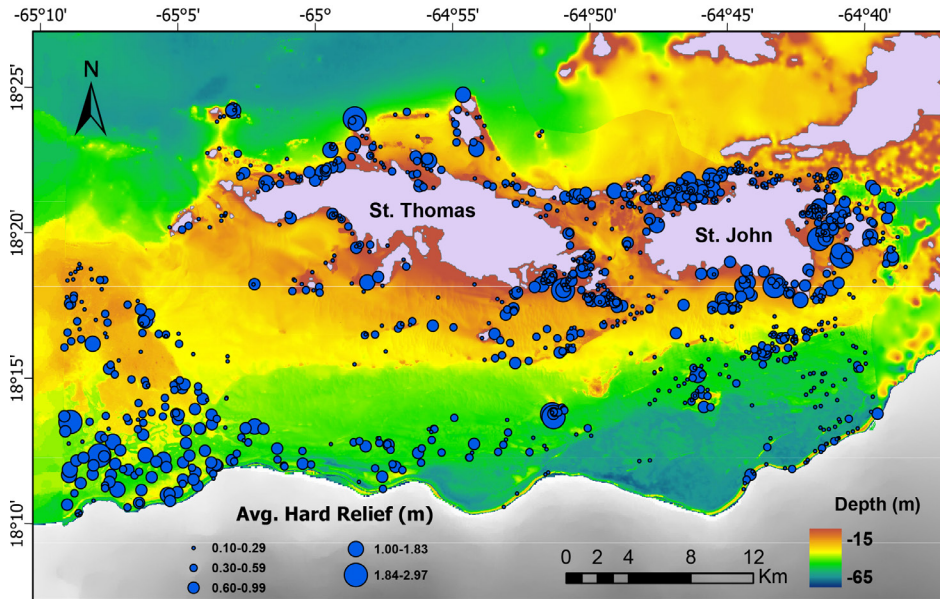


Figure 1. Locations of reef visual census sites surveyed around the northern USVI. Size of circle indicates the amount of average vertical relief of the site in meters. Bathymetry shallower than 65 m indicated by color ramp. Bathymetry deeper than 65 m indicated in grayscale and represents off-shelf habitats not surveyed in this project. Average relief and depth were predictor variables used in the analysis of fish communities.

surveyed by diver pairs using standard open circuit diving procedures (NCRMP) or open circuit technical diving with decompression procedures (DCRMP). All dives were conducted from an unmoored vessel (live-boat diving) that was piloted to within 5 m of the sampling point (i.e., center of 50 × 50 m grid cell). Upon entry, divers rapidly descended to the seafloor; ability to stay within the assigned sample grid was facilitated by sighting and descending to the first visible seafloor object.

Fish surveys were conducted using the Reef Visual Census Stationary Point Count (RVC-SPC) method (Bohnsack and Bannerot 1986, Brandt et al. 2009, CRCP 2022). Briefly, a dive flag was secured to the seafloor and each diver swam 7.5 m in opposite directions to create two imaginary 15-m diameter (177 m<sup>2</sup> area) non-overlapping cylinders. Each imaginary cylinder was centered on an individual diver and extended from the substrate to the sea surface or to the extent visible. Each diver identified fish to the species level, counting the number of individuals of each species. They then estimated for each species the minimum, maximum, and mean fork length to the nearest cm across all individuals seen. Groupers and snappers were sized individually when possible. Divers completed extensive training and in-water practice to ensure accurate measurements. Divers also recorded depth, visually estimated percent cover of general taxonomic groups (e.g., live coral, sponge, algae >1 cm, algae <1 cm), and categorized surface relief coverage by estimating the maximum vertical relief and the percentages of hard relief that fell into categories (in m; 0–0.2, 0.2–0.5, 0.5–1.0, 1.0–1.5, 1.5–max).

Diver pair data were deemed non-independent and were averaged at the site level. Data were entered into a standardized online data entry portal by the individual data collector. The data entry runs standard quality control for each species and

flags entries outside of species-specific expectations for number of individuals and individual sizes. The data are then “proofed” by the diver to ensure entries match the values recorded in the database, then again during a more comprehensive quality control process before the final cleaned data are made publicly available online (NCCOS and SEFSC 2018, 2020, 2022).

**DATA ANALYSIS.**—Data were analyzed to understand how fish density, diversity, and size were distributed across the seascape using common predictor variables. Predictor variables included site depth (m) and reef structure defined as the average vertical relief of hard substrate. The distribution of depth was roughly uniform across sites, so a transformation was not applied. Average hard relief, calculated by a weighted average of bin midpoints, was right skewed: most coverage of most sites lay predominantly in the first two bins and few sites had high average relief. Thus, average hard relief was log-transformed for analyses to achieve a more symmetric distribution. Distance to the southern shelf edge, defined as the 100 m bathymetric contour line, was also considered, but excluded because depth and shelf edge distance were significantly negatively correlated (Spearman’s rank correlation  $\rho = -0.70$ ,  $P < 0.001$ ). Therefore, the results are framed in reference to depth for ease of comparison to other studies but cannot be readily distinguished from effects of distance to the shelf edge on reef fish communities. In addition, diver-estimated coral cover was considered as a predictor variable but was also excluded because living coral cover and average hard relief were significantly negatively correlated (Spearman’s rank correlation  $\rho = 0.62$ ,  $P < 0.001$ ). We chose to focus on relief as the primary driver of fish community assemblages as fish associate primarily with reef structure regardless of whether it is living (e.g., Luckhurst and Luckhurst 1978, Kane and Tissot 2017), and a previous study in the region showed a weak relationship between fish abundance and live coral cover, with habitat and depth playing stronger roles (Garcia-Sais 2010). Furthermore, recent mass mortality events of corals have reduced living coral cover (Smith et al. 2013, 2016a, Brandt et al. 2021) such that site-wise differences are difficult to detect visually.

The full dataset was truncated to exclude fish with less than 1% occurrence across sites and small cryptic fish (Online Table S1) as their inconsistency obscured other patterns. Species were categorized into trophic groups (i.e., herbivore, invertivore, planktivore, piscivore) based on the primary literature (Online Table S1). Some species could be considered to fit within more than one of these groups or specialize on a subset of a group (i.e., sessile invertebrates); for the sake of simplicity we used broad categories of diet and only examined the primary trophic group in analyses. Fish density (ind 177m<sup>-2</sup>) was calculated on a species level for each site and converted to ind 100m<sup>-2</sup> for ease of comparison to other studies. Fish density was then aggregated as needed for each analysis into trophic groups or across all species combined. Fish diversity was calculated using the Simpson’s diversity index using the R package *vegan* (Oksanen et al. 2022).

To analyze the influence of environmental factors on total fish density, diversity, and presence-only trophic group density, we fit a generalized linear model (GLM) for each. Using the R package *stats* (R Core Team 2022), four model formulae were considered for each response variable: (1) response as a function of both depth and relief and their interaction (full model), (2) response as a function of only depth, (3) response as a function of only relief, and (4) no predictors (null model). Model



selection was informed by the Akaike Information Criterion (AIC), where the model with the lowest AIC value was deemed the best fit for the data. Response variables were transformed if needed to approximate a Gaussian distribution: total fish density was log-transformed, Simpson's diversity was cube-transformed, and trophic group densities were each log-transformed. To facilitate visual interpretation of interactions between predictor variables, two-way plots were created of each group of interest using depth and hard relief categorized into two groups by their median value (23.8 m and 0.3 m, respectively).

To examine patterns in the occurrence of fish species, we modeled species presence as a binary response variable using a logistic regression. We also investigated species density by fitting a linear regression on site-wise, presence-only data, log-transformed to approximate a Gaussian distribution, and examined patterns in size structure by fitting a weighted linear regression to individual fish lengths. For each analysis, the same model-selection process was followed using AIC as described above. For visualization, plots contrasting observed versus predicted values were generated. For the logistic regression of species presence/absence, the predicted values were the probabilities of presence, mapped in a gradient from blue (low probability) to red (high probability). For the presence-only linear regression on species density and the linear regression on species size, the observed versus predicted log densities were plotted, with points colored by depth and sized by relief. The fits of the models were evaluated using the Receiver Operating Characteristic (ROC) curves for the logistic regression, and Q-Q plots for the linear regressions to ensure assumptions of normally distributed residuals were met.

We applied a nonmetric multidimensional scaling (NMDS) to the species presence-absence data to examine compositional differences in the overall fish communities across sites. We used the Jaccard dissimilarity metric, which is appropriate for binary datasets. Due to convergence challenges in the NMDS, species present in fewer than the 25th percentile of sites were omitted from the analysis. This analysis was performed using the R package *vegan* (Oksanen et al. 2022).

All analyses were performed using the software language R (R Core Team 2022) in the RStudio environment (RStudio Team 2022). The results of all species-wise analyses are provided in the supplemental material.

## RESULTS

**SITE CHARACTERISTICS.**—A total of 1073 sites were surveyed between 2017 and 2022 across the NCRMP and DCRMP sampling programs (Fig. 1). Site depths varied from 1 m to 51 m (mean = 23.7 m, median = 23.8 m), and average hard relief at each site ranged from 0.1 m to 3.0 m (mean = 0.4 m, median = 0.3 m). Higher relief sites were associated with shallower nearshore habitats, particularly around St. John, and offshore sites in a mesophotic star coral (*Orbicella*) reef complex southwest of St. Thomas (Fig. 1; Smith et al. 2010). Low-relief sites were scattered around the shelf with a particular concentration offshore south of St. John. These sites were typically deeper areas (40–50 m depth) dominated by low calcium carbonate outcrops surrounded by rhodolith plains (Smith et al. 2019).

**FISH DENSITY AND DIVERSITY.**—Divers observed 290 unique fish species from 63 families. Of these, 141 species (37 families) had greater than 1% occurrence and were

Table 1. Outputs of overall generalized linear models of total fish density, Simpson's diversity index, planktivore density, herbivore density, piscivore density, and invertivore density against the potential predictors of site depth, bottom relief, and the interaction of the two.

Response	Predictors	Coefficient	P-value	R <sup>2</sup>
log(total fish density)	depth	-0.006	0.029	0.11
	log(relief)	0.383	<0.001	
	depth × relief	-0.004	0.023	
Simpson's diversity index	depth	0.001	0.24	0.06
	log(relief)	0.026	0.079	
	depth × relief	0.001	0.034	
log(planktivore density)	depth	0.056	<0.001	0.29
	log(relief)	0.351	0.004	
	depth × relief	-0.005	0.218	
log(herbivore density)	depth	-0.010	0.001	0.16
	log(relief)	0.359	<0.001	
	depth × relief	0.000	0.938	
log(piscivore density)	depth	0.008	0.049	0.14
	log(relief)	0.466	<0.001	
	depth × relief	-0.015	<0.001	
log(invertivore density)	depth	-0.020	<0.001	0.16
	log(relief)	0.323	<0.001	
	depth × relief	-0.002	0.403	

considered for more detailed analyses (Online Table S1). The mean fish density at each site was  $84.5 \pm 1.8$  fish per 100 m<sup>2</sup> (median 69.5 fish per 100 m<sup>2</sup>). The best-fit model for total fish density showed significant effects of depth, relief, and their interaction (Table 1). Higher-relief sites were associated with higher fish density across depths, but at low-relief sites, total fish density was higher at deeper sites (Fig. 2A, Online Fig. S2). Sites associated with lower fish density were common in nearshore areas and to a lesser degree in deeper lower-relief areas (Fig. 3A).

Fish diversity, as calculated by Simpson's diversity index (Table 1, Fig. 2B), was best explained by the full model, which showed suggestive evidence at an effect of relief and a significant interaction between depth and relief. Although the model was poorly fit ( $R^2=0.06$ ), diversity was high at higher-relief sites across all depths, whereas at lower-relief sites diversity was lower, particularly at deeper sites (Online Fig. 2B). Fish diversity was highly variable across the sampling area (Fig. 3B).

**TROPHIC TRENDS.**—Each trophic group was predominantly composed of only a few fish species by density. Invertivores were present in the highest density (41%), followed by herbivores (34%), planktivores (22%), and piscivores (3%). Species accumulation curves show that 50% of the total density in each trophic group was reached within two to four species (Fig. 4). Planktivores were dominated by blue chromis (*Chromis cyanea*), creole wrasse (*Clepticus parrae*), and chalk bass (*Serranus tortugarum*); herbivores were dominated by bicolor damselfish (*Stegastes partitus*), striped parrotfish (*Scarus iseri*), and princess parrotfish (*Scarus taeniopterus*); piscivores were dominated by tobaccofish (*Serranus tabacarius*), graysby (*Cephalopholis cruentata*), and blue runner (*Caranx crysos*); invertivores were dominated by bluehead wrasse (*Thalassoma bifasciatum*), yellowhead wrasse (*Halichoeres garnoti*), and slippery dick (*Halichoeres bivittatus*).

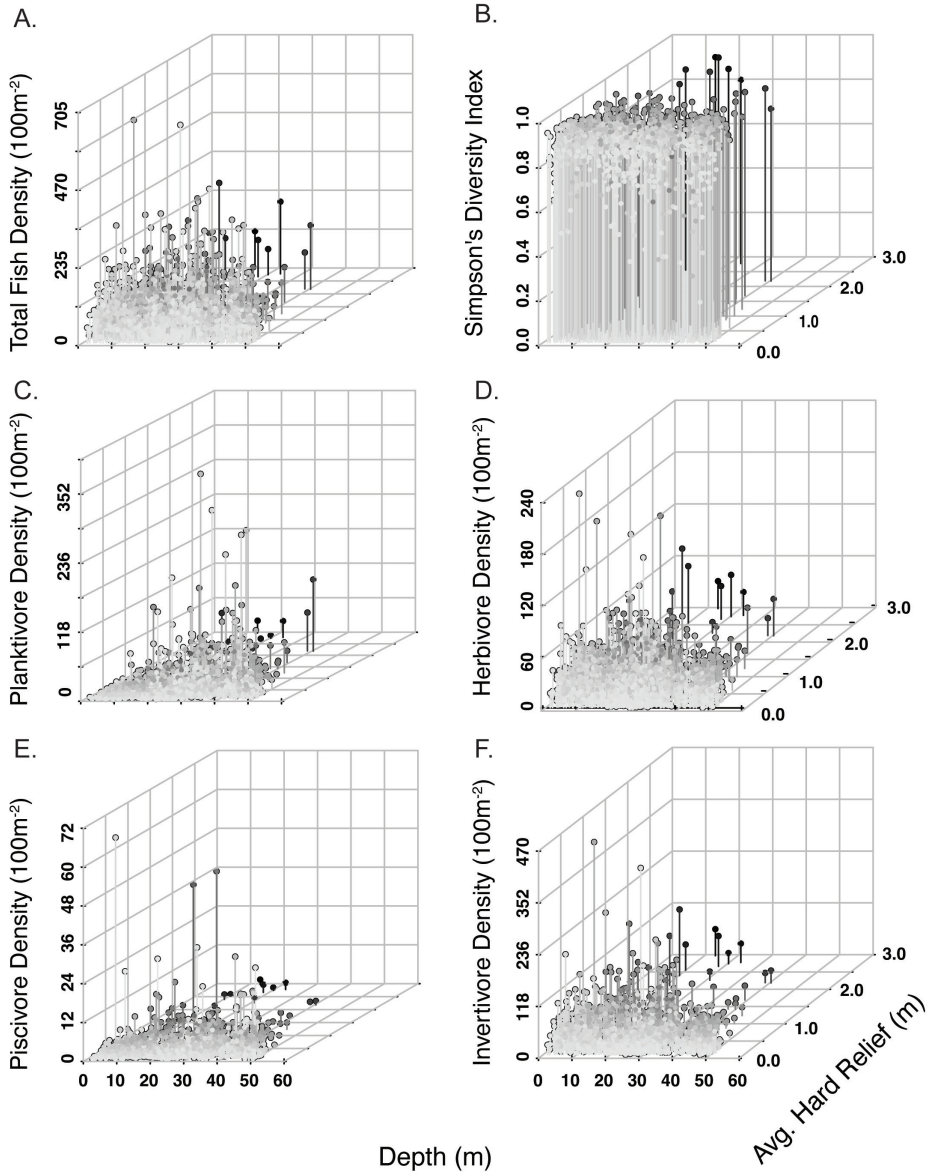


Figure 2. (A) Total fish density, (B) Simpson's diversity index, (C) planktivore density, (D) herbivore density, (E) piscivore density, and (F) invertivore density at sampling sites shown plotted against depth (m) and average hard relief (m). Density units are in fish per 100 m<sup>2</sup>. Point color illustrates relief, with light gray indicating low relief and black indicating high relief.

Planktivore density was well-fit to the full model, and significantly associated with both depth and relief, with no interaction (Table 1). Planktivores occurred in highest densities at deeper depths and higher relief (Fig. 2C, Online Fig. S2), and represented an increased share of total fish density at deeper sites (Fig. 5). Spatially, sites with higher planktivore density were associated with offshore deeper sites, with lower densities at shallower nearshore sites around St. Thomas and St. John



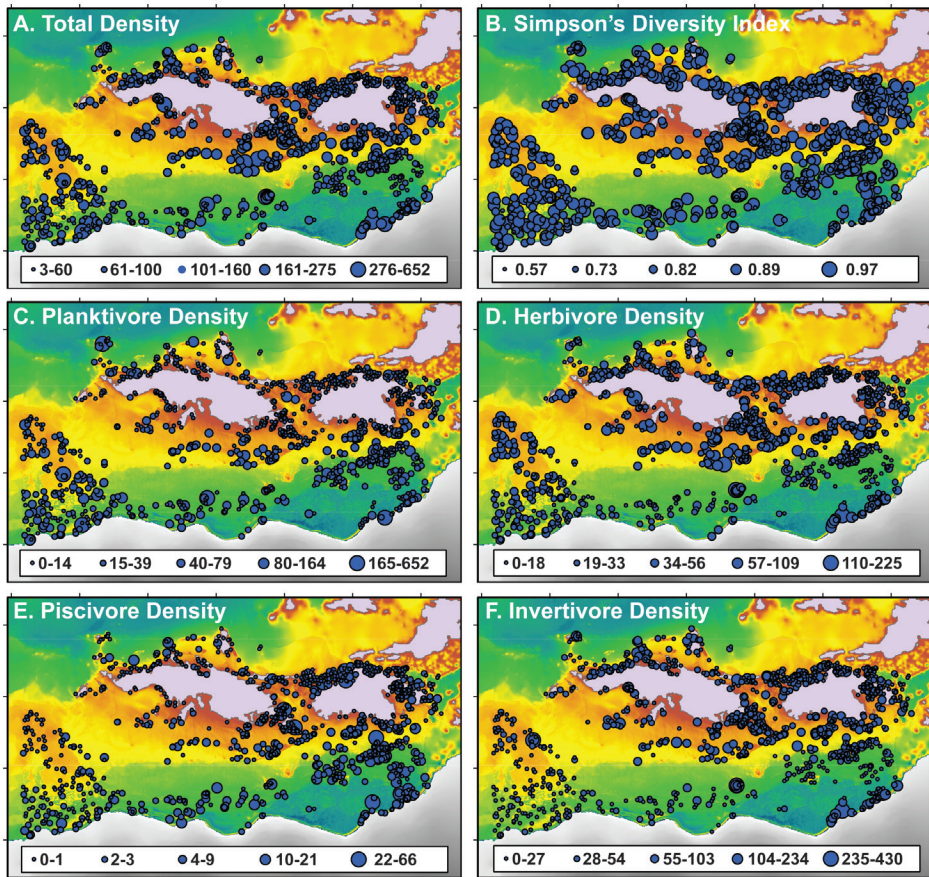


Figure 3. The northern US Virgin Islands sampling area with size of point showing the spatial pattern of (A) total fish density, (B) Simpson's diversity index, (C) planktivore density, (D) herbivore density, (E) piscivore density, and (F) invertivore density. All density estimates are shown as the number of fish per 100 m<sup>2</sup>.

(Fig. 3C). This pattern followed the occurrence of the three most common species (about 75% of density; Fig. 4), with *C. cyanea*, *C. parrae*, and *S. tortugarum* all showing an interaction between depth and relief. The nature of the interaction varied between species, with occurrence of *C. cyanea* and *C. parrae* most associated with deeper, higher-relief sites, whereas *S. tortugarum* were most associated with deeper, lower-relief sites. Of these common species, density was well-modeled only for *S. tortugarum*, which had highest densities at deeper, lower-relief sites, where it occurred most often. Other species which showed significant patterns included the commercially and recreationally important yellowtail snapper (*Ocyurus chrysurus*), which was most associated with deeper sites, especially those with higher relief. It also tended to be larger at deeper sites and those with higher relief and was especially small at shallower sites with lower relief. No other planktivores showed a clear size trend. Sunshinefish (*Chromis insolata*) were almost exclusively present at deeper sites. In contrast to the predominant planktivore pattern, sergeant major (*Abudefduf saxatilis*) had highest occurrence and density at shallower, higher-relief sites, and

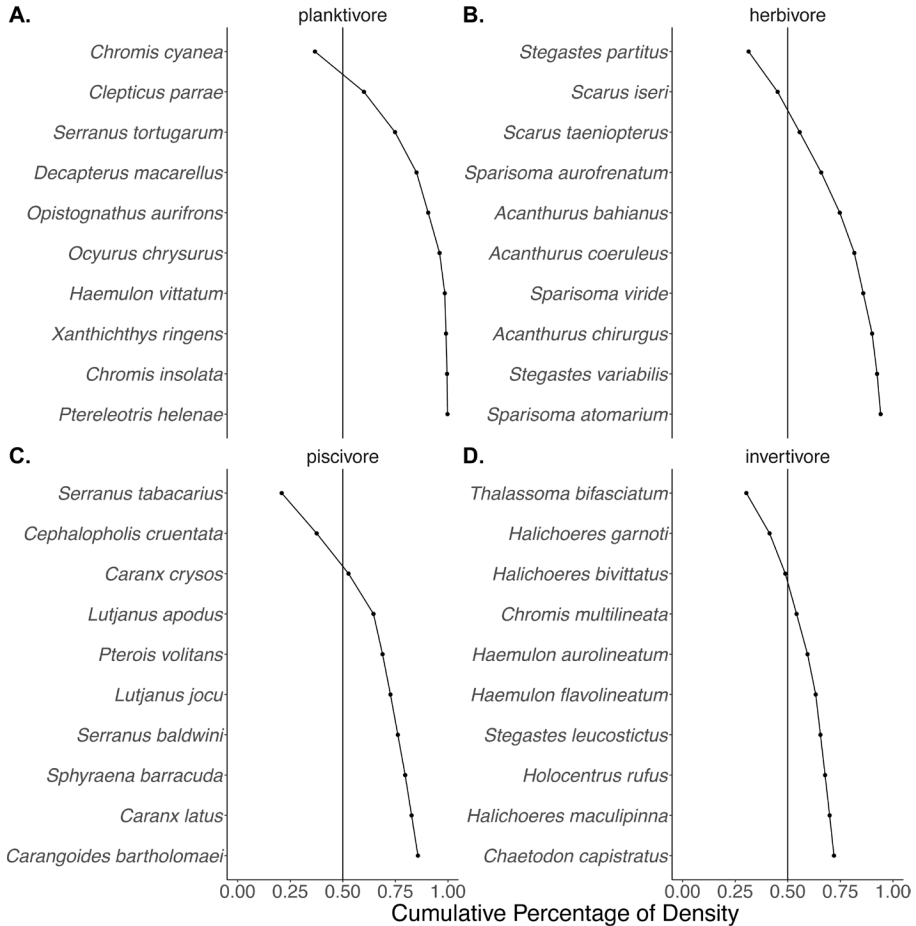


Figure 4. Fish species accumulation curves of cumulative percentage of trophic group density for (A) planktivores, (B) herbivores, (C) piscivores, and (D) invertivores. Only the 10 highest-density species are shown.

yellowhead jawfish (*Opistognathus aurifrons*) occurred most frequently at lower-relief sites.

Herbivore density was best explained by the full model, associated with both depth and relief, with no interaction (Table 1). Higher herbivore density was associated with higher relief, but in contrast to planktivores, was associated with shallower depths (Fig. 2D, Online Fig. S2). Herbivores represented a higher proportion of total fish density at shallower sites (Fig. 5). Spatially, higher overall herbivore density was predominantly found in nearshore and shallower midshelf sites (Fig. 3D). Among the most common herbivore species there were contrasting patterns of occurrence. *S. partitus* showed no ecologically significant patterns as it was nearly ubiquitous across sites (89% occurrence). *Scarus iseri* occurred most at higher-relief sites across depths, while *S. taeniopterus* occurrence increased with depth, particularly at higher-relief sites. Other herbivores with patterns of note included stoplight parrotfish (*Sparisoma viride*), which like *S. taeniopterus* was most common at deeper higher-relief sites, but relief was the stronger driver. Yellowtail damselfish (*Microspathodon chrysurus*)

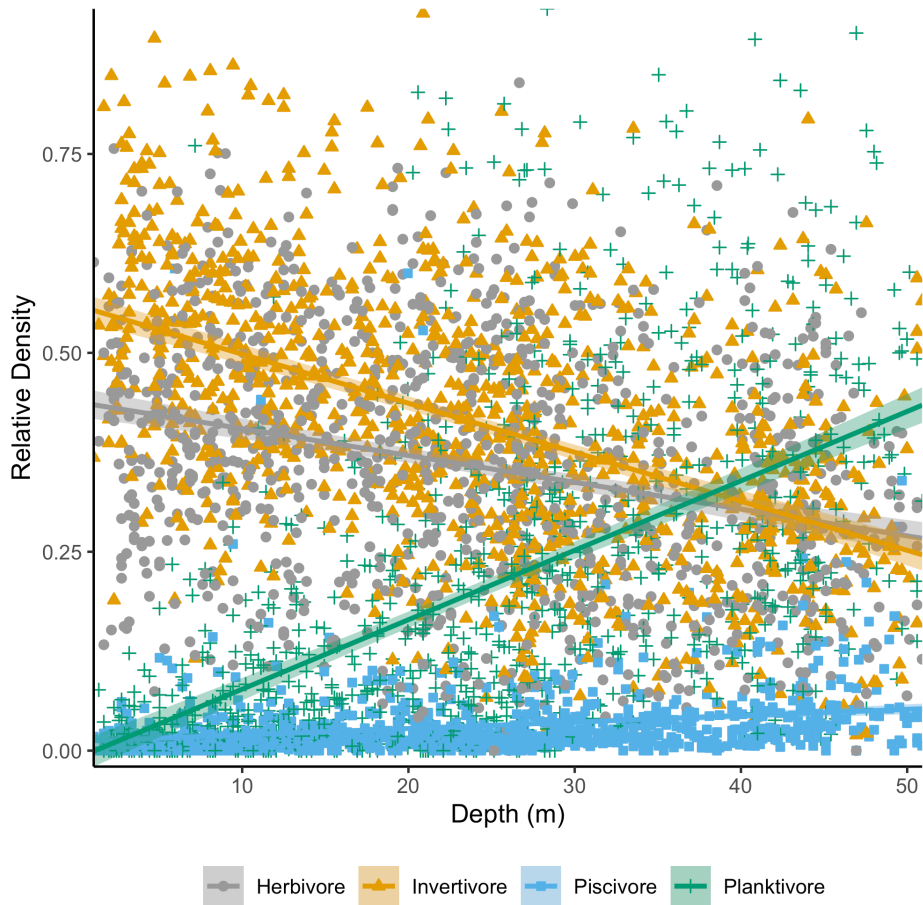


Figure 5. Relative density, as proportion of total density, of trophic groups (herbivores, invertivores, piscivores, planktivores) with increasing depth.

occurred most at shallower, higher-relief sites. Densities of redband parrotfish (*Sparisoma aurofrenatum*), beaugregory (*Stegastes leucostictus*), greenblotch parrotfish (*Sparisoma atomarium*), longfin damselfish (*Stegastes diencaeus*), and Bermuda chub (*Kyphosus sectatrix*) were all highest at shallower sites, with *S. atomarium* additionally increasing slightly in density at deeper lower-relief sites and *S. diencaeus* density increasing with higher relief. Increasing sizes of yellowtail parrotfish (*Sparisoma rubripinne*) were associated with increasing relief; further investigation of a significant interaction indicated uniform sizes except at shallower lower-relief sites where individuals were smaller. Queen parrotfish (*Scarus vetula*) increased in size with depth, and doctorfish (*Acanthurus chirurgus*) increased in size with both depth and relief.

Total piscivore density was best-fit by the full model, which showed significant positive effects of depth and relief and their interaction (Table 1). Although piscivores had the lowest density among the trophic groups presented (Fig. 5), the pattern was one of less variable density across depths in high-relief sites, but a stronger increase

in density with depth at low-relief sites (Fig. 2E, Online Fig. S2). Spatially, sites with higher piscivore density were associated with deeper, lower-relief sites south of St. John (Fig. 3E). The occurrence of the most common species of piscivores all showed significant effects of depth. *Cephalopholis cruentata* were very common and occurred at most sites (58%), but were more prominently associated with deeper, higher-relief sites. *Caranx crysos* were uncommon (6% occurrence), with high abundance at only a few sites due to large fish schools, and thus models fit poorly. *Serranus tortugarum* were rare in occurrence at higher-relief sites, with highest occurrence at deeper lower-relief sites. Other piscivores that were well-fit by models included the invasive lionfish (*Pterois volitans*) and the commercially important yellowmouth grouper (*Mycteroperca interstitialis*), which occurred most at deeper sites. Dog snapper (*Lutjanus jocu*) occurred most at sites that were deeper with higher relief. The endangered Nassau grouper (*Epinephelus striatus*) had overall low occurrence (6% of sites) but there was a suggestive positive effect of depth on its occurrence. Piscivore densities were highly variable and thus poorly fit by the linear regressions. In terms of patterns in size, spotted moray (*Gymnothorax moringa*) were larger at higher relief, and cero (*Scomberomerus regalis*) and black grouper (*Mycteroperca bonaci*) were larger deeper. We would like to note that *M. bonaci* had a small sample size of 10 individuals, and was only seen at two shallower sites, both within the Virgin Islands National Park; 7 of the other 8 individuals were seen at a depth of greater than 30 m.

Invertivore density was also best explained by the full model, which showed an interaction between depth and relief (Table 1). In contrast to piscivores, invertivore density was lower at deeper sites, regardless of relief, and increased at shallower sites, the effect of which was amplified at shallower higher relief sites (Online Fig. S2). Invertivores comprised a high proportion of total fish density at shallower sites, which decreased with depth (Fig. 5). Spatially, overall invertivore density was highest in nearshore environments of shallower and intermediate depths, particularly near and south of St. John (Fig. 3F). The most common invertivore species had distinct patterns of occurrence. *Thalassoma bifasciatum* were nearly ubiquitous across sites (87% occurrence), with highest occurrence and densities occurring at shallower higher-relief sites. *H. garnoti* occurrence was also high (91% across sites) but was significantly associated with deeper sites. Relief was a significant predictor of *H. garnoti* occurrence, but the coefficient was low and standard error high. In contrast to the other two common invertivore wrasses, there was an interaction between depth and relief driving occurrence of *H. bivittatus*, which were more common and found in higher densities at lower-relief sites in shallower water. Of the density models, only the commercially important schoolmaster snapper (*Lutjanus apodus*) was well-described: this species occurred more frequently at higher relief across depths, but had highest densities at shallower higher-relief sites. Of the occurrence models, there were many other invertivore species whose patterns were well-described. Red hind (*E. guttatus*), foureye butterflyfish (*Chaetodon capistratus*), and reef butterflyfish (*Chaetodon sedentarius*) all occurred generally at deeper sites and at sites with lower relief, but at deeper sites they were more common with higher relief. Fairy basslet (*Gramma loreto*) occurred more at sites that were deeper with higher relief. The commercially and recreationally important mutton snapper (*Lutjanus analis*) and queen triggerfish (*Balistes vetula*) showed weak positive associations with depth and relief individually, but both occurred much more at deeper lower-relief sites. The commercially and recreationally important hogfish (*Lachnolaimus maximus*)



showed a weak positive association with depth. Tobaccofish (*Serranus tabacarius*) showed no associations with depth or relief but had highest occurrence at deeper lower-relief sites. Yellowtail hamlet (*Hypoplectrus chlorurus*) and Spanish hogfish (*Bodianus rufus*) were strongly associated with depth and high relief, and especially together. Longsnout butterflyfish (*Prognathodes aculeatus*) was associated with deeper sites, especially those with higher relief, while puddingwife (*Halichoeres radiatus*) occurred most at shallower sites and those with higher relief, and especially both. Size analyses showed an increase in size with depth for yellow goatfish (*Mulloidichthys martinicus*) and porkfish (*Anisotremus virginicus*), and an increase in size with higher relief for green razorfish (*Xyrichtys splendens*). A few other species showed more complex patterns in size. Tomtate (*Haemulon aurolineatum*) were larger deeper and at higher relief, but there was more of an effect of relief at shallower sites; gray angelfish (*Pomacanthus arcuatus*) showed a similar pattern but a stronger interaction, with the largest individuals at deeper lower-relief sites. Squirrelfish (*Holocentrus adscensionis*) were generally larger deeper and at lower relief but were also larger at deeper higher-relief sites. Rock beauty (*Holacanthus tricolor*) were larger deeper, especially at deeper higher-relief sites.

**COMMUNITY COMPOSITION.**—Fish community composition showed clear differences across a gradient from shallower to deeper sites (Fig. 6), although there was marginal stress (0.2) in the NMDS. There were no apparent trends in community composition at different degrees of vertical relief, or across protected area boundaries. A follow-up ANOSIM confirmed that while there was a significant difference between sites inside an MPA and unprotected sites ( $P = 0.001$ ), the practical difference between them is small ( $R = 0.08$ ).

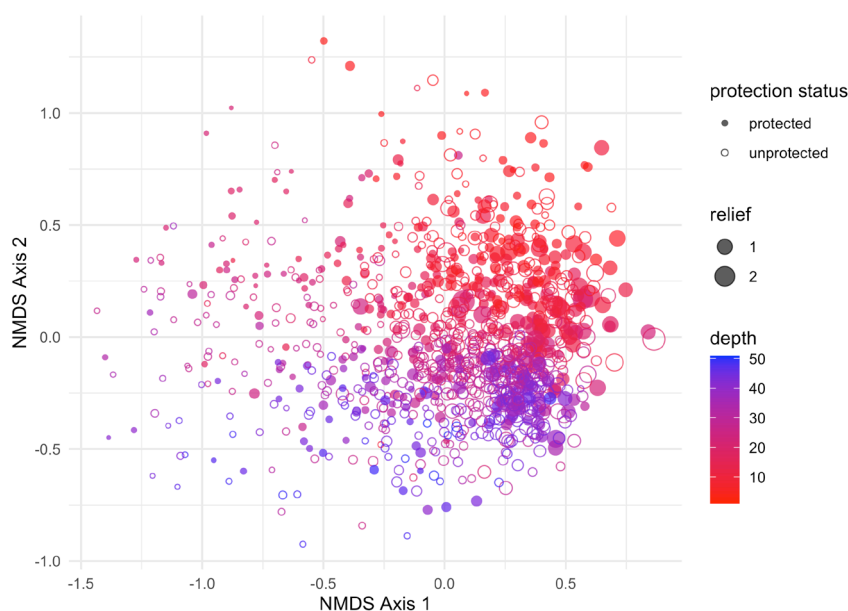


Figure 6. NMDS biplot on presence-absence of the 75% of species with greatest occurrences across surveyed sites where more than 10 species were observed. Points are colored by depth, point size corresponds to vertical relief, and filled points represent sites within marine protected areas.



## DISCUSSION

This study of seascape-scale patterns in Caribbean fish communities showed that both depth and surface relief act to influence community structure along a shallow to mesophotic gradient. In addition, interactions between depth and relief showed that changes in fish communities, particularly with regards to trophic structure, corresponded to complex patterns in individual species, adding to our understanding of what might drive fish community dynamics. We present here evidence that while patterns of association with relief and community structure changes with depth generally hold across the northern USVI, they are not universally true for all fish species.

Changes in overall fish density were driven by a positive association with relief, consistent with previous work (e.g., Gratwicke and Speight 2005, Wilson et al. 2007, Asher et al. 2017), however, we observed an increase in fish density with depth which contrasts other studies (e.g., Andradi-Brown et al. 2016, Appeldoorn et al. 2019). This could be due to the unique extensive *Orbicella* banks across the southern insular shelf of the USVI whose structural complexity harbors high numbers of fish in the upper mesophotic zone, which was the lower limit of our study (max depth 51 m). Other work has shown a faunal break at 60 m (e.g., Bejarano et al. 2014) so future studies venturing into the middle mesophotic zone may encounter additional community shifts.

Fish diversity was poorly explained and showed only a suggestive effect of relief on diversity, especially at deeper sites. Previous studies agree that fish diversity increases with relief (Appeldoorn et al. 2019), but others have observed that fish diversity decreases with depth (Andradi-Brown et al. 2016). While many species were observed across the depth range of this study, a few depth specialists emerged. We observed several deep specialists consistent with those identified by Garcia-Sais (2010) in Puerto Rico, such as sunshinefish (*C. insolata*), cherubfish (*Centropyge argi*), and longsnout butterflyfish (*P. aculeatus*). Specialization was stronger at depth; while some species were more associated with shallower sites (e.g., *H. bivittatus*, *H. radiatus*, *M. chrysurus*, *A. saxatilis*), none were seen exclusively shallow.

Regarding density, overall relative composition of trophic groups found here was like that observed by Friedlander et al. (2013) on hardbottom habitat, with invertivores (mostly small wrasses) being the most common, followed by herbivores, planktivores, then piscivores. It is a well-studied phenomenon that fish community structure changes with depth (e.g., Kahng et al. 2010, Kane and Tissot 2017, Stefanoudis et al. 2019), which is corroborated here. Fish communities shifted from herbivore- and invertivore-dominated communities at shallower depths to planktivore-dominated communities at deeper depths. In all three trophic groups there was also a pattern of higher density at higher-relief sites, which has been demonstrated locally in parrotfishes (Tzadik and Appeldoorn 2013). Depth was negatively correlated to distance from the shelf edge, so some apparent structuring by depth may also indicate the effect of a site being either in a nearshore or offshore environment. In tropical communities, structuring of herbivores and planktivores by both depth (e.g., Thresher and Colin 1986, Kahng et al. 2010, Bejarano et al. 2014, Pinheiro et al. 2016) and position on a shelf (e.g., Williams and Hatcher 1983, Cheal et al. 2012, Sanchez et al. 2022) have been consistently observed. These three trophic groups are likely to be structured by broad-scale patterns of resource availability. Increasing benthic

algal productivity in shallower, relatively high-light-intensity reef environments (Tebbett and Bellwood 2021) could provide an increase in primary food availability for herbivores (Nemeth and Appeldoorn 2009). Likewise, increasing plankton advection from oceanic environments may provide food resources for offshore planktivore communities (Hamner et al. 1988, Pinheiro et al. 2016, Appeldoorn et al. 2019). Invertivores like *Haemulon* spp., especially juveniles, require proximity to softbottom foraging habitats (Christensen et al. 2003), which may be more prevalent near shallow coral reefs, but seascape connectivity was not considered in this study. Other studies have found decreases in invertivores with depth (Kahng et al. 2010, Abesamis et al. 2018); invertivores may be supported more by high primary production in shallower water that feeds larger populations of invertebrates. Thus, for these trophic groups the overall pattern may have been driven by resources, but the local patterns are complex due to shifting species-specific preferences for structure. In addition, because the invertivore trophic classification was represented by the highest number of species (about half of the 141 species included in the analyses) it may have contributed to a pattern of increasing overall community diversity in shallow areas. Increased fish diversity in shallower water has been noted in other studies (Costello and Chaudhary 2017, Abesamis et al. 2018, Stefanoudis et al. 2019). Thus, at local scales, these trophic groups are positively driven by increasing reef structure that provides refuge from predation, while at larger scales communities are driven by shifting resource availability.

The patterns for piscivores were more complex, showing positive associations with depth and relief and an interaction between them. Piscivore distribution might be partly driven by resource availability and the way the numerically dominant species are differentially associated with reef structure. Although overall fish density was higher in shallower water, suggesting more food resources for piscivores, it may be that the prevalence of small planktivores in deeper environments (e.g., *C. cyanea*, *C. parrae*, and *S. tortugarum*) are supporting deeper piscivore populations. There may also be secondary food resources available that were not considered in this study, such as shrimp and crabs. Previous studies have observed increased dominance of piscivores with increasing depth (Andradi-Brown et al. 2016, Appeldoorn et al. 2019), which was not seen in this study, likely because of low densities overall. It should be noted that sharks are not prevalent on USVI reefs (6 species observed in this dataset, all with <7% occurrence), and trophic dynamics may change if top predators were more common. Piscivores showed highest mean densities in deeper and lower-relief environments despite being generally associated with higher relief, perhaps because the most common species, *S. tabacarius*, increased in density with depth, but associated more with lower-relief environments, commonly found in deep (>40 m) rhodolith plains. *Caranx crysos* were not common across sites but had very large abundances at a few deeper sites south of St. John and on the shelf edge where there is lower relief and coral cover (Smith et al. 2016b, 2019).

Commercially important fish species (Kadison et al. 2017) were relatively rare, and tended to occur more frequently and in some cases exhibit larger sizes in deeper, offshore environments. For example, one of the most commercially and recreationally important species in the USVI, *E. guttatus*, occurred most frequently in deeper habitats with higher relief. This corroborates an earlier study that also showed larger and more frequently encountered red hind at deeper sites in the northern USVI (Kadison et al. 2017), and another from Puerto Rico showing higher presence of

large-bodied snapper and grouper in MCEs (Bejarano et al. 2014). The invasive *P. volitans* occurred more often at deeper sites in this study, and in the past has been consistently more common on MCEs than shallower reefs in the USVI (Smith et al. 2019). There is some evidence that mesophotic reefs can be refuges for lionfish, where they are a characteristic species in some areas (Pinheiro et al. 2016, Stefanoudis et al. 2019) and may be protected from targeted fishing efforts concentrated in shallower areas (Andradi-Brown et al. 2017).

All species demonstrating increased size with depth (*O. chrysurus*, *S. rubripinne*, *S. vetula*, *A. chirurgus*, *M. bonaci*) are potentially caught by the trap fishery in the northern USVI, and this fishery can access deeper shelf waters. In fact, the deeper (>25 m) offshore areas of the northern USVI represent about 83% of the fishable area between the surface and 65 m depth (Kadison et al. 2017). While fishing pressure is concentrated on deeper reefs more so than shallower ones (pers observ), a dilution of fishing pressure across the large area covered by deeper reefs is likely and could contribute to the pattern. While we did not observe effects of spatial protection on the overall fish community, the MCD covers a large area of high-quality coral reef habitat (Armstrong et al. 2006) and might be offering some protection from fishing for these species.

This pattern of increased size with depth is also consistent with ontogenetic shifts in some species. Juveniles of several species settle in shallow habitats, such as seagrass beds and mangroves, at the edge of hard relief (Parrish 1989). This study sampled only hardbottom habitats, and thus, missed much of this nursery habitat. Despite this limitation, ontogenetic patterns were observed in some species. Occurrence as well as size of *O. chrysurus* increased with depth and relief. This species is known to settle in shallower seagrass habitats and shift to higher relief surfaces later in development (Watson et al. 2002), a pattern which has been observed previously in this species in the USVI (Christensen et al. 2003, Friedlander et al. 2013), Puerto Rico (Appeldoorn et al. 2019), and Honduras (Andradi-Brown et al. 2016). Haemulids also exhibit this ontogenetic habitat selection, which was also seen previously in the USVI (Christensen et al. 2003) and corroborated by this study in *H. aurolineatum*. Overall, it is likely that neither depth refuges nor ontogenetic shifts are working in isolation; the effects of each may be reinforcing the other to produce higher density and larger fish communities in the deeper offshore areas in the northern USVI.

We observed no clear effects of spatial protection from fishing on fish communities. We did notice that the three sites with the highest densities of piscivores all lie in less than 20 m depth within the boundaries of the Virgin Islands National Park, but upon further examination we found these were due to large schools of *C. crysos* and horse-eye jack (*Caranx latus*). Most of the other top ten sites for piscivore density were also high due to schools of jacks, which are highly transient. Two smaller individual *M. bonaci* were seen within the Virgin Islands National Park, while individuals seen in deeper waters were larger. If nearshore protected areas are safeguarding nursery habitats of commercially and recreationally important species, they could be allowing for ontogenetic migrations across protected boundaries. Previous studies of MPAs in the USVI have showed inconclusive effects of protection on fish communities because of inadequate enforcement, insufficient contiguous reef habitat, and a suite of stressors outside the control of park managers that are facing all territorial coral reefs, such as hurricanes and coastal development (Rogers and Beets 2001, Friedlander and Beets 2008, Friedlander et al. 2013). A lack of spatial

protection effects on overall fish community assemblages in this study could be due in part to the fact that fishery-targeted species are presently relatively uncommon in the USVI, so patterns in community assemblages are driven by untargeted species.

While species-specific effects of spatial protection were outside the scope of this study, future studies could more closely examine patterns in individual species across MPA boundaries, particularly those species targeted by fishing efforts. Some commercially and recreationally important species, such as *E. guttatus*, are well-represented in the data set and would be amenable to further analysis, especially since this species has responded strongly to the permanent spatial protection of its spawning grounds (Nemeth 2005). Even some species that are rarer but are of interest to species conservation have sufficient data to understand distribution and vulnerability to poaching. An example is the Nassau grouper, *E. striatus*, which is classified as critically endangered by the IUCN (Sadovy et al. 2018) and currently prohibited from landing in any area (NMFS and CFMC 2019). Nassau grouper are currently recovering in the USVI (Kadison et al. 2010), and several areas around the territory have been designated as critical habitat for the species (NOAA Fisheries 2024). While there is error inherent in the 2021 population estimate of 134,167 individuals across this study's survey domain of 307 km<sup>2</sup> (Online Table S1), we believe it is useful to evaluate the benefits that management actions have had on this species. Repeated surveys using nonextractive methodologies that encompass the primary depth range of the species are imperative to accurately track recovery.

This paper was limited to broad-scale patterns in fish communities, such as trophic structure, and more detailed studies could be conducted on species assemblages within each trophic group to understand finer ecological details. The study was also limited to hardbottom substrates for logistical and biological reasons, however, it should be noted that many economically important species, such as *B. vetula* and *L. analis*, are often associated with unconsolidated deep rhodolith communities. These habitats were inadvertently sampled in the study on the periphery of hardbottom and patch reefs environments, but not with any great frequency or intention. In the northern USVI, these habitats make up well over half the substrate type of the entire insular shelf (Smith et al. 2019) and, while they generally show low fish abundance and diversity (present study, Garcia-Sais 2010), their exclusion may lead to underestimates of the population sizes of the species that are associated with lower relief. Management actions taken for the benefit of certain targeted species must consider their specific habitat requirements, across all life stages.

This study represents the rare case of a stratified random seascape-scale survey of coral reef-associated fish communities from shallow areas through the upper mesophotic zone across the majority of the insular reef shelf in the northern USVI. The purpose of this paper was to highlight dominant overall patterns in fish communities and highlight areas where this dataset can benefit further ecological and fisheries research, such as stock assessment and ecological characterization. We encourage the further use of this spatially randomized data set to understand the ecology and conservation of fishes more completely in the western Atlantic.

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