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PRIMARY RESEARCH PAPER

Fish assemblage structure on a drowned barrier island in the northwestern Gulf of Mexico

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Abstract We investigated the assemblage structure of fishes associated with different habitats (inshore mud, shell bank, and offshore mud) over a drowned barrier island, Freeport Rocks Bathymetric High, on the inner continental shelf of the northwestern Gulf of Mexico (NW Gulf). Density data from otter trawls were used to examine spatial (habitat and site) and temporal differences in fish assemblage structure using multi- and univariate procedures. Eight species accounted for 69% of the total composition and in order of decreasing abundance included shoal flounder (*Syacium gunteri*), dwarf sand perch (*Diplectrum bivittatum*), red snapper (*Lutjanus campechanus*), least puffer (*Sphoeroides parvus*), silver seatrout (*Cynoscion nothus*), largescale lizardfish (*Saurida brasiliensis*), silver jenny (*Eucinostomus gula*), and sand seatrout (*Cynoscion arenarius*). Multivariate results indicated fish assemblage structure differed among habitats (ANOSIM; Global $R = 0.190$, $P < 0.001$) and survey dates (ANOSIM; Global $R = 0.541$, $P < 0.001$); however, differences among sites were negligible (ANOSIM; Global $R = -0.015$, $P = 0.749$). Highest densities of dwarf sand perch and least puffer were found on the shell bank, while densities of shoal flounder, largescale lizardfish, and silver jenny were highest on offshore mud. In addition, smallest sizes and highest densities of six of the eight abundant species were found in July, suggesting an important period for juvenile fishes. Diversity indices also varied relative to habitat with highest Shannon diversity (H') and species richness (S) values for fishes associated with the shell bank. Results of this study highlight the importance of a mosaic of habitat types to fish assemblages on a drowned barrier island in the NW Gulf.

Keywords Diversity · Fish assemblage structure · Freeport Rocks Bathymetric High · Habitat

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Introduction

Drowned barrier islands and natural banks are prominent features on the inner continental shelf of the northwestern Gulf of Mexico (NW Gulf) (Rezak et al., 1990). Several drowned barrier islands on the inner continental shelf of Texas represent relic depositional environments, and paleoenvironmental analyses of these natural banks indicate the original

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deposition in an estuarine environment with oyster beds (*Crassostrea virginica*) and other shell fragments as dominant features (Rodriguez et al., 2000). Areas of oyster beds combined with a gradation of depths and a variety of substrate types (i.e., mud, sand, and shell) over these drowned barrier islands provide important habitat to fishes and invertebrates on the inner continental shelf. Several studies have shown certain fishes occupy coarse substrates, such as packed sand or shell rubble, while others inhabit fine silt or mud-bottom habitat (Allen & Baltz, 1997; Ellis et al., 2000; Sullivan et al., 2000). In the NW Gulf, sediment discharged from the Mississippi River creates extensive mud-bottom habitat for many species, while others are found over non-mud substrates such as shell rubble (Rezak et al., 1990). As such, knowledge of the fishes associated with discrete habitats is an important first step in delineating essential fish habitat (EFH).

The role of habitat-mediated processes in post-settlement survival of continental shelf species has received increasing attention (Eggleston, 1995; Tupper & Boutilier, 1995; Rooker et al., 2004). Habitat selection may vary as a function of predation pressure and prey availability (Auster et al., 1997), physiological constraints (Allen & Baltz, 1997; Kupschus & Tremain, 2001), and physical processes (Boehlert & Mundy, 1988). Several studies have found positive relationships of both fish abundance and diversity with increasing structural complexity (Fraser et al., 1996; Rooker & Holt, 1997; Ohman & Rajasuriya, 1998), and abundance and diversity of associated prey items (Ohman & Rajasuriya, 1998; Harding & Mann, 2001). Thus, complexity afforded by structured habitats (i.e., oyster shell, sand ridges) may serve as physical and visual barriers between predators and prey, enhancing early life survival and recruitment (Eggleston, 1995; Rooker et al., 1998; Linehan et al., 2001).

The goals of this study were to characterize spatial and temporal patterns of habitat use for fishes associated with a drowned barrier island off the Texas coast. Specifically, fish assemblage structure was investigated over different habitats (inshore mud, shell bank, and offshore mud) associated with the Freeport Rocks Bathymetric High (FRBH). Density and size structure of the most common species were used to evaluate the importance of different habitats used by post-settled fishes in the NW Gulf.

Materials and methods

Study site

This study was conducted on a drowned barrier island, Freeport Rocks Bathymetric High (FRBH), and adjacent mud-bottom substrates located on the inner continental shelf of the NW Gulf (Fig. 1). FRBH is a relic barrier island with radiocarbon dating suggesting the bank to be 37,000–45,000 years old (Rodriguez et al., 2000). This bathymetric high runs northeast to southwest for $\sim$20 km with the ridge crest located between 15 and 20 m depth. FRBH was surveyed and mapped using a Global Positioning System (GPS) integrated side scan sonar (Edgetech 272 TD at 500 kHz) (Mikulas & Rooker, 2008). Results indicated substrates along the crest were composed of shell hash and sand with patches of relic oyster beds, while adjacent mud bottom was present on both the inshore and offshore areas surrounding the ridge crest.

Sampling methodology

Seven trawl surveys were performed from May to December of 2000. The study area was evenly divided into three sites: northern, central, and southern with three habitats (inshore mud, shell bank, and offshore mud) at each site. Two replicate trawl tows were performed over each habitat within each site, totaling 18 trawl tows per survey date. Trawling was conducted using a 6-m otter trawl with a 2-cm stretch mesh, a 1.25-cm mesh liner, and 0.6-cm tickler chain. Each trawl was towed 10 min in duration at a speed of 2.5 knots during daylight hours only (07:00–18:00 h), and direction was always against prevailing currents to standardize speed. GPS coordinates were taken at the beginning and end of each trawl to calculate the area sampled. Bottom water mass characteristics (temperature, salinity, and dissolved oxygen content) were measured at each sample location with a Hydrolab Scout. Trawl samples were sorted on board, and fishes were immediately frozen. All fishes captured during trawl surveys were identified to species and measured to the nearest mm standard length (SL).

Data analysis

Fish assemblage data were analyzed with the Plymouth Routines in Multivariate Ecological Research

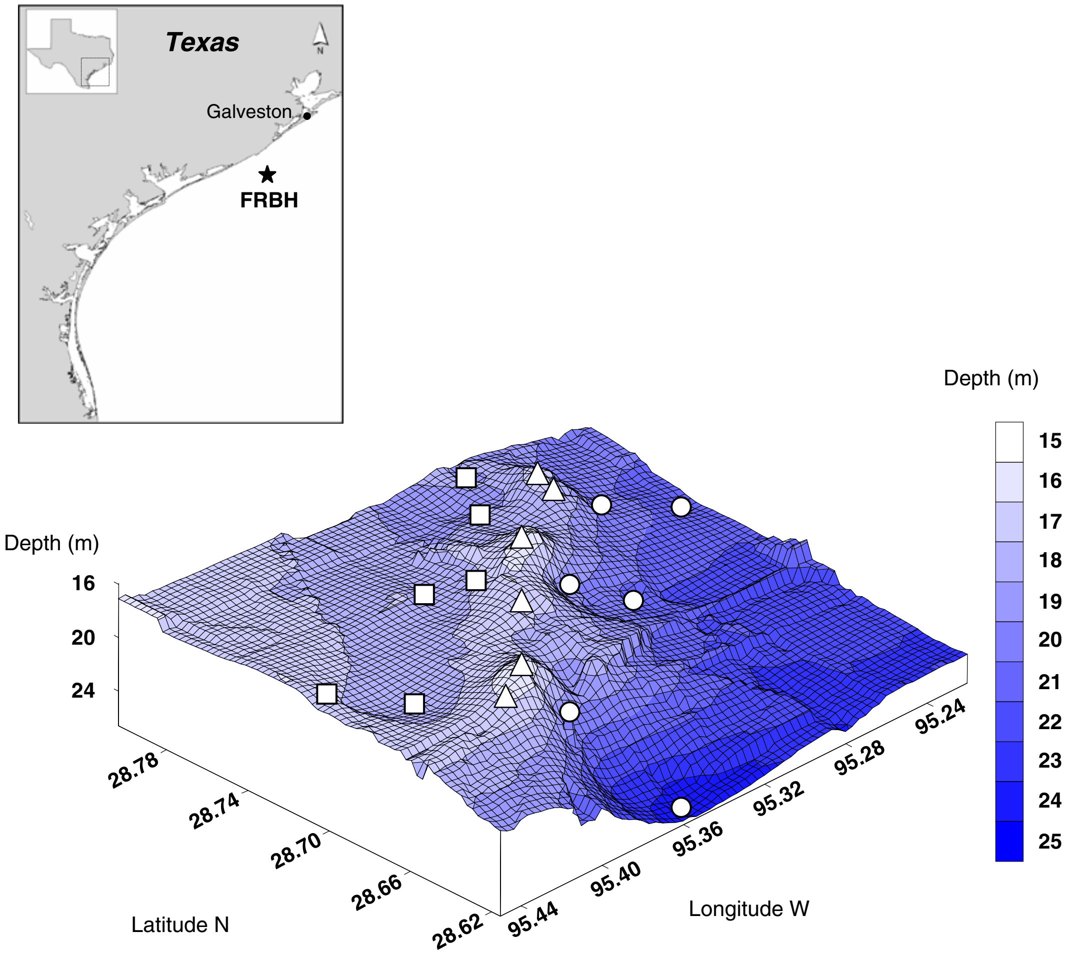

Fig. 1 Map of Freeport Rocks Bathymetric High (FRBH) drowned barrier island located on the NW Gulf inner continental shelf. Sample sites are coded by habitat type using different symbols: inshore mud (*squares*), shell bank (*triangles*), and offshore mud (*circles*)

(PRIMER) statistical package (Clarke & Warwick, 2001). Densities were transformed by using $\ln(x + 1)$ to down weight the abundant species and to retain information regarding some of the less abundant species. A Bray–Curtis similarity matrix then was computed with density data among all samples. Two-factor non-metric multi-dimensional scaling (MDS) models were computed for each survey date to visualize similarities and dissimilarities in fish assemblage structure among habitats and sites. Stress coefficients (residual modeling error) of 0.2 were treated as critical values to test goodness-of-fit of a given MDS model in two dimensions (Clarke & Warwick, 2001). The analysis of similarities (ANOSIM) permutation procedure was used to test for differences in fish assemblage structure among habitats, sites, and survey dates (Clark & Warwick, 2001). To assess species-specific contributions, Similarity Percentages (SIMPER) was used as the post hoc analysis to indicate the contribution of a particular species to the overall fish assemblage structure among habitats, sites, and survey dates (Clarke & Warwick, 2001).

Species richness (*S*), Shannon diversity (H'), and Pielou's evenness (J') were calculated and analyzed individually with a three-factor analysis of variance (ANOVA) in SAS (SAS Institute Inc, 2006), with survey date as a blocking factor and both habitat and site as main effects. Densities and sizes of the eight most abundant species in this study were also analyzed with a three-factor ANOVA (main effects: habitat, site; block: survey date). The equal variance assumption for each model was assessed by examining plots of the residuals versus the predicted values, and normality was tested with a Shapiro–Wilk test. A posteriori differences among means were detected with Tukey's HSD test with an alpha level of 0.05.

A comparison of fish assemblage composition with similar studies across the Gulf, Caribbean Sea, and western Atlantic was performed using total percent fish composition by family. Specifically, the 13 most abundant families (by number of individuals) across all studies were selected for comparisons. Care was taken to select comparable studies focusing on fish assemblage structure over continental shelf areas of similar substrates (i.e., sand, shell) using similar gears (i.e., otter trawls). Only otter trawl data from sand and shell habitats were used for comparisons, thus data from reef habitats were omitted from Wells et al. (2008), and only otter trawl data from Vasslides & Able (2008) were used. Selected study comparisons included the north-central Gulf (Wells et al., 2008), northeastern (NE) Gulf (Pierce & Mahmoudi, 2001), Middle and South Atlantic Bights (Love & Chase, 2007), NE USA off New Jersey (Vasslides & Able, 2008), southern Caribbean Sea (Garcia et al., 1998), and southeastern (SE) Brazil (Rocha & Rossi-Wongtschowski, 1998). Further, due to differences in sampling effort among studies, the total number of individuals per hectare was calculated according to family.

Results

Environmental parameters

Water mass properties near the substrate varied minimally among sites and habitats at FRBH during trawl surveys. Measurements were obtained for five of the seven surveys; no environmental data were acquired in June and December due to equipment malfunctions. In addition, dissolved oxygen content was only measured for two August survey dates and ranged from 5.1 to 6.4 mg/l, with an average of 5.6 mg/l. Salinity was relatively constant throughout the months sampled. Salinity was lowest in May, averaging 34.6, and was highest during the second August survey, with an average of 34.9. Salinity measurements never varied by more than 1 within each survey date among habitats or sites. Temperature was more variable than other parameters among survey dates, but never varied by more than 2.5°C among habitats and sites within a survey. Average temperature was lowest in May (24.0°C ± 0.2 standard error (SE)), and slightly increased during each survey date thereafter: July 5 (27.2°C ± 0.3 SE), July 17 (27.5°C ± 0.3 SE), August 17 (28.9°C ± 0.2 SE), and August 31 (29.7°C ± 0.1 SE).

Catch characteristics

A total of 29,000 fishes representing 41 families and 100 species were collected from trawl surveys (Table 1). The eight most abundant species comprised 69% of the total catch, with each represented by more than 1,000 individuals. In order of decreasing abundance, these species included shoal flounder (*Syacium gunteri*), dwarf sand perch (*Diplectrum bivittatum*), red snapper (*Lutjanus campechanus*), least puffer (*Sphoeroides parvus*), silver seatrout (*Cynoscion nothus*), largescale lizardfish (*Saurida brasiliensis*), silver jenny (*Eucinostomus gula*), and sand seatrout (*Cynoscion arenarius*) (Table 1). In addition, several other species were commonly found with percent frequency of occurrence greater than 50%; these included inshore lizardfish (*Synodus foetens*), lane snapper (*L. synagris*), bay whiff (*Citharichthys spilopterus*), fringed flounder (*Etropus crossotus*), and offshore tonguefish (*Symphurus civitatus*).

Spatial variability in habitat use

The composition of fishes associated with FRBH varied among habitats (ANOSIM; Global $R = 0.190$, $P < 0.05$); however, differences in species composition among sites were negligible using multivariate analyses (ANOSIM; Global $R = -0.015$, $P > 0.05$). When combined across sampling dates, pairwise comparisons showed significant differences among all three habitats (Tukey HSD, $P < 0.05$; Fig. 2a). Specifically, Fig. 2a shows distinct differences in assemblage structure between inshore mud and shell bank habitats, with offshore mud fish assemblage more intermixed with other habitats. Results of SIMPER analysis indicated shoal flounder, least puffer, and red snapper were the most ubiquitous species found among all habitats and accounted for over 40% of the variability within each habitat. Dwarf sand perch and pygmy sea bass (*Serraniculus pumilio*) accounted most toward the statistical

Table 1 Total number of species and total number of individuals collected by family during trawl surveys

Family	Common name	Species	Number of species	Total number	Mean density (number ha^{-1})	SD	% Freq
Achiridae	American soles		1	19			
Antennariidae	Frogfishes		1	1			
Ariidae	Sea catfishes		1	4			
Balistidae	Triggerfishes		1	243			
Batrachoididae	Toadfishes		1	33			
Bregmacerotidae	Codlets		1	1			
Carangidae	Jacks		6	227			
Clupeidae	Herrings		3	115			
Congridae	Conger eels		1	1			
Cynoglossidae	Tonguefishes		4	951			
Dactyloscopidae	Sand stargazers		1	4			
Diodontidae	Porcupinefishes		1	1			
Engraulidae	Anchovies		2	1,629			
Ephippidae	Spadefishes		1	1			
Gerreidae	Mojarras		3	1,589			
	Silver jenny	*Eucinostomus gula*		1,413	28.72	76.84	28.70
Gobiidae	Gobies		7	91			
Haemulidae	Grunts		2	73			
Labridae	Wrasses		2	69			
Lutjanidae	Snappers		3	2,840			
	Red snapper	*Lutjanus campechanus*		2,432	51.01	84.63	58.26
Monacanthidae	Filefishes		2	104			
Mullidae	Goatfishes		1	143			
Muraenidae	Moray eels		1	6			
Ogcocephalidae	Batfishes		3	128			
Ophichthidae	Snake eels		1	12			
Ophidiidae	Cusk-eels		4	25			
Ostraciidae	Boxfishes		1	10			
Paralichthyidae	Large-tooth flounders		10	6,205			
	Shoal flounder	*Syacium gunteri*		4,735	102.57	83.03	97.39
Polynemidae	Threadfins		1	94			
Priacanthidae	Bigeyes		1	3			
Sciaenidae	Croakers		7	4,080			
	Sand seatrout	*Cynoscion arenarius*		1,331	26.64	71.98	29.57
	Silver seatrout	*Cynoscion nothus*		2,043	45.67	108.05	52.17
Scombridae	Mackerels		1	2			
Scorpaenidae	Scorpionfishes		1	147			
Serranidae	Sea basses		5	5,136			
	Dwarf sand perch	*Diplectrum bivittatum*		4,386	89.26	277.29	68.70
Sparidae	Porgies		1	18			
Sphyraenidae	Barracudas		1	14			
Stromateidae	Butterfishes		2	54			
Syngnathidae	Pipefishes		3	113			

Table 1 continued

Family	Common name	Species	Number of species	Total number	Mean density (number ha^{-1})	SD	% Freq
Synodontidae	Lizardfishes		4	2,030			
	Largescale lizardfish	*Saurida brasiliensis*		1,476	31.24	151.42	31.30
Tetraodontidae	Puffers		2	2,256			
	Least puffer	*Sphoeroides parvus*		2,233	47.80	71.15	83.48
Trichiuridae	Cutlassfishes		1	127			
Triglidae	Searobins		5	401			

The eight most abundant species accounting for 69% of the total composition are included with mean density (number ha^{-1}), standard deviation (SD), and the percent frequency of occurrence (% Freq) representing the number of trawls each species was collected relative to the total number of trawls

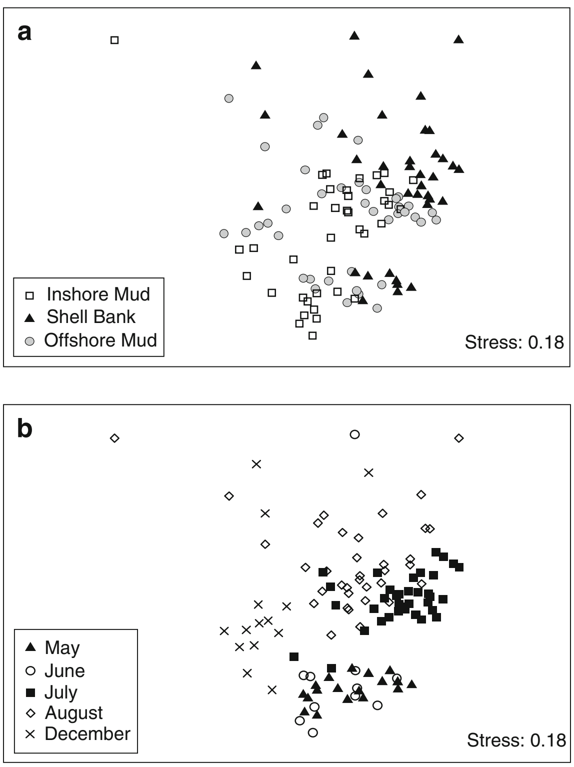

Fig. 2 Multi-dimensional scaling plots of trawl samples by **a** habitat and **b** month sampled. Stress coefficients represent goodness-of-fit criteria

differences in assemblage structure on the shell bank. Bay whiff and silver seatrout were important to assemblage structure on inshore mud, while offshore tonguefish and fringed flounder most affected statistical differences in assemblage structure on offshore mud. SIMPER analysis indicated each pair of species contributed over 20% of the variability within each habitat. Habitat-specific differences in density were observed for six of the eight most abundant species analyzed (Table 2). Shoal flounder, dwarf sand perch, least puffer, silver seatrout, largescale lizardfish, and silver jenny showed significant habitat effects, with no significant interactions between habitat and site ($P > 0.05$) (Table 2, Fig. 3). Highest densities of dwarf sand perch (average 189.7 ha^{-1} ± 55.4 SE) and least puffer (74.6 ha^{-1} ± 14.5 SE) were found on shell bank when compared to conspecific densities on inshore mud ($P < 0.05$) and offshore mud ($P < 0.05$). Highest densities of shoal flounder (143.7 ha^{-1} ± 16.2 SE), largescale lizardfish (82.7 ha^{-1} ± 27.4 SE), and silver jenny (57.6 ha^{-1} ± 19.6 SE) were found on offshore mud ($P < 0.05$), while silver seatrout had highest densities on both inshore mud (62.0 ha^{-1} ± 28.7 SE) and offshore mud (66.6 ha^{-1} ± 28.5 SE) (Tukey HSD, $P < 0.05$) (Fig. 3).

Significant density differences among sites were found for three of the eight most abundant species: shoal flounder, least puffer, and silver seatrout (Table 2, Fig. 3). Highest densities of both shoal flounder (119.2 ha^{-1} ± 16.2 SE) and least puffer (57.7 ha^{-1} ± 14.1 SE) were found in the central site; in contrast, silver seatrout densities were highest in the northern site (71.7 ha^{-1} ± 28.8 SE). Post hoc comparisons showed significantly higher densities of shoal flounder and least puffer in the central versus southern site ($P < 0.05$), while silver seatrout densities in the northern site were significantly higher than those in the southern site ($P < 0.05$).

Temporal variability in habitat use

Survey date was also a significant factor explaining fish assemblage structure on FRBH (ANOSIM; Global

Table 2 Univariate statistics of the eight most abundant species analyzed

Abundant species	Habitat (d.f. = 2)	Site (d.f. = 2)	Habitat × site (d.f. = 4)
Shoal flounder	6.16 (0.003)	9.44 (<0.001)	1.41 (0.238)
Dwarf sand perch	24.02 (<0.001)	2.50 (0.087)	0.32 (0.864)
Red snapper	1.85 (0.162)	2.49 (0.088)	2.44 (0.051)
Least puffer	8.16 (0.001)	4.40 (0.015)	0.48 (0.752)
Silver seatrout	16.93 (<0.001)	3.57 (0.032)	1.08 (0.372)
Largescale lizardfish	16.56 (<0.001)	0.67 (0.515)	0.47 (0.760)
Silver jenny	7.63 (0.001)	1.12 (0.330)	2.44 (0.051)
Sand seatrout	1.58 (0.212)	2.96 (0.056)	1.89 (0.118)

F-values are shown with associated *P*-values (in parentheses), based on a three-factor ANOVA using an alpha level of 0.05

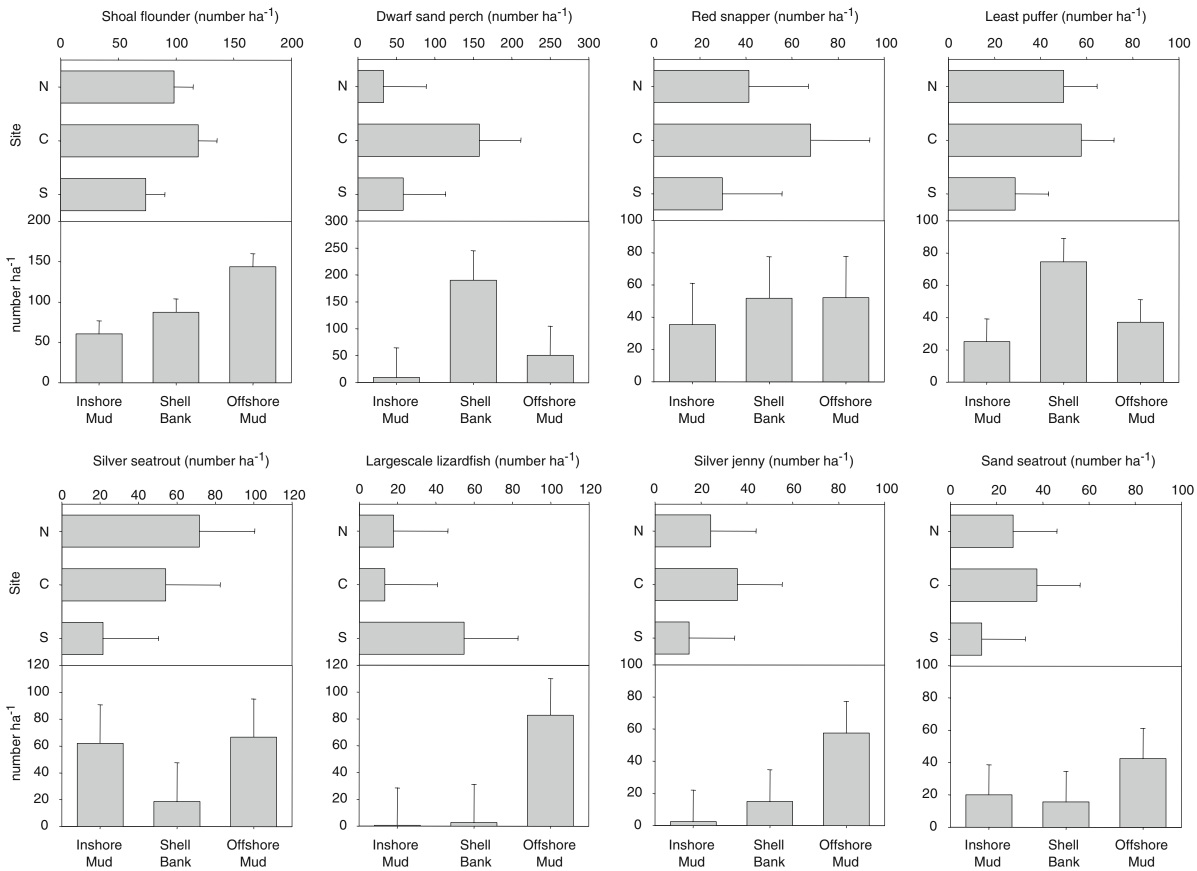

Fig. 3 Densities of the eight most abundant species collected by habitat and site (*N* = Northern, *C* = Central, *S* = Southern) listed in order of decreasing abundance. Error bars represent ±1SE

$R = 0.541$, $P < 0.05$; Fig. 2b). Pairwise comparisons between survey dates within the same month were statistically similar ($P > 0.05$), and therefore were combined to investigate habitat and site effects over the months sampled (May, June, July, August, and December). Temporal patterns of fish assemblages showed structure (May and June, July and August, and December) by the month sampled (Fig. 2b). A significant habitat effect was observed in May, July, and August ($P < 0.05$) (Fig. 4), but no significant effect of site was detected ($P > 0.05$). Shoal flounder was abundant on all habitats during each month, while several other species were abundant during specific months sampled. Sand seatrout were abundant on the shell bank in May, and both dwarf sand perch and least puffer were abundant in July and August. Similar

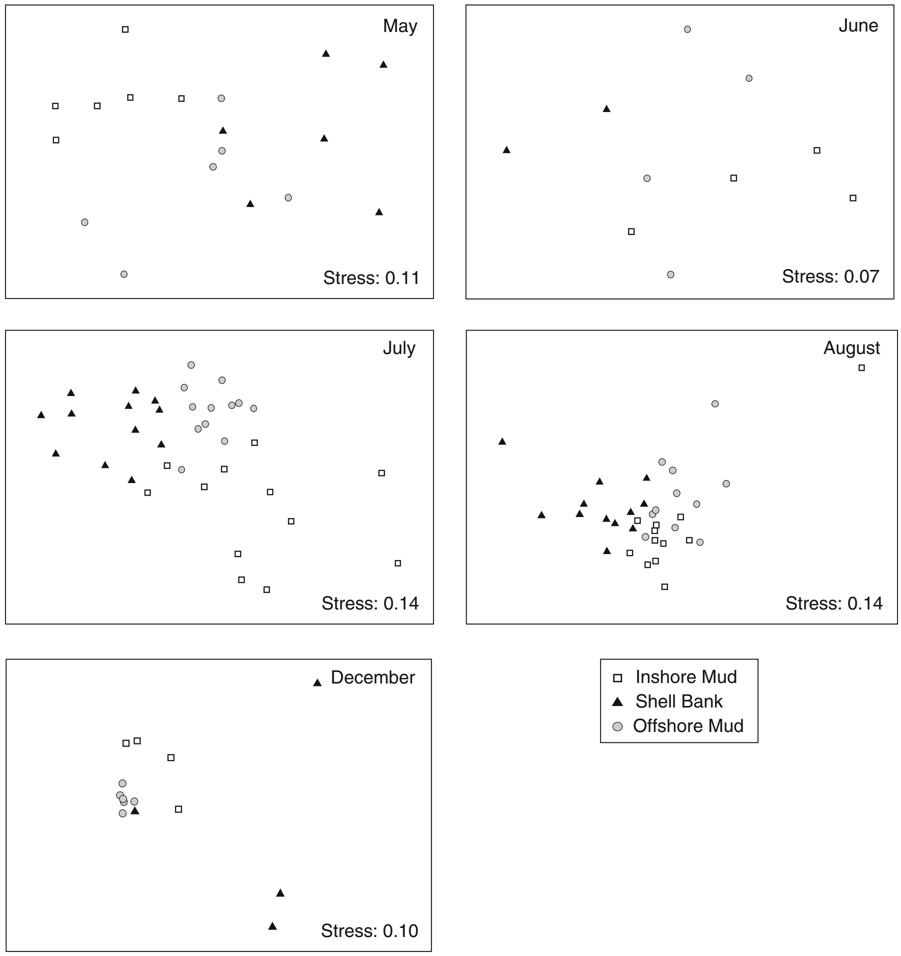

Fig. 4 Multi-dimensional scaling plots of trawl samples by habitat within each month sampled. Stress coefficients represent goodness-of-fit criteria

trends were seen on offshore mud with offshore tonguefish most abundant in May, and silver jenny and red snapper abundant in July and August, respectively. Seasonal changes were most pronounced for fish assemblage structure on inshore mud, with bay anchovy (*Anchoa mitchilli*) and sand seatrout most abundant in May, red snapper and bay whiff in July, and shoal flounder and least puffer in December. Peak abundance of six of the eight most common species was found in July (Fig. 5). Specifically, greater than 90% of the dwarf sand perch, inshore lizardfish, and silver jenny were collected in July. In contrast, silver seatrout showed two peaks in abundance, one in June and the other in December, while sand seatrout abundance peaked during May and June (Fig. 5).

Size

Smallest sizes of six of the eight common species were collected in early July (Table 3) suggesting that mid summer may be an important recruitment period on FRBH for these species. Mean length of dwarf sand perch, red snapper, least puffer, silver seatrout, large-scale lizardfish, and silver jenny were smallest from the July 5 survey date, and larger fish were collected during later survey dates for four of these six species (Table 3). In contrast, mean length of silver seatrout and largescale lizardfish was small during August survey dates, suggesting a second recruitment to the barrier island (Table 3). Similar sizes of shoal flounder were collected during all survey dates, and smallest

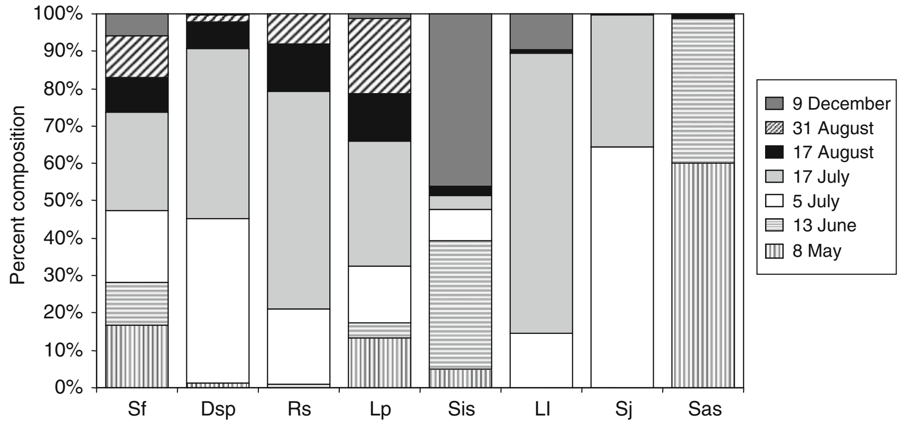

Fig. 5 Percent composition of the eight most abundant species collected by sample date. Sf = shoal flounder, Dsp = dwarf sand perch, Rs = red snapper, Lp = least puffer, Sis = silver seatrout, Ll = largescale lizardfish, Sj = silver jenny, Sas = sand seatrout. Values less than 1% are not represented

Table 3 Mean length (mm SL) of the eight most abundant species by sample date (±1 standard deviation)

Abundant species	May 8	June 13	July 5	July 17	August 17	August 31	December 9
Shoal flounder	71.7 (12.9)	76.7 (12.4)	78.1 (16.3)	72.3 (23.8)	75.0 (24.2)	70.6 (23.4)	75.6 (13.5)
Dwarf sand perch	77.2 (9.4)	68.6 (33.9)	24.9 (6.5)	30.8 (8.0)	48.4 (10.6)	56.3 (14.4)	78.1 (2.3)
Red snapper	NA	28.6 (2.5)	26.6 (14.6)	37.2 (10.8)	51.9 (14.7)	61.7 (16.2)	NA
Least puffer	40.8 (12.4)	53.5 (33.8)	26.3 (12.4)	31.5 (9.8)	35.2 (8.6)	38.8 (5.5)	44.6 (9.0)
Silver seatrout	102.2 (15.6)	41.3 (30.9)	30.8 (5.5)	89.4 (29.5)	78.5 (40.1)	41.2 (24.7)	52.3 (11.4)
Largescale lizardfish	NA	NA	29.9 (5.3)	41.7 (10.9)	36.2 (10.9)	37.6 (4.2)	75.6 (9.6)
Silver jenny	NA	NA	52.2 (7.7)	57.8 (6.3)	NA	NA	NA
Sand seatrout	36.0 (16.1)	61.6 (19.2)	NA	103.6 (25.4)	138.0 (29.5)	NA	NA

NA is not applicable because the species was not collected during the sample date

sizes of sand seatrout were collected in May with larger sizes collected during subsequent survey dates (Table 3). Finally, size differences of the eight common species were not significantly different among habitats or sites ($P > 0.05$).

Species diversity

Species richness (S), Shannon diversity (H'), and Pielou's evenness (J') were all significantly different among habitats (Table 4, Fig. 6). Significantly, higher H' and J' were found on both inshore mud ($H' = 2.01$; $J' = 0.75$) and shell bank ($H' = 2.02$; $J' = 0.72$) compared to offshore mud ($H' = 1.76$; $J' = 0.65$) (Tukey HSD, $P < 0.05$; Fig. 6); however, no differences were detected between inshore mud and shell bank. In addition, S was significantly higher on shell bank ($S = 18.65$) than inshore mud ($S = 15.83$) (Tukey HSD, $P < 0.05$; Fig. 6), but similar to offshore mud ($S = 16.67$, $P > 0.05$). No significant differences in S, H', and J' were found among sites ($P > 0.05$).

Fish assemblage comparison

Thirteen families accounted for 75–95% of the total fish composition according to the study region (Fig. 7). Five families (Paralichthyidae, Sciaenidae, Serranidae, Sparidae, and Synodontidae) were collected in all studies, albeit the total number per hectare varied considerably (Table 5). Sparidae accounted for the largest percent composition when averaged across all study regions and was the dominant family in the north-central Gulf, NE Gulf, and Middle and South Atlantic Bights accounting for 50, 33, and 28% of the total composition, respectively. In our study, four families accounted for 63% of the total composition and by order of decreasing abundance included Paralichthyidae, Serranidae, Sciaenidae, and Lutjanidae (Fig. 7, Table 5). The north-central and NE Gulf showed the most similar composition to our study with 12 of the 13 families found in each. In contrast, 8 of the 13 families were found in the NE USA and the three families contributing 92% of the total fish composition in

Table 4 Results of three-factor ANOVA comparing diversity indices with respect to habitat (inshore mud, shell bank, and offshore mud) and site (northern, central, and southern) over FRBH

Source of variation	d.f.	Shannon Diversity (H')	Pielou's Evenness (J')	Species richness (S)
Habitat	2	7.24 (0.001)	7.63 (< 0.001)	4.90 (0.009)
Site	2	0.28 (0.756)	1.68 (0.191)	1.16 (0.319)
Habitat x Site	4	0.89 (0.474)	0.61 (0.659)	0.76 (0.552)

Degrees of freedom (d.f.) for each source of variation are indicated along with F-values and associated P-values (in parentheses)

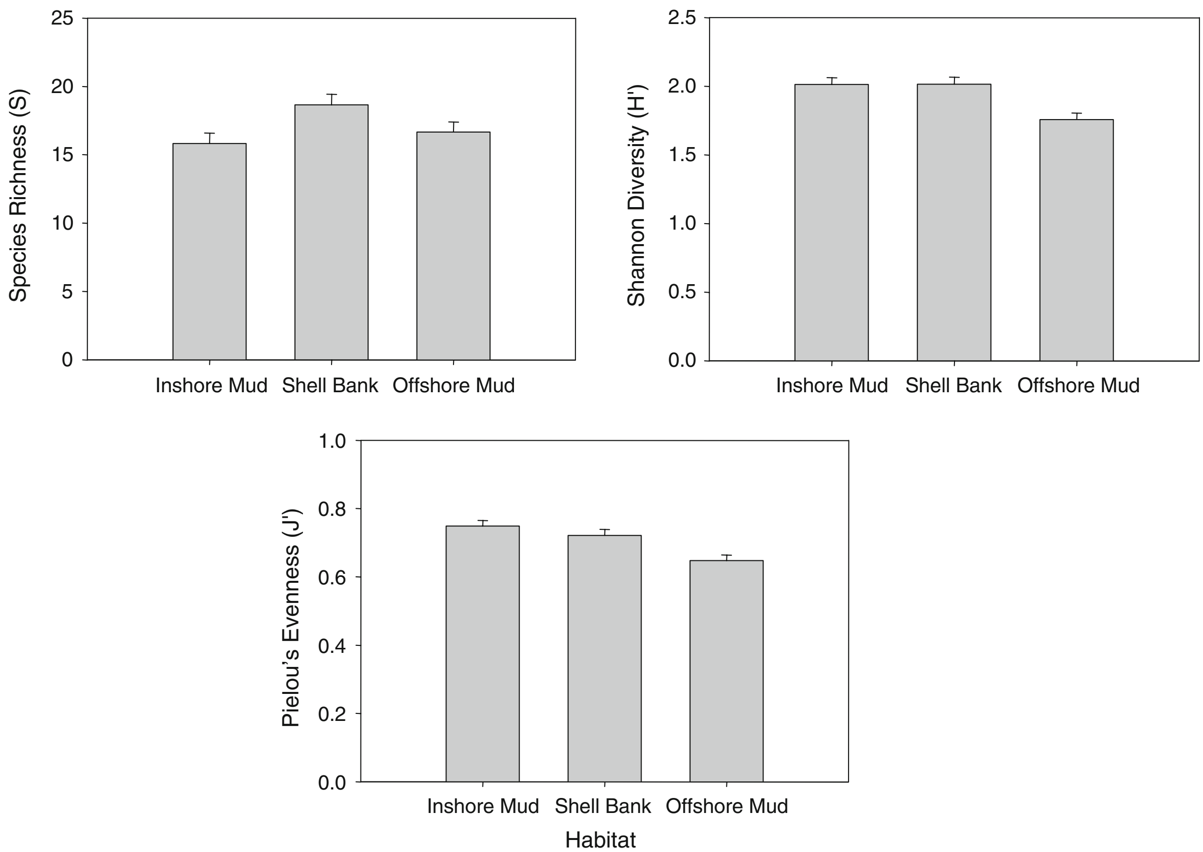

Fig. 6 Species richness (S), Shannon diversity (H'), and Pielou's evenness (J') of fish assemblage structure by habitat. Error bars represent ±1SE

the NE USA only contributed 20% at FRBH in the NW Gulf.

Discussion

The mosaic of habitat types associated with FRBH may be important to the early life survival of several fish species. Our results showed habitat-specific differences in assemblage structure; however, the eight most abundant species were found on all habitats, albeit in different densities. Other studies investigating fish assemblage structure have found similar trends, with the majority of species not unique to one habitat, but rather occupying multiple habitats (Pierce & Mahmoudi, 2001; Walsh et al., 2006). The proximity of biogenically complex (i.e., shell) and simple substrate types (i.e., sand and mud) was suggested to be important for fishes inhabiting similar features on the inner continental shelf of the Middle

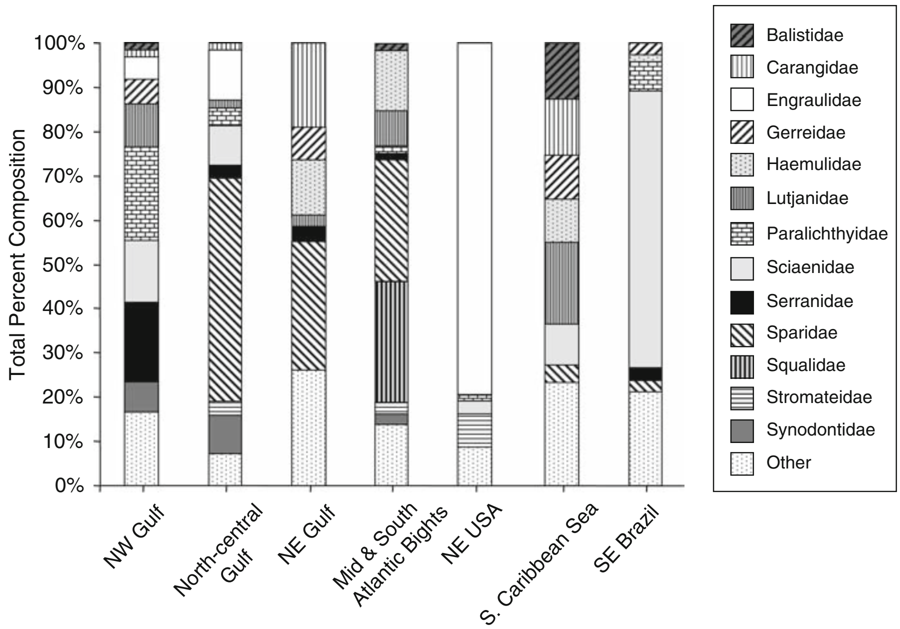

Fig. 7 Comparison of the percent composition of the 13 most abundant families among study regions. Comparisons were made with similar studies using otter trawls on continental shelf habitats in the Gulf, Caribbean Sea, and western Atlantic Ocean. North-central Gulf (Wells et al., 2008), NE Gulf (Pierce & Mahmoudi, 2001), Middle and South Atlantic Bights (Love & Chase, 2007), NE USA off New Jersey (Vasslides & Able, 2008), southern Caribbean Sea (Garcia et al., 1998), and SE Brazil (Rocha & Rossi-Wongtschowski, 1998). Families contributing <1% of the total composition by study region are not shown

Table 5 Total number of individuals (according to family) collected per hectare across studies

Family	Study location						
	NW Gulf	North-central Gulf	NE Gulf	Middle & South Atlantic Bights	NE USA	S. Caribbean Sea	SE Brazil
Balistidae	5.9	0.2	10.4	0.6	0	7.3	0.1
Carangidae	3.9	4.4	251.2	0.3	0.8	6.9	0
Engraulidae	27.9	52.1	0.2	0	1094.8	0	0
Gerreidae	27.2	2.6	98.9	0	0	5.6	8.0
Haemulidae	1.3	1.9	165.3	9.2	0	5.4	5.0
Lutjanidae	48.7	6.7	21.4	5.1	0	10.1	0
Paralichthyidae	106.4	15.2	1.4	0.8	7.5	<0.1	20.0
Sciaenidae	69.9	35.2	6.0	0.1	45.8	5.1	189.3
Serranidae	88.0	11.4	30.7	1.0	0.9	0.3	8.6
Sparidae	0.3	197.2	403.5	18.7	4.3	2.2	4.5
Squalidae	0	0	0	19.0	0	0	0
Stromateidae	0.9	12.6	0.4	1.6	129.4	0	0.5
Synodontidae	34.8	33.8	6.7	1.7	<0.1	0.2	0.3

Comparisons were made with similar studies using otter trawls on continental shelf habitats in the Gulf, Caribbean Sea, and western Atlantic Ocean. North-central Gulf (Wells et al., 2008), NE Gulf (Pierce and Mahmoudi, 2001), Middle and South Atlantic Bights (Love & Chase, 2007), NE USA off New Jersey (Vasslides & Able, 2008), southern Caribbean Sea (Garcia et al., 1998), and SE Brazil (Rocha & Rossi-Wongtschowski, 1998)

Atlantic Bight by providing refuge from predation on complex habitats and increased feeding resources over simple substratum (Diaz et al., 2003). These habitat-specific patterns of foraging and protection are not limited to shelf environments as other studies have found similar patterns in estuarine environments (Sheaves & Molony, 2000; Cocheret de la Moriniere et al., 2003). In our study, juvenile (<100 mm SL) red snapper were commonly collected on mud, sand, and shell habitats, similar to others (Rooker et al., 2004; Patterson et al., 2005; Geary et al., 2007), but habitat use is likely a function of protection afforded by shell and prey availability provided by soft substratum (Rooker et al., 2004). Additionally, dwarf sand perch have primarily been found on sand and mud habitats (Bortone et al., 1981), but our findings, as well as those of Wells & Cowan (2007), have found dwarf sand perch are also highly abundant on shell habitats in close proximity to simple substrates in the north-central and NW Gulf.

A suite of biotic and abiotic factors may have also contributed to fish assemblage structure. Here, depth differences among habitats and sites sampled at FRBH were negligible (i.e., <10 m). In addition, salinity, temperature, and dissolved oxygen of the water were relatively similar among habitats and sites, and did not appear to affect assemblage structure at FRBH. Nevertheless, differences in predation pressure, prey availability, and disturbance (trawling intensity) have been shown to influence benthic communities (Auster et al., 1997; Thrush & Dayton, 2002), and such factors may have affected the distribution and abundance of fishes associated with FRBH.

Estuarine-associated species were some of the most abundant species collected. Several species collected on FRBH have been reported from estuaries in different regions of the Gulf throughout various stages of their life history: least puffer (Shipp & Yerger, 1969), sand seatrout and silver seatrout (Sutter, 1987), silver jenny (Idelberger & Greenwood, 2005), lane snapper (Franks & VanderKooy, 2000), bay whiff, fringed flounder, and offshore tonguefish (Allen & Baltz, 1997). Moreover, least puffer, sand seatrout, silver seatrout, silver jenny, lane snapper, bay whiff, and fringed flounder have been reported in the Galveston Bay estuary (Sheridan, 1983). Given the proximity of the Freeport and Galveston Bay estuaries, this bathymetric feature, along with similar features located near estuaries along the Texas coast, may provide a corridor linking inshore and offshore movement for several species. For example, sand seatrout spawn in lower estuarine environments and inshore waters of the Gulf during spring months (March–May) at depths between 7 and 22 m (Shlossman & Chittenden, 1981). Increasing size over time of sand seatrout in this study suggests juveniles may recruit to FRBH following these estuarine or nearshore spawning events. In addition, distribution, abundance, and size patterns of bay whiff and fringed flounder in a Louisiana estuary showed evidence of spring spawning followed by movement toward the coast (Allen & Baltz, 1997). Increasing sizes over time for both species in this study suggests juveniles may recruit to offshore benthic habitats during spring and summer months. Further, juvenile lane snapper occur in nearshore and estuarine environments, whereas adults typically inhabit offshore reefs and hardbottom features (Franks & VanderKooy, 2000; Mikulas & Rooker, 2008). Lane snapper were not present on FRBH until July; however, increasing sizes were observed during summer surveys (July average = 35.6 mm SL, August average = 71.8 mm SL) suggesting movement from nearshore or estuarine to offshore areas may have occurred. Able (2005) examined fish estuarine dependence in southern New Jersey and concluded a large proportion of fishes use, both estuarine and ocean habitats, as juveniles and found this to be true for most of the dominant species in the Middle Atlantic Bight. This estuarine-ocean ecotone requires further study to understand species-specific movement patterns and associations between the estuary and nearshore bathymetric features such as FRBH.

Seasonal changes in fish assemblages were found over the sampling period. Results from MDS suggest habitat-specific fish assemblages change on a monthly scale with three unique assemblages found, and these included: May and June, July and August, and December. Changes in fish assemblages likely resulted from life history differences among species most contributing to assemblage structure. Species most responsible for structuring the May and June assemblage have known spring spawning events and have been found in highest numbers during these months in nearshore waters; sand and silver seatrout (Sutter, 1987), and bay anchovy (Robinette, 1983). July and August assemblage structure was most affected by dwarf sand perch, least puffer, red snapper, bay whiff, silver jenny, and inshore lizardfish, all species commonly found in nearshore waters during summer months (Allen & Baltz, 1997; Rooker et al., 2004; Wells & Cowan, 2007; Wells et al., 2008). Further, documented spawning events in the fall likely explain the abundance of silver seatrout in December collections (Sutter, 1987).

Habitat associations of the most abundant eight species in this study are similar to those reported by others in the Gulf. Previous studies have reported that dwarf sand perch, pygmy sea bass, and red snapper utilize shell habitats (Szedlmayer & Howe, 1997; Lingo & Szedlmayer, 2006; Wells & Cowan, 2007). In addition, species more abundant on mud habitats at FRBH have been observed over soft bottom habitats by other investigators; these include sand seatrout, silver seatrout, shoal flounder, largescale lizardfish, silver jenny, bay whiff, offshore tonguefish, and fringed flounder (Sutter, 1987; Allen & Baltz, 1997; Walsh et al., 1999; Brooks, 2004; Wells et al., 2008). Previous work has indicated that silver seatrout, sand seatrout, and shoal flounder were common members of the inner shelf fish assemblage in the NW Gulf, with Atlantic croaker (*Micropogonias undulatus*) and longspine porgy (*Stenotomus caprinus*) being most abundant (Moore et al., 1970; Chittenden & McEachran, 1976). In this study, shoal flounder were numerically dominant at FRBH. Brooks (2004) found high numbers of this species on a nearby bank while absent from other banks in this region, suggesting that the most abundant species within a fish assemblage may be bank specific.

Several families emerged as cosmopolitan inhabitants over continental shelf systems throughout the western Atlantic and adjacent seas. These families included Paralichthyidae, Sciaenidae, Serranidae, Sparidae, and Synodontidae. Four of the five families found among all study regions and Lutjanidae, which was found in five of the seven studies, comprised a majority (>60%) of the fish composition of FRBH. Geographic distribution of Lutjanidae is primarily limited to tropical and subtropical oceans (Allen, 1985), which likely explains why individuals were absent in the NE USA and SE Brazil collections. Numerical abundance of Sciaenidae fishes in SE Brazil has been suggested to replace reef fish families, such as Haemulidae and Lutjanidae, due to riverine influence on sediment type (Moyle & Cech, 1996) and a lack of hard bottom habitat in southern Brazil (Rocha & Rossi-Wongtschowski, 1998). Sparidae was the most abundant family across study regions; however, low numbers of only one species, *Lagodon rhomboides*, were collected on FRBH. This species was common in the north-central Gulf (Wells et al., 2008) and NE Gulf (Pierce & Mahmoudi, 2001), and several Sparidae species have been reported as common inhabitants occupying similar habitats on the NW Gulf shelf (Moore et al., 1970; Chittenden & McEachran, 1976; Brooks, 2004). Timing of our surveys may explain why two abundant Sparidae species (*L. rhomboides* and *S. caprinus*) with winter and early spring spawning events in offshore waters of the Gulf (Geoghegan & Chittenden, 1982; Darcy, 1985) were nearly absent from our collections. Differences in the timing of surveys may also play a part in the compositional differences in fish assemblages among studies.

Diversity estimates at FRBH were comparable to the findings from other studies investigating fish assemblage structure over similar habitats. Chittenden & McEachran (1976) reported Shannon diversity (H') and evenness (J') values on sand habitats in the NW Gulf inner shelf ranging from 0.89 to 2.59 and 0.29 to 0.94, respectively. Moreover, Wells et al. (2008) reported H' and J' values on shell and sand habitats in the north-central Gulf shelf from 1.03 to 2.07 and 0.39 to 0.73, respectively. In addition, species richness (S) values here were higher than those reported over similar bathymetric highs in the NW Gulf (ranging from 5 to 11) using similar gear types (Brooks, 2004). These findings suggest overall diversity in fish assemblages is relatively similar across the northern Gulf shelf. In addition, habitat-specific comparisons of diversity indices were minimal here, as well as in other studies (Wells & Cowan, 2007), suggesting the mosaic of habitats may be important to assemblage structure rather than a single habitat type on FRBH. Still, direct comparisons of diversity should be interpreted with caution because differences in sampling effort, gear, and the timing of each survey have been shown to influence estimates of diversity (Fock et al., 2002).

Freeport Rocks Bathymetric High appears to be an important relic drowned barrier island for fishes in the NW Gulf. Largest numbers of individuals found over FRBH belong to Paralichthyidae, Serranidae, Sciaenidae, and Lutjanidae, each containing important species under state or federal management. A combination of high densities, small sizes, and a large number of species that use estuaries at particular stages of their life history suggest this bank, and possibly others on the inner Gulf shelf, represent important habitat for juvenile fishes. This study has provided two (presence-absence and density) of the four habitat-specific levels of information needed to evaluate habitat quality and to assess whether a given habitat should be considered EFH (Minello, 1999). Future studies addressing the third (growth, reproduction, or survival) and fourth (production) components of EFH will be needed to assess whether FRBH enhances growth, production, and subsequent survival for several important fishes.

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