



Effects of environmental factors on reef fish assemblage structure in the southeastern US Atlantic

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ABSTRACT: Environmental variation influences fish assemblage structure; however, fish assemblage composition shifts due to natural or anthropogenic stressors have been observed in marine ecosystems worldwide, altering ecosystem structure and function, and fisheries sustainability. Previous research in waters off North and South Carolina (USA) was limited in scope and repeatability or did not quantify fish assemblages at a scale suitable for monitoring composition shifts. Concurrent chevron traps, underwater video, and environmental data from an annual fishery-independent survey were used to characterize the environment and enumerate demersal reef fishes caught in the traps, and priority fish species observed in video in depths ~15–110 m. Multivariate analyses detected assemblage patterns and environmental influences. An 8-variable (distance to shelf edge, depth, consolidated substrate size, latitude, percent biotic cover, temperature, undercut height, biotic class) model predicted assemblages, while 4 variables explained the greatest variation (distance to shelf edge [19%], depth [15%], consolidated substrate vertical relief [4%], size [4%]). The largest number of discriminator species occurred in mid- to outer shelf areas with greater substrate complexity (i.e. increasing substrate size and relief). Assemblages dominated by *Centropristis striata* at depths (~15–40 m) with little substrate complexity transitioned towards assemblages dominated by *Pagrus pagrus*, higher prevalence of larger-bodied predators, and invasive *Pterois* spp. at depths (~40–110 m) with greater substrate complexity. Understanding baseline assemblage characteristics and natural drivers of variability in fish assemblage structure is vital to conservation and management efforts that monitor changes in population abundance, the presence/absence of key species, and stressor-induced modifications of local assemblages, which are all measures of ecological health that underpin comprehensive assessments and management.

KEY WORDS: Assemblage structure · Environmental factors · Habitat · Reef fish · Fisheries · Atlantic

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1. INTRODUCTION

Spatial variation in fish assemblage structure is influenced by a variety of processes, including biotic and abiotic interactions and environmental stochasticity, that vary across multiple spatial and temporal scales (Waltho & Kolasa 1996, Friedlander et al. 2003, Richards et al. 2012, Anderson et al. 2013, Pearson &

Stevens 2015, MacDonald et al. 2016). Many studies have established strong connections between reef fish assemblage properties (e.g. species, abundance, biomass, richness, diversity) and depth (Miller & Richards 1980, Anderson et al. 2013, Geraldi et al. 2019). Depth is a physical gradient along which variability in oceanographic climatology (e.g. temperature and salinity), circulation processes (e.g. tidal flows,

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currents), and light attenuation (e.g. biotic complexity) influence biological and chemical processes (Menzel 1993) and the distribution of fish taxa (Fautin et al. 2010). Similarly, horizontal gradients such as distance to shore or open water have also been found to influence fish assemblages. Areas closer to shore are subject to increased habitat instability through environmental forcing and greater accessibility to fishing pressure, while areas closer to open water near the shelf edge may be influenced by upwellings, etc. (Miller & Richards 1980, Bacheler et al. 2019). As climate change, coastal development, and fishing pressure continue to impact fish species distributions, it is becoming increasingly important to understand mechanisms that underly cross-shelf and depth distributions (MacDonald et al. 2016). Additional strong associations have been established between structural complexity and fish assemblage properties, in that higher complexity is believed to reduce interspecific competition by providing a greater spectrum of resources and niches and reduces predator–prey interactions by providing refuges (Friedlander et al. 2003).

As commercial and recreational fish stocks decline due to anthropogenic or environmental factors, the loss of previously abundant and/or keystone species can alter the structure and function of fish assemblages and ecosystems (Pauly et al. 1998, Carr et al. 2002, Worm et al. 2009), and therefore, the overall sustainability of fisheries (Zhou et al. 2010). Such changes have been observed in marine ecosystems around the world (National Research Council 2006) and can have implications for fisheries management within, and across, jurisdictional boundaries.

To increase sustainability and augment traditional fisheries management methods in the USA, recent strategies are adopting a more holistic ecosystem-based approach that is being implemented through regional fishery management plans and fishery ecosystem plans (NMFS 2009). Ecosystem-based fishery management takes into account the entire ecosystem associated with a managed species, and management is guided by a number of principles, including the need to better understand a broad suite of ecosystem processes, drivers, and threats and the relative importance to fishery resources (NMFS 2016a,b). An integral step in implementing an ecosystem approach to fisheries is to define and determine the level of importance of marine habitats to fish populations (NMFS 2016b) and to quantify the co-occurrences of fish species within assemblages (Tolimieri & Levin 2006, Nogueira et al. 2013).

Previous demersal fish assemblage studies in the southeastern US Atlantic (SEUSA) vary in scale and

methods. Early studies concentrated on region-wide scales that subdivided areas by depth (Struhsaker 1969, Miller & Richards 1980, Grimes et al. 1982, Sedberry & Van Dolah 1984). More recent research includes studies focused on specific locations including marine protected areas (Quattrini & Ross 2006, Schobernd & Sedberry 2009) and Gray's Reef National Marine Sanctuary (Kendall et al. 2009), several hard-bottom habitat sites off North Carolina (NC) (Burge et al. 2012), hard bottom reefs, rock jetties and shipwreck sites across the shelf in Onslow Bay, NC (Whitfield et al. 2014), and broad-scale variation in fishes on temperate reefs by quantifying climate indices, water temperature, and fishing (Gerald et al. 2019). Previous studies have also analyzed assemblages based on commercial and recreational fishery-dependent data (Shertzer & Williams 2007, Shertzer et al. 2009). However, patterns of biodiversity are best extrapolated from fishery-independent data (Collie et al. 2008), as these data are collected during surveys that consistently adhere to standardized scientific protocols not influenced by specific management measures (e.g. season closures, mesh sizes, size and bag limits) or socioeconomic factors, and therefore provide a more unbiased account (Kilduff et al. 2009). Although many previous studies around the world have examined structures of reef fish assemblages across habitat, environmental, and other oceanographic gradients (e.g. Pearson & Stevens 2015, Fukunaga et al. 2017, Stefanoudis et al. 2019), these studies in the SEUSA do not provide information regarding reef fish assemblages and how they are structured across heterogeneous hard-bottom habitat types and other levels of environmental factors from which changes in structure can be monitored. Therefore, given the fluctuation in the status of many stocks in the SEUSA and recent advances in technology and the extent of gathering fisheries-independent data, it is feasible to examine how environmental drivers influence the structuring of fish assemblages. Understanding baseline assemblage structure characteristics and environmental drivers of variability in fish assemblage structure is vital to conservation and management efforts that monitor changes in population abundance, the presence/absence of key species, and stressor-induced modifications of local assemblages (Pauly 1995, Kendall et al. 2004, Tolimieri & Levin 2006, Nogueira et al. 2013), all of which are measures of ecological health that underpin comprehensive assessments and management.

The primary objectives of this study were to assess how distance to shelf edge, depth, latitude, tempe-

perature, surface geologic components, and biotic components (for details, see Table S1 in the Supplement at www.int-res.com/articles/suppl/m671p147_supp.pdf) influence fish assemblage structure, characterize assemblages at the finest taxonomic resolution possible (i.e. to species level), and identify species within the assemblages that may exhibit relative vulnerabilities to stressors off of NC and South Carolina (SC) using data obtained from 2 concurrently deployed gears (chevron traps and underwater video) in a long-term, annual, fishery-independent survey.

2. MATERIALS AND METHODS

2.1. Study area

We used data collected from approximately Cape Hatteras, NC, to Savannah, Georgia (GA), in the SEUSA continental shelf from 2013 to 2015 (Fig. 1). The width of the shelf extends from 30 km off Cape Hatteras out to its widest point of 120 km off GA and SC (Menzel 1993, Blanton et al. 2003). The depth contours generally parallel the shelf (Blanton et al. 2003) and can be divided into several depth zones: inner shelf (0–20 m), mid-shelf (21–40 m), outer shelf (41–75 m), and shelf break, which generally occurs at about 50–75 m depth, although depths can exceed 75 m off NC (Menzel 1993, Fautin et al. 2010). Relatively stable temperatures and salinity are observed near the bottom, just inshore of the shelf break, which is bordered by seasonally variable inshore waters on one side and fluctuating offshore waters on the other (Lee et al. 1991, Fautin et al. 2010). The outer shelf is subject to cold eddy/upwelling events and warm Gulf Stream intrusions (Lee et al. 1991, Fautin et al. 2010). Patchy areas of sand-veneered hard bottom areas and rocky outcrop hard bottom areas occur throughout the SEUSA (Powles & Barans 1980, Sedberry & Van Dolah 1984, Fautin et al. 2010). The amount of hard bottom available for development of a benthic community is influenced by morphology, geometry, and composition, as well as the thickness of the surface sand

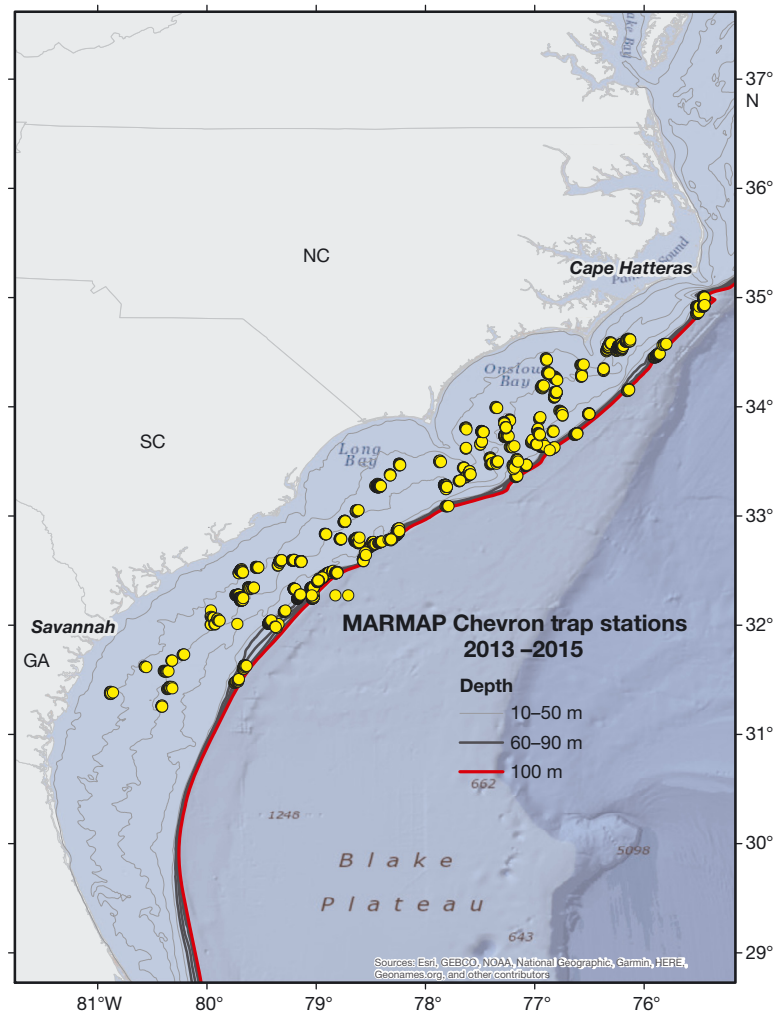


Fig. 1. 2013–2015 Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program chevron trap-video sampling areas (yellow dots) between approximately Cape Hatteras, North Carolina (NC), south to Savannah, Georgia (GA), USA; SC: South Carolina. The map was created using ArcGIS® software (Esri). ArcGIS® and ArcMap™ are the intellectual property of Esri (www.esri.com) and are used herein under license. Basemap © Esri

sheet (Riggs et al. 1996). These mesophotic hard-bottom areas provide substrate for persistent and dependent biological communities (Riggs et al. 1996) and are ecologically important resources that provide habitats necessary to the life history of many ecologically and economically important fish species (Powles & Barans 1980, Sedberry et al. 2006).

2.2. Survey design

We used fishery-independent data collected by the Southeast Reef Fish Survey (SERFS). SERFS repre-

sents the current collaborative work of 3 federally funded fishery-independent monitoring programs studying reef fish species of the SEUSA: The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program (1990–present), the Southeast Area Monitoring and Assessment Program–South Atlantic (SEAMAP–SA; 2009–present), and the Southeast Fishery-Independent Survey (SEFIS; 2010–present). The sampling season typically occurred between mid-April through mid-October. Stations were randomly sub-sampled from an archive of previously surveyed sites comprised of confirmed hard-bottom stations at depths ~15–100 m (Fig. 1). Chevron traps (see Collins 1990 for details) were one of several gear types used by MARMAP with standardized protocols since 1990. Each trap was baited with a combination of whole and cut clupeids, most often *Brevoortia* spp., and deployed during daylight hours with a target soak time of approximately 90 min. Up to 6 traps were deployed at the same time per trap set, one per station, with a minimum distance of at least 200 m between them to decrease the probability of nearby traps attracting fish from the same location; these were considered independent samples. Beginning in 2011, as part of the collaborative effort with the SEFIS, all traps used by the SERFS were equipped with a Canon Vixia HF200 video camera mounted above and facing away from the trap opening and a GoPro Hero (models 2, 3, and 4) video camera mounted above and facing away from the back of the traps. In 2015, all Canon cameras were replaced with GoPro Hero 4 cameras. All camera settings remained constant and were set to record 45 min video during the ~90 min soak period.

2.3. Environmental data collection

Environmental data used to investigate influences on fish assemblages in this study include data consistently collected as part of the SERFS fishery-independent survey and have been found to influence fish assemblages in many other previous studies (Friedlander et al. 2003, Richards et al. 2012, Anderson et al. 2013, MacDonald et al. 2016). Temperature and other physical oceanography data were collected using a SEABird Scientific (SBE 19 or 25) conductivity, temperature, and depth recorder (CTD). A single CTD deployment was conducted in the general vicinity of each trap set at a minimum distance of 200 m while each set of traps soaked. Depth (m), latitude, longitude, bottom temperature (°C, from CTD),

date, and soak time were recorded as part of the standard SERFS sampling protocol. Temporal, spatial, and other physical variables considered for analyses included date, position (decimal degrees), distance to shelf edge (km), depth, and bottom temperature (°C). Distance to shelf edge was selected as a proxy for potential influences from Gulf Stream (or conversely, distance from shore as a proxy for fishing pressure) and was calculated via a 'Near' analysis (NEAR_DIST) in ArcGIS using a straight-line distance from each sample point to the shelf edge where it parallels the general western boundary of the Gulf Stream (defined approximately as the 100 m isobath; Lee et al. 1991).

Habitat characterization criteria for surface geologic and biotic components were estimated from each video camera. Surface geologic components included: surface geologic class (dominant geologic type), seafloor morphology, consolidated substrate vertical relief, consolidated substrate size, and undercut height. Biotic components included biotic class (dominant biota type), biota height, and percent biotic cover. All environmental variables except for 'day of year' were coded as factors (ordinal, except geologic and biotic classes) to enable further examination of how assemblages differ across levels, or gradients, for each of these factors (Table S1). One unobstructed frame per video was used for habitat characterization. Videos where the trap moved, so that none of the initial view upon landing remained visible, were excluded. Videographic data from each trap-camera were combined to generate visual estimates of benthic parameters. Coral Point Count with Excel extensions (CPCe) (Kohler & Gill 2006) was used in cases where it was difficult for the observer to visually estimate percent of biotic cover. Each selected image frame imported into CPCe was analyzed via 25 randomized points for benthic characterization. The random point placement and identification process was repeated 3 times, after which the mean of the 3 trials and subsequent percentages were calculated and imported into an Excel spreadsheet.

2.4. Fish species data collection

All fishing gear types have specific selectivity for species, size, and species behavior that might vary among habitat types (Hayes et al. 2012, Baker et al. 2016). However, the use of multiple gears can mediate selectivity biases, provide complementary rather than redundant assemblage information, and therefore provide more robust estimates of assemblage

composition (Lapointe et al. 2006, Baker et al. 2016). Additionally, during this study, only priority species were annotated in video per SERFS protocol (see Bacheler et al. 2014 for details). Therefore, fish counts from individual chevron trap catches and video from cameras placed over the trap opening were utilized for analyses to reduce potential gear selectivity bias and to include the greatest number of species. Gear selection to estimate abundance was based on the following criteria so that only 1 gear source (trap or video) was used per species: (1) trap

catch abundances (total abundance per species per trap) for non-priority species not enumerated in videos; (2) video abundances for species not typically caught in traps; and (3) for species accounted for by both gears, only the gear with the highest percent frequency of occurrence over the sampling period (i.e. presence/absence over total number of traps or video). Selection of the data source was made to incorporate the widest range of environmental variation and/or distribution for that species (Table 1). Statistical differences between frequency of occurrence

Table 1. Complete list of enumerated reef fish species (n = 42) from 1510 samples taken in the southeastern US Atlantic from approximately Cape Hatteras, North Carolina, to Savannah, Georgia, (2013–2015) by frequency of occurrence (FO), percent frequency of occurrence (%FO), abundance per selected gear, and gear from which species data were derived

Common name	Scientific name	Family	FO	%FO	Abundance	Gear
Black sea bass	<i>Centropristis striata</i>	Serranidae	857	56.8	21 788	Trap
Tomtate	<i>Haemulon aurolineatum</i>	Haemulidae	608	40.3	11 630	Trap
Gray triggerfish	<i>Balistes capricus</i>	Balistidae	490	32.5	1559	Trap
Bank sea bass	<i>Centropristis ocyurus</i>	Serranidae	392	26.0	1156	Trap
White grunt	<i>Haemulon plumieri</i>	Haemulidae	340	22.5	1959	Trap
<i>Stenotomus</i> spp.	<i>Stenotomus</i> spp.	Sparidae	276	18.3	4045	Trap
Sand perch	<i>Diplectrum formosum</i>	Serranidae	248	16.4	678	Trap
Spottail pinfish	<i>Diplodus holbrookii</i>	Sparidae	116	7.7	486	Trap
Knobbed porgy	<i>Calamus nodosus</i>	Sparidae	106	7.0	172	Trap
Planehead filefish	<i>Stephanolepis hispidus</i>	Monacanthidae	72	4.8	110	Trap
Blue line tilefish	<i>Caulolatilus microps</i>	Malacanthidae	20	1.3	41	Trap
Red grouper	<i>Epinephelus morio</i>	Serranidae	20	1.3	21	Trap
Snowy grouper	<i>Hyporthodus niveatus</i>	Serranidae	17	1.1	28	Trap
Reef butterflyfish	<i>Chaetodon sedentarius</i>	Chaetodontidae	13	0.9	28	Trap
Reticulate moray	<i>Muraena retifera</i>	Muraenidae	13	0.9	13	Trap
Whitebone porgy	<i>Calamus leucosteus</i>	Sparidae	13	0.9	17	Trap
Blue angelfish	<i>Holocanthus bermudensis</i>	Pomacanthidae	11	0.7	13	Trap
Jackknife fish	<i>Equetus lanceolatus</i>	Scianidae	10	0.7	16	Trap
Speckled hind	<i>Epinephelus drummondhayi</i>	Serranidae	10	0.7	11	Trap
Sharksucker	<i>Echeneis naucrates</i>	Echeneidae	9	0.6	10	Trap
Whitespotted soapfish	<i>Rypticus maculatus</i>	Serranidae	9	0.6	11	Trap
Squirrelfish	<i>Holocentrus adscensionis</i>	Holocentridae	6	0.4	8	Trap
Red porgy	<i>Pagrus pagrus</i>	Chaetodontidae	782	51.8	2244	Video
Vermilion snapper	<i>Rhomboplites aurorubens</i>	Lutjanidae	403	26.7	4518	Video
Almaco	<i>Seriola rivoliana</i>	Carangidae	297	19.7	455	Video
Greater amberjack	<i>Seriola dumerili</i>	Carangidae	279	18.5	496	Video
Scamp	<i>Mycteroperca phenax</i>	Serranidae	240	15.9	371	Video
Lionfish	<i>Pterois volitans</i> and <i>P. miles</i>	Scorpaenidae	214	14.2	316	Video
Red snapper	<i>Lutjanus campechanus</i>	Lutjanidae	171	11.3	289	Video
Hogfish	<i>Lachnolaimus maximus</i>	Labridae	119	7.9	147	Video
Gag	<i>Mycteroperca microlepis</i>	Serranidae	103	6.8	136	Video
Banded rudderfish	<i>Seriola zonata</i>	Carangidae	72	4.8	219	Video
Sand tilefish	<i>Malacanthus plumieri</i>	Malacanthidae	67	4.4	75	Video
Atlantic sharpnose shark	<i>Rhizoprionodon terraenovae</i>	Carcharhinidae	66	4.4	116	Video
Cobia	<i>Rachycentron canadum</i>	Rachycentridae	30	2.0	46	Video
Graysby	<i>Cephalopholis cruentata</i>	Serranidae	27	1.8	43	Video
Rock hind	<i>Epinephelus adscensionis</i>	Serranidae	23	1.5	25	Video
Yellowmouth grouper	<i>Mycteroperca interstitialis</i>	Serranidae	14	0.9	14	Video
Sandbar shark	<i>Carcharhinus plumbeus</i>	Carcharhinidae	13	0.9	13	Video
Lesser amberjack	<i>Seriola fasciata</i>	Carangidae	12	0.8	19	Video
Gray snapper	<i>Lutjanus griseus</i>	Lutjanidae	11	0.7	14	Video
Nurse shark	<i>Ginglymostoma cirratum</i>	Ginglymostomatidae	7	0.5	7	Video

of each priority species within traps and video (Fig. 2) were tested with a 2-sample chi-squared test for equality of proportions with continuity correction in RStudio version 0.99.878 (RStudio Team 2015), and R version 3.2.3 (R Core Team 2015). Species that occurred less than 5 times over the entire sampling period were excluded from analyses. Video abundances were determined by the MaxN (MaxNO, MinCount) approach, in which the maximum number of each species observed in a single frame per video is determined. MaxN, at preselected reading intervals, is used commonly as a conservative estimate of relative abundance as it avoids repetitive counts of the same individuals (Gledhill 2001, Watson et al. 2005, Merritt et al. 2011). Using underwater video to enumerate fish can be time consuming, depending on target question (e.g. single species vs. assemblage characterizations). Therefore, for efficiency and inclusion of the greatest number of videos for this study as per standard SERFS protocol, view-

ing intervals began 10 min after the trap settled on the seafloor every 30 s over 20 consecutive minutes of footage (Bacheler & Shertzer 2015, Bacheler et al. 2016). Due to differences in resolution and field of view between Canons and the GoPros (used as replacements in 2015), a calibration factor developed by Bacheler & Ballenger (2018) was used to adjust 2015 species abundances.

2.5. Data analyses

Multivariate statistical tests and ordinations were performed to examine patterns in community structure using PRIMER-e with PERMANOVA+ (version 7.0.11) (Clarke & Gorley 2015). Permutational multivariate analysis of variance (PERMANOVA) is widely recognized and accepted for its use across many fields, including ecology, as it allows rigorous meaningful analysis of high dimensional systems. It is in-

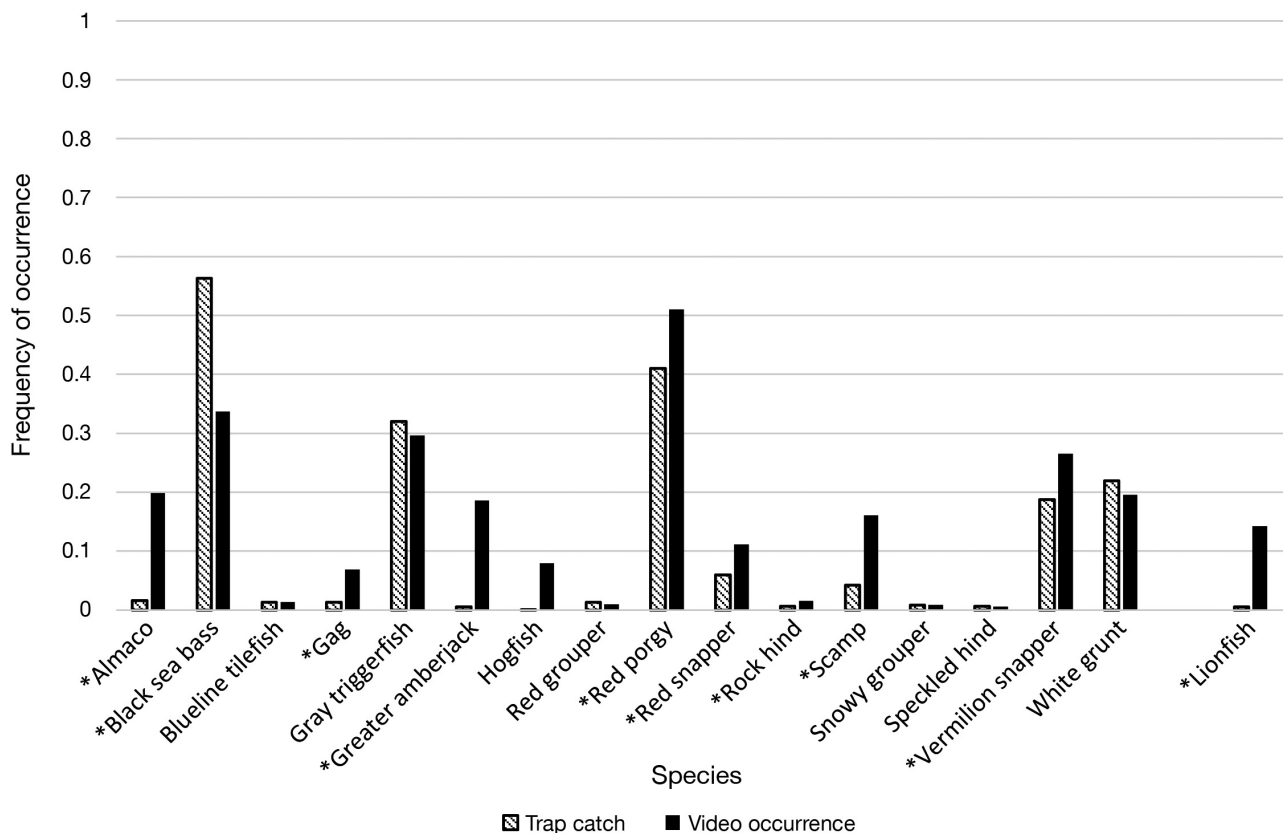


Fig. 2. Summary of the frequency of occurrence for managed reef fish species and lionfish (*Pterois volitans* and *P. miles*) captured in traps and observed in video between 2013 and 2015 on the southeastern US Atlantic continental shelf approximately between Cape Hatteras, NC, and Savannah, GA. Although not managed, lionfish are invasive in this region and were included to exemplify the statistically higher frequency of occurrence in videos. Statistical significance between frequency of occurrence within chevron traps and video was determined with a 2-sample test for equality of proportions with continuity correction with a 95% confidence interval. An asterisk indicates a statistically significant difference ($\alpha = 0.05$) in the frequency of occurrence between chevron traps and video for that species. Scientific names of species are given in Table 1

sensitive to multicollinearity and zero-inflated data, allows for multiple variables and differences in between-group variation, and assumes no distribution (Anderson 2014). Initially, pairwise scatterplots and an associated correlation matrix between all environmental factors were performed to detect collinearity (any correlation $|r| \geq 0.95$; Anderson et al. 2008). Environmental data were normalized where the values for each variable have their mean subtracted and divided by their standard deviation to put variables on a common scale and make it possible to derive meaningful distances between samples using Euclidean distance (Clarke & Gorley 2015). Species data were standardized by sample (i.e. relative percentages) to account for sampling differences in the number of fish that might be observed in trap catch vs. video 'capture' because the area sampled by each gear is difficult to enumerate (Clarke et al. 2014). Species data were fourth-root transformed to down-weight the contribution of numerically dominant species, and a Bray-Curtis similarity resemblance matrix was constructed from the transformed data.

2.6. Environmental data

Distance-based linear modeling (DistLM) was performed on the Bray-Curtis similarity resemblance matrix to determine the proportion of variation in fish assemblage structure explained by the environmental variables. The BEST (BioEnv + Stepwise) selection procedure, based on 999 permutations, was used to determine which environmental factors explained the greatest proportion of variance and to create an optimal model fit using the Bayesian information criterion (BIC; Schwarz 1978) by finding the most parsimonious model given the high number of environmental variables tested. The BEST procedure determines the best match between multivariate among-sample patterns of the assemblage and that from environmental variables associated with the samples (Clarke & Gorley 2015). The BEST procedure examines the value of the selection criterion for all possible combinations of predictor variables. A distance-based redundancy analysis (dbRDA) visualized the fitted model in multi-dimensional space by locating linear combinations of the environmental factors that explain the greatest variation in the data cloud (Legendre & Anderson 1999, Anderson et al. 2008, Clarke & Gorley 2015). The environmental factors selected by the DistLM procedure were analyzed for statistical significance with a 1-way PERMANOVA (Anderson et al. 2008) using 999 permu-

tions and Type III sums of squares partitioning for unbalanced designs having heterogeneous dispersions where some overlap occurs among the terms regarding the individual portions of variation they explain (Anderson et al. 2008). Post hoc pairwise PERMANOVAs were also used to test for significant differences in assemblage structure among levels of the environmental factors using 999 permutations, and a subsequent Bonferroni correction (α/n [$\alpha = 0.05$]) was applied to reduce the instance of a Type I error. PERMANOVA is sensitive to differences in multivariate dispersion among groups (Anderson et al. 2008, Warton et al. 2012); therefore, PERMDISP was used with distances calculated to centroids and 999 permutations to measure and test homogeneity of multivariate dispersions on the variables that explain the highest proportion of variation. Where a significant effect was indicated by PERMANOVA and PERMDISP, principal coordinates analysis (PCO, Torgerson 1958) was applied to the matrix of Bray-Curtis similarity to discern relevant patterns in the data due to dispersion and location effects (Anderson et al. 2008).

2.7. Fish assemblage structure

The similarity percentages (SIMPER) routine (Clarke 1993) was used to identify discriminator fish species that contributed most to within-group similarity using a 90 % cutoff (those which typified the groups, Clarke et al. 2014) across each environmental factor level selected by the DistLM marginal test and to examine turnover in assemblages (indicated by significant differences in fish assemblages between factor levels as determined by the pairwise PERMANOVA) across each environmental factor level.

3. RESULTS

Sampling occurred within latitudes 31.3–35° N, at 0.1–117.9 km distances to the shelf edge, and temperatures ranged from 16 to 21°C (see Table S1 for categorization of environmental factors). A total of 1510 trap deployments collected 43 800 specimens representing 22 species, while concurrent video-graphic data recorded 9563 specimens from 20 species. Black sea bass *Centropristis striata* had the highest frequency of occurrence (56.8 %) and abundance ($n = 21\,788$) in traps. In contrast, red porgy *Pagrus pagrus* had the highest frequency of occur-

rence (51.8%) observed in videographic surveys; however, it was the second most abundant species ($n = 2244$). Vermilion snapper *Rhomboplites aurorubens* recorded the highest abundance estimates in video surveys ($n = 4518$) but registered the second highest frequency of occurrence (27 %) (Table 1).

3.1. Environmental influences on reef fish assemblage structure

The DistLM analysis contained 8 variables: distance to shelf edge, depth, consolidated substrate size, latitude, % biotic cover, temperature, undercut height, and biotic class (Bayesian information criterion [BIC]: 11 718 and R^2 : 0.273). The first 2 dbRDA axes explained 89% of the fitted variation and 24 % of the total variation for the BEST BIC model (Fig. 3). One-way PERMANOVAs revealed that the environmental variables within the models selected by DistLM procedure showed a significant effect on fish assemblage structure ($p = 0.001$). However, the test also revealed multiple interactive effects between variables (Table S2 in the Supplement), which is expected as some environmental factors vary both spatially and temporally. Ad-

ditionally, indirect variables such as depth, geology, and habitat type can serve as proxies for, or typically replace, combinations of direct (e.g. temperature and pH) and resource variables (e.g. matter and energy consumed) (Austin et al. 1984, Guisan et al. 1999). The DistLM marginal tests indicated that each of the 13 variables was statistically significant ($p < 0.001$) in isolation; however, distance to shelf edge, depth, consolidated substrate size, and consolidated substrate vertical relief explained the greatest proportions of variation individually (19, 15, 4, and 4 %, respectively) (Table 2). These 4 variables were featured in the top 2 models selected by the BEST analysis. The remaining variables were not explored further. PERMDISP indicated significant differences in fish assemblage dispersion among distance to shelf edge ($p = 0.001$) and depth zones ($p = 0.001$) (Table 3).

3.2. Reef fish assemblage structure

The post hoc pairwise PERMANOVAs showed significant effects on community structure (Table 4) across factor levels (gradients) and were further examined in the SIMPER analyses. The Bonferroni test (α/n) also indicated statistical significance ($p < 0.001$) across all factor levels except between shelfzone groups (80–99) and (100–119) km. However, the permutation p-values provide an exact test of each individual null hypothesis of interest, while ad hoc experiment-wise corrections such as Bonferroni are known to be conservative and imprecise (e.g. Day & Quinn 1989, Anderson et al. 2008). The PERMDISP pairwise tests indicated statistically significant differences between all distance to shelf edge factor levels except between the (40–59) and (60–79) km shelf zones, and statistically significant differences between all depth zones ($p < 0.05$). Because PERMANOVA and PERMDISP both exhibited statistically significant differences for distance to shelf edge, depth zone, and across most factor levels (gradients), the influences of distance to shelf edge and depth on fish assemblages was visualized using PCO. The PCO biplots in Fig. 4 show the differential effects of distance to shelf edge and depth

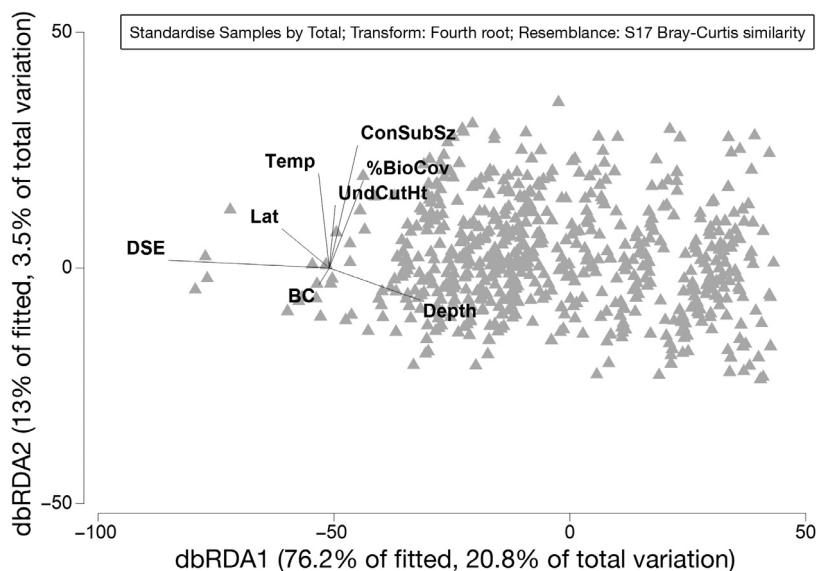


Fig. 3. Distance-based redundancy analysis (dbRDA) ordination of trap catches and video observation samples (Bray-Curtis resemblance matrix calculated from fourth-root transformed abundance data) overlaid with normalized environmental variables. Ordination is based on BEST-fit distance-based linear modeling (DistLM) using a Bayesian information criterion (BIC) model with vectors representing the variables from the model(s). Length and direction of vectors indicate the strength and direction of the relationship. Triangles represent samples ($N = 1510$). DSE: distance to shelf edge; Lat: latitude; Temp: temperature; ConSubSz: consolidated substrate size; %BioCov: percent biotic cover; UndCutHt: undercut height; BC: biotic class

effects on the fish assemblage structures. The SIMPER analysis revealed assemblage patterns for distance to shelf edge, depth, and consolidated substrate vertical relief and size. The greatest number

of discriminator species occurred at an approximate distance of 0–39 km (decreasing shoreward), within depth zones 41–60 m, and in areas of coarse to continuous substrate with moderate relief. Conversely,

the lowest number of discriminator species occurred furthest from the shelf edge in the shallowest depth zones (15–20 m), and in areas that did not exhibit any consolidated substrate (typically unconsolidated sandy substrate, Tables S3–S6 in the Supplement). The SIMPER results examining effects of distance to shelf edge (Fig. 4a, Table S3) revealed that the greatest assemblage differences occurred between (0–19) and (100–119) km gradients (average dissimilarity 95%), where red porgy dominated along the shelf edge with an individual contribution to within-group similarity (contributed percentage) of 51%. Black sea bass and red porgy were both dominant ~20–30 km from the shelf edge, after which a shift in species dominance to black sea bass occurred with an increasing individual contribution shoreward (84%). Interestingly, red porgy did not appear as a discriminator species at approximately 60 km and shoreward, whereas black sea bass was not included as a discriminator species approximately 19 km seaward. *Almaco Seriola rivoliana*, lionfish (*Pterois volitans* and *P. miles*), scamp *Mycteroperca phenax*, and hogfish *Lachnolaimus maximus* appear among the discriminator taxa at approximately 0–19 km from the shelf edge only. Additionally, the number of larger-bodied predatory species (i.e. jacks, groupers, blueline tilefish *Caulolatilus microps*), and lionfish that typify fish assemblages decreased shoreward (Fig. 4a, Table S3).

The SIMPER results examining the effect of depth zone on fish assemblage structure (and Fig. 4b, Table S4) revealed the greatest difference in assemblages between the inner shelf and shelf break depth zones (97% average dissimilarity). Red porgy (71% individual contribution) domi-

Table 2. Summary of distance-based linear modeling (DistLM) marginal test using the BEST selection procedure and the Bayesian information criterion (BIC) to examine the proportion of variation (Prop.) in fish assemblage structure explained by each factor individually (how much each variable explains in isolation, ignoring all other variables). Statistical significance is based on 999 permutations

Environmental factors	SS(trace)	Pseudo- <i>F</i>	Prop.	p
Distance to shelf edge	8.63×10^5	342.4	0.185	0.001
Depth	6.84×10^5	259.02	0.147	0.001
Consolidated substrate vertical relief	1.85×10^5	62.416	0.040	0.001
Consolidated substrate size	1.78×10^5	59.703	0.038	0.001
Surface geologic class	1.36×10^5	45.387	0.029	0.001
Latitude	1.35×10^5	44.955	0.029	0.001
% Biotic cover	1.32×10^5	44.099	0.028	0.001
Bottom temperature	1.32×10^5	43.97	0.028	0.001
Seafloor morphology	1.32×10^5	43.966	0.028	0.001
Undercut height	65231	21.394	0.014	0.001
Day of the year	48845	15.963	0.010	0.001
Biota height	47553	15.536	0.010	0.001
Biotic class	20956	6.8075	0.004	0.001
Residual df: 1508				

Table 3. Summaries of permutational multivariate analysis of variance (PERMANOVA) and PERMDISP results based on 999 permutations for tests to determine statistical significances of each of the 8 factors in the model (PERMANOVA), and each of the 4 factors explaining the highest proportion of variation (PERMDISP) selected by the distance-based linear modeling (DistLM)

Source of variation	df	SS	MS	Pseudo- <i>F</i>	p(perm)
PERMANOVA					
Distance to shelf edge	5	1.96×10^5	39266	18.638	0.001
Latitude	3	1.16×10^5	38559	18.302	0.001
Depth	3	72953	24318	11.542	0.001
Consolidated substrate size	2	38383	19191	9.1093	0.001
Bottom temperature	3	50137	16712	7.9326	0.001
Undercut height	3	26393	8797.6	4.1758	0.001
Biotic class	4	28990	7247.6	3.4401	0.001
% Biotic cover	3	16708	5569.5	2.6436	0.001
Residual	1483	3.12×10^6	2106.8		
Total	1509	4.66×10^6			
PERMDISP					
	df1, df2			<i>F</i>	p(perm)
Distance to shelf edge	5, 1504			119.54	0.001
Depth	3, 1510			88.183	0.001
Consolidated substrate vertical relief	3, 1506			0.38478	0.821
Consolidated substrate size	2, 1507			0.5222	0.643

Table 4. Summary of pairwise permutational multivariate analysis of variance (PERMANOVA) results based on 999 permutations for pairwise statistical differences between each factor level of each of the 4 factors that explain the greatest proportion of variation determined by the marginal tests. Groups = factor levels

Environmental factors	Factor levels	<i>t</i>	p(perm)
Distance to shelf edge (km)	(0–19), (20–39)	8.218	0.001
	(0–19), (40–59)	15.042	0.001
	(0–19), (60–79)	14.837	0.001
	(0–19), (80–99)	6.321	0.001
	(0–19), (100–119)	5.481	0.001
	(20–39), (40–59)	6.241	0.001
	(20–39), (60–79)	7.094	0.001
	(20–39), (80–99)	4.280	0.001
	(20–39), (100–119)	4.324	0.001
	(40–59), (60–79)	2.173	0.001
	(40–59), (80–99)	2.790	0.001
	(40–59), (100–119)	3.568	0.001
	(60–79), (80–99)	2.122	0.001
	(60–79), (100–119)	2.899	0.001
	(80–99), (100–119)	2.281	0.007
Depth zone	Inner shelf, mid-shelf	5.901	0.001
	Inner shelf, outer shelf	9.841	0.001
	Inner shelf, shelf break	10.579	0.001
	Mid-shelf, outer shelf	14.272	0.001
	Mid-shelf, shelf break	10.831	0.001
	Outer shelf, shelf break	3.811	0.001
Consolidated substrate vertical relief	None, low	5.660	0.001
	None, moderate	5.851	0.001
	None, high	5.896	0.001
	Low, moderate	2.877	0.001
	Low, high	3.947	0.001
	Moderate, high	1.759	0.002
Consolidated substrate size	None, small-coarse	4.150	0.001
	None, coarse-continuous	7.704	0.001
	Small-coarse, coarse-continuous	3.896	0.001

nated the assemblage along the shelf break, and black sea bass dominated the assemblage at depths along the inner shelf (85 % individual contribution). The number of large-bodied species (e.g. jacks, groupers) that typify fish assemblages occurred at outer shelf and shelf break depths. Here, lionfish had the fourth largest contribution (6 %) within the outer shelf depth zones (Fig. 4b, Table S4).

The SIMPER results examining the effect of consolidated substrate vertical relief on fish assemblage structure (Table S5) revealed that the greatest number of discriminator species ($n = 12$) typifying community structure, which accounted for 90 % of the cumulative percentage, occurred in areas exhibiting moderate vertical relief (0.3–1 m). Areas with lower and higher relief had similar numbers of discriminator species ($n = 11$ and 10, respectively), although the pairwise PERMANOVA showed significant differ-

ences between each gradient (Table S5). The smallest number of species typifying assemblages occurred in areas with no visible consolidated substrate (Table S5), where 7 species characterized the assemblage. The greatest difference in assemblages occurred between areas with no consolidated substrate and areas of high substrate relief with 85 % average dissimilarity. Tomtate *Haemulon aurolineatum*, red porgy, and lionfish dominated areas of high relief and accounted for 55 % of the cumulative percentage, whereas black sea bass dominated the assemblage in areas with no consolidated substrate and accounted for an individual contribution of 53 %. Although large-bodied species (e.g. jacks, groupers) occurred in all areas that exhibited consolidated substrate relief, these species were more dominant in areas of moderate and high relief. Lionfish assemblage contribution increased with relief from 0.05 % contribution in areas with no visible consolidated substrate relief to 12 % in areas that exhibit high relief (Table S5).

The SIMPER results examining the effect of consolidated substrate size on fish assemblage structure (Table S6) revealed that the greatest number of discriminator species ($n = 11$) typifying community structure contributed 90 % of the cumulative percentage and occurred in areas exhibiting coarse to continuous substrate size (≥ 50 % of consolidated sediment is > 1 m in diameter). The smaller number, 7, of discriminator species typifying assemblages occurred in areas with no visible consolidated substrate (Table S6) and characterized the assemblage similar to areas with no vertical relief. The greatest difference in assemblages (79 % average dissimilarity) occurred between areas with no consolidated substrate and areas of coarse to continuous substrate. Red porgy, tomtate, and black sea bass dominated areas of coarse to continuous substrate, contributing 57 % to the cumulative percentage, whereas black sea bass, with an individual 53 % of the cumulative percentage, dominated the assemblage in areas with no visible consolidated substrate. Large-bodied species (e.g. jacks, groupers) were more dominant in areas that exhibited coarse to continuous consolidated substrate, whereas lionfish con-

tributed the assemblage along the shelf break, and black sea bass dominated the assemblage at depths along the inner shelf (85 % individual contribution). The number of large-bodied species (e.g. jacks, groupers) that typify fish assemblages occurred at outer shelf and shelf break depths. Here, lionfish had the fourth largest contribution (6 %) within the outer shelf depth zones (Fig. 4b, Table S4).

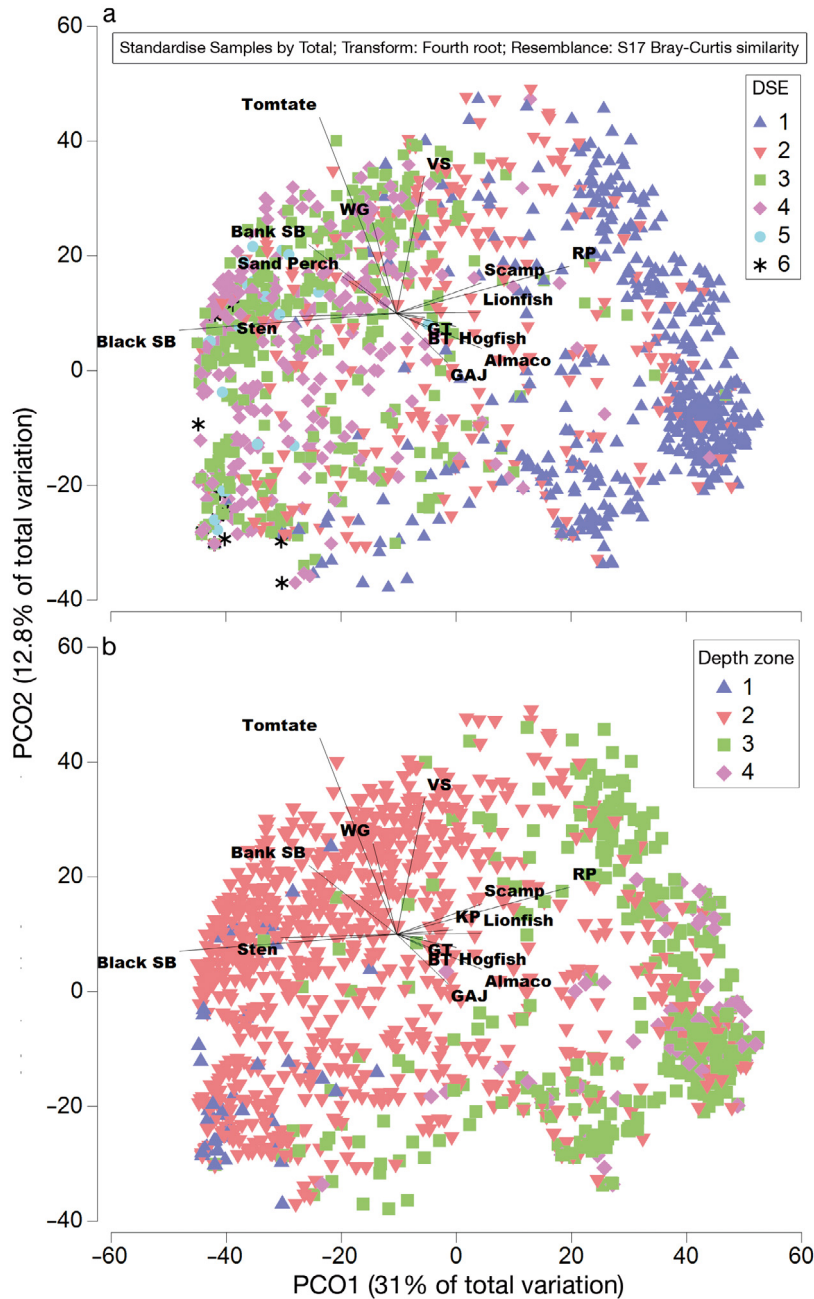


Fig. 4. Principal coordinates analyses (PCO) of site centroids for the trap catch and video observation samples (Bray-Curtis resemblance matrix calculated from fourth-root transformed abundance data) overlaid with discriminator species selected by the SIMPER analyses for (a) distance to shelf edge (DSE) and (b) depth zone. DSE (km): (1) 0–19, (2) 20–39, (3) 40–59, (4) 60–79, (5) 80–99, (6) 100–119, and depth zones (m): (1) Inner shelf (15–20), (2) mid-shelf (21–40), (3) outer shelf (41–60), (4) shelf break (61–110). Bank SB: bank sea bass; Black SB: black sea bass; BT: blueline tilefish; GT: gray triggerfish; GAJ: greater amberjack; KP: knobbed porgy; RP: red porgy; Sten: *Stenotomus* spp.; VS: vermilion snapper; WG: white grunt. Scientific names of species are given in Table 1

tribution (eighth highest, 5%) increased in areas of coarse to continuous substrate (Table S6).

3.3. Habitat specificity

Although observed species overlapped across levels for each of these factors (gradients), as depicted by the SIMPER analyses, there were significant differences (e.g. habitat partitioning, species turnover) in overall assemblage structure between the levels of each factor tested (Table 4), and the individual percent contribution differed (Tables S3–S6). Several species (e.g. black sea bass, red porgy, tomtate, vermilion snapper, gray triggerfish *Balistes caprisicus*) appear to be habitat generalists (species with relatively broad across-shelf distributions; Fitzpatrick et al. 2012) and occurred across most environmental gradients tested. Black sea bass and red porgy were the most dominant species and therefore appear to exhibit more habitat generality than tomtate, vermilion snapper, and gray triggerfish. Additionally, black sea bass and red porgy exhibited a shift in dominance across the environmental gradients tested. Black sea bass exhibited greater dominance moving shoreward at shallower depths with less consolidated substrate present, whereas red porgy dominance was observed moving seaward with increasing depth zones and increasing consolidated substrate vertical relief and size. This study also highlighted several species that appear to exhibit greater habitat specificity (more restricted to limited environmental gradients; Fitzpatrick et al. 2012). For example, as discriminator species, almaco, lionfish, scamp, and hogfish mainly appeared in areas close to the shelf edge, and scamp and almaco were more prevalent in outer shelf and shelf break depth zones. Lionfish appeared only in outer shelf depth zones, and blueline tilefish only occurred in shelf break depth zones. Furthermore, scamp, lionfish, almaco, greater amberjack, white grunt *Haemulon plumieri*, vermilion snapper, and hogfish appear to be more strongly associated with hard-bottom habitats of varying relief,

whereas scamp and lionfish appear to have a stronger preference for areas with coarse to continuous substrate.

4. DISCUSSION

The primary objectives of this study were to assess how environmental variables influence fish assemblage structure, identify species that typify the assemblage structure, and identify species within the assemblages that may exhibit relative vulnerabilities to stressors off NC and SC. Fish species data were compiled from chevron trap catches and priority species enumerated in underwater video (see Bacheler et al. 2014). A total of 1510 random trap-video camera deployments at depths of 15–110 m included data for a total of 53 363 specimens representing 42 species. An 8-variable (distance to shelf edge, depth, consolidated substrate size, latitude, percent biotic cover, temperature, undercut height, biotic class) model best predicted assemblages, while 4 variables explained the greatest proportion of variation (distance to shelf edge [19%], depth [15%], consolidated substrate vertical relief [4%], and size [4%]). The largest number of discriminator species occurred in mid- to outer shelf areas with greater substrate complexity (i.e. increasing substrate size and relief). Assemblages dominated by black sea bass at shallower depths (~15–40 m) with little substrate complexity transitioned towards assemblages dominated by red porgy, a higher prevalence of larger-bodied predators, and invasive lionfish at depths (~40–110 m) with increasing substrate size and relief.

4.1. Environmental influences on reef fish assemblage structure

Effects of some environmental factors on fish assemblage structure vary both spatially and temporally, and effects are often the result of multiple interacting factors. Here, the effects of distance to shelf edge, depth, temperature, percent biotic cover, and consolidated substrate size appear to vary with latitude, while temperature, biotic class, and undercut height vary with depth. For example, because of differences in water mixing and other factors, shallow depths experience lower temperatures in winter than areas further offshore (Willems et al. 2007). Furthermore, effects of environmental variables can be classified into 3 broad types: resource (e.g. matter and energy consumed), direct (e.g. physiological rele-

vance such as temperature and pH), and indirect (e.g. depth, geology, habitat type, etc.) (Austin et al. 1984). Most variables in this study were indirect, which typically replace combinations of different resource and direct variables (Guisan et al. 1999).

When examined independently, distance to shelf edge exhibited the greatest influence on fish assemblage structure, followed by depth, consolidated substrate vertical relief, and consolidated substrate size (Table 2). Distance to shelf edge and depth explain the greatest proportion of variation in this study, and as indirect factors, most likely serve as proxies for a multitude of more specific environmental mechanisms such as wave energy, light penetration, proximity to Gulf Stream, and influences from intrusions and/or fronts such as productivity, temperature, and salinity (Tolimieri & Levin 2006), or anthropogenic factors such as accessibility to fishing grounds. Accordingly, there might be some areas close to shore with what appear to be suitable or preferred habitat, but which are low in richness or abundance. As changes in climate, coastal development, and fishing pressure continue to impact fish species distributions, it is becoming increasingly important to understand mechanisms that underly cross-shelf and depth distributions (MacDonald et al. 2016). To disentangle environmental and anthropogenic effects, it is essential to obtain information regarding specific environmental factors associated with shelf edge areas (e.g. currents, upwellings), as well detailed information regarding fishing effort.

Substrate vertical relief and size also were key factors explaining the structure of the fish assemblages across the shelf. The role of geologic factors and complexity in structuring reef fish assemblages has been well-documented globally (Kendall et al. 2009, Coker et al. 2012). However, hard-bottom habitats are patchy in the SEUSA, and while environmental data in this region such as depth, salinity, etc. are consistently collected, there remains a paucity of data regarding extent and character of hard-bottom habitats. Given the importance of geologic factors as structuring drivers for fish assemblages, bathymetric surveys should be expanded to obtain more accurate, detailed geologic measurements and to determine habitat availability and connectivity in this region.

4.2. Reef fish assemblage structure

We found the greater number of discriminator species within mid- to outer shelf depth zones (21–60 m) at 0–39 km from the shelf edge. This supports previ-

ous studies in the region that also determined depth plays a strong role in shaping fish assemblages (Geraldi et al. 2019), and a greater number of species persist at intermediate locations on the continental shelf approximately 24–51 m in depth (Miller & Richards 1980). However, effects of distance to shelf edge and depth zone on assemblages also vary. For instance, areas of shallow depths where the shelf narrows to approximately 30 km off Cape Hatteras, NC, might be more heavily influenced by effects from the Gulf Stream, especially by temperature, than those same depths off Savannah, GA, where the shelf widens to approximately 120 km (Fig. 1). A greater number and diversity of species (including subtropicals) can persist in the intermediate shelf area where the warmest bottom temperatures remain the most stable due to less influence by inshore cooling and offshore cold-water intrusions (Miller & Richards 1980, Bacheler et al. 2019). While temperature is widely known to influence species distributions, the lack of SERFS survey sampling during the months of October through March makes it difficult to determine these effects explicitly. Notwithstanding, the greater number of species found at similar depths in this study might also be the effect of a more stable, warmer environment than what typically occurs nearer to the shore and shelf edge.

A greater number of large-bodied predator species serve as discriminator species in reef fish assemblages at deeper depth zones and areas closest to the shelf edge (furthest from shore; Fig. 4, Tables S3 & S4). This finding is similar to that of Richards et al. (2012), who reported a negative association between large-bodied reef fishes and human population density with additional influences on distribution associated with depth, temperature, and distance to deep water. Geraldi et al. (2019) found that bigger and longer-lived fishes were positively correlated with winter temperature and depth. However, the significance of depth diminished over their long-term analysis, indicating that climate- and temperature-related variables may play a stronger role in decadal-scale changes in fish assemblages (Geraldi et al. 2019). The prevalence of bigger, long-lived fishes at greater depths may be indicative of a natural ontogenetic deepening in which the average size of many marine fish species increases with depth (Heincke 1913, Macpherson & Duarte 1991), or these species might prefer areas deeper and closer to the shelf edge due to environmental preferences (e.g. currents, nutrients, prey abundances, thermoclines, and opportunities for reproduction; Costa et al. 2014). It might also be a result of increased fishing pressure

closer to shore, as fisheries typically target large-bodied predacious individuals such as snappers and groupers, that is consistent with the 'ontogenetic-like deepening' suggested for the resident cod stock on the eastern Scotian Shelf (Frank et al. 2018).

This study also indicates that small-scale habitat characteristics play a role in shaping reef fish assemblages. Although substrate size and vertical relief explained limited variance compared to depth and distance to shelf edge, the role of geologic factors and structural complexity have proven to be strong drivers of species distributions and indicators of increased richness in previous studies (Kendall et al. 2009, Coker et al. 2012). Increased structure and complexity provide a greater amount of surface area for bottom-up trophic processes and refuge from predators (Wilson et al. 2007). We found statistically significant differences between gradients within consolidated substrate sizes and within consolidated substrate vertical relief; however, low to moderate vertical reliefs had a greater number of discriminator species defining assemblages than areas with high relief, but areas with highest relief had a greater number of large-bodied predators. This might be due to the presence of suitable habitat that provides greater refuge and food availability than traps (Robichaud et al. 2000, Dupuch et al. 2011) or a decreased detectability of smaller species in video due to disrupted views by large reef or rock formations (Bacheler et al. 2014).

4.3. Relative vulnerability

Differences in assemblage structure and number of discriminator species across environmental gradients (e.g. depth zones) were inherently driven by differences in abundances and, therefore, might reflect vulnerability to disturbances. Establishing a baseline of fish assemblage structure characteristics and environmental drivers of variability, and then highlighting those SEUSA species that vary in habitat specificity (especially in regard to habitats that exhibit little natural variation), can assist in assessing vulnerability to large-scale disturbance such as fishing pressure, major storms, climate change, and invasive species. If habitat specialists are not as resilient to disturbance as generalists, disturbance can have severe ramifications for the comprehensive management of fish stocks (Vázquez & Simberloff 2002) and could ultimately result in overall changes in community structure. For example, a moratorium on an overexploited species can lead to increased fishing

pressure on co-occurring species. Overfishing of one species could leave a particular niche vacant and subsequently filled by another species. This study has indicated scamp overlap with almaco and red porgy in outer shelf areas where exposed hard bottom has greater surface area and relief. In this instance, a seasonal closure or moratorium on scamp can lead to increased fishing pressure on almaco or red porgy. Although almaco and red porgy do not appear to be as specialized in habitat preferences as scamp, and given that almaco might be less resilient to fishing pressure than the more generalist red porgy, separate additional management measures might need to be considered for these species to prevent subsequent overexploitation.

This research also provides further evidence and supports similar findings by Bacheler et al. (2017), that lionfish are well-established in the study region. Lionfish, which are invasive, also appear to be a discriminator taxon for assemblages in areas with coarse-continuous substrate of moderate–high vertical relief (>0.3) in the outer shelf depth zones (Tables S5 & S6). Overexploitation of co-occurring species such as scamp, and increasing temperatures associated with climate change, might promote the continued expansion of the lionfish range by extending distributions shoreward and northward and occupy niches left vacant by exploited or other range-shifting species.

4.4. Implications for management

‘Shifting baseline syndrome’ occurs when fish assemblage characterization is left unquantified, and each generation of fisheries scientists accepts species composition and stock size as it occurred at the beginning of their careers (Pauly 1995). Without a more recent baseline from which to assess change, long-term declines in managed resources might remain undetected (Kendall et al. 2004). Therefore, it is of importance to identify how the environment structures fish assemblages and to isolate the effects of stressors that contribute to shifts in fish assemblage structure to manage fisheries more effectively (Tolimieri & Levin 2006, Nogueira et al. 2013).

Species differences in habitat preference can reflect the use of physiologically optimal environments, or habitat preference can also be attributed to predator and prey interactions or interactions among competitors (Helfman et al. 2009). Both species interactions with the environment and inter- and intraspecific interactions are important for ecosystem function and stability, and a disruption to either could

have reverberating effects on entire communities and the ecosystem (Díaz et al. 2013, Valiente-Banuet et al. 2015). However, the investigation of inter- and intraspecific interactions within assemblages is not within the scope of this paper, as this study focuses only on those species retained by chevron traps and priority species enumerated in concurrent video (see Bacheler et al. 2014) following SERFS protocol as part of the annual SERFS trap-video survey off NC and SC. Nonetheless, this study does provide insight regarding co-occurring species across environmental gradients. Additionally, current efforts are underway to record the presence of all fish species observed in video across the entire survey region. The expansive spatial coverage of the SERFS long-term survey coupled with the ability to obtain a large amount of unbiased fishery-independent, complementary trap and video data, provides the best opportunity to develop a region-wide, baseline assessment of assemblages that incorporates non-targeted and non-priority fish species. These data, in turn, can provide additional insight into the behavioral inter- and intraspecific mechanisms (e.g. predator–prey relationships, diets), that shape structure within assemblages. Providing this information to fisheries managers enhances conservation and management efforts, including efforts to implement ecosystem-based fishery management, aids in the development of marine protected areas, and helps monitor changes in population abundance, the presence/absence of key species, and modifications of local assemblages, all of which are measures of ecological health that underpin comprehensive stock assessments and management plans that focus on the maintenance of biological integrity.

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