Using Opportunistic Datasets to Infer Spatial Management Strategies of Local Fisheries in the U.S. Caribbean Region

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A Red hind *Epinephelus guttatus* and a French grunt *Haemulon flavolineatum* swimming on a reef in St. Croix. Photo Credit: NOAA Photo Library.

As an initial step towards the implementation of an ecosystem-based approach to management, the Caribbean Fishery Management Council has recently ratified three island-based fishery management plans that will supplant the existing regional plans. The newly formed management plans account for nuances among the island platforms in the U.S. Caribbean, including ecological, cultural, and social considerations. The island-based approach represents a novel strategy among the eight fishery management councils in the United States and therefore remains an untested technique. This study evaluated the decision to separate fishery management among the island platforms by comparing fish assemblages through time in the region. The results suggest that the structure and function of fish communities are spatially driven, with little temporal influence. Combined with the ecological, cultural, and social differences among the islands, the spatial nature of the fish community data support the Caribbean Fishery Management Council decision to transition to island-based management plans.

INTRODUCTION

Traditional fisheries management has predominately relied on single species stock assessments to generate reference points that are enforceable across the distribution of the stock. This approach has utility in specific circumstances, but often fails to take ecosystem considerations into account, particularly with regard to ecological interactions and anthropogenic influences beyond fishing (Simberloff 1998; Levin et al. 2013; Marshall et al. 2018). As such, many countries have begun to adopt ecosystem approaches to fisheries management (EAFM) by including consideration of environmental factors in single fisheries stock management, while others have developed plans organized by fisheries sector and focusing on multiple stocks, thus moving to ecosystem-based fisheries management (EBFM; Pitcher et al. 2009; Nguyen 2012). In the United States, the National Oceanic and Atmospheric Administration (NOAA) has identified a shift to EBFM as a top priority and has recently unveiled EBFM implementation plans in every region under U.S. jurisdiction (NMFS 2018a). The U.S. Caribbean region, which includes the U.S. territories of Puerto Rico and the U.S. Virgin Islands (i.e., St. Thomas, St. John, and St. Croix), has already taken initial steps to adopt EBFM as the Caribbean Fishery Management Council (CFMC) has elected to convert its fishery management plans from regional stock-based plans to island-based fishery management plans (IBFMP). Under the new IBFMPs, each island platform (i.e., Puerto Rico, St. Thomas/St. John, and St. Croix) would have its own fishery management plan, and the nuances of each plan would reflect the differences among the islands (CFMC 2018). The IBFMPs would include several ecosystem considerations that are central to effective EBFM implementation (Link 2002), such as increased protection for reef herbivores, and represent the initial step for EBFM implementation in the U.S. Caribbean region (NMFS 2018a).

While the development of the IBFMPs represents an important step towards the eventual implementation of EBFM, the division by island platform remains a partition with rationale that is rooted in cultural and socio-economic differences among the islands as opposed to biophysical considerations (CFMC 2018). Specifically, the differences among the plans reflect the market preference for fish species as well as the local traditional fishing practices within each island platform. The geomorphology of the Caribbean archipelago suggests differing levels of connectivity among the islands, as shallow shelves connect some fish populations, but not others (Jansma et al. 2000; Locker et al. 2010). Therefore, fish populations with differing levels of connectivity among the islands also experience different levels of fishing pressure based solely on market preferences (Campbell et al. 2018). In addition, stocks are often shared across international boundaries, and/or among other regions of the United States, adding a further level of complexity to the ecosystem and the methods of management (Roberts 1997; Salas et al. 2007).

Like many other small island developing states worldwide, fishery-dependent data in the U.S. Caribbean region are limited and inconsistent (Salas et al. 2007; Seijo 2007; Newman et al. 2015). Specifically, fishery-dependent data in the U.S. Caribbean is considered "data-poor," and therefore unsuitable for traditional single-species stock assessment techniques (Newman et al. 2015). Moreover, there is a history of poor performance of traditional stock assessments in tropical, multi-species fisheries associated with coral reef ecosystems, primarily due to high occurrences, but low abundances, of individual species (SEDAR 2016). Efforts are ongoing in the region to improve data reporting to address these issues, but analyses using those data will only be possible after several years of continuous collection. Conversely, substantial fishery-independent data have been gathered in the region by various researchers and government agencies, albeit highly dispersed among the institutions that gathered them.

This study aims to evaluate the decision made by the CFMC and by NOAA's National Marine Fisheries Service Southeast Regional Office, and championed by fishers in the region, with regard to the spatial scales chosen for island-based management, and whether other considerations such as temporal variability, seasonality, and depth should factor into the new IBFMPs. The current study uses several opportunistic datasets to describe the patterns of temporal and spatial variability among the fish communities in the U.S. Caribbean. Then, we evaluate the degree to which ecological structure and function among the islands is captured by the new IBFMPs towards EAFM based on the analyses presented. Here, the term function refers to the mathematical descriptions of patterns, and not to ecological or ecosystem function (akin to ecosystem services). Last, we suggest several approaches towards EAFM based on the analyses presented.

MATERIALS AND METHODS
Study Sites

The U.S. Caribbean includes the islands of Puerto Rico and the U.S. Virgin Islands (St. Thomas, St. John, and St. Croix), with an exclusive economic zone totaling 196,029 km^2 in area (Figure 1). The major islands in the U.S. Caribbean differ biophysically, economically, and socially. Puerto Rico is the largest island, measuring 177 km by 56 km at its widest points. The majority of Puerto Rico residents are Hispanic, and the official languages of the island are both Spanish and English (Nash 1970). In addition, the size of Puerto Rico supports an agricultural sector, which is largely absent on the smaller U.S. Virgin Islands (USVI). The USVI are situated approximately 64 km to the east of Puerto Rico. The official language of the USVI is English, though some residents also speak French, Virgin Islands
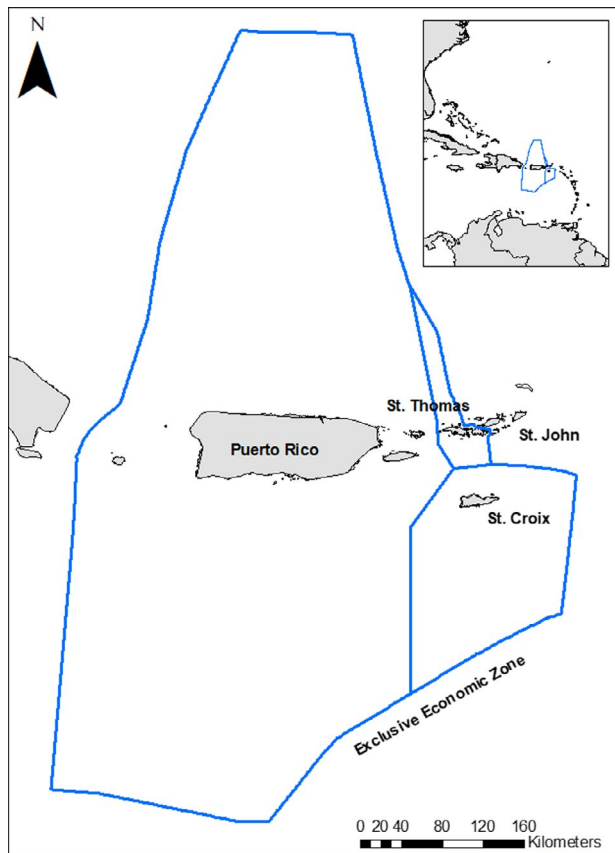
Figure 1. Map of the U.S. Caribbean, including the exclusive economic zone of each of the three island platforms.

Creole, and on St. Croix in particular, Spanish. St. Croix is the largest of the U.S. Virgin Islands and measures 44.8 km by 11.2 km at its widest points. St. Thomas and St. John are much smaller, measuring 22.1 km by 6 km and 12 km by 8.4 km, respectively, at their widest points. Locally, St. Thomas and St. John are governed as one district due to their proximate geographical location and due to the significant economic differences between these northern islands and St. Croix, which lies approximately 64.5 km to the south (Legislature of the Virgin Islands 2019). The human populations of the islands are roughly 3.2 million for Puerto Rico, 51,600 for St. Thomas, 50,600 for St. Croix, and 4,200 for St. John (U.S. Census Bureau 2010, 2018). These differences among the islands, as well as each island's unique heritage, have led to distinct cultures, values, fishing practices, and ultimately the status of the local coral reefs and associated fisheries (Rouse 1951; Mintz 1965).

Opportunistic Datasets

Three datasets were chosen for this study. Each dataset is open access and freely available via online platforms. The datasets include: (1) Legacy data from the National Centers for Coastal Ocean Science (NCCOS), (2) data from the Coral Reef Ecosystem Studies (CRES) program, and (3) contemporary data from the National Coral Reef Monitoring Program (NCRMP). All three datasets were federally funded by NOAA. Federal datasets were chosen for analysis due to their accessibility, open access nature, reliability, relative ease of use, and applicability as they were evaluated to answer questions regarding federal management plans. These datasets

were therefore considered "opportunistic," as they were not designed specifically for this study and are freely available for use by anyone inclined to do so. Unless otherwise noted, the data presented in this study are those directly derived from online platforms where these data are stored, and each dataset was analyzed independently of one another.

NCCOS Legacy Dataset

The NCCOS legacy dataset spans 2000 through 2011. The NCCOS monitoring program is widespread throughout U.S. territorial waters and complete details of the monitoring protocol can be found in Brandt et al. (2009), Smith et al. (2011), and Friedlander et al. (2013). For this study, the data used was collected at three main locations: La Parguera in Puerto Rico, Buck Island in St. Croix, and the Virgin Islands National Park in St. John (Figure 2). It is important to note that the use of only a single location on each island platform likely suggests non-representative sampling of the entire insular platform. The following is a brief summary of the protocol with regard to fish community monitoring.

Sampling in the U.S. Caribbean occurred seasonally among the three locations, but varied in annual frequency at each location, ranging from a single season to four seasons. Prior to each sampling season, individual monitoring sites were selected using a random stratified, two-stage sampling design. Stratifications were based on geographic sub-region, depth, and habitat class (i.e., hard-bottom, soft-bottom, and mangrove).

Once in the field, belt transect surveys (25 × 4 m) were conducted at each previously identified sampling site. Two divers (one fish and one benthos specialist) were dropped as close to the centroid of the sample site as possible. They then deployed the transect line along a random compass heading and recorded fish, invertebrates, and benthic features detected within 2 m on either side of the transect line. All fishes within the bounds of the belt transect, including cryptic individuals, were recorded to species and sized using 5-cm bins up to 35 cm. Fishes over 35 cm were recorded in an "over" category. All transects were 15 minutes in duration and occurred at depths equal to or shallower than 30 m.

CRES Dataset

The CRES dataset spans 2004 through 2006, and data were collected solely at forereef locations in La Parguera, Puerto Rico. Visual surveys were conducted via belt transects (25 × 4 m) at permanently marked transect locations by teams of two divers following essentially the same protocol as described for the NCCOS surveys. Eight reefs were surveyed in total, six of which were situated on the insular shelf, while the remaining two sites were considered as shelf-edge reefs (Figure 3). There were nine transects conducted at each sampling site. Each transect was situated parallel to the depth contour, with three replicate transects at each of the 3-, 10-, 15-, and 20-m depth intervals. Three depth intervals were surveyed on insular-shelf reefs (i.e., 3, 10, and 15 m), while only a single depth interval (i.e., 20 m) was surveyed at shelf-edge sites. Sampling generally occurred seasonally (i.e., four times per year), although time between sampling events varied by year and location. During each survey, fishes were identified and sized by 5-cm bins until 35 cm, after which they were classified as "over 35 cm." Survey efforts focused on the identification and quantification of all non-cryptic diurnal fish species present within the transect at the time of sampling.
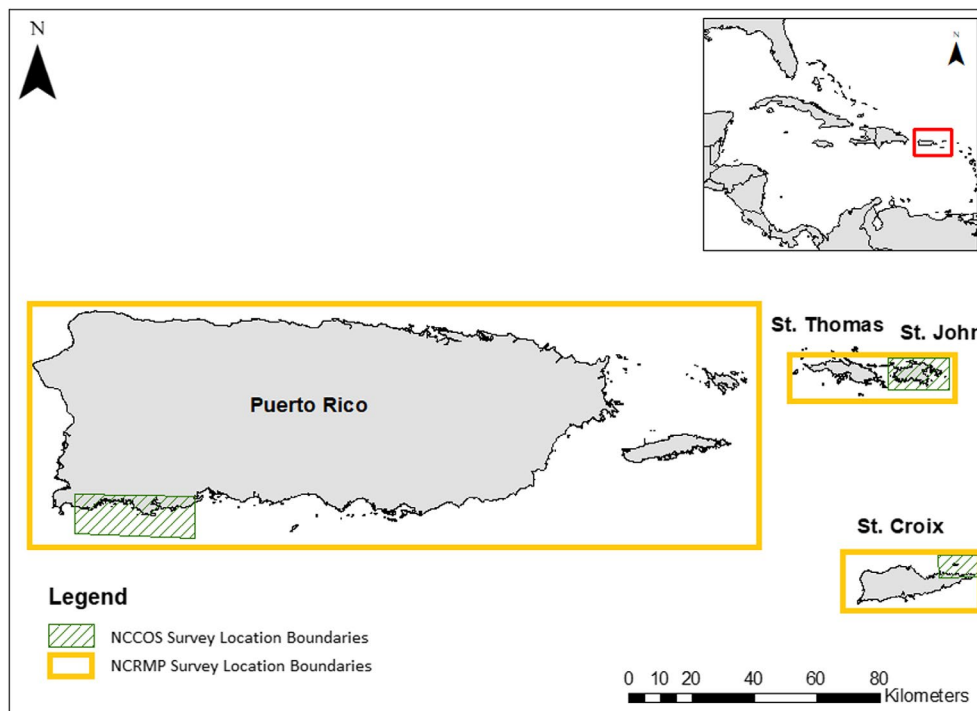
Figure 2. Map of the study areas included in the National Centers for Coastal Ocean Science (NCCOS) legacy data set and the National Coral Reef Monitoring Program (NCRMP) data set. Study sites for the NCCOS program include La Parguera in Puerto Rico, the territorial waters of St. John, and Buck Island in St. Croix.

NCRMP Dataset

In 2013, the NCCOS monitoring program was replaced by the NCRMP program as the primary method to monitor coral reef fishes in U.S. territorial waters. As the goal of the NCRMP program is to capture status and trends of U.S. coral reef ecosystems, sampling shifted to biennially across the insular shelves of Puerto Rico, Vieques, Culebra, St. Croix, St. Thomas, and St. John in the U.S. Caribbean. The NCRMP data set used here includes data from the years 2013 and 2015 for St. Thomas and St. John, for 2015 only for St. Croix (due to data availability), and for the years 2014 and 2016 for Puerto Rico. During this period, the visual survey protocol for fish community monitoring was identical to that of the NCCOS protocol, but the area surveyed differed. Site selection was performed in a similar random stratified design, but the sampling domain for the NCRMP dataset included the entire insular shelves of the islands sampled, instead of being limited to small subsets of the shelf as with the NCCOS legacy data. Geographic subdivisions of the sampling domain on each insular shelf were established and represented a stratification layer for the site selection methods. These subdivisions were arbitrarily assigned, and do not represent known differences in community structure and function. The visual surveys currently being conducted include the use of a new protocol that involves stationary divers performing a point count in imagined cylinders of 7.5-m radii. This new method has recently been applied to the U.S. Caribbean (as of 2017) but will not be considered in this study.

Statistical Analyses

The statistical analyses performed for this study comprised primarily distance-based, non-parametric multivariate techniques found in the Fathom Toolbox (Jones 2014) and implemented in MATLAB (MATLAB R 2017b). In the case of the NCCOS legacy dataset, to derive fish community groupings, analyses were initially performed on the entire dataset, excluding those species that occurred at less than 5% of the study sites, and subsequently implemented on a subset of the data that only consisted of the hard-bottom substrata among the three main study locations (i.e., excluding single-season datasets in Jobos in the summer of 2009 and Vieques in the spring of 2007). As appropriate, fish abundance datasets were square root transformed to minimize the effects of rare or overly abundant species. As part of the distance-based approach, a Bray–Curtis distance matrix was used to infer pairwise measurements of beta diversity, while accounting for zero inflation, among the datasets (Legendre and Legendre 2012). Permutation based P-values were derived and significance levels (α) were set at 0.05 for all statistical analyses involving hypothesis testing (Legendre and Legendre 2012).

To test the assumption that temporal trends were absent in the data, a non-parametric multivariate analysis of variance (MANOVA) was conducted using a yearly grouping vector on the NCCOS dataset. Additionally, a second MANOVA was performed on the "La Parguera" samples to test for seasonal variance. The La Parguera subset was chosen due to the robust nature of dataset (i.e., representative of all years) and the representation of all seasons therein.

To infer spatial and temporal trends in each dataset, exploratory analyses were performed as initial indicators to inform further analyses. To derive hypotheses about potential fish community groupings in both the NCCOS and the CRES datasets, exploratory analyses consisted primarily of principal coordinate analyses (PCoA), which were used to
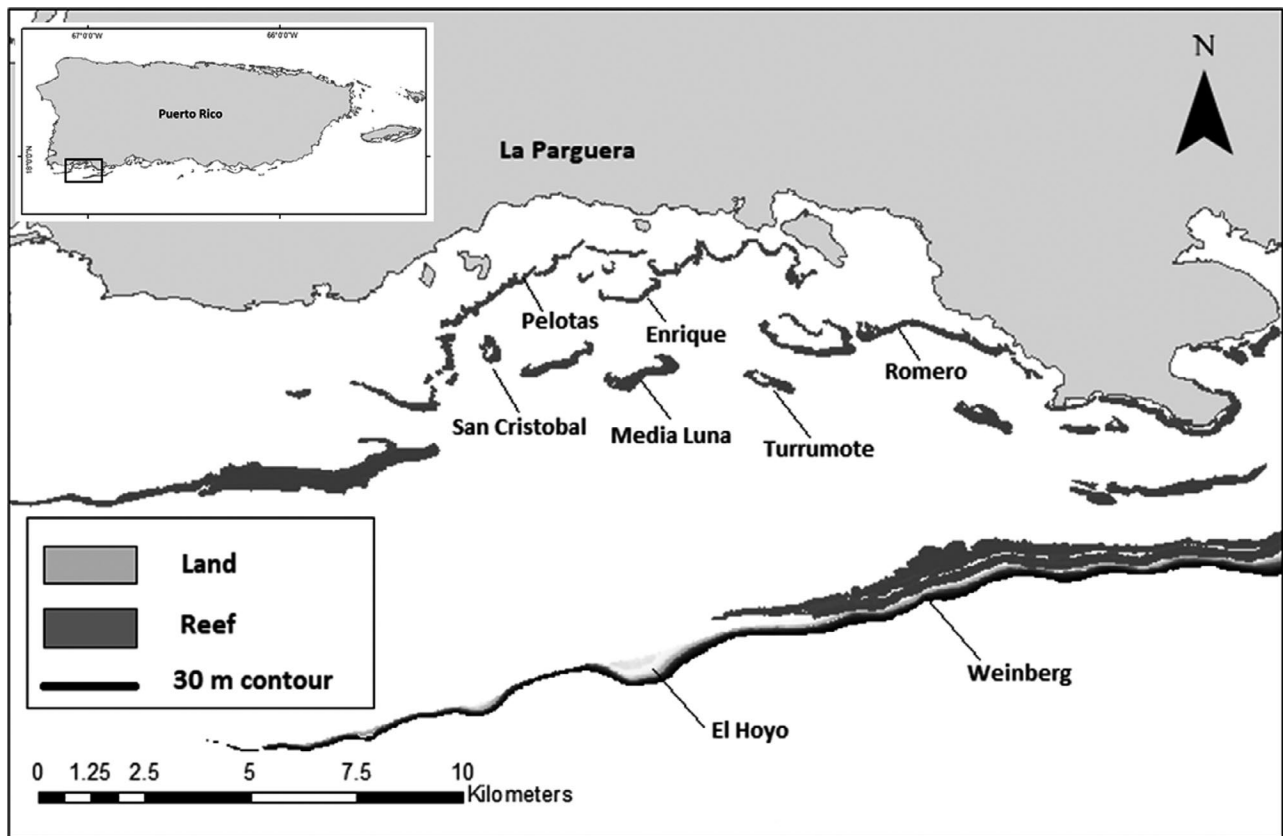
Figure 3. Map of the study areas included in the Coral Reef Ecosystem Studies (CRES) data set. Insular-shelf study sites included Pelotas, Enrique, and Romero. Mid Shelf study sites included San Cristobal, Media Luna, and Turrumote. Shelf-edge study sites included Weinberg and El Hoyo. All study sites were located within the La Parguera reef system in southwestern Puerto Rico.

visualize sample sites with respect to their multivariate characteristics. Further hypothesis testing of group divisions, included the implementation of MANOVA, and further visualized and tested using canonical analyses of principal coordinates (CAP; Anderson and Willis 2003; Legendre and Legendre 2012), constrained by island platform. To test the predictability of the model, a leave-one-out (LOO) cross validation method was incorporated into the CAP, which tested the ability of the model to correctly classify random samples from the initial dataset. Outputs from the CAP were compared to that of a random-allocation model via the use of a proportional chance criterion (McGarigal et al. 2000; Jones 2014). In all cases where the assumption of homogenous dispersions was made (i.e., MANOVA and CAP), this assumption was verified using a multivariate version of Levene's test (Anderson 2006). Last, to identify individual species that are indicative of a particular grouping, the IndVal method was used to compare relative abundance to relative frequency of occurrence, thereby deriving species with disproportional influence (Dufrene and Legendre 1997).

RESULTS
Opportunistic Datasets

Within each of the three datasets, data were averaged within sampling seasons to create individual sample sites and to overcome the temporally inconsistent nature of the data (i.e., each "sample site" variable comprises the mean values of all species across the sampling season). Thus, derived data for each site consisted of the mean number of fishes observed in a single season at a single location. Of the datasets used for this study, the NCCOS legacy dataset was the largest, with 132 sample sites spread among 48 sampling seasons. The CRES dataset was the next largest with 87 sample sites, among 12 sampling seasons, while the NCRMP dataset had 16 sample sites spread among five sampling seasons. The NCCOS legacy data also represented the longest running dataset, with 12 years of consecutive data collection.

NCCOS Legacy Dataset

The graphical representation of the PCoA suggested that the composition and abundance of the fish community differed spatially, with little to no temporal variation (Figure 4). Fish community structure was driven almost entirely by habitat class (i.e., hard-bottom, soft-bottom, and mangrove). This apparent difference was tested and verified using an np-MANOVA ($F = 8.64$, $P = 0.001$, df = 131), and followed up with a CAP (Trace stat = 1.47, P = 0.001, variability explained = 76.24%, CA-1 correlation = 0.94, m = 9) to further demonstrate the apparent differences. The LOO analysis that accompanied the CAP, reclassified random samples into the appropriate habitat class based on the output model produced by the CAP with a 97% success rate. When compared to a 32.7% success rate by the random allocation model, the CAP model reclassified samples with a far superior success rate than that of random chance.

Spatial variation was further tested using only the sites within the hard-bottom habitat class. The apparent spatial division
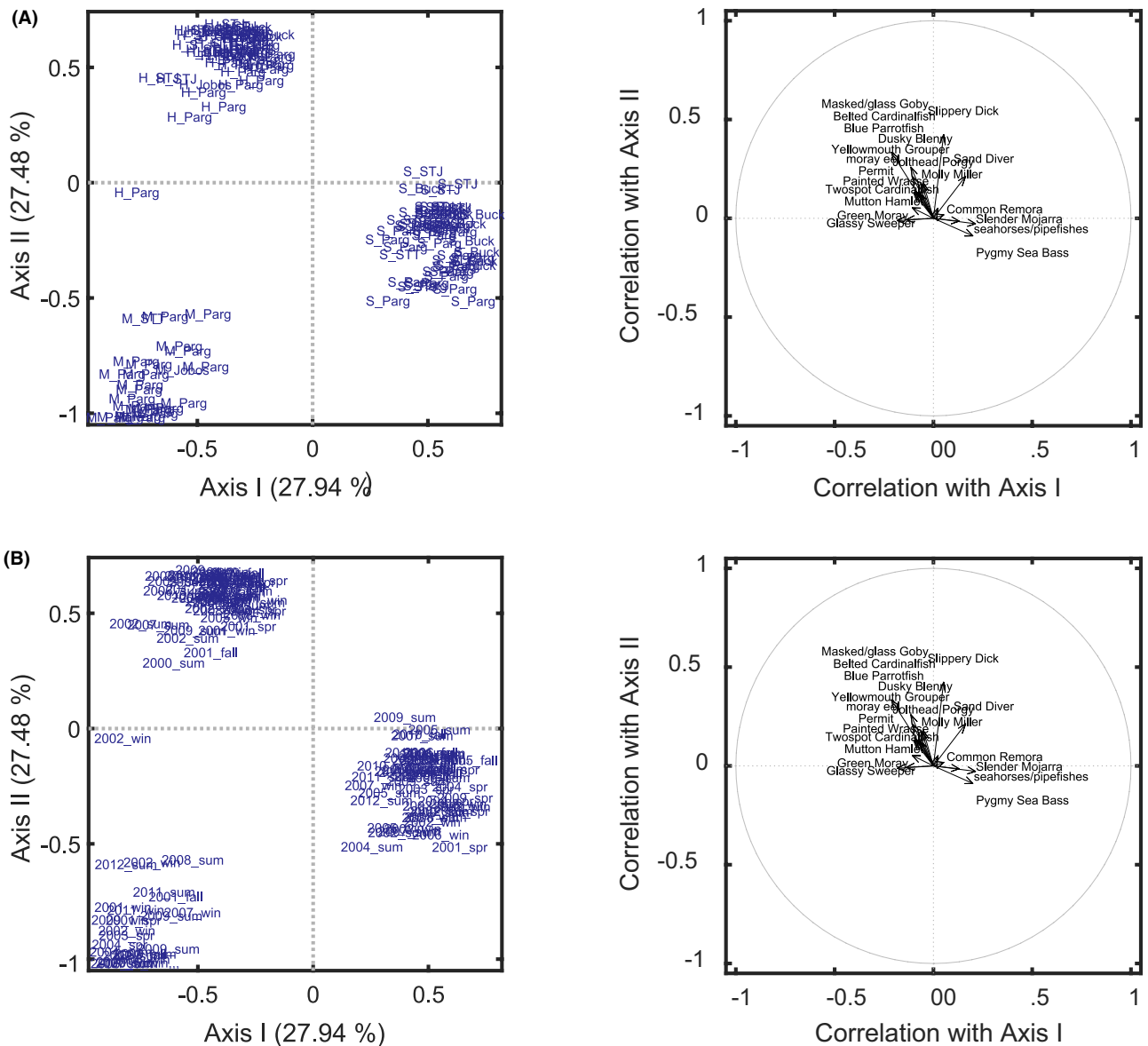
Figure 4. Principal Coordinate Analysis (PCoA) visualization of fish communities using beta diversity of the National Centers for Coastal Ocean Science (NCCOS) legacy dataset. Sampling units are labeled to indicate the substrate type (hard bottom, soft bottom, mangrove), site, year, and season. For visual clarity, the ordination is presented twice as Figures 4A (substrate and site) and Figure 4B (year and season). Note that Figures 4A, B represent the same ordination but are simply presented twice with different labels. The ordination visualization represents the dissimilarity among sampling sites and highlights the division among substrate types. The percentages on the axes refer to the percent variability explained by each canonical axis. The fish biplot vectors next to the ordination plot represent the relative correspondence with the first two canonical axes. Vector lengths and direction represent the strength and grouping tendency, respectively. All fish species were used to perform the PCoA analysis, but only the top 20 most influential species, as determined by indicator value, are presented here.

by island was tested and verified using an np-MANOVA (F = 15.77, P = 0.001, df = 51), and further verified with a CAP (Trace stat = 1.83, P = 0.001, variability explained = 57.92%, CA-1 correlation = 0.98, m = 4). The model produced by the CAP reclassified random samples to the appropriate island-group with a 100% success rate. Compared to the success rate of 33.4% of the random allocation model, the model produced by the CAP was once again superior. Fish communities among islands were unique and statistically identifiable by their assemblages (Figure 5). A total of 132 significant indicator species (α = 0.05) were derived for the division of the entire assemblage at hard-bottom only sites, as determined by the IndVal analysis (Table 1), while several commercially-important species (per NMFS 2018b) were also identified as significant indicators (Figure 6).

Temporal variation based on yearly groupings was not identified in the NCCOS dataset, as verified by an np-MANOVA (F = 0.72, P = 0.968, df = 12), nor were seasonal groupings, as demonstrated with the La Parguera subset of the NCCOS dataset (F = 0.63, P = 0.883, df = 3).
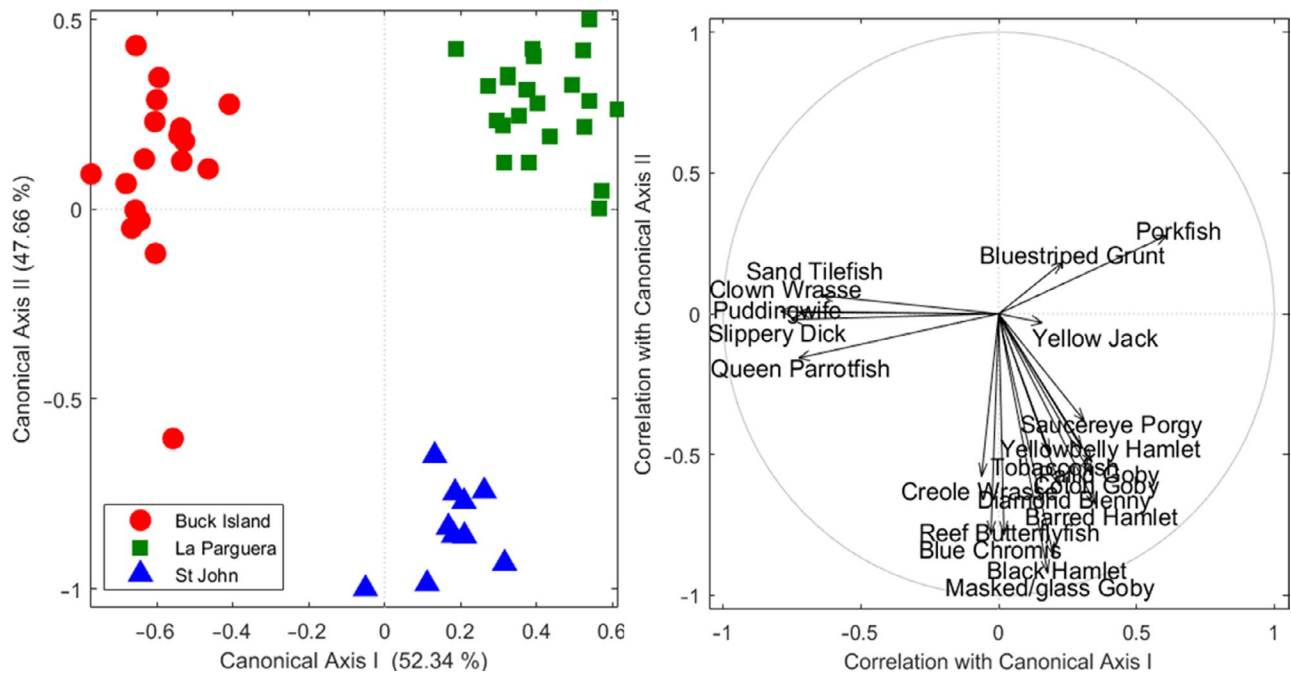
Figure 5. Canonical Analysis of Principal Coordinates (CAP) visualization of fish communities using beta diversity of the National Centers for Coastal Ocean Science (NCCOS) legacy dataset among hard-bottom sites only. Sampling units are labeled to indicate location (i.e., La Parguera, St. John, and Buck Island). The ordination visualization represents the dissimilarity among sampling sites and highlights the division among island platforms. The percentages on the axes refer to the percent variability explained by each canonical axis. The fish biplot vectors next to the ordination plot represent the relative correspondence with the first two canonical axes. Vector lengths and direction represent the strength and grouping tendency, respectively. All fish species were used to perform the CAP analysis, but only the top 20 most influential species, as determined by indicator value, are presented here.

CRES Dataset

Spatial differences among study sites were tested and verified using an np-MANOVA ($F = 31.70$, $P = 0.001$, df = 86), and further explored using a CAP (Trace stat = 5.47, P = 0.001, variability explained = 83.23%, CA-1 correlation = 0.99, m = 9). Spatial differences were apparent, while temporal differences were not noticeable. Differences were primarily driven by depth, with shelf-edge reefs differing from insular shelf reefs (Figure 7). Further, each sample location was statistically unique and largely driven by depth along the secondary principal coordinate (Figure 7). The LOO analysis reclassified individual samples with a 100% success rate to each individual sample reef, using the model output from the CAP. Compared to a 12.9% success rate from the random allocation model, the CAP model was superior to a model of random chance. The division among reefs was largely driven by 92 significant indicator species ($\alpha = 0.05$), as determined from the IndVal analysis (Table 2). While each species has a specific indicator value for each reef in the sample set, indicator species predominantly drove the division between insular-shelf and shelf-edge reefs (Figure 7).

NCRMP Dataset

Spatial differences were tested and verified among "biotope" locations on all islands using np-MANOVAs (Table 3). Further hypothesis testing was not used due to the limited temporal range of the dataset, therefore limiting inference beyond basic differences. Biotopes were classified within the dataset and represented geographically unique areas within each island (e.g., east, north, and southwest coasts of Puerto Rico). Statistical differences were observed among all locations within island groups, among every dataset tested. Importantly, each of the sampling locations for the original NCCOS dataset (i.e., La Parguera in Puerto Rico, Buck Island in St. Croix, and the Virgin Islands National Park in St. John) were included as unique biotopes in the NCRMP dataset. As noted above, the fish community within each of these locations was unique within its own island platform, and therefore not representative of the entire island platform.

DISCUSSION
Using Opportunistic Datasets in Fisheries Management

The analyses of the opportunistic datasets used in this study suggest that fish communities in the U.S. Caribbean are not spatially homogenous, therefore supporting the notion of a sub-regional management structure. The specific spatial scale that fish communities differ remains unclear, but divisions were apparent among islands as well as within individual island platforms. Future management considerations should explore the possibility of further resolving spatial management to incorporate differences (e.g., leeward vs windward regions) within each island platform. The shift from regional strategies to the recognition of smaller management units (i.e., individual island management areas of Puerto Rico, St. Thomas/St. John, and St. Croix) represents a significant step towards the implementation of an ecosystem-based approach to fisheries management.

The most notable assumption that was made during the analyses of the opportunistic datasets, was that all the datasets used were representative. Due to the short temporal range of the data (e.g., 2 years within island platforms for NCRMP data), the utility of these analyses are limited in inference to the timeframe that data collection occurred. In addition,

Table 1. Significant indicator species (α = 0.05) for the hard-bottom sites of the National Centers for Coastal Ocean Science legacy dataset, as determined by the IndVal analysis. Ind = Indicator value, P = P value, Group = Island Indication, Species = Indicator Species.

Ind	P	Group	Species
98.18	0.001	St. John	Masked/glass Goby
87.53	0.001	St. John	Rainbow Wrasse
86.00	0.001	St. John	Chalk Bass
84.10	0.001	St. John	Black Hamlet
78.14	0.001	St. John	Tobaccofish
77.01	0.001	St. John	Colon Goby
76.77	0.001	St. John	Blue Chromis
76.50	0.001	St. John	Diamond Blenny
75.30	0.001	Buck Island	Slippery Dick
73.91	0.001	Buck Island	Queen Parrotfish
72.06	0.001	St. John	Cero
71.47	0.001	St. John	hamlets
71.30	0.005	La Parguera	Bluestriped Grunt
70.96	0.001	St. John	Barred Hamlet
69.72	0.001	St. John	Rock Beauty
69.45	0.001	St. John	Saucereye Porgy
67.84	0.001	Buck Island	Clown Wrasse
67.03	0.001	Buck Island	Sand Tilefish
66.30	0.004	St. John	Creole Wrasse
66.05	0.001	St. John	Slender Filefish
63.80	0.001	St. John	Pallid Goby
62.56	0.001	Buck Island	Puddingwife
62.49	0.001	St. John	Butter Hamlet
61.99	0.001	La Parguera	Hogfish
61.65	0.002	St. John	Boga
61.40	0.001	La Parguera	Orangespotted Goby
61.24	0.001	St. John	Cocoa Damselfish
60.10	0.001	La Parguera	Yellowtail Hamlet
58.56	0.001	Buck Island	Longfin Damselfish
57.12	0.001	Buck Island	Yellowfin Mojarra
56.93	0.004	St. John	Lane Snapper
56.84	0.001	Buck Island	Yellowtail Damselfish
56.66	0.002	Buck Island	Redlip Blenny
54.93	0.001	St. John	Sand Diver
54.39	0.001	Buck Island	Beaugregory
54.06	0.002	La Parguera	Gray Angelfish
53.82	0.001	St. John	French Angelfish
53.09	0.001	St. John	Yellowhead Wrasse
52.83	0.001	St. John	Red Hind
52.83	0.001	St. John	Princess Parrotfish
52.16	0.002	St. John	Dog Snapper
51.32	0.003	Buck Island	Blue Runner
51.18	0.006	St. John	Gray Snapper
50.76	0.001	St. John	Sharpnose Puffer
50.58	0.003	St. John	Spotted Goatfish
50.46	0.002	La Parguera	Goldspot Goby

(Continues)

Table 1.   (Continued)

Ind	P	Group	Species
50.41	0.001	Buck Island	Platefish
50.01	0.001	Buck Island	Coney
49.97	0.004	La Parguera	Sharknose Goby
49.24	0.001	Buck Island	Ocean Surgeonfish
48.70	0.002	St. John	Shy Hamlet
47.88	0.003	St. John	Graysby
47.74	0.001	St. John	Striped Parrotfish
47.43	0.002	St. John	Bridled Goby
46.09	0.014	Buck Island	Saddled Blenny
45.78	0.035	St. John	Brown Chromis
45.75	0.015	St. John	Great Barracuda
45.66	0.008	St. John	Queen Triggerfish
45.63	0.002	Buck Island	Harlequin Bass
45.34	0.001	St. John	Peppermint Basslet
45.30	0.04	St. John	Queen Angelfish
44.68	0.049	La Parguera	Bucktooth Parrotfish
44.09	0.006	Buck Island	Bicolor Damselfish
44.01	0.001	La Parguera	Tube blenny
43.52	0.018	St. John	Smooth Trunkfish
42.87	0.03	La Parguera	Yellowtail Snapper
42.82	0.002	St. John	Barfin Blenny
42.74	0.003	St. John	Spinyhead Blenny
42.15	0.019	Buck Island	Spanish Hogfish
41.89	0.037	La Parguera	Lantern Bass
41.78	0.008	Buck Island	Mutton Snapper
41.37	0.006	St. John	Nassau Grouper
41.15	0.029	Buck Island	Mahogany Snapper
40.59	0.001	Buck Island	Cottonwick
40.52	0.002	St. John	Longjaw Squirrelfish
39.96	0.003	St. John	Redband Parrotfish
82.32	0.001	St. John	Reef Butterflyfish
77.35	0.001	St. John	Yellowbelly Hamlet
63.96	0.001	La Parguera	Porkfish
58.53	0.001	La Parguera	Pluma Porgy
57.72	0.001	Buck Island	Blue Tang
51.67	0.002	Buck Island	Bluehead
51.42	0.001	La Parguera	Foureye Butterflyfish
50.00	0.002	St. John	Atlantic Creolefish
46.06	0.014	La Parguera	Dusky Damselfish
41.96	0.014	St. John	Spotted Drum
39.88	0.038	Buck Island	Redspotted Hawkfish
39.15	0.008	St. John	herring
38.66	0.001	Buck Island	Yellowcheek Wrasse
38.46	0.027	Buck Island	Black Durgon
38.35	0.004	La Parguera	Orangesided Goby
37.38	0.019	La Parguera	Hovering Goby
36.62	0.020	La Parguera	Peppermint Goby
35.15	0.003	St. John	Horse-eye Jack

(Continues)

Table 1. (Continued)

Ind	P	Group	Species
34.74	0.026	St. John	Spotfin Butterflyfish
34.16	0.002	Buck Island	Spotfin Goby
33.64	0.015	La Parguera	Secretary Blenny
32.72	0.01	St. John	Barred Cardinalfish
32.62	0.05	St. John	Dash Goby
32.34	0.02	St. John	Sharksucker
30.80	0.006	Buck Island	Spotted Scorpionfish
30.43	0.019	St. John	scads
29.29	0.005	St. John	Shortnose batfish
28.07	0.042	St. John	Longsnout Seahorse
27.41	0.004	St. John	Tiger Grouper
27.09	0.024	St. John	Chub (Bermuda/Yellow)
26.36	0.014	La Parguera	Rusty Goby
25.41	0.009	St. John	Sheepshead Porgy
25.06	0.012	St. John	Longsnout Butterflyfish
24.36	0.027	St. John	Glassy Sweeper
23.92	0.042	St. John	Reef Croaker
23.04	0.047	St. John	Seaweed Blenny
22.94	0.015	La Parguera	Seminole Goby
21.74	0.013	La Parguera	Sea bream
21.56	0.034	La Parguera	Highhat
20.93	0.016	Buck Island	Broadstripe Goby
20.93	0.029	St. John	Fringed Filefish
20.82	0.032	St. John	Blue Parrotfish
19.97	0.028	La Parguera	Green Moray
19.58	0.013	Buck Island	Purplemouth moray
19.21	0.036	St. John	Striped Grunt
19.02	0.016	St. John	Shortfin Pipefish
18.30	0.022	St. John	goby Elacatinus
17.39	0.028	La Parguera	Whitefin Sharksucker
17.16	0.039	St. John	Filefish
16.86	0.047	St. John	Margate (White)
15.79	0.023	Buck Island	Greenbanded Goby
15.79	0.024	Buck Island	Neon Goby
15.79	0.028	Buck Island	Eyed Flounder
15.79	0.032	Buck Island	moray eel Gymnothorax
15.06	0.048	St. John	Mutton Hamlet
14.42	0.039	Buck Island	Night Sergeant

sampling did not occur representatively across time. For example, in the NCCOS legacy dataset, nearly all St. John sampling occurred during the summer months. However, previous studies suggest minimal intra-annual temporal changes in reef-associated fish communities in the region (e.g., Tzadik et al. 2017). The assumption of representative sampling, even over a limited temporal range, was therefore accepted.

The two main limitations of the study were a restricted temporal range, as discussed above, and the use of non-targeted

sampling protocols. Several indicator species that were derived in the above analyses, such as Rainbow Wrasse *Halichoeres pictus* and Tobaccofish *Serranus tabacarius*, are not of management interest, nor are they commonly thought to act as ecological engineers, or ecosystem indicators. While the structure and function of the endemic fish communities depends on the presence or absence of these species, their importance to current management strategies remains indirect, and primarily only under EAFM approaches. Future studies that aim to address similar questions could instead focus sampling efforts on species that directly impact management decisions, such as those of commercial and/or ecological importance.

Fish Community Structure and Function Across Spatial Scales

Sub-regional differences in the fish community have been noted in previous studies and in anecdotal accounts, particularly with regard to fishery-dependent monitoring data in the form of landings and fisher communications (Matos-Caraballo and Agar 2008). These sub-regional differences should be studied further to develop the best monitoring and management practices that can be tailored to the nuances of each location. Further, fish assemblages are highly dependent on the habitats they occupy, the quality of those habitats, and connectivity to adjacent habitat types (Nagelkerken et al. 2001; Brown et al. 2018). The health and extent of each of these individual habitats often depend on the interplay among habitat types, also termed seascape nurseries or seascape habitats (Nagelkerken et al. 2013; Sambrook et al. 2019). The presence, abundance, and quality of particular habitats play key roles in the composition of fish assemblages by way of availability of nursery habitat, feeding grounds, structure, and energy transfer (Nagelkerken et al. 2002; Dorenbosch et al. 2004; Dorenbosch et al. 2005).

Spatial differences at multiple spatial scales were readily observed across all three datasets used in this study. The most apparent and robust (i.e., the most data points) divisions occurred within the NCCOS Legacy dataset. Among islands, fish communities differed by habitat type (Figure 4). Differences among such distinct habitat types were expected and has been frequently observed in previous studies in the region (Dahlgren and Eggleston 2000; Harbone et al. 2006) and worldwide (Shibuno et al. 2008; Kimirei et al. 2013). Further exploration of only the hard-bottom sites revealed a more interesting trend that suggests that fish communities differ by sample location (i.e., La Parguera, St. John, and Buck Island). These locations represent reefs around three islands that are in close proximity to one another, compared to the extent of the Caribbean, yet show consistent differences in the fish community structure and function, which supports the ecological argument for management at a finer spatial scale (Figure 5). This could include measures that are currently under development (such as island-specific annual catch limits of indicator stocks, as appropriate) but could also set the stage for more holistic approaches that underpin EAFM. Considering the data limitations in the region, a pressing need exists to incorporate alternative approaches to EAFM, including the development of conceptual models, ecosystem indicators, and risk assessments as viewed by the local experts and regional stakeholders. These components can not only inform management, but can also act to guide queries within the datasets that do exist (Levin et al. 2018).

The indicator species identified for each location offer potential insight into the nuances of each fish community
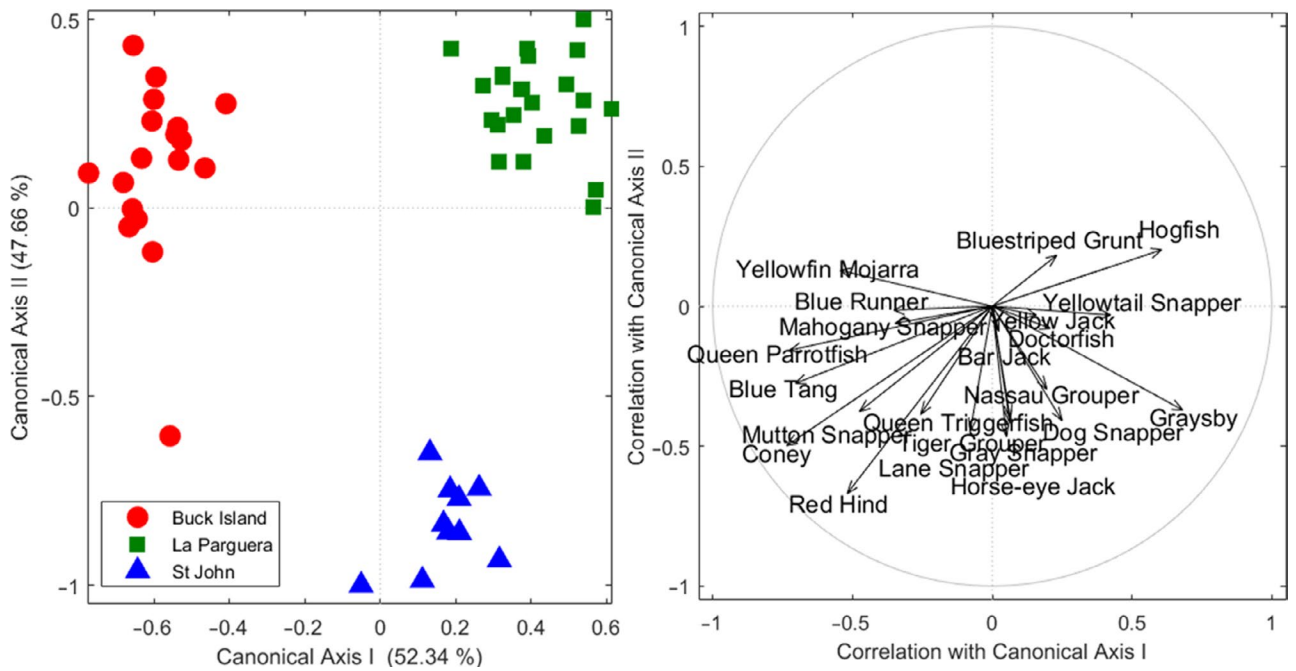
Figure 6. Visual representation of the same Canonical Analysis of Principal Coordinates (CAP) as in Figure 5, with only the top 22 commercially important species, as determined by indicator value, visualized as influence vectors.
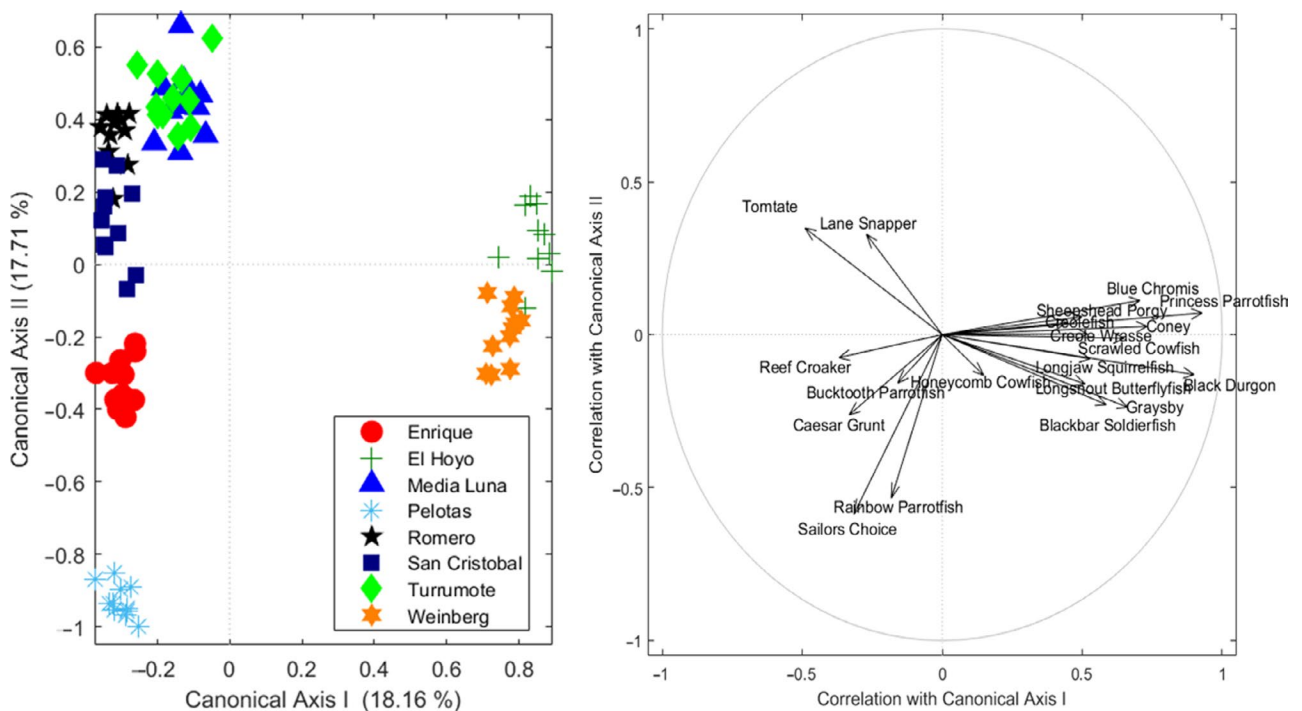

Figure 7. Canonical Analysis of Principal Coordinates (CAP) visualization of fish communities using beta diversity of the Coral Reef Ecosystem Studies (CRES) dataset. Sampling units are labeled to indicate location (i.e., eight distinct forereef locations). The ordination visualization represents the dissimilarity among sampling sites and highlights the division among sites. A strong division is apparent along the primary axis, which separates shelf-edge sites (on the right) from insular-shelf sites (on the left). The ordination of sites along the secondary axis represents a depth gradient along the insular shelf (increasing depth corresponding to shelf location, as values increase along axis II). The percentages on the axes refer to the percent variability explained by each canonical axis. The fish biplot vectors next to the ordination plot represent the relative correspondence with the first two canonical axes. Vector lengths and direction represent the strength and grouping tendency, respectively. All fish species were used to perform the CAP analysis, but only the top 20 most influential species, as determined by indicator value, are presented here.

Table 2. Significant indicator species (α = 0.05) for the Coral Reef Ecosystem Studies sample sites, as determined by the IndVal analysis. Ind = Indicator value, P = P value, Reef = Sampling site, Shelf Location = reef location on the shelf platform, Species = Indicator Species.

Ind	P	Reef	Shelf Location	Species
93.4167	0.001	El Hoyo	Shelf edge	Coney
87.8788	0.001	Weinberg	Shelf edge	Creole Wrasse
87.5307	0.001	Romero	Insular shelf	Lane Snapper
82.7436	0.001	Weinberg	Shelf edge	Longjaw Squirrelfish
81.7807	0.001	Weinberg	Shelf edge	Blackbar Soldierfish
78.9571	0.001	El Hoyo	Shelf edge	Scrawled Cowfish
77.5401	0.001	Weinberg	Shelf edge	Longsnout Butterflyfish
77.0026	0.001	Romero	Insular shelf	Tomtate
75.7556	0.001	Weinberg	Shelf edge	Blue Chromis
74.7903	0.001	Weinberg	Shelf edge	Black Durgon
69.697	0.001	El Hoyo	Shelf edge	Harlequin Bass
66.449	0.001	Pelotes	Insular shelf	Threespot Damselfish
64.9604	0.001	Enrique	Insular shelf	Caesar Grunt
63.6364	0.001	Pelotes	Insular shelf	Rainbow Parrotfish
56.4474	0.001	El Hoyo	Shelf edge	Sheepshead Porgy
54.5828	0.001	Weinberg	Shelf edge	Princess Parrotfish
50.1274	0.001	Romero	Insular shelf	Reef Croaker
48.7988	0.001	Weinberg	Shelf edge	Graysby
47.3118	0.001	El Hoyo	Shelf edge	Creolefish
47.1495	0.001	Enrique	Insular shelf	Sailors Choice
46.9697	0.001	Turrumote	Insular shelf	Bermuda Chub
46.5518	0.001	El Hoyo	Shelf edge	Bicolor Damselfish
46.1392	0.001	El Hoyo	Shelf edge	Longspine Squirrelfish
45.4203	0.001	Pelotes	Insular shelf	Yellow Goatfish
45.3466	0.001	Pelotes	Insular shelf	Hogfish
42.8236	0.001	El Hoyo	Shelf edge	Yellowhead Wrasse
42.4134	0.001	Enrique	Insular shelf	Bluestriped Grunt
41.3937	0.001	Weinberg	Shelf edge	Caribbean Reef Shark
37.2881	0.001	El Hoyo	Shelf edge	Black Seabass
37.2583	0.001	Pelotes	Insular shelf	Doctorfish
37.2001	0.001	Enrique	Insular shelf	Sergeant Major
36.6667	0.001	El Hoyo	Shelf edge	Rock Beauty
35.6273	0.001	Pelotes	Insular shelf	Beaugregory
35.4839	0.001	Enrique	Insular shelf	Schoolmaster
35.3982	0.001	San Christobal	Insular shelf	Queen Angelfish
34.4928	0.001	Turrumote	Insular shelf	Redlip Blenny
34.492	0.004	San Christobal	Insular shelf	Smallmouth Grunt
34.3471	0.001	Media Luna	Insular shelf	Fairy Basslet
33.192	0.001	Romero	Insular shelf	Spanish Hogfish
32.5159	0.001	Pelotes	Insular shelf	French Grunt
32.4895	0.001	El Hoyo	Shelf edge	Redtail Parrotfish
32.197	0.002	Weinberg	Shelf edge	Dusky Squirrelfish

(Continues)

Table 2. (Continued)

Ind	P	Reef	Shelf Location	Species
31.9276	0.001	San Christobal	Insular shelf	Bar Jack
31.1321	0.001	El Hoyo	Shelf edge	Queen Triggerfish
31.0519	0.001	El Hoyo	Shelf edge	Bluehead
30.9792	0.001	Weinberg	Shelf edge	Greenblotch Parrotfish
30.976	0.001	San Christobal	Insular shelf	Yellowtail Damselfish
30.5485	0.001	Pelotes	Insular shelf	Marbled Pufferfish
30.24	0.001	Pelotes	Insular shelf	Yellowtail Parrotfish
29.8938	0.001	El Hoyo	Shelf edge	Spotted Goatfish
29.2492	0.001	El Hoyo	Shelf edge	Ocean Surgeonfish
28.7879	0.001	Pelotes	Insular shelf	Yellowtail Hamlet
28.6511	0.001	Pelotes	Insular shelf	Porkfish
28.2828	0.002	Weinberg	Shelf edge	Bigeye
28.0851	0.001	El Hoyo	Shelf edge	Red Hind
28.0436	0.001	San Christobal	Insular shelf	Blue Tang
27.9263	0.001	Pelotes	Insular shelf	Gray Angelfish
26.1045	0.001	Weinberg	Shelf edge	Foureye Butterflyfish
25.7222	0.007	Turrumote	Insular shelf	Brown Chromis
25.4018	0.005	Turrumote	Insular shelf	Clown Wrasse
24.2424	0.006	Weinberg	Shelf edge	Spotfin Butterflyfish
23.6125	0.001	San Christobal	Insular shelf	Slippery Dick
23.2955	0.001	Pelotes	Insular shelf	Mahogany Snapper
23.0762	0.002	Romero	Insular shelf	Yellowtail Snapper
22.113	0.002	San Christobal	Insular shelf	Puddingwife
21.2121	0.003	Pelotes	Insular shelf	Gray Snapper
20.5882	0.004	Enrique	Insular shelf	Longfin Damselfish
20.1076	0.007	Turrumote	Insular shelf	Sharpnose Pufferfish
19.9071	0.014	Media Luna	Insular shelf	Butter Hamlet
19.6642	0.011	Enrique	Insular shelf	Cleaning Goby
19.2877	0.007	Pelotes	Insular shelf	Striped Parrotfish
19.0372	0.001	Turrumote	Insular shelf	Stoplight Parrotfish
18.8433	0.030	San Christobal	Insular shelf	Queen Parrotfish
18.1818	0.011	Media Luna	Insular shelf	Cubera Snapper
18.1818	0.012	Pelotes	Insular shelf	Mutton Snapper
18.1818	0.019	Weinberg	Shelf edge	Masked/Glass Goby
18.0653	0.026	Media Luna	Insular shelf	Barred Hamlet
17.4852	0.018	Media Luna	Insular shelf	White Grunt
17.4081	0.011	Pelotes	Insular shelf	Porcupinefish
17.3258	0.001	Turrumote	Insular shelf	Redband Parrotfish
17.0122	0.022	Weinberg	Shelf edge	Horse-eye Jack
16.9848	0.023	Romero	Insular shelf	Smooth Trunkfish

(Continues)

Table 2. (Continued)

Ind	P	Reef	Shelf Location	Species
16.8972	0.019	Pelotes	Insular shelf	Squirrelfish
16.637	0.013	Weinberg	Shelf edge	Redspotted Hawkfish
16.3636	0.013	Weinberg	Shelf edge	Glasseye
16.1791	0.049	San Christobal	Insular shelf	Trumpetfish
14.4628	0.008	Romero	Insular shelf	Dog Snapper
14.0762	0.030	Weinberg	Shelf edge	Spotted Drum
13.5616	0.006	El Hoyo	Shelf edge	Greater Soapfish
12.987	0.009	Pelotes	Insular shelf	Cocoa Damselfish
12.3967	0.020	Weinberg	Shelf edge	Spanish Grunt
11.1888	0.019	San Christobal	Insular shelf	Striped Grunt
11.1111	0.041	Turrumote	Insular shelf	Blackear Wrasse
8.08081	0.042	Enrique	Insular shelf	Bucktooth Parrotfish
7.95181	0.033	El Hoyo	Shelf edge	Honeycomb Cowfish

Table 3. Multivariate analysis of variance tables that identify differences among all sampling units within the National Coral Reef Monitoring Program dataset from 2013–2016. DF = Degrees of Freedom, SS = Sum of squares, MS = Mean Square, F = F ratio, P = iterated p value (1000 iterations). Factor 1 is the grouping vector for each dataset and differs according to the grouping convention of that particular year.

Source	DF	SS	MS	F	P
Puerto Rico Manova 2014					
Factor 1	2	2.8431	1.4215	5.8225	0.001
Residual	227	55.4216	0.2441		
Total	229	58.2646			
Puerto Rico Manova 2016					
Factor 1	2	2.5269	1.2635	6.4542	0.001
Residual	237	46.3953	0.1958		
Total	239	48.9222			
St Thomas/St John 2013 Manova					
Factor 1	3	3.4756	1.1585	5.2782	0.001
Residual	279	61.2386	0.2195		
Total	282	64.7142			
St Thomas/St John 2015 Manova					
Factor 1	4	4.2384	1.0596	4.4705	0.001
Residual	250	59.2552	0.2370		
Total	254	63.4936			
St Croix Manova 2015					
Factor 1	3	3.8098	1.2699	6.7036	0.001
Residual	235	44.5190	0.1894		
Total	238	48.3288			

resulting from differences in the ecological, physical, and fishery dynamics in each place. Species with the highest indicator values were clearly representative of individual sampling locations (Figure 5). Of the top 20 most influential indicator species, labrids were highly indicative of Buck Island fish communities, while haemulid indicators were representative of La Parguera. Several indicator species of smaller reef fishes (i.e.,

gobiids, small serranids, and pomacentrids) were representative of the fish community of St. John (Figure 5; Table 1). Further research should focus on causal relationships of these patterns, but the differences in the structure and function of the fish communities is clear among sampling locations. Commercial indicators were not as clearly identified by sampling location (Figure 6). Two of the sampling locations are designated no-take reserves (i.e., St. John and Buck Island), and exhibited commercial indicator species that were representative of these closures. Of the commercially important indicator species, the large lutjanids and serranids were predominantly indicative of St. John. In contrast, Buck Island in St. Croix, had indicator species with lower desirability in fish markets such as Blue Tang *Acanthurius coeruleus* and Mahogany Snapper *Lutjanus mahogoni*. This trend was surprising considering the similar lengths of closure (since 1961 and 1962 for Buck Island and St. John, respectively), and consequent expansion (2001 for both). However, it may be explained in part by fishing practices, proximity of spawning aggregations, and fishable area (Kadison et al. 2017). Targeted species also differ between St. Croix and St. John. Fishes such as Queen Parrotfish *Scarus vetula* and Coney *Cephalopholis fulva* were indicative of the Buck Island closed area, even though both fishes are important to the commercial fishery of St. Croix (NMFS 2018b), further suggesting that the study area is a naturally productive area for these populations. In addition, large lutjanids and serranids off St. John are highly ciguatoxic compared to other locations within the region (Loeffler et al. 2018), which may offer an additional level of protection against poaching, as fishers would likely avoid species with known histories of *ciguatera*. The trend of large lutjanids and serranids around St. John may partially explain the strong association of small reef fishes as well. The prevalence of these two groups may suggest a mutualistic relationship associated with cleaning stations (Trivers 1971; Darcy et al. 1974), or as a mesopredator controlled fish community (Stallings 2008).

Additional spatial differences were observed in the CRES dataset. The trends observed highlight the differences in fish communities across depth gradients. Previous studies have noted similar patterns across depth gradients (e.g., Bejarano et al. 2014), but the strong separation of the shelf edge reefs compared to the insular shelf reefs was greater than expected, and extended further into the unequivocal delineation of each reef that was sampled (Figure 7). The clear division of each reef suggests that the structure and function of fish communities may differ on much smaller scales than previously noted, with regard to depth and/or distance from shore. Confounding factors such as wave energy and upwelling highlight these differences, but the depth gradient itself encompasses these variations, and therefore is the primary variable associated with fish community structure. Indicator species for the divide between shelf edge reefs and insular shelf reefs were largely characteristic of feeding differences between the two general locations. For example, Black Durgon *Melichthys niger* were indicative of the shelf edge sites when compared to the insular shelf reefs (Figure 7). Black Durgon are opportunistic feeders that typically forage across the entire water column (Turingan et al. 1995). Their presence on the shelf edge reefs could be attributed to the larger water column and the upwelling of nutrients along the shelf. Similarly, Blackbar Soldierfish *Myripristis jacobus* feed on plankton in the water column and may therefore prefer shelf edge reefs due to the upwelling of nutrients that promotes the planktonic community there (Randall 1967). The indicator

species among the insular shelf reefs did not show as clear of a pattern with regard to diet-based groupings (Figure 7). The differences observed may be influenced by ontogenetic migration patterns, but further analysis of fish size structure and maturity levels, is required to explore that possibility.

Since 2012, the NCRMP monitoring program has supplanted the NCCOS system and is now used exclusively in the region. The new sampling design should improve representative sampling due to its inclusion of all regions among the islands as opposed to three distinct locations. This distinction is an important one, given that the sub-regions that were sampled in the NCCOS legacy dataset were not in fact representative of the island platform within which they were embedded, as indicated by the NCRMP data (Table 3). In fact, the structure and function of the fish community differed among all biotopes that were tested (Table 3).

The divisions identified in the present study represent preliminary interpretations of complex data. As noted above, the temporal limitations of the study preclude any definitive conclusions from the NCRMP dataset. However, within the scope of the available data, the sub-regions (as defined by the sampling protocol) differ with regard to the structure and function of the fish community and should therefore be considered distinct from one another.

Fish Community Structure as a Function of Spatial, not Temporal Scale

No discernable temporal trends were observed across any of the available datasets. Further, when sample units within each dataset were spatially grouped (i.e., by island or by individual reef) they were reclassified with 100% accuracy using the LOO analysis. The reclassification success suggests that spatial differences override any temporal variation and that little, if any, temporal trends exist within the datasets analyzed. The longest running dataset, the NCCOS legacy data, sampled across 12 years failed to group fish communities along temporal axes. Indeed, when considered as individual sampling events, neither sample seasons nor sample years varied enough within site to consider temporal trends (Figure 4). Neither annual nor seasonal variation was observed, further suggesting that fish communities in the region do not differ over the relatively short temporal scales considered here.

Similarly, within the limited temporal scale of the CRES dataset, no temporal trends were observed. Differences on an annual time scale would not be representative with such a short dataset, although seasonal differences could emerge. There were no such differences observed, further suggesting that fish communities in the region do not differ across seasonal temporal scales. Considering the temporal limitations of the NCRMP dataset no trends were expected, and none were observed.

Island Based Spatial Divisions for Fisheries Management

The exploration of opportunistic datasets in the region highlighted the spatial variability in the structure and function of the endemic fish communities. No temporal trends were observed, although this may be due to the limited temporal range of the datasets themselves. However, seasonal differences were not observed among any of the datasets, suggesting relatively static fish community composition among the species sampled over a yearly temporal scale. The trends that were derived and analyzed in the opportunistic datasets as presented above are indicative of a spatial management structure in the U.S. Caribbean due to the small-scale spatial differences within the regional fish community, and therefore support the notion of Island Based Fishery Management Plans. Ecosystem-based fisheries management calls for a spatially explicit approach (Berkeley et al. 2004), though many countries, including the USA still manage fisheries regionally, through a stock-based approach. More localized fisheries management has been successfully implemented in several countries, especially through co-management regimes (Cinner et al. 2012). Lack of understanding about optimal spatial scales for management and concern about complex spatial policies may explain why regulators have difficulty implementing EBFM (Takashina and Baskett 2016; Bode et al. 2016). This study demonstrates that there are differences in fish community structure across island platforms that are temporally consistent. That coupled with differences in fishing communities, gears, and harvesting preferences make for a rational, yet not overly complex management structure for the CFMC, which can be a model for other U.S. regional fishery management councils and countries with regionally dispersed fisheries. Future work should aim to elicit if finer spatial scales of management units would be more practical and, ultimately, more effective.

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