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ARTICLE

Benthic Habitats, as Derived from Classification of Side-Scan-Sonar Mapping Data, Are Important Determinants of Reef-Fish Assemblage Structure in the Eastern Gulf of Mexico

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Abstract
Increasingly restrictive management regulations have greatly reduced the utility of fishery-dependent data for characterizing temporal changes in the abundance of managed fish populations, so fishery-independent data are becoming more important for the accurate assessment of stock status. A notable downside to fishery-independent data is the high cost of conducting surveys, and efforts to maximize survey efficiency are critical given ongoing reductions in agency funding. We conducted a pilot study to explore the utility of classifying side-scan-sonar mapping data to provide a practical a priori characterization of reef habitat in the eastern Gulf of Mexico. An analysis of side-scan-sonar mapping data identified five distinct reef habitat types (low-relief hard bottom, mixed hard bottom, fragmented hard bottom, ledges, and potholes) that were subsequently sampled with stereo baited remote underwater video (S-BRUV) arrays and trap-mounted GoPro cameras. The permutational analysis of variance indicated that the assemblage structure of reef fish differed significantly ($P < 0.01$) among all of the pairs of habitats except ledges and fragmented hard bottom; assemblage structure did not differ among cameras ($P = 0.45$). Overall species richness and diversity were significantly higher in the habitats with greater vertical relief, as were the abundances of several economically and ecologically important reef fishes, although many taxa were observed across all of the habitat types. Benthic habitats that are identified from side-scan-sonar mapping data are important determinants of reef-fish assemblage structure and may prove to be useful as a stratification scheme for reef-fish surveys, although additional research is necessary to explore the transferability of these results to the rest of the eastern Gulf of Mexico.

Fishery-independent data are becoming increasingly important in the southeastern United States because restrictive management regulations, including such measures as individual fishing quotas and complete fishery closures, have altered fishing behavior and eroded the utility of fishery-dependent data for assessing population trends (Bryan and McCarthy 2015; Smith et al. 2015; SEDAR 2018). Accordingly, the use of fishery-independent survey data to characterize reef-fish populations has increased dramatically, especially that of data that are obtained through visual sampling. Visual surveys are less selective than those that use traditional capture gear such as traps (Bacheler et al. 2013), trawls (Wells et al. 2008), and hooks (Willis et al. 2000; Parker et al. 2016), and they are typically less strongly influenced by depth, bottom relief, or fish behavior (Cappo et al. 2003). Visual-based sampling methods used to target reef fishes in the southeastern United States include stereo baited remote underwater video

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(S-BRUV) arrays (Saul et al. 2013; Campbell et al. 2015; Thompson et al. 2017; Keenan et al. 2018), towed cameras (Lembke et al. 2017), diver visual surveys (Smith et al. 2011; Harford et al. 2016), and trap-mounted video cameras (Bacheler et al. 2013, 2014, 2016).

Due to the high cost of conducting fishery-independent surveys and the broad geographic range of reef fishes in the southeastern United States, it is critical to improve the efficiency of surveys so as to maximize statistical power while minimizing sampling effort. In the Florida Keys, the sampling design of an ongoing diver visual survey effectively stratifies sampling effort based on spatial and habitat criteria (Smith et al. 2011). By defining strata that are important in structuring reef-fish assemblages and allocating higher sampling intensity in strata with higher diversity of managed reef fishes, Smith et al. (2011) dramatically improved survey effectiveness, thereby improving the precision of the estimates of abundance for managed and nonmanaged reef fishes alike. This method relied on the availability of accurate digital benthic habitat maps for shallow reef areas (in waters < 33 m deep) throughout the Florida Keys reef tract (FMRI 1998; Franklin et al. 2003), which included data on reef type and reef rugosity.

The use of habitat-based stratification and effort allocation in other reef-fish surveys would likely result in efficiency improvements that are similar to those that were documented for the Florida Keys diver survey. But unlike for the Florida Keys, detailed information on the distribution and quantity of available reef habitats or on habitat-specific variability in reef-fish assemblage structure is generally lacking for most of the Gulf of Mexico and U.S. South Atlantic. Consequently, the implementation of habitat-based stratification and effort allocation within existing broad-scale surveys are currently not feasible. The evolution of the diver visual survey for the Florida Keys does, however, provide a conceptual framework for improving the survey design for the Gulf of Mexico. A first step toward a habitat-based survey design is to identify habitat metrics that are important correlates of reef-fish assemblage structure that also can be characterized at spatial scales that can be identified easily and integrated into the design of reef-fish surveys.

Accordingly, we conducted a pilot study in a small area of the eastern Gulf of Mexico to (1) identify and classify reef habitat types from side-scan-sonar mapping data and (2) conduct a habitat-based, stratified-random survey to evaluate whether reef-fish assemblage structure, as determined from underwater camera surveys, differed with habitat. The results from this study will determine whether habitat types that are derived from the classification of side-scan-sonar mapping data are important determinants of reef-fish assemblage structure and so merit consideration as a habitat stratification scheme more broadly for reef-fish surveys throughout the eastern Gulf of Mexico.

METHODS

Study area.— This study was conducted in the eastern Gulf of Mexico within the Elbow Reef area (Moe 1963), covering an area of 166 km^2 approximately 145 km northwest of Tampa Bay, Florida (Figure 1). Initially described by Moe (1963), the Elbow is dominated by a narrow ridge of limestone rock that rises 7–14 m above the surrounding sand-and-shell bottom. Surrounding the primary ridge are areas of low-relief reef habitat as well as isolated areas of exposed rock (1–3 m). These habitats are rife with crevices, ledges, and caverns that are covered extensively with corals, sponges, and colonial tunicates. Given the diversity of hard-bottom habitat within a generally compact area, the Elbow was an ideal location for which to develop a habitat-classification system and test a habitat-based, stratified-random sampling design for assessing reef-fish populations.

Collection and processing of acoustic data.— An L-3 Klein 3900 towfish was used to acquire side-scan-sonar

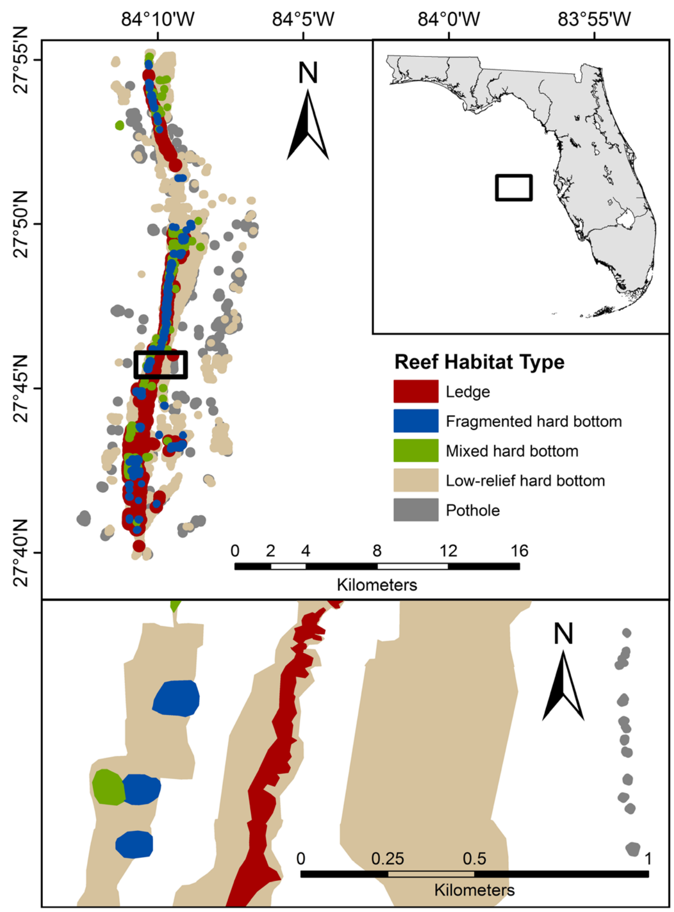

FIGURE 1. Distribution of reef habitats within the Elbow as determined via side-scan sonar. The location of the Elbow Reef area is delineated in the upper right inset. The lower panel depicts the fine-scale details of the spatial distribution and orientation of habitats in a portion of the study area. Note that the boundaries of individual reef habitat features have been exaggerated to facilitate visualization.

mapping data covering an area of approximately 166 km^2 that was bounded by 27°55′N and 27°40′N and 84°6′W and 84°12′W; mapping was conducted in 153 latitudinal passes (i.e., moving from east to west, then west to east). All of the acoustic data were collected during February 20–25, 2012 aboard the FV *Florida Fisherman.* The data were collected at 455 kHz at a range of 125 m per channel, providing a swath width of 250 m with 10% overlap between successive passes. Navigation data, including speed, heading, and position, were collected by using a WAAS-enabled Garmin GPSMap76. The towfish was towed at approximately 2.6 m/s at a range of 12–24 m above the seafloor. Information that is required to compute the layback of the towfish (i.e., navigation offset, length of cable out, and water depth) was recorded during data acquisition. The raw imagery was viewed by using SonarPro 11.3 and archived as 5-min XTF files.

The acoustic data were processed by using Hypack software. To streamline the processing, we divided the raw data files into 52 sections consisting of three east–west passes each. The towfish navigation data were used to determine heading and position, and a smoothing filter was applied to minimize pitch/roll/yaw anomalies. The towfish bottom-tracking software successfully identified the bottom throughout the survey, so minimal processing of bottom tracking was necessary. The time varied gain was normalized prior to exporting the mosaic as a geotiff at a 0.25-m resolution.

Side-scan sonar produces imagery that represents acoustic returns of varying strength and not quantitative measures of depth or bottom hardness, so the habitats were manually classified and delineated by using the ArcGIS 9.3 habitat digitizer extension (https://coastalscience.noaa.gov/project/habitat-digitizer-extension/). The geotiffs that were created during the mosaicking process were imported into the GIS environment, and polygons were then manually drawn around the areas of hard bottom and individual reef features that were classified. The habitat-classification scheme that was used was adapted from the geoform component of the Coastal and Marine Ecological Classification Standard (FGDC 2012). Specifically, we developed definitions for Level 2 geoform types that represented generally small-scale features (that were <1 km^2 in area) that upon initial examination appeared to represent unique habitats that were distinguishable in the side-scan-sonar mapping data (Table 1; Figure 2). Because several people were involved in the habitat classification, we implemented a rigorous quality assurance process whereby the polygons that were drawn and classified by each reader were reviewed by a second reader. All of the discrepancies were then reviewed to formulate a consensus. Following habitat classification, all of the polygons were merged by habitat type and divided into 0.3-nm high ×0.1-nm wide primary sampling units ($N = 1{,}618$) for the subsequent reef-fish surveys. The height (0.3 nm) of each sampling unit was chosen to allow for three overlapping passes of the side-scan sonar to aid in the correction of positional inaccuracies, while the North–South orientation of the sampling units was chosen to align with reef features that are presumably associated with relic shorelines.

Collection and processing of video data.— During the fall of 2012, sampling was conducted to assess whether the reef-fish assemblages differed among the five habitat types that are common in the Elbow: ledges, fragmented hard bottom, mixed hard bottom, low-relief hard bottom, and potholes (Figure 1). Sampling was conducted by using three gear types: S-BRUV arrays, chevron traps, and Antillean *Z* traps. Each S-BRUV array consisted of two independent stereo-video systems that were mounted orthogonally. Each stereo-video system consisted of one video camera (Arecont 2015DN camera equipped with a Computar H2Z0414C-MP lens; 90.4° horizontal field of view; 1,600 × 1,200 image resolution) and a pair of stereo still-image cameras (Videre STH-MDCS3-9CM; 103.6° horizontal field of view; 1,280 × 960 image resolution) set to record one image per second. GoPro HD Hero 1 cameras (94.4° horizontal field of view; 1,280 × 960 image resolution) were mounted 90° from each stereo-video system. Each S-BRUV was freshly baited with four cut Atlantic mackerel halves (*Scomber* spp.) that were secured inside of a bait box and deployed for at least 30 min. Both the chevron and Antillean *Z* traps were equipped with GoPro HD Hero 1 cameras that were positioned inside of the trap to the right of the throat facing outward and were baited with cut Atlantic mackerel before being deployed for 90–120 min. All of the underwater camera systems were unlighted. Each gear type was deployed on 18 randomly selected sampling sites for each of the five habitat strata.

Videos from the chevron traps, Antillean *Z* traps, and S-BRUV arrays were read to quantify MaxN, the maximum number of individuals of each species that was observed on a single screen shot. For both S-BRUV and GoPro cameras, a total of 20 min of video was read beginning approximately 10 min after each camera reached the bottom to allow for the dissipation of any resultant sediment plume. The stations where the videos were extremely turbid or stations with less than 10 min of usable video (because either the camera did not record or the recording ended prematurely) were not processed. All of the fishes were identified to the lowest possible taxon, but due to difficulties in counting individuals in extremely large schools species-specific MaxN values were capped at 300 individuals.

Analytical methods.— Variations in reef-fish assemblages were explored using the Bray–Curtis similarity matrix, which was calculated by using fourth-root-transformed abundance (MaxN) data to reduce the influence of

TABLE 1. Definitions of habitats that were classified within the Elbow Reef area as derived from the geoform component of the Coastal and Marine Ecological Classification Standard (FGDC 2012).

Habitat type	Definition
Ledge	A linear change in elevation of the seafloor that is associated with a rocky outcrop or underwater ridge of rocks. Ledges are defined spatially as the area within 5 m of the identified ledge. Within this area, boulders, rocks, and other types of hard bottom may be associated with the ledge system. The acoustic image will generally show a linear, jagged edge with evidence of some relief >0.2 m. Relief will exhibit a hard return (coloration much brighter than the surrounding area) when looking at the face of a ledge and an acoustic shadow (black coloration due to a lack of a detectable acoustic return) when the ledge is facing away from the side-scan beam.
Low-relief hard bottom	Flat or nearly flat areas (<0.1 m of relief) of hard bottom that is generally colonized by benthic biota. The acoustic image will appear rough, showing evidence of hard bottom and possibly some epifaunal growth but lacking the presence of acoustic shadows or hard returns that are associated with fragmented hard bottom.
Mixed hard bottom	Mainly flat areas of hard bottom containing some features with relief >0.1 m that represents a transition between low-relief hard bottom and fragmented hard bottom. The acoustic image will generally be rough, showing evidence of hard bottom with evidence of small, scattered acoustic shadows or hard returns.
Fragmented hard bottom	Areas dominated by exposed rock or coral that may be separated by narrow channels of finer sediment that has been eroded by currents, leaving the rock elevated above the seafloor with relief of >0.1 m. The acoustic image will appear to be bumpy, showing evidence of patchy hard bottom with large acoustic shadows or hard returns. The features present in this habitat type will show some connectivity, whereas boulder fields will contain large, distinctly separate pieces of rock.
Pothole	Small (0.5–10 m in diameter) indentations or depressions that are lower than the surrounding surface, usually occurring in unconsolidated sediments. The acoustic image will show an elliptical or circular feature with an acoustic shadow on one side and a hard return on the opposite side. The excavated area in the center of a pothole may contain exposed rock as evidenced by a hard return.

highly abundant taxa. To visualize the patterns of assemblage structure among gear types and habitats, an ordination was constructed by using nonmetric multidimensional scaling that was calculated on the gear type by habitat centroids. The statistical significance and relative importance of gear type (gear, a fixed factor with three levels: S-BRUV, GoPro-Chevron Trap, and GoPro-Z Trap) and habitat (geoform, a fixed factor with five levels: ledge, fragmented hard bottom, mixed hard bottom, low-relief hard bottom, and pothole) were investigated by using a permutational multivariate analysis of variance (PERMANOVA) on the full set of data at the replicate level, with significance set at $\alpha = 0.05$. The analyses included all of the interaction terms and were conducted by using type III sums of squares. The *P*-values were obtained by using 9,999 permutations under a reduced model. For all of the factors that were found to be significant, post hoc pairwise comparisons were made, also by using PERMANOVA, to compare the assemblage structure between factor levels. For significant factors, similarity percentages analyses (SIMPER) were conducted (fourth-root-transformed data) by pooling over the nonsignificant factors to identify the taxa that contributed to the top 80% in the differences in assemblage structure between factor levels. Further, the average number of taxa, taxonomic richness, abundance, and taxonomic diversity were compared among the levels of factors that were found to be significant by using a one-way ANOVA. All of the analyses were conducted by using PRIMER 7 software with the PERMANOVA+ add-on (Anderson et al. 2008; Clarke et al. 2014; Clarke and Gorley 2015).

RESULTS

We identified five natural reef habitat types that were widely distributed throughout the Elbow study area (Figure 3). In terms of total coverage, low-relief hard bottom ($14.80\ km^2$) covered the most area and potholes covered very little area ($0.03\ km^2$). Spatially, low-relief hard bottom occurred in more of the sampling units than any other habitat did, but potholes and the other three habitats were also widely distributed, occurring in 5–10% of all of the sampling units. Despite the prevalence of reef habitats within the Elbow study area ($16.81\ km^2$ of reef habitat was identified), approximately 90% of the total mapped area consisted of unconsolidated sediment.

Videos from 87 S-BRUV and 176 trap-associated GoPro deployments were viewed for analysis (Table 2).

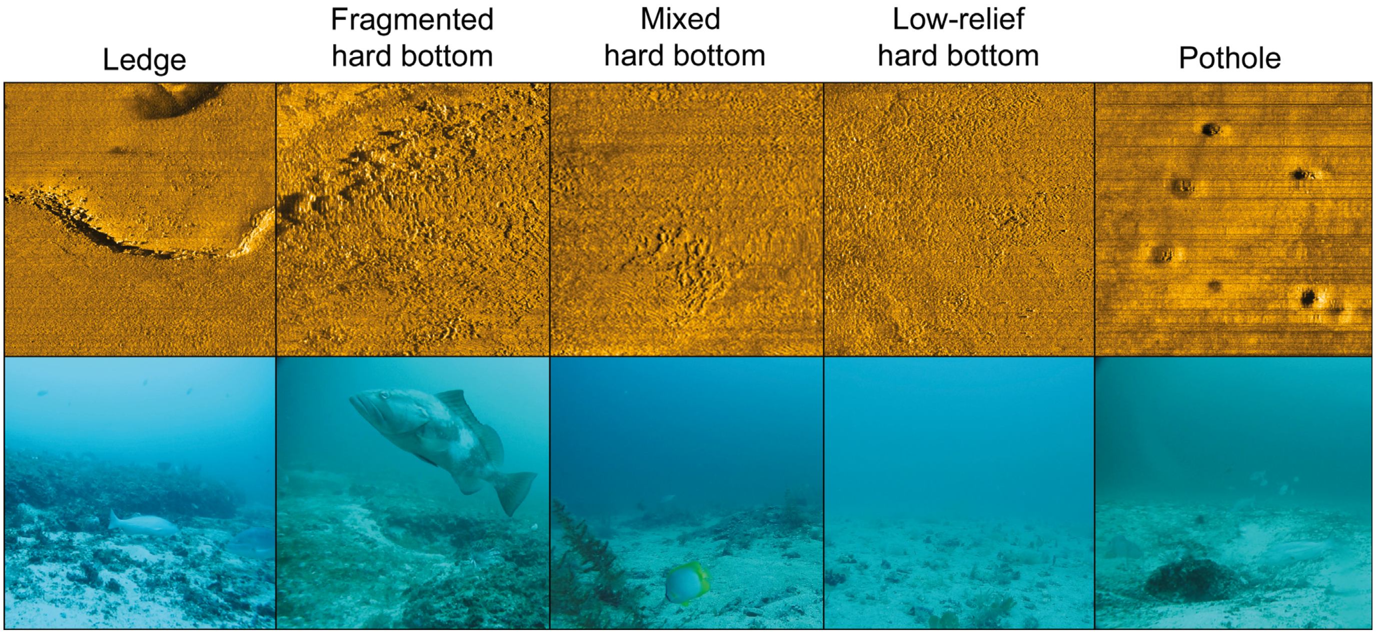

FIGURE 2. Representative imagery from side-scan sonar (upper panels) and underwater cameras (lower panels) from the five common reef habitats that were identified in the Elbow.

Data were unavailable from 3 S-BRUV and 4 trap-associated GoPro deployments due to highly turbid conditions or because less than 10 min of usable video was recorded. A total of 131 taxa were observed on video, 81 of which were identified to species. The total number of observed taxa were highest on fragmented hard bottom ($N_{TAXA} = 83$; $N_{SPP} = 57$), ledges ($N_{TAXA} = 80$; $N_{SPP} = 54$), and mixed hard bottom ($N_{TAXA} = 81$; $N_{SPP} = 48$); markedly less taxa were observed on potholes ($N_{TAXA} = 62$; $N_{SPP} = 36$) and low-relief hard bottom ($N_{TAXA} = 55$; $N_{SPP} = 35$). The results from the multidimensional scaling ordinations indicated that reef-fish assemblages differed by habitat but not gear type (Figure 4). The observed differences were most distinct between potholes and low-relief hard bottom and the remaining three habitats (Figure 5).

Within-group multivariate dispersion differed significantly among gear type × habitat groups ($F_{14,\ 248} = 2.33$; $P = 0.02$), but because the sample sizes were similar among the groups (16–18 observations per group) the data met the criteria for PERMANOVA. The results from the main-test PERMANOVA indicated that the reef-fish assemblages differed significantly among habitats but not among gear types and the gear type × habitat interaction was not significant (Table 3). The results from the PERMANOVA post hoc pairwise comparisons of assemblage structure between habitat types indicated that the assemblages did not differ between ledges and fragmented hard bottom ($t_{99} = 1.11$; $P = 0.24$) but did differ between all of the other pairs of habitats ($t \geq 1.35$; $P \leq 0.05$ for all of the pairwise comparisons).

Because the assemblages differed by habitat but not gear type, the data were pooled across gear type for all of the subsequent analyses. The results from the SIMPER analyses identified 39 taxa that cumulatively contributed

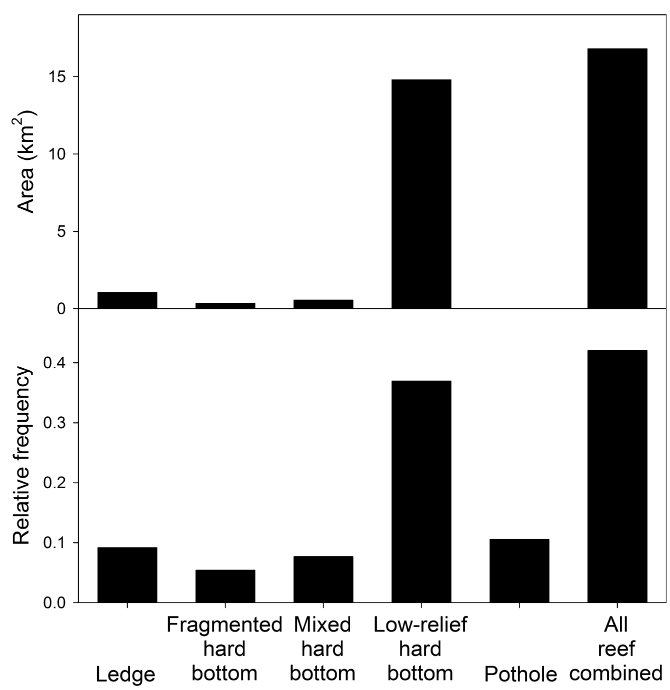

FIGURE 3. Overall areal extent and frequency of occurrence within the primary sampling units of the five common reef habitats in the Elbow.

TABLE 2. Summary of the overall sampling effort. The numbers represent the individual gear deployments per habitat type as classified from the interpretation of the side-scan-sonar mapping data.

Habitat type	GoPro *Z* traps	GoPro chevron traps	S-BRUVs
Ledge	18	16	17
Pothole	18	18	17
Low-relief hard bottom	17	18	17
Mixed hard bottom	18	17	18
Fragmented hard bottom	18	18	18
Total	89	87	87

to the top 80% of the habitat-specific differences in assemblage structures (Figure 6). Unidentified wrasses *Halichoeres* spp. were the most abundant taxa that was observed over all of the habitat types, although their abundance was generally lowest over low-relief hard-bottom and pothole habitats. Many other taxa also exhibited their lowest abundance over low-relief habitats (e.g., low-relief hard bottom and potholes), including Greater Amberjack *Seriola dumerili*, Hogfish *Lachnolaimus maximus*, Blue Angelfish *Holacanthus bermudensis*, Tattler *Serranus phoebe*, unidentified jacks *Seriola* spp., Sand Tilefish *Malacanthus plumieri*, Scamp *Mycteroperca phenax*, and Spotfin Butterflyfish *Chaetodon ocellatus*. Red Porgy *Pagrus pagrus* and the *Decapterus*/*Selar*/*Trachurus* complex were most abundant in low-relief hard-bottom habitats, while unidentified baitfish, Vermilion Snapper *Rhomboplites aurorubens*, unidentified sand perches *Diplectrum* spp., and unidentified lionfish *Pterois* spp. were most abundant on potholes (Figure 6).

The average number of taxa, taxonomic richness, and taxonomic diversity were significantly lower on low-relief hard-bottom and pothole habitats than on ledge, fragmented, and mixed hard-bottom habitats (Figure 7). In contrast, the average number of individuals that was observed did not differ among the habitats.

DISCUSSION

Through this study, we effectively classified and delineated reef habitats through the interpretation of side-scan-sonar mapping data, and the utility of these classifications was validated because the derived habitat-classes were important determinants of reef-fish assemblage structure. The results yielded valuable insight into the spatial dynamics of reef habitats and their associated fish assemblage structures that will likely facilitate efforts to improve and expand reef-fish surveys. Accordingly, the identification of habitats through the interpretation of side-scan-sonar mapping data represents an important step for the improvement of survey design through the incorporation of an optimized habitat-based stratification scheme in the Gulf of Mexico.

In this pilot study, the reef-fish assemblage structure in the Elbow differed significantly relative to the types of reef habitat that were identified through side-scan-sonar imagery. The distribution of fish populations is often related to habitat characteristics ranging from microhabitats (e.g., substrate composition, attached biota) to broad-scale habitat features (e.g., water depth) throughout their range (Anderson and Yoklavich 2007; Purcell et al. 2014; Bacheler and Ballenger 2015; Laman et al. 2015; Bacheler et al. 2016). Determining which measures of habitat are the most important to the statistical design of a fisheries survey requires careful consideration. Stratifying survey effort among defined habitat types can increase the efficiency of surveys as long as the habitat designations correspond in some way to the composition and variance in abundance of the species populations and assemblages that are being assessed (Hilborn and Walters 1992; Smith et al. 2011). For sampling effort to be allocated appropriately to each sampling stratum, the habitats must also have been defined in such a way that they can be assessed and quantified before sampling is conducted. The habitat-classification approach that we tested appears to meet those criteria. We delineated five common reef habitat types, including potholes as small as 2 m in diameter. Subsequently, the reef-fish assemblage structure differed among all of the habitat types except ledges and fragmented hard bottom, indicating that the habitat-classification scheme that we used in this study captured some physical factors that are important in structuring different reef-fish assemblages. Accordingly, these methods show promise as a component of habitat classification and stratification protocols that would improve reef-fish surveys in the eastern Gulf of Mexico. An important advantage of a stratified-random sampling design is that stratification may improve the precision of the parameter estimates by subdividing a heterogeneous population into relatively homogeneous strata. Because the reef-fish assemblage structure did not differ between ledges and fragmented hard bottom in the present study, it may be possible to simplify the habitat-stratification scheme that was tested in the current study by merging these two habitats into a single stratum. It should be noted that nonreef habitats, which covered approximately 90% of the total area that was mapped, are important habitats for certain reef fishes (e.g., Red Snapper); however, as sediment-dominated habitats are effectively sampled by ongoing Gulf-wide trawl and bottom longline surveys (Switzer et al. 2015; Karnauskas et al. 2017), they were not sampled in the present study.

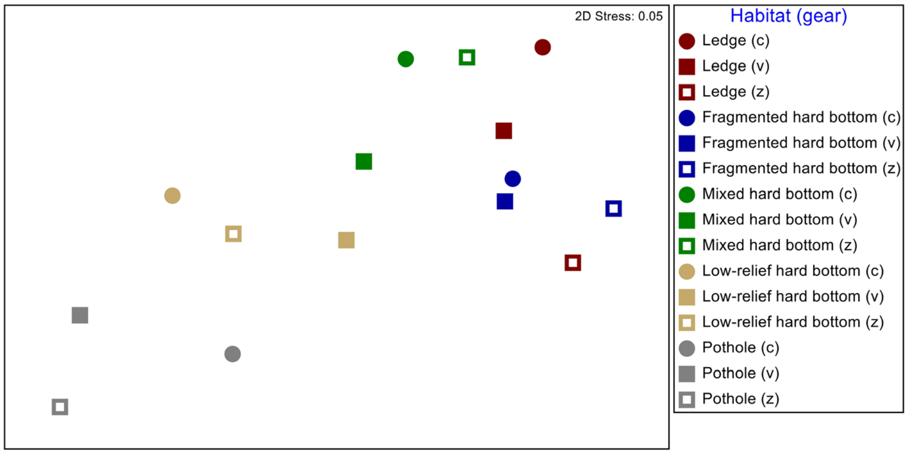

FIGURE 4. Nonmetric multidimensional scaling plot of the average assemblage structure that was observed on S-BRUV (ledge c; filled circles) and trap-mounted GoPro video surveys on chevron (ledge v: filled squares) and *Z* traps (ledge z: open squares) over the five habitat types in the Elbow.

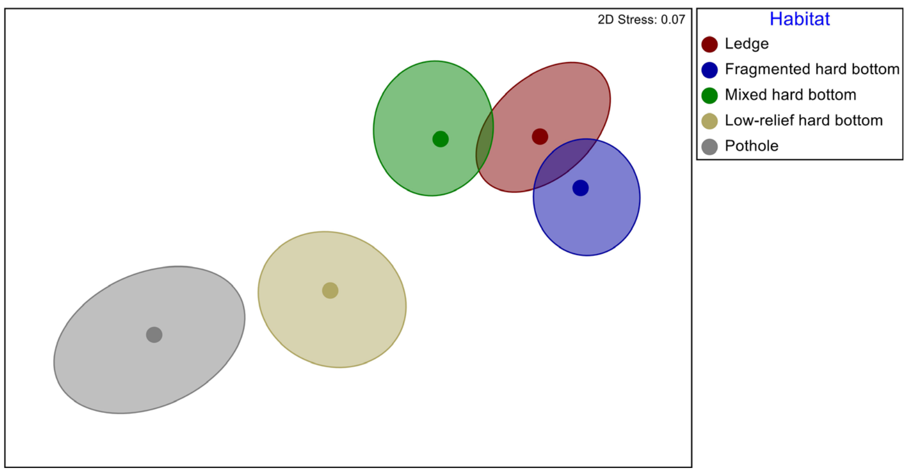

FIGURE 5. Nonmetric multidimensional scaling plot of the habitat centroids and corresponding bootstrap-averaged ellipses of the separation of reef-fish assemblages that is associated with the five habitat types in the Elbow.

TABLE 3. PERMANOVA results for the analysis of the reef-fish assemblages based on the Bray–Curtis dissimilarity measure in relation to gear type (Gr) and habitat (Hab); MS = mean squares, Sqrt = square root, and Res = residuals.

Source	df	MS	Pseudo-*F*	*P*	Sqrt (component of variation)	% of variation
Gr	2	2,231	1.01	0.45	0.55	0.8
Hab	4	13,247	6.01	<0.01	14.50	22.3
Gr × Hab	8	2,047	0.93	0.67	−3.00	
Res	248	2,205			49.96	76.9
Total	262					

Although it was not quantitatively assessed in the present study, vertical relief appeared to be strongly associated with assemblage structure in the habitats that were examined. We classified hard-bottom habitats by visually interpreting the spatial patterns in the strong acoustic returns that are associated with specific habitat features. Side-scan-sonar data cannot provide absolute estimates of depth, so it is not possible to measure the vertical relief of specific reef features. But shadow zones are evident in side-scan-sonar imagery and can be interpreted here as a relative, qualitative measure of vertical relief that informed the habitat definitions that we developed. The

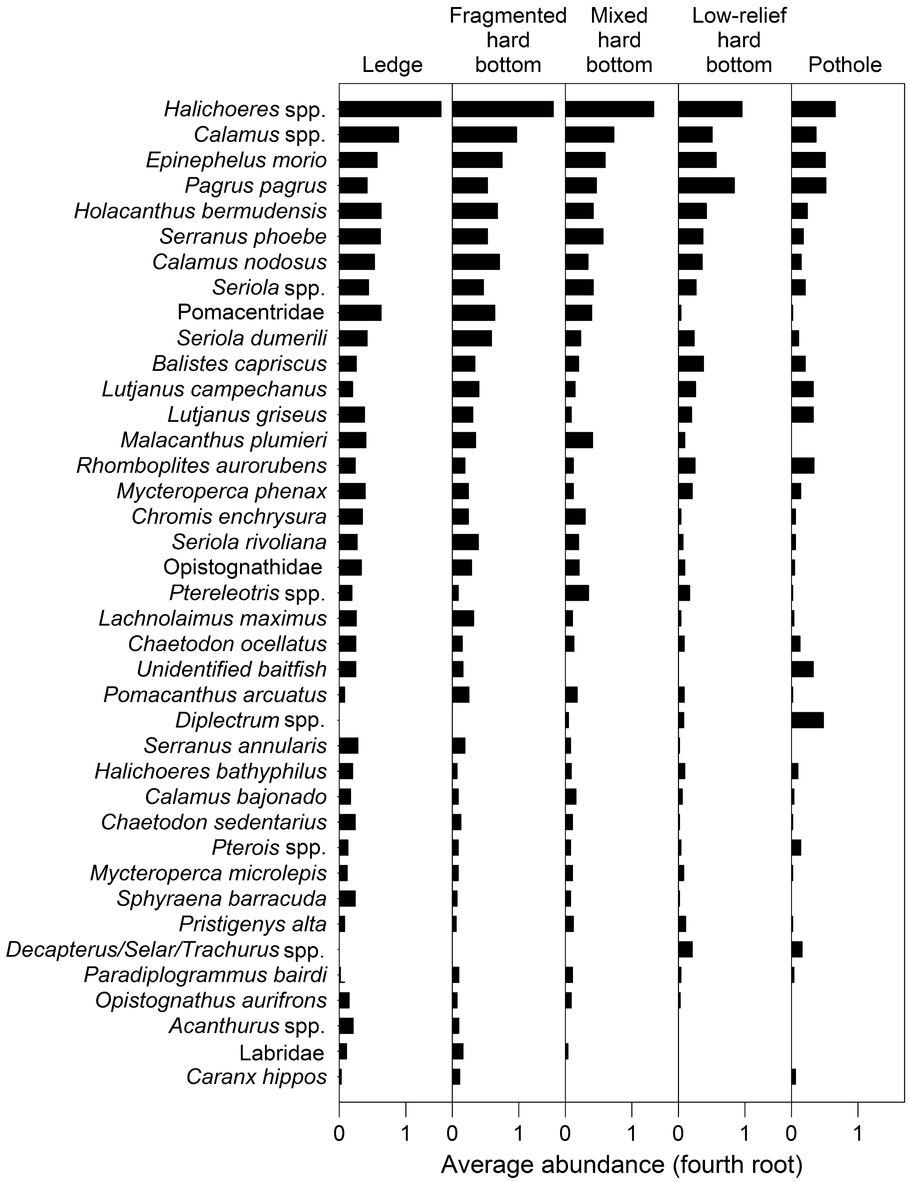

FIGURE 6. Average transformed relative abundance of the taxa that were identified via similarity percentages analyses as contributing to the observed differences in assemblage structure between the five reef habitats in the Elbow.

results from this study indicate that overall taxonomic richness and diversity, as well as the relative abundance of many reef-associated fishes, were generally highest for habitat types with the greatest relative vertical relief (e.g., ledges and fragmented hard bottom). These results largely corroborate the notion that, for many reef-associated taxa, overall diversity and species abundance are generally higher on high-relief reef habitats (Sluka et al. 2001; Gledhill and David 2004; Koenig et al. 2005; Harford et al. 2016; McLean et al. 2016). Given its importance as a correlate of abundance and reef-fish assemblage structure, vertical relief in some measure will be essential in developing an optimal habitat-based sampling strategy. What is less clear is how exactly to stratify relief for the purposes of survey design throughout the Gulf of Mexico. Most studies and surveys have used a qualitative delineation of relief (e.g., low, medium, high), although the designation of habitat as high relief has ranged from tens of centimeters (Anderson and Yoklavich 2007; Love et al. 2009) to a meter or more, depending on the study area (Harford et al. 2016; McLean et al. 2016). In the present study, the relief ranged from 0.2 to 4.0 m in the habitat types that were characterized by notable vertical relief (e.g., fragmented hard bottom and ledge habitat),

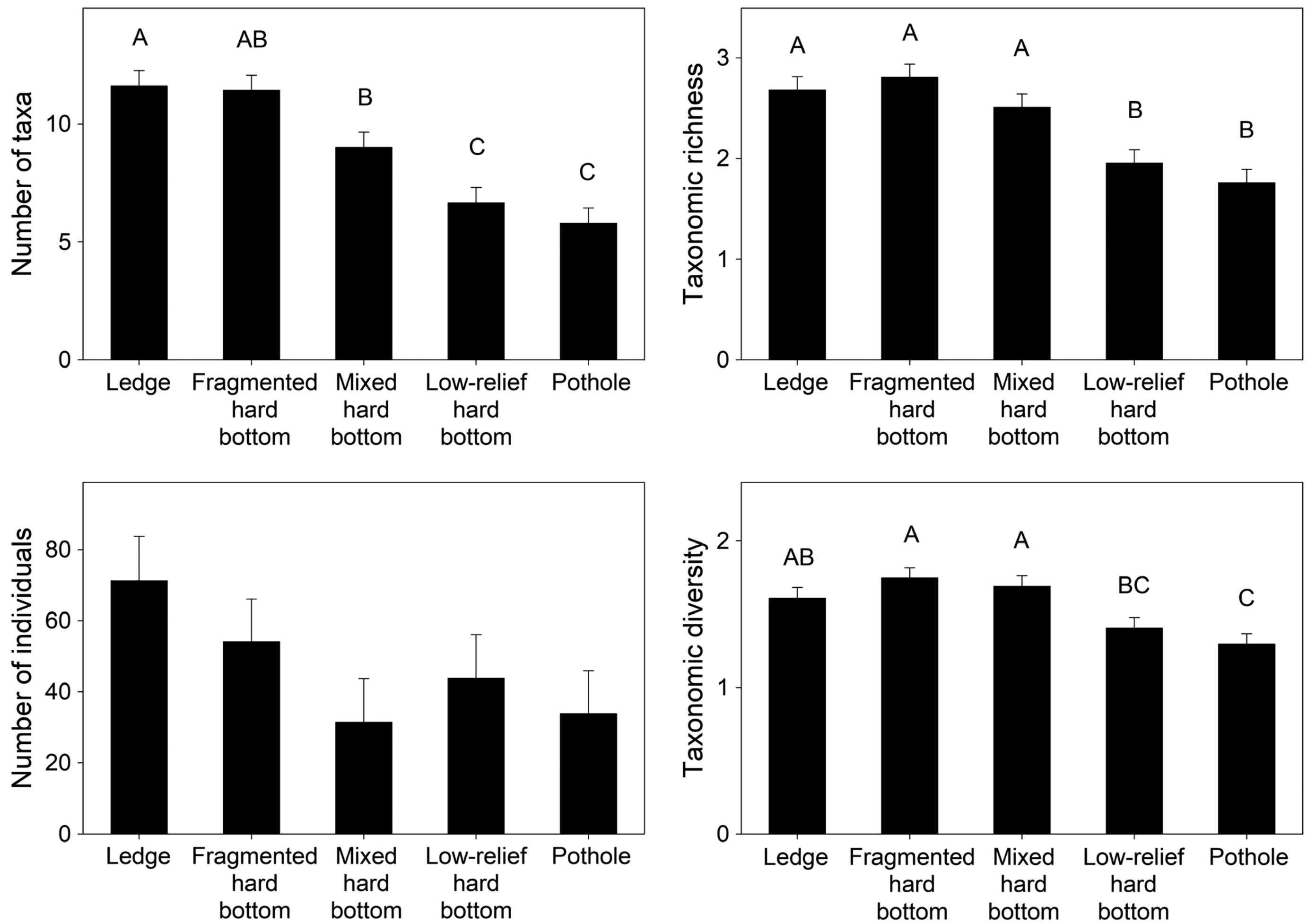

FIGURE 7. Average (±SE) taxonomic diversity metrics by habitat type in the Elbow. The mean values for each of the diversity metrics were compared among the habitat types via a one-way ANOVA, and the letters designate post hoc Tukey groupings where significant differences were observed.

although pinnacles of 10 m or more occurred along the eastern Gulf of Mexico shelf break and in several artificial habitats (Keenan et al. 2018). Additional efforts to more finely tune the qualitative designation of vertical-relief strata may facilitate the integration of data from side-scan-sonar mapping surveys with data from other mapping approaches (e.g., satellites or multibeam sonar) into a universal habitat-classification scheme and resolve known discrepancies in the identification and delineation of hard-bottom habitats between mapping technologies (Ilich 2018).

We detected no significant difference in the observed assemblage structure between the S-BRUV and GoPro cameras. We had expected that differences in field of view and image resolution between the two camera types might influence our ability to count and identify individuals, but they did not. The use of a baited survey may partly negate the benefits of using a higher-resolution camera. Many reef-fish taxa, including predatory and scavenging species, have been observed in greater numbers at baited stations than at unbaited stations (Willis and Babcock 2000; Harvey et al. 2007; Watson et al. 2010), although this is not universal (Watson and Huntington 2016). Bait may attract individuals closer to the camera than they would otherwise get, allowing for accurate identification and counting even when lower-resolution video is used. Accordingly, the use of GoPro cameras or other inexpensive camera systems are a viable alternative to the more costly, custom-built S-BRUV systems when resources are limited. As the use of underwater video becomes more common in reef-fish surveys, careful consideration is required as to how rapidly changing technology may affect the ability to estimate fish populations. Should new technologies improve the ability to detect or quantify a species, the effects of a change in catchability will need to be appropriately accounted for in statistical models of relative abundance so that changes in the size of populations can accurately be assessed through time. Ultimately, these effects may be mitigated through the use of baited systems in combination with accurate estimates of the volume of water that is sampled (Harvey et al. 2007). Nevertheless, comparative studies such as the present study would be beneficial before implementing significant technological advancements in long-term surveys.

Before habitat stratification is incorporated into reef-fish surveys in the eastern Gulf of Mexico, careful consideration is required with respect to allocating sampling effort among identified habitats. Because a main objective of the current study was to compare reef-fish assemblages among identified habitats, we implemented a balanced design, where sampling effort was allocated equally among all of the habitat types. Moving forward, accurate estimates of the quantity of each habitat that is available is essential to the implementation of a probabilistic sampling design, especially when the goal of survey efforts is to extrapolate site-specific density data to broad-scale estimates of abundance or biomass (Anderson et al. 2005; Wakefield et al. 2005). Nevertheless, an optimized survey design may require disproportionately higher efforts within sampling strata that exhibit either high variability in relative abundance or high taxonomic diversity (Smith et al. 2011), especially when it is important to maximize the ability of a survey to detect rare taxa (Sanderlin et al. 2014). In the present study, approximately 88% of the entire reef habitat that was identified was low-relief, hard-bottom habitat. However, given that taxonomic richness and diversity were significantly lower on low-relief hard bottom than on several other reef habitats (e.g., ledge, fragmented hard bottom, mixed hard bottom), the efficiency of survey efforts would likely be improved upon by down-weighting sampling efforts on low-relief hard bottom. To a large extent, the accurate quantification of available habitat is a function of the minimum mapping unit, or the smallest areal entity to be mapped and identified as a unique feature. In this study, we chose a minimum mapping unit of 2.0×2.0 m, or $4.0\,m^2$, to delineate individual potholes that represent small-scale areas that are maintained by the activity of Red Grouper *Epinephelus morio* and are of tremendous ecological importance (Coleman et al. 2010; Ellis et al. 2017; Harter et al. 2017). Ideally, a minimum mapping unit should be selected that corresponds to the scale of important biological processes (Anderson et al. 2005), but the resolution of information on available habitat is seldom that high (Smith et al. 2011).

In the eastern Gulf of Mexico, small-scale habitat features, including the potholes that were identified in the present study, are of vital importance ecologically and economically. They often result from habitat modification by fishes such as Red Grouper that clear away surficial sediments, expose underlying rock, and provide important settlement habitat for the larvae of sessile invertebrates (Coleman et al. 2010). The active maintenance of potholes and similar features by Red Grouper results in larger features with demonstrably steeper slopes and greater depths (Wall et al. 2011; Ellis et al. 2017), ultimately contributing to significantly greater abundance and diversity of fishes and macroinvertebrates than in such features in which Red Grouper are no longer present (Coleman et al. 2010; Ellis et al. 2017; Harter et al. 2017). Other studies from the eastern Gulf of Mexico have identified Red Grouper holes that were generally larger (Wall et al. 2011) or smaller (Ellis et al. 2017) than the potholes that we identified. The mechanisms that contribute to regional differences in the physical characteristics of potholes or Red Grouper holes are not yet clear, but it does appear that the influence of these habitats likely extends well beyond their physical boundary. Additional research that is designed to better define the sphere of influence of these and other habitats (e.g., ledges) that may occupy a small spatial footprint will be instrumental in determining the measure of habitat quantity to incorporate into future survey design.

Before incorporating this habitat-classification scheme into reef-fish survey design, the transferability of the observed results to the greater eastern Gulf of Mexico needs further study. At broad spatial scales, the composition and structure of reef-fish assemblages as well as overall species richness and diversity often vary markedly with depth and latitude (Love et al. 2009; Zintzen et al. 2012; Easton et al. 2015; Bacheler et al. 2016; Harford et al. 2016) and depth-associated patterns may vary regionally (Saul et al. 2013). At the species level, many reef-associated fishes exhibit strong ontogenetic differences in depth and habitat preferences; larger individuals typically prefer higher-relief habitats and deeper waters (Sluka et al. 2001; Love et al. 2009; Bacheler and Ballenger 2015; Laman et al. 2015; Heyns-Veale et al. 2016). Aside from several areas that have received focused study (Gledhill and David 2004; Wall et al. 2011; Harter et al. 2017), little is known regarding the overall quantity and quality of reef habitat throughout the eastern Gulf of Mexico. In addition, insights into species–habitat associations that are developed from a study at one spatial scale do not necessarily translate directly to broader or finer spatial scales (Lecours et al. 2015). Additional efforts are clearly needed to expand our understanding of the distribution and availability of reef habitats throughout the eastern Gulf of Mexico. Only then can we adequately test whether the lessons that have been learned from the present study are more broadly applicable. Preliminarily, however, it appears that the derivation of habitat classification from side-scan-sonar data may be effective for stratifying and optimizing reef-fish surveys.

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REFERENCES

Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth, UK.

Anderson, T. J., M. M. Yoklavich, and S. L. Eittreim. 2005. Linking fine-scale groundfish distributions with large-scale seafloor maps: issues and challenges of combining biological and geological data. Pages 667–678 *in* P. W. Barnes and J. P. Thomas, editors. Benthic habitats and the effects of fishing. American Fisheries Society, Symposium 41, Bethesda, Maryland.

Anderson, T. J., and M. M. Yoklavich. 2007. Multiscale habitat associations of deepwater demersal fishes off central California. U.S. National Marine Fisheries Service Fishery Bulletin 105:168–179.

Bacheler, N. M., and J. C. Ballenger. 2015. Spatial and temporal patterns of Black Sea Bass sizes and catches in the southeastern United States inferred from spatially explicit nonlinear models. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 7:523–536.

Bacheler, N. M., D. J. Berrane, W. A. Mitchell, C. M. Schobernd, Z. H. Schobernd, B. Z. Teer, and J. C. Ballenger. 2014. Environmental conditions and habitat characteristics influence trap and video detection probabilities for reef fish species. Marine Ecology Progress Series 517:1–14.

Bacheler, N. M., Z. H. Schobernd, D. J. Berrane, C. M. Schobernd, W. A. Mitchell, B. Z. Teer, K. C. Gregalis, and D. M. Glasgow. 2016. Spatial distribution of reef fish species along the southeast U.S. Atlantic coast inferred from underwater video survey data. PLOS (Public Library of Science) ONE [online serial] 11:e0162653.

Bacheler, N. M., C. M. Schobernd, Z. H. Schobernd, W. A. Mitchell, D. J. Berrane, G. T. Kellison, and M. J. M. Reichert. 2013. Comparison of trap and underwater video gears for indexing reef fish presence and abundance in the southeast United States. Fisheries Research 143:81–88.

Bryan, M. D., and K. McCarthy. 2015. Standardized catch rates for Red Grouper from the United States Gulf of Mexico vertical line and longline fisheries. SEDAR (System for Electronic Document Analysis and Retrieval), SEDAR42-AW-02, North Charleston, South Carolina.

Campbell, M. S., A. G. Pollack, C. T. Gledhill, T. S. Switzer, and D. A. DeVries. 2015. Comparison of relative abundance indices calculated from two methods of generating video count data. Fisheries Research 170:125–133.

Cappo, M., E. Harvey, H. Malcolm, and P. Speare. 2003. Potential of video techniques to monitor diversity abundance and size of fish in studies of marine protected areas. Pages 455–464 *in* J. P. Beumer, A. Grant, and D. C. Smith, editors. Aquatic protected areas: what works best and how do we know? Australian Society for Fish Biology, North Beach, Australia.

Clarke, K. R., and R. N. Gorley. 2015. PRIMER v7: user manual/tutorial. PRIMER-E, Plymouth, UK.

Clarke, K. R., R. N. Gorley, P. J. Somerfield, and R. M. Warwick. 2014. Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition. PRIMER-E, Plymouth, UK.

Coleman, F. C., C. C. Koenig, K. M. Scanlon, S. Heppell, S. Hep-Pell, and M. W. Miller. 2010. Benthic habitat modification through excavation by Red Grouper, *Epinephelus morio*, in the northeastern Gulf of Mexico. Open Fish Science Journal [online serial] 3:1–15.

Easton, R. R., S. S. Heppell, and R. W. Hannah. 2015. Quantification of habitat and community relationships among nearshore temperate fishes through analysis of drop camera video. Marine and Coastal Fishes: Dynamics, Management, and Ecosystem Science [online serial] 7:87–102.

Ellis, R. D., F. C. Coleman, and C. C. Koenig. 2017. Effects of habitat manipulation by Red Grouper, *Epinephelus morio*, on faunal communities associated with excavations in Florida Bay. Bulletin of Marine Science 93:961–983.

FGDC (Federal Geographic Data Committee). 2012. Coastal and marine ecological classification standard. FGDC, Report FGDC-STD-018-2012, Reston, Virginia.

FMRI (Florida Marine Research Institute). 1998. Benthic habitats of the Florida Keys. FMRI, Technical Report TR-4, St. Petersburg, Florida.

Franklin, E. C., J. S. Ault, S. G. Smith, J. Luo, G. A. Meester, G. A. Diaz, M. Chiappone, D. W. Swanson, S. L. Miller, and J. A. Bohnsack. 2003. Benthic habitat mapping in the Tortugas region, Florida. Marine Geodesy 26:19–34.

Gledhill, C., and A. David. 2004. Survey of fish assemblages and habitat within two marine protected areas on the west Florida shelf. Proceedings of the Gulf and Caribbean Fisheries Institute 55:614–625.

Harford, W. J., S. G. Smith, J. S. Ault, and E. A. Babcock. 2016. Cross-shelf habitat occupancy probabilities for juvenile groupers in the Florida Keys coral reef ecosystem. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 8:147–159.

Harter, S. L., H. Moe, J. K. Reed, and A. W. David. 2017. Fish assemblages associated with Red Grouper pits at Pulley Ridge, a mesophotic reef in the Gulf of Mexico. U.S. National Marine Fisheries Service Fishery Bulletin 115:419–432.

Harvey, E. S., M. Cappo, J. J. Butler, N. Hall, and G. A. Kendrick. 2007. Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. Marine Ecology Progress Series 350:245–254.

Heyns-Veale, E. R., A. T. F. Bernard, N. B. Richoux, D. Parker, T. J. Langlois, E. S. Harvey, and A. Götz. 2016. Depth and habitat determine assemblage structure of South Africa's warm-temperate reef fish. Marine Biology 163:article 158.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Ilich, A. R. 2018. Integrating towed underwater video with multibeam acoustics for mapping benthic habitat and assessing reef fish communities on the West Florida Shelf. Master's thesis. University of South Florida, St. Petersburg.

Karnauskas, M., J. F. Walter III, M. D. Campbell, A. G. Pollack, J. M. Drymon, and S. Powers. 2017. Red Snapper distribution on natural habitats and artificial structures in the northern Gulf of Mexico. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 9:50–67.

Keenan, S. F., T. S. Switzer, K. A. Thompson, A. J. Tyler-Jedlund, and A. R. Knapp. 2018. Comparison of reef-fish assemblages between artificial and geologic habitats in the northeastern Gulf of Mexico: implications for fishery-independent surveys. Pages 141–163 *in* S. A. Bortone, editor. Marine artificial research and development: integrating fisheries management objectives. American Fisheries Society, Symposium 86, Bethesda, Maryland.

Koenig, C. C., A. N. Shepard, J. K. Reed, F. C. Coleman, S. D. Brooke, J. Brusher, and K. M. Scanlon. 2005. Habitat and fish populations in the deep-sea *Oculina* coral ecosystem of the western Atlantic. Pages 795–805 *in* P. W. Barnes and J. P. Thomas, editors. Benthic habitats and the effects of fishing. American Fisheries Society, Symposium 41, Bethesda, Maryland.

Laman, E. A., S. Kotwicki, and C. N. Rooper. 2015. Correlating environmental and biogenic factors with abundance and distribution of Pacific Ocean Perch (*Sebastes alutus*) in the Aleutian Islands, Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 113:270–289.

Lecours, V., R. Devillers, D. C. Schneider, V. L. Lucieer, C. J. Brown, and E. N. Edinger. 2015. Spatial scale and geographic context in benthic habitat mapping: review and future directions. Marine Ecology Progress Series 535:259–284.

Lembke, C., S. Grasty, A. Silverman, H. Broadbent, S. Butcher, and S. Murawski. 2017. The camera-based assessment survey system (C-BASS): a towed camera platform for reef fish abundance surveys and benthic habitat characterization in the Gulf of Mexico. Continental Shelf Research 151:62–71.

Love, M. S., M. Yoklavich, and D. M. Schroeder. 2009. Demersal fish assemblages in the Southern California Bight based on visual surveys in deep water. Environmental Biology of Fishes 84:55–68.

McLean, D. L., T. J. Langlois, S. J. Newman, T. H. Holmes, M. J. Birt, K. R. Bornt, T. Bond, D. L. Collins, S. N. Evans, M. J. Travers, C. B. Wakefield, R. C. Babcock, and R. Fisher. 2016. Distribution, abundance, diversity and habitat associations of fishes across a bioregion experiencing rapid coastal development. Estuarine, Coastal and Shelf Science 178:36–47.

Moe, M. A. 1963. A survey of offshore fishing in Florida. Florida State Board of Conservation, Professional Paper 4, Tallahassee.

Parker, D., H. Winker, A. T. F. Bernard, E. R. Heyns-Veale, T. J. Langlois, E. S. Harvey, and A. Götz. 2016. Insights from baited video sampling of temperate reef fishes: how biased are angling surveys? Fisheries Research 179:191–201.

Purcell, S. W., K. R. Clarke, K. Rushworth, and S. J. Dalton. 2014. Defining critical habitats of threatened and endemic reef fishes with a multivariate approach. Conservation Biology 28:1688–1698.

Sanderlin, J. S., W. M. Block, and J. L. Ganey. 2014. Optimizing study design for multi-species avian monitoring programmes. Journal of Applied Ecology 51:860–870.

Saul, S. E., J. F. Walter III, D. J. Die, D. F. Naar, and B. T. Donahue. 2013. Modeling the spatial distribution of commercially important reef fishes on the West Florida Shelf. Fisheries Research 143:12–20.

SEDAR (System for Electronic Document Analysis and Retrieval). 2018. SEDAR 51: Gulf of Mexico Gray Snapper stock assessment report. SEDAR, North Charleston, South Carolina.

Sluka, R. D., M. Chiappone, and K. M. Sullivan-Sealey. 2001. Influence of habitat on grouper abundance in the Florida Keys, U.S.A. Journal of Fish Biology 58:682–700.

Smith, S. G., J. S. Ault, J. A. Bohnsack, D. E. Harper, J. Luo, and D. B. McClellan. 2011. Multispecies survey design for assessing reef-fish stocks, spatially explicit management performance, and ecosystem condition. Fisheries Research 109:25–41.

Smith, M. W., D. Goethel, A. Rios, and J. Isley. 2015. Standardized catch rate indices for Gulf of Mexico Gray Triggerfish (*Balistes capriscus*) landed during 1993–2013 by the commercial handline fishery. SEDAR (System for Electronic Document Analysis and Retrieval), SEDAR43-WP-05, North Charleston, South Carolina.

Switzer, T. S., E. J. Chesney, and D. M. Baltz. 2015. Habitat use by juvenile Red Snapper in the northern Gulf of Mexico: ontogeny, seasonality, and the effects of hypoxia. Transactions of the American Fisheries Society 144:300–314.

Thompson, K. A., T. S. Switzer, M. C. Christman, S. F. Keenan, C. Gardner, M. Campbell, and A. Pollack. 2017.Indices of abundance for Gray Snapper (*Lutjanus griseus*) using combined data from three independent video surveys. SEDAR (System for Electronic Document Analysis and Retrieval), SEDAR51-DW-15, North Charleston, South Carolina.

Wakefield, W. W., C. E. Whitmire, J. E. R. Clemons, and B. N. Tissot. 2005. Fish habitat studies: combining high-resolution geological and biological data. Pages 119–138 *in* P. W. Barnes and J. P. Thomas, editors. Benthic habitats and the effects of fishing. American Fisheries Society, Symposium 41, Bethesda, Maryland.

Wall, C. C., B. T. Donahue, D. F. Naar, and D. A. Mann. 2011. Spatial and temporal variability of Red Grouper holes within Steamboat Lumps Marine Reserve, Gulf of Mexico. Marine Ecology Progress Series 431:243–254.

Watson, D. L., E. S. Harvey, B. M. Fitzpatrick, T. J. Langlois, and G. Shedrawi. 2010. Assessing reef fish assemblage structure: how do different stereo-video techniques compare? Marine Biology 157:1237–1250.

Watson, J. L., and B. E. Huntington. 2016. Assessing the performance of a cost-effective video lander for estimating relative abundance and diversity of nearshore fish assemblages. Journal of Experimental Marine Biology and Ecology 483:104–111.

Wells, R. J. D., K. M. Boswell, J. H. Cowan Jr., and W. F. Patterson III. 2008. Size selectivity of sampling gears targeting Red Snapper in the northern Gulf of Mexico. Fisheries Research 89:294–299.

Willis, T. J., and R. C. Babcock. 2000. A baited underwater video system for the determination of relative density of carnivorous reef fish. Marine and Freshwater Research 51:755–763.

Willis, T. J., R. B. Millar, and R. C. Babcock. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. Marine Ecology Progress Series 198:249–260.

Zintzen, V., M. J. Anderson, C. D. Roberts, E. S. Harvey, A. L. Stewart, and C. D. Struthers. 2012. Diversity and composition of demersal fishes along a depth gradient assessed by baited remote underwater stereo-video. PLOS (Public Library of Science) ONE [online serial] 7: e48522.