Relative Value of Deep Subtidal Oyster Reefs to Other Estuarine Habitat Types using a Novel Sampling Method

Author(s): Megan M. Reese Robillard, Gregory W. Stunz and James Simons
Source: Journal of Shellfish Research, 29(2):291-302.
Published By: National Shellfisheries Association
https://doi.org/10.2983/035.029.0203
URL: http://www.bioone.org/doi/full/10.2983/035.029.0203

Journal of Shellfish Research, Vol. 29, No. 2, 291–302, 2010.

RELATIVE VALUE OF DEEP SUBTIDAL OYSTER REEFS TO OTHER ESTUARINE HABITAT TYPES USING A NOVEL SAMPLING METHOD

MEGAN M. REESE ROBILLARD,[1] GREGORY W. STUNZ[1]* AND JAMES SIMONS[2]
[1]*Texas A&M University–Corpus Christi, Harte Research Institute for Gulf of Mexico Studies, Department of Life Sciences, 6300 Ocean Drive, Corpus Christi, TX 78412;* [2]*Texas Parks and Wildlife Department, 6300 Ocean Drive, NRC 2509, Corpus Christi, TX 78412*

ABSTRACT Subtidal eastern oyster *Crassostrea virginica* (Gmelin) cover large expanses of many Gulf of Mexico estuaries; however, few researchers have attempted to quantify the value of deep, open-water, subtidal reefs as habitat for fishes and crustaceans as a result of gear limitations. We developed quantitative sampling gear for live oyster reefs by slightly modifying an epibenthic sled. Gear comparison trials showed similar effectiveness among marsh edge, submerged aquatic vegetation, and nonvegetated bottom for both epibenthic sled types. We then quantified the density and community assemblage of nekton and benthic crustaceans on deep subtidal oyster reefs in Lavaca Bay, TX, and compared it with densities found in nearby marsh edge, submerged aquatic vegetation, and nonvegetated bottom habitats. We found significantly fewer nektonic and benthic crustaceans on nonvegetated bottom and oyster reefs than in marsh edge and submerged aquatic vegetation over all seasons and regions, and community analysis revealed similar differences among habitat assemblages. Using gill nets, the greatest catch of transient fishes and crustaceans were collected on oyster reefs and nonvegetated bottom. Although relatively low densities of small juvenile fishes were observed over deep oyster reefs, our community analyses and the high catch-per-unit-effort of large, transient species provide evidence that subtidal reefs are a critical habitat for numerous estuarine fishes and crustaceans.

KEY WORDS: oyster reef, essential fish habitat, nekton habitat use, estuarine habitat

INTRODUCTION

Estuaries are productive natural ecosystems, with 75% of the economically important fishes and crustaceans in the Gulf of Mexico using estuaries for ''nursery'' habitat (Chambers 1992, Minello 1999, Beck et al. 2001, Jackson et al. 2001). Legislative mandates have required resource managers to identify essential fish habitat (EFH) for fishes and crustaceans, and take measures to restore, protect, and preserve these areas (2007 Magnuson-Stevens Fishery Conservation and Management Act Public Law 94-265). Estuarine habitat types such as submerged aquatic vegetation (e.g., seagrasses), emergent intertidal marshes, and nonvegetated bottom have been thoroughly investigated, and their role as EFH is well documented (see reviews by Minello (1999) and Waycott et al. (2009)). Fishes and crustaceans occur at high densities in vegetated areas (Rozas & Minello 1998, Minello 1999, Beck et al. 2001, Stunz et al. 2002a), and experimental research has shown high growth rates and relatively low mortality (Stunz & Minello 2001, Stunz et al. 2001) among these vegetated estuarine habitats (Coen et al. 1999, Stunz & Minello 2001, Beck et al. 2001, Stunz et al. 2002b). However, eastern oyster reefs (*Crassostrea virginica* Gmelin) cover large expanses of many Gulf and Atlantic coast estuaries and are conspicuously missing from many of these comparative analyses. Research has largely focused on fringing intertidal oyster reefs and has clearly documented these areas as important habitat for fishes and crustaceans (Zimmerman et al. 1989, Coen et al. 1999, Posey et al. 1999, Peterson et al. 2003, Coen & Grizzle 2007, Stunz et al. 2010); however, very little research has assessed the habitat value of deep, subtidal oyster reefs.

Oyster reefs are both an estuarine habitat and fishery resource (Peterson et al. 2003). The majority of oyster reefs on the Gulf coast are subtidal (Kilgen & Dugas 1989), and oyster reef coverage has been greatly reduced in many areas as a result of overharvesting, reduced water quality, disease, and habitat destruction (Wenner et al. 1996, Coen et al. 1999, Kirby 2004, Johnson et al. 2009). For example, the percent coverage of oyster reefs has decreased by 60% in Lavaca Bay, TX, since 1913 (Simons et al. 2004). The continued loss of this estuarine habitat could affect numerous ecological processes, and scientists have limited data on fish and crustacean use of these areas to make informed decisions on the impact of this habitat loss. Clearly, subtidal oysters themselves are EFH because the oysters could not survive without the supporting reef structure (Coen et al. 1999), but it is far less certain what role these subtidal habitats offer estuarine fishes and crustaceans.

Few studies have been done on subtidal oyster reefs primarily because of difficulties with conventional gear in these deep, structurally complex habitat types. During the past 3 decades, several sampling techniques have been used to quantify habitat value of oyster reefs (see the review by Coen and Grizzle (2007)). For example, researchers sampling intertidal oyster reefs have used throw traps (Glancy et al. 2003), epibenthic pumps (Hosack et al. 2006), reef removal (Dame 1979), and drop samplers (Zimmerman et al. 1989, Shervette & Gelwick 2008, Stunz et al. 2010). However, these gear types have been met with various levels of success, and many are not an option, or have substantial limitations, on deep subtidal reefs. The studies that have described nekton abundance on subtidal oyster reefs have suggested that these deep habitats are essential habitat. Lehnert and Allen (2002) used experimental trays filled with oyster shells to determine nekton use of subtidal oyster shell accumulations, intertidal reefs, and nonvegetated bottom in North Inlet estuary, SC, and found high diversity and abundance of fishes on the subtidal oyster shells. Using similar experimental trays with oyster shells in Barataria Bay, LA, Plunket and La Peyre (2005) found that decapod crustaceans were twice as abundant on subtidal oyster reefs as on mud bottom. Gregalis et al. (2009)

---

*Corresponding author. E-mail: greg.stunz@tamucc.edu also used trays filled with oyster shell, as well as experimental gill nets, on restored oyster reefs and found high abundances of fishes and crustaceans using the deep reef habitats. Although these studies provided important evidence that subtidal oyster reefs may be an important habitat for numerous species, these sampling methods may not provide accurate density estimates (Rozas & Minello 1997), and many studies have only considered individual or groups of certain species. Moreover, it is also necessary to simultaneously compare relative value of oyster reef with other habitat types such as nonvegetated bottom and vegetated habitats (e.g., marsh).

The lack of quantitative data on nekton, benthic crustaceans, and transient fishes using subtidal oyster reefs, especially in relation to other putative estuarine habitat types, has hindered scientists from assessing the role reefs play in estuarine ecosystems. Thus, the overall goal of this study was to modify a traditional, quantitative gear that could effectively sample subtidal live oyster reefs and characterize their habitat role in estuarine ecosystems. Specifically, we addressed the following objectives: (1) modify a traditional sampling device to quantitatively sample deep subtidal oyster reefs, (2) determine the effectiveness of the modified gear in several estuarine habitats, and (3) quantify the density and community assemblage of fishes and crustaceans using subtidal oyster reefs, as well as marsh edge, submerged aquatic vegetation, and deep nonvegetated bottom habitats.

METHODS

Modified Sampling Gear Trials

To test quantitatively for nekton density differences among subtidal and intertidal habitats, we slightly modified a type of commonly used sampling gear—an epibenthic sled (EBS)—for use in deep subtidal habitats. The EBS is towed by hand and consists of a metal frame with an opening of 0.75 m (height) by 0.6 m (length) with a 1-mm mesh conical plankton net. The EBS has been shown to be effective and efficient in many studies (for examples and detailed descriptions see, Stunz et al. (2002a), Burfeind and Stunz (2006), and Reese et al. (2008)) among various habitat types, but is not designed to sample complex oyster reef structure. Therefore, we made slight modifications to the epibenthic sled (MES) for use in subtidal reefs by attaching steel teeth to the canvas-covered rectangular frame (78 cm wide × 30 cm high × 45 cm deep). The row of tines along the 0.78-m front bottom was designed to agitate and disrupt the oyster reef as the gear is towed. A coarse mesh (7 × 7-cm) panel was attached to the rear of the frame. This mesh was designed to exclude large oysters while allowing animals to pass through the netting to the cod end. The frame was covered in canvas, but the bottom of the MES was lined with chain mesh (9 × 9 cm) to disrupt and suspend momentarily oyster shell/clumps, and dislodge nekton and benthic crustaceans into the water column before being excluded, which could then be collected by the plankton net while oyster were excluded through the bottom. In all other respects, the MES was identical to the EBS in that it included a 1-mm mesh conical plankton net attached to the back of the frame, and aluminum runners/sleds along the sides for stability.

To calculate the effectiveness of the gear, we first standardized the MES with the original EBS among various habitat types. We sampled several shallow estuarine habitats using both gear types, allowing us to compare densities and therefore determine the effectiveness of the MES. Samples were collected in upper Laguna Madre, TX, in June 2006. We collected 10 replicate samples with each gear type, MES and EBS, in seagrass (*Halodule wrightii*), marsh edge (*Spartina alterniflora*), and shallow nonvegetated bottom, for a total of 30 samples per gear. The marsh edge interface is the ecotonal zone between open water and the emergent vegetation (Zimmerman et al. 1984, Baltz et al. 1993), and in our gear trials, marsh edge samples were within 1 m of the marsh vegetated edge over nonvegetated bottom. The MES was pulled by hand approximately 13 m and the EBS was pulled approximately 17 m, both covering 10 m^2 of bottom. Each adjacent pull (at least 10 m apart) occurred alternately along a marsh edge or seagrass transect. Samples were rough sorted in the field, removing large algae, and preserved in 10% formalin. In the laboratory, fishes and crustaceans were sorted, identified, quantified, and preserved in 70% ethanol.

Delineation of Sites and Sampling in Lavaca Bay, TX

We conducted the large-scale habitat use study in Lavaca Bay, TX, which is located in the northwest corner of the Matagorda Bay system on the central Texas coast (Fig. 1). Matagorda Bay is the 3rd largest bay system on the Texas coast, covering about 1,100 km^2 (Kilgen & Dugas 1989). The Lavaca and Navidad rivers combine and empty into the northeast corner of Lavaca Bay, providing the majority of freshwater and sediments to the bay system. Subtidal oyster reefs (*C. virginica*) are a large biogenic habitat in Lavaca Bay found in deep, open-water areas of the bay, and are commercially harvested. The other predominant habitat types in Lavaca Bay are submerged aquatic vegetation (*H. wrightii*) and intertidal salt marshes (*S. alterniflora*). This study focused on quantifying the density of fishes and crustaceans in 2 separate regions (upper and lower) and 4 different habitat types in Lavaca Bay: marsh edge, submerged aquatic vegetation (found only in lower Lavaca Bay), subtidal oyster reef, and deep nonvegetated bottom adjacent to subtidal reefs. In the upper regions, the marsh edges sampled were over nonvegetated bottom; in the lower regions, the marsh edge was often interspersed with submerged aquatic vegetation. Sampling was conducted in summer (July) and fall (October) 2006, and winter (February) and spring (April) 2007, for a total of 4 sampling events. There were 2 replicate sites per available habitat in both upper (except submerged aquatic vegetation) and lower Lavaca Bay, and triplicate samples were collected at all habitat sites, for a total of 42 samples for each sampling event.

The gear trials showed the MES has similar effectiveness to the EBS, but the steel teeth on the MES severely disrupt vegetated habitats. Because the EBS was not designed and was ineffective at sampling the subtidal oyster habitat type, and the MES severely damaged shallow vegetated habitats, we used the EBS in marsh and submerged aquatic vegetation habitats and the MES in the deep reef and nonvegetated bottom habitats. The EBS was pulled by hand about 17 m, covering 10 m^2 of bottom, and the MES was towed by boat to cover 100 m^2. We selected a tow length of 100 m^2, because in preliminary testing on deep reefs we found very low abundance of organisms in subtidal habitats (Rozas & Minello 1997). Transient fishes and crustaceans were collected using 1 gill net (29 × 1 m, with 5-cm and 2.5-cm monofilament panels) per habitat site in both

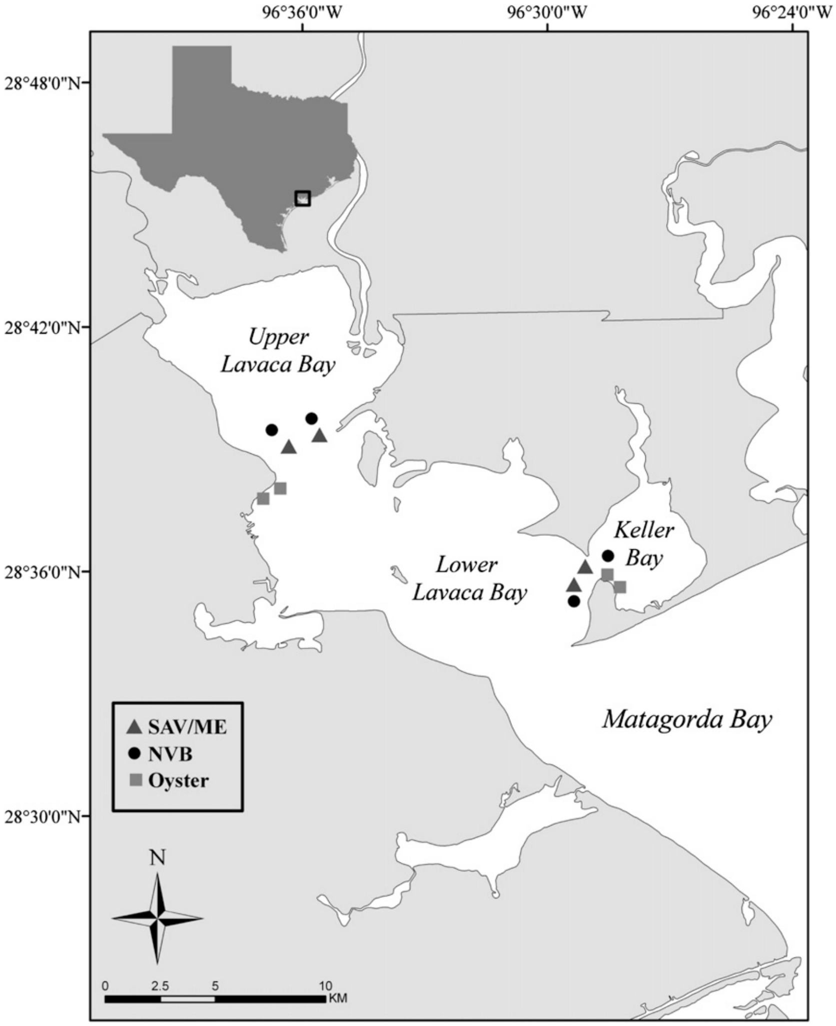

Figure 1. Study site locations of habitats sampled in Lavaca Bay, TX. Submerged aquatic vegetation (SAV) was found only in the lower Lavaca Bay sampling sites. ME, marsh edge; NVB, nonvegetated bottom; Oyster, subtidal oyster reef.

the upper and lower Lavaca Bay for a total of 12 per sampling event. Gill nets were set perpendicular to the shoreline for submerged aquatic vegetation and marsh edge sites; therefore, only 1 net was used for each marsh edge/submerged aquatic vegetation site. Soak times varied (4 h in summer; 2 h in fall, winter, and spring), and standardized catch-per-unit-effort was calculated for each set.

Samples collected with the EBS and MES were rough sorted in the field and preserved in 10% formalin. In the laboratory, fish and crustaceans were sorted, identified to lowest feasible taxon, measured to the nearest 0.1 mm standard length, and preserved in 70% ethanol. If more than 20 individuals were caught for each species or group, the largest and smallest, and 20 other random individuals were measured. Large, transient fishes collected from gill nets were counted, identified, and measured to the nearest millimeter total length. Seasonally at each site, water temperature (measured in degrees Celsius), dissolved oxygen (measured in milligrams per liter), salinity (psu), and depth (measured in meters) were measured using a Hydrolab Quanta (Hydrolab Corporation®, Austin Texas). At subtidal oyster reef and nonvegetated bottom sites, we measured temperature, dissolved oxygen, and salinity from the surface and bottom. Marsh edge and submerged aquatic vegetation environmental parameters were combined into 1 site because they were directly adjacent to each other and, in upper Lavaca Bay, there was no submerged aquatic vegetation.

Data Analysis

We tested for differences in gear effectiveness among habitats with analysis of variance (ANOVA; $\alpha = 0.05$) using the general linear model procedure in SAS version 9.1. Total catches were converted to number per square meter. We used a 2-way ANOVA with habitat (marsh edge, submerged aquatic vegetation, and nonvegetated bottom) and gear (EBS and MES) as the fixed main effects. We found a significant habitat–gear interaction in the ANOVA model ($F_{2,54} = 21.10$; $P < 0.001$); therefore, we used a 1-way main effects model using each habitat × gear combination ($n = 6$) as levels in the main treatment with *a priori* linear contrasts ($\alpha = 0.05$) to test for density differences among gear and habitat. Habitat use patterns of total macrofauna collected in Lavaca Bay were analyzed using a partially nested hierarchical ANOVA model in SAS version 9.1. Densities were calculated for each habitat by converting total catches to number per square meter. The overall ANOVA model included region (upper and lower), season (summer, fall, winter, spring), and habitat (marsh edge, subtidal oyster reef, nonvegetated bottom) as fixed effects, and sites as random effects. Sites were nested within habitat, and season was used as a blocking variable because samples were only collected once each season. Submerged aquatic vegetation was not sampled in upper Lavaca Bay because it did not occur; therefore, we did not include it in the overall model. Using a 2nd ANOVA model, we tested differences of total macrofauna density in lower Lavaca Bay, which included all 4 habitat types. The fixed and random effects were the same as noted earlier, except region was excluded from the analysis. Catch data from the gill nets (measured as catch per unit effort (CPUE); number of fish per hour) was analyzed using the overall model with 3 habitats (marsh edge/submerged aquatic vegetation, subtidal oyster reef, and nonvegetated bottom). Physical parameters were also analyzed for differences among habitats, regions, and seasons using the overall model with 3 habitats (marsh edge/submerged aquatic vegetation, subtidal oyster reef, and nonvegetated bottom). For each model, the distribution of the residuals was analyzed using the UNIVARIATE procedure, and data were transformed (log10 $(x + 1)$) to reduce heteroskedasticity. Mean differences in density and CPUE among regions and habitat types were tested using Tukey's Honestly Significant Difference (HSD) ($\alpha = 0.05$).

We used a multivariate analysis to test for significant differences in community assemblages among habitats in Lavaca Bay, TX, using several routines from PRIMER v.6 (Clarke & Gorley 2006). We examined mean density of species collected seasonally for each habitat (16 total samples). Data were 4th root transformed prior to analysis to reduce the differential effects of dominant species and to differentiate between habitats having many or few rare species (Clarke & Green 1988). We determined community assemblage patterns among habitats using nonmetric multidimensional scaling (MDS) based on Bray-Curtis similarity, with Bray-Curtis cluster groups superimposed for interpretation (Clarke & Warwick 2001). We also used the BVSTEP procedure in the BEST routine to identify the species that contributed the most to the whole community pattern, which is a more holistic approach than the SIMPER routine. Using the identified species, we then created another resemblance matrix based on Bray-Curtis similarity and compared it with the original matrix (all species included) using the RELATE routine, with the null hypothesis that there is no relationship between the 2 similarity matrices, to determine whether we would find a similar community pattern with only the selected species (Clarke & Gorley 2006).

RESULTS

Sampling Gear Trials

We examined the effectiveness of the MES versus the EBS and found they collect similar densities of fish and crustaceans. Catch data are reported as mean ± SE throughout the Results section. There was no significant difference between the MES ($2.15 \pm 0.52/\text{m}^2$) and EBS ($2.90 \pm 0.98/\text{m}^2$) in submerged aquatic vegetation ($F_{1,54} = 0.010$, $P = 0.936$). Similarly, in marsh edge there was no difference ($F_{1,54} = 0.980$; $P = 0.326$) between gear (MES, $4.79 \pm 0.84/\text{m}^2$; EBS, $3.33 \pm 0.49/\text{m}^2$). Densities were also similar (MES, $0.16 \pm 0.04/\text{m}^2$; EBS, $0.07 \pm 0.04/\text{m}^2$) in nonvegetated bottom ($F_{1,54} = 0.150$, $P = 0.703$). We also found no difference between the MES and the EBS among all habitats ($F_{1,54} = 0.560$, $P = 0.458$).

Lavaca Bay Physical Parameters

We found seasonal and regional differences in physical parameters, with some differences among habitat types. There were no habitat–region interactions; therefore, we were able to interpret habitat, season, and region main effects. Water depth was the only parameter that was different among habitats, with subtidal oyster reef and nonvegetated bottom significantly deeper than marsh edge and submerged aquatic vegetation sites. Regions were significantly different for all parameters and upper Lavaca Bay had significantly higher temperatures ($F_{1,45} = 8.17$) and higher dissolved oxygen concentrations ($F_{1,45} = 10.41$). Lower Lavaca Bay had significantly higher salinity ($F_{1,45} = 142.58$) and greater depth ($F_{1,45} = 12.74$). All physical parameters measured were different among seasons (Table 1).

Lavaca Bay Density and CPUE

We collected a total of 2,961 fishes from all habitats, representing at least 42 species from 23 families, and 15,056 crustaceans (13 species from 12 families) during the study period (Table 2). In the marsh edge habitat, we collected the most organisms, with 695 fishes (representing at least 28 species from 17 families) and 7,772 crustaceans (representing 9 species from 8 families). We collected 579 fishes and 5,847 crustaceans from the submerged aquatic vegetation habitat, representing 22 species from 12 families and 7 species from 6 families, respectively. The highest catch of fishes was on nonvegetated bottom, with 1,254 organisms collected (representing 21 species from 14 families). Bay anchovy (*Anchoa mitchilli* Valenciennes) was the dominant fish captured on nonvegetated bottom, accounting for 48% of total fishes collected. We also collected 802 crustaceans from nonvegetated bottom (12 species from 11 families). The fewest organisms were collected from the subtidal oyster reef habitat; we collected 433 fishes (representing 18 species from 13 families) and 635 crustaceans (representing 10 species from 9 families; Table 2). Crustaceans outnumbered fishes, accounting for about 84% of the total catch, with grass shrimp (*Palaemonetes* spp. Heller) representing 67% and penaeid shrimp accounting for 18% of the total crustaceans collected. Six species of fishes (bay anchovy, Atlantic croaker *Micropogonias undulatus* Linnaeus, pipefishes *Syngnathus* spp. Linneaus, naked goby *Gobiosoma bosc* Lacepède, Gulf menhaden *Brevoortia patronus* Goode, and pinfish *Lagodon rhomboides* Linneaus) represented 81% of the total fishes collected over all seasons (Table 2).

We examined overall density of nekton and benthic crustaceans collected among the habitats found in both regions and found significantly fewer in nonvegetated bottom ($4.28 \pm 0.28/\text{m}^2$) and subtidal oyster reef ($2.23 \pm 0.99/\text{m}^2$) than in marsh edge ($17.65 \pm 2.38/\text{m}^2$) over all seasons and regions (Table 3, Fig. 2A). There was no region–habitat interaction, but season was significant. We also assessed density of all 4 habitats in lower Lavaca Bay and found the highest densities of nekton and benthic crustaceans in submerged aquatic vegetation (26.76 ±

TABLE 1.

Mean environmental parameters (SE) for habitats in both upper and lower Lavaca Bay collected seasonally from July 2006 through April 2007.

	Marsh Edge/Submerged Aquatic Vegetation				Subtidal Oyster Reef				Nonvegetated Bottom				*P* Value for Habitat Effect	*P* Value for Region Effect	*P* Value for Season Effect
	Upper		Lower		Upper		Lower		Upper		Lower				
Parameter	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
Water temperature (°C)	22.1	(6.6)	22.6	(4.7)	19.7	(5.9)	21.9	(5.5)	21.1	(6.3)	21.9	(5.5)	0.218	0.006*	<0.001*
Dissolved oxygen (mg/L)	8.7	(1.5)	7.3	(1.5)	8.7	(2.1)	7.9	(1.8)	8.2	(1.7)	8.0	(1.9)	0.764	0.002*	<0.001*
Salinity (psu)	13.0	(3.1)	18.0	(2.8)	11.8	(3.2)	19.0	(2.7)	12.8	(3.8)	18.7	(2.7)	0.905	<0.001*	<0.001*
Water depth (m)	0.7	(0.2)	0.5	(0.1)	2.0	(0.4)	1.8	(0.2)	2.0	(0.3)	1.6	(0.3)	<0.001*	<0.001*	<0.001*

Mean and SE were calculated from measurements taken twice per season over 4 seasons ($n = 8$). During July 2006, only 1 sample was collected the subtidal oyster reef; therefore, $n = 7$ for all parameters. ANOVA was used to test for differences among habitats, regions, and seasons. Season was used as a blocking variable because samples were only collected once each season and the region × habitat interaction was not significant.
* Value was significant.

4.92/m^2) and marsh edge (20.26 ± 3.31/m^2) compared with nonvegetated bottom (2.91 ± 1.06/m^2) and subtidal oyster reef (1.72 ± 0.34/m^2) over all seasons (Table 3, Fig. 2B).

We found the greatest CPUE of transient fishes and crustaceans on subtidal oyster reef (13.33 ± 2.45 CPUE) and nonvegetated bottom (13.73 ± 2.37 CPUE) compared with shallow marsh edge/submerged aquatic vegetation habitats (3.34 ± 0.99 CPUE; Table 3, Fig. 3). Summer (14.92 ± 2.96 CPUE), fall (12.17 ± 2.41 CPUE), and spring (12.71 ± 2.35 CPUE) catches were similar, with winter having the lowest CPUE (0.75 ± 0.29). We also captured more fishes in the upper region (12.00 ± 2.07 CPUE) than in the lower region (8.27 ± 0.29 CPUE; Table 3). We collected a total of 1,079 fishes and crustaceans. Gulf menhaden dominated the total catch and had a mean size of 166 ± 1.2 mm. Gafftopsail catfish (*Bagre marinus* Mitchill) and hardhead catfish (*Ariopsis felis* Linnaeus) also contributed to the total catch and were collected primarily in subtidal oyster reef and nonvegetated bottom habitats. Most species were collected among all habitats; however, red drum (*Sciaenops ocellatus* Linnaeus) and black drum (*Pogonias cromis* Linnaeus) were collected only in the marsh edge/submerged aquatic vegetation habitat. Similarly, blacktip shark (*Carcharhinus limbatus* Valenciennes), Spanish mackerel (*Scomberomorus maculatus*), and bonnethead sharks (*Sphyrna tiburo* Linnaeus) were only collected in subtidal oyster reef and nonvegetated bottom habitats (Table 4).

Lavaca Bay Community Assemblage

Community assemblage analysis showed similar results to the density patterns among habitats throughout both upper and lower Lavaca Bays. Bray-Curtis cluster analysis with SIMPROF test revealed 2 clusters—marsh edge and submerged aquatic vegetation, and subtidal oyster reef and nonvegetated bottom—at the 50% similarity level ($P < 0.001$; Fig. 4A). The MDS plot showed the same separation between vegetated habitats and subtidal habitats, and the separation was very clear with the cluster analysis superimposed at the 50% similarity level (Fig. 4B). We also assessed differences in species composition based on the 2 groups from the cluster and MDS analyses. Using the BEST routine, we found 14 species (Table 2) that correlated 95.2% of the community assemblages. We found a strong correlation between the original matrix (all species) and the BEST matrix (selected species) using the RELATE routine indicating that the matrices were similar ($R = 0.952$, $P = 0.001$). In general, the most abundant species were identified in the BEST routine as contributing to the community assemblage such as anchovies, pipefishes, several goby species, grass shrimp, penaeid shrimp species, blue crabs, and stone crabs (*Menippe* sp. De Haan). However, several flatfish species (*Citharichthys spilopterus* Gunter, *Paralichthys lethostigma* Jordan and Gilbert, *Symphurus plagiusa* Linnaeus, and *Achirus lineatus* Linnaeus) that had relatively low densities contributed to the overall community structure among habitats. Snapping shrimp (*Alpheus heterochaelis* Say) were also collected in low densities, but did contribute to community assemblage differences (Table 2).

DISCUSSION

Sampling Gear Trials

A major focus of this study was to assess whether an MES could quantitatively sample deep, structurally complex oyster reef. We collected similar densities of fishes and crustaceans between the MES and EBS gear types in all habitats sampled (submerged aquatic vegetation, marsh edge, and nonvegetated bottom), indicating that the MES is effective at capturing small fishes and crustaceans from numerous estuarine habitat types. Because the EBS cannot be used in deep habitats, it was not possible to include subtidal oyster reef into the initial gear comparison trials. Despite these limitations, we are confident in the functionality of the MES's effectiveness on deep subtidal habitats, and initial observational testing in clear water showed the MES was turning over the oysters while simultaneously collecting small organisms. However, a limitation of the MES was that it severely disrupts vegetated habitats as the front teeth dig into the substrate. This was by design, because the dredging is ideal for disrupting and sampling oyster reef, but it made the gear difficult to tow by hand, and we do not recommended it for

TABLE 2.

Overall mean density as number per square meter and SE of all collected fishes and crustaceans in 4 habitat types, including BEST analysis results.

Common Name	Scientific Name	Total Catch	RA (%)	Marsh Edge Mean	Marsh Edge SE	Submerged Aquatic Vegetation Mean	Submerged Aquatic Vegetation SE	Subtidal Oyster Reef Mean	Subtidal Oyster Reef SE	Nonvegetated Bottom Mean	Nonvegetated Bottom SE
Total fishes		2,961	16.4								
Bay anchovy*	*Anchoa mitchilli*	894	5.0	0.31	(0.14)	0.00	(0.00)	0.28	(0.09)	1.27	(0.62)
Atlantic croaker	*Micropogonias undulates*	502	2.8	0.27	(0.12)	0.11	(0.05)	0.34	(0.12)	0.38	(0.12)
Pipefish	*Syngnathus* spp.	321	1.8	0.37	(0.21)	0.56	(0.15)	0.00	(0.00)	0.02	(0.01)
Naked goby*	*Gobiosoma bosc*	261	1.4	0.08	(0.03)	0.54	(0.22)	0.11	(0.03)	0.09	(0.04)
Gulf menhaden*	*Brevoortia patronus*	243	1.3	0.00	(0.00)	0.00	(0.00)	0.04	(0.02)	0.46	(0.17)
Pinfish	*Lagodon rhomboids*	183	1.0	0.09	(0.03)	0.59	(0.22)	0.00	(0.00)	—	—
Green goby	*Microgobius thalassinus*	163	0.9	0.02	(0.01)	0.13	(0.07)	0.05	(0.01)	0.21	(0.07)
Darter goby	*Gobionellus boleosoma*	58	0.3	0.01	(0.00)	0.15	(0.06)	0.01	(0.00	0.03	(0.01)
Star drum	*Stellifer lanceolatus*	45	0.2	0.06	(0.03)	0.05	(0.04)	0.00	(0.00)	—	—
Goby species	Gobiidae	32	0.2	0.00	(0.00)	0.02	(0.01)	0.03	(0.02)	0.03	(0.01)
Red drum	*Sciaenops ocellatus*	32	0.2	0.05	(0.02)	0.03	(0.01)	—	—	0.00	(0.00)
Bay whiff*	*Citharichthys spilopterus*	30	0.2	0.00	(0.00)	0.01	(0.01)	0.02	(0.01)	0.03	(0.01)
Code goby	*Gobiosoma robustum*	29	0.2	—	—	0.11	(0.04)	0.00	(0.00)	0.00	(0.00)
Spotfin mojarra	*Eucinostomus argenteus*	23	0.1	0.04	(0.01)	0.03	(0.02)	—	—	—	—
Southern flounder*	*Paralichthys lethostigma*	18	0.1	0.04	(0.01)	0.00	(0.00)	—	—	—	—
Blackcheek tonguefish*	*Symphurus plagiusa*	16	0.1	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)
Lined sole*	*Achirus lineatus*	15	0.1	0.02	(0.01)	0.01	(0.01)	—	—	0.01	(0.01)
Diamond killfish	*Adinia xenica*	14	0.1	0.03	(0.02)	—	—	—	—	—	—
Spotted seatrout	*Cynoscion nebulosus*	12	0.1	0.01	0.03	(0.10)	—	—	0.00	(0.00)	
Sheepshead minnow	*Cyprinodon variegates*	10	0.1	0.02	(0.01)	—	—	—	—	—	—
Black drum	*Pogonias cromis*	9	0.0	—	—	—	—	0.00	(0.00)	0.01	(0.01)
Unidentified fish	Unidentified Fish	0	0.0	—	—	—	—	0.00	(0.00)	0.01	(0.01)
Stripped mullet	*Mugil cephalus*	5	0.0	0.01	(0.01)	—	—	—	—	—	—
Clown goby	*Microgobius gulosus*	4	0.0	0.00	(0.00)	0.00	(0.00)	—	—	0.00	(0.00)
Silver perch	*Bairdiella chrysoura*	3	0.0	0.00	(0.00)	—	—	—	—	0.00	(0.00)
Dwarf seahorse	*Hippocampus zosterae*	3	0.0	—	—	0.01	(0.01)	—	—	—	—
Frillfin gobies*	*Bathygobius* spp.	2	0.0	—	—	—	—	—	—	0.00	(0.00)
Clingfish	*Gobisox* spp.	2	0.0	—	—	—	—	0.00	(0.00)	0.00	(0.00)
Tripletail	*Lobotes surinamensis*	2	0.0	0.00	(0.00)	—	—	0.00	(0.00)	—	—
Rainwater killfish	*Lucania parva*	2	0.0	0.00	(0.00)	—	—	—	—	—	—
Atlantic silverside	*Menidia menidia*	2	0.0	—	—	0.01	(0.01)	—	—	—	—
Shrimp eel	*Ophichthus gomesii*	2	0.0	0.00	(0.00)	—	—	—	—	0.00	(0.00)
Tonguefish	*Symphurus* spp.	2	0.0	0.00	(0.00)	—	—	—	—	0.00	(0.00)
Inshore lizardfish	*Synodus foetens*	2	0.0	—	—	0.00	(0.00)	0.00	(0.00)	—	—
Needlefish	Belonidae	1	0.0	0.00	(0.00)	—	—	—	—	—	—
Striped blenny	*Chasmodes bosquianus*	1	0.0	—	—	—	—	0.00	(0.00)	—	—
Mojarra species	*Eucinostomus spp.*	1	0.0	—	—	0.00	(0.00)	—	—	—	—
Sharptail goby	*Gobionessus oceanicus*	1	0.0	0.00	(0.00)	—	—	—	—	—	—
Lined Seahorse	*Hippocampus erectus*	1	0.0	—	—	0.00	(0.00)	—	—	—	—
Grey snapper	*Lutjanus griseus*	1	0.0	0.00	(0.00)	—	—	—	—	—	—
Inland silverside	*Menidia beryllina*	1	0.0	—	—	—	—	—	—	0.00	(0.00)
Southern kingfish	*Menticirrhus americanus*	1	0.0	0.00	(0.00)	—	—	—	—	—	—
Pigfish	*Orthopristis chrysoptera*	1	0.0	—	—	—	—	0.00	(0.00)	—	—
Least puffer	*Sphoeroides parvus*	1	0.0	—	—	—	—	—	—	0.00	(0.00)
Hogchoker	*Trinectes maculatus*	1	0.0	—	—	—	—	—	—	0.00	(0.00)
Total crustaceans		15,056	83.6								
Grass shrimp	*Palaemonetes* ssp.	10,063	55.8	11.88	(2.23)	17.77	(4.56)	0.09	(0.02)	0.11	(0.07)
Penaeid shrimp*	Penaeidae	2,649	14.7	2.29	(0.47)	4.25	(1.12)	0.45	(0.10)	0.66	(0.16)
White shrimp*	*Litopenaeus setiferus*	568	3.2	1.03	(0.35)	0.26	(0.08)	0.02	(0.01)	0.01	(0.01)
Grooved penaeid shrimp*	*Farfantepenaeus* spp.	371	2.1	0.29	(0.09)	0.50	(0.11)	0.13	(0.04)	0.10	(0.05)
Arrow shrimp	*Tozeuma carolinense*	342	1.9	0.02	(0.01)	1.02	(0.38)	—	—	0.19	(0.18)
Blue crab	*Callinectes sapidus*	312	1.7	0.41	(0.08)	0.35	(0.13)	0.02	(0.01)	0.04	(0.02)
Xanthid crabs	Xanthidae	290	1.6	0.19	(0.06)	0.15	(0.09)	0.27	(0.06)	0.07	(0.04)

continued on next page

TABLE 2.

continued

Common Name	Scientific Name	Total Catch	RA (%)	Marsh Edge		Submerged Aquatic Vegetation		Subtidal Oyster Reef		Nonvegetated Bottom	
				Mean	SE	Mean	SE	Mean	SE	Mean	SE
Longeye shrimp	*Ogyrides* spp.	216	1.2	—	—	0.01	(0.01)	0.05	(0.02)	0.40	(0.15)
Stone crabs*	*Menippe* spp.	108	0.06	0.04	(0.02)	—	—	0.14	(0.04)	0.05	(0.02)
Porcelain crabs	Porcellanidae	73	0.04	0.00	(0.00)	—	—	0.13	(0.06)	0.02	(0.01)
Brown shrimp	*Farfantepenaeus aztecus*	52	0.3	0.04	(0.02)	0.06	(0.02)	0.02	(0.01)	0.02	(0.01)
Snapping shrimp*	*Alpheus heterochaelis*	5	0.0	0.00	(0.00)	—	—	0.00	(0.00)	0.01	(0.01)
Mantis shrimp	Stomatopoda	4	0.0	—	—	—	—	0.01	(0.00)	—	(0.00)
Pea crabs	*Pinnixa* spp.	2	0.0	—	—	—	—	—	—	0.00	(0.00)
Longnose spider crab	*Libinia dubia*	1	0.0	—	—	—	—	—	—	0.00	(0.00)

The EBS was used for marsh edge and submerged aquatic vegetation samples, and the MES was used for subtidal oyster reef and nonvegetated bottom samples. The total number and relative abundance (RA; number of individuals/total number of animals collected × 100) also are given.
* Species that contribute the most to the community structure for each habitat from BEST analysis. A dash (—) indicates no catch.

use in shallow or vegetated habitat types. Overall, our results show evidence that the MES functions well, and we recommend this gear for sampling deep reef, although caution should be taken when extrapolating our relative density estimates in subtidal oyster reef to absolute abundance numbers.

Lavaca Bay Density and CPUE

We found differences in fish and crustacean density among habitats in Lavaca Bay, TX. Most notably were differences between the shallow vegetated habitats and the deep subtidal oyster reef and adjacent nonvegetated bottom. Fish and crustacean densities in shallow vegetated marsh habitat were 3-fold higher than both deep nonvegetated bottom and subtidal oyster reef in both upper and lower Lavaca Bay. Environmental water characteristics most likely did not contribute to these differences because water temperature, dissolved oxygen, and salinity were similar among habitats. The only parameter that differed was depth, but subtidal and nonvegetated bottom habitats were expected to be much deeper than submerged

TABLE 3.

ANOVA table for total macrofauna density (sum of total fishes and crustaceans; overall model and lower Lavaca Bay model) and transient fish CPUE (gill net model) in Lavaca Bay, TX.

Source	*df*	Sum of Squares	Mean Square	F Value	*P* Value
Overall model					
Region	1	0.013	0.013	0.450	0.5048
Season	3	0.308	0.103	3.530	0.0167*
Habitat	2	2.904	1.452	50.020	<0.001*
Sites (habitat)	3	0.047	0.016	0.550	0.6521
Region × habitat	2	0.053	0.027	0.910	0.4036
Residual	132	3.831	0.029		
Lower Lavaca Bay model					
Season	3	0.150	0.050	1.090	0.3568
Habitat	3	4.863	1.621	35.300	<0.001*
Sites (habitat)	4	0.101	0.025	0.550	0.6977
Residual	157	7.210	0.046		
Gill net model					
Region	1	0.303	0.303	6.980	0.0132*
Season	3	4.633	1.544	35.600	<0.001*
Habitat	2	2.050	1.025	23.630	<0.001*
Sites (Habitat)	3	0.106	0.035	0.810	0.4983
Region × habitat	2	0.141	0.070	1.620	0.2144
Residual	29	1.258	0.043		

The overall model for macrofauna density tested for the main effects of region (2 levels), season, and only 3 habitat levels, because submerged aquatic vegetation did not occur in upper Lavaca Bay. We also tested for differences in total macrofauna density among all 4 habitats in the lower Lavaca Bay only (no region effect, lower Lavaca Bay model). Data collected from gill nets (CPUE) were also tested for the main effects of region (2 levels), habitat (3 levels), and season. Season was blocked for all models to control for seasonal variability.
* ANOVA probability value significant at the 5% level.

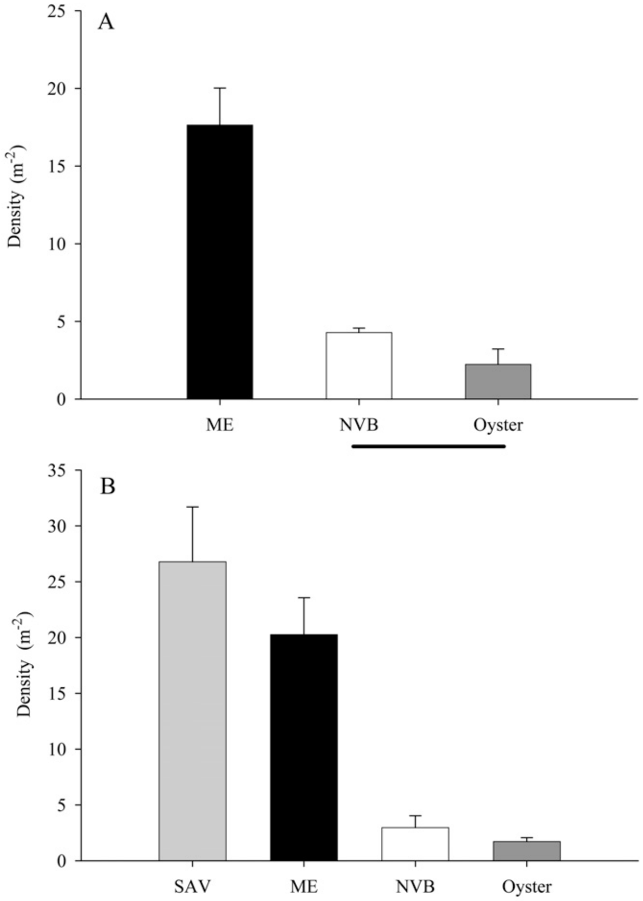

Figure 2. (A) Mean nekton and benthic crustacean density of total nekton collected in marsh edge (ME), nonvegetated bottom (NVB), and subtidal oyster reef (Oyster) from all sites over all seasons. (B) Mean nekton density among all habitats in only lower Lavaca Bay, where submerged aquatic vegetation (SAV) is found. ANOVA was used to test for differences among habitats. Habitats that share a common line are not different. The EBS was used for marsh edge and submerged aquatic vegetation samples, and the MES was used for subtidal oyster reef and nonvegetated bottom samples.

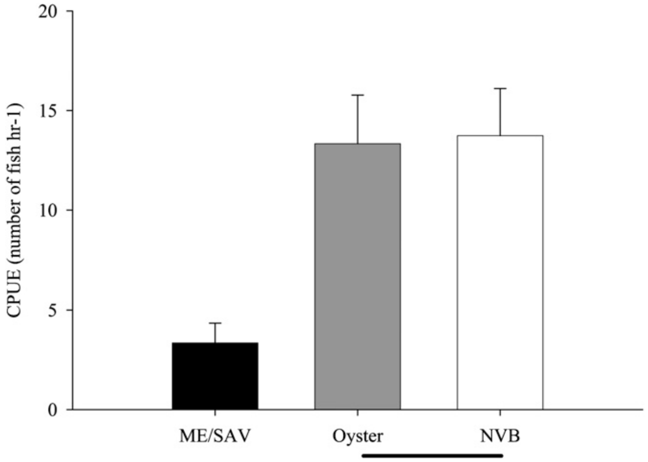

Figure 3. Mean CPUE of transient fish collected in each habitat with gill nets over all seasons. ANOVA was used to test for differences among habitats. Habitats that share a common line are not different. ME/SAV, marsh edge/submerged aquatic vegetation; NVB, nonvegetated bottom; Oyster, subtidal oyster reef.

aquatic vegetation and marsh edge. High nekton and benthic crustacean densities in shallow vegetated habitats over nonvegetated bottom is consistent with much current research that has shown that these organisms use shallow vegetated areas because these habitats provide increased growth and survival compared with areas with limited or no structure (Stunz & Minello 2001, Stunz et al. 2002a, Nanez-James et al. 2009, Stunz et al. 2010).

We found very low densities of fishes and crustaceans on subtidal oyster reef, which contrasts numerous studies showing that structurally complex oyster reef systems support very high density, biomass, and richness of estuarine nekton and benthic crustaceans (Coen et al. 1999, Coen & Grizzle 2007, Stunz et al. 2010). However, most of these studies described assemblages and densities on shallow intertidal reefs or on shell accumulations, not deep oyster beds. The low densities we observed could be the result of several reasons. First, the subtidal reefs we sampled are commercially fished via dredging, and may have low vertical relief as a result of this fishing pressure (Coen et al. 1999). Without vertical relief, there is reduced complexity resulting from limited refuge available to them and their prey (Zimmerman et al. 1989, Lenihan et al. 2001, Gregalis et al. 2009). Second, deep oyster habitats were separated from shallow vegetated habitats by large expanses of nonvegetated bottom. Without a connection to shallower vegetated areas, there may be minimal movement of nekton to deep, complex habitats, also attributing to the low densities on subtidal oyster reefs (Lehnert & Allen 2002). Moreover, these results clearly point toward a need for a direct comparison of subtidal and intertidal oyster reefs. This is particularly the case for Gulf coast estuaries, where the daily tidal range is very limited and these reefs and nearby marshes stay submerged at least 78% of time (Minello & Webb 1997). Finally, we did not directly assess the predation fields among these habitat types, and there is the potential that very different trophic cascade dynamics may exist on the deeper reefs that may affect community structure and abundance (Grabowski 2004, Grabowski & Powers 2004).

Several studies have demonstrated that different trophic linkages and connectivity between different estuarine habitats can affect nekton and benthic crustacean assemblage, density, prey mortality, and growth (Irlandi & Crawford 1997, Micheli & Peterson 1999, Grabowski et al. 2005). Lehnert and Allen (2002) showed that subtidal shell rubble directly adjacent to intertidal reefs sustains very high densities of fishes compared with nonvegetated bottom. The subtidal reef accumulations were directly adjacent to intertidal reef and were connected via a large tidal range (1.7 m), and the authors proposed to include these shell habitats as EFH (Lehnert and Allen 2002). Gain (2009) showed that estuarine habitats that are connected have synergistic relationships. Gain (2009) found that oyster reefs embedded in other structurally complex habitat types, such as submerged aquatic vegetation, sustained higher densities of fishes and crustaceans than when they were near nonvegetated bottom alone. Unlike these studies, we sampled subtidal habitats with limited or no connectivity to shallow vegetated habitats with a very small tidal range (0.4 m) (Britton & Morton 1989). The deep reefs were isolated from other structurally

TABLE 4.

Overall mean CPUE, size (in millimeters), SE, and total catch of all fishes and crustaceans collected from gill nets in Lavaca Bay, TX.

				Marsh Edge/Submerged Aquatic Vegetation					Subtidal Oyster Reef					Nonvegetated Bottom				
Common Name	Scientific Name	Total Catch	RA (%)	Mean CPUE	SE	Mean Size (mm)	SE	*n*	Mean CPUE	SE	Mean Size (mm)	SE	*n*	Mean CPUE	SE	Mean Size (mm)	SE	*n*
Gulf menhaden	*Brevoortia patronus*	507	47.0	0.91	(0.6)	151	(1.5)	29	6.67	(1.5)	168	(2.0)	229	6.83	(1.7)	167	(1.3)	249
Gafftopsail	*Bagre marinus*	136	12.6	—	—	—	—	—	1.72	(0.4)	404	(16.5)	68	1.84	(0.6)	402	(17.4)	68
Hardhead catfish	*Ariopsis felis*	131	12.1	0.97	(0.6)	244	(8.4)	32	1.45	(0.5)	231	(6.1)	49	1.42	(0.5)	240	(8.5)	50
Spot	*Leiostomus xanthurus*	65	6.0	0.03	(0.0)	70	(0.0)	1	1.00	(0.6)	176	(2.6)	32	0.95	(0.5)	165	(2.4)	32
Gulf kingfish	*Menticirrhus littoralis*	57	5.3	0.16	(0.1)	230	(9.1)	5	0.59	(0.3)	228	(5.4)	21	0.89	(0.6)	220	(3.5)	31
Atlantic threadfin	*Polydactylus octonemus*	48	4.4	0.093	(0.0)	203	(0.0)	1	0.47	(0.2)	178	(2.7)	15	1.00	(0.5)	182	(1.5)	32
Sand seatrout	*Cynoscion arenarius*	24	2.2	—	—	—	—	—	0.42	(0.2)	273	(9.0)	18	0.14	(0.1)	287	(26.7)	6
Gizzard shad	*Dorosomapetenense*	16	1.5	—	—	—	—	—	0.22	(0.2)	171	(3.3)	7	0.16	(0.1)	172	(1.9)	9
Atlantic croaker	*Micropogonias undulates*	15	1.4	0.03	(0.0)	201	(0.0)	1	0.19	(0.1)	179	(2.2)	10	0.11	(0.1)	178	(4.6)	4
Spotted seatrout	*Cynoscion nebulosus*	13	1.2	0.14	(0.1)	269	(5.5)	5	0.11	(0.1)	374	(46.5)	5	0.06	(0.0)	247	(13.5)	3
Sheepshead	*Archosargus probatocephalus*	10	0.9	0.31	(0.1)	303	(29.3)	10	—	—	—	—	—	—	—	—	—	—
Silver perch	*Bairdiella chrysoura*	9	0.8	0.13	(0.1)	186	(3.3)	4	0.06	(0.0)	175	(0.5)	2	0.09	(0.1)	174	(3.5)	3
Crevalle jack	*Caranx hippos*	7	0.6	0.02	(0.0)	141	(0.0)	1	0.09	(0.1)	154	(7.1)	4	0.03	(0.0)	152	(3.5)	2
Black drum	*Pogonias cromis*	6	0.6	0.19	(0.1)	327	(12.1)	6	—	—	—	—	—	—	—	—	—	—
Red drum	*Sciaenops ocellatus*	6	0.6	0.19	(0.1)	445	(29.3)	6	—	—	—	—	—	—	—	—	—	—
Striped mullet	*Mugil cephalus*	5	0.5	0.14	(0.1)	276	(39.5)	5	—	—	—	—	—	—	—	—	—	—
Blacktip shark	*Carcharhinus limbatus*	4	0.4	—	—	—	—	—	0.03	(0.0)	509	(81.5)	2	0.03	(0.0)	419	(15.5)	2
Spanish mackerel	*Scomberomorus maculates*	4	0.4	—	—	—	—	—	0.09	(0.1)	548	(7.6)	3	003	(0.0)	539	(0.0)	1
Bonnethead shark	*Sphyrna tiburo*	4	0.4	—	—	—	—	—	0.03	(0.0)	629	(23.5)	2	0.03	(0.0)	618	(17.0)	2
American harvestfish	*Peprilus paru*	3	0.3	—	—	—	—	—	0.03	(0.0)	166	(0.0)	1	0.05	(0.0)	143	(67.0)	2
Blue crab	*Callinectes sapidus*	2	0.2	0.03	(0.0)	161	(0.0)	1	0.03	(0.0)	120	(0.0)	1	—	—	—	—	—
Ladyfish	*Elops saurus*	2	0.2	0.02	(0.0)	360	(0.0)	1	—	—	—	—	—	0.03	(0.0)	348	(0.0)	1
Pinfish	*Lagodon rhomboids*	2	0.2	—	—	—	—	—	0.02	(0.0)	118	(0.0)	1	0.03	(0.0)	126	(0.0)	1
Bluefish	*Pomatomus saltatrix*	1	0.1	0.03	(0.0)	183	(0.0)	1	—	—	—	—	—	—	—	—	—	—
White shrimp	*Litopenaeus setiferus*	1	0.1	—	—	—	—	—	0.03	(0.)	162	(0.0)	1	—	—	—	—	—
Pigfish	*Orthopristis chrysoptera*	1	0.1	—	—	—	—	—	0.03	(0.)	163	(0.0)	1	—	—	—	—	—

Mean values were calculated from 16 total samples per habitat type. The total number and relative abundance (RA; number of individuals/total number of animals collected × 100) also are given. An em dash (—) indicates no catch.

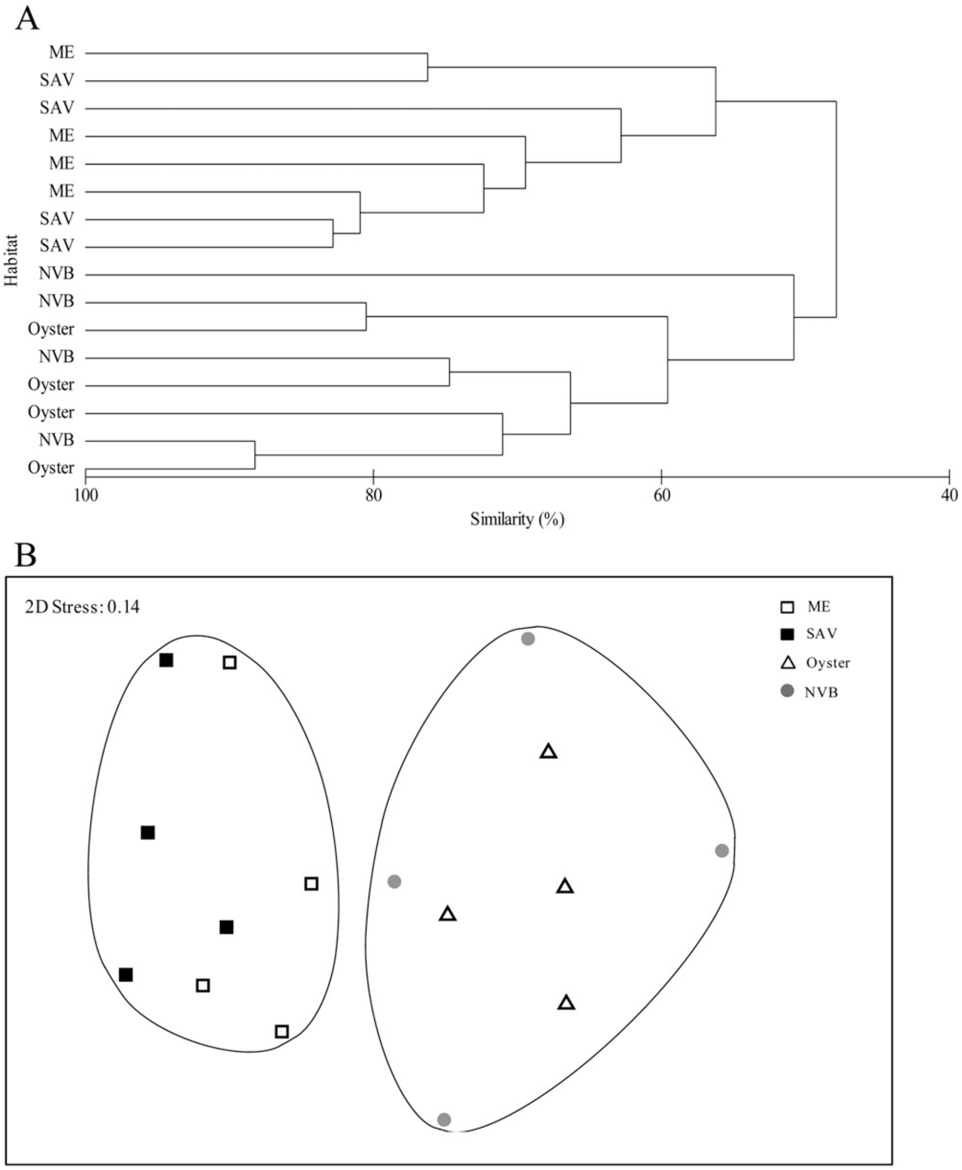

Figure 4. Bray-Curtis cluster analysis (A) and MDS ordination with Bray-Curtis cluster analysis superimposed using 50% similarity (B) of mean seasonal nekton and benthic crustacean density from each habitat. Densities were averaged among sites and regions by season, for a total of 16 samples. ME, marsh edge; NVB, nonvegetated bottom; Oyster, subtidal oyster reef; SAV, submerged aquatic vegetation.

complex, shallow habitats, which may account for the very low density of small fishes and crustaceans collected in these areas (Grabowski et al. 2005).

Despite the low densities collected, our community analysis did show different assemblages of nekton and benthic crustaceans over deep reefs and nonvegetated bottom. Resident species dominated the catch on subtidal reef, such as xanthid, porcelain, and stone crabs; as well as bay anchovies and several goby species. Bay anchovies are typically ubiquitous throughout the bay and water column, and may have been collected as the MES was pulled to the surface (North & Houde 2004). However, the benthic crustaceans and fishes captured use subtidal oyster shell throughout their life history, because it provides appropriate spawning habitat (Breitburg 1999, Harding & Mann 2001, Lehnert & Allen 2002). The majority of estuarine-dependent species such as red drum, pinfish, Atlantic croaker, and blue crab were absent from subtidal oyster reef. Most juvenile estuarine-dependent species were found in marsh and submerged aquatic vegetation, similar to many other studies (Day et al. 1989, Minello 1999, Beck et al. 2001, Stunz et al. 2002a, Stunz et al. 2010), suggesting that subtidal oyster reef may not be EFH for these particular recruiting species. Although estuarine-dependent species were not collected in these deep areas, the community analysis distinctly shows differences in assemblage that provides evidence that these areas are required habitat for numerous other estuarine fishes and crustaceans.

Although the density estimates of small fishes and crustaceans were low, we collected nearly twice as many large, transient fish over subtidal oyster reef and nonvegetated bottom than in the shallow habitats. In a companion trophic study in Lavaca Bay, TX, Wrast (2008) found that subtidal oyster reef supports a more robust food web than nonvegetated bottom and shallow vegetated habitats. Our findings are consistent with a large number of fishes collected over both subtidal reef and nonvegetated bottom—in particular, large predators such as Gafftopsail and hardhead catfish, as well as Gulf kingfish and several shark species. Because nonvegetated bottom habitats were sampled adjacent to oyster reefs, there was most likely movement and integration between these habitats, explaining why catches were similar. Although depth may have affected CPUE in deep and shallow habitats because gill nets typically work better in deeper habitats, we feel our data suggest open-water areas are very important for large, transient fishes, because they may be critical foraging grounds for these larger estuarine predators.

This study provides evidence of the role deep subtidal oyster reefs play in the complex matrix of estuarine habitats. We used a novel sampling approach to quantify use of subtidal reefs by fishes and crustaceans to compare densities with well-studied vegetated habitats. The MES provides a viable and effective way of sampling subtidal oyster reefs when other conventional gear is not feasible. However, as with any gear, the potential exists for certain limitations and biases; therefore, our density estimates should be interpreted cautiously, particularly as they relate to calculating absolute density estimates. Although we found relatively low density of nekton and decapod crustaceans over subtidal reef compared with vegetated habitat types, these areas are clearly important for numerous estuarine resident species as well as large, transient predators. Moreover, given the large areal coverage in many estuaries, these oyster reefs have the potential for high production of estuarine nekton. More studies on the habitat role of subtidal reefs are warranted—in particular, those that directly compare nekton and benthic crustacean density between subtidal and intertidal reefs, given that recent research has shown intertidal oyster reefs support very high densities of estuarine nekton (Coen et al. 1999, Coen & Grizzle 2007, Stunz et al. 2010). This information would have clear restoration implications and will be essential in determining the habitat role oyster reefs serve along the Gulf of Mexico.

ACKNOWLEDGMENTS

The authors thank Texas Parks and Wildlife Department (TPWD) State Wildlife Grant and Texas A&M University-Corpus Christi (TAMU-CC) for funding this research. They particularly thank J. Wrast for assisting with field logistics and data collection. This research would not have been possible without the members of the Fisheries Ecology Lab at TAMU-CC, and the authors particularly thank J. Froeschke for helping with the analysis; and R. Aguayo, S. Bayer, L. Brown, A. Bushon, R. Calderon, and M. Castrorena for their field and laboratory assistance. They also thank 2 anonymous reviewers that greatly improved this manuscript.

LITERATURE CITED

Baltz, D. M., C. Rakocinski & J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* 36:109–126.

Beck, M. W., K. L. Heck, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan & M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641.

Breitburg, D. L. 1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? In: M. W. Luckenbach, R. Mann, & J. Wesson, editors. Oyster reef habitat restoration: a synopsis and synthesis of approaches. Gloucester Point: Virginia Institute of Marine Science Press. Pp. 239–250.

Britton, J. C. & B. Morton. 1989. Shore ecology of the Gulf of Mexico, 3rd edition. Austin: University of Texas Press. pp. 387.

Burfeind, D. D. & G. W. Stunz. 2006. The effects of boat propeller scarring intensity on nekton abundance in subtropical seagrass meadows. *Mar. Biol.* 148:953–962.

Chambers, J. R. 1992. Coastal degradation and fish population losses. In: R. H. Stroud, editor. Stemming the tide of coastal fish habitat loss. Savannah, GA: National Coalition for Marine Conservation. pp. 45–51.

Clarke, K. R. & R. N. Gorley. 2006. PRIMER v6: user manual/tutorial. Plymouth, UK: PRIMER-E. 190 pp.

Clarke, K. R. & R. H. Green. 1988. Statistical design and analysis for a "biological effects" study. *Mar. Ecol. Prog. Ser.* 46:213–226.

Clarke, K. R. & R. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. Plymouth, UK: PRIMER-E.

Coen, L. & R. Grizzle. 2007. The importance of habitat created by molluscan shellfish to managed species along the Atlantic Coast of the United States. Atlantic States Marine Fisheries Commission Habitat Management Series no.8, Washington DC. pp 1–108.

Coen, L. D., M. W. Luckenbach & D. L. Breitburg. 1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *Am. Fish. Soc. Symp.* 22:438–454.

Dame, R. F. 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. *Proc Natl. Shellfish. Assoc.* 69:6–10.

Day, J. W., C. A. S. Hall, W. M. Kemp & A. Yanez-Arancibia. 1989. Estuarine ecology, vol. 1. New York: Wiley. pp. 558.

Gain, I. 2009. Oysters as nekton habitat in estuarine ecosystems. MS thesis, Texas A&M University-Corpus Christi. pp. 92.

Glancy, T. P., T. K. Frazer, C. E. Cichra & W. J. Lindberg. 2003. Comparative patterns of occupancy by decapod crustaceans in seagrass, oyster, and marsh-edge habitats in a northeast Gulf of Mexico estuary. *Estuaries* 26:1291–1301.

Grabowski, J. H. 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.

Grabowski, J. H., A. R. Hughes, D. L. Kimbro & M. A. Dolan. 2005. How habitat setting influences restored oyster reef communities. *Ecology* 86:1926–1935.

Grabowski, J. H. & S. P. Powers. 2004. Habitat complexity mitigates trophic transfer on oyster reefs. *Mar. Ecol. Prog. Ser.* 277:291–295.

Gregalis, K. C., M. W. Johnson & S. P. Powers. 2009. Restored oyster reef location and design affect responses of resident and transient fish, crab, and shellfish species in Mobile Bay, Alabama. *Trans. Am. Fish. Soc.* 138:314–327.

Harding, J. M. & R. Mann. 2001. Oyster reefs as fish habitat: opportunistic use of restored reefs by transient fishes. *J. Shellfish Res.* 20:951–959.

Hosack, G. R., B. R. Dumbauld, J. L. Ruesink & D. A. Armstrong. 2006. Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. *Estuaries Coasts* 29:1150–1160.

Irlandi, E. A. & M. K. Crawford. 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230.

Jackson, E. L., A. A. Rowden, M. J. Attrill, S. J. Bossey & M. B. Jones. 2001. The importance of seagrass beds as a habitat for fishery species. *Oceanogr. Mar. Biol. Annu. Rev.* 39:269–303.

Johnson, M. W., S. P. Powers, J. Senne & K. Park. 2009. Assessing in situ tolerances of Eastern oysters (*Crassostrea Virginica*) under moderate hypoxic regimes: implications for restoration. *J. Shellfish Res.* 28:185–192.

Kilgen, R. H. & R. J. Dugas. 1989. The ecology of oyster reefs of the northern Gulf of Mexico: an open file report. NWRC-open file report no. 89-02. Washington, DC: US Dept of Interior. 113 pp.

Kirby, M. X. 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. *Proc. Natl. Acad. Sci. USA* 101:13096–13099.

Lehnert, R. L. & D. M. Allen. 2002. Nekton use of subtidal oyster shell habitat in a southeastern US estuary. *Estuaries* 25:1015–1024.

Lenihan, H.S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer, & D. R. Colby. 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. *Ecol. Appl.* 11:764–782.

Micheli, F. & C. H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conserv. Biol.* 13:869–881.

Minello, T. J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat.

Minello, T. J. & J. W. Webb. 1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* 151:165–179.

Nanez-James, S. E., G. W. Stunz & S. A. Holt. 2009. Habitat use patterns of newly settled southern flounder, *Paralichthys lethostigma*, in Aransas-Copano Bay, Texas. *Estuaries Coasts* 32:350–359.

North, E. W. & E. D. Houde. 2004. Distribution and transport of bay anchovy (*Anchoa mitchilli*) eggs and larvae in Chesapeake Bay. *Estuar. Coast. Shelf Sci.* 60:409–429.

Peterson, C. H., J. H. Grabowski & S. P. Powers. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Mar. Ecol. Prog. Ser.* 264:249–264.

Plunket, J. & M. K. La Peyre. 2005. Oyster beds as fish and macroinvertebrate habitat in Barataria Bay, Louisiana. *Bull. Mar. Sci.* 77:155–164.

Posey, M. H., T. D. Alphin & C. M. Powell. 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. In: M. W. Luckenbach, R. Mann, & J. A. Wesson, editors. Oyster reef restoration: a synopsis and synthesis of approach. Gloucester Point: Virginia Institute of Marine Science Press. pp. 229–237.

Reese, M. M., G. W. Stunz & A. M. Bushon. 2008. Recruitment of estuarine-dependent nekton through a new tidal inlet: the opening of Packery Channel in Corpus Christi, TX, USA. *Estuaries Coasts* 31:1143–1157.

Rozas, L. P. & T. J. Minello. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20:199–213.

Rozas, L. P. & T. J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bull. Mar. Sci.* 63:481–501.

Shervette, V. R. & F. Gelwick. 2008. Relative nursery function of oyster, vegetated marsh edge, and nonvegetated bottom habitats for juvenile white shrimp *Litopenaeus setiferus*. *Wetlands Ecol. Manage.* 16:405–419.

Simons, J. D., J. Harper, T. Dellapenna, J. Bronikowski, W. Sager & M. Patch. 2004. Mapping bathymetry, oyster reefs, sedimentary facies, subbottom structures and anthropogenic impacts in Lavaca Bay, Texas. Final report submitted to Texas General Land Office. Texas Parks and Wildlife Department, Austin. pp. 207.

Stunz, G. W., P. S. Levin & T. J. Minello. 2001. Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. *Environ. Biol. Fishes* 61:305–313.

Stunz, G. W. & T. J. Minello. 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 260:13–25.

Stunz, G. W., T. J. Minello & P. S. Levin. 2002a. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. *Estuaries* 25:76–85.

Stunz, G. W., T. J. Minello & P. S. Levin. 2002b. Growth of newly settled red drum *Sciaenops ocellatus* in different estuarine habitat types. *Mar. Ecol. Prog. Ser.* 238:227–236.

Stunz, G. W., T. J. Minello & L. P. Rozas. 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. *Mar. Ecol. Prog. Ser.* 406:147–159.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, Jr., A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short & S. L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. USA* 106:12377–12381.

Wenner, E., H. R. Beatty & L. Coen. 1996. A method for quantitatively sampling nekton on intertidal oyster reefs. *J. Shellfish Res.* 15:769–775.

Wrast, J. L. 2008. Spatiotemporal and habitat-mediated food web dynamics in Lavaca Bay, Texas. MS thesis, Texas A&M University-Corpus Christi.

Zimmerman, R., T. Minello, T. Baumer & M. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. NOAA technical memorandum. *NMFS-SEFC* 249:16.

Zimmerman, R., T. J. Minello & G. Zamora. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in Galveston Bay salt marsh. *Fish. Bull.* 82:325–336.