OYSTER REEFS AS NEKTON HABITAT IN ESTUARINE ECOSYSTEMS

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ABSTRACT

Oyster reefs are important components of marine ecosystems and function as essential habitat for many estuarine species. However, few studies have focused on the interaction and synergy of oyster reefs with other estuarine habitat types (e.g., seagrasses, marsh). This research was designed to characterize the macrofaunal community associated with shallow water, intertidal oyster reefs. I examined the functional habitat relationships of oyster reefs and the effects of structural complexity, spatial synergy, and predator influence on habitat selection. Two sites in Corpus Christi Bay, Texas, were sampled using a throw-trap sampler. Replicate, intertidal oyster reef plots, marsh edge, and seagrass habitats were compared. Results showed higher overall densities of nekton and benthic crustaceans on oyster reefs compared to seagrass and marsh edge habitat types. Oyster reefs supported a distinctive community of nekton and benthic crustaceans. The spatial relationships of habitat types was evaluated by sampling oyster reef adjacent to mud bottom, oyster reef adjacent to seagrass, and oyster reef adjacent to marsh edge. Highest densities were collected on oyster reefs near seagrass and mud bottom. Predator exclusion cages were used to evaluate community differences on oyster reefs with and without predation pressure. Differences in nekton densities were found among predator exclusion treatments during fall. To evaluate the role of structural complexity on oyster reefs, habitat selection of a fish, juvenile red drum (*Sciaenops ocellatus*), and a crustacean, brown shrimp (*Farfantepaneaus aztecus*), were examined using experimental mesocosms. Selection patterns were also evaluated in the presence and absence of large predators, pinfish (*Lagodon rhomboides*). Red drum habitat selection was not influenced by structured habitats in the absence of a predator. However, when exposed to predators,

red drum showed clear selection patterns for more structured, complex habitat. Brown shrimp were not exposed to predators, and did not show a strong selection pattern for more or less complex reefs. These results suggest that the structurally complex estuarine habitat provided by oyster reef may function similarly to seagrass or marsh edge habitat types and may provide a refuge from predation for some fish and crustaceans.

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INTRODUCTION

Estuaries provide a variety of habitat types to organisms. The benefits of the variety of habitat types available to estuarine organisms are many and include services including predation refuge and food sources (Weinstein 1979, Corona et al. 2000, Beck et al. 2001, Minello et al. 2003, Saintilan et al. 2007). Moreover, the arrangement of these habitat types, such as seagrasses, soft-bottom substrates, macroalgae, and other hard substrates, produces high habitat heterogeneity (Leber 1985, Corona et al. 2000). Given these characteristics, estuarine habitats often support high densities of nekton (Leber 1985, Minello & Zimmerman 1991, Corona 2000, Stunz et al. 2002). Many studies have shown that seagrass beds, salt marsh habitats, and even non-vegetated bottom can provide essential services for many fisheries species (Leber 1985, Stunz et al. 2002, Zeug et al. 2007).

Oysters are an important fishery species whose dense aggregations into reefs provide essential habitat for many species of fish and invertebrates. Oyster reefs, composed of eastern oysters (*Crassostrea virginica*), were once dominant features in estuarine systems along the Atlantic and Gulf of Mexico coasts (Powell 1993, Wenner et al. 1996). The ecosystem goods and services provided by this habitat have been endangered by disease, reduced water quality, and many anthropogenic impacts including over-harvesting and outright destruction (Eggleston et al. 1999, Meyer & Townsend 2000, Grabowski et al. 2005; Grabowski & Peterson 2007). These habitat alterations have led to fragmentation and decline in areal coverage of oyster reefs, which now occupy only a small portion of their historic habitat (Wenner et al. 1996, Coen et al. 1999). This loss concerns many scientists since the value of these reefs in terms of habitat to nekton is relatively unknown for many areas, and studies of the value of oyster reefs as essential fish habitats are relatively rare compared to studies of other estuarine habitats (but see Posey et al. 1999, Harding & Mann 2001, Glancy et al. 2003, Hosack et al. 2006, Coen & Grizzle 2007, Shervette & Gelwick 2008a, Reese et al. in review, Stunz et al. in review).

The habitat provided by intertidal oyster reefs may be particularly beneficial to fish and crustaceans due to its spatial and geographic arrangement in estuaries. Intertidal oyster reefs develop in three configurations: (1) fringing reefs that border the edges of salt marshes, (2) reefs that extend outward from a point of marsh, and (3) isolated patches that may be surrounded by seagrass beds or unvegetated bottom (Bahr & Lanier 1981). Estuaries ranging from southern North Carolina to northern Florida and northern Gulf Coast estuaries generally lack large expanses of submerged aquatic vegetation, but have well-developed oyster reefs in intertidal areas (Lehnert & Allen 2002). Despite the lack of submerged vegetation, these areas are productive for several finfish and shellfish species (Lehnert & Allen 2002). Intertidal oyster reefs are three-dimensional, biogenic habitats with physical complexity and vertical relief arising from the settling of new generations of oysters upon the foundation laid by previous generations (Grabowski & Kimbro 2005; Boudreaux et al. 2006). Approximately 50 m^2 of surface area is available as habitat for epifauna for every square meter of reef area (Bahr & Lanier 1981). These estimates demonstrate the potential value of oyster reefs as habitats for fish and invertebrates. This structural complexity may increase prey availability in both quantity and quality, while reducing predation risk to many juvenile fish and invertebrates

(Minello 1999). In these estuaries, oyster reef may be functioning as essential estuarine fish habitat.

The three-dimensional structure of the oyster reefs provides habitat for many macrofauna (Tolley & Volety 2005), and they are recognized for maintaining high densities of nekton, polychaetes, mollusks, and benthic crustaceans (Grabowski et al. 2005, Boudreaux et al. 2006, Rodney & Paynter 2006, Stunz et al. in review). Biogenic services generated by intertidal oyster reefs generally result in higher densities of macroinvertebrate prey species than unstructured mud habitats (Grabowski & Powers 2004). Oysters make food available to various benthic organisms by capturing organic carbon from the water column and repackaging it in different forms such as body mass, pseudofeces, and feces. Oysters assimilate 70% of the organic matter they filter and the rest, when coupled with the structural complexity of the reef, provides sustenance for high densities of both sessile and mobile benthic macrofauna (Tolley & Volety 2005). In temperate estuaries, polychaetes, bivalves, and decapods, all of which may be found on oyster reefs, account for more than 90% of the diet of juvenile fish (Grabowski et al. 2005), further supporting the importance of oyster reefs in estuarine ecosystems.

The mosaic of habitats in estuaries includes seagrasses, mangroves, saltmarshes, oyster reefs, and unvegetated sand and mudflats. The proximity of these different habitats to one another may influence the community assemblages of organisms in these areas as well as the abundance of certain species. Movement between adjacent habitats may provide access to different resources and refuge from predation (Skilleter et al. 2005). Habitat linkages between saltmarshes, mangroves, and seagrass beds have recently been investigated (see Irlandi & Crawford 1997, Skilleter et al. 2005, Saintilan et al. 2007). The synergistic relationships among these habitats should be taken into account when studying habitat use by nekton of intertidal oyster reefs; however, few studies have investigated these types of relationships with regard to oyster reefs. The spatial arrangement of seagrass meadows to mangroves influences the abundance of the bay prawn (*Metapenaeus bennettae*) and eastern king prawn (*Penaeus plebejus*) (Skilleter et al. 2005). The abundance of both prawns was greater in seagrass meadows adjacent to mangroves even when seagrass density was low. Greater numbers of pinfish used intertidal salt marshes near seagrass beds and their growth was greater where marshes were bordered by seagrass beds (Irlandi & Crawford, 1997). Seagrass beds and salt marshes that surround oyster reefs can impact the abundance and diversity of benthic macroinvertebrates living on the reefs (Micheli & Peterson 1999; Grabowski et al. 2005). Moreover, Zeug et al. (2007) suggested that oyster reefs are an important habitat feature limiting the capacity of created marsh areas to support the dominant species that are found in natural marshes. The authors found several species were abundant in natural marsh areas containing oyster reef that were not found in created marsh, further supporting the idea that oyster reef is an important estuarine habitat that may increase species diversity. These findings clearly support the need to examine the synergistic relationships among the various habitat types available to nekton with direct comparison among other putative estuarine habitat types.

Elevated risk of predation and physical stress causes many organisms to avoid the unstructured flat bottoms that may surround the structured habitats of seagrass meadows, kelp beds, and oyster reefs (Micheli & Peterson 1999). The risk of predation can greatly influence prey behavior, densities, growth rates, and reproductive effort (Werner &

Peacor 2003, Grabowski et al. 2005). Changes in behavior and phenotypes can lead to indirect effects being transmitted through the food web (Trussell et al. 2004). For example, in the presences of the oyster toadfish (*Opsanus tau*), Atlantic mud crabs (*Panopeus herbstii*) will abandon their normal foraging area on top of the oyster reefs to seek refuge within the reefs. The crabs may experience a reduction in mobility within the refuge that decreases encounters with both juvenile hard clams and juvenile oysters, thereby increasing the survival of the bivalves (Grabowski & Kimbro 2005). Predator-prey relationships play an important role in community structure of these habitats and as the predation risks increase, structural complexity becomes more relevant (Laegdsgaard & Johnson 2001). Pink shrimp (*Farfantepenaeus duorarum*) had a greater potential to reduce prey densities in simple habitats than in more complex habitats (Leber 1985). In areas with greater structural complexity, amphipods were afforded greater protection from predation and most prey organisms were subject to less predation pressure. Other experimental studies have also demonstrated that nekton preferentially select for complex habitats, such as oyster reef, and have lower mortality rates in structured habitats (Stunz et al. 2002; Grabowski 2004).

The quality of refuge provided by a structure may depend upon the complexity of that structure or habitat type and may also influence habitat selection by fish and crustaceans. Gratwicke & Speight (2005) manipulated the height, rugosity, growth forms, and variety of hole sizes found on artificial coral reefs to evaluate the effects of structural complexity on fish abundance. Attributes such as height, surface area, and distance to neighboring structures have been used to measure levels of habitat complexity (McElhinny et al. 2005). Vertical relief in habitats may be an important factor in habitat selection (Soniat et al. 2004, Grabowski & Kimbro 2005, Tolley & Volety 2005). Seagrass habitats support large numbers of fish species (Horinouchi 2007), and epifaunal abundances are often correlated with plant biomass (Leber 1985). Fish recruitment to seagrass beds has been shown to be positively influenced by the structure of individual seagrass beds (Jenkins et al. 1998). The habitat complexity is an important component of habitat selection by fish and decapod crustaceans which has yet to be thoroughly investigated for oyster reefs, especially its effects on habitat selection by mobile nekton.

Oyster reef complexity creates refuges for organisms at lower trophic levels by reducing effectiveness of predators (Grabowski & Kimbro 2005). Corona et al. (2000) found that as habitat complexity increased, consumption of amphipods by pink shrimp decreased. In addition, pinfish utilized mixed vegetation habitats with greater complexity more than areas of low complexity, where predation rates were higher (Adams et al. 2004). Greater habitat complexity may increase prey survival and reduce foraging success of higher-order consumers, thereby increasing survival of intermediate predators (Grabowski & Powers 2004). Thus, it is important to evaluate the role of predation in influencing habitat selection by nekton on oyster reefs with varying complexity.

In accordance with the 1996 Magnuson-Stevens Fisheries Conservation and Management Act (reauthorized in 2007), the quantification of the habitat role of oyster reefs is a necessary step to identify and protect Essential Fish Habitat (http://www.nmfs.noaa.gov/sfa). A factor that restricts the effectiveness of management and conservation of oyster reefs is our limited understanding of their role as habitat for fisheries species. Few studies have quantitatively assessed the use of oyster reef habitat by fisheries species or examined the functional relationships associated with the nekton utilizing the reefs, primarily due to the difficulty in sampling these areas and gear limitations (Zimmerman et al. 1989; Wenner et al. 1996; Rozas & Minello 1997; Coen et al. 1999; Minello 1999; Stunz et al. 2002, Tolley & Volety 2005). There are many differences in protective value and feeding functions among habitat types that have yet to be well defined (Zimmerman et al. 1989), and there is a need to more precisely identify the potential for oyster reefs to serve as Essential Fish Habitat. Two recent studies have shown that oyster reefs are important estuarine habitat. Stunz et al. (in review) found greater abundances of nekton and benthic crustaceans on intertidal oyster reefs when compared to abundance from shallow non-vegetated bottom and marsh edge. Reese et al. (in review) found lower abundances of nekton on subtidal oyster reefs compared to abundance in other estuarine habitats, however a distinct community was found on these reefs and abundances of transient fish species were high. Clearly, these studies show high use by marine life, but there is a need to make simultaneous comparisons of submerged aquatic vegetation, marsh edge, and oyster reef, as well as a need to further investigate the role of oyster reefs in estuarine ecosystems, especially regarding the effects of synergy among oyster reefs and adjacent habitat types and the role of predation on the community structure of the reefs.

This project was designed to characterize the macrofaunal community of intertidal oyster reefs and to examine functional habitat relationships among oyster reefs and adjacent habitat types in a Gulf coast estuary. Specifically, the goals of this research were to: (1) characterize the macrofauna using intertidal oyster reefs; (2) address the effects of synergy among seagrass, marsh edge, and oyster reef habitat types; (3) examine the role of predation on fish recruitment to oyster reefs; and (4) explore the role of oyster reef structural complexity on habitat selection of red drum and brown shrimp in the presence and absence of a predator. Highly efficient enclosure sampling was used to make comparisons among three habitat types: intertidal oyster reef, marsh edge, and seagrass beds to quantify the diversity of marine life using intertidal oyster reefs. Multiple habitat types were simultaneously sampled to address synergistic effects on diversity of their associated nekton. A manipulative predator exclusion caging experiment was used to evaluate the role of predation on fish recruitment to oyster reefs. Finally, a laboratory study was performed to assess the effects of structural complexity of oyster reefs on the habitat selection of juvenile red drum and brown shrimp.

MATERIALS AND METHODS

Study Site. Sampling occurred in East Flats, a region of Corpus Christi Bay, which is a shallow estuary located along the central Texas coastline (Fig. 1.). The average depth of the bay is 3 m (USEPA 1999) with the exception of the ship channel that reaches a maximum depth of 15 m (Flint & Younk 1983). East Flats is located along the interior of Mustang Island (Fig. 1.). Two replicate study locations were chosen: along Piper Channel (East Flats 1) and near Coyote Island (East Flats 2). Both study areas were comprised of many habitat types including: *Spartina alterniflora* intertidal marsh, seagrass (mixed but primarily *Halodule wrightii)* and extensive intertidal oyster reefs (*C. virginica*).

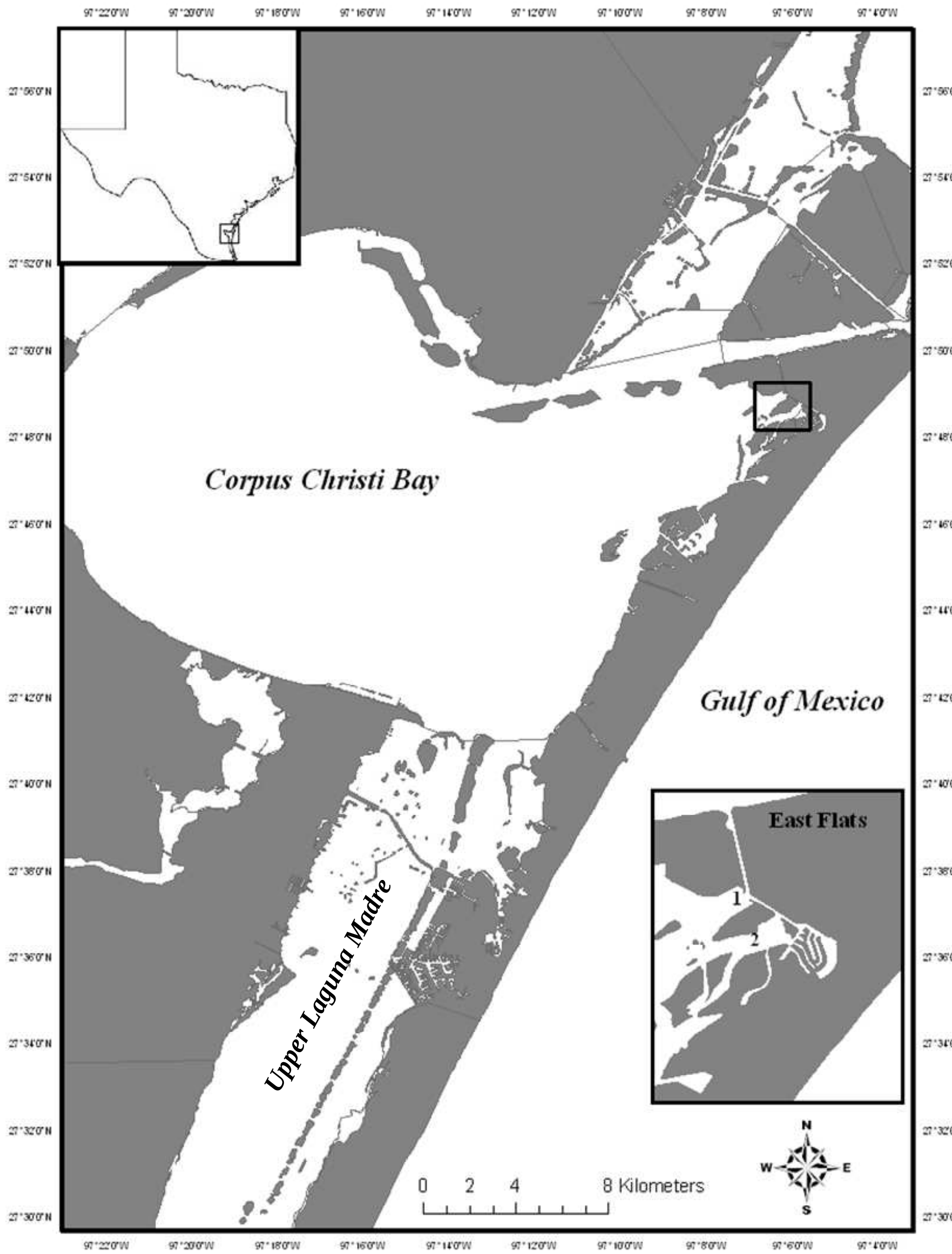


Fig. 1. Oyster reef study sites in East Flats, Corpus Christi Bay, Texas. There were two study sites within this area (marked as 1 and 2 on the inset map). Both of these study sites included *Spartina alterniflora* marsh, seagrass beds, and oyster reef.

Assessment of oyster reef habitat nekton. The seasonal diversity and density of nekton on oyster reefs was quantified at the two study sites in East Flats during spring (May 2008) and fall (November 2008). I constructed 15 oyster sampling units (OSU) in the spring and 12 in the fall. The OSUs consisted of a 58 cm [W] x 58 cm [L] tray, constructed from a wooden framing (2.5 cm x 2.5 cm) with 1-cm^2 mesh attached to the bottom, and 50 live oysters, obtained from a local commercial oyster provider, that were placed in the center of the flat tray. The OSUs were secured into the bottom using two pieces of rebar and left in the field for three months (see the next section below for the detailed arrangement of the OSUs for the spatial synergy study). Any large clumps of "natural" oysters were cleared from just around the OSU plots (1 m x 1 m total area including the OSU) to allow proper deployment of the modified drop sampler used to sample nekton (Fig. 2). The frames and bottom mesh were rapidly covered by the natural substrate leaving only the oyster exposed (personal observation).

Samples from all three habitat types were collected using a modified drop sampler, “throw trap,” which enclosed a one meter squared area. The 1-m^2 throw trap samplers were 60 cm, 70 cm, or 80 cm in height and were lined with a 1.6-mm nylon netting that was reinforced along the edges with canvas. A 7.6-cm metal skirt on the bottom of each sampler, which could be pushed into the sediment, ensured that no organisms escaped from the sampler (see Fig. 2). This is an efficient sampling device and has been used by numerous investigators (Rozas and Minello 1997). Throw trap samplers were rapidly dropped by two people to enclose the sampling area. Samples were also collected in natural stands of seagrass beds (SG) and marsh edge (ME). Marsh edge was defined as the ecotonal zone between the emergent vegetation and open water (Stunz et al. 2002). A total of fifteen oyster replicates were collected in the spring and 12 replicates were collected in the fall using the drop sampler. There were 20 SG and 20 ME replicates collected in both seasons (Table 1). The replicates were as equally distributed between the two study sites between East Flats 1 and East Flats 2 as possible. After the sampler was secure, the OSUs were rinsed thoroughly and removed from the enclosed area. Oysters were sorted and any animals were removed by hand. The enclosed area was swept with sweep nets until no new organisms were collected (a minimum of 5 passes). Any remaining organisms in the sample area, attached to the sampler, were removed by hand. Large fish and crabs were identified, tallied, measured to the nearest millimeter, and released. Large crabs were identified to species and carapace width (distance between the two outermost anteriolateral spines) was measured. Large fish were identified to species and total length was measured. Small organisms were collected and preserved for later analysis. These samples were fixed in a 10% formalin solution in the field. Organisms were sorted, identified to the lowest practical taxon, counted, and then stored in 70% ethanol in the laboratory. Hydrological parameters (e.g., pH, DO, temperature) were measured once at each study site on the day the samples were collected

The mean and standard error (SE) for the total number of fish, crustaceans, and individual species was calculated for each habitat type sampled. Percent relative abundance (RA %) was calculated by season for the total number of fish and crustaceans collected as well as for each individual species collected. Average species richness was calculated as number of species per square meter. Only organisms that were identified to species were accounted for in this calculation, with the exception of grass shrimp which were collectively grouped as *Palaemonetes* species.

Analysis of Variance (SAS 9.2) was used to examine differences in abundance of nekton among habitat types with $\alpha = 0.05$. All counts were extrapolated to density (number of organisms m^{-2}) prior to analysis. A two-factor ANOVA was used to examine differences in mean densities of nekton among habitats, with habitat as a fixed main effect and site as a random effect. Data were transformed (log10[x+1]) to ensure homogeneity of variance and the normality of the residuals. Linear contrasts were performed if there was a significant interaction between site and habitat. If no interaction was detected, then a Tukey's post-hoc test was used. Spring and fall as well as fish and crustaceans were analyzed separately. Species richness, and individual species that occurred in high densities were analyzed separately with the use of ANOVAs to compare habitat types and three a priori contrasts to test different habitat combinations (Table 2). Alpha values were adjusted as described by Rice (1989) using a Bonferonni correction.

Community similarity/dissimilarity among habitats was explored using a variety of non-parametric multivariate analyses using PRIMER v.6 (Clarke and Gorley 2006). I examined the mean densities of nekton collected from each habitat type in the spring and fall. Data were 4th root transformed prior to analysis. Bray-Curtis resemblance matrices were constructed for both seasons and community assemblages were further investigated by using a non-metric multidimensional scaling (MDS) that was based on the Bray-Curtis similarity with the Bray-Curtis similarity groups superimposed for better interpretation (Clarke and Warwick 2001). A one-way SIMPER analysis was used to determine the dominant species for each habitat.

(A)

(B)

Figure 2. (A) Throw trap sampler deployed in the field for sampling seagrass. (B) Left: Sweep net used to collect organisms captured in the throw trap sampler. Right: Throw trap sampling gear used to sample estuarine habitat types.

Table 1. Habitat types examined in this study and the sample size (N) by season. (A) General habitat characterization, (B) Synergistic relationships, (C) Predator exclusion study.

(A)

Habitat Category	Description of Habitat Types	Sample Size (N)	
		Spring	Fall
OR	Oyster reef	15	12
SG	Seagrass Beds (*Halodule wrightii*)	20	20
ME	Marsh Edge = emergent vegetation < 2m from the shoreline	20	20
	Total	55	52

(B)

Habitat Category	Description of Habitat Types	Sample Size (N)	
		Spring	Fall
OO	Oyster Reef	5	4
OSG	Oyster reef embedded in seagrass beds (*Halodule wrightii*)	5	4
OME	Oyster reef adjacent to marsh edge = emergent vegetation < 2m from the shoreline	5	4
	Total	15	12

(C)

Habitat Category	Description of Habitat Types	Sample Size (N)	
		Spring	Fall
OSU	Oyster sampling unit	15	12
2C	2-sided predator exclusion control	15	12
FS	Fully enclosed predator exclusion cage	15	12
	Total	45	36

Table 2. Examples of (A) Analysis of Variance table for comparing three habitat types including Oyster Reef (OSU), Marsh Edge (ME), and Seagrass (SG). The model tests for the main effect of habitat type, and a priori contrasts compare specific habitat types. (B) Analysis of variance table comparing three synergistic relationships between habitats including, oyster reef only, oyster reef adjacent to marsh edge, and oyster reef adjacent to seagrass. (C) Analysis of Variance table for comparing three predator exclusion treatments including an Oyster Sampling Unit, 2-sided control, and a full enclosure. The log(x+1) transformation of the total macrofauna density was used in these examples.

(A)

Source	df	SUM OF SQUARES	MEAN SQUARE	F VALUE	P VALUE
Spring (May 2008)					
HABITAT TYPE	5	1.116	0.558	9.36	< 0.001
CONTRASTS					
ME vs SG	1	0.145	0.145	2.44	0.125
ME vs OSU	1	0.487	0.487	8.16	0.006
SG vs OSU	1	1.102	1.102	18.50	< 0.001
RESIDUAL ERROR	49	2.920	0.060		

(B)

Source	df	SUM OF SQUARES	MEAN SQUARE	F VALUE	P VALUE
Spring (May 2008)					
Synergy	2	0.027	0.135	6.59	0.017
Site	1	0.424	0.424	20.74	0.001
Synergy*Site	2	0.034	0.017	0.84	0.464
RESIDUAL ERROR	9	0.184	0.020		

(C)

Source	df	SUM OF SQUARES	MEAN SQUARE	F VALUE	P VALUE
Spring (May 2008)					
Predator Treatment	2	0.048	0.024	0.72	0.491
Site	1	1.082	1.082	32.55	< 0.001
Predator Treatment*Site	2	0.055	0.027	0.82	0.446
RESIDUAL ERROR	39	1.297	0.033		

Affects of synergy on oyster reef habitat nekton. To assess the relative importance of synergy among habitats and how it affects oyster reef as a fishery habitat, the OSUs described previously were placed in multiple habitat types within the two study sites in East Flats. There were three distinct spatial localities: (1) oyster reef in oyster reef complex (OO), oyster reef adjacent to seagrass beds (OSG), and in oyster reef adjacent to marsh edge (OME). In the spring 5 OSUs were placed in each of these localities (15 total); in the fall 4 OSUs were placed in each of the three distinct spatial locales (12 total) which were as equally dispersed as possible between East Flats 1 and East Flats 2. The trays were placed a minimum of 10 m apart. The OSUs were left in the field for three months each season. Throw trap samplers were used to sample these areas and all samples were collected and processed as previously described.

Relative abundance (RA %) was calculated by season for the total number of fish and crustaceans collected as well as for each individual species collected. The mean and standard error (SE) for the total number of fish, crustaceans, and individual species was also calculated for each synergy relationship sampled.

Analysis of Variance (ANOVA) was used to examine differences in overall mean density of nekton among synergy types with $\alpha = 0.05$. All counts were extrapolated to density (number of organisms m^{-2}) prior to analysis. A two-factor ANOVA was used to determine significant differences in mean densities of nekton between synergy types, with synergy as a fixed main effect and site as a random effect. A transformation (log10 [x+1]) was used to reduce heteroskedasticity. Since no interaction was detected between synergy type and site, a Tukey's post-hoc test was used to determine differences. Spring and fall and fish and crustacean densities were analyzed separately. Those species that occurred in high densities were analyzed also separately with ANOVAs to compare synergy types and three a priori contrasts to test different synergy combinations.

Community similarity/dissimilarity among habitat combinations was explored using a variety of non-parametric multivariate analyses using PRIMER v.6 (Clarke and Gorley 2006). I examined the mean densities of nekton collected from each habitat type in the spring and fall. Data were 4^{th} root transformed prior to analysis. Bray-Curtis resemblance matrices were constructed for both seasons and community assemblages were further investigated by using a non-metric multidimensional scaling (MDS) that was based on the Bray-Curtis similarity with the Bray-Curtis similarity groups superimposed for better interpretation (Clarke and Warwick 2001). A one-way SIMPER analysis was used to determine dominant species for each habitat.

Predator exclusion. I examined the role of predation on fish recruitment using predator exclusion cages. Each experimental block contained one OSU, one 2-sided control, and one completely enclosed predator exclusion cage. All the cages were constructed from a wood frame and modified from the above description. The 2-sided control (58 cm [W] x 58 cm [L]) was constructed with two adjacent sides 32 cm tall. The bottom of the cage was covered with 1-cm^2 mesh and the two sides were covered with 6.45-cm^2 mesh. The two open sides allowed predator access. The fully enclosed cage had the same dimensions as the two-sided control but with all four sides present, with predators fully excluded from OSU. A total of 15 and 12 experimental blocks were placed in the field during the spring and fall of 2008, respectively. The cages were equally distributed between the two sites in East Flats as in the habitat study. Each cage was secured to the bottom with rebar and contained 50 live oysters obtained from a local commercial plant. The cages were left in the field for three months prior to the sampling date. To avoid disturbance, all three cage types were simultaneously sampled using three throw trap samplers. All samples collected were treated in the same manner as previously described.

The mean and standard error (SE) for the total number of fish, crustaceans, and individual species was also calculated for each predator exclusion cage sampled. Relative abundance (RA %) was calculated by season for the total number of fish and crustaceans collected as well as for each individual species collected. Analysis of Variance (ANOVA) was used to examine differences in density of nekton among predator exclusion cage types with $\alpha = 0.05$. All counts were extrapolated to density (number of organisms m^{-2}) prior to analysis. A two-factor ANOVA was used to determine significant differences in mean densities of nekton between predator exclusion cage types, with cage type as a fixed main effect and site as a random effect. A transformation (log10 [x+1]) was used to reduce heteroskedasticity. Since no interaction was detected between cage type and site, a Tukey's post-hoc test was used to determine differences. Spring and fall and fish and crustacean densities were analyzed separately. Those species that occurred in high densities were analyzed separately with ANOVAs to compare synergy types and three a priori contrasts to test different synergy combinations.

Community similarity/dissimilarity among habitat combinations was explored using a variety of non-parametric multivariate analyses using PRIMER v.6 (Clarke and Gorley 2006). I examined the mean densities of nekton collected from each predator exclusion cage in the spring and fall. Data were 4th root transformed prior to analysis. Bray-Curtis resemblance matrices were constructed for both seasons and community assemblages were further investigated by using a non-metric multidimensional scaling (MDS) that was based on the Bray-Curtis similarity with the Bray-Curtis similarity groups superimposed for better interpretation (Clarke and Warwick 2001). A one-way SIMPER analysis was used to determine the dominant species for each habitat.

Oyster reef complexity. ***Experimental organisms.*** I experimentally examined the habitat selection of two common and economically important estuarine species: juvenile red drum and brown shrimp. Red drum and brown shrimp were seined from seagrass beds in Corpus Christi Bay and Aransas Bay. Red drum ranged in size from 15 mm to 30 mm SL and brown shrimp ranged in size from 40 mm to 60 mm TL. Both experimental organisms were maintained in separate tanks in a seawater laboratory system and fed to satiation daily. I used pinfish, as the experimental predator. Pinfish are important predators of juvenile red drum and have been successfully used in numerous experimental trials (Fuiman 1994, Rooker et al. 1998). During preliminary trials pinfish readily consumed red drum prey. Pinfish were collected by hook and line in Corpus Christi Bay and ranged in size from 114 mm to 152 mm SL. Pinfish were maintained in a separate tank in the seawater system under the same conditions as the red drum and brown shrimp.

Experimental mesocosms. The experimental system used consisted of 18, 151.42 L rectangular fiberglass tanks. This system was connected to a recirculating seawater treatment system consisting of UV disinfection, sand filtration, and biofiltration. The tanks were aerated by a common 2.5 hp blower. Oyster shells were obtained from a commercial processing plant and sun dried before being added to the experimental mesocosms. The sand filter and biofilter were bypassed while the system was run with freshwater for three days once the oyster shell and sand were in place. The system was then filled with seawater from the Laguna Madre.

The effect of habitat complexity on habitat selection was evaluated using laboratory mesocosms (for examples see Stunz et al. 2001 and Stunz and Minello 2001) and simulating four levels of complexity: (1) no complexity, (2) low complexity, (3) medium complexity, and (4) high complexity. The bottom of each mesocosm was covered with coarse beach sand and the complexity levels of the habitats were controlled by constructing reefs with the desired attributes. The measured attributes included height, volume, and number of oyster clusters. The no complexity habitat consisted of a sand bottom. The low complexity habitat consisted of a sand bottom and an average of 1.5 L of oyster shell, all of which were placed flat on the sand. For the medium complexity the average volume of oyster shell was 3.2 L and placed on top of the sand bottom. A small amount of vertical relief (2 cm to 10 cm) was present because some of the shells were placed vertically. The high complexity level consisted of 4.3 L of oyster shells with a much greater vertical relief (2-23 cm) and 4 large oyster clusters per mesocosm. The oyster clusters were constructed by securing oyster shells together using epoxy until the desired height was achieved. The artificial oyster clusters were designed to simulate natural oyster clusters found in the field. Once the structures were built they were allowed to air dry for a minimum of 24 hours before being placed in the water. Each mesocosm was divided in half and each contained a complexity treatment replicate on each side. To strictly assess the effect of the habitat structures on habitat selection, no food was introduced into the experimental mesocosms.

Habitat selection in the absence of a predator. To examine the effects of habitat complexity on the habitat selection of red drum and brown shrimp every possible pairwise combination of habitat complexity levels was used, and complexity treatment within each mesocosm was randomized. Prior to the beginning of each trial air stones were removed, and three juvenile red drum or three brown shrimp were placed in the center of each mesocosm and monitored for a three hour acclimation period. After the acclimation period the location of each of the organisms in the experimental mesocosms were visually recorded every 30 minutes for five hours. Each trial was repeated with different fish and shrimp for a total of 10 replicates per treatment with each study organism.

Habitat Selection in the presence of a predator. To examine the effects of a predator on habitat selection of red drum, the previous experiment was repeated using tethered pinfish. The pinfish were tethered to a large weight using a small metal clip attached to the lower jaw which was secured to a 30 cm monofilament line. Two tethered pinfish were placed in each mesocosm, one on each side. Every possible pairwise comparison was performed. Predators were allowed a 30-minute acclimation period prior to the introduction of red drum, and observation began 30 minutes after introduction of the red drum. The location of the red drum was recorded every 30 minutes for five hours. Each trial was repeated with different fish for a total of 10 replicates per treatment.

Statistical Analysis. For each replicate mesocosm the percent occurrence of the organisms in each complexity level was determined. Mean percent occurrence was calculated and these data were arcsine transformed to normalize the distribution of the percentage data. Selection patterns were analyzed using a paired student's t-test (α = 0.05).

RESULTS

Assessment of oyster reef habitat nekton. Salinity, DO, and temperature were measured once in spring and fall of 2008 on the day the samples were collected in East Flats 1 and East Flats 2. Salinity was similar in both East Flats 1 and East Flats 2 in spring. There was an increase in salinity in fall. Dissolved oxygen levels were similar between the two study sites in both spring and fall. Temperatures varied from 28.05^{o} C in the spring to 20.34^{o}C in the fall (Table 3).

A total of 11,246 organisms were collected during spring (May) and fall (November) of 2008 in East Flats, with a total of 28 fish species and 15 species of decapod crustaceans (Table 4). Species richness was significantly greater in oyster reef (OR) with an average of 11.2 and 10 species m^{-2} in spring (F=40.19; df=5,49; p<0.001) and fall (F=34.30; df=5,46; p<0.001), respectively (Fig. 3). In May 2008 the highest nekton abundance (7,292) was observed. Crustaceans were the most abundant group in both seasons, 5,344 and 3,190 during spring and fall, respectively. Darter gobies (*Gobionellus boleosoma*), pinfish, gulf toadfish (*Opsanus beta*), bay anchovies (*Anchoa mitchilli*), and code gobies (*Gobiosoma robustum*), were the most abundant fish in spring. Mud crabs (Panopeidae) were the most abundant benthic crustacean and grass shrimp, brown and pink shrimp, and blue crabs (*Callinectes sapidus*) were the most abundant nektonic crustaceans in the spring. Darter gobies, code gobies, and gulf toadfish were the most abundant fish in fall. With the addition of the arrow shrimp (*Tozeuma carolinense),* the most abundant crustaceans in fall were the same as in spring (Table 4).

I determined if there were differences between the habitat types by using ANOVA. Overall densities of organisms were significantly different among habitats during both spring ($F= 9.36$; $df=5,49$; $p < 0.001$) and fall ($F= 29.60$; $df=5,46$; $p<0.001$). There were no differences in overall densities of organisms between seagrass and marsh edge habitats, but densities on oyster reefs were substantially higher (Fig. 4). Crustacean density was also significantly different among habitats during both spring ($F= 11.09$; $df=5,49$; $p < 0.0001$) and fall ($F=36.93$; $df=5,46$; $p<0.0001$). There were also significant differences between crustacean densities among all three habitats (Fig. 5), however, mean densities in oyster reef were more than double those in marsh edge and seagrass habitats in fall, and were substantially higher than marsh edge in spring. There were no significant differences in fish densities among habitats in spring ($F=1.95$; $df=5,49$; $p=0.153$) (Fig 6). However, there were significant differences in fish densities among habitats in fall ($F=4.49$; $df=5,46$; $p=0.017$); oyster reef densities were greater than seagrass densities, but marsh edge densities were not significantly different from either of the other habitats.

The densities of the most abundant fish and crustaceans were compared across habitats to discern any differences among habitat types (Table 5). In spring, darter gobies were most abundant in SG followed by ME and OR. Pinfish densities were similar in OR and SG habitats and highest in ME habitat. Toadfish were present almost solely in OR with only two collected from ME during spring. Grass shrimp were the most abundant decapod crustacean in both spring and fall with greatest densities occurring in OR and

ME habitats in spring and OR and SG habitats in fall. Mud crabs had the greatest abundance in OR in both seasons. Blue crab densities in fall were similar in OR (15.50 ± 5.85) and SG (14.30 ± 2.02). Brown and pink shrimp were more abundant in spring than in fall. The highest densities were recorded in ME in the spring and SG in fall.

Table 3. Environmental variables recorded on the day the habitats were sampled in the spring and fall of 2008 for the two study sites located in East Flats, Corpus Christi Bay, Texas**.**

	East Flats	
Environmental Variable	Site 1	Site 2
Spring 2008		
Temperature (^oC)	27.15	28.05
Salinity (ppt)	31.50	31.00
Dissolved Oxygen (mg l^{-1})	6.47	6.08
Fall 2008		
Temperature (^oC)	22.50	20.34
Salinity (ppt)	35.40	36.05
Dissolved Oxygen (mg l^{-1})	6.13	5.78

Table 4. Overall mean densities as number m^{-2} and (SE, one standard error) of all collected fishes and crustaceans in three habitat types including marsh edge, seagrass beds, and oyster reef in the Spring and Fall of 2008. The total number and relative abundance (number of individuals/total number of animals collected x 100) are also given.

				Oyster Reef		Seagrass		Marsh Edge	
COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	MEAN	SE	MEAN	SE	MEAN	SE
SPRING 2008									
Total Fishes		1948	26.71	31.8	(2.10)	41.25	(4.11)	32.3	(3.17)
Darter goby	*Gobionellus boleosoma*	1429	19.60	21.80	(1.10)	31.75	(3.82)	23.35	(2.98)
Pinfish	*Lagodon rhomboides*	197	2.70	2.60	(0.62)	2.05	(0.43)	5.85	(1.63)
Gobies (unknown)		138	1.89	0.20	(0.11)	4.75	(1.08)	2.00	(0.62)
Gulf toadfish	*Opsanus beta*	50	0.69	3.20	(0.81)	0.00	(0.00)	0.10	(0.10)
Bay anchovy	*Anchoa mitchilli*	37	0.51	0.00	(0.00)	1.85	(1.21)	0.00	(0.00)
Code goby	*Gobiosoma robustum*	34	0.47	1.87	(0.43)	0.30	(0.13)	0.00	(0.00)
Pipefish	*Syngnathus* sp.	18	0.25	0.27	(0.15)	0.05	(0.05)	0.65	(0.27)
Pigfish	*Orthopristis chrysoptera*	13	0.18	0.67	(0.29)	0.10	(0.07)	0.05	(0.05)
Silver perch	*Bairdiella chrysoura*	7	0.10	0.47	(0.47)	0.00	(0.00)	0.00	(0.00)
Inland silverside	*Menidia beryllina*	4	0.05	0.00	(0.00)	0.20	(0.16)	0.00	(0.00)
Mangrove snapper	*Lutjanus griseus*	4	0.05	0.27	(0.15)	0.00	(0.00)	0.00	(0.00)
Striped mullet	*Mugil cephalus*	4	0.05	0.00	(0.00)	0.00	(0.00)	0.20	(0.14)
Spotfin mojarra	*Eucinostomus argenteus*	2	0.03	0.13	(0.09)	0.00	(0.00)	0.00	(0.00)
Spotted seatrout	*Cynoscion nebulosus*	2	0.03	0.07	(0.07)	0.00	(0.00)	0.05	(0.05)
Gulf killifish	*Fundulus grandis*	2	0.03	0.00	(0.00)	0.10	(0.10)	0.00	(0.00)
Striped blenny	*Chasmodes bosquianus*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)

Table 4. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	Oyster Reef MEAN	Oyster Reef SE	Seagrass MEAN	Seagrass SE	Marsh Edge MEAN	Marsh Edge SE
Naked goby	*Gobiosoma bosc*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Green goby	*Microgobius thalassinus*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Spot	*Leiostomus xanthurus*	1	0.01	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Atlantic croaker	*Micropogonias undulatus*	1	0.01	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Blackwing searobin	*Prionotus rubio*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Longnose killifish	*Fundulus similis*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.05	(0.05)
Total Crustaceans		5344	73.29	171.00	(27.81)	42.50	(6.29)	96.45	(29.74)
Grass shrimp	*Palaemonetes* spp.	3538	48.52	91.53	(22.66)	25.30	(3.93)	82.95	(27.57)
Mud crabs	Panopeidae	1076	14.76	62.20	(10.00)	6.40	(2.26)	0.75	(0.40)
Brown / Pink shrimp (grooved)	*Farfantepenaeus* spp.	225	3.09	2.60	(0.67)	1.20	(0.27)	8.10	(2.31)
Blue crab	*Callinectus sapidus*	217	2.98	2.07	(0.57)	7.10	(1.21)	2.20	(0.56)
Ridgeback mud crab	*Panopeus turgidus*	103	1.41	6.13	(0.88)	0.45	(0.35)	0.10	(0.10)
Snapping shrimp	*Alpheus heterochaelis*	63	0.86	4.07	(0.69)	0.10	(0.10)	0.00	(0.00)
Penaeid shrimp		37	0.51	0.47	(0.27)	0.40	(0.17)	1.10	(0.33)
Arrow shrimp	*Tozeuma carolinense*	33	0.45	0.00	(0.00)	0.60	(0.33)	1.05	(0.41)
Thinstripe hermit crab	*Clibanarius vittatus*	27	0.37	1.00	(0.37)	0.55	(0.22)	0.05	(0.05)
Hermit crab		10	0.14	0.20	(0.14)	0.30	(0.13)	0.05	(0.05)
Atlantic mud crab	*Panopeus herbstii*	6	0.08	0.40	(0.16)	0.00	(0.00)	0.00	(0.00)
Longeye shrimp	*Ogyrides* spp.	2	0.03	0.00	(0.00)	0.10	(0.07)	0.00	(0.00)
Longnose spider crab	*Libinia dubia*	2	0.03	0.00	(0.00)	0.00	(0.00)	0.10	(0.07)
Hermit crab (left-handed)		2	0.03	0.13	(0.13)	0.00	(0.00)	0.00	(0.00)

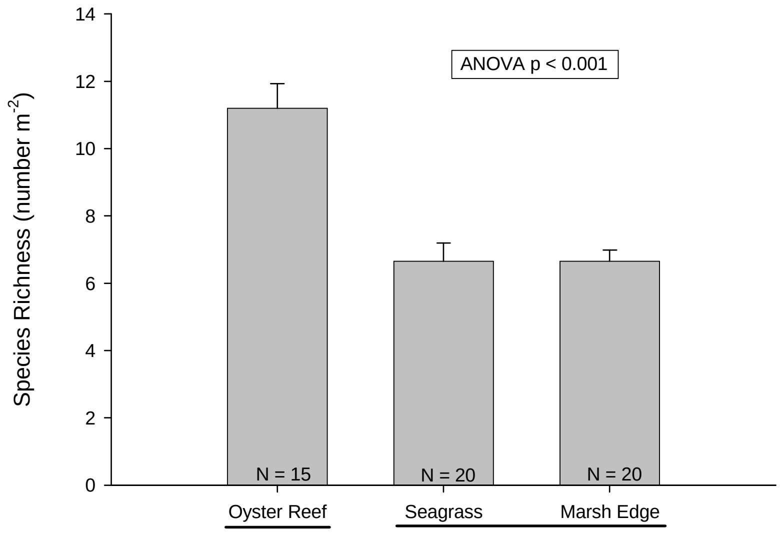
Table 4. (Continued)

				Oyster Reef		Seagrass		Marsh Edge	
COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	MEAN	SE	MEAN	SE	MEAN	SE
Flatback mud crab	*Eurypanopeus depressus*	2	0.03	0.13	(0.09)	0.00	(0.00)	0.00	(0.00)
Dark shore crab	*Pachygrapsus gracilis*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
FALL 2008									
Total Fishes		764	19.32	18.33	(2.81)	10.40	(2.08)	16.80	(3.35)
Darter goby	*Gobionellus boleosoma*	658	16.64	14.42	(2.49)	9.10	(2.21)	15.15	(3.40)
Code goby	*Gobiosoma robustum*	27	0.68	0.42	(0.19)	1.10	(0.59)	0.00	(0.00)
Gulf toadfish	*Opsanus beta*	21	0.53	1.75	(0.51)	0.00	(0.00)	0.00	(0.00)
Spotfin mojarra	*Eucinostomus argenteus*	16	0.40	0.58	(0.34)	0.00	(0.00)	0.45	(0.25)
Sheepshead minnow	*Cyprinodon variegatus*	12	0.30	0.00	(0.00)	0.00	(0.00)	0.60	(0.60)
Frillfin goby	*Bathygobius soporator*	5	0.13	0.42	(0.15)	0.00	(0.00)	0.00	(0.00)
Pipefish	*Syngnathus* spp.	5	0.13	0.00	(0.00)	0.00	(0.00)	0.25	(0.10)
Green goby	*Microgobius thalassinus*	4	0.10	0.00	(0.00)	0.00	(0.00)	0.20	(0.12)
Striped blenny	*Chasmodes bosquianus*	3	0.08	0.25	(0.18)	0.00	(0.00)	0.00	(0.00)
Mangrove snapper	*Lutjanus griseus*	3	0.08	0.25	(0.13)	0.00	(0.00)	0.00	(0.00)
Naked goby	*Gobiosoma bosc*	2	0.05	0.08	(0.08)	0.00	(0.00)	0.05	(0.05)
Pinfish	*Lagodon rhomboides*	2	0.05	0.08	(0.08)	0.00	(0.00)	0.05	(0.05)
Gulf menhaden	*Brevoortia patronus*	1	0.03	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Blackcheek tonguefish	*Symphurus plagiusa*	1	0.03	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Gobies (unknown)	Gobiidae	1	0.03	0.00	(0.00)	0.00	(0.00)	0.05	(0.05)

Table 4. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	Oyster Reef MEAN	Oyster Reef SE	Seagrass MEAN	Seagrass SE	Marsh Edge MEAN	Marsh Edge SE
Dwarf seahorse	*Hippocampus zosterae*	1	0.03	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Emerald sleeper	*Erotelis smaragdus*	1	0.03	0.08	(0.08)	0.00	(0.00)	0.00	(0.00)
Cusk eel	Ophidiidae	1	0.03	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Total Crustaceans		3190	80.68	143.25	(32.65)	46.30	(7.05)	27.25	(5.35)
Grass shrimp	*Palaemonetes* spp.	1342	33.94	44.50	(10.72)	26.35	(4.35)	14.05	(3.83)
Mud crabs	Panopeidae	712	18.01	54.67	(14.99)	1.45	(0.53)	1.35	(1.15)
Blue crab	*Callinectus sapidus*	617	15.60	15.50	(5.85)	14.30	(2.02)	7.25	(1.43)
Ridgeback mud crab	*Panopeus turgidus*	172	4.35	14.25	(2.58)	0.05	(0.05)	0.00	(0.00)
Arrow shrimp	*Tozeuma carolinense*	91	2.30	0.67	(0.36)	0.70	(0.33)	3.45	(1.69)
Snapping shrimp	*Alpheus heterochaelis*	79	2.00	6.42	(1.13)	0.10	(0.07)	0.00	(0.00)
Brown / Pink shrimp (grooved)	*Farfantepenaeus* spp.	47	1.19	0.75	(0.35)	1.75	(0.39)	0.15	(0.11)
Thinstripe hermit crab	*Clibanarius vittatus*	43	1.09	3.33	(1.82)	0.15	(0.08)	0.00	(0.00)
penaeid shrimp		27	0.68	0.83	(0.83)	0.45	(0.22)	0.40	(0.18)
Hermit Crab		21	0.53	0.25	(0.25)	0.65	(0.25)	0.25	(0.10)
White Shrimp	*Litopenaeus setiferus*	15	0.38	0.17	(0.11)	0.30	(0.15)	0.35	(0.17)
Porcelain crab	*Petrolisthes* spp.	9	0.23	0.75	(0.30)	0.00	(0.00)	0.00	(0.00)
Atlantic mud crab	*Panopeus herbstii*	5	0.13	0.42	(0.19)	0.00	(0.00)	0.00	(0.00)
Dark shore crab	*Pachygrapsus gracilis*	3	0.08	0.25	(0.18)	0.00	(0.00)	0.00	(0.00)
Green Porcelain Crab	*Petrolisthes armatus*	3	0.08	0.25	(0.18)	0.00	(0.00)	0.00	(0.00)
Flatback mud crab	*Eurypanopeus depressus*	2	0.05	0.17	(0.17)	0.00	(0.00)	0.00	(0.00)
Longnose spider crab	*Libinia dubia*	1	0.03	0.00	(0.00)	0.05	(0.05)	0.00	(0.00)
Stone crab	*Menippe adina*	1	0.03	0.08	(0.08)	0.00	(0.00)	0.00	(0.00)

(A)



(B)

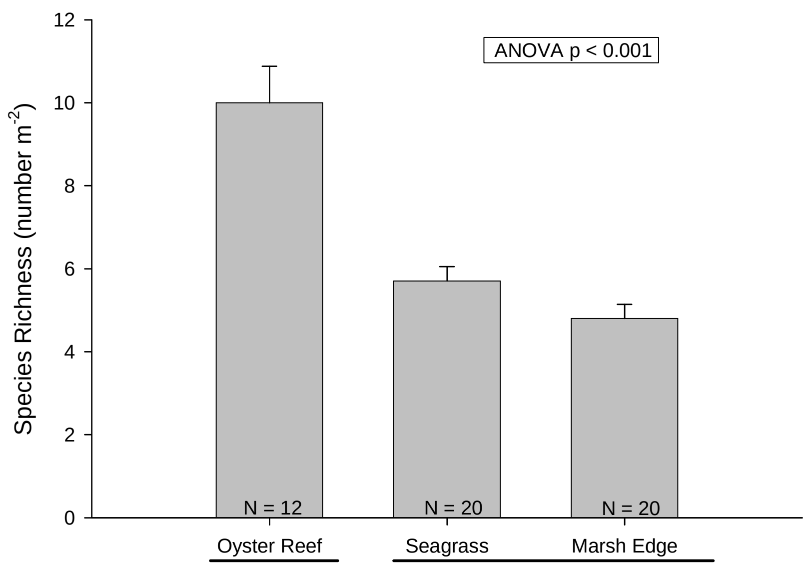
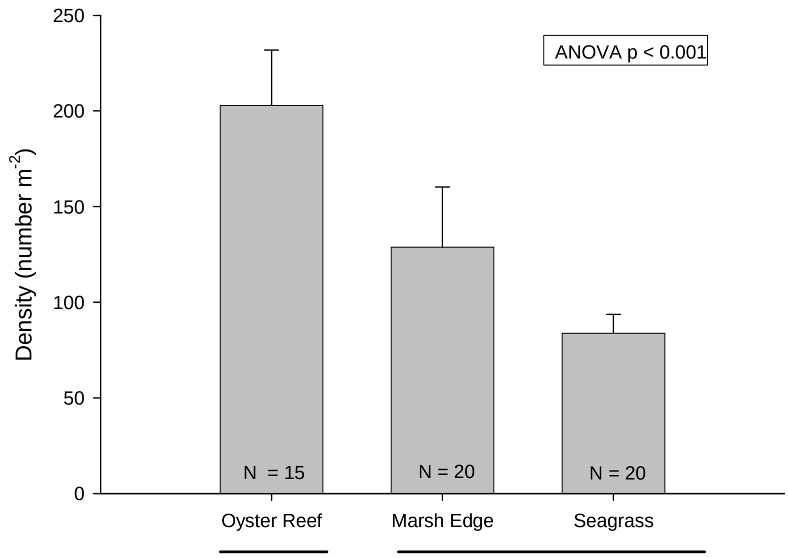


Fig. 3. Species richness (number of species m^{-2}) in oyster reef, seagrass, and marsh edge habitats during (A) spring and (B) fall 2008. Habitats that share a common line were not significantly different.

(A)



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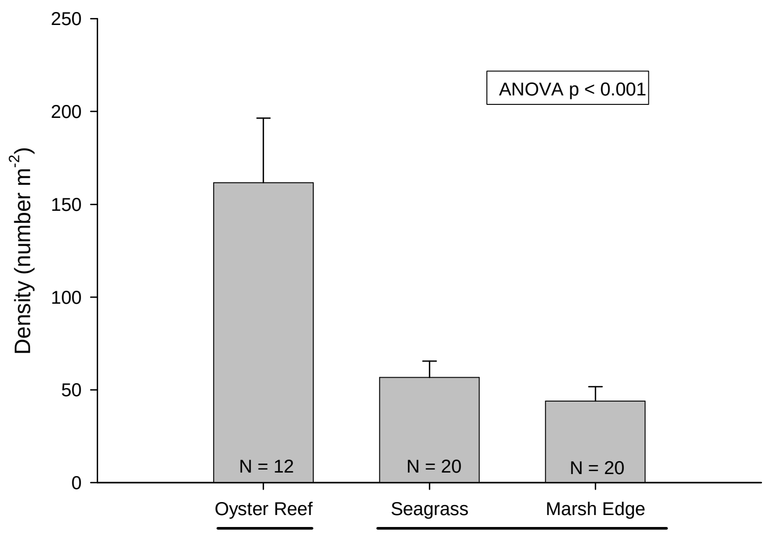
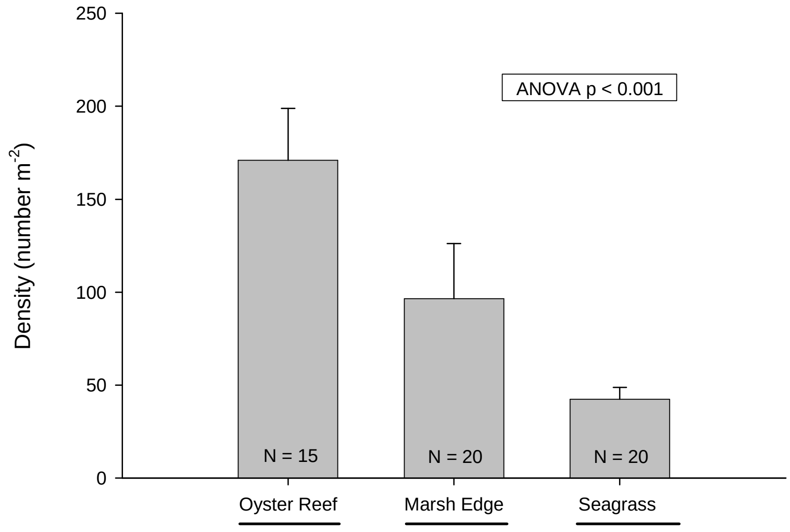


Fig. 4. Mean densities (number m^{-2}) of nekton and decapod crustaceans (combined) collected from oyster reef, seagrass, and marsh edge, habitats in (A) spring and (B) fall of 2008. Samples were collected using a 1-m^2 drop sampler. Habitats that share a common line were not significantly different.

(A)



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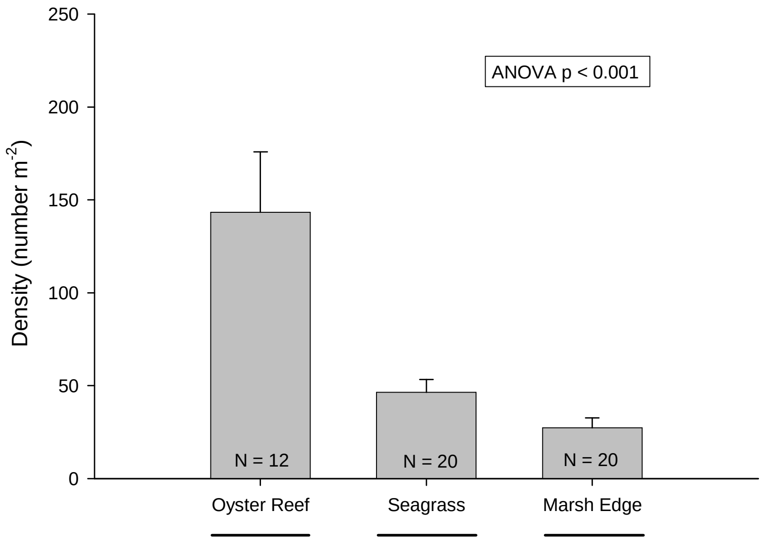
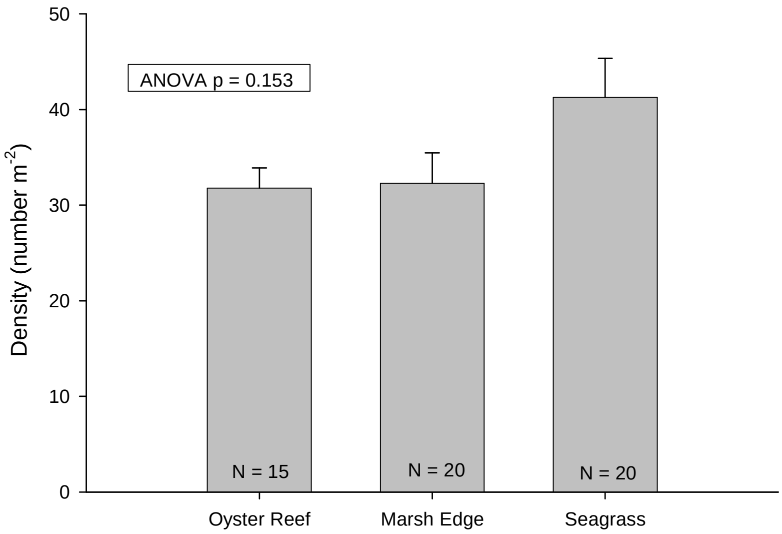


Fig. 5. Mean densities (number m^{-2}) of crustaceans collected from oyster reef, seagrass, and marsh edge habitats during (A) spring and (B) fall 2008. Habitats that share a common line were not significantly different.

(A)



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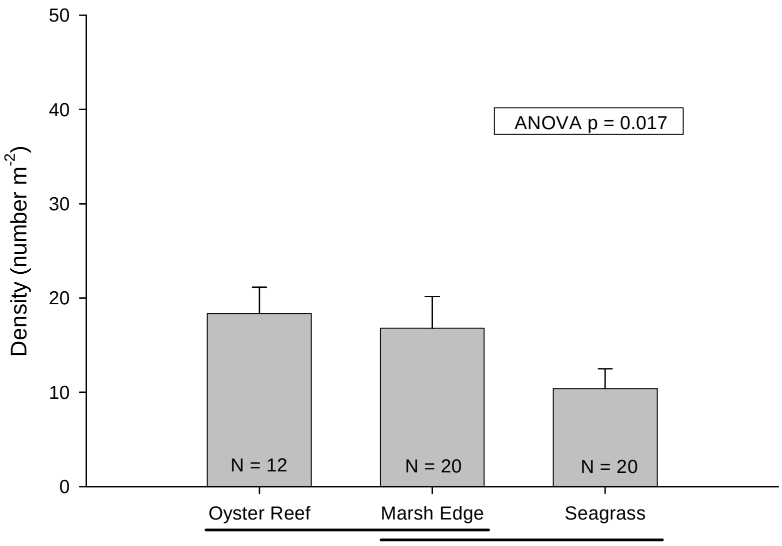


Fig. 6. Mean densities (number m^{-2}) of fish collected from oyster reef, seagrass, and marsh edge during (A) spring and (B) fall 2008.. Habitats that share a common line were not significantly different.

Community analyses revealed differences in overall community structure among the three habitat types. Differences were seen in both cluster analysis and MDS ordination. The Bray-Curtis cluster analyses delineated three distinct groups in spring and two groups in fall with 65% and 64% similarity, respectively. The MDS ordination of data from fall shows a dissimilarity in community structure among all three habitats (Fig 7) whereas in spring, SG and ME communities are similar but oyster reef communities were distinct (Fig 8).

A one-way SIMPER analysis was used to determine which species contributed the most to the differences among habitat types (Table 6). In spring, mud crabs, bay anchovies, pipefish (*Syngnathus* sp.), grass shrimp, and arrow shrimp contributed most to the dissimilarity between ME and SG, and in fall brown and pink shrimp, mud crabs, arrow shrimp, hermit crabs, and white shrimp contributed to the dissimilarity. Mud crabs, snapping shrimp, gulf toadfish, and code gobies contributed most to the dissimilarity between ME and OR in both seasons. Species contributing most to the difference between OR and SG in spring include gulf toadfish, snapping shrimp, mud crabs, gobies, and bay anchovies. In fall mud crabs, snapping shrimp, gulf toadfish, and porcelain crabs contributed to dissimilarity between oyster reef and seagrass.

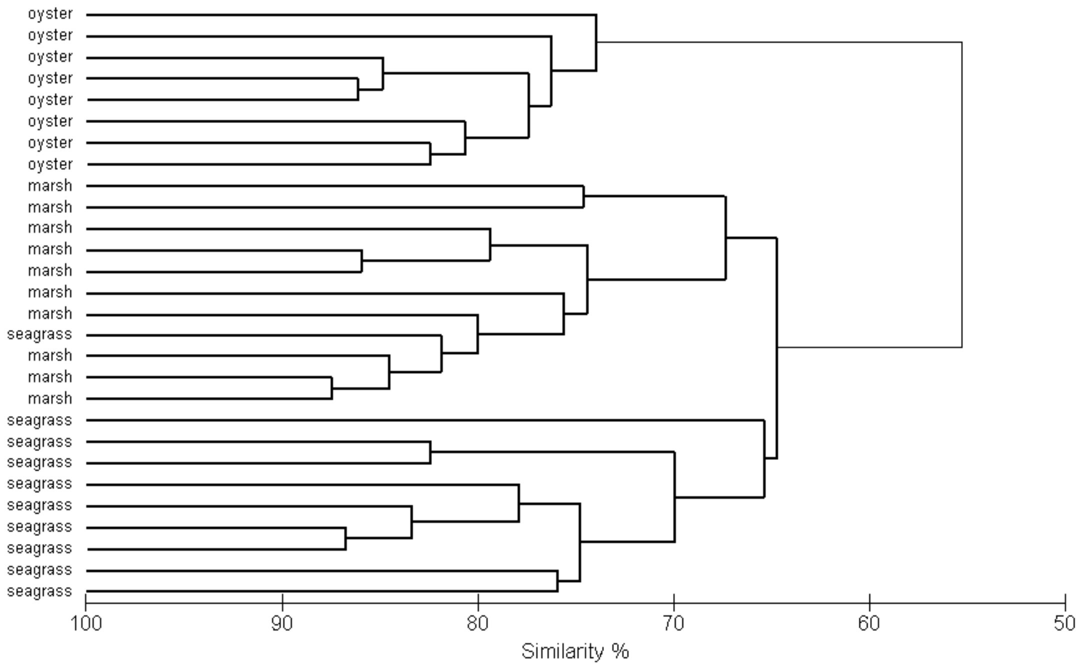
Table 5. Mean densities as number m^{-2} and (SE, one standard error) of abundant fishes and crustaceans collected from three habitat types: oyster reef (OR), seagrass (SG), and marsh edge (ME) during spring and fall 2008. Refer to Table 1 for sample size of each mean. Results (p-values) are given from ANOVAs used to compare habitat types (HABITAT EFFECT) and three a priori contrast testing different habitat combinations. The ANOVA probability value was significant at the 5% level after alpha values were adjusted as described by Rice (1989). Contrast p-values were not adjusted.

	Oyster Reef		Seagrass		Marsh Edge		TOTAL	HABITAT	Contrast p values		
							NUMBER	EFFECT	OR Vs	OR vs	ME vs
COMMON NAME	MEAN	SE	MEAN	SE	MEAN	SE	COLLECTED	p value	SG	ME	SG
SPRING 2008											
Fishes											
Darter goby	21.80	(1.10)	31.75	(3.82)	23.35	(2.98)	1429	0.003	0.153	0.632	0.042
Pinfish	2.60	(0.62)	2.05	(0.43)	5.85	(1.63)	197	0.003	0.673	0.152	0.047
Gobies (unknown)	0.20	(0.11)	4.75	(1.08)	2.00	(0.62)	138	< 0.001	< 0.001	0.003	0.001
Gulf toadfish	3.20	(0.81)	0.00	(0.00)	0.10	(0.10)	50	< 0.001	< 0.001	< 0.001	0.660
Crustaceans											
Grass shrimp	91.53	(22.66)	25.30	(3.93)	82.95	(27.57)	3538	0.000	0.012	0.946	0.008
Mud crabs	62.20	(10.00)	6.40	(2.26)	0.75	(0.40)	1076	< 0.001	< 0.001	< 0.001	< 0.001
Brown / Pink shrimp	2.60	(0.67)	1.20	(0.27)	8.10	(2.31)	225	< 0.001	0.063	0.000	< 0.001
Blue crab	2.07	(0.57)	7.10	(1.21)	2.20	(0.56)	217	< 0.001	< 0.001	0.894	< 0.001
Ridgeback mud crab	6.13	(0.88)	0.45	(0.35)	0.10	(0.10)	103	< 0.001	< 0.001	< 0.001	0.348
Snapping shrimp	4.07	(0.69)	0.10	(0.10)	0.00	(0.00)	63	< 0.001	< 0.001	< 0.001	0.449
Penaeid shrimp	0.47	(0.27)	0.40	(0.17)	1.10	(0.33)	37	0.010	0.927	0.071	0.042
FALL 2008											
Fishes											
Darter goby	14.42	(2.49)	9.10	(2.21)	15.15	(3.40)	658	0.002	0.025	0.445	0.080

Table 5. (Continued)

COMMON NAME	Oyster reef MEAN	Oyster reef SE	Seagrass MEAN	Seagrass SE	Marsh Edge MEAN	Marsh Edge SE	TOTAL NUMBER COLLECTED	HABITAT EFFECT p value	Contrast p values: OR vs SG	Contrast p values: OR vs ME	Contrast p values: ME vs SG
Code goby	0.42	(0.19)	1.10	(0.59)	0.00	(0.00)	27	0.013	0.719	0.030	0.035
Gulf toadfish	1.75	(0.51)	0.00	(0.00)	0.00	(0.00)	21	0.000	< 0.001	< 0.001	1.000
Crustaceans											
Grass shrimp	44.50	(10.72)	26.35	(4.35)	14.05	(3.83)	1342	< 0.001	0.358	< 0.001	< 0.001
Mud crabs	54.67	(14.99)	1.45	(0.53)	1.35	(1.15)	712	< 0.001	< 0.001	< 0.001	0.170
Blue crab	15.50	(5.85)	14.30	(2.02)	7.25	(1.43)	617	< 0.001	0.129	0.127	< 0.001
Ridgeback mud crab	14.25	(2.58)	0.05	(0.05)	0.00	(0.00)	172	< 0.001	< 0.001	< 0.001	0.703
Arrow shrimp	0.67	(0.36)	0.70	(0.33)	3.45	(1.69)	91	0.004	0.950	0.030	0.011
Snapping shrimp	6.42	(1.13)	0.10	(0.07)	0.00	(0.00)	79	< 0.001	< 0.001	< 0.001	0.628
Brown / Pink shrimp	0.75	(0.35)	1.75	(0.39)	0.15	(0.11)	47	0.002	0.034	0.141	< 0.001

(A)



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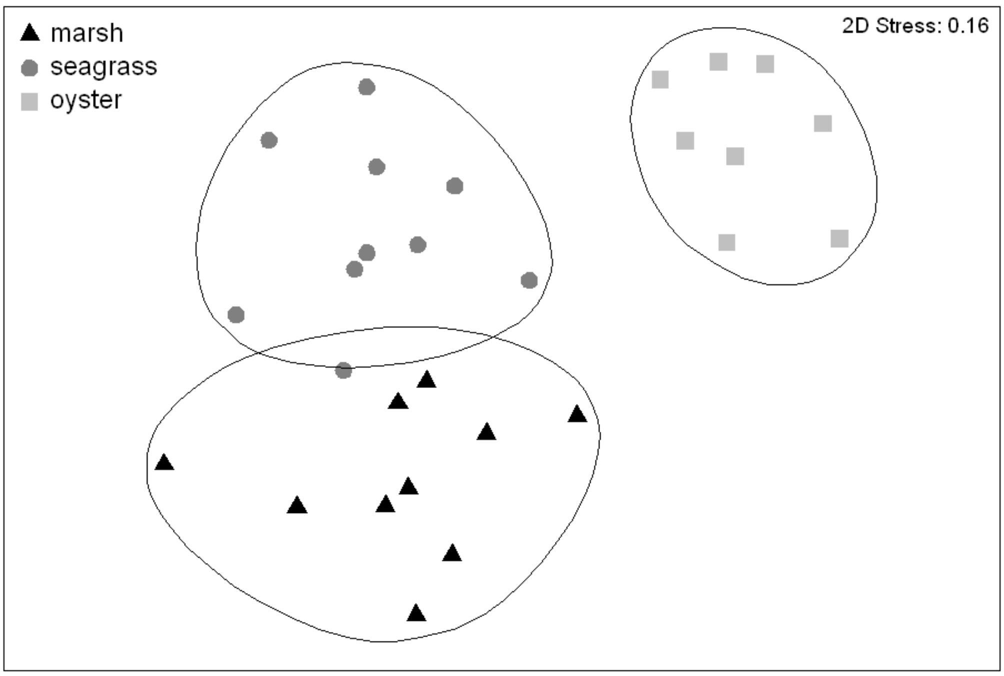
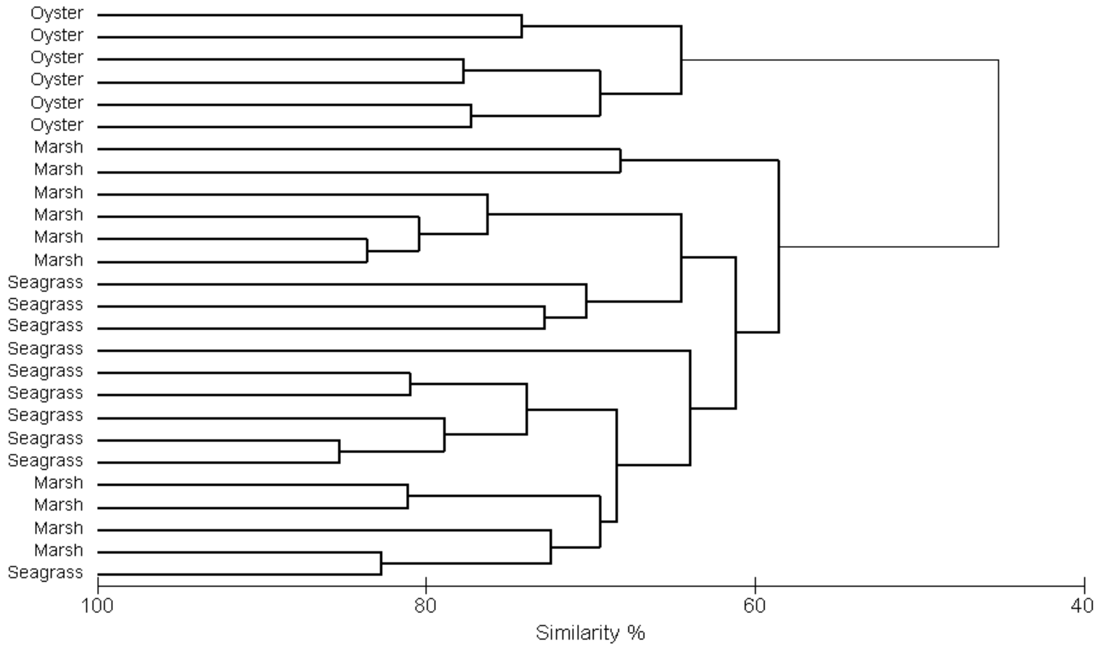


Fig. 7. Bray-Curtis cluster analysis for spring 2008 (A) and MDS ordination (B) with Bray-Curtis cluster analysis superimposed using 65% similarity of mean density of nekton and benthic crustaceans from each habitat.

(A)



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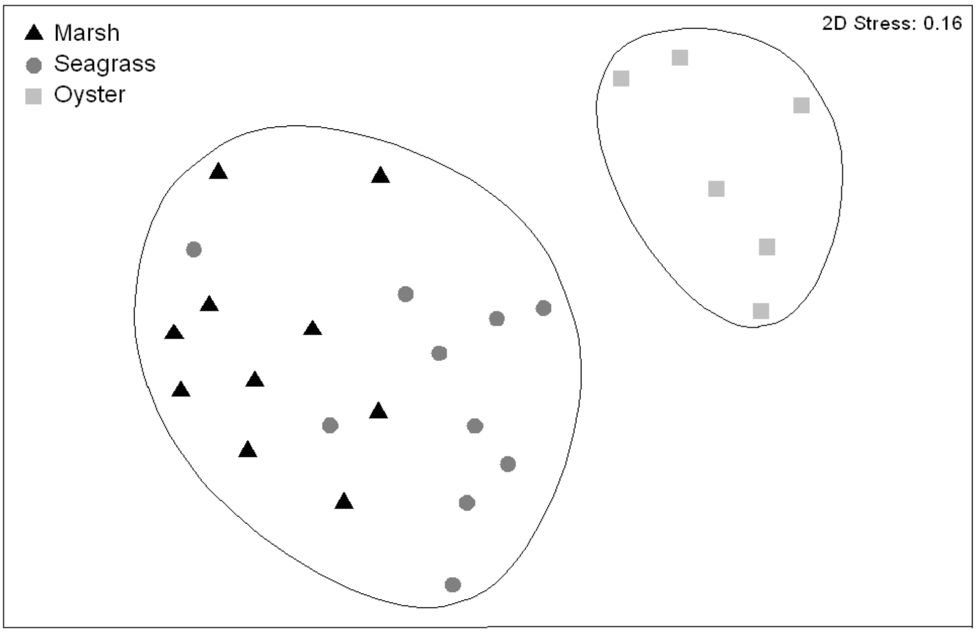


Fig. 8. Bray-Curtis cluster analysis for fall 2008 (A) and MDS ordination (B) with Bray-Curtis cluster analysis superimposed using 64% similarity of mean density of nekton and benthic crustaceans from each habitat.

Table 6. Summary of one-way SIMPER analysis for all habitat types sampled showing species which contributed more than 1% to either the within group similarity or dissimilarity between groups in the spring and fall of 2008. Data were fourth-root transformed. Mean densities, as number m^{-2}, are given. Values < 1% are represented by a dash (-).

	Oyster Reef		Seagrass		Marsh Edge		Seagrass and Oyster Reef	Marsh Edge and Oyster Reef	Marsh Edge and Seagrass
	Mean Density	% Similarity	Mean Density	% Similarity	Mean Density	% Similarity	% Dissimilarity	% Dissimilarity	% Dissimilarity
Spring 2008									
Grass Shrimp	91.53	15.92	25.30	17.09	82.95	22.12	4.86	3.56	6.57
Mud Crabs (unidentified)	62.20	14.12	6.40	11.34	0.75	1.23	6.78	12.57	10.47
Darter Goby	21.80	12.05	31.75	18.77	23.35	18.82	1.37	1.08	2.57
Snapping Shrimp	4.07	7.61	0.10	-	0.00	-	8.03	8.23	-
Gulf Toadfish	3.20	6.84	0.00	-	0.00	-	8.22	7.23	-
Brown/ Pink Shrimp	2.60	6.45	1.20	6.18	8.10	13.65	2.41	2.32	5.97
Pinfish	2.60	7.01	2.05	8.13	5.85	10.63	1.86	2.54	5.06
Blue Crab	2.07	6.20	7.10	13.06	2.20	8.39	2.72	1.88	4.80
Code Goby	1.87	6.32	0.30	0.39	0.00	-	4.71	6.84	3.93
Pigfish	0.67	1.21	0.10	-	0.05	-	3.44	-	-
Atlantic Mud Crab	0.40	1.96	0.00	-	0.00	-	3.87	-	-
Pipefish	0.27	-	0.05	-	0.65	4.31	2.42	3.74	6.76
Gobies (< 14mm SL)	0.20	-	4.75	11.89	2.00	11.35	7.27	5.82	2.67
Ridgeback Mud Crab	0.13	8.29	0.00	-	0.00	-	7.37	8.29	3.62
Arrow Shrimp	0.00	-	0.60	1.86	1.05	3.13	3.54	4.20	6.39
Bay Anchovy	0.00	-		2.95	0.00	-	4.94	-	7.49
Fall 2008									
Mud Crabs (unidentified)	54.67	16.00	1.45	6.42	1.35	-	10.25	11.46	9.87
Grass Shrimp	44.50	14.34	26.35	26.54	14.05	24.07	3.19	3.68	4.63

Table 6. Continued

	Oyster Reef		Seagrass		Marsh Edge		Seagrass and Oyster Reef	Marsh Edge and Oyster Reef	Marsh Edge and Seagrass
	Mean Density	% Similarity	Mean Density	% Similarity	Mean Density	% Similarity	% Dissimilarity	% Dissimilarity	% Dissimilarity
Blue Crab	15.50	11.18	14.30	22.98	7.25	21.40	-	1.92	3.76
Darter Goby	14.42	11.94	9.10	19.98	15.15	23.05	2.06	1.86	4.57
Ridgeback Mud Crab	14.25	11.70	0.05	-	0.00	-	10.64	9.99	-
Snapping Shrimp	6.42	10.49	0.10	-	0.00	-	8.54	8.60	2.00
Gulf Toadfish	1.75	7.28	0.00	-	0.00	-	6.91	6.18	-
Brown/ Pink Shrimp	0.75	1.62	1.75	8.85	0.15	-	2.03	3.38	9.94
Porcelain crabs	0.75	2.91	0.00	-	0.00	-	4.59	4.10	-
Arrow Shrimp	0.67	1.34	0.70	4.41	3.45	15.59	3.78	4.29	8.23
Spotfin Mojarra	0.58	-	0.00	-	0.45	1.95	2.39	3.10	5.54
Code Goby	0.42	2.76	1.10	2.06	0.00	-	4.19	3.75	6.43
Atlantic Mud Crab	0.42	1.35	0.00	-	0.00	-	3.14	2.81	-
Frillfin goby	0.42	1.20	0.00	-	0.00	-	2.72	2.43	-
White Shrimp	0.17	-	0.30	-	0.35	3.04	0.33	2.83	6.60
Pipefish	0.00	-	0.00	-	0.25	2.85	-	2.58	5.62

Affects of synergy on oyster reef habitat. A total of 5,201 organisms were collected during spring and fall 2008 from three oyster habitat types in East Flats: oyster reef within oyster reef complex (OO), oyster reef adjacent to seagrass (OSG), and oyster reef adjacent to marsh edge (OME); 16 fish species and 15 crustacean species were identified (Table 7). Nekton abundance (3,262) was greatest in the spring. Nektonic and benthic crustaceans were more abundant than fish regardless of season. Darter gobies and gulf toadfish were the two most abundant fish species collected in both seasons. Pinfish were collected primarily in the spring. Grass shrimp, mud crabs, brown and pink shrimp, snapping shrimp, and blue crabs were the most abundant crustaceans in both seasons.

An ANOVA was used to determine differences in the overall nekton density, fish density, and crustacean density among habitats. There were significant differences in the densities of nekton (fish+decapods) in both spring ($F=6.59$; $df=5,9$; $p = 0.017$) and fall ($F=6.63$; $df=5,6$; $p=0.030$). In both spring and fall there were no significant differences in overall nekton densities between oyster reef in OO and OSG (Fig. 9). In spring nekton densities on OME were significantly lower than densities in both OO and OSG habitats whereas in fall, there were only significant differences between densities in OO and OME. Differences in the densities of crustaceans appear to be driving the differences in the densities all nekton. Like total nekton, there were significant differences in the densities of crustaceans in spring ($F=5.75$; $df=5,9$; $p = 0.025$) and fall ($F= 5.51$; $df=5,6$; $p = 0.044$). Patterns of significant differences in crustacean densities among habitats were identical to those seen in total nekton (Fig. 10). There were no significant differences in fish densities among the three synergistic habitat types in the spring (F=2.56; df=5,9; p=0.132) or fall (F=1.36; df=5,6; p=0.325) (Fig. 11).

Community analysis revealed no differences in overall community structure among the three synergistic habitat relationships. The MDS ordination does not show a distinct separation between OO, OME, or OSG (Fig 12). The low densities of nekton collected from OME were not due to the absence of any particular species, but just overall lower abundance of fish and crustaceans. Grass shrimp, mud crabs, and gulf toadfish were less abundant in OME than in either OSG or OO. Gulf toadfish had a significantly lower abundance in OME in the fall (F=4.44; df=5,6; p = 0.049) and the highest abundance in OSG in fall. In spring gulf toadfish had similar densities across all synergy treatments. Also, mud crabs had significantly higher densities in OSG (F=8.07; df=5,6; p = 0.004) and OO, than in OME (Fig 13).

Table **7.** Overall mean densities (number m^{-2}) and standard error (SE, one standard error) of all fishes and crustaceans collected in three habitat types: oyster reef in oyster reef complex (OO), oyster reef in seagrass bed (OSG), and oyster reef in marsh edge(OME) in spring and fall 2008. Total numbers and relative abundances (number of individuals/total number of animals collected x 100) of each species and group are also given.

				OO		OSG		OME	
COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	MEAN	SE	MEAN	SE	MEAN	SE
SPRING 2008									
Total Fishes		477	15.68	33.00	(1.14)	36.00	(3.24)	26.40	(4.72)
Darter goby	*Gobionellus boleosoma*	327	10.75	20.80	(1.74)	24.00	(2.30)	20.60	(1.63)
Gulf toadfish	*Opsanus beta*	48	1.58	3.80	(1.16)	4.20	(2.06)	1.60	(0.51)
Pinfish	*Lagodon rhomboides*	39	1.28	2.80	(0.37)	3.00	(0.84)	2.00	(1.76)
Code goby	*Gobiosoma robustum*	28	0.92	2.00	(1.10)	2.20	(0.49)	1.40	(0.68)
Pigfish	*Orthopristis chrysoptera*	10	0.33	1.00	(0.63)	0.40	(0.24)	0.60	(0.60)
Silver perch	*Bairdiella chrysoura*	7	0.23	0.00	(0.00)	1.40	(1.40)	0.00	(0.00)
Mangrove snapper	*Lutjanus griseus*	4	0.13	0.80	(0.37)	0.00	(0.00)	0.00	(0.00)
Pipefish	*Syngnathus* sp.	4	0.13	0.40	(0.24)	0.40	(0.40)	0.00	(0.00)
Gobies (unknown)		3	0.10	0.40	(0.24)	0.00	(0.00)	0.20	(0.20)
Spotfin mojarra	*Eucinostomus argenteus*	2	0.07	0.40	(0.24)	0.00	(0.00)	0.00	(0.00)
Striped blenny	*Chasmodes bosquianus*	1	0.03	0.20	(0.20)	0.00	(0.00)	0.00	(0.00)
Naked goby	*Gobiosoma bosc*	1	0.03	0.00	(0.00)	0.20	(0.20)	0.00	(0.00)
Green goby	*Microgobius thalassinus*	1	0.03	0.00	(0.00)	0.20	(0.20)	0.00	(0.00)
Spotted seatrout	*Cynoscion nebulosus*	1	0.03	0.20	(0.20)	0.00	(0.00)	0.00	(0.00)
Blackwing searobin	*Prionotus rubio*	1	0.03	0.20	(0.20)	0.00	(0.00)	0.00	(0.00)
Total Crustaceans		2785	91.55	215.20	(44.32)	215.60	(53.42)	82.20	(18.53)
Grass shrimp	*Palaemonetes* spp.	1373	45.13	117.00	(39.11)	130.20	(46.85)	27.40	(10.09)

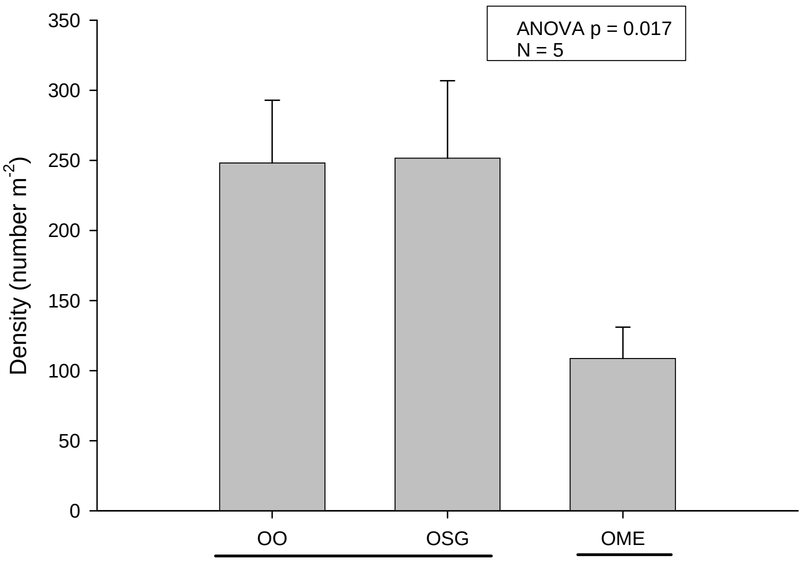
Table 7. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	OO		OSG		OME	
				MEAN	SE	MEAN	SE	MEAN	SE
Mud crabs	Panopeidae	933	30.67	78.40	(12.02)	69.40	(24.32)	38.80	(9.92)
Ridgeback mud crab	*Eurypanopeus turgidus*	92	3.02	8.80	(1.36)	5.20	(1.69)	4.40	(0.87)
Snapping shrimp	*Alpheus heterochaelis*	61	2.01	3.20	(0.80)	4.20	(1.32)	4.80	(1.53)
Brown / Pink shrimp	*Farfantepenaeus* spp.	39	1.28	3.40	(1.63)	2.80	(1.24)	1.60	(0.40)
Blue crab	*Callinectus sapidus*	31	1.02	2.00	(0.89)	2.20	(0.97)	2.00	(1.30)
Thinstripe hermit crab	*Clibanarius vittatus*	15	0.49	1.20	(0.37)	0.40	(0.40)	1.40	(0.98)
Penaeid shrimp		7	0.23	0.40	(0.24)	0.20	(0.20)	0.80	(0.80)
Atlantic mud crab	*Panopeus herbstii*	6	0.20	0.20	(0.20)	0.40	(0.24)	0.60	(0.40)
Hermit crab		3	0.10	0.60	(0.40)	0.00	(0.00)	0.00	(0.00)
Hermit crab (Left-handed)		2	0.07	0.00	(0.00)	0.40	(0.40)	0.00	(0.00)
Flatback mud crab	*Eurypanopeus depressus*	2	0.07	0.00	(0.00)	0.20	(0.20)	0.20	(0.20)
Dark shore crab	*Pachygrapsus gracilis*	1	0.03	0.00	(0.00)	0.00	(0.00)	0.20	(0.20)
FALL 2008									
Total Fishes		220	11.35	22.75	(4.31)	19.00	(6.26)	13.25	(3.71)
Darter goby	*Gobionellus boleosoma*	173	8.92	19.25	(4.33)	13.25	(4.55)	10.75	(4.03)
Gulf toadfish	*Opsanus beta*	21	1.08	1.25	(0.48)	3.25	(1.11)	0.75	(0.48)
Spotfin mojarra	*Eucinostomus argenteus*	7	0.36	1.00	(0.71)	0.75	(0.75)	0.00	(0.00)
Code goby	*Gobiosoma robustum*	5	0.26	0.25	(0.25)	0.50	(0.50)	0.50	(0.29)
Frillfin goby	*Bathygobius soporator*	5	0.26	0.50	(0.29)	0.75	(0.25)	0.00	(0.00)
Striped blenny	*Chasmodes bosquianus*	3	0.15	0.00	(0.00)	0.00	(0.00)	0.75	(0.48)
Mangrove snapper	*Lutjanus griseus*	3	0.15	0.25	(0.25)	0.25	(0.25)	0.25	(0.25)
Naked goby	*Gobiosoma bosc*	1	0.05	0.00	(0.00)	0.00	(0.00)	0.25	(0.25)

Table 7. (Continued)

				OO		OSG		OME	
COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	MEAN	SE	MEAN	SE	MEAN	SE
Pinfish	*Lagodon rhomboides*	1	0.05	0.25	(0.25)	0.00	(0.00)	0.00	(0.00)
Emerald sleeper	*Erotelis smaragdus*	1	0.05	0.00	(0.00)	0.25	(0.25)	0.00	(0.00)
Total Crustaceans		1719	88.65	169.75	(35.91)	185.25	(85.66)	74.75	(26.75)
Mud crabs	Panopeidae	656	33.83	64.75	(20.11)	70.00	(39.05)	29.25	(14.66)
Grass shrimp	*Palaemonetes* spp.	534	27.54	46.75	(6.98)	61.75	(27.57)	25.00	(15.06)
Blue crab	*Callinectus sapidus*	186	9.59	17.75	(9.26)	23.75	(14.98)	5.00	(2.16)
Ridgeback mud crab	*Eurypanopeus turgidus*	171	8.82	22.50	(5.61)	12.25	(0.85)	8.00	(1.96)
Snapping shrimp	*Alpheus heterochaelis*	77	3.97	8.75	(1.89)	5.75	(2.02)	4.75	(1.89)
Thinstripe hermit crab	*Clibanarius vittatus*	40	2.06	5.00	(4.36)	5.00	(3.44)	0.00	(0.00)
penaeid shrimp		10	0.52	0.00	(0.00)	2.50	(2.50)	0.00	(0.00)
Brown / Pink shrimp (grooved)	*Farfantepenaeus* spp.	9	0.46	1.00	(0.71)	0.50	(0.50)	0.75	(0.75)
Porcelain crab	*Petrolisthes* spp.	9	0.46	0.00	(0.00)	1.50	(0.65)	0.75	(0.48)
Arrow shrimp	*Tozeuma carolinense*	8	0.41	1.75	(0.85)	0.25	(0.25)	0.00	(0.00)
Atlantic mud crab	*Panopeus herbstii*	5	0.26	0.50	(0.29)	0.25	(0.25)	0.50	(0.50)
Hermit crab		3	0.15	0.00	(0.00)	0.75	(0.75)	0.00	(0.00)
Dark shore crab	*Pachygrapsus gracilis*	3	0.15	0.25	(0.25)	0.50	(0.50)	0.00	(0.00)
Green porcelain crab	*Petrolisthes armatus*	3	0.15	0.75	(0.48)	0.00	(0.00)	0.00	(0.00)
White shrimp	*Litopenaeus setiferus*	2	0.10	0.00	(0.00)	0.25	(0.25)	0.25	(0.25)
Flatback mud crab	*Eurypanopeus depressus*	2	0.10	0.00	(0.00)	0.00	(0.00)	0.50	(0.50)
Stone crab	*Menippe adina*	1	0.05	0.00	(0.00)	0.25	(0.25)	0.00	(0.00)

(A)



(B)

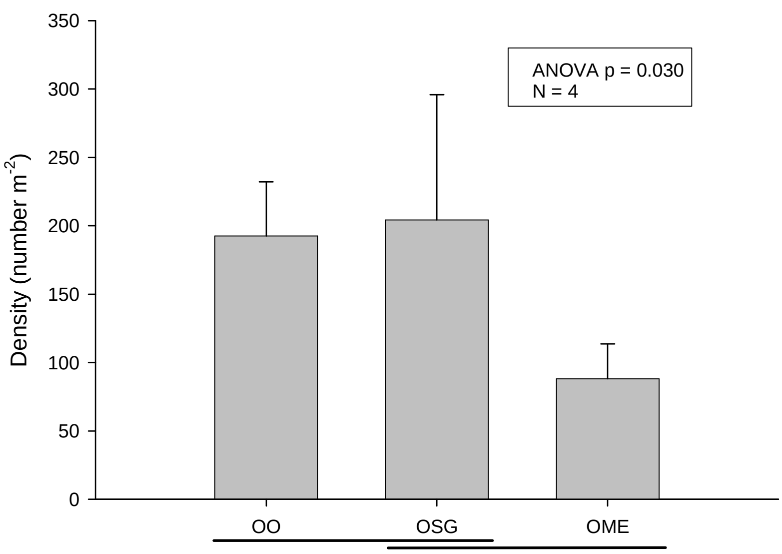
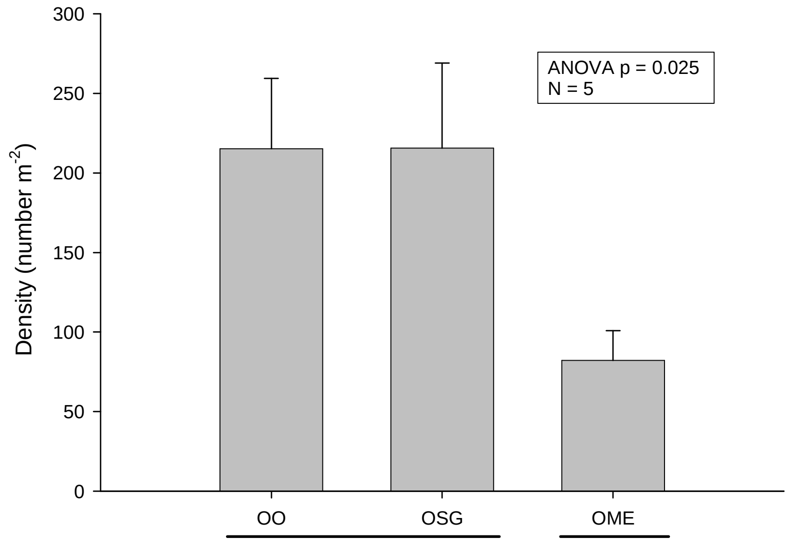


Fig. 9. Mean densities of nekton (fish + crustaceans) collected from oyster reefs in spring (A) and fall (B) 2008 with three different synergistic habitat relationships: OO= Oyster reef within oyster reef complex, OSG= Oyster reef by seagrass, and OME= Oyster reef by marsh edge.

(A)



(B)

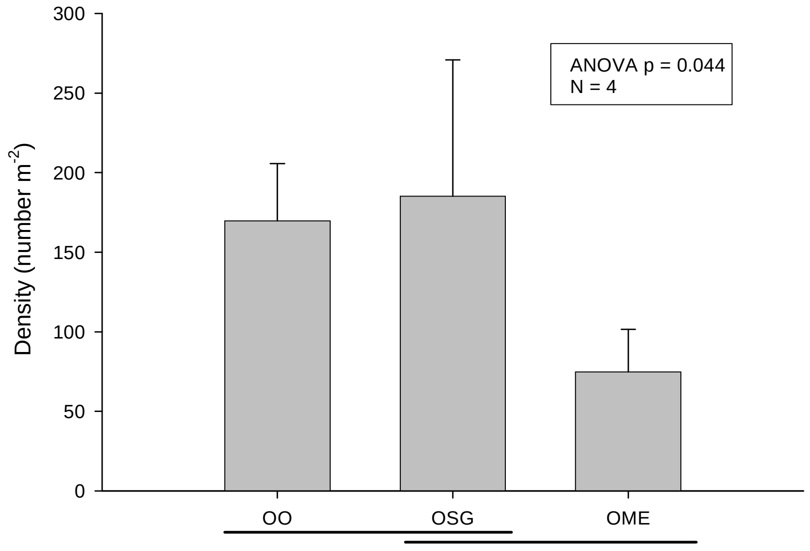
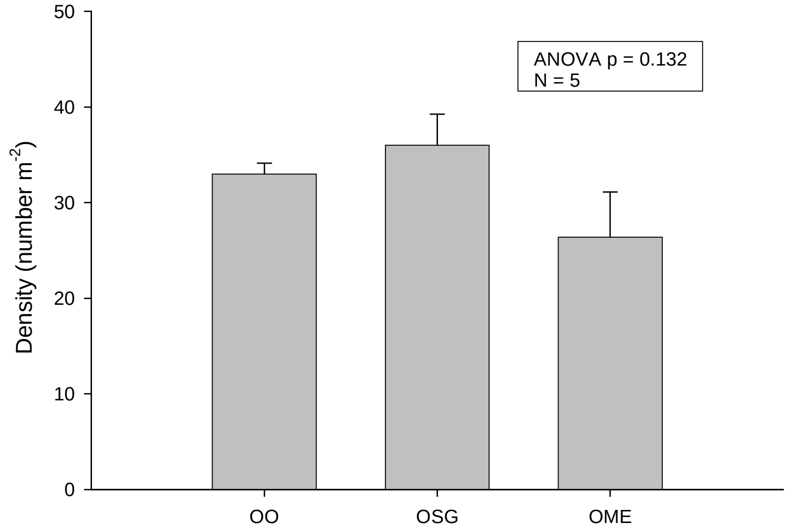


Fig. 10. Mean densities of crustaceans collected from oyster reefs in spring (A) and fall (B) 2008 with three different synergistic habitat relationships: OO= Oyster reef within oyster reef complex, OSG= Oyster reef by seagrass, and OME= Oyster reef by marsh edge.

(A)



(B)

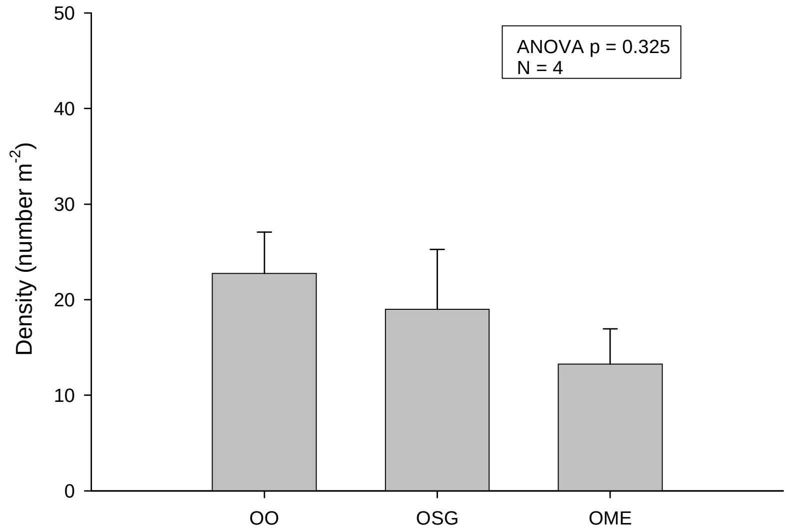
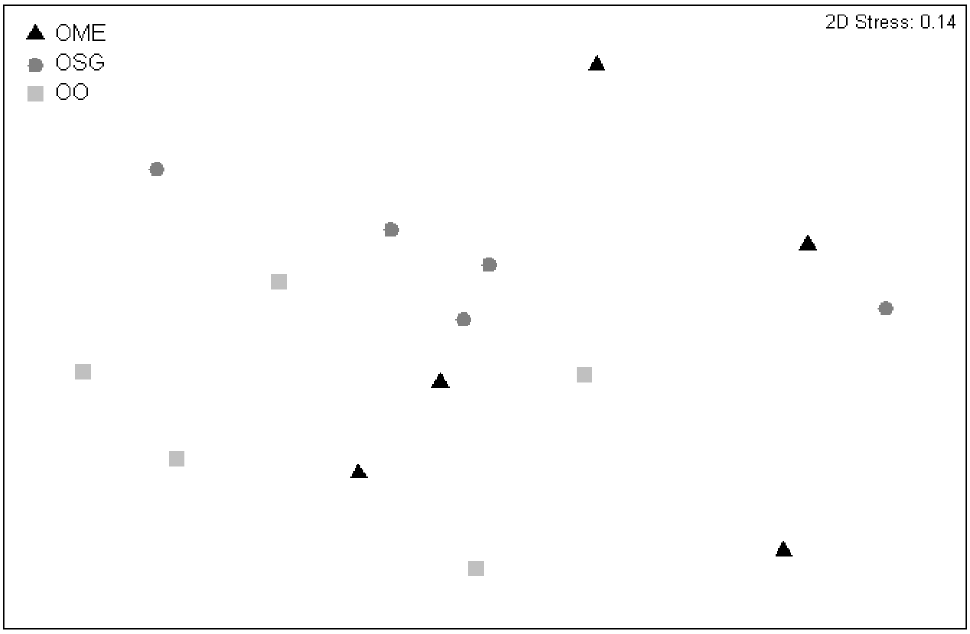


Fig. 11. Mean densities of fish collected from oyster reefs in spring (A) and fall (B) 2008 with three different synergistic habitat relationships: OO= Oyster reef within oyster reef complex, OSG= Oyster reef by seagrass, and OME= Oyster reef by marsh edge.

(A)



(B)

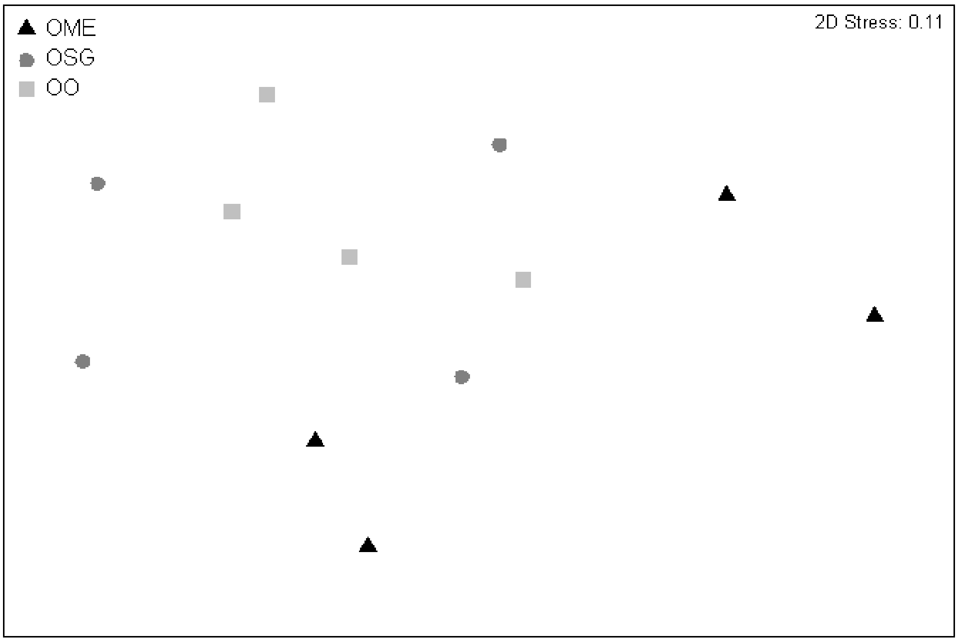
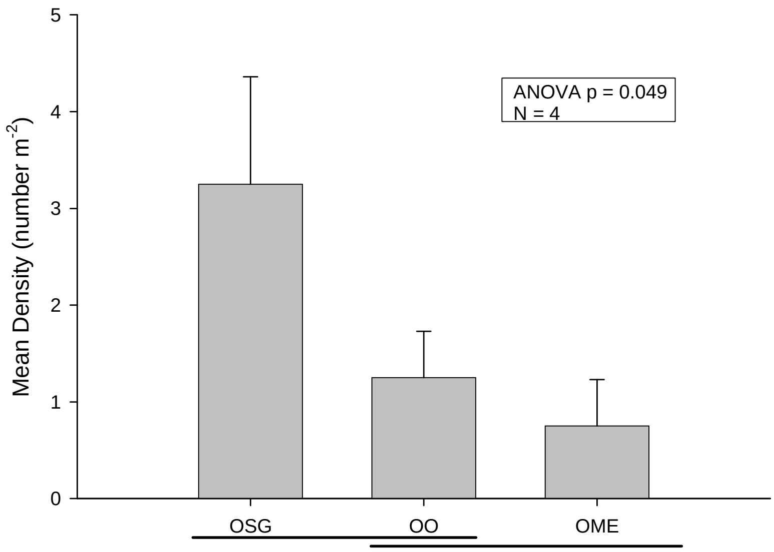


Fig. 12. MDS ordination for spring 2008 (A) and Fall 2008 (B) of mean density of nekton and benthic crustaceans from three different synergistic habitat relationships OO= Oyster reef within oyster reef complex, OSG= Oyster reef by seagrass, and OME= Oyster reef by marsh edge.

(A)



(B)

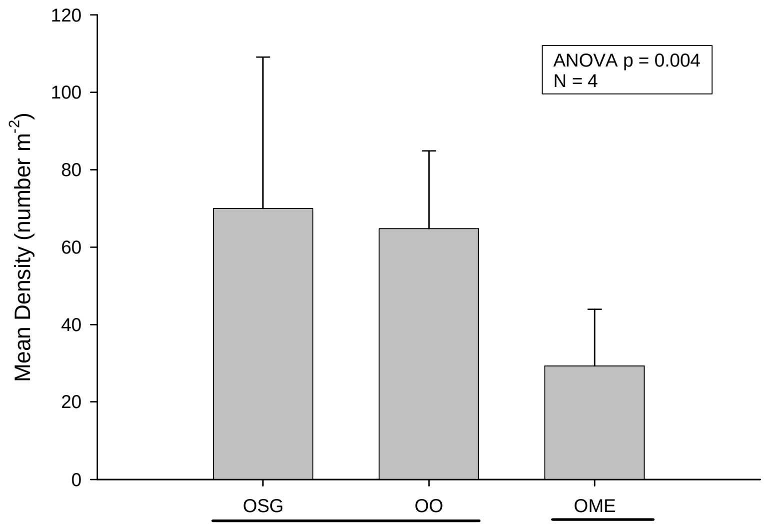


Fig. 13. Mean density of gulf toadfish (A) and mud crabs (B) in fall of 2008. Results are given from ANOVAs used to compare habitat types and three a priori contrast testing different synergistic habitat relationships: OO= Oyster reef within oyster reef complex, OSG= Oyster reef by seagrass, and OME= Oyster reef by marsh edge.

Predator Exclusion. A total of 18,068 organisms were collected during spring and fall of 2008 from three predator exclusion treatments in East Flats: oyster sampling unit (OSU), 2-sided control (2C), and a full enclosure (FE); 28 identified species of fish and 15 identified species of crustaceans were identified (Table 8). Nekton abundance (9,767) was greatest in spring, with 8,231 total crustaceans collected. The most abundant fishes in spring were darter gobies, pinfish, gulf toadfish, code gobies, pigfish, and silver perch. In fall darter gobies, spotfin mojarra (*Eucinostomus argenteus*), gulf toadfish, and frillfin goby (*Bathygobius soporator*) were the most abundant fishes. Mud crabs, specifically the ridgeback mud crab (*Eurypanopeus turgidus*), and snapping shrimp were the most abundant benthic crustaceans. Grass shrimp, brown and pink shrimp, and blue crabs were among the most abundant nektonic crustaceans collected in both spring and fall.

A two-factor ANOVA was used to determine differences in the overall density, fish density, and crustacean density among predator exclusion treatments. There were no significant differences in densities of nekton (fish+decapods) in spring ($F=0.72$; $df=5,39$; $p=0.491$). In fall there was a significant difference in nekton densities ($F=10.69$; $df=5,30$; $p < 0.001$). In fall the full enclosure (FE) had a significantly higher overall density (Fig 14). This pattern was driven primarily by the abundance of crustaceans. There were significant differences in the densities of crustaceans in fall ($F=11.00$;$df=5,30$; $p < 0.001$) but not in spring ($F=0.67$; $df= 5,39$; $p= 0.515$). In fall crustacean densities were greatest in FE (Fig. 15). Overall density of fish was greater in spring than in fall (Table 8), however, there was no significant difference among the treatments in either spring ($F=0.12$; $df=5,39$; $p=0.891$) or fall ($F=0.27$; $df=5,30$; $p=0.762$) (Fig 16).

Community analyses did not reveal any differences in overall community structure within predator exclusion treatments. The Bray-Curtis cluster analysis and MDS ordination show no distinct separation between the OSU, 2-sided control (2C), and the FE (Fig 17). However ANOVAs used to compare predator exclusion treatments with three a priori contrasts comparing each of the different treatment combinations revealed differences in densities of a few species in spring and fall (Table 9). In spring, pinfish densities were significantly higher in FE than in OSU. Gulf toadfish densities were significantly lower in FE than 2C during spring. In fall densities of grass shrimp and grooved shrimp were significantly higher in FE than OSU.

Table 8. Overall mean densities (number m^{-2}) and (SE, one standard error) of all collected fishes and crustaceans collected in three predator exclusion treatments in oyster reef: oyster sampling unit, 2-sided control; and a full enclosure in the spring and fall of 2008. Total numbers and relative abundances (number of individuals/total number of animals collected x 100) of each species and group are also given.

				Oyster Sampling Unit		2-Sided Control		Full Enclosure	
COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	MEAN	SE	MEAN	SE	MEAN	SE
SPRING 2008									
Total Fishes		1536	15.73	31.80	(2.10)	32.27	(2.79)	38.33	(4.86)
Darter goby	*Gobionellus boleosoma*	858	8.78	21.80	(1.10)	17.87	(2.34)	17.53	(3.72)
Pinfish	*Lagodon rhomboides*	241	2.47	2.60	(0.62)	4.20	(1.42)	9.27	(2.43)
Gulf toadfish	*Opsanus beta*	149	1.53	3.20	(0.81)	4.47	(0.66)	2.27	(0.51)
Code goby	*Gobiosoma robustum*	129	1.32	1.87	(0.43)	1.87	(0.53)	4.87	(2.37)
Pigfish	*Orthopristis chrysoptera*	76	0.78	0.67	(0.29)	1.93	(0.89)	2.47	(1.46)
Silver perch	*Bairdiella chrysoura*	27	0.28	0.47	(0.47)	0.33	(0.19)	1.00	(0.86)
Gobies (unknown)		18	0.18	0.20	(0.11)	0.93	(0.36)	0.07	(0.07)
Spotfin mojarra	*Eucinostomus argenteus*	6	0.06	0.13	(0.09)	0.13	(0.09)	0.13	(0.13)
Pipefish	*Syngnathus* spp.	6	0.06	0.27	(0.15)	0.13	(0.09)	0.00	(0.00)
Mangrove snapper	*Lutjanus griseus*	5	0.05	0.27	(0.15)	0.07	(0.07)	0.00	(0.00)
Naked goby	*Gobiosoma bosc*	4	0.04	0.07	(0.07)	0.07	(0.07)	0.13	(0.09)
Gulf killifish	*Fundulus grandis*	4	0.04	0.00	(0.00)	0.07	(0.07)	0.20	(0.14)
Gulf menhaden	*Brevoortia patronus*	2	0.02	0.00	(0.00)	0.07	(0.07)	0.07	(0.07)
Bathygobius spp.	*Bathygobius* spp.	2	0.02	0.00	(0.00)	0.00	(0.00)	0.13	(0.09)
Atlantic needlefish	*Strongylura marina*	1	0.01	0.00	(0.00)	0.07	(0.07)	0.00	(0.00)
Striped blenny	*Chasmodes bosquianus*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Feather blenny	*Hypsoblennius hentz*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.07	(0.07)
Skilletfish	*Gobiesox strumosus*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.07	(0.07)
Green goby	*Microgobius thalassinus*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)

Table 8. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	Oyster Sampling Unit MEAN	Oyster Sampling Unit SE	2-Sided Control MEAN	2-Sided Control SE	Full Enclosure MEAN	Full Enclosure SE
Spotted seatrout	*Cynoscion nebulosus*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Sheepshead	*Archosargus probatocephalus*	1	0.01	0.00	(0.00)	0.07	(0.07)	0.00	(0.00)
Blackwing searobin	*Prionotus rubio*	1	0.01	0.07	(0.07)	0.00	(0.00)	0.00	(0.00)
Shrimp eel	*Ophichthus gomesii*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.07	(0.07)
Total Crustaceans		8231	84.27	171.00	(27.81)	198.93	(28.64)	178.80	(29.27)
Grass shrimp	*Palaemonetes* spp.	4852	49.68	91.53	(22.66)	121.20	(24.69)	110.73	(25.34)
Mud crabs	Panopeidae	2528	25.88	62.20	(10.00)	58.53	(8.95)	47.80	(10.47)
Ridgeback mud crab	*Eurypanopeus turgidus*	284	2.91	6.13	(0.88)	6.13	(0.98)	6.67	(1.23)
Brown / Pink shrimp	*Farfantepenaeus* spp.	193	1.98	2.60	(0.67)	5.53	(1.12)	4.73	(0.85)
Snapping shrimp	*Alpheus heterochaelis*	174	1.78	4.07	(0.69)	3.93	(0.73)	3.60	(0.84)
Thinstripe hermit crab	*Clibanarius vittatus*	81	0.83	1.00	(0.37)	1.93	(0.45)	2.47	(0.75)
Blue crab	*Callinectus sapidus*	65	0.67	2.07	(0.57)	1.00	(0.43)	1.27	(0.33)
Atlantic mud crab	*Panopeus herbstii*	16	0.16	0.40	(0.16)	0.33	(0.13)	0.33	(0.21)
Arrow shrimp	*Tozeuma carolinense*	8	0.08	0.00	(0.00)	0.07	(0.07)	0.47	(0.40)
penaeid shrimp		8	0.08	0.47	(0.27)	0.00	(0.00)	0.07	(0.07)
Hermit crab		8	0.08	0.20	(0.14)	0.00	(0.00)	0.33	(0.27)
Dark shore crab	*Pachygrapsus gracilis*	7	0.07	0.07	(0.07)	0.13	(0.09)	0.27	(0.18)
Hermit crab (left-handed)		4	0.04	0.13	(0.13)	0.07	(0.07)	0.07	(0.07)
Flatback mud crab	*Eurypanopeus depressus*	2	0.02	0.13	(0.09)	0.00	(0.00)	0.00	(0.00)
Stone crab	*Menippe adina*	1	0.01	0.00	(0.00)	0.07	(0.07)	0.00	(0.00)
FALL 2008									
Total Fishes		688	8.29	18.33	(2.81)	20.08	(2.47)	18.92	(2.39)
Darter goby	*Gobionellus boleosoma*	500	6.02	14.42	(2.49)	14.83	(2.13)	12.42	(2.45)
Spotfin mojarra	*Eucinostomus argenteus*	62	0.75	0.58	(0.34)	1.75	(0.81)	2.83	(1.21)

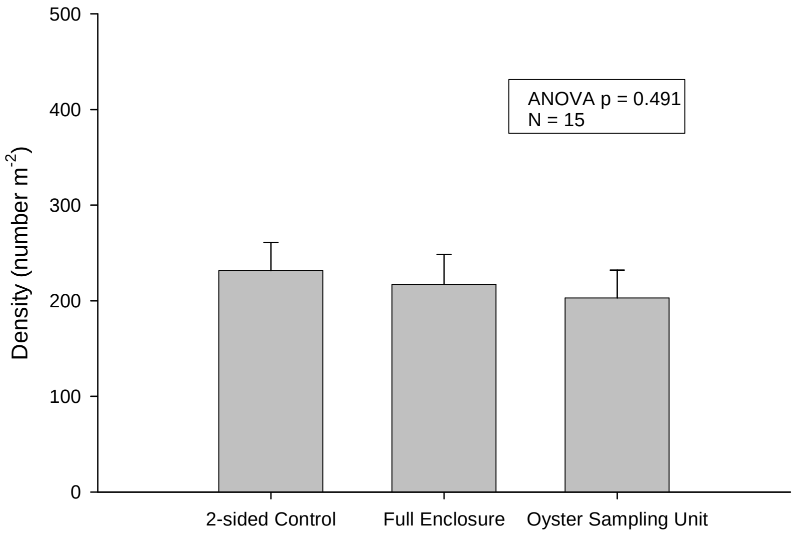
Table 8. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	Oyster Sampling Unit		2-Sided Control		Full Enclosure	
				MEAN	SE	MEAN	SE	MEAN	SE
Gulf toadfish	*Opsanus beta*	56	0.67	1.75	(0.51)	2.00	(0.49)	0.92	(0.34)
Frillfin goby	*Bathygobius soporator*	30	0.36	0.42	(0.15)	1.08	(0.31)	1.00	(0.35)
Code goby	*Gobiosoma robustum*	14	0.17	0.42	(0.19)	0.33	(0.19)	0.42	(0.29)
Pinfish	*Lagodon rhomboides*	7	0.08	0.08	(0.08)	0.00	(0.00)	0.50	(0.19)
Mangrove snapper	*Lutjanus griseus*	5	0.06	0.25	(0.13)	0.00	(0.00)	0.17	(0.17)
Striped blenny	*Chasmodes bosquianus*	3	0.04	0.25	(0.18)	0.00	(0.00)	0.00	(0.00)
Green goby	*Microgobius thalassinus*	2	0.02	0.00	(0.00)	0.00	(0.00)	0.17	(0.17)
Red drum	*Sciaenops occelatus*	2	0.02	0.00	(0.00)	0.00	(0.00)	0.17	(0.17)
Emerald sleeper	*Erotelis smaragdus*	2	0.02	0.08	(0.08)	0.00	(0.00)	0.08	(0.08)
Blackcheek tonguefish	*Symphurus plagiusa*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.08	(0.08)
Naked goby	*Gobiosoma bosc*	1	0.01	0.08	(0.08)	0.00	(0.00)	0.00	(0.00)
Bay whiff	*Citharichthys spilopterus*	1	0.01	0.00	(0.00)	0.08	(0.08)	0.00	(0.00)
Barbfish	*Scorpaena brasiliensis*	1	0.01	0.00	(0.00)	0.00	(0.00)	0.08	(0.08)
Pipefish	*Syngnathus* spp.	1	0.01	0.00	(0.00)	0.00	(0.00)	0.08	(0.08)
Total Crustaceans		7613	91.71	143.25	(32.65)	178.00	(25.33)	313.17	(54.91)
Grass shrimp	*Palaemonetes* spp.	3588	43.22	44.50	(10.72)	43.17	(9.29)	211.33	(50.55)
Mud crabs	Panopeidae	2185	26.32	54.67	(14.99)	74.17	(14.97)	53.25	(8.99)
Ridgeback mud crab	*Eurypanopeus turgidus*	617	7.43	14.25	(2.58)	20.92	(4.38)	16.25	(2.00)
Blue crab	*Callinectus sapidus*	575	6.93	15.50	(5.85)	21.00	(3.59)	11.42	(2.98)
Snapping shrimp	*Alpheus heterochaelis*	303	3.65	6.42	(1.13)	10.00	(1.28)	8.83	(1.16)
Thinstripe hermit crab	*Clibanarius vittatus*	148	1.78	3.33	(1.82)	3.83	(1.54)	5.17	(1.68)
Brown / Pink shrimp	*Farfantepenaeus* spp.	68	0.82	0.75	(0.35)	1.83	(0.51)	3.08	(0.62)
Arrow shrimp	*Tozeuma carolinense*	34	0.41	0.67	(0.36)	0.92	(0.51)	1.25	(0.99)
Hermit crab		18	0.22	0.25	(0.25)	0.67	(0.67)	0.58	(0.42)
Atlantic mud crab	*Panopeus herbstii*	17	0.20	0.42	(0.19)	0.67	(0.36)	0.33	(0.14)
Penaeid shrimp		16	0.19	0.83	(0.83)	0.00	(0.00)	0.50	(0.29)
Green porcelain crab	*Petrolisthes armatus*	14	0.17	0.25	(0.18)	0.33	(0.26)	0.58	(0.29)
Dark shore crab	*Pachygrapsus gracilis*	12	0.14	0.25	(0.18)	0.33	(0.19)	0.42	(0.19)

Table 8. (Continued)

COMMON NAME	SCIENTIFIC NAME	TOTAL NUMBER	RELATIVE ABUNDANCE (%)	Oyster Sampling Unit		2-Sided Control		Full Enclosure	
				MEAN	SE	MEAN	SE	MEAN	SE
Porcelain crab	*Petrolisthes* spp.	10	0.12	0.75	(0.30)	0.00	(0.00)	0.08	(0.08)
White Shrimp	*Litopenaeus setiferus*	3	0.04	0.17	(0.11)	0.00	(0.00)	0.08	(0.08)
Stone crab	*Menippe adina*	3	0.04	0.08	(0.08)	0.17	(0.11)	0.00	(0.00)
Flatback mud crab	*Eurypanopeus depressus*	2	0.02	0.17	(0.17)	0.00	(0.00)	0.00	(0.00)

(A)



(B)

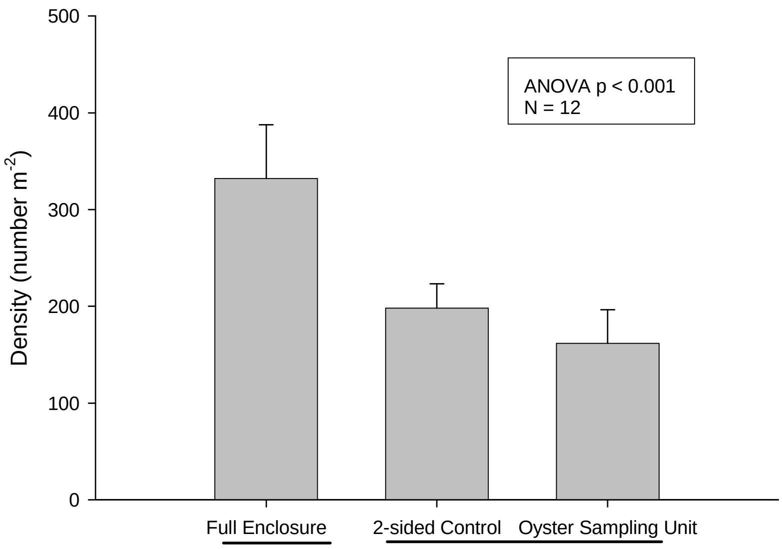
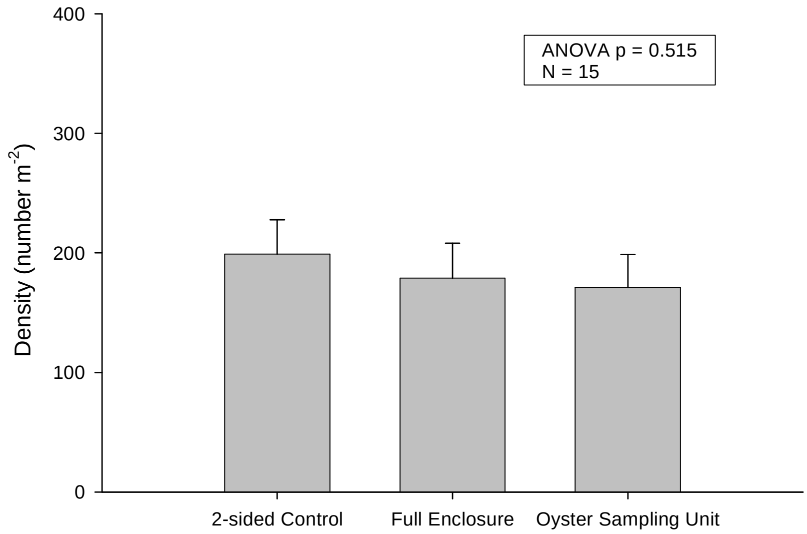


Fig. 14. Mean densities of nekton (fish+crustaceans) collected from oyster reefs in spring (A) and fall (B) with three experimental predator exclusion treatments: oyster sampling unit, 2-sided control, and fully enclosed predator exclusion.

(A)



(B)

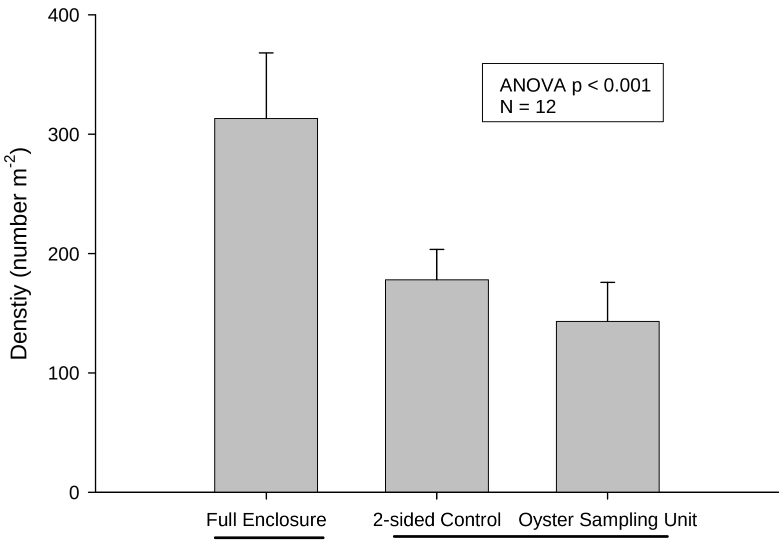
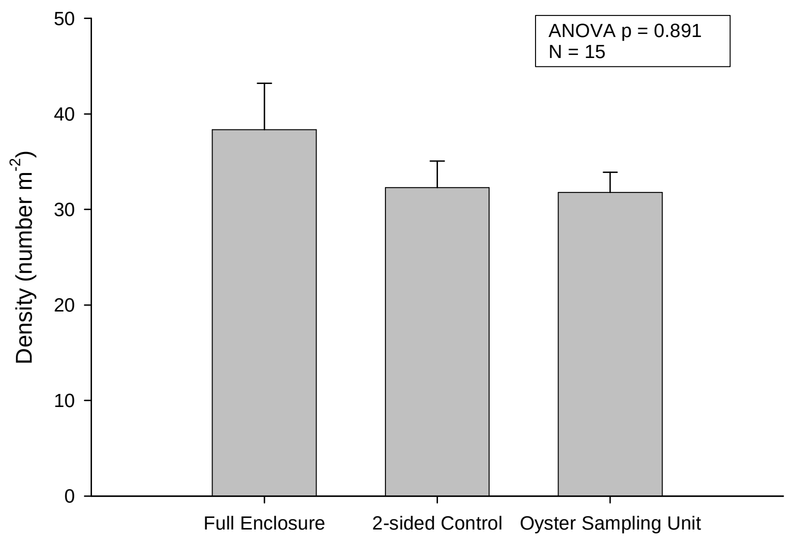


Fig. 15. Mean densities of crustaceans collected from oyster reefs in spring (A) and fall (B) with three experimental predator exclusion treatments: oyster sampling unit, 2-sided control, and fully enclosed predator exclusion.

(A)



(B)

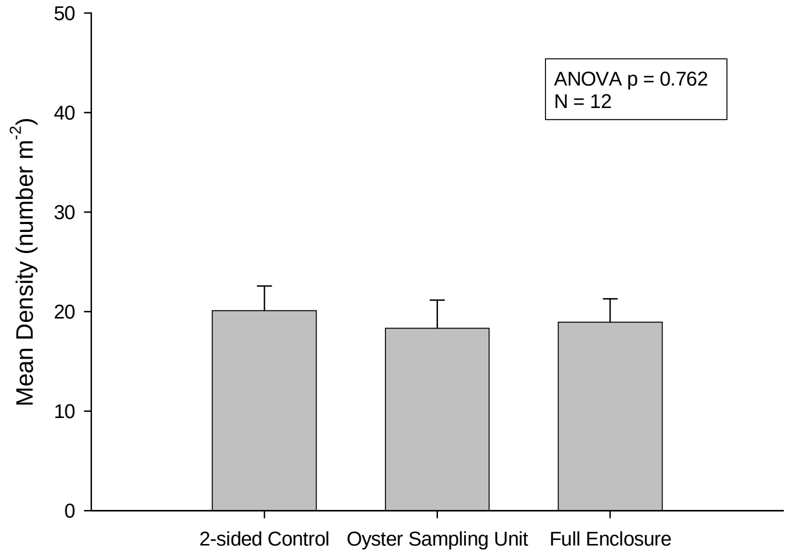
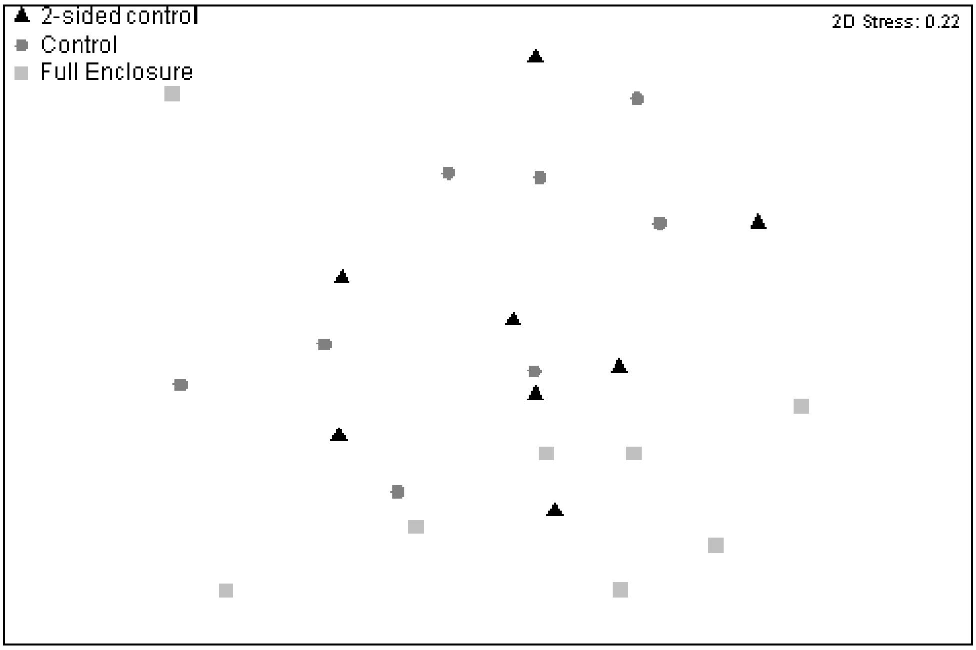


Fig. 16. Mean densities fish collected from oyster reefs in spring (A) and fall (B) with three experimental predator exclusion treatments: oyster sampling unit, 2-sided control, and fully enclosed predator exclusion.

(A)



(B)

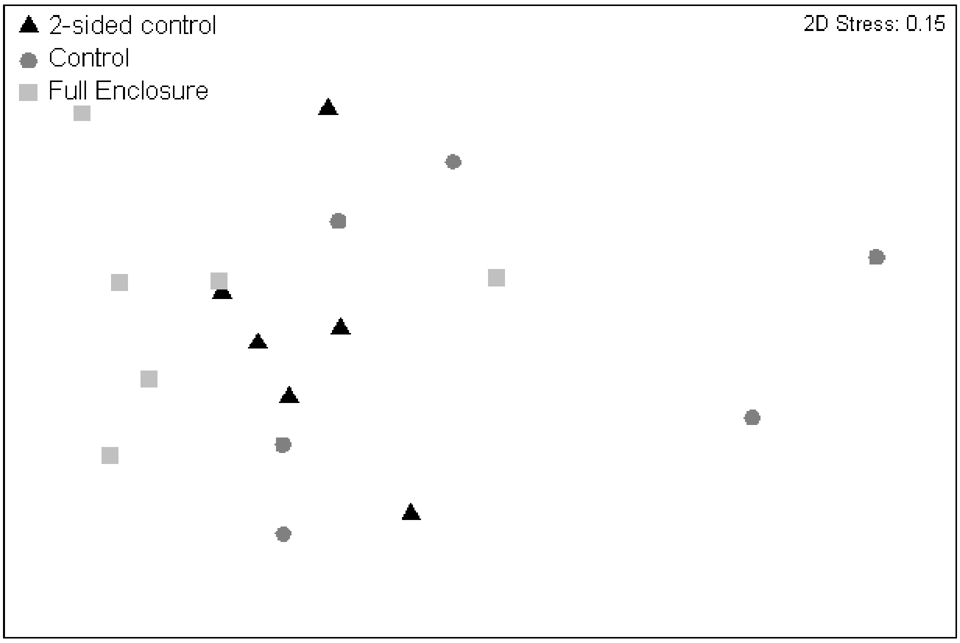


Fig. 17. MDS ordination for spring 2008 (A) and fall 2008 (B) of nekton and benthic crustaceans from the three predator exclusion treatments in oyster reef: oyster sampling unit, 2-sided control, and full enclosure. Mean densities of organisms collected from East Flats 1 and East Flats 2 were used. Data were fourth-root transformed.

Table 9. Mean densities as number m^{-2} and (SE, one standard error) of abundant fishes and crustaceans collected among three predator exclusion treatments, including an oyster sampling unit (OSU), 2-sided control (2C), and a full enclosure(FE) during the spring and fall of 2008. Refer to Table 1 for sample size of each mean. Results (p-values) are given from ANOVAs used to compare habitat types (HABITAT EFFECT) and three a priori contrast testing different habitat combinations.

		Oyster Sampling Unit		2-sided Control		Full Enclosure				Contrast p values		
COMMON NAME	SCIENTIFIC NAME	MEAN	SE	MEAN	SE	MEAN	SE	TOTAL NUMBER COLLECTED	HABITAT EFFECT p value	OSU vs 2C	OSU vs FE	FE vs 2C
SPRING 2008												
Fishes												
Pinfish	*Lagodon rhomboides*	2.60	(0.62)	4.20	(1.42)	9.27	(2.43)	241	0.037	0.484	0.014	0.068
Gulf toadfish	*Opsanus beta*	3.20	(0.81)	4.47	(0.66)	2.27	(0.51)	149	0.049	0.125	0.575	0.039
FALL 2008												
Crustaceans												
Grass shrimp	*Palaemonetes* spp.	44.50	(10.72)	43.17	(9.29)	211.33	(50.55)	3588	0.001	0.691	< 0.001	0.003
Blue crab	*Callinectus sapidus*	15.50	(5.85)	21.00	(3.59)	11.42	(2.98)	575	0.036	0.036	0.823	0.021
Brown / Pink shrimp	*Farfantepenaeus* spp.	0.75	(0.35)	1.83	(0.51)	3.08	(0.62)	68	0.014	0.075	0.001	0.088

Oyster reef complexity. Selection patterns of red drum and brown shrimp were analyzed using a Student's paired t-test. Red drum and brown shrimp did not exhibit a strong preference for complex oyster reefs. Brown shrimp chose low complexity over bare sand bottom significantly more often ($p = 0.044$) and medium complexity significantly more than low complexity ($p = 0.005$). One notable brown shrimp behavior was the tendency to bury themselves in the sand, even in the more complex habitats. Red drum generally did not exhibit strong preferences for any complexity treatment. When a preference was exhibited, it was for lower complexity treatments (Figs. 18 and 19). They selected for bare sand ($p < 0.001$) and medium ($p < 0.01$) complexity treatments significantly more often than the high complexity treatment.

The presence of a predator (pinfish) altered the selection pattern of red drum. Prior to the addition of pinfish, red drum strongly selected no complexity over medium complexity ($p< 0.001$) and medium complexity over high complexity ($p=0.002$). However, after pinfish were introduced they tended to select for more structured, complex oyster reefs (Fig. 20). When a tethered pinfish was present they selected low over no complexity ($p = 0.022$), high over low complexity ($p = 0.008$), and high over medium complexity ($p < 0.001$).

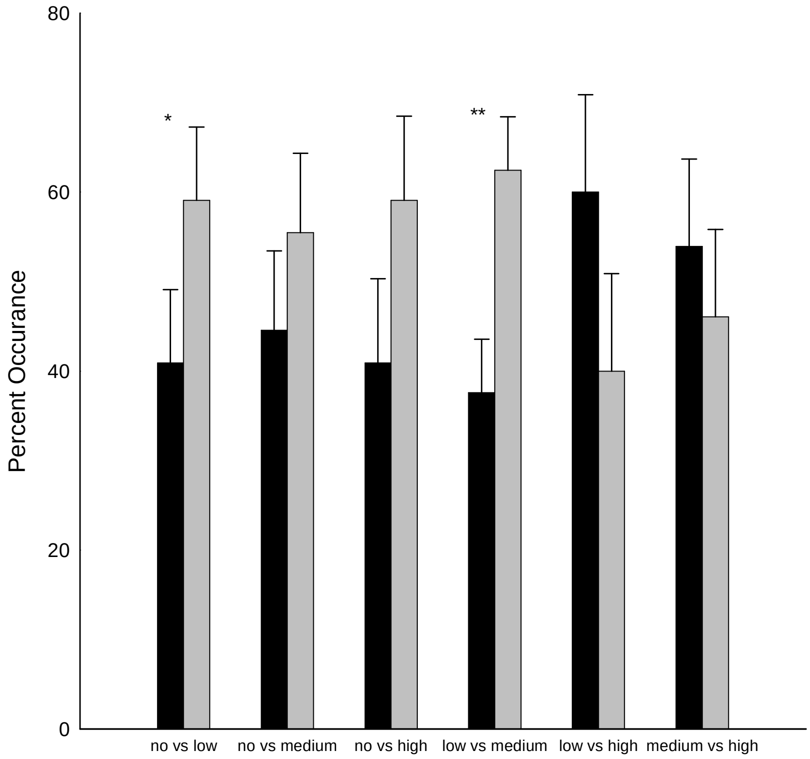


Fig. 18. Mean percentages of occurrence (± SE) of brown shrimp in each oyster reef complexity level for all possible comparisons. Each comparison represents 10 replicate mesocosms. Significant results from a paired Student's t-tests are indicated by * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

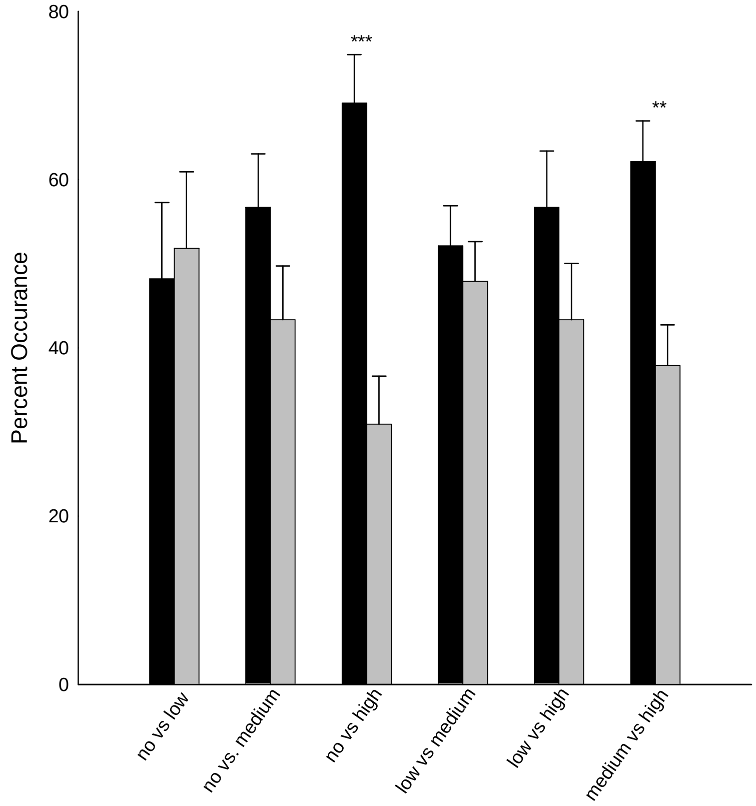


Fig. 19. Mean percent occurrence (± SE) of red drum in each oyster reef complexity level for all possible comparisons. Each comparison represents 10 replicate mesocosms. Significant results from a paired Student's t-tests are indicated by * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

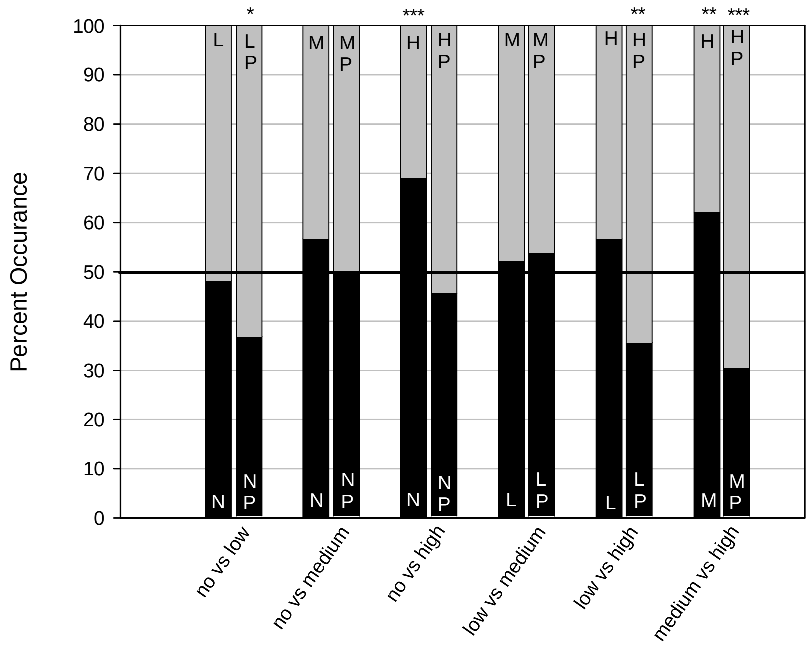


Fig. 20. Effects of a pinfish predator on habitat selection by red drum. Mean percentages of occurrence are indicated for each habitat complexity treatment comparison. Complexity designations are N= no complexity, L= low complexity, M = medium complexity, and H = high complexity. The first bar in each pair represents the selection pattern without predators; the presence of a predator is indicated by a 'P' on the bar. Each comparison represents 10 replicate mesocosms. Significant results from a Student's t-tests are indicated by *= $p < 0.05$, ** = $p < 0.01$, and ***= $p < 0.001$.

DISCUSSION

The objectives of this project were to characterize the macrofaunal community of intertidal oyster reefs, examine the effects of synergy among habitat types on nekton diversity and abundance, evaluate the role of predation on recruitment, and assess effects of oyster reef structural complexity on the habitat selection by brown shrimp and red drum. I found strong evidence that intertidal oyster reef supports not only significantly higher densities of nekton, but also that community structure was different than either seagrass or marsh edge habitats. Synergy among oyster reef, seagrass, and marsh edge may not contribute to differences in community structure. There was strong evidence that it does play a role in the number of organisms living within these areas, as oyster reef adjacent to marsh edge supported significantly lower densities of fish and crustaceans. The results of this study show that depending on season, predation may influence abundance of crustaceans using oyster reefs. These data also indicate that complexity of oyster reefs is important in habitat selection by juvenile red drum, especially in the presence of a predator. Overall, I found prominent differences in nekton density and community structure on oyster reefs compared to surrounding habitats, which may be affected by predation and habitat structure.

Oyster reef habitat nekton. Oyster reefs are recognized for supporting high densities of resident polychaetes, mollusks, and crustaceans (Wells 1961, Grabowski et al. 2005, Boudreaux et al. 2006). In this study, oyster reef sampling yielded 29 species in 18 families, including16 fish and 13 decapod species. Macrofaunal densities and species richness were both greater in oyster reef samples than in either seagrass and marsh edge samples regardless of season.

Densities of crustaceans were greater than densities of fish in all three habitats in both seasons. Crustacean densities are often higher than densities of other taxa on oyster reefs (Zimmerman et al. 1989; Micheli & Peterson 1999; Minello 1999; Meyer & Townsend 2005; Tolley & Volety 2005, Stunz et al. in review). Grass shrimp were the most abundant nektonic crustacean collected from all habitats. Mud crabs, including the ridgeback mud crab (*Eurypanopeus turgidus*), Atlantic mud crab (*Panopeus herbstii*), and the flatback mud crab (*Eurypanopeus depressus*), were the most abundant benthic crustaceans collected in oyster reef habitats. In Minello's (1999) study, Atlantic mud crabs were the second most abundant crustacean on oyster reefs. Atlantic mud crabs feed extensively on oysters (Tolley & Volety 2005), however, in this study 11 Atlantic mud crabs were collected. The most abundant mud crab was the ridgeback mud crab, for which there is very limited information. Few studies of oyster reef communities have identified the ridgeback mud crab as a common resident but many studies group all mud crabs into a single category (Shubart et al. 2000). Stunz et al. (in review) collected ridgeback mud crabs from both oyster reef and shallow non-vegetated bottom in West Galveston Bay, but their abundance was low. Mud crabs play an important role in shaping benthic communities of shallow estuarine habitats since clams, oysters, and barnacles are among their main prey items (Shubart et al. 2000; Grabowski 2004; Tolley & Volety 2005).

Other crustaceans collected in relatively high abundance include blue crabs and brown and pink shrimp. These species were very abundant in collections regardless of season. In spring most were collected from seagrass. In fall, blue crabs were found primarily in oyster reef and seagrass. Although densities of blue crabs were high, they were generally small (< 25 mm) suggesting blue crabs may be using oyster reef and seagrass as nurseries. Most studies suggest that submerged aquatic vegetation is the primary location where juvenile blue crabs settle (Epifanio 2007). However, data collected in this study show that densities of juvenile blue crabs on oyster reefs in the fall were similar to densities in seagrass habitats. Although previous studies have noted juvenile blue crabs in oyster reefs, their abundances have been relatively low (see Coen et al. 1999; Lehnert & Allen 2002). The importance of oyster reef habitat for blue crabs, although recognized, is not fully understood (Hines 2007). The high abundance of blue crabs found in oyster reef in this study may demonstrate the importance of both seagrass and oyster reef habitats for juvenile blue crabs. Densities of brown and pink shrimp were higher in the spring than in the fall and were most common in marsh edge in the spring and seagrass in the fall. This supports previous observations on the importance of vegetated habitat for these decapods (Kneib 1984, Baltz et al. 1993, Minello 1999, Stunz et al. in review).

Twenty-eight species of fish were collected from all three habitats. Darter gobies (*Gobionellus boleosoma*) were the most abundant fish in spring and fall. Some gobies use oyster shell as a spawning substrate and many resident fish will feed on commensal invertebrates (Tolley & Volety 2005). Other important species that were found in high densities included gulf toadfish, pinfish, bay anchovy and code goby. Gulf toadfish play an important role in structuring oyster reef communities because they primarily feed on mud crabs (Grabowski 2004; Grawboski & Kimbro 2005). Some fish species were collected primarily from oyster reef, but their densities were low: mangrove snapper (*Lutjanus griseus*), silver perch (*Bairdiella chrysoura*), and spotfin mojarra (*Eucinostomus argenteus*). Since diets of many juvenile fish are comprised primarily of polychaetes, bivalves, and decapod crustaceans (Grabowski 2002), the density patterns of crustaceans found in this study further supports the importance of oyster reef habitat in estuarine ecosystems, since decapods had significantly lower abundances in adjacent seagrass and marsh edge habitats.

Differences in community structure among seagrass, marsh edge, and oyster reef were found using community analyses. The oyster reef macrofaunal assemblage was notably different in both spring and fall, whereas macrofaunal community composition of seagrass and marsh edge habitats were similar. Mud crabs, mainly ridgeback mud crab, snapping shrimp, and gulf toadfish were collected mainly from oyster reef habitats and contributed most to community differences among oyster reef, seagrass, and marsh edge. Both the Bray-Curtis cluster analysis and the MDS ordination clearly show that oyster reefs are structured differently than either seagrass or marsh edge habitat types.

This study has focused solely on fish and crustaceans associated with oyster reefs, which are often not fully accounted for due to the difficulty of sampling in these areas. There are many other species that depend on oyster reefs that were not accounted for in this study such as other bivalves, polychaetes, and gastropods. Oyster reefs support a very diverse assemblage of species as shown in this study and many others (see Wells 1961; Boudreaux et al. 2006; Zimmerman et al. 1989; Meyer & Townsend 2000; among others). Wells (1961) identified 303 species in areas with *C. virginica* and referenced several other studies that catalogued upwards of 100 species. Other species that have been collected include various polychaetes, mollusks, decapods, anemones, and sponges to name a few (Wells 1961, Zimmerman et al. 1989, Minello 1999, Boudreaux et al. 2006, Rodney & Paynter 2006). The importance of the complex architecture of oyster reefs for several species can be recognized and should be studied further in order to fully understand the role that this habitat plays in estuarine ecosystems.

Affects of synergy on oyster reef habitat nekton. Another important factor that may affect nekton density and community composition of oyster reefs is spatial proximity of the reef to other estuarine habitats. The spatial relationship of habitats is important in determining densities of organisms and community composition in any given habitat (see

Irlandi & Crawford 1997, Micheli & Peterson 1999, Grabowski et al. 2005, Saintilan et al. 2007). Within estuaries many habitat types are often in close proximity to one another. In Caribbean systems, higher densities of fish used seagrass beds when they were adjacent to mangroves even though mangroves did not supply a large amount of plant material to their diets (Saintilan et al. 2007). The results of this study showed that when habitats were adjacent to one another they shared a common assemblage, but the relative density of nekton varied.

In this study, nekton densities were significantly greater on oyster reef in oyster reef complex and on oyster reef by seagrass than in areas adjacent to marsh edge. The pattern described by Micheli and Peterson (1998) was similar; oyster reefs that were spatially isolated from marsh by either non-vegetated bottom or seagrass supported greater densities of macroinvertebrates than areas near saltmarsh habitats. Densities of darter gobies, code gobies, gulf toadfish, and pinfish in this study were within each spatial arrangement of habitat types, with the exception of spring gulf toadfish densities, which were lower in oyster reef by marsh edge than in oyster reef adjacent to seagrass.

The patterns seen in this study were primarily driven by the density of crustaceans. The differences seen in overall nekton abundance were driven primarily by the presence of grass shrimp, blue crabs, and mud crabs in oyster reef in oyster reef complex and oyster reef by seagrass. Although grass shrimp densities were not significantly different among habitats, fewer were collected from oyster reef by marsh edge than other habitat types. Grass shrimp spring densities in marsh edge were similar to those found on oyster reef in oyster reef complex suggesting that grass shrimp were using both habitats; however, when oyster reef and marsh edge are in close proximity, marsh edge may be a more suitable habitat. The highest densities of blue crabs were collected in oyster reef in oyster reef complex and oyster reef by seagrass. These juvenile blue crabs may be using these more structurally complex areas as a refuge and foraging ground. However, since submerged aquatic vegetation is thought to be the primary location for settlement of blue crabs (Epifanio 2007) this pattern may be a result of the spatial proximity of these two habitat types. Further study is needed to fully understand the habitat selection patterns of juvenile blue crabs.

In previous studies, higher densities of nekton were typically found in habitats adjacent to marsh edge (Zimmerman et al. 1989, Minello 1999, Stunz et al. 2002). Irlandi and Crawford (1997) found that pinfish were more abundant in seagrass which was in close proximity to marsh than in areas adjacent to non-vegetated bottom. In addition, brown shrimp and pinfish were found in higher densities near marsh edge than in shallow non-vegetated bottom that was far from marsh edge (Stunz et al. in review). In this study, however, this same pattern was not observed. My results indicate that oyster reefs play a more important habitat role, primarily for crustaceans, when they are further from marsh edge and either isolated or adjacent to seagrass habitats.

Predator exclusion and oyster reef complexity. Habitat complexity can create refuges for organisms in lower trophic levels by reducing the ability of predators to find and access them (Leber 1985, Laegdsgaard & Johnson 2001, Werner & Peacor 2003, Grabowski & Kimbro 2005, Hughes & Grabowski 2006). Risk of predation is elevated in low complexity bottoms that are surrounded by more structured habitats (Micheli & Peterson 1999). Increased vertical habitat structure may increase prey survival and reduce foraging success of higher-order consumers, thereby increasing survival of intermediate predators (Grabowski & Powers 2004). Mud crabs will leave their normal foraging area on top of the oyster reefs to seek refuge within the reefs in the presence of the oyster toadfish (*Opsanus tau*), thereby increasing the survival of juvenile bivalves (Grabowski 2004; Grobowski & Kimbro 2005). The foraging efficiency of predators is inversely related with habitat structural heterogeneity and complexity (Hughes & Grabowski 2006). Habitats with higher complexity may offer better protection for prey from multiple predators.

In spring, densities were similar across all predator exclusion treatments: oyster sampling unit, 2-sided control, and full enclosure. This could be because the primary organisms using oyster reef are crustaceans and the oyster reef complex may provide the same amount of protection from predation as the full enclosures. Densities were significantly greater in the full predator exclusion treatment in fall and differences were driven by the abundance of crustaceans, primarily grass shrimp. Brown and pink shrimp were the only other species with significantly different densities in the full enclosure in the fall. The increased abundances of shrimp in the full enclosure may be a result of the absence of predators in fall. In spring pinfish densities were significantly higher in the full enclosure. The abundance of mud crabs was unaffected by the absence of predators. Their response to the lack of predators may be a change in behavior rather than in a change of habitat preference or abundance as was mentioned in Grabowski (2004). Fish may forage on oyster reefs rather than relying on them as refuges from predation. In this study, there were no significant differences in fish densities among habitat types and their densities were not affected by the absence of large predators. Grass shrimp and brown and pink shrimp were the only two nektonic crustaceans found in higher abundances in the full enclosures. These species may not be afforded the same amount of protection from predation on oyster reefs as some of the benthic crustaceans.

Structural complexity is a characteristic that is generally compared between habitats and not within one habitat type. Juvenile red drum that were placed in the experimental mesocosms and allowed to choose among different oyster reef structures with no predator used both complex and simple habitats and when there was a difference they selected for simple reefs. However, with equal predation pressure occurring on both sides of the mesocosm, red drum regularly selected for the more complex reefs. Grabowski (2004) explored the idea of oyster reef complexity in relation to trophic cascades and others have investigated the role of habitat complexity in various habitats including seagrass beds, coral reefs, and mangroves (see Laegdsgaard & Johnson 2001, Charbonnel et al. 2002, Schofield 2003, Gratwicke & Speight 2005, Horinouchi 2007), but few have evaluated the effects of oyster reef complexity in relation to habitat selection and value to juvenile fish. Predator-prey relationships play an important role in structuring the communities of these habitats and structural heterogeneity and complexity becomes more relevant as predation risks increase (Laegdsgaard & Johnson 2001); this pattern was observed in this study as well. Prey are more likely to depend on the structural complexity of an area for refuge in the presence of predators (Laegdsgaard & Johnson 2001). Habitat selection can be affected by the presence of a predator and there may be a switch in habitat preference. In another mesocosm study, wild-caught juvenile red drum showed a preference for oyster reef over other habitats when no predators were present (Stunz et al. 2001). However, when a pinfish was introduced to the system and present in the oyster reef habitats they selected for another habitat.

While complex oyster reefs may offer refuge from predation, other factors may play a role in influencing their community assemblages. The effects of habitat complexity on predation refuge may only be effective to a certain point and can be affected by many factors including predator and prey type, prey availability, and predator and prey behavior (Adams et al. 2004, Horinouchi 2007). For example, the mobility of large predators will be restricted in complex reefs; however, this may also restrict the movement of juvenile fish and may be disadvantageous. Overly complex habitats may restrict the ability of prey to visually detect a predator and employ anti-predator behavior, yet it may be beneficial for ambush-type predators by allowing more areas from which to attack (Horinouchi 2007). This may explain the abundance of crustaceans on oyster reefs and the similarity of fish densities among habitats in this study. Oyster reefs may provide greater refuge for crustaceans, such as ridgeback mud crabs and flatback mud crabs because they are able to hide in small crevices and avoid predation by most large predators. Fish that employ behaviors such as group formation to avoid predation or that rely on the visual detection of predators, may be too restricted in overly complex reefs, and may simply use the reefs as a foraging area. Blennies and gobies, on the other hand, may select for more complex reefs; they are only present in areas with a great deal of vertical relief and spatial heterogeneity (Soniat et al. 2004). Therefore, oyster reefs may be a better habitat in terms of refuge for less mobile species, such as benthic crustaceans, while providing good foraging grounds for fish that may find refuge in other nearby habitats, such as seagrass.

Conclusions and Future Studies. Oyster reefs are a valuable habitat that should be protected. They are a highly structured habitat that supports a high abundance of marine life. A distinctive community of fish and crustaceans depend on oyster reefs for food, refuge, and reproduction. Oyster reefs provide a structurally complex habitat with high refuge value especially for crustaceans and reefs may provide a valuable forage area for fish. The results of this study show densities of nekton and benthic crustaceans on oyster reefs to be greater on oyster reef in an oyster reef complex or adjacent to seagrass. The absence of predators on reefs had greater impact on more mobile species, such as pinfish and brown shrimp, which may not generally use oyster reef as a refuge because the complex architecture restricts mobility and impedes visual detection of predators. Red drum altered their habitat selection from low complexity to greater complexity in the presence of a predator. Therefore complexity of oyster reefs may be an important factor for the habitat selection of juvenile fish, especially in regard to refuge value, and should be further investigated.

Oyster reef restoration efforts might need to be focused on areas closer to other habitat types and it may be beneficial to restore them in conjunction with other habitat types such as seagrass. The complexity of restored reefs should also be taken into account as it can affect not only fish and crustacean densities, but oyster recruitment as well (Soniat et al. 2004). Further studies of the effects of reef complexity on fish abundance and behavior should be undertaken with different species of predators and prey since this study only focused on the effects of pinfish on the habitat selection of juvenile red drum. Other fish and crustaceans may demonstrate different behaviors, especially when exposed to a variety of predators with different foraging tactics. Many studies have examined the role of complexity in regards to habitats such as seagrasses and coral reefs, but there is a lack of information on the effects of oyster reef structural complexity on fish communities. Moreover, this study only assessed intertidal oyster reef. Much areal coverage of this habitat type includes large subtidal reefs. The high abundances of nekton and benthic crustaceans in intertidal reefs in this study as well as by Stunz et al. (in review) are in drastic contrast to the relatively low abundances Reese et al. (in review) found in open water deep subtidal oyster reefs in the nearby estuaries. There is a need to make a direct comparison of intertidal oyster reefs and subtidal reefs in order to fully understand their habitat role in estuarine ecosystems.

Finally, as the use of ecosystem-based management increases, it is necessary to understand the functional roles and linkages among habitats in estuarine systems including effects of species interactions. The importance of structural complexity and habitat heterogeneity has only been touched on in this study. A better understanding of how these interactions vary across habitats with different structural complexity is necessary to guide conservation decisions and to inform decision makers charged with implementing management plans for restoration efforts of oyster reefs.

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