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CHARACTERIZING NEKTON USE OF THE LARGEST UNFISHED OYSTER REEF IN THE UNITED STATES COMPARED WITH ADJACENT ESTUARINE HABITATS

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ABSTRACT Characterizing density patterns of fish and crustaceans across estuarine habitat types can provide useful information regarding their relative value. The oyster reef complex within Sabine Lake Estuary is the largest known in the United States with no record of commercial harvest, and it presents a unique opportunity to understand the habitat value of an unfished reef system in comparison with adjacent estuarine habitats. High abundances of relatively large oysters with complex formations were observed throughout the 2-y study period. Average densities of fish and crustaceans were 6 times greater at the marsh edge than the nonvegetated shallow habitats, and 40 times greater than both the oyster reef and nonvegetated deep habitats. Low faunal densities observed in the oyster reef habitat may be the result of spatial configuration and connectivity to surrounding habitats, collection limitation resulting from its large vertical relief (>1 m) and complex 3-dimensional structure, or habitat selection resulting from water depth. Because the majority of crustaceans and resident and transient fish were observed within the marsh edge and nonvegetated shallow habitats, it is difficult to determine whether oyster reefs within Sabine Lake Estuary provide essential habitats for these species. Although low densities of organisms were observed in the oyster reef habitat, multivariate analysis indicates that the unfished reef supports a unique community of fish and crustaceans. Results provide a valuable baseline for future conservation, restoration, and management actions as we seek to understand more completely and to protect important estuarine habitat types.

KEY WORDS: community composition, essential fish habitat, estuarine organisms, oyster reefs, population structure, Sabine Lake Estuary

INTRODUCTION

High-quality estuarine habitats such as intertidal marshes and oyster reefs are essential for supporting reproduction, growth, and persistence of dense aggregations of estuarine fauna (Boesch & Turner 1984, Kneib 1984, Levin & Stunz 2005, Stunz et al. 2010). These habitats are highly productive for fish and crustaceans (Coen et al. 1999, Hendon et al. 2000), and their biophysical structures play a strong role in shaping estuarine community structure (Breitburg et al. 1995, Hosack et al. 2006) via enhanced deposition of food (Commito & Rusignuolo 2000), settlement of larvae (Gutiérrez et al. 2003), survival of postlarvae and prey species (Tupper & Boutilier 1995, Dittel et al. 1996, Stunz & Minello 2001, Humphries et al. 2011a), and food resources for a variety of fauna (Runyan 1961, Breitburg et al. 1999, Harding & Mann 2001, Grabowski 2004). Oysters are unique in their ability to form hard substrate in estuaries that are otherwise dominated by soft sediment or vegetated environments. These hard structures can support unique assemblages of fauna compared with other estuarine habitat types (Posey et al. 1999, Stunz et al. 2001, Humphries et al. 2011b) and, as such, may influence trophic cascades and food web functions (Grabowski 2004, Grabowski et al. 2008). Oyster reefs are generally considered essential habitats for resident nekton such as the naked goby (*Gobiosoma bosc*), feather blenny (*Hypsoblennius hentz*), and skilletfish (*Gobiesox strumosus*) (Coen et al. 1999), as well as oysters themselves (Harding & Mann 2001, Lehnert & Allen 2002). However, less is known about nekton use of open-water, subtidal reefs as a result of gear limitations (but see Stunz et al. (2010) and Robillard et al. (2010)).

Worldwide, oyster reef coverage has been reduced by an estimated 90% as a result of fishing pressure, reduced water quality, disease, and habitat destruction (Kirby 2004, Jackson 2008, Beck et al. 2011). Oyster reefs support major commercial and recreational fisheries (VanderKooy 2012), and typical harvest methods using dredges and/or hand tongs can decrease habitat complexity (Lenihan et al. 2001). Comparisons of shell-bottom with mud-bottom habitats indicate that prolonged overharvest can lead to significant reductions in reef-dependent species (Plunket & La Peyre 2005, Shervette & Gelwick 2008, Stunz et al. 2010). Outside of habitat provisioning and enhancement of fishery resources, oyster reefs are recognized for providing numerous other ecosystem services, including water filtration (Nelson et al. 2004), habitat stabilization (Piazza et al. 2005, Meyer et al. 2008), and carbon sequestration (Peterson & Lipcius 2003). Oyster reef restoration is used to ameliorate lost ecosystem services such as fish production (e.g., Peterson et al. 2003, Luckenbach et al. 2005), but an ongoing challenge is to describe the natural condition to which a system can be restored (Seaman 2007).

Although previous studies characterizing estuarine fauna across habitat types have enhanced our understanding of relative habitat values, studies of natural, unfished oyster reefs are rare (e.g., Louisiana Department of Wildlife and Fisheries 2010, Beck 2012). The objectives of this study were (1) to quantify the population structure and density of oysters on a natural, unfished reef complex, and (2) to quantify the abundance and diversity of finfish and crustaceans within the reef complex compared with nonvegetated and marsh edge habitats. Understanding the oyster population structure on a natural, unfished reef, and characterizing the associated nekton community in comparison with adjacent estuarine habitats can help inform restoration and management actions, particularly with respect to

potential changes that may result from future commercial harvest.

METHODS

Study Site

Sabine Lake Estuary is an approximately 259-km^2 estuary located on the Texas–Louisiana border along the Gulf of Mexico (Fig. 1). The estuary receives freshwater inflow from both the Sabine and Neches rivers along with tidal inputs from the Gulf of Mexico through Sabine Pass (Rappleye 2005). A defining characteristic of Sabine Lake Estuary is its extensive, high-vertical relief (1 m) oyster reef with no record of commercial harvest, presenting a unique opportunity to understand the habitat value of an unfished reef system in comparison with adjacent estuarine habitats. The oyster reef complex in Sabine Lake Estuary is likely the largest in the United States to remain in its natural, unfished state (Moore 2008). The reef is an estimated 10 km^2 in total areal extent, with crest depth averaging 3–4 m below the water's surface (Morton 1996), and it is 1 of only 2 estuaries in the United States to show stable or increasing oyster biomass since 1900 (zu Ermgassen et al. 2012). In addition, approximately 9,400 m^2 of marsh surround the estuary, making it one of the largest coastal ecosystems in Texas. In response to substantial oyster mortalities throughout Louisiana estuaries resulting from hurricane activity (e.g., Buck 2005, Louisiana Department of Wildlife and Fisheries 2005) and freshwater releases post-Macondo oil spill (Williams 2010, Upton 2011), Louisiana expressed strong interest in pursuing commercial oyster harvest in Sabine Lake Estuary (Moore 2008). Although the estuary has not yet been opened to commercial harvest, the decision to evaluate harvest potential drove the gathering of critical baseline data on reef- and estuarine-associated fauna.

Field Sampling

Sampling was conducted biannually from fall 2011 to spring 2013 (4 sampling periods). Thirty fixed locations were visited during each sampling trip: 12 oyster reef, 6 marsh edge, 6 nonvegetated shallow bottom (<3 m), and 6 nonvegetated deep bottom (>3 m) habitats (Fig. 1). Equal numbers of oyster reef and nonvegetated deep stations were located on both the Texas and Louisiana sides of the estuary. All nonvegetated shallow and marsh edge stations were located on the Louisiana side of the estuary because similar sites were not available in the Texas portion. During the period of study, commercial oyster harvest was not allowed on either side of the estuary.

At each oyster station, a modified epibenthic sled (MES) was used to collect reef-associated crustaceans and fish from the subtidal reef (see Stunz et al. (2002a) and Robillard et al. (2010) for details). Briefly, the MES is a canvas-covered rectangular steel frame (0.78 m wide × 0.30 m high × 0.45 m deep) with a row of attached steel teeth along the front bottom edge that worked to agitate and dislodged nekton and benthic crustaceans living on the oyster reef. These organisms were then retained in a 1-mm mesh plankton net attached to the back of the sled. The MES was towed at 2.5 m/sec for 100 m, covering approximately 78 m^2. This device has been calibrated against well-established nekton collecting gear and has been shown to be very effective at sampling small nekton and other crustaceans over deep-water oyster reefs (Rozas & Minello 1998, Stunz et al. 2002a, Robillard et al. 2010).

After collecting reef-associated organisms, an oyster dredge (0.50 m wide, 5-cm mesh) was then towed at 2.5 m/sec for 60 sec, covering approximately 75 m^2 to sample the oyster reef. All live
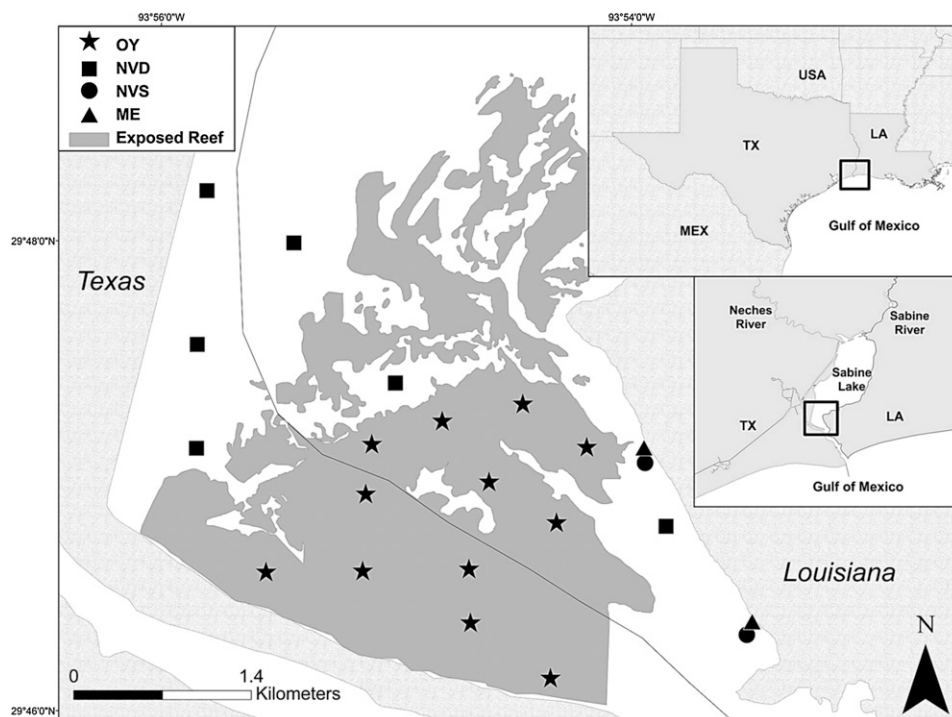

Figure 1. Sampling locations in Sabine Lake Estuary, Texas. Marsh edge and nonvegetated shallow habitats were sampled on the eastern side of the estuary only. ME, marsh edge; NVD, nonvegetated deep; NVS, nonvegetated shallow; OY, subtidal oyster reef.

and dead oysters were counted in the field, and 20 live oysters were selected for processing in the laboratory. Because of the potential for bias and limitation with the oyster dredge resulting from the complex 3-dimensional structure of the oyster reef, these data represent relative values (Powell et al. 2007, Beseres Pollack et al. 2011).

At each marsh edge and nonvegetated shallow station, an epibenthic sled was used to collect all fish and crustaceans (see Stunz et al. (2002a) for details). Briefly, the epibenthic sled consists of a metal frame (0.75 m high × 0.6 m wide) with a 1-mm mesh conical plankton net. It was towed by hand for 17 m, covering 10 m² of bottom either within the flooded marsh edge habitat or at a distance of 5 m from the shoreline, parallel to the marsh edge (nonvegetated shallow habitat). All crustaceans and fish were fixed in 10% formalin and seawater and stored for laboratory analysis. The MES was used at each nonvegetated deep station, where it was towed at 2.5 m/sec for 50–75 m covering 40–60 m². Both of these gear types are very similar, except for the design of the MES to work in deep water and over oyster reefs. Gear efficiency studies have been performed (Robillard et al. 2010) and show no difference in nekton collected from marsh edge, submerged aquatic vegetation, and nonvegetated bottom for both epibenthic sled types.

Fauna were classified as either resident or transient species. Oyster reefs are generally considered essential habitat for resident species—those that feed, breed, or seek shelter on reefs—including various species of gobies (e.g., naked goby, *Gobiosoma bosc*), blennies (e.g., feather blenny, *Hypsoblennius hentz*), skilletfish (*Gobiesox strumosus*), and toadfish (e.g., oyster toadfish, *Opsanus tau*) (Coen et al. 1999, Harding & Mann 2000). Transient species are more widely distributed, using oyster reefs as well as other estuarine habitats, including Atlantic croaker (*Micropogonias undulatus*), silver perch (*Bairdiella chrysoura*), and spotted seatrout (*Cynoscion nebulosus*) (Harding & Mann 2001, Lederhouse 2009).

Monthly environmental water-quality indicators (salinity, temperature, and dissolved oxygen) for the subtidal oyster reef were obtained from Texas Parks and Wildlife Department (TPWD) from 2011 through 2013. Environmental variables were also measured at each station using a Hydrolab data sonde. Bottom water samples were collected using a horizontally mounted Van Dorn bottle to quantify chlorophyll *a* and total suspended solids. Monthly hydrological data were also obtained from TPWD's Coastal Fisheries Division.

Laboratory Sample Processing

All fish and crustaceans were identified to the lowest possible taxon, enumerated, and measured to the nearest 0.1 mm standard length. If more than 20 individuals were caught for each species or group, then the largest, smallest, and 20 other random individuals were measured (see Stunz et al. (2010) for details). Oysters were measured in the field for shell height (measured in millimeters, distance from umbo to ventral shell margin). Twenty oysters were selected randomly and measured additionally for wet tissue weight, dry weight, and ash-free dry weight in the laboratory. A condition index was then calculated for each site as the ratio of ash free dry weight to shell height × 100 (Lucas & Beninger 1985, Zarnoch & Schreibman 2012). An oyster condition index is a measure of the metabolic condition related to the amount of glycogen stored (Lucas & Beninger

1985) and can be useful to estimate how environmental variables influence oyster growth.

Data Analysis

All statistical analyses were conducted using R version 2.15.3. Faunal densities, lengths, live and dead oyster counts, and oyster shell heights were $\log_{10}$ transformed before analysis to improve homogeneity of variance and normality. One-way analysis of variance (ANOVA; $\alpha = 0.05$) tests were run to determine whether there were significant differences in the numbers of live and dead oysters as well as the live-to-dead ratio across all 4 sampling periods. Analysis of variance was also used to test for differences in shell height (in millimeters) and oyster condition index among sampling periods. Tukey's post hoc tests were performed when significant differences were found.

Allometric relationships were calculated between oyster shell length and biomass: wet weight (measured in grams), dry weight (measured in grams), and ash-free dry weight (measured in grams). The relationship between mean shell length and mean weight can be used as an index of oyster growth using the power function $L = aW^b$, where L is the shell height in millimeters; W is wet, dry, or ash-free dry weight; and a and b are model-derived coefficients (Dame 1972, Beseres Pollack et al. 2011).

Two-way ANOVA ($\alpha = 0.05$) was used to test for differences in total faunal densities, fish and crustacean size, and densities of dominant major taxa between habitat type (marsh edge, nonvegetated shallow, nonvegetated deep, and subtidal oyster reef), and season (fall 1, spring 1, fall 2, and spring 2), representing fall 2011, spring 2012, fall 2012, and spring 2013, respectively. Tukey's post hoc tests were also run when significant differences were found.

Community similarity among the 4 habitat types was evaluated using the Shannon diversity index ($H = -\Sigma p_i \log p_i$) (Shannon 1948), where p_i is the proportion of the total number of individuals occurring in species i, and Margalef's richness index ($D = (S - 1)/\ln N$), where S is the number of species recorded and N is the total number of individuals summed over all S species. Analysis of variance was used to test for differences in diversity and richness across habitat type.

PRIMER version 6 was used to test for significant differences in community assemblages (Clarke & Gorley 2006). Nonmetric multidimensional scaling (MDS) was used based on a Bray–Curtis similarity matrix with SIMPROF to determine differences in community assemblages among all 4 habitats. Bray–Curtis cluster groups were superimposed on the plot for better interpretation (Clarke & Warwick 2001). The BIOENV routine was used to determine the species that best contributed to the overall community structure.

RESULTS

Environmental Variables

Monthly averaged salinity ranged from 4.2–27.5, water temperature from 13.3–31.9°C, and dissolved oxygen from 4.3–9.7 mg/L during the study period. Chlorophyll *a* levels ranged from 2.4–4.9 µg/L.

Oyster Reef

Live oyster abundance varied significantly among sampling periods ($P \leq 0.0001$), with spring 2013 having the highest
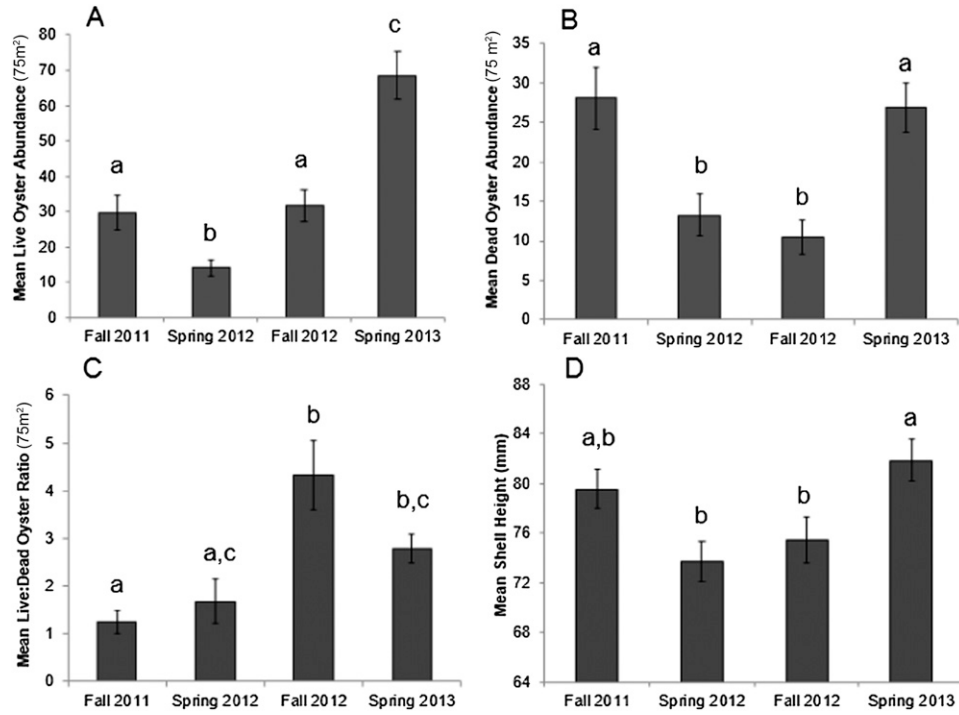
Figure 2. (A) Average live oyster abundances collected. (B) Average dead oyster abundances collected. (C) Average live-to-dead oyster ratio. (D) Average shell height of collected oysters. All data collected in Sabine Lake Estuary, Texas. Bars with different letters have significantly different Tukey groupings ($P < 0.05$). Error bars represent SE.

abundance per 75 m^2 tow (Fig. 2A). Dead oyster abundance was highest in fall 2011 and spring 2013 ($P \leq 0.0001$; Fig. 2B). The ratio of live to dead oysters was significantly different among seasons ($P \leq 0.001$), and was lowest in fall 2011 and highest in fall 2012 (Fig. 2C). Live oyster shell heights ranged from 13–203 mm

throughout the 4 collection periods (Fig. 3). During 3 of the 4 sampling periods, the average shell height of oysters collected was greater than the harvestable size (76 mm; Fig. 2D). Almost half (45%) of all live oyster heights measured were 80 mm or larger. The largest oyster observed ($\sim$203 mm in spring 2013) was on par
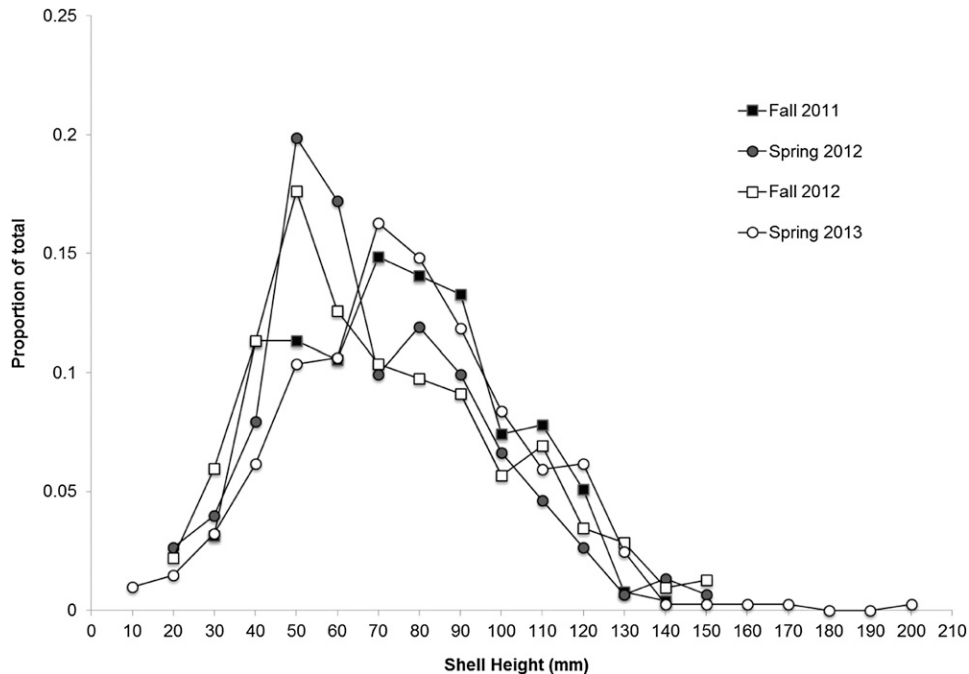

Figure 3. Oyster shell height distribution as a proportion of the total collected in each sampling period from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas.

with the maximum shell height of *Crassostrea virginica* recorded in Texas (203.4 mm; TPWD data).

Oyster condition index was significantly greater ($P \leq 0.001$) in fall 2012 (0.70 ± 0.03) than fall 2011 (0.59 ± 0.02) and spring 2012 (0.58 ± 0.02), indicating that metabolic condition may have been affected by environmental variability across sampling periods. Estimated coefficients for allometric relationships between shell height and oyster biomass were similar to those reported previously for *Crassostrea virginica* shell height and wet weight ($a = 10^{1.582}$, $b = 0.33$), dry weight ($a = 10^{1.846}$, $b = 0.258$), and ash-free weight ($a = 10^{1.957}$, $b = 0.266$) (Dame 1972, Beseres Pollack et al. 2011).

Faunal Densities

A total of 2,562 fish from 26 species and 12,327 decapod crustaceans from 10 species were collected from all habitats throughout the course of the study (Table 1, Table 2). The greatest number of organisms was collected within the marsh habitat, with 1,099 fish from 18 species and 9,020 decapod crustaceans from 8 species. The most abundant organisms in marsh habitat included grass shrimp (*Palaemonetes* spp.), Atlantic croaker (*Micropogonias undulatus*), and red drum *Sciaenops ocellatus*). The oyster reef habitat had the second highest number of organisms collected, with 1,001 fish from 15 species and 1,411 decapod crustaceans from 10 species. Atlantic croaker, grass shrimp, postlarval penaeid shrimp, and xanthid crabs were

present in the highest densities in the oyster reef. The fewest organisms were captured in the nonvegetated shallow (309 fish from 15 species and 1,469 decapod crustaceans from 6 species) and nonvegetated deep (153 fish from 11 species and 427 decapod crustaceans from 9 species) habitats. The greatest densities of organisms in the nonvegetated shallow habitat included grass shrimp, postlarval penaeid shrimp, Atlantic croaker, and red drum. For the nonvegetated deep habitat, postlarval penaeid shrimp and longeye shrimp (*Ogyrides* spp.) were present in the greatest densities. Decapod crustaceans accounted for 83% of the total catch across all habitats, with 84% found within the marsh edge habitat. Grass shrimp and postlarval penaeid shrimp accounted for 86% of all decapod crustaceans collected (54% and 32%, respectively). Four species (Atlantic croaker, red drum, darter goby *Ctenogobius boleosoma*, and naked goby *Gobiosoma bosc*) represented 81% of all fish collected, with Atlantic croaker representing 44% of all fish. Approximately 70% of all fish were found within the marsh edge and 19% within nonvegetated shallow habitats.

Decapod crustaceans were observed in both spring and fall; however, white shrimp (*Litopenaeus setiferus*) were observed primarily in the fall, and brown shrimp (*Farfantepenaeus aztecus*) were collected predominantly in the spring. Porcelain crabs (Porcellanidae) and pea crabs (*Pinnixa* spp.) were the only decapod crustaceans found exclusively in the fall; no decapod crustaceans were found exclusively in the spring (Table 3). Ten species of fish were only collected in the spring: black drum

TABLE 1.

Overall mean species densities and SE of fish in marsh edge, nonvegetated deep, nonvegetated shallow, and oyster reef biannually from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas.

Common name	Scientific name	Total catch	RA* (%)	Marsh edge (mean ± SE)	Nonvegetated deep (mean ± SE)	Nonvegetated shallow (mean ± SE)	Oyster reef (mean ± SE)
Total fish		2,562	17.2				
Atlantic croaker	*Micropogonias undulatus*	1,124	7.5	4.12 ± 2.86	0.11 ± 0.05	0.62 ± 0.24	0.60 ± 0.45
Red drum	*Sciaenops ocellatus*	440	3.0	3.03 ± 1.49	0.06 ± 0.02	0.62 ± 0.28	0.04 ± 0.01
Darter goby	*Ctenogobius boleosoma*	245	1.6	0.34 ± 0.06	0.06 ± 0.01	0.57 ± 0.09	0.03 ± 0.01
Naked goby	*Gobiosoma bosc*	245	1.6	0.87 ± 0.44	0.04 ± 0.01	0.24 ± 0.05	0.03 ± 0.00
Bay anchovy	*Anchoa mitchilli*	109	0.7	0.88 ± 0.28	—	0.17 ± 0.07	0.02 ± 0.01
Black drum	*Pogonias cromis*	108	0.7	1.53 ± 0.74	0.06 ± 0.01	0.10 ± 0.00	0.02 ± 0.00
Silver perch	*Bairdiella chrysoura*	104	0.7	1.21 ± 0.55	—	0.38 ± 0.16	—
Pinfish	*Lagodon rhomboides*	33	0.2	0.29 ± 0.07	—	0.14 ± 0.02	—
Bay whiff	*Citharichthys spilopterus*	30	0.2	—	0.04 ± 0.01	0.15 ± 0.05	0.03 ± 0.01
Skilletfish	*Gobiesox strumosus*	28	0.2	0.28 ± 0.09	0.01 ± 0.00	0.13 ± 0.02	0.01 ± 0.00
Green goby	*Microgobius thalassinus*	25	0.2	—	0.04 ± 0.01	—	0.01 ± 0.00
Blackcheek tonguefish	*Symphurus plagiusa*	15	0.1	—	0.04 ± 0.01	0.10 ± 0.00	0.03 ± 0.01
Southern kingfish	*Menticirrhus americanus*	12	0.1	0.24 ± 0.07	—	—	—
Spotted seatrout	*Cynoscion nebulosus*	11	0.1	0.23 ± 0.08	—	—	0.03 ± 0.00
Striped mullet	*Mugil cephalus*	9	0.1	0.14 ± 0.02	—	0.10 ± 0.00	—
Ladyfish	*Elops saurus*	4	0.0	0.10 ± 0.00	—	0.10 ± 0.00	—
Shrimp eel	*Ophichthus gomesii*	4	0.0	—	0.02 ± 0.00	—	—
Pipefish	*Syngnathus* spp.	4	0.0	0.15 ± 0.05	—	—	0.01 ± 0.00
Gulf menhaden	*Brevoortia patronus*	3	0.0	0.10 ± 0.00	—	0.10 ± 0.00	—
Feather blenny	*Hypsoblennius hentz*	2	0.0	—	0.01 ± 0.00	—	0.01 ± 0.00
Inland silverside	*Menidia beryllina*	2	0.0	0.10 ± 0.00	—	—	—
Emerald sleeper	*Erotelis smaragdus*	1	0.0	0.01 ± 0.00	—	—	—
Spot	*Leiostomus xanthurus*	1	0.0	—	—	0.10 ± 0.00	—
Blackwing searobin	*Prionotus rubio*	1	0.0	0.10 ± 0.00	—	—	—
Least puffer	*Sphoeroides parvus*	1	0.0	—	—	—	0.01 ± 0.00
Inshore lizardfish	*Synodus foetens*	1	0.0	0.10 ± 0.00	—	—	—

* RA = (No.ofindividuals/Total) × 100. RA, relative abundance.

TABLE 2.

Overall mean species densities and SE of crustaceans in 4 habitat types (marsh edge, nonvegetated deep, nonvegetated shallow, and oyster reef) biannually from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas.

Common name	Scientific name	Total catch	RA* (%)	Marsh edge (mean ± SE)	Nonvegetated deep (mean ± SE)	Nonvegetated shallow (mean ± SE)	Oyster reef (mean ± SE)
Total crustaceans		12,327	82.8				
Grass shrimp	*Palaemonetes* spp.	6,718	45.1	23.96 ± 4.88	0.08 ± 0.04	1.09 ± 0.18	0.23 ± 0.08
Postlarval penaeid shrimp	Penaeidae	4,002	26.9	10.34 ± 1.78	0.20 ± 0.05	3.90 ± 0.61	0.16 ± 0.06
Brown shrimp	*Farfantepenaeus aztecus*	405	2.7	2.58 ± 0.57	0.05 ± 0.01	0.60 ± 0.14	0.02 ± 0.00
White shrimp	*Litopenaeus setiferus*	392	2.6	2.05 ± 0.29	0.04 ± 0.02	0.71 ± 0.18	0.03 ± 0.01
Swimming crab	*Callinectes* spp.	301	2.0	0.73 ± 0.18	0.04 ± 0.01	0.52 ± 0.08	0.03 ± 0.01
Mud crabs	Xanthidae	269	1.8	0.33 ± 0.07	0.05 ± 0.02	0.31 ± 0.07	0.10 ± 0.03
Longeye shrimp	*Ogyrides* spp.	216	1.5	0.50 ± 0.00	0.18 ± 0.04	—	0.04 ± 0.02
Snapping shrimp	*Alpheus heterochaelis*	10	0.1	0.10 ± 0.00	0.03 ± 0.01	—	0.01 ± 0.01
Porcelain crabs	Porcellanidae	9	0.1	—	—	—	0.02 ± 0.00
Pea crabs	*Pinnixa* spp.	5	0.0	—	0.03 ± 0.01	—	0.01 ± 0.00

* RA = (No.ofindividuals/Total) × 100. RA, relative abundance.

Pogonias cromis, silver perch *Bairdiella chrysoura*, southern kingfish *Menticirrhus americanus*, stripped mullet *Mugil cephalus*, ladyfish *Elops saurus*, pipefish *Syngnathus* spp., inland silverside *Menidia beryllina*, spot *Leiostomus xanthurus*, least puffer *Sphoeroides parvus*, and inshore lizardfish *Synodus foetens*. Five fish species were observed in the fall only: Atlantic croaker, red drum, shrimp eel *Ophichthus gomesii*, emerald sleeper *Erotelis smaragdus*, and blackwing searobin *Prionotus rubio*.

Eighteen fish and nine invertebrates were collected in two or more habitats (Table 3). Five species were found exclusively in the marsh edge habitat (southern kingfish, inland silverside, emerald sleeper, blackwing searobin, and inshore lizardfish), one species (shrimp eel) only within the nonvegetated deep habitat, one species (spot) only within the nonvegetated-shallow habitat, and two species (least puffer and Porcellanidae) only within the oyster reef.

Faunal densities were greatest at the marsh edge, followed by nonvegetated shallow habitats across all sampling periods (Fig. 4). For the dominant (≥90% of total collected) fauna, grass shrimp, postlarval penaeid shrimp, brown shrimp, and white shrimp were found at the greatest densities within the marsh edge, followed by the nonvegetated shallow habitat (Fig. 5A). The dominant fish comprised 7 species —4 transients (Atlantic croaker, red drum, bay anchovy, and black drum) and 3 residents (darter goby, naked goby, and skilletfish *Gobiesox strumosus*). Similar to the crustaceans, the dominant transient fish were generally found at greater densities within the marsh edge, followed by the nonvegetated shallow habitat (Fig. 5B). The bay anchovy was the only dominant transient fish not collected from the nonvegetated deep habitat. Because of wide variability in Atlantic croaker densities, there were no significant differences among habitat types. Greater densities of naked goby and skilletfish were found within the marsh edge habitat, whereas the darter goby was observed at greater densities within the nonvegetated shallow habitat (Fig. 5C).

Community Analysis

Mean species diversity (H′ ± SE) was greatest in the nonvegetated deep habitat (H′ = 2.7 ± 0.1) and least in the

marsh edge habitat (H′ = 1.9 ± 0.2). Species richness was greatest in nonvegetated deep habitats (D = 2.3 ± 0.3) and least in marsh edge habitats (D = 1.8 ± 0.2). There were no significant differences in species diversity or richness across habitat types.

The Bray–Curtis cluster analysis with SIMPROF demonstrated differences in community structure among the 4 habitat types (P ≤ 0.001). The MDS analysis revealed 4 distinct clusters with communities that were at least 36% similar to one another: 1 containing all marsh edge and all nonvegetated shallow sites, 1 containing the majority of oyster reef sites, 1 containing all nonvegetated deep sites, and 1 containing a single oyster reef site (Fig. 6). The single clustered oyster reef site had the greatest number of species (n = 16) of all oyster reef sites. The BIOENV in the BEST routine found 4 species that had a 96.2% correlation with the total community structure (R = 0.962). Three of the 4 indicator species were abundant throughout all sampling periods: Atlantic croaker, grass shrimp, and postlarval penaeid shrimp. Each of these species was found at greater densities within the marsh edge habitat. The fourth indicator species, longeye shrimp, was found predominantly within the nonvegetated deep habitat.

DISCUSSION

Average densities of fish and crustaceans in Sabine Lake Estuary were 6 times greater in the marsh edge than the nonvegetated shallow habitats, and 40 times greater than both the oyster reef and nonvegetated deep habitats. This result contrasts with numerous studies showing that intertidal and shallow subtidal oyster reef habitats can support high densities and diversities of estuarine fauna (Coen et al. 1999, Coen & Grizzle 2007, Stunz et al. 2010). However, it supports results reported by Robillard et al. (2010), showing relatively low densities of fish and crustaceans on deep subtidal reefs compared with vegetated habitats. Low faunal densities observed in the oyster reef habitat could be the result of several factors. First, faunal assemblages can depend on the spatial configuration and proximity of surrounding habitats (Raposa & Oviatt 2000, Grabowski et al. 2005, Kanouse et al. 2006). Because the subtidal oyster reef in Sabine Lake Estuary is separated from marsh habitats by large

TABLE 3.

Seasonal occurrence, habitat occurrence, and total average density (measured in number per square meter) of fish and crustaceans biannually from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas.

| Common name	Scientific name	Seasonal occurrence	Habitat occurrence	Total abundance	RA* (%)	Mean ± SE
Fish				2,562	17.2	
Atlantic croaker	*Micropogonias undulatus*	Fall	ME, NVD, NVS, OY	1,124	7.5	1.02 ± 0.49
Red drum	*Sciaenops ocellatus*	Fall	ME, NVD, NVS, OY	440	3.0	1.09 ± 0.48
Darter goby	*Ctenogobius boleosoma*	Spring, fall	ME, NVD, NVS, OY	245	1.6	0.32 ± 0.05
Naked goby	*Gobiosoma bosc*	Spring, fall	ME, NVD, NVS, OY	245	1.6	0.30 ± 0.12
Bay anchovy	*Anchoa mitchilli*	Spring, fall	ME, NVS, OY	109	0.7	0.54 ± 0.19
Black drum	*Pogonias cromis*	Spring	ME, NVD, NVS, OY	108	0.7	0.61 ± 0.32
Silver perch	*Bairdiella chrysoura*	Spring	ME, NVS	104	0.7	0.87 ± 0.33
Pinfish	*Lagodon rhomboides*	Spring, fall	ME, NVS	33	0.2	0.24 ± 0.05
Bay whiff	*Citharichthys spilopterus*	Spring, fall	NVD, NVS, OY	30	0.2	0.05 ± 0.01
Skilletfish	*Gobiesox strumosus*	Spring, fall	ME, NVD, NVS, OY	28	0.2	0.14 ± 0.04
Green goby	*Microgobius thalassinus*	Spring, fall	NVD, OY	25	0.2	0.04 ± 0.00
Blackcheek tonguefish	*Symphurus plagiusa*	Spring, fall	NVD, NVS, OY	15	0.1	0.05 ± 0.01
Southern kingfish	*Menticirrhus americanus*	Spring	ME	12	0.1	0.24 ± 0.07
Spotted seatrout	*Cynoscion nebulosus*	Spring, fall	ME, OY	11	0.1	0.19 ± 0.07
Striped mullet	*Mugil cephalus*	Spring	ME, NVS	9	0.1	0.13 ± 0.02
Ladyfish	*Elops saurus*	Spring	ME, NVS	4	0.0	0.10 ± 0.00
Shrimp eel	*Ophichthus gomesii*	Fall	NVD	4	0.0	0.02 ± 0.00
Pipefish	*Syngnathus* spp.	Spring	ME, OY	4	0.0	0.10 ± 0.05
Gulf menhaden	*Brevoortia patronus*	Spring, fall	ME, NVS	3	0.0	0.10 ± 0.00
Feather blenny	*Hypsoblennius hentz*	Spring, fall	NVD, OY	2	0.0	0.01 ± 0.00
Inland silverside	*Menidia beryllina*	Spring	ME	2	0.0	0.10 ± 0.00
Emerald Sleeper	*Erotelis smaragdus*	Fall	ME	1	0.0	0.01 ± 0.00
Spot	*Leiostomus xanthurus*	Spring	NVS	1	0.0	0.10 ± 0.00
Blackwing searobin	*Prionotus rubio*	Fall	ME	1	0.0	0.10 ± 0.00
Least puffer	*Sphoeroides parvus*	Spring	OY	1	0.0	0.01 ± 0.00
Inshore lizardfish	*Synodus foetens*	Spring	ME	1	0.0	0.10 ± 0.00
Crustaceans				12,327	82.8	
Grass shrimp	*Palaemonetes* spp.	Spring, fall	ME, NVD, NVS, OY	6,718	45.1	6.22 ± 1.56
Postlarval penaeid shrimp	Penaeidae	Spring, fall	ME, NVD, NVS, OY	4,002	26.9	3.31 ± 0.58
Brown shrimp	*Farfantepenaeus aztecus*	Spring, fall	ME, NVD, NVS, OY	405	2.7	1.15 ± 0.28
White shrimp	*Litopenaeus setiferus*	Spring, fall	ME, NVD, NVS, OY	392	2.6	1.01 ± 0.18
Swimming crab	*Callinectes* spp.	Spring, fall	ME, NVD, NVS, OY	301	2.0	0.41 ± 0.07
Mud crabs	Xanthidae	Spring, fall	ME, NVD, NVS, OY	269	1.8	0.21 ± 0.03
Longeye shrimp	*Ogyrides* spp.	Spring, fall	ME, NVD, OY	216	1.5	0.15 ± 0.03
Snapping shrimp	*Alpheus heterochaelis*	Spring, fall	ME, NVD, OY	10	0.1	0.03 ± 0.01
Porcelain crabs	Porcellanidae	Fall	OY	9	0.1	0.02 ± 0.00
Pea crabs	*Pinnixa* spp.	Fall	NVD, OY	5	0.0	0.02 ± 0.00

* RA = (No.ofindividuals/Total) × 100. ME, marsh edge; NVD, nonvegetated deep; NVS, nonvegetated shallow; OY, subtidal oyster reef; RA, relative abundance.

areas of nonvegetated bottom, this may decrease connectivity and reduce movement of nekton between structured habitats (Lehnert & Allen 2002, Robillard et al. 2010). Because the nonvegetated shallow habitat was sampled adjacent to the marsh edge habitat, it is likely there was connectivity and movement between these paired habitats, resulting in similar communities. Second, low faunal densities from the oyster reef habitat may have resulted from collection limitation because of its large vertical relief (>1 m) and complex 3-dimensional structure. Alternatively, habitat selection resulting from water depth may have influenced the distribution of estuarine fauna (Rozas & Minello 1998). Additional research is warranted to compare directly unfished with fished oyster reefs, as well as deep subtidal reefs with their intertidal and shallow subtidal counterparts.

Because the majority of crustaceans and fish were observed within the marsh edge and nonvegetated shallow habitats, it is difficult to determine whether subtidal oyster reefs within Sabine Lake Estuary provide essential habitat for these species (Beck et al. 2001, Stunz et al. 2002a). The MDS analysis indicates a distinct faunal community inhabits the oyster reef compared with the intertidal marsh and nonvegetated habitats in Sabine Lake Estuary. Soniat et al. (2004) found reef-associated fish species to show a greater affinity for vertically oriented oyster shell structures such as those maintained by live oyster populations, rather than those with horizontal orientation. Because there was no commercially harvested oyster reef within Sabine Lake Estuary for comparison, it is not known how the faunal community might change as a result of dredging activities. However, Robillard et al. (2010) found the nekton community associated with commercially harvested oyster reefs in Lavaca Bay, Texas, to be similar to that inhabiting nonvegetated bottom. Therefore, should the oyster reef of Sabine Lake Estuary be opened to
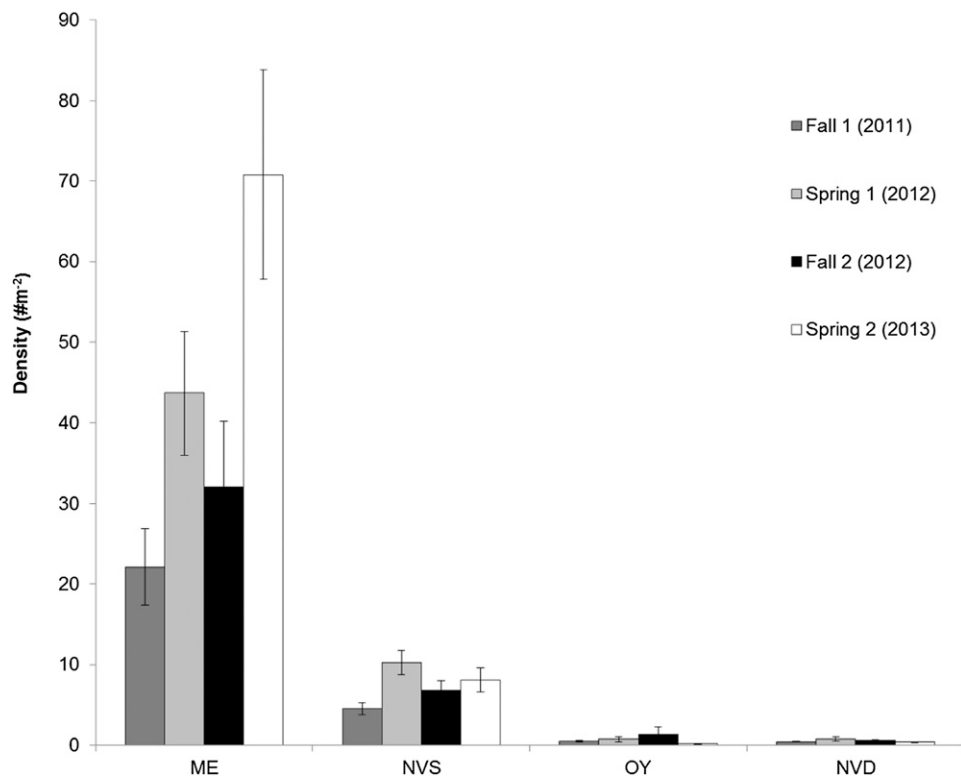
Figure 4. Seasonal mean nekton and crustacean densities of total fauna collected in marsh edge (ME), nonvegetated shallow (NVS), nonvegetated deep (NVD), and subtidal oyster reef (OY) habitats from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas. Error bars represent SE.

commercial harvest, the associated faunal community may not support the same unique species assemblage as the current, natural state.

The value of oyster reefs to resident fauna may depend more on the 3-dimensional habitat structure than the number of live oysters (Lenihan 1999, Tolley & Volety 2005, zu Ermgassen et al. 2012, but see Humphries et al. 2011b). Fish may select oyster reef habitats preferentially (Posey et al. 1999, Stunz et al. 2001), and there is evidence that nekton incur lower mortality in oyster reefs compared with other estuarine habitat types (Stunz et al. 2002a, Grabowski 2004). Given the extreme vertical relief of Sabine Lake Estuary's oyster reef, it may be of greater value to resident nekton than reflected in this study—for example, by increasing habitat heterogeneity and decreasing interspecific competition (Stunz et al. 2010, Bonin et al. 2011). In addition, previous evidence of high catch-per-unit effort of large, transient species associated with subtidal reefs substantiates their use for foraging and other critical habitat requirements (Robillard et al. 2010, Stunz et al. 2010). Overall, conserving the 10 km² of unfished, structurally complex oyster reef in Sabine Lake Estuary should have positive benefits for fish and crustaceans (Hixon 1998).

Salt marshes are well recognized as important habitats for estuarine fish and crustaceans (e.g., Bozeman & Dean 1980, Peterson & Turner 1994, Rozas & Minello 1998). Porcelain crabs and pea crabs were the only crustacean species not found within the marsh edge habitat. Previous studies have shown salt marsh and shallow vegetated estuarine habitats to support greater densities of nekton than nearby nonvegetated habitats, perhaps as a result of increased production, growth, and survival (Minello
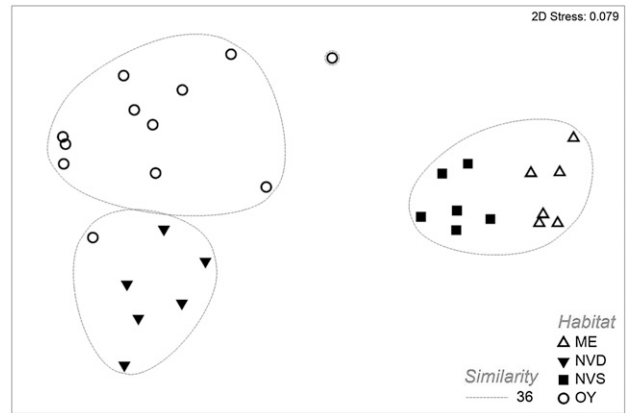
& Zimmerman 1983, Rozas & Zimmerman 2000, Kanouse et al. 2006). These shallow estuarine habitats may provide food and/or refugia for small nekton vulnerable to predation (Zimmerman & Minello 1984, Minello & Webb 1997, Paterson & Whitfield 2000). In addition, marsh edge habitats and surrounding nonvegetated habitats provide a variety of areas for juvenile fish to exploit critical resources (Neahr et al. 2010). Resident nekton such as the naked goby (*Gobiosoma bosc*) are abundant components of marsh edge communities in the northern Gulf of Mexico and are likely to play a vital link in the trophic web within these habitats (Hendon et al. 2000). Although not targeted in the current study, transient nekton also use marsh edge habitats seasonally for increased survival and growth compared with areas with limited structure (Stunz et al. 2002b, Neahr et al. 2010). Stunz et al. (2002a) found marsh edge habitats to support greater densities of newly settled red drum than near nonvegetated bottom and oyster reef habitats.

Of the 3 dominant resident fish (naked goby, darter goby, and skilletfish) only the naked goby and skilletfish were caught at greater densities within the marsh edge habitat, whereas the darter goby was dominant within the nonvegetated shallow habitat. Previous studies have demonstrated high densities of these fish within oyster reef habitat, perhaps as a result of food availability, protection from predation, and substrate for egg deposition (Crabtree & Middaugh 1982, Lehnert & Allen 2002, Tolley & Volety 2005). Harding and Mann (2000) reported fish densities to be 14 times greater for shell substrate bottom compared with areas lacking shell. However, species such as the naked goby have also been found at high densities within vegetated habitats compared with nonvegetated areas (Rozas & Minello 1998).
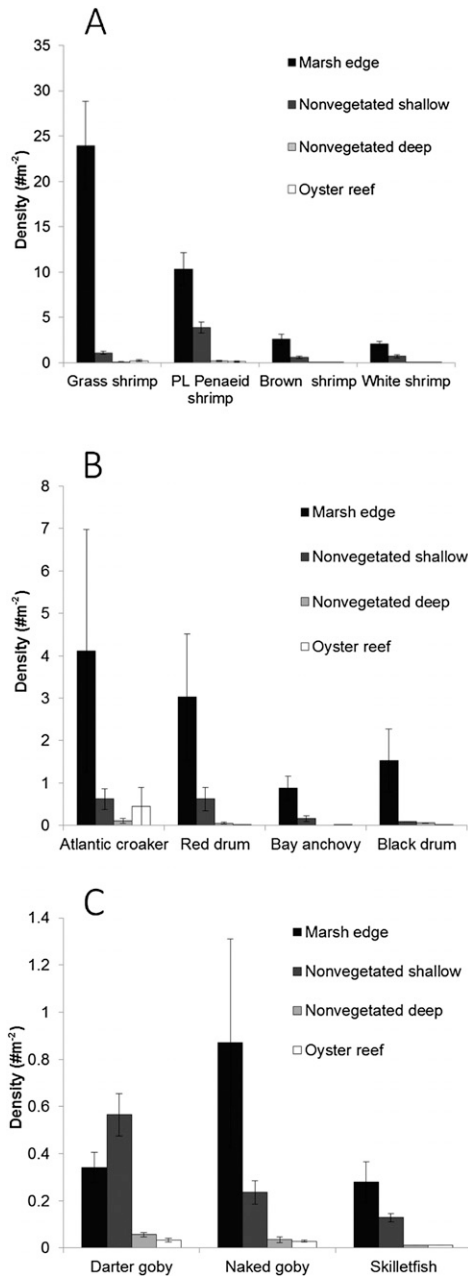
Figure 5. (A–C) Mean densities of dominant crustaceans (A), dominant transient fish (B), and dominant resident fish (C) collected in marsh edge, nonvegetated shallow, nonvegetated deep, and subtidal oyster reef habitats from fall 2011 through spring 2013 in Sabine Lake Estuary, Texas. Error bars represent SE.

Figure 6. A nonmetric multidimensional scaling plot with a Bray-Curtis cluster analysis superimposed using 36% similarity ($P \leq 0.001$) of mean nekton and crustacean density from each habitat (6 marsh edge (ME), 6 nonvegetated shallow (NVS), 6 nonvegetated deep (NVD), and 12 subtidal oyster reef (OY)) in Sabine Lake Estuary, Texas.

Transient fish habitat association may be more related to structure or associated fauna of the habitat than the habitat itself (Zimmerman & Minello 1984, Harding & Mann 2001). Red drum, bay anchovy, and black drum all occurred at greater densities within marsh edge habitats compared with nonvegetated deep bottom habitats. The Atlantic croaker did not seem to select for any particular habitat type, likely because of the highly opportunistic nature of this species (Miller & Dunn 1980, Petrik et al. 1999). However, some transient fish (Atlantic croaker, bay anchovy) have shown greater occurrence within nonvegetated bottom habitats compared with surrounding submerged aquatic

vegetation (Rozas & Minello 1998, Castellanos & Rozas 2001, Robillard et al. 2010).

Water depth may also play a significant role in shaping faunal community structure. For example, deep nonvegetated areas may serve as critical foraging grounds for large, transient fish (Robillard et al. 2010). Depth-related habitat selection can be important because horizontal transfer of production occurs across estuarine landscapes via predator–prey interactions (Kneib 1997). However, in areas prone to stratification, habitats located in deep water will be at greater risk of hypoxia/anoxia, which can lead to mortality and changes in abundance and distribution of associated fauna (Lenihan et al. 2001). In areas with high rates of sediment deposition or subsidence, increasing reef elevation may increase flow speed and ameliorate the effects of sedimentation (Lenihan 1999).

Results from this study provide a valuable baseline for future conservation and restoration efforts, particularly with respect to potential changes in estuarine community structure where commercial harvest occurs. Despite relatively low densities of fish and crustaceans collected within the subtidal oyster reef in Sabine Lake Estuary, previous long-term assessments have shown these areas form key habitats for important game fish (red drum, Atlantic croaker, and spotted seatrout) as well as other commercially important crustaceans (white shrimp, brown shrimp, blue crab) that use the estuary during selected periods of their life cycle (Rappleye 2005, TPWD 2005). In addition, unfished oyster reefs may offer unique ecosystem services that lower vertical relief, or degraded reefs, do not, including a more structurally complex habitat for fish and crustaceans (Lenihan & Peterson 1998), greater shoreline/marsh stabilization (Piazza et al. 2005, Meyer et al. 2008), higher filtration rates (Newell 1988, Grizzle et al. 2008), and increased nitrogen regulation (Beseres Pollack et al. 2013, Kellogg et al. 2013, Smyth et al. 2013), suggesting strong management implications if the reef is opened to commercial fishing in the future.

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