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ARTICLE

A Comparison of Fish Community Structure at Mesophotic Artificial Reefs and Natural Banks in the Western Gulf of Mexico

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Abstract

Oil and gas platforms along the northwestern Gulf of Mexico (GOM) shelf have served as artificial reefs since oil and gas exploration intensified in the 1950s. As these structures are decommissioned, they must be removed; however, some are converted to permanent artificial reefs. Despite the potential effects these artificial habitats may have on marine fisheries, investigations that assess the fish communities inhabiting these structures relative to natural habitats are rare. During fall 2012, we used remotely operated vehicle surveys to compare fish communities between artificial reefs (i.e., reefed platforms; $n = 5$) and adjacent natural banks ($n = 5$) in the western GOM. Our surveys successfully documented 79 species representing 28 families. Multivariate analyses suggested that fish communities at artificial reefs were distinct from those at natural banks. Post hoc analyses indicated that the differences were driven by high abundances of transient, midwater pelagics and other gregarious species at artificial reefs. Many fisheries species, like the Red Snapper *Lutjanus campechanus*, were found in both habitat types, with density at artificial reefs estimated to be nearly eight times greater than at natural banks. Despite lower densities at natural banks, the disproportionately large areas of these habitats resulted in relatively high total abundance estimates—approximately 5% of the 2012 GOM Red Snapper annual catch limit (3.67 million kg [8.08 million lb])—a finding that has significant implications for Red Snapper and artificial reef management in the GOM. Our study suggests that although fish community structure may differ between these two habitats, artificial reefs serve as important habitat for species like Red Snapper by potentially diverting fishing pressure from natural habitats; however, future studies that address species-specific life history traits will be needed to better understand the function and performance of artificial reefs in supporting fisheries productivity.

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Artificial reefs are constructed from a diverse assortment of materials and serve a variety of purposes, but they are often widely regarded as habitat for fishes (Bohnsack and Sutherland 1985; Seaman 2000; Baine 2001; Baine and Side 2003; Broughton 2012). In the northwestern Gulf of Mexico (GOM), oil and gas infrastructure represents the largest artificial reef complex in the world (Dauterive 2000). Currently, about 2,300 oil and gas platforms (hereafter, “platforms”) are installed across the northern GOM shelf (BSEE 2016), providing additional hard substrate (on an otherwise unstructured bottom) that becomes suitable “reef” habitat for a variety of marine life (Gallaway and Lewbel 1982; Dauterive 2000; Stanley and Wilson 2000; Kaiser and Pulsipher 2005). Prior to the introduction of platforms, hard substrate was relatively scarce, as the northwestern GOM shelf is dominated by soft sediments consisting of clay, silt, and sand (Parker et al. 1983; Rezak et al. 1985). Consequently, platforms and other artificial reefs and the high abundances of fish that occur on these structures have become an integral component of the region’s fisheries.

Many of the platforms in the northwestern GOM are nearing the end of their production life spans and will soon be decommissioned (Macreadie et al. 2011; Fowler et al. 2014). Typically, this process entails severing the platform below the seafloor and towing it to shore (i.e., complete removal); however, platforms may also be accepted into a state-run reefing program known as “Rigs to Reefs” (RTR), in which structures can be retained as permitted artificial reefs. Accepted structures can be towed to permitted reefing areas, toppled in place (i.e., laid on the seafloor), or partially removed (i.e., only the top portion of the steel jacket removed) and thus continue to serve as habitat for fish and other reef species (Dauterive 2000; Kaiser and Pulsipher 2005). Although a proportion of these platforms will be accepted into RTR programs, much of this habitat will be permanently removed from the northern GOM ecosystem. As such, it is critical to determine the effects these changes in habitat may have on marine fish populations (e.g., Claisse et al. 2015).

Several studies assessing fish communities at artificial reefs have shown that densities of many important fisheries species are higher on artificial reefs than in nearby natural habitats (Stanley and Wilson 1996, 1997, 2000; Wilson et al. 2003, 2006; Love and York 2005; Love et al. 2005, 2006; Reubens et al. 2013). Whether these observed increases in fish densities represent increased production (i.e., stock enhancement) or simply the redistribution (i.e., aggregation) of existing biomass has been and is currently vigorously debated (Bohnsack 1989; Carr and Hixon 1997; Grossman et al. 1997; Lindberg 1997; Shipp and Bortone 2009; Cowan et al. 2011; Claisse et al. 2014, 2015). Generally, this uncertainty is driven by a lack of fishery-independent studies comparing artificial reefs with their natural counterparts, leaving significant knowledge gaps regarding the relative value and function of artificial reefs in supporting fisheries productivity.

Determining the effects of artificial reefs on marine fish populations necessitates information on species composition and abundances from both natural and artificial habitats (Carr and Hixon 1997). In the northern GOM, previous investigations

of community composition have primarily focused on assessing the fish populations that inhabit standing platforms. Although less common, natural banks providing hard substrate and substantial vertical relief are scattered across the mid- to outer shelf (Rezak et al. 1985). In fact, these prominent bathymetric features are thought to be the historical centers of abundance for diverse reef species and also for the economically important Red Snapper *Lutjanus campechanus* and Vermilion Snapper *Rhomboplites aurorubens* (Camber 1955; Dennis and Bright 1988; Gledhill 2001). Despite the likely importance of these habitats, limited studies comparing fish communities on artificial reefs to those on nearby natural habitats in the northern GOM have been conducted (e.g., Rooker et al. 1997; Wilson et al. 2003, 2006; Patterson et al. 2014; Langland 2015). With the exception of Patterson et al. (2014), who compared fish community structure at smaller-scale artificial reefs and natural reef habitat in the northeastern GOM, the studies to date have focused on comparisons of diapiric shelf-edge banks (e.g., the intensively studied Flower Garden Banks), standing platforms, and a limited number of artificial reefs in the northwestern GOM. Certainly, more research is needed to better understand these dynamics.

Natural bank habitats farther south off the coast of Texas have much different geological and physical characteristics than the shelf-edge banks of the northern GOM (i.e., drowned corallgal banks rather than diapiric banks with extensive vertical relief; Berryhill 1987). In fact, relatively little is known about fish community structure at natural banks or artificial reefs in the western GOM region given the difficulties in sampling these deep offshore habitats (Dennis and Bright 1988; Ajemian et al. 2015a). Dennis and Bright (1988) presented the first quantitative study of fish communities at natural banks off the coast of Texas by using data from submersible transects. Using remotely operated vehicle (ROV) surveys, Ajemian et al. (2015b) recently performed the first comprehensive assessment of fish community structure among artificial reefs (standing platforms, RTR artificial reefs, and liberty ship reefs) in the region. In their assessment, bottom depth alone best explained the observed patterns in fish community structure, and Ajemian et al. (2015b) speculated that variation in artificial reef fish communities was driven by the ambient communities present among the various depth strata.

In this paper, we present the first comparative study of reef fish community structure among RTR artificial reefs and drowned corallgal banks in the western GOM region. Despite the importance of these two habitats for fish and fisheries in the GOM, such comparative investigations have not been conducted. The primary goal of this study was to assess fish community structure at mesophotic natural banks and RTR artificial reefs in the western GOM by using ROV surveys. Our specific objectives were to (1) compare and contrast fish community structure between RTR artificial reefs and the nearby natural bank habitats and (2) estimate Red Snapper densities at these artificial reefs and natural banks. Considering the social and economic importance of Red Snapper in the region, we discuss Red Snapper density estimates with respect to the known area of the surveyed artificial

and natural habitats, and we highlight the implications for artificial reef development and Red Snapper management in the GOM.

STUDY AREA

Our study area encompassed five artificial reef sites and five natural banks interspersed along the Texas shelf in the western GOM (Figure 1). The region is characterized by a gently sloping shelf, substrates dominated by terrigenous sediments consisting of silt and clay muds, and a generally low availability of natural hard substrates with 1-m or greater vertical relief (Parker et al. 1983; Rezak et al. 1985). The artificial reefs surveyed were part of the Texas Parks and Wildlife Department's Artificial Reef Program and consisted of multiple RTR structures at each reef site (i.e., within a permitted reef site, 2–4 structures were present). Ambient bottom depths of these reefs ranged from 36 to 75 m (mean = 58 m), while vertical relief ranged from 16 to 40 m (mean = 25 m; Table 1). The natural habitats surveyed were part of a group of bathymetric features collectively known as the

South Texas Banks (Rezak et al. 1985; Nash et al. 2013). Unlike the natural banks in the northern GOM, which formed atop diapiric salt intrusions, the South Texas Banks have been classified as drowned remnant corallgal reefs that flourished during the Pleistocene (Rezak et al. 1985; Belopolsky and Droxler 1999). The surveyed natural banks were characterized by ambient bottom depths ranging from 70 to 96 m (mean = 79 m) and vertical relief ranging from 12 to 16 m (mean = 13 m; Table 1). All of the sites surveyed in this study are influenced by a persistent but variable nepheloid layer, which can be up to 35 m thick (Shideler 1981; Rezak et al. 1985). The nepheloid layer is formed from re-suspended sediments and undoubtedly affects the ecology of biota inhabiting the reefs (Dennis and Bright 1988; Rezak et al. 1990; Tunnell et al. 2009).

METHODS

Community surveys.—Surveys of fish communities were conducted using the Global Explorer MK3 ROV (Deep Sea Systems International, Inc.) during two cruises aboard the R/V

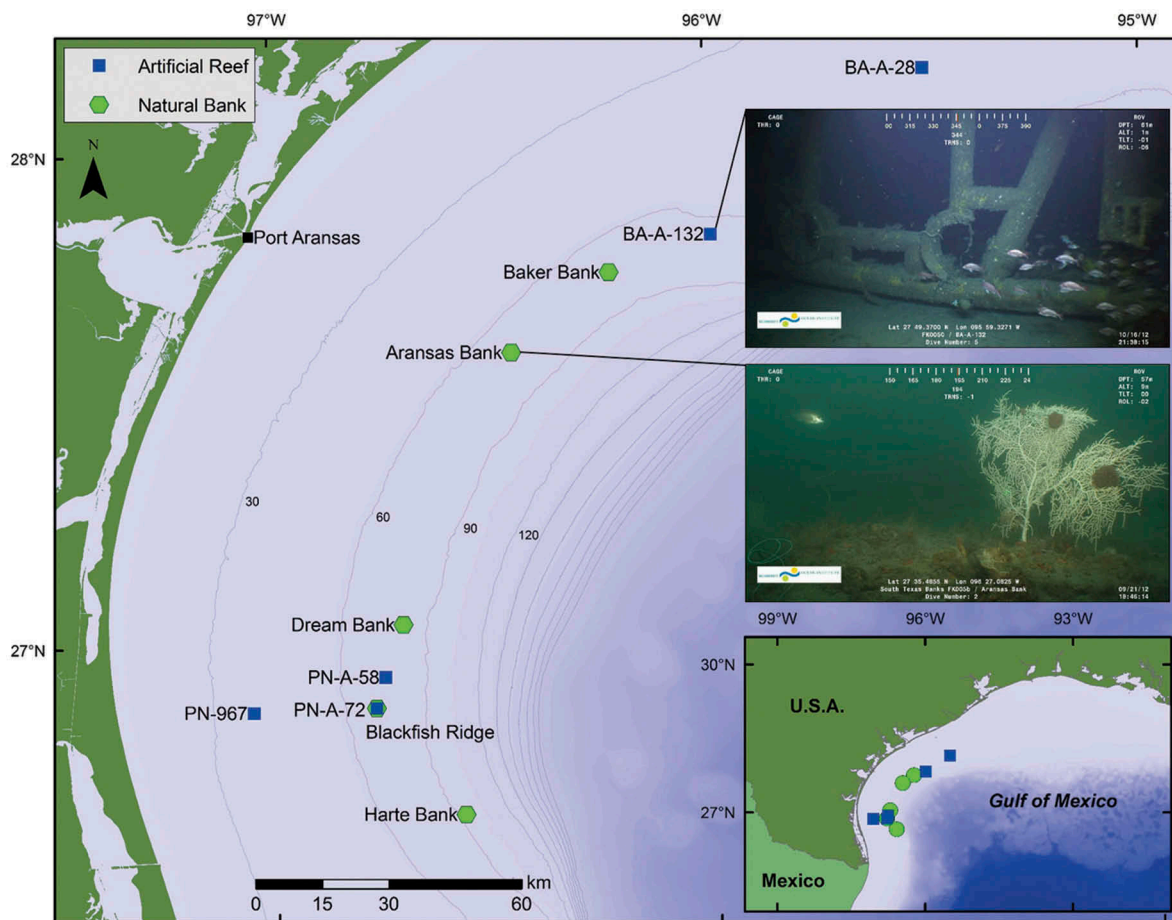


FIGURE 1. Map depicting locations of artificial reefs (blue squares) and natural banks (green circles) that were surveyed using a remotely operated vehicle, the Global Explorer, in the western Gulf of Mexico (GOM) during September and October 2012. Bathymetric contours (gray lines) are displayed in 30-m intervals. Inset map (bottom right) shows the study area relative to the western GOM region. Inset pictures provide examples of each habitat type.

TABLE 1. Physical characteristics of natural banks and artificial reefs surveyed with a remotely operated vehicle (ROV) in the Gulf of Mexico along the Texas shelf during fall 2012. Structure depth is the shallowest depth of structure at the site, while relief is the vertical extent from the seafloor to the top of structure. Nepheloid thickness is the estimated vertical extent (m) of the nepheloid layer at each site at the time of the ROV surveys.

Site	Survey date (2012)	Bottom depth (m)	Structure depth (m)	Relief (m)	Survey temperature (°C)	Area (km ²)	Nepheloid thickness (m)
Natural banks							
Baker Bank	Sep 19	74	58	16	24.0	1.33	3
Aransas Bank	Sep 21	70	58	12	24.0	0.50	1
Dream Bank	Sep 23	82	68	14	24.6	2.29	4
Blackfish Ridge	Sep 26	72	60	12	25.5	1.12	1
Harte Bank	Sep 27	96	83	13	22.9	0.31	6
Artificial reefs							
BA-A-28	Oct 9	46	27	19	27.1	3.90×10^{-3}	2
PN-A-58	Oct 15	75	52	23	27.1	1.65×10^{-3}	3
PN-A-72	Oct 15	72	32	40	27.1	1.08×10^{-3}	3
PN-967	Oct 15	36	20	16	27.3	1.60×10^{-3}	2
BA-A-132	Oct 16	61	32	29	27.0	6.73×10^{-3}	0

Falkor spanning September 17–29, 2012 (natural banks), and October 8–20, 2012 (artificial reefs). The Global Explorer is a large, working-class ROV (1,451.5 kg [3,200 lb]; 3,000-m depth rating) equipped with Ocean ProHD cameras (160° tilt and 105° viewing angle), a digital camera with laser scaler, multibeam imaging and scanning sonar, real-time conductivity–temperature–depth sensor, LED lights, and a manipulator arm. During ROV deployments, the R/V *Falkor* maintained a fixed distance away from the artificial reef or natural bank under investigation by using a dynamic positioning system. The position of the Global Explorer was logged by using a Sonardyne Ranger 2 Ultra-Short BaseLine (USBL) acoustic positioning system, which allowed for estimation of the distance surveyed. The ROV lights remained on during all ROV deployments. Real-time observations were made possible via live-feed video in the ROV control room, and all video was recorded and saved for further viewing and processing.

We surveyed the fish communities of both artificial reefs and natural banks by using continuous transects that began as soon as the ROV entered the water and terminated when the ROV surfaced (i.e., one continuous transect per site; artificial reefs: $n = 5$; natural banks: $n = 5$). However, the distinct differences in physical constraints of the structure at the two habitats (e.g., artificial reefs were complex with high relief; natural banks had a lower relief and were spread over a large area; Table 1) necessitated some slight modifications to our survey methods. Continuous roving transects (CRTs) were used to survey reef fish communities at artificial reefs (Ajemian et al. 2015a). Generally, CRTs entailed a horizontal rove around the top of the artificial reef and then at 10-m depth intervals for 1-min periods until the bottom was reached or until the nepheloid layer prevented further observations. When this depth was reached, the ROV performed another rove around the outer surface of the down-current side

of the reef. This method was recently demonstrated to be effective in documenting the reef fish community over the large vertical expanse of RTR structures (Ajemian et al. 2015a, 2015b). Because artificial reef sites contained multiple RTR structures, we attempted to survey at least two structures when currents and other conditions allowed. During CRTs, the ROV maintained a distance of approximately 1–2 m from the artificial reef structures to minimize the possibility of entanglement.

Transect placement on natural banks was guided by georeferenced multibeam maps of bank bathymetry. Transects typically started at the upper limit of the nepheloid layer on the bank slope, ascended over the terraces and across the reef crest, and continued down the slope to the upper limit of the nepheloid layer on the opposite side. Accordingly, ROV transects generally spanned the range of habitat zones present at each natural bank surveyed. We used direct observations from these ROV transects to document the fish communities inhabiting the five natural banks surveyed. The ROV maintained a consistent camera tilt, viewing angle (105°), and height above the bank (~1 m). Visual field width was estimated by using the laser scale to measure the field of view at approximately fixed intervals along the transects. Measurements were then averaged to provide a visual field width for each transect. Visual field width (~3.5 m) and ROV speed (0.1 m/s) during natural bank surveys were the same as those for CRT surveys on artificial reefs except when the ROV occasionally paused to photograph species with uncertain identification or to obtain collections of rock, coral, or other invertebrate fauna.

Recorded video was examined in the laboratory by two independent viewers. Viewing began as soon as the ROV entered the water and ended when the ROV surfaced. Fish were identified to the lowest possible taxon, enumerated, and recorded each time they entered the field of view. If directionality of large schools was

apparent, enumeration was completed by viewing paused frames in succession and then summing the counts. Time of day, depth, salinity, temperature, and ROV heading were also recorded with each count. Species-specific counts produced by the two viewers were compared and jointly reviewed only if the counts differed by more than 5%. For each survey, we generated a minimum count (MinCount) for each species that was observed (i.e., the minimum number of individuals that were present during the survey). The MinCount, also commonly referred to as MaxN, is a conservative metric that minimizes the probability of double-counting. It represents the maximum number of individuals on the screen at any one time during the survey, and its use as an index of relative abundance is widespread throughout the literature (Ellis and DeMartini 1995; Cappo et al. 2004; Wells and Cowan 2007; Campbell et al. 2015; Ajemian et al. 2015a, 2015b).

Community analyses.—We began our comparison of fish communities on artificial reefs and natural banks by assessing species frequency of occurrence and by identifying and enumerating species that were unique to either habitat. Patterns of diversity were investigated using traditional diversity measures, including species richness, the Shannon diversity index (H'), and Pielou's evenness index (J'). Diversity metrics were calculated using the DIVERSE routine in Primer version 7 (Clarke and Warwick 2001). Potential differences in richness, H' , and J' between artificial reefs and natural banks were tested using Welch's t -test. MinCounts were examined for each species within each ROV survey.

Patterns in the observed fish community data were investigated with multivariate methods in Primer version 7 (Clarke et al. 2014a). Species-specific MinCounts were first square-root transformed to downweight the contribution of dominant species to subsequent analyses. These data were then converted into a resemblance matrix by using Bray–Curtis similarities. Nonmetric multidimensional scaling (NMDS) was run on the resemblance matrix to visually assess group structure among our samples. Overall effects of habitat type on the observed reef fish communities were tested with permutational multivariate ANOVA (PERMANOVA; Anderson 2001). We used a one-way design to test the null hypothesis that there was no difference in fish community structure between artificial and natural habitats. Species-specific contributions to the observed similarity within or dissimilarity between habitats were investigated with similarity percentage (SIMPER) analysis (Clark 1993). We followed this analysis with hierarchical agglomerative clustering (via CLUSTER) and similarity profile (SIMPROF) testing to determine whether it was appropriate to interpret the resulting NMDS groupings. We used SIMPER to identify which species were responsible for the variation among resulting groups. Because species do not arrive independently in samples (Clarke et al. 2006), we also performed an inverse analysis (e.g., Field et al. 1982) to determine whether species were positively associated in our samples (i.e., whether the MinCounts fluctuated in proportion across samples). Prior to beginning this analysis, we used type 2 SIMPROF testing to evaluate the null hypothesis that species were not associated with

each other (Sommerfield and Clark 2013). The species-specific count data set was reduced to include only those species with MinCounts that accounted for over 5% in any one sample. A species similarity matrix was then created using standardized species counts and Whittaker's index of association (Whittaker 1952). Hierarchical agglomerative clustering in combination with type 3 SIMPROF testing were used to evaluate the null hypothesis that species were coherently associated (Sommerfield and Clarke 2013). The MinCounts of identified species groups were visualized in a shade plot to qualitatively describe species' associations with habitat and habitat characteristics (Clarke et al. 2014b).

Considering that our surveys spanned two distinct habitats with varying physical characteristics, we performed additional analyses to determine whether abiotic factors, including structure depth (i.e., depth to the top of the reef or bank), bottom depth, relief, reef area, and survey water temperature (i.e., taken as the temperature at the median depth of all fish observations; Table 1), potentially influenced the fish communities we observed. Abiotic data were normalized and converted to a resemblance matrix based on Euclidean distance measures. We conducted a RELATE test to assess the agreement between the biotic and abiotic resemblance matrices. Given a significant RELATE test, we then performed a BEST analysis (i.e., BIO-ENV) to determine which combination of abiotic factor(s) best explained the variation in observed reef fish communities (i.e., highest Spearman's rank correlation coefficient ρ ; Clarke 1993; Clarke and Ainsworth 1993). All tests of significance were conducted using an α value of 0.05.

Red Snapper density estimates.—We estimated Red Snapper density on artificial reefs and natural banks within the study area by using standardized transects from the previously described ROV community surveys. We standardized the abundance estimates by estimating the area surveyed (mean visual field width \times transect length). Visual field width was estimated as described for community transects, and transect length was estimated from the USBL position data. On artificial reefs, 40-m transects (the approximate length of a toppled RTR structure) representing subsets of the entire CRT used for analysis of community structure were selected if the ROV was traveling (1) forward at a constant speed (0.1 m/s) and (2) along an approximately straight path. To control visual field width, only Red Snapper that were within 1 m of the outer plane of the reef were counted (i.e., fish were not counted if they were >1 m inside the reef). We chose these criteria to help minimize double-counting of fish and to allow better estimates of the surface area surveyed, thus providing more accurate density estimates. Generally, transects at artificial reefs were located along piles (toppled RTR structures) or crossbeams (partially removed RTR structures) close to the benthos because the ROV often traveled along these features as it moved from one side of the structure to the next. One transect was analyzed for each structure that was surveyed at an artificial reef site (i.e., two transects were possible at the artificial reefs where two structures were surveyed and where the ROV path during the CRT met the two criteria described above). On the natural banks,

transects included the entire distance surveyed from the base of the structure, across the bank crest, and down to the opposite base. Red Snapper counts from the community data set (i.e., counts that fell within transect start and end times) were summed to generate a total Red Snapper count for each transect. This total count was then divided by the surface area of each transect surveyed to estimate Red Snapper density (number of individuals/m²). Because we had a limited number of transects (artificial reefs: $n = 8$ transects; natural banks: $n = 5$ transects), nonparametric bootstrapping with replacement ($n = 1,000$) was used to generate bias-adjusted 95% confidence intervals for Red Snapper density without making assumptions about the population distribution (Efron 1987; Efron and Tibshirani 1993). We used the nonparametric bootstrap test for equality ($n = 1,000$) to determine whether there was statistical evidence that mean Red Snapper density differed between artificial reef and natural bank habitats (Bowman and Azzalini 1997). Significance of differences was assessed at an α value of 0.05. All analyses of Red Snapper density were carried out in R version 3.2.3 (R Core Team 2015) using functions from the “boot” (Canty and Ripley 2015) and “sm” (Bowman and Azzalini 2014) packages. Total Red Snapper abundance at each site was calculated by multiplying the known area (m²; i.e., the “footprint”) of a given bank or reef site by the density estimate (fish/m²) for that site. Average total abundance was also calculated for each habitat type.

RESULTS

Community Analyses

Video-based surveys from the ROV deployments resulted in 22.2 h of footage. Survey times at artificial reef sites (mean = 118.0 min) and natural banks (mean = 148.8 min) were similar (Welch's t -test: $t = 2.78$, $df = 4$, $P = 0.324$), and these surveys were successful in documenting 79 species representing 28 families (48 species at artificial reefs and 51 species at natural reefs; Table 2). We observed the highest species richness at Baker Bank, with 33 species. Among artificial sites, BA-A-132 had the highest richness, with 30 species observed. The lowest species richness was observed at the southernmost natural sites: Blackfish Ridge (15 species) and Harte Bank (16 species). Water temperatures among survey sites ranged from 20.1°C to 29.2°C at the natural banks and from 23.1°C to 28.2°C at the artificial reefs. Survey water temperatures ranged from 22.9°C to 25.5°C at the natural bank sites and from 27.0°C to 27.3°C at the artificial reef sites (Table 1). Salinity was similar at both habitats and averaged 36.5 psu.

Interestingly, no single species was observed at all 10 sites; however, five species were observed at eight or nine sites, including economically important species like the Red Snapper (9 sites), Greater Amberjack (8 sites), and Almaco Jack (8 sites; Table 2). Many of the documented species were only observed at one of the habitat types we surveyed. For example, 28 species, including seven species of carangid, were observed at artificial reef sites but not at natural banks. Conversely, 31 species were documented on natural banks but not at artificial reefs; these

included eight species of small serranid (e.g., the Wrasse Basslet, Roughtongue Bass, and several *Serranus* spp.) and three species of pomacentrid damselfish (Purple Reef fish, Sunshinetail, and Yellowtail Reef fish). Twenty species of fish occurred on both artificial and natural habitats. Included in this group was the invasive Red Lionfish, which was observed at one artificial reef (BA-A-132) and one natural bank (Baker Bank). Species richness was not significantly different between habitats ($t = 2.78$, $df = 8$, $P = 0.860$). Diversity was generally higher at natural banks (mean $H' = 2.31$, $SE = 0.09$) than at artificial reefs (mean $H' = 1.98$, $SE = 0.14$; Table 2). We observed the highest diversity at Baker Bank ($H' = 2.59$) and the lowest diversity at PN-A-58, an artificial reef ($H' = 1.73$); however, the effect of habitat type on H' was not significant ($t = 2.31$, $df = 8$, $P = 0.078$). Similarly, J' was also higher on natural banks (mean $J' = 0.74$, $SE = 0.04$) than on artificial reefs (mean $J' = 0.62$, $SE = 0.03$), but statistical evidence for an effect of habitat type on J' was marginal ($t = 2.31$, $df = 8$, $P = 0.056$).

Species-specific MinCounts were highly variable between and within habitats. At artificial reefs, proportional counts were dominated by pelagic schooling species, such as the Horse-eye Jack, Blue Runner, Bar Jack, Rainbow Runner, and Lookdown. On average, the pelagic schooling group accounted for 47% of the total counts at artificial reefs, but among surveys this group represented as little as 3% (BA-A-132) or as much as 77% (PN-A-72) of the total count. At natural bank sites, pelagic schooling carangids accounted for less than 1% of the total counts. As a group, federally managed lutjanids, including the Red Snapper, Gray Snapper, and Vermilion Snapper, accounted for similar proportions of the total fish counts at artificial and natural sites (20% and 21%, respectively), despite the fact that Gray Snapper were not observed during any of the natural bank surveys. The MinCounts of federally managed species were highly variable among sites and between habitats (Table 3). Vermilion Snapper MinCounts ranged widely among artificial sites: from a high of 255 fish at BA-A-28 to a low of zero at two different sites. The highest Vermilion Snapper MinCount at natural habitats was observed at Aransas Bank (76 fish). Red Snapper were observed at all five artificial reefs, with MinCounts ranging from 4 fish at PN-A-72 to as many as 65 fish at BA-A-132. Red Snapper were observed at four of the five natural bank sites, with the highest MinCounts occurring at Aransas Bank (31 fish) and Baker Bank (22 fish). Although no Gray Snapper were observed on the natural banks we surveyed, as many as 95 individuals were observed on artificial reefs (PN-967). Gray Triggerfish occurred sporadically in our surveys, and MinCounts never exceeded 2 individuals at either habitat type. Greater Amberjacks were consistently found in low numbers across both habitat types, with the highest MinCount (8 fish) recorded at Harte Bank—the deepest site surveyed in this study.

Ordination using NMDS revealed clear grouping of reef fish communities by habitat type (Figure 2). When tested using PERMANOVA, the effect of habitat type on reef fish community structure was significant ($F_{1, 8} = 6.54$, $P = 0.007$). The SIMPER analysis revealed that this divergence was driven

TABLE 2. Record of the various fish taxa that were observed during remotely operated vehicle surveys at five natural banks and five artificial reef sites in the Gulf of Mexico along the Texas shelf during fall 2012.

Family, species, or metric	Natural banks					Artificial reefs				
	Baker	Aransas	Dream	Blackfish	Harte	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967
Acanthuridae										
Blue Tang <i>Acanthurus coeruleus</i>						X				
Doctofish <i>Acanthurus chirurgus</i>						X				
Apogonidae										
Twospot Cardinalfish <i>Apogon pseudomaculatus</i>			X	X	X					
Balistidae										
Gray Triggerfish <i>Balistes caprisicus</i>		X		X		X				X
Carangidae										
African Pompano <i>Alectis ciliaris</i>						X				X
Bar Jack <i>Caranx ruber</i>										
Black Jack <i>Caranx lugubris</i>						X			X	
Blue Runner <i>Caranx crysos</i>						X		X	X	
Crevalle Jack <i>Caranx hippos</i>						X		X	X	
Horse-eye Jack <i>Caranx latus</i>						X		X	X	
Yellow Jack <i>Caranx bartholomaei</i>						X		X	X	
Rainbow Runner <i>Elagatis bipinnulata</i>						X		X	X	
Lookdown <i>Selene vomer</i>		X						X	X	
Almaco Jack <i>Seriola rivoliana</i>		X	X		X	X		X	X	
Greater Amberjack <i>Seriola dumerili</i>		X	X	X	X	X		X	X	
Carcharhinidae										
Sandbar Shark <i>Carcharhinus plumbeus</i>		X								
Chaetodontidae										
Banded Butterflyfish <i>Chaetodon striatus</i>	X									X
Reef Butterflyfish <i>Chaetodon sedentarius</i>	X		X	X	X			X		X
Spotfin Butterflyfish <i>Chaetodon ocellatus</i>		X				X		X		X
Bank Butterflyfish <i>Prognathodes aya</i>			X							
Ephippidae										
Atlantic Spadefish <i>Chaetodipterus faber</i>						X		X		X
Epinephelidae										
Atlantic Goliath Grouper <i>Epinephelus itajara</i>						X		X		X
Rock Hind <i>Epinephelus adscensionis</i>	X							X		X
Black Grouper <i>Mycteroperca bonaci</i>	X							X		X
Groupers <i>Mycteroperca</i> spp.	X							X		X
Scamp <i>Mycteroperca phenax</i>		X						X		X

TABLE 2. Continued.

Family, species, or metric	Natural banks					Artificial reefs				
	Baker	Aransas	Dream	Blackfish	Harte	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967
Yellowmouth Grouper <i>Mycteroperca interstitialis</i>							X			
Atlantic Creolefish <i>Paranthias furcifer</i>						X	X	X	X	X
Gobiidae										
White-eye Goby <i>Bollmannia boqueronensis</i>			X							
Neon Goby <i>Elacatinus oceanops</i>	X									
Haemulidae										
Porkfish <i>Anisotremus virginicus</i>										X
Tomtate <i>Haemulon aurolineatum</i>						X	X			X
Holocentridae										
Squirrelfish <i>Holocentrus adscensionis</i>	X		X	X	X					
Deepwater Squirrelfish <i>Sargocentron bullisi</i>	X	X	X							
Kyphosidae										
Bermuda Chub <i>Kyphosus saltatrix</i>						X				
Labridae										
Spanish Hogfish <i>Bodianus rufus</i>						X	X	X	X	X
Spotfin Hogfish <i>Bodianus pulchellus</i>	X	X	X	X		X	X	X	X	X
Creole Wrasse <i>Clepticus parrae</i>							X			
Greenband Wrasse <i>Halichoeres bathyphilus</i>	X	X	X							
Parrotfish <i>Sparisoma</i> spp.							X			
Bluehead <i>Thalassoma bifasciatum</i>							X			
Lutjanidae										
Gray Snapper <i>Lutjanus griseus</i>						X	X	X	X	X
Lane Snapper <i>Lutjanus synagris</i>		X								
Red Snapper <i>Lutjanus campechanus</i>	X	X	X		X	X	X	X	X	X
Yellowtail Snapper <i>Ocyurus chrysurus</i>										
Vermilion Snapper <i>Rhomboplites aurorubens</i>	X	X	X			X	X	X	X	X
Muraenidae										
Spotted Moray <i>Gymnothorax moringa</i>	X									
Ostraciidae										
Scrawled Cowfish <i>Acanthostracion quadricornis</i>								X		
Pomacanthidae										
Cherubfish <i>Centropyge argi</i>	X			X						
Blue Angelfish <i>Holacanthus bermudensis</i>	X	X		X		X	X	X	X	X
Queen Angelfish <i>Holacanthus ciliaris</i>	X			X		X	X	X	X	X

TABLE 2. Continued.

Family, species, or metric	Natural banks					Artificial reefs				
	Baker	Aransas	Dream	Blackfish	Harte	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967
Townsend Angelfish <i>Holacanthus</i> sp.						X				
French Angelfish <i>Pomacanthus paru</i>	X	X				X				
Pomacentridae										
Brown Chromis <i>Chromis multilineata</i>		X	X	X			X			
Purple Reeffish <i>Chromis scotti</i>	X	X	X	X						
Sunshinefish <i>Chromis insolata</i>	X	X	X	X						
Yellowtail Reeffish <i>Chromis enchrysur</i>	X	X	X	X						
Bicolor Damselfish <i>Stegastes partitus</i>	X	X	X	X			X	X	X	X
Damselfish <i>Stegastes</i> spp.										
Priacanthidae										
Bigeye <i>Priacanthus arenatus</i>	X	X	X	X	X					
Short Bigeye <i>Pristigeyus alta</i>	X	X	X							
Ptereleotridae										
Blue Dartfish <i>Ptereleotris calliura</i>	X	X	X							
Rachycentridae										
Cobia <i>Rachycentron canadum</i>								X		X
Sciaenidae										
Jackknife-fish <i>Equetus lanceolatus</i>		X								
Cubbyu <i>Pareques umbrosus</i>	X	X								
Scorpaenidae										
Red Lionfish <i>Pterois volitans</i>	X								X	
Serranidae										
Threadnose Bass <i>Choranthias tenuis</i>	X		X		X					
Candy Basslet <i>Liopropoma carmabi</i>	X									
Wrasse Basslet <i>Liopropoma eukrines</i>	X	X	X	X	X					
Roughtongue Bass <i>Pronotogrammus martinicensis</i>	X	X	X	X	X					
Freckled Soapfish <i>Rypticus bistrispinus</i>		X			X					
Orangeback Bass <i>Serranus annularis</i>	X									
Snow Bass <i>Serranus chionarata</i>			X							
Tattler <i>Serranus phoebe</i>	X	X	X		X					
Sparidae										
Sheepshead <i>Archosargus probatocephalus</i>						X				X
Porgies <i>Calamus</i> spp.		X		X						
Sphyraenidae										
Great Barracuda <i>Sphyraena barracuda</i>						X	X	X	X	X

TABLE 2. Continued.

Family, species, or metric	Natural banks					Artificial reefs				
	Baker	Aransas	Dream	Blackfish	Harte	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967
Synodontidae			X							
Inshore Lizardfish <i>Synodus foetens</i>					X					
Tetraodontidae										
Pufferfish <i>Canthigaster</i> sp.	X	X	X		X					
Species richness (total = 79 species)	33	32	26	15	16	26	30	20	18	24
Shannon diversity (H')	2.589	2.354	2.146	2.366	2.106	1.892	2.518	1.730	1.960	1.790
Pielou's evenness (J')	0.741	0.679	0.659	0.874	0.760	0.581	0.740	0.577	0.678	0.563

TABLE 3. Relative abundance (i.e., minimum counts [MinCounts]) of five federally managed species observed during remotely operated vehicle surveys of artificial reefs and natural banks in the western Gulf of Mexico, fall 2012.

Species	Artificial reefs					Natural banks				
	BA-A-28	BA-A-132	PN-A-58	PN-A-72	PN-967	Baker	Aransas	Dream	Blackfish	Harte
Gray Snapper	15	37	0	9	95	0	0	0	0	0
Gray Triggerfish	2	0	0	0	2	0	1	0	1	0
Greater Amberjack	3	5	1	1	0	0	1	2	2	8
Red Snapper	7	65	10	4	32	22	31	1	0	3
Vermilion Snapper	255	3	0	21	0	39	76	5	0	0

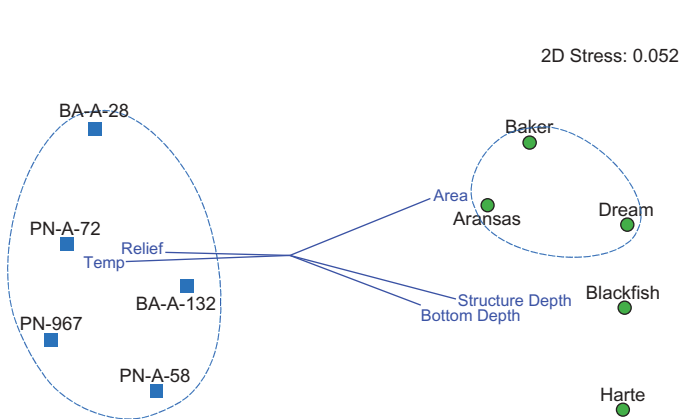


FIGURE 2. Nonmetric multidimensional scaling ordination using square-root-transformed minimum counts (MinCounts) and Bray–Curtis similarities from remotely operated vehicle surveys of artificial reefs (blue squares) and natural banks (green circles) in the western Gulf of Mexico. Significant groups determined with similarity profile testing ($P < 0.005$) are denoted by the dashed ellipses. The relationships among the five habitat variables (Temp = temperature) tested with BIO-ENV are displayed in the blue vector plot.

by gregarious or schooling species, such as the Horse-eye Jack, Atlantic Spadefish, Lookdown, and Vermilion Snapper, all of which were more abundant on artificial reefs (Table 4). A subsequent cluster analysis of the samples with SIMPROF testing ($P < 0.005$) revealed four groups with distinct community structure: an artificial reef group containing all artificial reef sites (37% similarity), a group containing the three northernmost natural banks (i.e., Baker, Aransas, and Dream banks; 57% similarity) and two groups containing only one site each (i.e., Blackfish Ridge and Harte Bank; Figure 2). Investigation of these groups with SIMPER suggested that differences in community structure between the artificial reef group and each of the three natural bank groups were driven by higher contributions of pelagic schooling species. Higher MinCounts of Vermilion Snapper, Purple Reefish, and Red Snapper at the three northernmost natural banks differentiated that group from Blackfish Ridge. A prevalence of Threadnose Bass and a lack of pomacentrid damselfishes at Harte Bank distinguished this single-site group from Blackfish Ridge and the other natural bank group (i.e., the three northernmost banks).

TABLE 4. Species that contributed most to the dissimilarity between artificial reefs and natural banks surveyed in the western Gulf of Mexico during fall 2012. Mean abundance in each habitat ($Mean_{Artificial}$ and $Mean_{Natural}$), contribution to mean dissimilarity (DIS), the dissimilarity : SD ratio (DIS : SD), and the percent contribution of species derived via similarity percentage analysis using a 50% cut-off for cumulative percent contribution are presented.

Species	$Mean_{Artificial}$	$Mean_{Natural}$	DIS	DIS : SD	Contribution (%)	Cumulative contribution (%)
Horse-eye Jack	7.42	0.00	7.15	1.40	8.57	8.57
Atlantic Spadefish	5.24	0.00	4.28	1.10	5.13	13.69
Lookdown	4.62	0.20	4.21	0.79	5.04	18.73
Vermilion Snapper	4.46	3.43	4.18	1.14	5.01	23.74
Gray Snapper	4.54	0.00	3.93	1.29	4.71	28.45
Blue Runner	4.83	0.00	3.90	0.78	4.68	33.12
Rainbow Runner	3.78	0.00	3.24	1.10	3.88	37.01
Purple Reefish	0.00	3.67	3.10	1.41	3.71	40.72
Atlantic Creolefish	3.04	0.00	2.90	1.51	3.47	44.19
Red Snapper	4.31	2.59	2.68	1.29	3.21	47.40
Sunshinefish	0.00	2.58	2.19	1.82	2.62	50.02

Our inverse analysis generated strong evidence of an association among species observed in our surveys, thus warranting further investigation (type 2 SIMPROF: π [sum of absolute departures of observed profile from mean profile under H_0] = 2.19, $P < 0.001$). After the removal of rare species (i.e., those that contributed $<5\%$ in any one sample), 22 species were retained for further analysis. Clustering based on the resulting species similarity matrix and type 3 SIMPROF testing ($P < 0.001$) identified four species groups whose member species co-occurred in a similar fashion throughout our surveys (Figure 3). The first group (group A in Figure 3) contained many of the gregarious or schooling species that could potentially be found in extremely high abundances at artificial reefs and that—with the exception of Vermilion Snapper—were not observed at natural banks. The second group (group B in Figure 3) included Red Snapper and several other fisheries species that were generally detected at both habitats but were usually found in higher abundances at artificial reefs (with exceptions). The third group of species (group C in Figure 3) typified natural bank habitats and comprised the Reef

Butterflyfish, three pomacentrid damselfish species, and Roughtongue Bass. Generally, these species were consistently observed across all natural bank sites and, with the exception of Reef Butterflyfish, were not observed on artificial reefs. The final species group identified (group D in Figure 3) contained a single species, the Threadnose Bass, which was observed only on natural banks and exhibited high abundances only on Harte Bank.

There was significant agreement between biotic and abiotic similarity matrices (RELATE: $\rho = 0.76$, $P = 0.001$). Among the five abiotic variables tested, the BEST analysis (BIO-ENV) suggested that structure depth and survey temperature best matched the observed patterns in reef fish communities ($\rho = 0.78$, $P < 0.001$). Spearman's ρ for individual variables was greater for structure depth ($\rho = 0.78$) than for survey temperature ($\rho = 0.68$).

Red Snapper Density Estimates

Red Snapper density was estimated from eight transects on artificial reefs and from five transects on natural banks. The

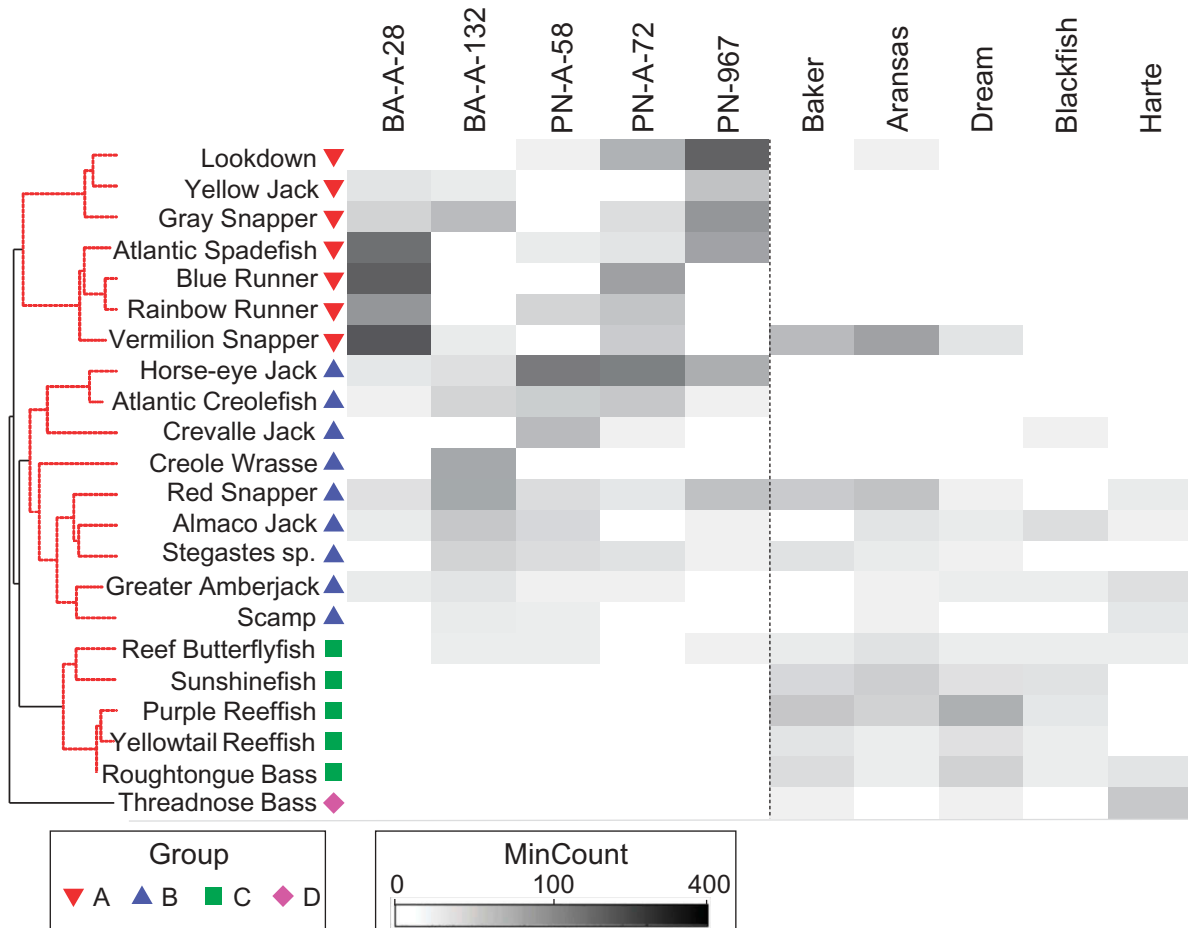


FIGURE 3. Shade plot of square-root-transformed species counts (only species accounting for $\geq 5\%$ of the total counts in any one sample are shown) by sample site in the western Gulf of Mexico. The linear gray scale shows back-transformed minimum counts (MinCounts). The dendrogram on the left displays the hierarchical clustering of species groups based on Whittaker's (1952) index of association resemblances computed on species-standardized MinCounts. Species groups identified using type 3 similarity profile testing ($P < 0.001$) are indicated by connected red lines in the dendrogram and by the symbols displayed next to species names (e.g., red inverted triangles = group A).

bootstrap test of equality suggested that mean density at artificial reefs and natural banks was significantly different ($P = 0.011$). In fact, estimated Red Snapper density at artificial reefs (mean = 0.169 fish/m², 95% CI = 0.103–0.315) was nearly 7.8 times greater than density on natural banks (mean = 0.022 fish/m², 95% CI = 0.005–0.047; **Figure 4A**). Density estimates from artificial reefs were nearly five times more variable than those from natural banks (SD = 0.14 and 0.03, respectively; **Figure 4**). Estimated Red Snapper densities from individual transects at artificial reefs ranged from a low of 0.03 fish/m² at BA-A-28 to as high as 0.49 fish/m² at BA-A-132. Among natural banks, Blackfish Ridge had the lowest Red Snapper density (0 fish/m²), whereas Aransas Bank had the highest estimated density (0.06 fish/m²; **Figure 4B**). Total Red Snapper abundance estimates at artificial reef sites ranged from 61 fish at PN-A-72 to 2,242 fish at BA-A-132 (**Figure 5**). Mean total abundance at artificial reefs averaged 638 Red Snapper (SE = 404). Red Snapper abundance estimates at natural banks ranged from zero individuals at Blackfish Ridge to 43,788 individuals at Baker Bank and averaged 16,028 fish/bank (SE = 9,124). Scaling this estimate to the five banks examined here suggested that approximately 80,140 Red Snapper (SE = 45,620) inhabited natural bank sites at the time of the survey.

DISCUSSION

Concurrent surveys of artificial and natural habitats that provide basic information on species composition and abundance

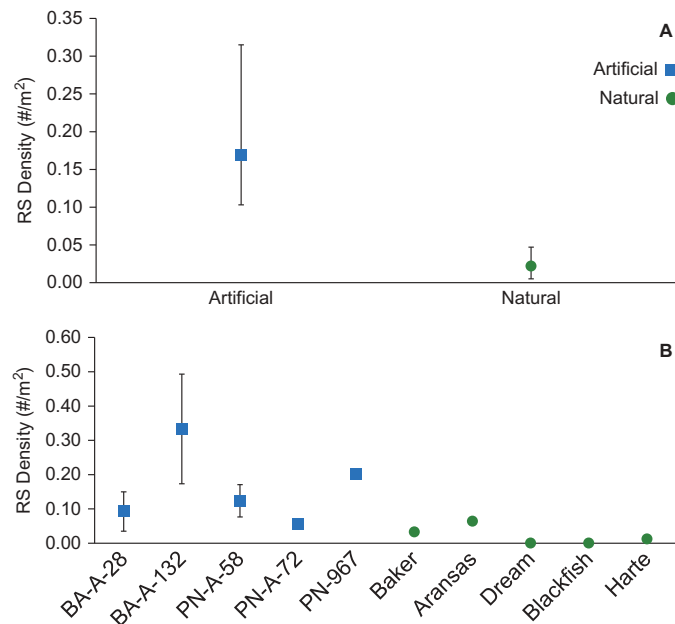


FIGURE 4. Red Snapper (RS) density estimates (number of individuals/m²) from remotely operated vehicle transects on artificial reefs (squares) and natural banks (circles) in the western Gulf of Mexico during fall 2012. Density is displayed for **(A)** each habitat type (error bars represent bootstrapped 95% confidence intervals) and **(B)** each site (error bars represent SEs for sites that had two transects) to show variation in individual estimates.

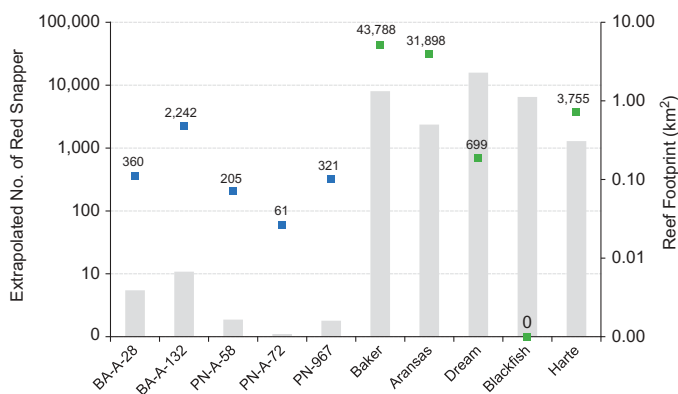


FIGURE 5. Estimated total abundance of Red Snapper (based on the site-specific density estimate multiplied by the reef area [footprint]) at artificial reefs (blue squares) and natural banks (green circles) in the western Gulf of Mexico. Reef area (gray bars) is plotted on the secondary y-axis. Note that both the number of Red Snapper and the reef area are plotted on log scales. For ease of interpretation, the estimated number of Red Snapper is printed above each data point.

are essential to gaining a better understanding of the role of artificial reefs as habitat for marine fish populations (Carr and Hixon 1997). Our study represents the first attempt to quantify the differences in fish communities at RTR artificial reefs and coralgal banks, two disparate yet understudied habitats in the western GOM. Despite the vast physical differences between these two habitats, video-based ROV methods documented 79 species of fish ranging from small, reef-dependent species to large, highly mobile apex predators. Our analyses suggested that fish communities at artificial reefs were different than fish communities at natural bank habitats—a finding that is supported by several studies of community structure in the northern GOM (Rooker et al. 1997; Wilson et al. 2003, 2006; Langland 2015). Although many species were shared between natural and artificial habitats, several reef-dependent species were only observed on natural banks, suggesting that artificial reefs may not be suitable for all species. Nevertheless, many economically important species, including Red Snapper, Vermilion Snapper, Greater Amberjack, Almaco Jack, and Scamp, were observed at both natural and artificial habitats. Furthermore, our data suggested that Red Snapper occurred in higher densities on RTR artificial reefs than natural banks, consistent with the findings of Wilson et al. (2003), who reported that Red Snapper densities at two RTR artificial reefs were higher than at the West Flower Garden Bank, where no Red Snapper were observed. The observation of invasive Red Lionfish at both natural and artificial habitats is notable given their negative impacts on native fish recruitment (Albins and Hixon 2008). Furthermore, subsequent ROV-based surveys of artificial reefs in our region indicate that Red Lionfish have become more common (Ajemian et al. 2015b); therefore, we recommend continued monitoring of these habitats to determine the Red Lionfish’s potential impacts on fish community structure.

Differences in fish community composition at RTR artificial reefs and coralgal banks were observed for several taxa—many of which were undetected or absent in surveys of one habitat or the other. For example, 31 species were only observed on natural banks, and 28 species were only observed on artificial reefs. Several species that we did not observe at the South Texas Banks but that have been recorded in the literature included the Gray Snapper (Tunnell et al. 2009), Great Barracuda (Dennis and Bright 1988), and Blue Runner (Dennis and Bright 1988). Although the majority of these presence/absence observations are likely real (e.g., the Roughtongue Bass is an obligate natural reef species), some may be attributable to varying environmental conditions, sampling effort, or our ability to detect rare, cryptic, or behaviorally secretive species (Gu and Swihart 2004). For example, at all sites except for BA-A-132, the nepheloid layer was present and generally prohibited observations from the bottom 2–6 m of structured habitat (mean nepheloid depth = 2 m at artificial reefs, 3 m at natural reefs). Thus, MinCounts for more benthic species were likely underestimated. In addition, the large ROV and its lights may have caused some species to avoid the ROV (e.g., gobies and other species that burrow or hide in crevices). In contrast, species like the Greater Amberjack appeared to be less disturbed by the presence of the ROV and sometimes swam along with the ROV for brief periods. These behaviors seemed to hold for both natural and artificial habitats; however, differences in species behavior and detectability at each habitat must be considered, as such differences may have led to bias in the resulting MinCounts and subsequent analyses.

Our community indices suggested that species richness and H' were similar at natural banks and RTR artificial reefs, supporting several previous studies (Clark and Edwards 1999; Fowler and Booth 2012). In contrast to this finding, other investigations have indicated that natural habitats support higher species richness and higher diversity than artificial habitats (Carr and Hixon 1997; Rooker et al. 1997; Patterson et al. 2014; Langland 2015). In a comparative study of fish communities in the northern GOM, Rooker et al. (1997) reported higher species richness at the Flower Garden Banks than at HI-389, a standing platform; those authors cited the increased complexity of habitats available over a larger area at the Flower Garden Banks as a possible driver of this difference. The Flower Garden Banks are well-developed coral reefs, providing significant amounts of reef habitat with high diversity (e.g., 280 fish species have been reported; Schmahl et al. 2008). However, unlike the Flower Garden Banks and other diapiric shelf-edge banks in the northern GOM, the South Texas Banks surveyed in this study are less complex, providing relatively little true “reef” habitat due to the lack of contemporary reef-building activity (Dennis and Bright 1988). The South Texas Banks also have fewer benthic habitat zones than the Flower Garden Banks—a difference that is driven largely by their comparatively low relief (e.g., Flower Garden Banks exhibit over 50 m of relief; banks in our survey averaged 13 m of relief) and consequently their more prevalent

interaction with the nepheloid layer (Rezak et al. 1985, 1990; Dennis and Bright 1988). Accordingly, lower species richness and diversity at the South Texas Banks—comparable to those at the RTR artificial reefs we surveyed—may be driven by more frequent interactions with the nepheloid layer and its associated high turbidity. Although potential differences in species detectability could also play a role, these conditions likely prevent the development of diverse epibenthic communities, which in turn may limit food and habitat availability for reef fish (Dennis and Bright 1988).

Our multivariate analyses indicated that differences in reef fish communities inhabiting RTR artificial reefs and natural banks largely resulted from high counts of schooling species, such as the Atlantic Spadefish, Vermilion Snapper, and carangids (e.g., Horse-eye Jack and Lookdown), at artificial reefs. This finding is supported by previous work in the northern GOM, which also demonstrated high abundances of transient midwater carangids (Rooker et al. 1997; Ajemian et al. 2015b), Atlantic Spadefish (Gallaway et al. 1979; Stanley and Wilson 2000), and Vermilion Snapper (Ajemian et al. 2015b) at artificial habitats. Several of these species, including the Atlantic Spadefish, Blue Runner, and Lookdown, are generally less dependent on food resources living directly on platform reefs, but they can often account for most of the fish biomass (Gallaway et al. 1979; Gallaway and Lewbel 1982; Stanley and Wilson 1997, 2000). Increased concentrations of planktonic prey near platform reefs have been attributed to local changes in hydrographic conditions associated with the high vertical relief of these structures—a finding that may explain the high abundances of these more planktivorous, reef-associated fish species at platform habitats (Hernandez et al. 2003; Keenan et al. 2003; Lindquist et al. 2005). In contrast, natural banks in our study were typified by more reef-dependent taxa, including the Purple Reef fish, Yellowtail Reef fish, Sunshinefish, Reef Butterflyfish, and small serranids, such as the Roughtongue Bass and Wrasse Basslet. Several previous studies have also identified species of this reef-dependent assemblage as characteristic of the South Texas Banks (Dennis and Bright 1988; Tunnell et al. 2009; Hicks et al. 2014). Certainly, food-web-based examination to better understand these ecological linkages is warranted.

Although artificial reef communities in this study were generally similar, our analyses suggested the relatively rare natural banks could be further divided into three groups with differing community composition: (1) the three northernmost banks (i.e., Baker, Aransas, and Dream banks); (2) Blackfish Ridge; and (3) Harte Bank. Nash et al. (2014) derived similar bank groupings based on geomorphic variables, including regional depth, shallowest depth, rugosity, number of terraces, distance to nearest neighbor, and bank area. In the present study, Harte Bank and Blackfish Ridge generally had lower species richness, possibly because of the unique physical characteristics of each site. Harte Bank differed from the

other banks we surveyed because it was located in deeper water (e.g., base depth at Harte Bank = 96 m; mean depth at the other banks = 75 m). Blackfish Ridge was unique because PN-A-72, an artificial reef surveyed in this study, was located in extremely close proximity to the main bank feature (~300 m). Interestingly, Blackfish Ridge and PN-A-72 each represented the lowest species richness of their respective habitat types. Previous work has reported that Blackfish Ridge experiences persistent high turbidity that often covers the entire bank, a condition that limits epibenthic primary production and is generally associated with lower observed species richness (Rezak et al. 1985, 1990; Dennis and Bright 1988; Tunnell et al. 2009); however, when we surveyed Blackfish Ridge, its terrace did extend out of the nepheloid layer. Nevertheless, we noticed lower MinCounts for several pomacentrid damselfishes at Blackfish Ridge, possibly an indication of nepheloid effects on benthic primary productivity. The proximity of the artificial reef to Blackfish Ridge provides another potential explanation for the lower species richness and diversity—namely that the artificial reef may concentrate high abundances of large piscivores, which in turn could negatively influence community structure by increasing predation rates (Hixon and Beets 1993; Cowan et al. 2011) or by decreasing postsettlement survival of fish that would normally recruit to the natural habitat (Carr and Hixon 1997). Despite this possibility, we documented low abundances of potential predators like Red Snapper at both of these sites. Although the effects of the nepheloid layer probably influenced the communities we observed, further investigation of the manner in which proximity to artificial reefs can affect natural reef fish communities is warranted, as new artificial reefs may fail to meet management objectives depending on their proximity to existing reef habitat (e.g., Mudrak and Szedlmayer 2012).

Environmental factors, including bottom depth and vertical relief, have often been identified as important drivers of fish community structure at natural and artificial reef habitats (Gallaway et al. 1981; Stanley and Wilson 2000; Wilson et al. 2003; Zintzen et al. 2012; Bryan et al. 2013; Patterson et al. 2014). Seminal work by Gallaway et al. (1981) classified standing platform communities across the Texas–Louisiana shelf into three groups: a coastal group (<30 m), an offshore group (30–60 m), and a blue water group (>60 m). In a more recent study of artificial reefs across the shelf in our study region, Ajemian et al. (2015b) detected a similar transition in fish communities around the 60-m isobath. Our analyses identified structure depth (i.e., the shallowest depth of structure at a site) and survey temperature as the most important factors influencing the fish communities we observed—a difference that may have been related to the bottom depths of the sites in our survey. For example, with the exception of BA-A-28, PN-967, and Harte Bank, the surveyed sites were located in bottom depths of 61–82 m rather than a wide range of depths across the shelf. Our analyses also suggested that survey temperature was important for explaining the patterns in fish

community structure, but it is difficult to assess the relative importance of structure depth and survey temperature because they were highly correlated. Specifically, survey temperature was generally warmer on artificial reefs because the CRTs spanned the greater vertical relief of the artificial reefs and thus spent more time higher in the water column. Structure depth, however, was nearly twice as shallow at artificial reefs (mean structure depth = 33 m at artificial reefs and 65 m at natural reefs). Previous studies have shown that many species responsible for the dissimilarity between the two habitats we surveyed (e.g., Atlantic Spadefish, Blue Runner, Horse-eye Jack, Lookdown, and Vermilion Snapper) are commonly found at high but variable abundances in the middle to upper portions of the water column around reefs with high vertical relief (Rooker et al. 1997; Stanley and Wilson 1997, 2000; Wilson et al. 2006; Ajemian et al. 2015a, 2015b). Similarly, the highest abundances for many of these species were observed at BA-A-28 and PN-967, two artificial reefs with the shallowest structure depths. While we recognize that bottom depth and vertical relief influence the structure depth at a site, our data support previous studies suggesting that the presence of structure high in the water column influences the occurrence and possibly the abundances of these pelagic schooling species (Wilson et al. 2003). Thus, as standing platforms are removed throughout the northern GOM, the RTR artificial reefs may become increasingly valuable habitat for these types of fish. For these reasons, we recommend that future video-based surveys for assessing fish community structure at these habitats apply more appropriate survey designs and dedicate the effort necessary to assess species that are more transient and that typically occur higher in the water column.

Species-specific habitat requirements likely influenced the occurrence of several species in our samples; we identified several species groups that occurred in a similar fashion throughout our samples. For example, species in the reef-dependent group (i.e., group C in Figure 3 [excluding Reef Butterflyfish]) only occurred at the natural banks. Bright and Rezak (1976) regarded one of these species, the planktivorous Roughtongue Bass, as the most characteristic species of the South Texas Banks. The Roughtongue Bass is reported as a common member of the deep-reef fish community and is an important forage base for larger fish, like groupers and snappers (Weaver et al. 2006). Among artificial habitats, Sheepsheads were only observed at the two shallowest sites (BA-A-28 and PN-967), aligning well with the species' life history and dependency on biofouling communities at shallower reefs (Gallaway and Lewbel 1982; Parker et al. 1994; Stanley and Wilson 1997). Collectively, the consistency with which these species appeared in our samples suggests that their association is not by chance (Somerfield and Clarke 2013). Indeed, different habitats are characterized by differing food resources, shelter, and abiotic conditions—all of which affect growth, survival, and successful recruitment—resulting

in consistent and distinct fish assemblages (Rezak et al. 1985, 1990; Dennis and Bright 1988; Beck et al. 2001; Somerfield and Clark 2013).

Our analysis of Red Snapper density at platform reefs compared to natural-bottom South Texas Banks suggested that densities at artificial reefs were nearly 7.8 times greater and were more variable than estimates from natural structure. These results are supported by other studies that have also found high but variable abundances of Red Snapper at standing platforms, likely due to the patchy nature of their populations over large expanses of structured habitat. For example, Stanley and Wilson (1997) noted that Red Snapper abundance varied up to a factor of 4 between months, a finding they attributed to Red Snapper movement away from the platform. Inferences regarding our density estimates must be made with the following considerations. First, our ability to estimate Red Snapper density was hindered by visibility constraints imposed by the nepheloid layer (Shideler 1981; Ajemian et al. 2015a). Because the Red Snapper is a demersal species that derives a portion of its food resources from soft sediments surrounding reefs (McCawley and Cowan 2007; Gallaway et al. 2009), the Red Snapper densities in our study likely represent conservative underestimates of the true densities. For example, we routinely observed Red Snapper moving into and out of the nepheloid layer, but observations within this feature were not possible due to the near-zero visibility. An exception was BA-A-132, where no nepheloid layer was present; however, even when we excluded density estimates from that site, the resulting mean Red Snapper density at artificial reefs (0.115 fish/m²) was still 5.2 times greater than the density estimated at natural banks (0.022 fish/m²). Second, our density estimates were based on relatively few transects given the nature of offshore research logistics, ship time costs, and the self-imposed sample criteria that were used to minimize double-counting. Despite these issues, our results are similar to those of previous investigations documenting higher densities of Red Snapper at artificial reefs than at natural habitats (Wilson et al. 2003, 2006; Patterson et al. 2014). Furthermore, in a comparative study of reef fish community structure at artificial and natural reefs in the northern GOM, Patterson et al. (2014) reported that Red Snapper densities were approximately 6 times greater at artificial reefs than at natural reefs—remarkably similar to our estimate of 7.8-fold. The Red Snapper total abundances we estimated at artificial reefs were also similar to the range reported by hydroacoustic surveys at standing platforms and RTR artificial reefs in the northern GOM (Stanley and Wilson 1997, 2000; Wilson et al. 2003, 2006) and to Red Snapper abundance estimates based on explosive platform removals (Gitschlag et al. 2003). However, our estimates appear low, possibly due to characteristics such as the presence of RTR structures near some of our reef sites (i.e., previous estimates of Stanley and Wilson [1997, 2000] and Wilson et al. [2003, 2006] were based on single structures). This difference could simply be attributed to

visibility constraints causing the underestimation of density, but it may also be a function of artificial reef density (i.e., the number of structures in close proximity). Strelcheck et al. (2005) observed decreasing Red Snapper abundance and size with increasing artificial reef abundance and density. Our estimates of Red Snapper density and total abundance at the five natural banks in our study suggest that at least 80,140 (likely more) Red Snapper inhabited these sites at the time of our survey (see Figure 5). If we multiply the estimated number of individuals by the average weight of Red Snapper from natural banks in our area (2.3 kg; estimated from fishery-independent vertical line surveys; M. K. Streich, unpublished data), this implies that the five natural banks held approximately 184,322 kg (406,360 lb) of Red Snapper, or approximately 5% of the GOM annual catch limit (ACL) set by the National Oceanic and Atmospheric Administration—Fisheries in 2012 (3.67 million kg [8.08 million lb]; NOAA 2012). Thus, despite higher Red Snapper densities at artificial reefs, natural banks likely support much higher total abundances of Red Snapper because of their comparatively large habitat area (i.e., footprint). Given that the stock has recovered substantially since our survey was conducted (SEDAR 2015), these Red Snapper estimates also likely underestimate the true current abundance based on visibility constraints and sampling design and because our survey was performed in 2012.

Our estimate of Red Snapper total abundance on the five relatively small natural banks (i.e., total area of the five banks = 5.55 km²; Table 1), which account for less than 0.4% of the estimated natural reef habitat area in the northern GOM (1,578 km²; Gallaway et al. 2009), indicates that the natural banks in this region likely hold a large biomass of Red Snapper. Thus, these areas warrant further investigation, particularly given the Red Snapper management uncertainties in the GOM. Moreover, there are hundreds of known bathymetric features scattered across the northern GOM shelf (Ludwick and Walton 1957; Rezak et al. 1985; Shroeder et al. 1988, 1995; Weaver et al. 2001; Rooker et al. 2004; Dufrene 2005; VERSAR 2009). Although the vast majority of these features have yet to be characterized, many are well known from anecdotal fishing reports to harbor large concentrations of Red Snapper. Moreover, many features have not yet been discovered; for example, a prominent unknown bank—now formally known as Harte Bank—was described and mapped during this cruise. Although Harte Bank was the smallest natural bank surveyed in this study (0.31 km²), it represents a significant bathymetric feature and highlights the likelihood of additional unmapped natural reef habitat for Red Snapper in the GOM.

The dynamics between natural and artificial reefs may also have important implications for reef fish management. Other work has shown that fishing mortality and fish density are not equally distributed between artificial and natural habitats, with natural banks often serving as a refuge from at least some fishing mortality. The fishing mortality refuge provided by known and unknown natural banks may to some extent explain the observed

lack of a clear spawner–recruit relationship in this Red Snapper population (Cowan et al. 2011; SEDAR 2015). For example, Garner and Patterson (2015) observed that for-hire captains fishing during the open Red Snapper season targeted artificial reef sites. Consequently, fishing mortality may often be concentrated at artificial reefs (Polovina 1991; Grossman et al. 1997; Garner and Patterson 2015). Although fishing mortality can be quite high at these habitats (e.g., Addis et al. 2016), artificial reefs have the potential to divert fishing effort away from more sensitive natural habitats and—based on the findings here—away from a large portion of the Red Snapper population in the western GOM. This inference is supported by a recent survey of recreational anglers in Texas, which suggested that over 70% of the anglers used artificial reefs, with nearly 40% of these anglers targeting standing platforms (Schuett et al. 2015). Moreover, in a GOM-wide study, Porch et al. (2015) observed the highest Red Snapper spawning frequencies at natural habitats in our region, further highlighting the potential benefits of the RTR artificial reefs and the diversion of fishing pressure away from natural habitats. Although more detailed study of fishing effort among habitat types is needed, these findings certainly reveal several management implications for RTR habitats versus natural banks. As the number of standing platforms in the GOM continues to decline (Pulsipher et al. 2001), RTR artificial reefs will likely become increasingly important for supporting the Red Snapper fishery in the northwestern GOM, which in recent decades has relied on the abundance of standing platforms and the habitat they provide. Subsequently, future levels of fishing effort at natural habitats may increase if the amount of RTR habitat or other artificial habitat available to fishermen does not replace the current abundance of standing platforms. Nonetheless, we caution against strict interpretation of our estimates for direct management advice due to the relatively small sample size and restricted geography. However, the estimates clearly point to the beneficial aspects of both natural and artificial reef effects on fisheries species, such as Red Snapper, in the GOM. We recommend that future surveys increase replication and geographic coverage of natural and artificial reefs to gain better estimates across the northern GOM. Although our study provides new information necessary for evaluating the effects of RTR artificial reefs in comparison with natural bank habitats of the western GOM, we stress the need for additional comparisons of species-specific life history traits (e.g., reproductive potential, age distribution, growth, mortality, and site fidelity) at artificial and natural habitats as well. Only with more thorough characterization of these habitat types and comparative performance metrics will it be possible to fully understand the value and function of natural and artificial reefs as fish habitat.

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