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Macrofauna using intertidal oyster reef varies in relation to position within the estuarine habitat mosaic

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Abstract Oyster reefs are important components of marine ecosystems and function as essential habitat for estuarine species; however, few studies have simultaneously compared natural intertidal reefs to more well-studied seagrass meadows and marsh habitats. We investigated habitat use within an estuarine mosaic consisting of intertidal oyster reef (*Crassostrea virginica*), seagrass (*Halodule wrightii*), and marsh edge (*Spartina alterniflora*) habitats in Corpus Christi Bay, Texas. Oyster sampling units (OSUs) were deployed within intertidal oyster reef, and modified throw traps were used to collect macrofauna inhabiting the OSU and other adjacent vegetated habitats. Habitat arrangement and proximity as it relates to macrofaunal density, species richness, and community composition were also evaluated by comparing communities in oyster reef within the oyster reef complex, oyster reef adjacent to a seagrass complex, and oyster reef adjacent to marsh edge. Higher macrofaunal densities and species richness were observed within oyster reefs compared to seagrass and marsh edge. Oyster reef also supported a distinct community, while seagrass and marsh shared similar species composition and richness. The highest densities of macrofauna were collected on oyster reefs near seagrass and oyster reef located within the oyster reef complex. These results indicate the importance of intertidal oyster reefs to macrofauna and that reef location within the estuarine mosaic influences density and community assemblages. These findings are important because in many areas there are large efforts to restore oyster reef in estuarine systems, and for these programs to be successful, it is necessary to understand the functional roles and linkages among habitats.

Introduction

Estuaries represent one of the most productive ecosystems, and much of their function is derived from the plentiful habitat types that characterize these systems. Studies have shown seagrass beds, salt marshes, oyster reefs, and even non-vegetated bottom are essential for persistence of many fishery species (Leber 1985; Posey et al. 1999; Stunz et al. 2002; Zeug et al. 2007). Ecologists are beginning to focus more effort on understanding how the proximity and interaction among these habitats influence the ecosystem services (e.g., predation refuges, plentiful food resources) they provide both spatially and temporally (Beck et al. 2001; Minello et al. 2003; Grabowski et al. 2005; Smyth et al. 2015). This information is especially critical as restoration and conservation efforts increasingly focus on estuarine nursery habitats (Peterson et al. 2003, Grabowski et al. 2005; Geraldi et al. 2009), and for these programs to be successful, a thorough understanding of the functional role these biogenic habitats play in the estuarine mosaic is required.

Eastern oysters (*Crassostrea virginica*) are an ecologically and economically important fishery species whose

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dense reef aggregations provide essential habitat for many species of fish and invertebrates (e.g., blue crabs (*Callinectes sapidus*), red drum (*Sciaenops ocellatus*); Coen and Grizzle 2007; Stunz et al. 2010). Oyster reefs were once dominant features in estuarine systems along the Atlantic and Gulf of Mexico coasts (Powell 1993; Kirby 2004); however, the ecosystem goods and services provided by oysters have been compromised by disease, reduced water quality, over-harvesting, and predation (Eggleston et al. 1999; Grabowski et al. 2005; Grabowski and Peterson 2007; Johnson and Smee 2014). Oyster habitat alterations have led to fragmentation and decline in areal coverage of 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 and resource managers, since studies have shown the importance of these habitats to macrofauna, particularly intertidal oyster reefs (Posey et al. 1999; Glancy et al. 2003; Coen and Grizzle 2007; Stunz et al. 2010). Additionally, few studies have simultaneously compared natural intertidal reefs to more well-studied seagrass meadows and marsh habitats, as most of these comparisons have focused on the relative functionality of restored oyster reefs (Peterson et al. 2003; Grabowski et al. 2005; Geraldi et al. 2009; Smyth et al. 2015).

The habitat provided by shallow intertidal oyster reefs may be particularly beneficial to fish and crustaceans due to their spatial and geographic arrangement in estuaries. Intertidal oyster reefs commonly occur 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 non-vegetated bottom (Bahr and Lanier 1981; Micheli and Peterson 1999). These reefs are three-dimensional, biogenic habitats with physical complexity and vertical relief, arising from the settlement of new generations of oysters upon the foundation laid by previous generations (Grabowski and Kimbro 2005; Boudreaux et al. 2006). Ecosystem services generated by intertidal oyster reefs generally result in higher densities of macroinvertebrate prey species than unstructured mud habitats (Grabowski and Powers 2004). Greater abundances of nekton and benthic crustaceans have been found on oyster reefs when compared to abundance from non-vegetated bottom and marsh edge (Stunz et al. 2010; Humphries et al. 2011), and these relationships to structured and unstructured bottom are well known; however, these comparisons did not include seagrass meadows. Thus, it is important to first discern the relative value of intertidal oyster reef, marsh edge, and seagrass meadows to fishes and crustaceans, which will provide much needed information as scientists seek to understand how the spatial arrangement of these habitat types play in supporting estuarine ecosystem processes.

Effective management of marine resources depends on understanding the relationships between estuarine habitats (Skilleter and Loneragan 2003), particularly as restoration efforts continue to increase. Often, these conservation and restoration programs focus on individual habitats, which may restore ecosystem structure, but not necessarily function (Simenstad et al. 2006). A better examination of habitat linkages between salt marshes, seagrass beds, and intertidal oyster reefs is needed, and it provides a benchmark for restoration success. For example, studies have found that restored oyster reefs near established vegetated habitats do not enhance fish and crustacean productivity (Geraldi et al. 2009) and other ecosystem benefits, such as denitrification, are reduced (Smyth et al. 2015), leading to habitat redundancy. Thus, information about how habitat arrangement and proximity in a natural setting affect ecosystem services is greatly needed.

Thus, the purpose of this study was to characterize the macrofaunal community of intertidal oyster reefs in the context of functional relationships among oyster reefs and adjacent habitat types. Specifically, the primary objectives of this research were to: (1) characterize the macrofauna using intertidal oyster reefs within various habitat mosaic settings and (2) assess the effects of habitat arrangement and proximity among seagrass, marsh edge, and intertidal oyster reef habitat types. Highly efficient enclosure sampling was used to make comparisons among three habitat types to quantify the density and richness of marine life, and habitats were simultaneously sampled to look for effects of habitat arrangement and proximity on diversity of the community structure and abundances of associated nekton.

Materials and methods

Study site and design

Sampling occurred in Corpus Christi Bay, a shallow estuary located along the central Texas coast (Fig. 1) with an average depth of 3 m (USEPA 1999). Two replicate study locations were chosen within Corpus Christi Bay that comprised a mosaic of several habitat types including: intertidal salt marsh (*Spartina alterniflora*), seagrass (primarily *Halodule wrightii*), and extensive intertidal oyster reefs (*C. virginica*). During each sampling event, dissolved oxygen (DO) (mg l^{-1}) and temperature (°C) were measured at each site using an YSI DO 200, and salinity was measured using a refractometer. We quantified seasonal diversity and density of macrofauna among intertidal oyster reef (OR), seagrass (SG), and marsh edge (ME) habitats in Corpus Christi Bay during spring (May) and fall (November) 2008. Because of the inherent difficultly of sampling intertidal

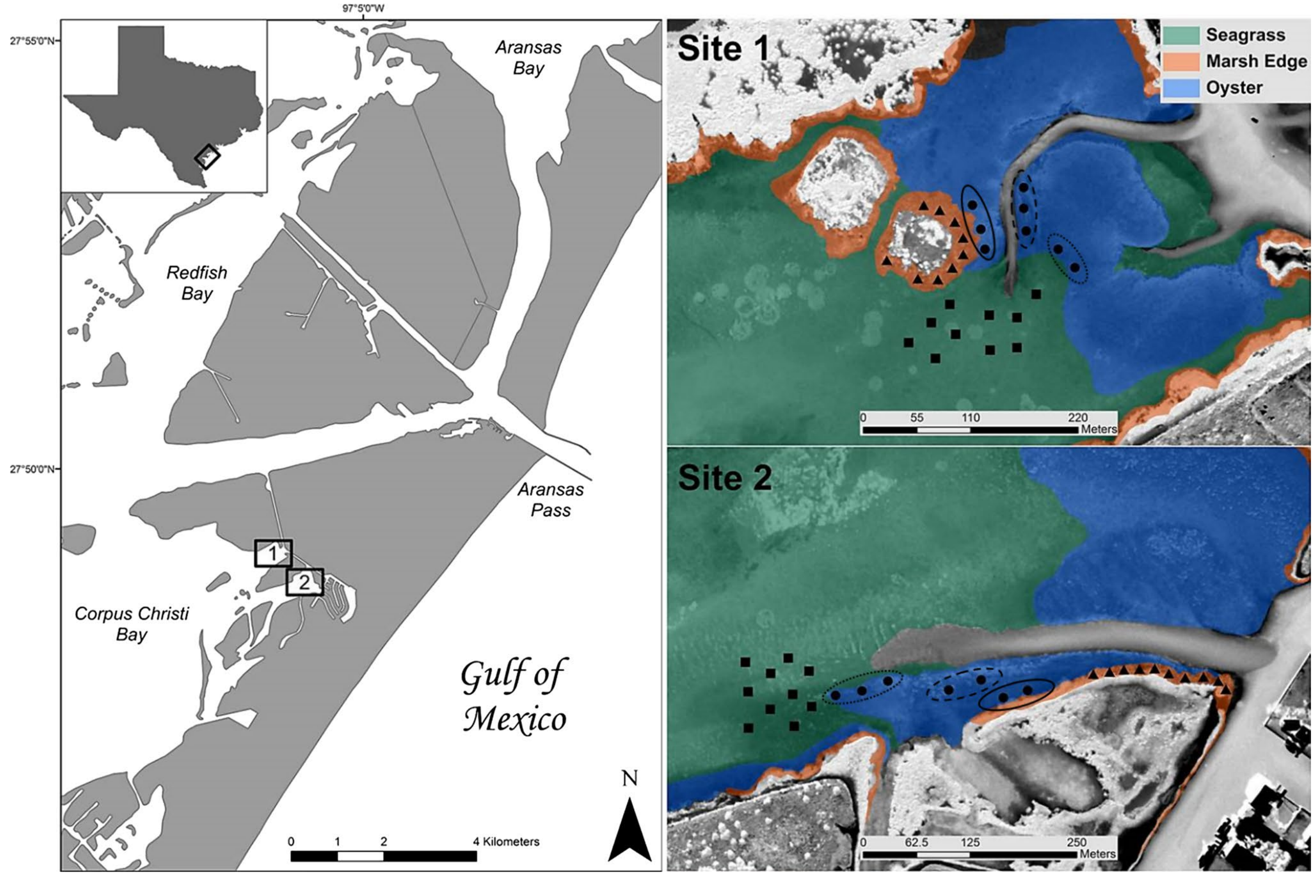

Fig. 1 General sampling locations (Spring 2008 only) and spatial arrangement of habitats in two study sites in Corpus Christi Bay, Texas. Habitats sampled include marsh edge (*Spartina alterniflora*), seagrass beds (*Halodule wrightii*), and intertidal oyster reef (*Crassostrea virginica*). *Circle* oyster sampling units; *square* seagrass samples; *triangle* marsh edge samples. Oyster sampling units that were also used for habitat arrangement and proximity analyses are indicated by: *dashed ellipse* OO (oyster reef in oyster reef complex); *dotted ellipse* OSG (oyster reef adjacent to seagrass beds); *solid ellipse* OME (oyster reef adjacent to marsh edge)

oyster reefs with traditional methods (Stunz et al. 2010), we constructed oyster sampling units (OSUs) to act as a surrogate for natural oyster reef that consisted of a 58 cm [W] × 58 cm [L] tray, made from a wooden frame (2.5 cm [W] × 2.5 cm [H]) with 1-cm^2 mesh attached to the bottom that, once filled with oysters and secured in the environment, would be flush with the bottom sediment leaving only the oysters as habitat. Each tray was filled with 50 live oysters (76–152 mm shell length) obtained from a local commercial oyster provider. The OSUs were placed within the natural intertidal oyster reef, pressed into the sediment and secured to the bottom using two pieces of rebar, and left in the environment for three months prior to first measurements in May and November, respectively. No macrofauna were included with the oysters in the OSUs during deployment. Macrofauna density and diversity were also seasonally quantified in natural stands of nearby SG and ME. Marsh edge was defined as the ecotonal zone between the emergent vegetation and open water (Stunz et al. 2002). The tides in this region are typically mixed and microtidal and with a mean range of 0.3 m (Minello et al. 2012). Thus, ME vegetation is usually inundated and available for nekton to inhabit throughout the year (Britton and Morten 1989; Minello et al. 2012), and samples were collected when all habitats were flooded.

During spring 2008, a total of 15 replicate OSUs were sampled (Site 1 = 8 and Site 2 = 7), and in fall 2008, a total of 12 OSUs were sampled (6 from each site). Additionally, there were 20 SG and 20 ME replicate samples collected in both seasons (10 from each site). To collect fishes and macrofauna inhabiting the OSUs, a 1-m^2 throw trap with 1-mm mesh sides and a modified 7.6-cm metal skirt on the bottom was pressed securely into the sediment over the tray so that no organisms could escape. Multiple throw traps (6–8 traps depending on number of OSUs at each site) were deployed by hand simultaneously at each site over the OSUs in an effort to minimize disturbance. After the samplers were secured in the habitat, the tray was thoroughly rinsed and removed from the enclosed area. Oysters from the trays were sorted and inspected for marine life, and the enclosed area swept with an approximately 0.99 m wide, fixed rigid-frame sweep net with 1 mm mesh until no new organisms were collected (a minimum of 5 passes). The same multiple throw traps and sweep net were used to simultaneously sample the nearby SG and ME habitats (see Fig. 1) at each site. To ensure mobile nekton did not escape during sampling of ME habitats, the sampler was deployed on the edge of the marsh by two people who were able to quickly and efficiently secure it over the habitat. After the sampler was secure in the habitat, fishes and macrofauna were collected in the enclosed area using the sweep net until no new organisms were collected (a minimum of 5 passes). Because we sampled marsh edge, the emergent marsh was relatively sparse in the sampler ensuring proper efficiency of the sweep net (Stunz et al. 2002). At all sites, larger fish and crabs were identified, counted, measured to the nearest mm (carapace width for crustaceans and total length for fishes), and released. The remaining organisms were preserved in a 10% formalin solution for later identification and enumeration. In the laboratory, individuals were sorted, identified to the lowest practical taxon, counted, measured to the nearest mm, and stored in 70% ethanol. All the organisms, both released and collected, were combined for analyses.

Effects of habitat arrangement and proximity

When assessing relative nekton abundance among habitat types, we chose sites where all three habitat types were nearby to avoid confounding the experiment with site-specific differences. For example, some intertidal oyster reef had areas with seagrass, marsh, or other oyster reef directly adjacent to the experimental plots. We were able to take advantage of this natural experimental design to test how habitat arrangement and proximity might influence organism abundance. For example, a subset of OSUs were placed within intertidal oyster reefs and were isolated and surrounded completely by oyster reef (>15 m from other habitats), while some of them were placed within the oyster reef so that they were also adjacent (<10 m) to seagrass meadows, and others were adjacent (<10 m) to marsh edge habitats (Fig. 1). To assess the relative importance of this spatial arrangement and how it affects macrofaunal usage of oyster reef, we did a separate analysis using the OSU samples collected above. These were categorized in three distinct spatial locales: (1) oyster reef in oyster reef complex (OO), oyster reef adjacent to seagrass beds (OSG), and oyster reef adjacent to marsh edge (OME) in the spring ($N = 5$ per locale) and the fall ($N = 4$ per locale).

Statistical design

The mean and standard error (SE) for the total number of fish, crustaceans, and individual species were calculated for each habitat type. Percent relative abundance (RA%) was calculated by season for the total number of fish and crustaceans collected. Mean species richness was calculated based on the number of species per m^2. Analysis of variance (SAS 9.2) was used to examine differences in abundance of macrofaunal groups among habitat types and spatial arrangement and proximity at $\alpha = 0.05$. All counts were extrapolated to density (number of organisms m^{-2}) prior to analyses. A two-factor ANOVA was used to examine differences in mean densities of macrofauna among habitats, with habitat as a fixed main effect and site as a random effect. A two-factor ANOVA was also used to determine significant differences in mean densities of macrofauna between spatial arrangement and proximity, with habitat locale (OO, OSG, OME) as a fixed main effect and site as a random effect. Data were log10 [x + 1] transformed to meet homogeneity of variance and the normality of the residuals for analyses. A priori 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 fish and crustacean densities were analyzed separately. Species richness and individual species that occurred in high densities were also analyzed separately with the above statistical design. To account for multiple comparisons, a Bonferroni correction was performed by adjusting Alpha values as described by Rice (1989).

Community composition among habitats and habitat combinations was explored with a variety of nonparametric multivariate analyses using PRIMER version 7 (Clarke et al. 2014). The mean densities of all organisms collected from each habitat type during each season (spring and fall) were examined, and data were 4th root transformed prior to analysis to reduce the differential effects of dominant species and to differentiate between habitats having many or few rare species (Clarke and Green 1988). Bay anchovies were removed from this analysis as they are pelagic and likely not using the benthic habitat (North and Houde 2004). Bray–Curtis resemblance matrix was constructed, and community assemblages were further investigated with a cluster analysis and non-metric multidimensional scaling (nMDS) that was based on the Bray–Curtis similarity, with the Bray–Curtis similarity groups superimposed for better interpretation (Clarke and Warwick 2001). A two-way crossed SIMPER analysis was used to determine the dominant species for each habitat across both seasons.

Results

Assessment of oyster reef as habitat

We found little variation in physical parameters among sites. In spring, salinity was 31.5 at site 1 and 31.0 at site 2; in fall, there was slightly higher salinity at both sites (35.4 and 36.1, respectively). Dissolved oxygen ranged from a low of 5.78 mg-l^{-1} at site 2 in the fall to a high of 6.47 mg-l^{-1} at site 1 in the spring, and temperatures ranged from 27.15 °C at site 1 to 28.05 °C at site 2 in the spring and from 22.50 to 20.34 °C in the fall.

We collected a total of 11,246 organisms during spring and fall, with a total of 28 fish species and 15 species of decapod crustaceans (Table 1). Species richness was significantly different in spring (ANOVA, F(5,49) = 23.79, $p < 0.001$) and fall (ANOVA, F(5,46) = 16.66). During spring, an interaction was found between habitat and site ($p < 0.001$) and linear contrasts showed that OR was greater than ME and SG (OR vs. ME $p < 0.001$; OR vs. SG $p < 0.001$) with a mean of 11.2 species m^{-2} (Fig. 2a). In fall, there was no interaction between habitat and site and habitats were significantly different (p < 0.001). Post hoc analyses showed a similar pattern to spring with OR being significantly greater than ME and SG (Fig. 2b). Darter gobies, pinfish, gobies (unknown), and Gulf toadfish were the most abundant fishes in spring. Similarly, Darter gobies were very abundant in the fall, along with code gobies and Gulf toadfish. Crustaceans were the most abundant group in both spring and fall with 5344 and 3190 individuals, respectively. Mud crabs (Panopeidae) were the most abundant benthic crustacean group. Grass shrimp, penaeid shrimp (*Farfantepenaeus* spp.), and blue crabs were the most abundant nektonic crustaceans in the spring. Overall, the most abundant crustaceans in the fall were similar to the spring with the addition of arrow shrimp (Table 1).

Overall seasonal densities of organisms were significantly different during spring (ANOVA, F(5,49) = 7.92, $p < 0.001$) and fall (ANOVA, F(5,46) = 26.53, $p < 0.001$). During spring, a significant interaction was found between habitat and site ($p = 0.001$), and linear contrasts indicated that here were no differences in overall densities of organisms between SG and ME habitats ($p = 0.125$), and OR densities were substantially higher than both vegetated habitats (ME vs. OR $p = 0.006$; SG vs. OR $p < 0.001$) (Fig. 2c). No interaction was found during fall ($p = 0.667$), and habitats were significantly different ($p < 0.001$) with post hoc analyses revealing SG and ME habitats were similar, and OR densities were substantially higher (Fig. 2d). Crustacean density was also significantly different during spring (ANOVA, F(5,49) = 11.09, $p < 0.001$) and fall (ANOVA, F(5,46) = 30.62, $p < 0.0001$). There was a significant interaction between habitat and site with spring samples ($p < 0.001$); thus, linear contrasts showed that mean densities in OR were more than double those in ME and SG habitats in spring (ME vs. OR $p = 0.002$; SG vs. OR $p < 0.001$), and SG was also significantly higher than ME ($p = 0.013$) (Fig. 3a). During the fall, no interaction was found ($p = 0.092$) and habitats were significantly different ($p < 0.001$). Post hoc analyses showed that OR densities were higher than ME and SG habitats, and ME was higher than SG (Fig. 3b). There were significant differences in spring fish densities (ANOVA, F(5,49) = 2.49, $p = 0.043$); however, no habitat differences were found ($p = 0.153$) (Fig. 3c). During the fall, there were also significant differences in fish densities (ANOVA, F(5,46) = 6.23, $p < 0.001$) and no interaction was found between habitat and site ($p = 0.283$). Habitats were significantly different ($p = 0.017$), and post hoc analyses indicated that OR densities were greater than SG densities, but ME and SG were similar (Fig. 3d).

The densities of the most abundant fish and crustaceans were compared across habitats to discern any differences among habitat types (Table 1). 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 and SG. Penaeid shrimp were more abundant in spring than in fall; their highest densities were recorded in ME in the spring and SG in fall.

Community assemblage analysis complimented differences in densities of the representative taxa within the OR habitat from the vegetated habitats. A cluster analysis of Bray–Curtis similarity values revealed there were two significant habitat groups (ME and SG vs. OR) discerned at the 60% similarity level using SIMPROF, regardless of season. The MDS plot showed the same patterns with separation of all three habitats into two groups, whereas SG and ME communities were similar but oyster reef communities were distinct (Fig. 4). A two-way SIMPER analysis showed which taxa contributed to differences in habitats (Table 2). Mud crabs, ridgeback mud crab, snapping shrimp, Gulf toadfish, and grass shrimp contributed most to the dissimilarity between both SG and OR, as well as ME and OR. Although we found that SG and ME communities were not statistically different with the SIMPROF test, SIMPER results showed that grass shrimp, penaeid shrimp,

Table 1 Overall mean densities as number per 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

Common name	Scientific name	Count	RA %	Oyster reef		Seagrass		Marsh edge		*p* value	Contrast *p* values		
				Mean	SE	Mean	SE	Mean	SE		OR/SG	OR/ME	ME/SG
Spring													
Total fishes		1948	26.7	31.8	(2.10)	41.25	(4.11)	32.3	(3.17)	–	–	–	–
Darter goby	*Gobionellus boleosoma*	1429	19.6	21.8	(1.10)	31.75	(3.82)	23.35	(2.98)	0.003	0.153	0.632	0.042
Pinfish	*Lagodon rhomboides*	197	2.7	2.6	(0.62)	2.05	(0.43)	5.85	(1.63)	0.003	0.673	0.152	0.047
Gobies (unknown)		138	1.89	0.2	(0.11)	4.75	(1.08)	2	(0.62)	<0.001	<0.001	0.003	0.001
Gulf toadfish	*Opsanus beta*	50	0.69	3.2	(0.81)	0	(0.00)	0.1	(0.10)	<0.001	<0.001	<0.001	0.660
Bay anchovy	*Anchoa mitchilli*	37	0.51	0	(0.00)	1.85	(1.21)	0	(0.00)	–	–	–	–
Code goby	*Gobiosoma robustum*	34	0.47	1.87	(0.43)	0.3	(0.13)	0	(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)	0.1	(0.07)	0.05	(0.05)	–	–	–	–
Silver perch	*Bairdiella chrysoura*	7	0.1	0.47	(0.47)	0	(0.00)	0	(0.00)	–	–	–	–
Inland silverside	*Menidia beryllina*	4	0.05	0	(0.00)	0.2	(0.16)	0	(0.00)	–	–	–	–
Mangrove snapper	*Lutjanus griseus*	4	0.05	0.27	(0.15)	0	(0.00)	0	(0.00)	–	–	–	–
Striped mullet	*Mugil cephalus*	4	0.05	0	(0.00)	0	(0.00)	0.2	(0.14)	–	–	–	–
Spotfin mojarra	*Eucinostomus argenteus*	2	0.03	0.13	(0.09)	0	(0.00)	0	(0.00)	–	–	–	–
Spotted seatrout	*Cynoscion nebulosus*	2	0.03	0.07	(0.07)	0	(0.00)	0.05	(0.05)	–	–	–	–
Gulf killifish	*Fundulus grandis*	2	0.03	0	(0.00)	0.1	(0.10)	0	(0.00)	–	–	–	–
Striped blenny	*Chasmodes bosquianus*	1	0.01	0.07	(0.07)	0	(0.00)	0	(0.00)	–	–	–	–
Naked goby	*Gobiosoma bosc*	1	0.01	0.07	(0.07)	0	(0.00)	0	(0.00)	–	–	–	–
Green goby	*Microgobius thalassinus*	1	0.01	0.07	(0.07)	0	(0.00)	0	(0.00)	–	–	–	–
Spot	*Leiostomus xanthurus*	1	0.01	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Atlantic croaker	*Micropogonias undulatus*	1	0.01	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Blackwing searobin	*Prionotus rubio*	1	0.01	0.07	(0.07)	0	(0.00)	0	(0.00)	–	–	–	–
Longnose killifish	*Fundulus similis*	1	0.01	0	(0.00)	0	(0.00)	0.05	(0.05)	–	–	–	–
Total crustaceans		5344	73.3	171	(27.81)	42.5	(6.29)	96.45	(29.74)	0.000	0.012	0.946	0.008
Grass shrimp	*Palaemonetes* spp.	3538	48.5	91.53	(22.66)	25.3	(3.93)	82.95	(27.57)	<0.001	<0.001	<0.001	<0.001
Mud crabs	Panopeidae	1076	14.8	62.2	(10.00)	6.4	(2.26)	0.75	(0.40)	<0.001	0.063	0.000	<0.001
Brown/Pink shrimp	*Farfantepenaeus* spp.	225	3.09	2.6	(0.67)	1.2	(0.27)	8.1	(2.31)	<0.001	<0.001	0.894	<0.001
Blue crab	*Callinectus sapidus*	217	2.98	2.07	(0.57)	7.1	(1.21)	2.2	(0.56)	<0.001	<0.001	<0.001	0.348
Ridgeback mud crab	*Panopeus turgidus*	103	1.41	6.13	(0.88)	0.45	(0.35)	0.1	(0.10)	<0.001	<0.001	<0.001	0.449
Snapping shrimp	*Alpheus heterochaelis*	63	0.86	4.07	(0.69)	0.1	(0.10)	0	(0.00)	0.010	0.927	0.071	0.042
Penaeid shrimp		37	0.51	0.47	(0.27)	0.4	(0.17)	1.1	(0.33)	–	–	–	–
Arrow shrimp	*Tozeuma carolinense*	33	0.45	0	(0.00)	0.6	(0.33)	1.05	(0.41)	–	–	–	–

Table 1 continued

Common name	Scientific name	Count	RA %	Oyster reef		Seagrass		Marsh edge		*p* value	Contrast *p* values		
				Mean	SE	Mean	SE	Mean	SE		OR/SG	OR/ME	ME/SG
Thinstripe hermit crab	*Clibanarius vittatus*	27	0.37	1	(0.37)	0.55	(0.22)	0.05	(0.05)	–	–	–	–
Hermit crab		10	0.14	0.2	(0.14)	0.3	(0.13)	0.05	(0.05)	–	–	–	–
Atlantic mud crab	*Panopeus herbstii*	6	0.08	0.4	(0.16)	0	(0.00)	0	(0.00)	–	–	–	–
Longeye shrimp	*Ogyrides* spp.	2	0.03	0	(0.00)	0.1	(0.07)	0	(0.00)	–	–	–	–
Longnose spider crab	*Libinia dubia*	2	0.03	0	(0.00)	0	(0.00)	0.1	(0.07)	–	–	–	–
Hermit crab (left-handed)		2	0.03	0.13	(0.13)	0	(0.00)	0	(0.00)	–	–	–	–
Flatback mud crab	*Eurypanopeus depressus*	2	0.03	0.13	(0.09)	0	(0.00)	0	(0.00)	–	–	–	–
Dark shore crab	*Pachygrapsus gracilis*	1	0.01	0.07	(0.07)	0	(0.00)	0	(0.00)	–	–	–	–
Fall													
Total fishes		764	19.3	18.33	(2.81)	10.4	(2.08)	16.8	(3.35)	–	–	–	–
Darter goby	*Gobionellus boleosoma*	658	16.6	14.42	(2.49)	9.1	(2.21)	15.15	(3.40)	0.002	0.025	0.445	0.080
Code goby	*Gobiosoma robustum*	27	0.68	0.42	(0.19)	1.1	(0.59)	0	(0.00)	0.013	0.719	0.030	0.035
Gulf toadfish	*Opsanus beta*	21	0.53	1.75	(0.51)	0	(0.00)	0	(0.00)	0.000	<0.001	<0.001	1.000
Spotfin mojarra	*Eucinostomus argenteus*	16	0.4	0.58	(0.34)	0	(0.00)	0.45	(0.25)	–	–	–	–
Sheepshead minnow	*Cyprinodon variegatus*	12	0.3	0	(0.00)	0	(0.00)	0.6	(0.60)	–	–	–	–
Frillfin goby	*Bathygobius soporator*	5	0.13	0.42	(0.15)	0	(0.00)	0	(0.00)	–	–	–	–
Pipefish	*Syngnathus* spp.	5	0.13	0	(0.00)	0	(0.00)	0.25	(0.10)	–	–	–	–
Green goby	*Microgobius thalassinus*	4	0.1	0	(0.00)	0	(0.00)	0.2	(0.12)	–	–	–	–
Striped blenny	*Chasmodes bosquianus*	3	0.08	0.25	(0.18)	0	(0.00)	0	(0.00)	–	–	–	–
Mangrove snapper	*Lutjanus griseus*	3	0.08	0.25	(0.13)	0	(0.00)	0	(0.00)	–	–	–	–
Naked goby	*Gobiosoma bosc*	2	0.05	0.08	(0.08)	0	(0.00)	0.05	(0.05)	–	–	–	–
Pinfish	*Lagodon rhomboides*	2	0.05	0.08	(0.08)	0	(0.00)	0.05	(0.05)	–	–	–	–
Gulf menhaden	*Brevoortia patronus*	1	0.03	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Blackcheek tonguefish	*Symphurus plagiusa*	1	0.03	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Gobies (unknown)	Gobiidae	1	0.03	0	(0.00)	0	(0.00)	0.05	(0.05)	–	–	–	–
Dwarf seahorse	*Hippocampus zosterae*	1	0.03	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Emerald sleeper	*Erotelis smaragdus*	1	0.03	0.08	(0.08)	0	(0.00)	0	(0.00)	–	–	–	–
Cusk eel	Ophidiidae	1	0.03	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Total crustaceans		3190	80.7	143.3	(32.65)	46.3	(7.05)	27.25	(5.35)	–	–	–	–
Grass shrimp	*Palaemonetes* spp.	1342	33.9	44.5	(10.72)	26.35	(4.35)	14.05	(3.83)	<0.001	0.358	<0.001	<0.001
Mud crabs	Panopeidae	712	18	54.67	(14.99)	1.45	(0.53)	1.35	(1.15)	<0.001	<0.001	<0.001	0.170
Blue crab	*Callinectus sapidus*	617	15.6	15.5	(5.85)	14.3	(2.02)	7.25	(1.43)	<0.001	0.129	0.127	<0.001
Ridgeback mud crab	*Panopeus turgidus*	172	4.35	14.25	(2.58)	0.05	(0.05)	0	(0.00)	<0.001	<0.001	<0.001	0.703
Arrow shrimp	*Tozeuma carolinense*	91	2.3	0.67	(0.36)	0.7	(0.33)	3.45	(1.69)	0.004	0.950	0.030	0.011

Table 1 continued

Common name	Scientific name	Count	RA %	Oyster reef		Seagrass		Marsh edge		*p* value	Contrast *p* values		
				Mean	SE	Mean	SE	Mean	SE		OR/SG	OR/ME	ME/SG
Snapping shrimp	*Alpheus heterochaelis*	79	2	6.42	(1.13)	0.1	(0.07)	0	(0.00)	<0.001	<0.001	<0.001	0.628
Brown/pink shrimp	*Farfantepenaeus* spp.	47	1.19	0.75	(0.35)	1.75	(0.39)	0.15	(0.11)	0.002	0.034	0.141	<0.001
Thinstripe hermit crab	*Clibanarius vittatus*	43	1.09	3.33	(1.82)	0.15	(0.08)	0	(0.00)	–	–	–	–
penaeid shrimp		27	0.68	0.83	(0.83)	0.45	(0.22)	0.4	(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)	0.3	(0.15)	0.35	(0.17)	–	–	–	–
Porcelain crab	*Petrolisthes* spp.	9	0.23	0.75	(0.30)	0	(0.00)	0	(0.00)	–	–	–	–
Atlantic mud crab	*Panopeus herbstii*	5	0.13	0.42	(0.19)	0	(0.00)	0	(0.00)	–	–	–	–
Dark shore crab	*Pachygrapsus gracilis*	3	0.08	0.25	(0.18)	0	(0.00)	0	(0.00)	–	–	–	–
Green porcelain crab	*Petrolisthes armatus*	3	0.08	0.25	(0.18)	0	(0.00)	0	(0.00)	–	–	–	–
Flatback mud crab	*Eurypanopeus depressus*	2	0.05	0.17	(0.17)	0	(0.00)	0	(0.00)	–	–	–	–
Longnose spider crab	*Libinia dubia*	1	0.03	0	(0.00)	0.05	(0.05)	0	(0.00)	–	–	–	–
Stone crab	*Menippe adina*	1	0.03	0.08	(0.08)	0	(0.00)	0	(0.00)	–	–	–	–

The total number (Count) and relative abundance (%RA; number of individuals/total number of animals collected × 100) are also given. Results (*p* values) are given from ANOVAs used to compare habitat types and three a priori contrast testing different habitat combinations for the most common species

–, species not analyzed

mud crabs, and arrow shrimp did contribute to differences between these groups.

Effects of habitat arrangement and proximity

Clear patterns of abundance in OR habitats were found based on spatial arrangement and proximity of other habitat types, but there were no such differences observed in community structure. We collected a total of 5201 organisms from three habitat arrangements (OO, OSG, OME) comprising 16 fishes and 15 crustacean species (Table 3). Total macrofaunal abundance (3262) was greatest in the spring. We found no differences in species richness among the habitat locales for both spring (ANOVA, F(2,12) = 1.64, $p = 0.235$) and fall (ANOVA, F(2,9) = 1.25, $p = 0.332$). 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, penaeid shrimp, snapping shrimp, and blue crabs were the most abundant crustaceans in both seasons.

We found significant differences in the densities of macrofauna in both spring (ANOVA, F(5,9) = 8.52, $p = 0.003$) and fall (ANOVA, F(5,6) = 8.29, $p = 0.011$). There was no interaction between site and habitat arrangement factors in spring ($p = 0.464$) or fall ($p = 0.258$), and significant differences were found during both seasons in habitat arrangement (spring $p = 0.017$; fall $p = 0.030$) with post hoc analyses revealing that low densities in OME are driving differences found. In both spring and fall, there were no significant differences in overall macrofaunal densities between OO and OSG. In spring, macrofaunal densities on OME were significantly lower than densities in both OO and OSG habitats (Fig. 5a), whereas in fall, there were only significant differences between densities in OO and OME (Fig. 5b). Differences in the densities of crustaceans appear to be driving the differences in the densities of all macrofauna (Fig. 5c, d). Similar to the total macrofauna, there were significant differences in the densities of crustaceans in spring (ANOVA, F(5,9) = 7.71, $p = 0.004$) and fall (ANOVA, F(5,6) = 6.37, $p = 0.022$). Additionally, crustacean differences among habitat locales followed the same pattern that we observed with total macrofauna, with no interaction of habitat arrangement and site and lower OME densities driving differences during both seasons. There were no significant differences in fish densities among the three habitat arrangements in the spring (ANOVA, F(5,9) = 2.94, $p = 0.076$) or fall (ANOVA, F(5,6) = 1.72, $p = 0.263$). However, we found density differences in the most abundant macrofauna collected. Grass shrimp, mud crabs, and Gulf toadfish were less abundant in OME than in either OSG or OO. In spring Gulf toadfish had similar densities across all habitat arrangement and

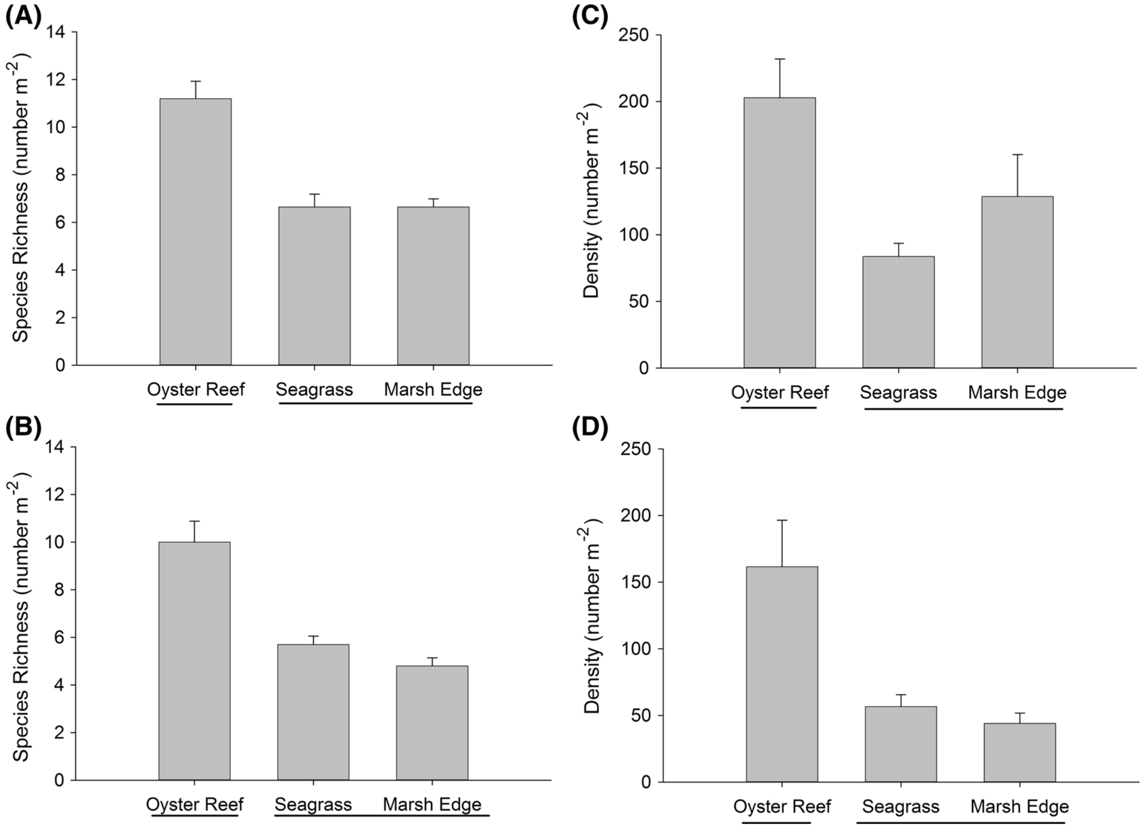

Fig. 2 Mean species richness (number m^{-2}) and mean densities (number m^{-2}) of macrofauna collected from oyster reef, seagrass, and marsh edge habitats in spring (**a**, **c**) and fall (**b**, **d**) 2008 with standard error. Oyster reef sample size for spring $N = 15$ and fall $N = 12$; seagrass and marsh edge $N = 20$ for spring and fall. ANOVA was used to test for differences among habitats. Habitats that share a common line were not significantly different

proximity treatments (ANOVA, F(5,9) = 2.60, $p = 0.101$). However, in the fall, Gulf toadfish had a significantly lower abundance in OME than OSG (ANOVA, F(5,6) = 4.44, $p = 0.049$; linear contrasts OME vs. OSG $p = 0.018$). In the fall, mud crabs had significantly higher densities (ANOVA, F(5,6) = 12.04, $p = 0.004$) in OSG and OO than in OME (linear contrasts OME vs. OSG $p = 0.029$, OME vs. OO $p = 0.014$) (Table 3).

Community analysis revealed no differences in overall community structure among the three habitat arrangements, and the Bray–Curtis nMDS ordination in conjunction with cluster analysis did not distinguish any of the habitat groups. The species composition was similar among locales; thus, the low densities of macrofauna collected from OME were not due any particular species, but rather to overall lower abundances of fishes and crustaceans.

Discussion

The goals of this study were to compare the macrofaunal community of intertidal oyster reefs to seagrass and marsh edge and examine how the spatial arrangement affects habitat use. Overall, macrofaunal densities and species richness were greater in intertidal oyster reef than in seagrass or marsh edge habitats, regardless of season, and crustaceans dominated. Spatial arrangement of habitat types involving oyster reef, seagrass, and marsh edge did not significantly contribute to differences in species richness or community structure; however, there was strong evidence that it does play a role in the abundances of organisms inhabiting these areas, as oyster embedded within marsh edge supported lower densities of fish and crustaceans than oyster within seagrass and the oyster reef complex. Thus, differences in macrofaunal density and community structure on oyster reefs may be affected by the spatial arrangement of adjacent habitat types.

We found much higher densities of crustaceans than fishes in all three habitats in both seasons with grass shrimp being the most abundant epibenthic crustacean collected. Additionally, crustacean densities were higher on oyster reefs than other taxa, which is similar to numerous studies (Micheli and Peterson 1999; Minello 1999; Meyer and Townsend 2000; Stunz et al. 2010). In

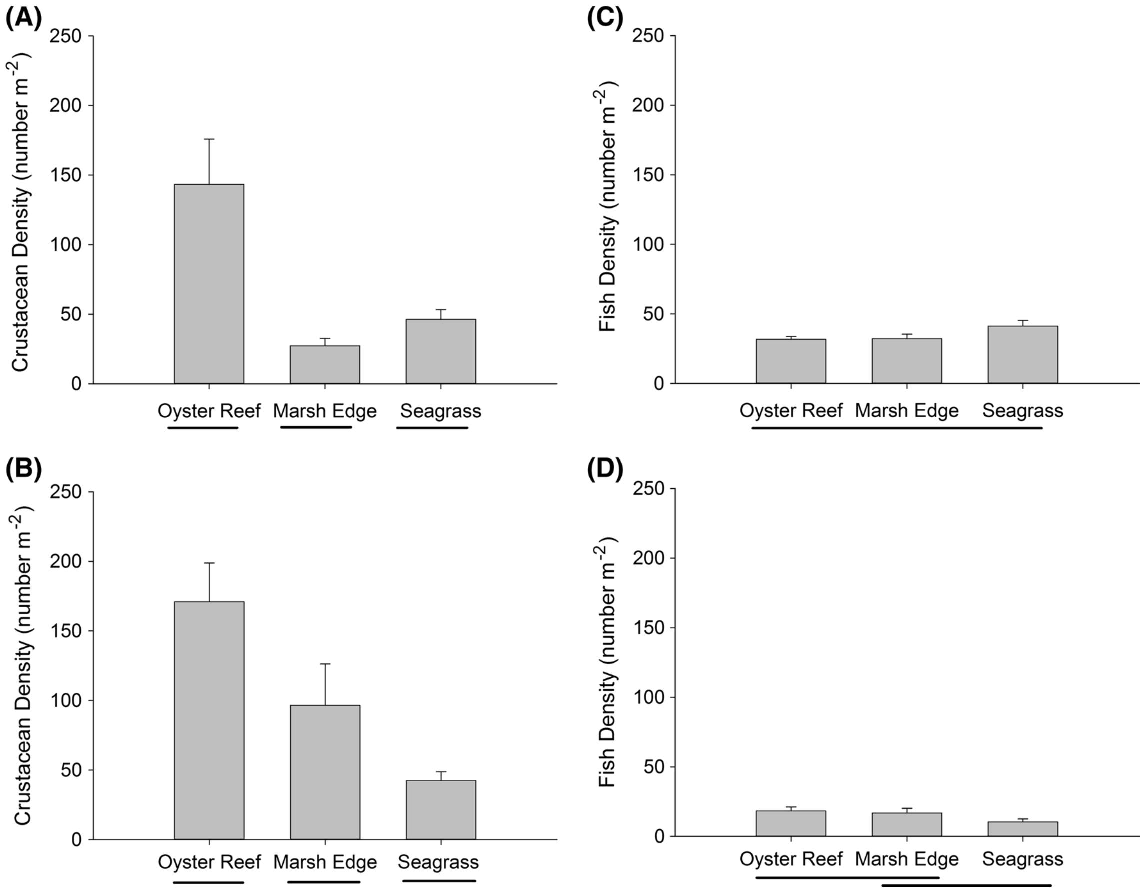

Fig. 3 Mean densities (number m^{-2}) and standard error of crustaceans (**a**, **b**) and fish (**c**, **d**) collected from oyster reef, seagrass, and marsh edge habitats during spring (**a**, **c**) and fall (**b**, **d**) 2008. Oyster reef sample size for spring $N = 15$ and fall $N = 12$; seagrass and marsh edge $N = 20$ for spring and fall. ANOVA was used to test for differences among habitats. Habitats that share a common line were not significantly different

particular, benthic crustaceans dominated the catch from intertidal oyster reefs, with panopeid mud crabs being the most numerous. Interestingly, we found the ridgeback mud crab was the most numerous benthic crustacean on oyster reefs, which contrasts several studies from other areas. Stunz et al. (2010) collected ridgeback mud crabs from both oyster reef and shallow non-vegetated bottom, but their abundance was low. Additionally, few studies of oyster reef communities have identified the ridgeback mud crab as a common resident although many studies group all mud crabs into a single category (Shubart et al. 2000). The numerical dominance of mud crabs suggests they play an important role in shaping oyster reef community structure, as clams, oysters, and barnacles are among their main prey items (Shubart et al. 2000; Grabowski 2004; Tolley and Volety 2005; Lunt and Smee 2014). Finally, we found that mud crabs, including the ridgeback mud crab, are contributing to the community composition differences between oyster reef and vegetated habitats, as we collected far fewer mud crabs in seagrass and marsh, further supporting the importance of intertidal oyster reefs to these benthic crustaceans.

Other economically important crustaceans collected in relatively high abundance include blue crabs and penaeid shrimp. We found differences in abundances of these species between seasons and habitats, and they also contributed to community differences among habitats. Densities of penaeid shrimp were higher in marsh edge in the spring, and this provides evidence that they may prefer marsh over seagrass and oyster reef when all three habitats are available. Additionally, the high densities of blue crabs found in the fall primarily in oyster reef and seagrass indicate they may be using oyster reef and seagrass areas as nurseries, as they were generally small (<25 mm). The importance of oyster reef habitat for blue crabs, although recognized, is not fully understood (Hines 2007). Submerged aquatic vegetation is thought to be the primary habitat 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

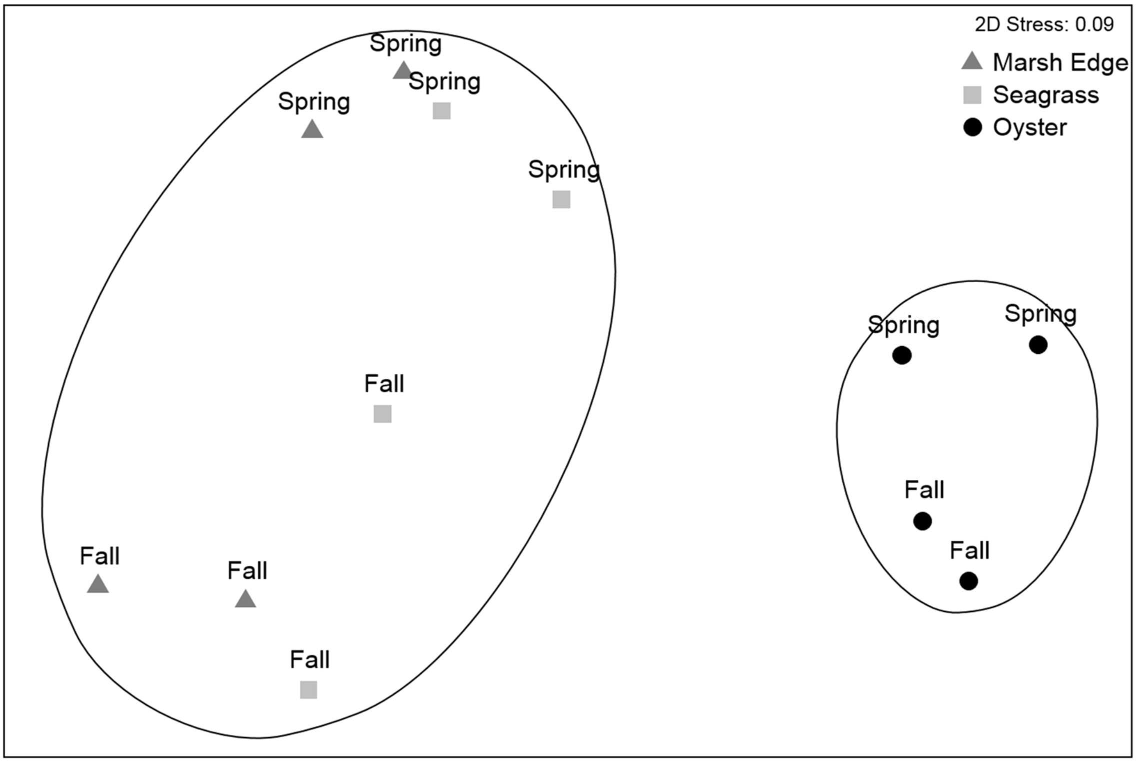

Fig. 4 Non-metric multi-dimensional scaling (nMDS) ordination with Bray–Curtis cluster analysis superimposed using 60% similarity of mean macrofauna density. Within seasons and habitats, data were averaged across sites, for a total of 12 samples

Table 2 Summary of two-way SIMPER analysis for all habitat types showing species that contributed to the between group dissimilarity across both seasons

Seagrass & oyster reef	Contribution (%)	Marsh edge & oyster reef	Contribution (%)	Marsh edge & seagrass	Contribution (%)
Mud crabs (unidentified)	13.07	Mud crabs (unidentified)	16.34	Grass shrimp	11.6
Ridgeback mud crab	12.18	Ridgeback mud crab	11.91	Brown/pink shrimp	11.42
Snapping shrimp	9.92	Snapping Shrimp	9.53	Mud crabs (unidentified)	10.72
Gulf toadfish	7.08	Grass shrimp	7.1	Arrow shrimp	9.27
Grass shrimp	6.77	Gulf toadfish	6.52	Blue crab	8.36
Brown/pink shrimp	5.31	Code goby	4.8	Darter goby	7.86
Code goby	5.14	Blue crab	4.15	Penaeid shrimp	7.00
Blue crab	4.48	Arrow shrimp	4.04	Gobies (<14 mm SL)	5.44

Data were fourth-root transformed, and species contributing to at least 4% dissimilarity were included

habitats, supporting previous observations that blue crabs also use oyster reef as nursery habitat (Coen et al. 1999; Lehnert and Allen 2002). 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.

There were also key differences in the community assemblages of fishes among habitats. Pinfish were most abundant in marsh habitats, but were also commonly found in both oyster reef and seagrass. Gulf toadfish was particularly common in oyster reef, likely because mud crabs are a major food source for Gulf toadfish which we found in very high densities (Grabowski 2004; Grabowski and Kimbro 2005). Important fish species, such as Mangrove Snapper, Silver Perch, and Spotfin mojarra, were collected primarily from oyster reef, and diets of many juvenile fish which are known to inhabit oyster reef are comprised of polychaetes, bivalves, and decapod crustaceans. Thus, while few fish were collected from oyster reef, the high density patterns of crustaceans found in this

Table 3 Overall mean densities (number m-2) and standard error (SE, one standard error) of all fishes and crustaceans collected in habitat arrangements: 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

Common name	Scientific name	Count	RA%	OO		OSG		OME	
				Mean	SE	Mean	SE	Mean	SE
Spring									
Total fishes		477	15.68	33.00	(1.14)	36.00	(36.00)	26.40	(26.40)
Darter goby	*Gobionellus boleosoma*	327	10.75	20.80	(1.74)	24.00	(24.00)	20.60	(20.60)
Gulf toadfish	*Opsanus beta*	48	1.58	3.80	(1.16)	4.20	(4.20)	1.60	(1.60)
Pinfish	*Lagodon rhomboides*	39	1.28	2.80	(0.37)	3.00	(3.00)	2.00	(2.00)
Code goby	*Gobiosoma robustum*	28	0.92	2.00	(1.10)	2.20	(2.20)	1.40	(1.40)
Pigfish	*Orthopristis chrysoptera*	10	0.33	1.00	(0.63)	0.40	(0.40)	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		2565	84.32	215.20	(44.32)	215.60	(215.60)	82.20	(82.20)
Grass shrimp	*Palaemonetes* spp.	1373	45.13	117.00	(39.11)	130.20	(130.20)	27.40	(27.40)
Mud crabs	*Panopeidae*	933	30.67	78.40	(12.02)	69.40	(69.40)	38.80	(38.80)
Ridgeback mud crab	*Eurypanopeus turgidus*	92	3.02	8.80	(1.36)	5.20	(5.20)	4.40	(4.40)
Snapping shrimp	*Alpheus heterochaelis*	61	2.01	3.20	(0.80)	4.20	(4.20)	4.80	(4.80)
Brown/Pink shrimp	*Farfantepenaeus* spp.	39	1.28	3.40	(1.63)	2.80	(2.80)	1.60	(1.60)
Blue crab	*Callinectus sapidus*	31	1.02	2.00	(0.89)	2.20	(2.20)	2.00	(2.00)
Thinstripe hermit crab	*Clibanarius vittatus*	15	0.49	1.20	(0.37)	0.40	(0.40)	1.40	(1.40)
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	(0.40)	0.60	(0.60)
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									
Total Fishes		220	11.35	22.75	(4.31)	19.00	(19.00)	13.25	(13.25)
Darter goby	*Gobionellus boleosoma*	173	8.92	19.25	(4.33)	13.25	(13.25)	10.75	(10.75)
Gulf toadfish	*Opsanus beta*	21	1.08	1.25	(0.48)	3.25	(3.25)	0.75	(0.75)
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	(0.50)
Frillfin goby	*Bathygobius soporator*	5	0.26	0.50	(0.29)	0.75	(0.75)	0.00	(0.00)
Striped blenny	*Chasmodes bosquianus*	3	0.15	0.00	(0.00)	0.00	(0.00)	0.75	(0.75)
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)
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	(185.25)	74.75	(74.75)
Mud crabs	*Panopeidae*	656	33.83	64.75	(20.11)	70.00	(70.00)	29.25	(29.25)
Grass shrimp	*Palaemonetes* spp.	534	27.54	46.75	(6.98)	61.75	(61.75)	25.00	(25.00)

Table 3 continued

Common name	Scientific name	Count	RA%	OO		OSG		OME	
				Mean	SE	Mean	SE	Mean	SE
Blue crab	*Callinectus sapidus*	186	9.59	17.75	(9.26)	23.75	(23.75)	5.00	(5.00)
Ridgeback mud crab	*Eurypanopeus turgidus*	171	8.82	22.50	(5.61)	12.25	(12.25)	8.00	(8.00)
Snapping shrimp	*Alpheus heterochaelis*	77	3.97	8.75	(1.89)	5.75	(5.75)	4.75	(4.75)
Thinstripe hermit crab	*Clibanarius vittatus*	40	2.06	5.00	(4.36)	5.00	(5.00)	0.00	(0.00)
Penaeid shrimp		10	0.52	0.00	(0.00)	2.50	(2.50)	0.00	(0.00)
Brown/pink shrimp	*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	(1.50)	0.75	(0.75)
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)

Total numbers and relative abundances (number of individuals/total number of animals collected × 100) of each species and group are also given

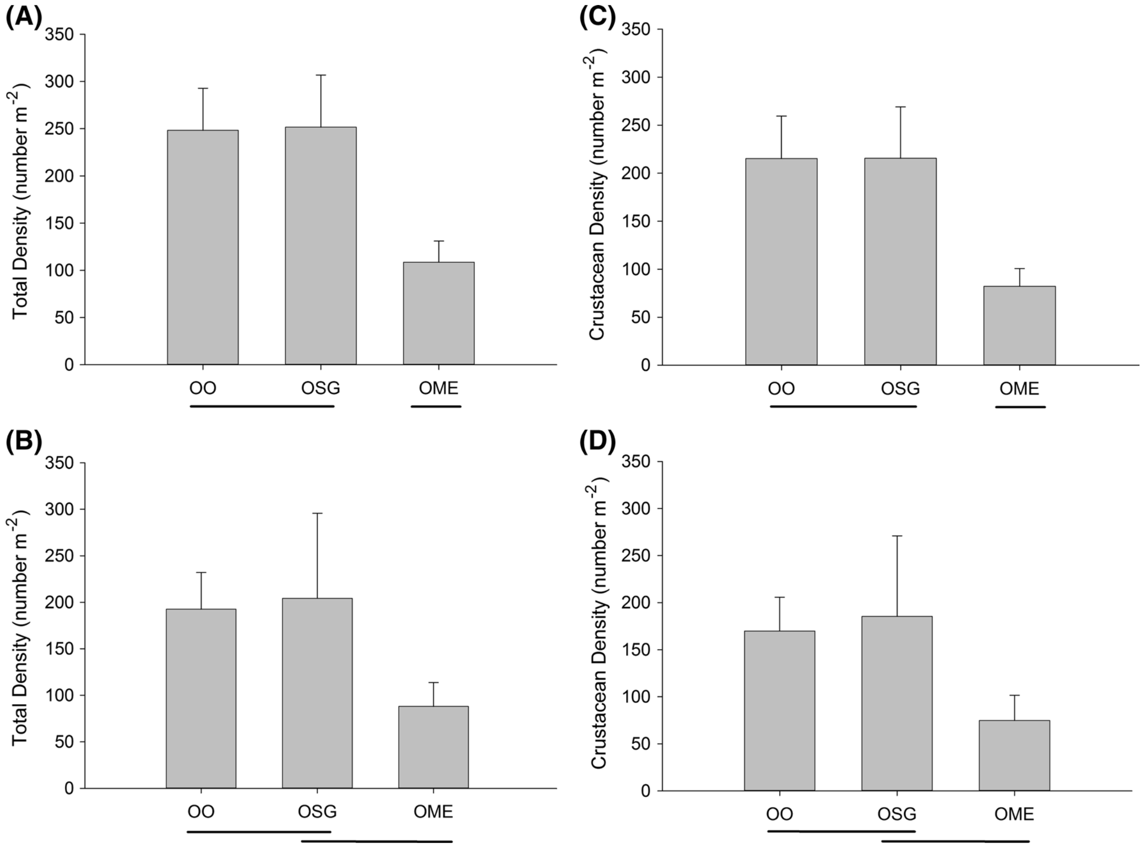

Fig. 5 Mean densities (number m^{-2}) and standard error of total macrofauna (**a**, **b**) and crustaceans (**c**, **d**) collected from oyster reefs in spring (**a**, **c**; $N = 5$) and fall (**b**, **d**; $N = 4$) 2008 with three different habitat arrangements: OO = oyster reef within oyster reef complex, OSG = oyster reef adjacent to seagrass, and OME = oyster reef adjacent marsh edge. ANOVA was used to test for differences among habitats. Habitats that share a common line were not significantly different

study show they are likely a valuable food resource for small fishes, as well as larger more transient fishes that are commonly observed using oyster reefs, and further support the importance of intertidal oyster reef habitat in estuarine ecosystems.

We had a unique opportunity to test for the effects of spatial arrangement of habitat types among oyster reef, seagrass, and marsh edge because of the mosaic landscape in which they naturally occurred. We found that spatial proximity of oyster reefs to other estuarine habitat types is a key factor affecting macrofauna density and community composition. The spatial relationship to other habitats is important in determining densities of organisms and community composition in any habitat type (see Irlandi and Crawford 1997; Micheli and Peterson 1999; Grabowski et al. 2005; Saintilan et al. 2007). Within estuaries, many habitat types are often in close proximity to one another forming diverse mosaics (Skilleter and Loneragan 2003). 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 adjacent habitats shared a common assemblage of fishes and macroinvertebrates; however, the relative density of macrofauna varied between habitats. For example, macrofaunal densities were greater on oyster reef within a larger oyster reef complex and on oyster reef near seagrass than in areas adjacent to marsh edge. The pattern described by Micheli and Peterson (1999) was similar; oyster reefs that were spatially isolated (10–15 m) from marsh by either non-vegetated bottom or seagrass supported greater densities of macroinvertebrates than areas near salt marsh habitats. Our results indicate that oyster reefs play a more important habitat role, primarily for crustaceans, when they are further (>10 m) from marsh edge and either isolated or adjacent to seagrass habitats.

Further investigation of the effects of spatial arrangement of habitats to community structure showed that the overall macrofaunal abundances were primarily driven by the presence of grass shrimp, blue crabs, and mud crabs in the OO complex and in the OSG complex. Although grass shrimp densities were not significantly different among habitat complexes, fewer were collected from OME than other habitat complexes. Spring densities of grass shrimp in marsh edge were similar to those found in OO complex, suggesting that grass shrimp were using both areas; however, when oyster reef and marsh edge are in close proximity, marsh edge may be a more suitable habitats. It also indicates that when oyster reefs are near marsh edge they are redundant and not providing any additional value to grass shrimp (Geraldi et al. 2009). Similarly, the highest densities of blue crabs were collected in OO and OSG arrangements. 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. Additional research is needed to fully understand the driving factors behind habitat selection patterns of juvenile blue crabs and other nektonic species; however, these results show that selection and use are complex when animals have access to a variety of habitat types.

Despite a reduction in the valuable biogenic habitats provided by oyster reef that have been compromised by disease, reduced water quality, over-harvesting, and predation, we clearly show that intertidal reefs are important estuarine habitats supporting high abundances of a distinct community of fishes and crustaceans. We observed the greatest densities of macrofauna in both the large oyster reef complex, as well as oyster reef that was adjacent to seagrass. The oyster reef habitat used in this study was in the water three months prior to sampling, but there is a chance this may not have been long enough for full colonization by some animals. However, results from this study clearly support our conclusions that these areas provide a structurally complex habitat, which provide predation refuges especially for crustaceans, and reefs may provide a valuable forage area for fishes. These findings will be of value to the extensive oyster reef restoration programs in estuarine systems (Peterson et al. 2003; Grabowski et al. 2005; Smyth et al. 2015) and indicate that intertidal reefs are most effective in maximizing macrofaunal abundance when placed close (10–15 m) to existing estuarine habitats such as seagrasses and other oyster reefs. Moreover, this study assessed shallow intertidal oyster reef; much areal coverage of this habitat type includes large expanses of subtidal reefs. The high abundances of nekton and benthic crustaceans found on intertidal reefs are similar to those reported by other studies (Tolley and Volety 2005; Shervette and Gelwick 2008; Stunz et al. 2010; Humphries et al. 2011) but are in drastic contrast to the relatively low abundances found in open water deep subtidal oyster reefs in nearby estuaries (Robillard et al. 2010; Nevins et al. 2014; Froeschke et al. 2016). These differences certainly have restoration implications. Thus, there is a high need to make a direct comparison of intertidal and subtidal oyster reefs within the same habitat mosaic to fully understand their habitat role in estuarine ecosystems. Finally, as management progresses toward more ecosystem-based approaches, it will be even more necessary to understand the functional roles and linkages among habitats in estuarine systems including effects of species interactions across broad landscapes.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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