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Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs

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ABSTRACT

Structurally complex habitats are often associated with more diverse and abundant species assemblages in both aquatic and terrestrial ecosystems. Biogenic reefs formed by the eastern oyster (*Crassostrea virginica*) are complex in nature and are recognized for their potential habitat value in estuarine systems along the US Atlantic and Gulf of Mexico coasts. Few studies, however, have examined the response of nekton to structural complexity within oyster reefs. We used a quantitative sampling technique to examine how the presence and complexity of experimental oyster reefs influence the abundance, biomass, and distribution of nekton by sampling reefs 4 months and 16 months post-construction. Experimental oyster reefs were colonized immediately by resident fishes and decapod crustaceans, and reefs supported a distinct nekton assemblage compared to mud-bottom habitat. Neither increased reef complexity, nor age of the experimental reef resulted in further changes in nekton assemblages or increases in nekton abundance or diversity. The presence of oyster reefs per se was the most important factor determining nekton usage.

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1. Introduction

Variations in abiotic and biotic factors influence species interactions and community assemblages (Grabowski et al., 2008; Lenihan, 1999). For example, structural complexity can determine the success of some organisms in colonizing or using habitats, and dictate the energetic benefits and constraints of organisms (MacArthur and Pianka, 1966). In theory, structurally complex habitats are expected to sustain higher densities of organisms and more diverse communities than structurally simple ones (Diehl, 1992; Luckhurst and Luckhurst, 1978). By altering resource availability and predation risk (Hixon and Menge, 1991), the habitat structure has the ability to shape community assemblages via direct and indirect interactions.

A variety of ecological theories have been suggested to explain demographic patterns in structurally complex habitats (e.g., Christensen and Persson, 1993; Gratwicke and Speight, 2005; Hicks, 1980; MacArthur and MacArthur, 1961). In shallow water estuarine environments, biogenic reefs formed by the eastern oyster (*Crassostrea virginica*; hereafter oyster) are recognized for their ability to create structure (Jones et al., 1994) and support large populations of resident organisms (Breitburg, 1999; Shervette and Gelwick, 2008; Stunz et al., 2010; Tolley and Volety, 2005). This complex structure can increase the number of habitats and thus the effective niche space within an environment, thereby potentially decreasing the physical stress of resident organisms (Dean and Connell, 1987). As a result, reef habitat may allow potentially competing species to coexist within a structurally complex environment (Beukers and Jones, 1997). Organisms may use structure provided by oyster reefs as nursery or foraging habitat, spawning substrate, refugia, or attachment space. However, it is unclear how nekton abundance and diversity are related to the relative structural complexity of different reefs.

Oyster reefs provide significant structure in shallow marine ecosystems worldwide, yet are often underrepresented in studies of estuarine nekton community and population dynamics as compared to other biogenic structures (e.g., seagrass meadows, salt marshes, mangroves, coral reefs) (see review in Minello et al., 2003). For example, Heck et al. (2003) concluded that very few differences exist in the abundance, growth, or survival of associated nekton assemblages when comparing seagrass meadows to other biogenic structures (i.e., oyster or cobble reefs, macroalgal beds). In their review, however, only one (Eggleston et al., 1998) of the sixty-four cited references explicitly included oyster reefs. Studies that focus on community assemblages at oyster reefs often compare reefs to other biogenic structures or mud-bottom, ignoring possible structural differences within reefs that may influence nekton use (e.g., Geraldi et al., 2009; Harding and Mann, 2001; Plunket and La Peyre, 2005; Shervette and Gelwick, 2008; Stunz et al., 2001, 2002, 2010; but see Tolley and Volety,

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2005). An exception is Soniat et al. (2004), who reported that shell orientation affects the availability of refugia, and fish species may show a higher affinity for vertically- rather than horizontally-oriented oyster shell.

In this study, we used a quantitative sampling technique to simultaneously compare nekton use of bare, mud bottom and experimental oyster reefs that differed in structural complexity. Our objectives were to examine whether: (1) the presence of structure influences nekton assemblages, (2) the level of reef complexity affects nekton communities (abundance, diversity, biomass, assemblage), and (3) the nekton communities at biogenic reefs change over time. We predicted distinct assemblages and an increase in species abundance, biomass, and diversity at oyster reefs compared to mud-bottom, and as reef structural complexity (i.e., shell density) increased. We also predicted that communities would become more diverse and support a higher biomass over time.

2. Materials and methods

2.1. Study site

The study was conducted along the northern shore of Caillou (Sister) Lake, located in Terrebonne Parish, Louisiana, USA (29°15′ N, 90°55′W). Sister Lake is a mesohaline salt marsh system comprised of primarily open water habitat with water depths ranging from 1 to 3 m and a mean tidal range of 0.3 ± 0.03 m (1 SE) (National Geodetic Vertical Datum). Mean (± 1 SE) water temperature and salinity in the study area between 1997 and 2009 were 23.5 ± 1.9 °C and 12.0 ± 2.8 respectively (LDWF/USGS 07381349 — Caillou Lake southwest of Dulac, LA, USA). Dominant winds are typically from the southeast, except during winter following the passage of cold fronts when northerly winds prevail. Sister Lake has served as a state public oyster seed reservation since 1940, and oyster beds are abundant within the system.

2.2. Experimental reef construction

Treatments (0.45 m^2) were created by varying the density of clean, unaggregated oyster shells and placing them in cylindrical wire cage structures (2.54-cm mesh), with the top left open. Unaggregated shell treatments were used in these experiments as a surrogate for oyster reef. The use of clean, nonliving oyster shell and the relatively small size of the treatments in our experiments were chosen to conservatively test for a nekton response to the addition of reef on mud-bottom habitat. The cages enabled us to simulate three-dimensional reefs by containing the unaggregated shell and preventing the destruction or movement of the reefs in the field. Four treatments were tested, two control and two experimental. Treatments varied by shell volume (L) and vertical relief (cm) with the assumption that an increase in shell volume and vertical relief increases the 3-dimensional structure. Treatments included: (1) mud-bottom, no cage (MUD), (2) mud-bottom, with cage (CAGE), (3) low oyster shell density (4 L shell, approx. 5 cm vertical relief; LOW), and (4) high oyster shell density (8 L shell, approx. 20 cm vertical relief; HIGH). We created the CAGE treatment to determine whether the structure of the cages alone had an effect on nekton communities. In July 2009, we chose two sampling shorelines (each spanning at least 225 m in length) for the placement of treatments in Sister Lake. At each sampling shoreline within shallow water, we randomly selected 30 sites approximately 15 m apart and 25 m from shore and randomly assigned treatment types. Thus, in total 60 sites (10 MUD + 10 CAGE + 20 LOW + 20 HIGH) were distributed evenly by treatment type between the two sampling shorelines. The experimental oyster reefs were deployed in July 2009.

2.3. Field sampling

We planned two sampling events, the first (October 2009) to occur shortly after the reefs were constructed to examine the immediate response of nekton to the addition of reef, and a second (October 2010) a year after the first to examine more long-term colonization of reefs by nekton. We collected a total of 59 nekton samples (note: one MUD treatment was lost between sampling events). Fishes and decapod crustaceans were quantitatively sampled using a 1-m^2 drop sampler (Zimmerman et al., 1984). The drop sampler rapidly encloses a sample unit area and has been shown to have a 96% sampling efficiency (Zimmerman et al., 1986). Reefs were sampled non-sequentially along each shoreline to avoid disturbing sites just prior to sampling. Immediately after the drop sampler was deployed, water clarity (cm) was measured using a secchi disc, water depth (m) measurements were taken in triplicate inside the drop sampler, and a YSI model 556 Multiprobe (YSI Inc., Yellow Springs, OH, USA) was used to measure salinity, temperature (°C) and dissolved oxygen ($mg\ L^{-1}$) inside the drop sampler. We removed animals by using dip nets and filtering the water pumped from the sampler through a 1-mm mesh net. When the sampler was completely drained, we removed by hand any oyster shells present and used a 5-mm mesh sieve to capture the organisms inside. All samples were taken over a 3 day sampling event in 2009 and in 2010. Samples were placed on ice and returned to the laboratory for processing where we identified organisms to the lowest feasible taxon. We weighed all individuals of a species in each sample to the nearest 0.1 g (wet weight) to determine biomass. We recorded the total abundance and total biomass of all species collected.

2.4. Statistical analyses

All data were checked for normality using Shapiro–Wilk's W test to evaluate the assumption of the statistical analyses. Subsequent logarithmic ($\log_{10}[x+1]$) transformations were necessary for only the nekton biomass data. All data are reported as untransformed mean ± 1 standard error unless indicated differently.

We used multivariate analysis of variance (MANOVA) (SAS Institute, Inc., Cary, NC, U.S.A.) to test whether water quality variables (secchi, temperature, salinity, dissolved oxygen) and site characteristics (water depth), compared simultaneously, differed by reef treatment type (MUD, CAGE, LOW, HIGH), and sample year (2009, 2010). Comparisons of least-squared means, using a two-way analysis of variance (factor: treatment, year) were conducted for any significant ($\alpha<0.05$) MANOVAs.

We used MANOVA to test whether abundance (ind m^2), species diversity (Shannon index; H'), or biomass, compared simultaneously, differed by reef treatment type (MUD, CAGE, LOW, HIGH), and sample year (2009, 2010), blocking on sample shoreline. Analyses were performed on the entire nekton data set, and broken down by fish and decapod crustaceans separately. Comparisons of least-squared means, using a two-way analysis of variance (factor: treatment, year) were conducted for any significant ($\alpha<0.05$) MANOVA models.

To examine the overall similarity of nekton assemblages at each treatment, we performed multidimensional scaling (MDS) on a reduced, raw species abundance matrix using PRIMER statistical software (version 6.1.9; Clarke and Warwick, 2001). We used only species whose abundance and biomass accounted for more than 5% of the total catch for the MDS analysis (Gauch, 1982), and we displayed this using 2-dimensional ordination. To test for differences in the similarity of nekton assemblages at each treatment, we performed a one-way analysis of similarity (ANOSIM). Lastly, a similarity percentage (SIMPER) analysis was also conducted to determine which species contributed the most to the similarities or dissimilarities among treatments. We performed the analyses by comparing treatment type for each year separately, because some species were

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Table 1
Range and mean (with ±1 standard error) of temperature, salinity, dissolved oxygen, water depth, secchi depth, and oyster reef shell volume at Sister Lake for each sampling year. Significant differences (α<0.05) between years are indicated by an asterisk.

Environmental variable	2009	2010
Temperature (°C)*	17.8–20.4	19.3–22.4
	19.1 ± 0.1	21.1 ± 0.2
Salinity*	9.8–13.4	12.2–13.7
	11.4 ± 0.3	13.2 ± 0.1
Dissolved oxygen (mg L^{-1})*	6.2–8.9	4.8–6.4
	7.6 ± 0.1	5.8 ± 0.1
Water depth (m)	0.8–1.4	0.7–1.3
	1.1 ± 0.1	0.9 ± 0.2
Secchi depth (cm)*	36–63	41–72
	49.9 ± 1.3	59.2 ± 1.4
Low shell volume (L)	4.0–4.0	2.5–5.5
	4.0 ± 0.0	4.0 ± 0.3
High shell volume (L)	8.0–8.0	5.5–9.5
	8.0 ± 0.0	7.6 ± 0.4

only abundant enough to include in the statistical analysis in a single year.

3. Results

3.1. Environmental variables

All environmental variables differed between 2009 and 2010, but not between treatments or shorelines (Table 1). Water temperature, salinity, and secchi depth were higher in 2010 than 2009. Dissolved oxygen was lower in 2010 than 2009.

3.2. Nekton assemblages

We collected a total of 551 individuals (188 fishes and 363 decapod crustaceans) representing 23 species (17 fishes and 6 decapod crustaceans) with a total biomass of 8375 g wet weight (6941 g and 1434 g for fishes and decapod crustaceans, respectively) in 2009 (Tables 2 and 3). In 2010, we collected a total of 220 individuals (120 fishes and 100 decapod crustaceans) representing 14 species (10 fishes and 4 decapod crustaceans) and a total biomass of 2436 g wet weight (818 g and 1618 g for fishes and decapod crustaceans, respectively) (Tables 2 and 3).

Across all treatments in 2009, decapod crustaceans outnumbered fishes and accounted for 65.9% of individuals collected (Table 3). Fishes accounted for 82.9% of the total biomass. Without sheepshead (*Archosargus probatocephalus*), however, fish biomass would account for only 32.9% of the total. Although sheepshead was excluded from our multivariate analyses, it was only collected at oyster reefs. Freckled blenny (*Hypsoblennius ionthas*), naked goby (*Gobiosoma bosc*), and skilletfish (*Gobiesox strumosus*) accounted for 60.6% of all fishes. Other species contributing to the catch included silver perch (*Bairdiella chrysoura*), gray snapper (*Lutjanus griseus*), clown goby (*Microgobius gulosus*), and striped mullet (*Mugil cephalus*); no other species of fish accounted for more than 5% of the total fish collected in 2009. The only fish present at all 4 treatment types was *G. bosc* (Table 2). The only species absent from oyster reefs were *M. cephalus* and southern flounder (*Paralichthys lethostigma*) (Table 2). The mud crab (*Panopeus* spp.) and white shrimp (*Litopenaeus setiferus*) accounted for 64.2% of all decapod crustaceans and were the only crustacean species collected at all 4 treatment types (Table 2). We were unable to classify mud crabs at the species level, but given the geographic region of this experiment, they were most likely the congeners *P. obesus* and *P. simpsoni* (Reames and Williams, 1984). Bigclaw snapping shrimp (*Alpheus heterochaelis*), blue crab (*Callinectes sapidus*), and brown shrimp (*Farfantepenaeus aztecus*) also were collected; no other species of decapod crustacean accounted for more than 5% of the total decapod crustacean catch in 2009.

In 2010, fishes outnumbered decapod crustaceans and accounted for 54.5% of the total (Table 3). Decapod crustaceans accounted for 66.4% of the total biomass; however, without *C. sapidus*, decapod crustacean biomass would account for only 12.3% of the total. *G. bosc* and Atlantic spadefish (*Chaetodipterus faber*) accounted for 70.8% of

Table 2
Mean abundance (ind m^{-2} ± 1 standard error) and total (individuals) by oyster treatment and year for all species collected via drop sampling at Sister Lake. Means and SEs were computed from 5 MUD, 5 CAGE, 10 LOW, and 10 HIGH samples each year, except only 4 MUD samples in 2010.

Species	Mud bottom		Cage structure		Low oyster density		High oyster density	
	2009	2010	2009	2010	2009	2010	2009	2010
Fishes	1.8 (1.32)	1.5 (1.50)	1.4 (0.24)	1.8 (1.11)	6.6 (0.93)	4.1 (1.16)	10.0 (1.38)	5.8 (1.68)
Archosargus probatocephalus	0	0	0	0	0.2 (0.12)	0.1 (0.09)	0.3 (0.15)	0.3 (0.21)
Bairdiella chrysoura	0	0	0	0	1.0 (0.33)	0	0.5 (0.22)	0
Bathygobius soporator	0	0	0	0	0.1 (0.09)	0	0.1 (0.10)	0
Chaetodipterus faber	0	1.5 (1.50)	0	0.6 (0.40)	0	2.6 (1.86)	0	0.3 (0.21)
Citharichthys spilopterus	0	0	0	0	0	0	0.1 (0.10)	0
Ctenogobius boleosoma	0	0	0	0	0.2 (0.12)	0	0.2 (0.10)	0
Cyprinodon variegatus	0	0	0	0	0.4 (0.15)	0	0.3 (0.15)	0
Gobiesox strumosus	0	0	0	0	1.3 (0.38)	0	1.8 (0.55)	0.3 (0.15)
Gobiosoma bosc	0.3 (0.21)	0	0.4 (0.24)	0.4 (0.40)	1.0 (0.33)	2.2 (0.74)	2.5 (1.08)	2.8 (1.04)
Hypsoblennius ionthas	0	0	0.4 (0.24)	0	1.4 (0.64)	0.1 (0.11)	2.5 (0.79)	0.5 (0.27)
Lutjanus griseus	0	0	0.2 (0.20)	0	0.2 (0.18)	0.2 (0.15)	0.7 (0.21)	0
Microgobius gulosus	0	0	0.2 (0.20)	0	0.4 (0.36)	0	0.3 (0.15)	0
Mugil cephalus	1.3 (1.15)	0	0	0	0	0	0	0
Myrophis punctatus	0	0	0	0	0.1 (0.09)	0.2 (0.22)	0.2 (0.13)	0.9 (0.48)
Micropanope sculptipes	0	0	0	0	0	0.2 (0.15)	0	0.1 (0.10)
Opsanus beta	0	0	0	0	0.1 (0.09)	0	0.3 (0.15)	0.1 (0.10)
Paralichthys lethostigma	0	0	0.2 (0.20)	0	0	0	0	0
Symphurus plagiusa	0	0	0	0	0.3 (0.19)	0	0.2 (0.20)	0.5 (0.17)
Decapod crustaceans	2.0 (0.89)	0.3 (0.25)	5.0 (2.55)	1.6 (0.81)	14.6 (1.92)	1.9 (0.63)	16.6 (1.92)	4.5 (1.25)
Alpheus heterochaelis	0	0	0	0	1.5 (0.47)	0.4 (0.34)	4.2 (0.83)	1.8 (0.71)
Callinectes sapidus	0.3 (0.21)	0	1.0 (0.45)	0.4 (0.40)	2.7 (0.70)	0.4 (0.34)	0.8 (0.51)	1.8 (1.07)
Farfantepenaeus aztecus	0	0.3 (0.25)	1.6 (1.36)	1.0 (0.63)	0.6 (0.37)	0.8 (0.36)	0.2 (0.20)	0.9 (0.71)
Palaemonetes pugio	1.2 (0.48)	0	0.4 (0.24)	0	0.2 (0.18)	0	0	0
Panopeus spp.	0.2 (0.17)	0	0.4 (0.24)	0.1 (0.1)	4.4 (1.54)	1.1 (0.38)	7.8 (1.83)	1.8 (0.62)
Litopenaeus setiferus	0.8 (0.65)	0	1.6 (1.12)	0	5.0 (2.02)	0	3.6 (1.33)	0
Total	3.8 (1.36)	1.8 (1.44)	6.4 (2.73)	3.4 (1.03)	21.3 (2.39)	7.2 (1.51)	26.6 (2.53)	12.1 (2.22)

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Table 3
Total number of individuals and biomass (g) by year for all species collected via drop sampling at Sister Lake.

Species	Total number		Total biomass	
	2009	2010	2009	2010
Fishes	188	120	6940.60	818.54
Archosargus probatocephalus	5	4	6235.40	425.47
Bairdiella chrysoura	16	0	30.76	0
Bathygobius soporator	2	0	19.52	0
Chaetodipterus faber	0	35	0	290.49
Citharichthys spilopterus	1	0	0.15	0
Ctenogobius boleosoma	4	0	1.08	0
Cyprinodon variegatus	7	0	22.36	0
Gobiesox strumosus	32	3	66.69	3.08
Gobiosoma bosc	40	50	19.53	14.29
Hypsoblennius ionthas	42	6	179.24	15.21
Lutjanus griseus	10	2	64.72	24.61
Microgobius gulosus	8	0	2.57	0
Mugil cephalus	8	0	158.97	0
Myrophis punctatus	3	11	4.04	35.91
Micropanope sculptipes	0	3	0	1.13
Opsanus beta	4	1	23.22	0.96
Paralichthys lethostigma	1	0	100.84	0
Symphurus plagiusa	5	5	11.53	7.39
Decapod crustaceans	363	100	1434.70	1618.00
Alpheus heterochaelis	58	22	72.31	13.89
Callinectes sapidus	45	24	782.32	1502.67
Farfantepenaeus aztecus	16	22	58.28	35.53
Palaemonetes pugio	11	0	2.39	0
Panopeus spp.	129	32	399.65	65.91
Litopenaeus setiferus	104	0	119.77	0
Total	551	220	8375.30	2436.50

all fishes and were collected at all treatment types. Other species in our samples included *H. ionthas* and the speckled worm-eel (*Myrophis punctatus*); no other species of fish accounted for more than 5% of the total fish catch in 2010. *Panopeus* spp., *C. sapidus*, *F. aztecus*, and *A. heterochaelis* were the only decapod crustacean species collected in 2010 and each species accounted for at least 22% of the total crustacean catch. The only species collected at all 4 treatment types was *F. aztecus* (Table 2). *L. setiferus* was not collected in 2010. *C. faber* was the second most abundant fish species in 2010, while *B. chrysoura*, *G. strumosus*, and *H. ionthas* were either absent or occurred only at low densities in 2010. *L. setiferus* was the second most abundant decapod crustacean species in 2009, but absent from all 4 treatment types in 2010, whereas *C. faber* was the second most abundant fish species in 2010, but absent from all 4 treatment types in 2009 (Table 2).

Table 4
Summary of the F-values of 2-way analysis of variance tests for abundance (ind m^{-2}), diversity (H') and biomass (g m^{-2}) of total nekton, fish and decapod crustaceans collected at experimental reefs in Sister Lake. Year = October 2009, October 2010. Treatment = MUD, CAGE, LOW volume reef, HIGH volume reef. Numbers in parentheses indicate degrees of freedom. Significant results (α<0.05) are indicated by an asterisk.

Variable	Main effects		Interaction
	Year (1)	Treatment (3)	Reef×Treatment (7)
Abundance			
Nekton	22.47*	20.06*	3.67*
Fish	4.07*	10.44*	0.60
Decapod crustacean	34.44*	11.61*	4.98*
Diversity			
Nekton	35.43*	35.13*	0.91
Fish	7.66*	16.75*	1.97
Decapod crustacean	33.42*	6.09*	1.92
Biomass			
Nekton	22.75*	12.32*	0.61
Fish	18.66*	5.43*	0.40
Decapod crustacean	32.41*	11.70*	7.91*

B. chrysoura, *G. strumosus*, and *H. ionthas* were all abundant fish species in 2009, but were either absent or occurred at low densities in 2010.

Total nekton abundance differed significantly by year, and year interacted significantly with treatment in the analysis (Table 4; Fig. 1). Nekton abundance was lower in mud-bottom treatments (MUD, CAGE) than oyster reef treatments (LOW, HIGH), with no significant differences within either oyster reef or mud-bottom treatments. Between years, mud-bottom nekton abundances remained unchanged while 2010 oyster reef abundances were significantly lower than 2009 abundances. No significant interactions were detected for total nekton diversity or biomass. Total nekton diversity was significantly higher in 2009 than 2010. MUD sites had significantly lower diversity than CAGE sites, and diversity at CAGE sites was significantly lower than either LOW or HIGH oyster reef sites (Fig. 2). While uneven sample size may bias diversity indices, it did not appear to confound our analysis. Total nekton biomass was higher in 2009 than 2010, and higher at oyster reef treatments (LOW, HIGH) than mud-bottom treatments (MUD, CAGE), with no significant differences within either oyster reef or mud-bottom treatments. The pattern in 2009 was an exception in that no significant difference was detected in total biomass between mud-bottom treatments and the LOW oyster reef treatment (Fig. 1).

Decapod crustacean abundance and biomass followed the same patterns, with a significant year by treatment interaction (Table 4; Fig. 1). Decapod crustacean abundance and biomass were lower in mud-bottom treatments (MUD, CAGE) than oyster reef treatments (LOW, HIGH), with no significant differences within either oyster reef or mud-bottom treatments. Between years, mud-bottom nekton (fish and decapod crustacean) abundances remained unchanged while oyster reef abundances were significantly lower in 2010 than 2009. Decapod crustacean diversity was higher in 2009 than 2010, and significantly lower in MUD than the other three treatments (CAGE, LOW, HIGH), which did not differ from one another (Fig. 2).

Fish abundance, diversity and biomass were all significantly higher in 2009 than 2010 (Table 4, Figs. 1 and 2). Both abundance and biomass followed a similar pattern with lower fish abundance at both mud-bottom treatments (MUD, CAGE) than the oyster reef treatments (LOW, HIGH), with no difference within mud-bottom or oyster reef treatments. In contrast, fish diversity was significantly lower at mud-bottom treatments (MUD, CAGE) than oyster reef treatments (LOW, HIGH), but diversity was also lower at the LOW than HIGH treatment (Fig. 2).

Multivariate analysis revealed differences in nekton assemblages between oyster reefs and mud-bottom habitat, with LOW and HIGH treatments grouping more discretely than MUD and CAGE in both 2009 (stress = 0.17) and 2010 (stress = 0.24) (Fig. 3). ANOSIM indicated that assemblages were significantly different from one another in 2009 ($r = 0.416$, $\alpha < 0.001$) and 2010 ($r = 0.220$, $\alpha = 0.002$). In both years, oyster reef treatments (LOW, HIGH) were significantly different from MUD and CAGE (2009: $r = 0.406$, $\alpha < 0.001$; 2010: $r = 0.336$, $\alpha = 0.013$), but not from one another (2009: $r = 0.061$, $\alpha = 0.127$; 2010: $r = 0.070$, $\alpha = 0.143$).

SIMPER analysis indicated that in 2009 the species composition of LOW and HIGH treatments was 69.56% and 75.78% different, respectively, than the CAGE treatment. These differences were driven by the presence of *A. heterochaelis*, *Panopeus* spp., and *L. setiferus* at the oyster reefs. The species composition at oyster reefs was also 84.7% and 89.6% different, respectively, compared to the MUD treatment. These differences were driven largely by the presence of *A. heterochaelis*, *Panopeus* spp., and *C. sapidus* at the oyster reefs. Oyster reefs differed from one another by 53.59% with significantly greater densities of *C. sapidus* at LOW treatments and significantly greater densities of *A. heterochaelis* at HIGH treatments.

SIMPER analysis indicated that in 2010 the species compositions of LOW and HIGH treatments were 88% and 80.5% different,

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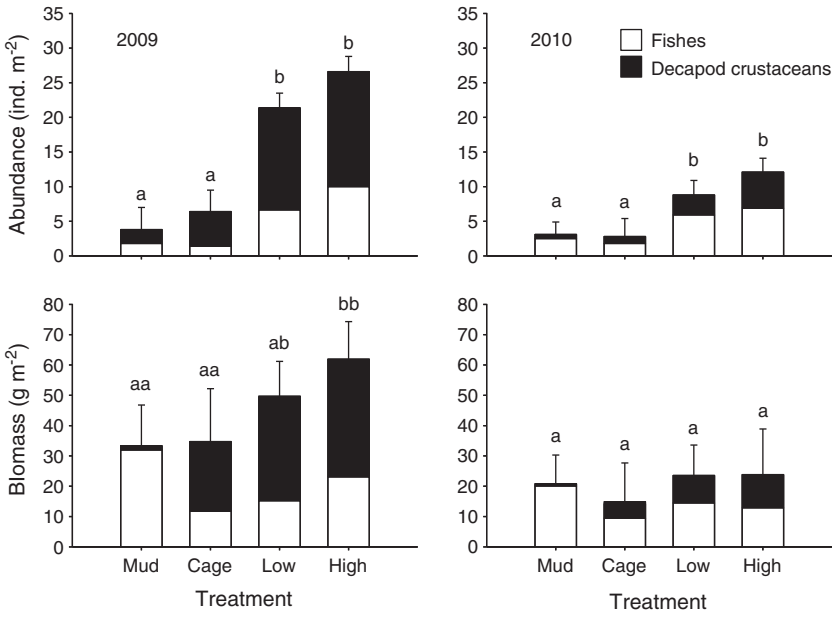

Fig. 1. Mean species abundance and biomass (±1 standard error) for all species combined by treatment type for 2009 and 2010. Stacked bars indicate the relative contribution of fishes and decapod crustaceans for each treatment. Means and SEs were computed from 5 MUD, 5 CAGE, 10 LOW, and 10 HIGH samples each year, except only 4 MUD samples in 2010. Treatments with different letters indicate significant differences.

respectively, than the CAGE treatment, and that the species composition at oyster reefs was 97.3% and 92.0% different, respectively, than the MUD treatment. These differences were driven primarily by the high abundance of *G. bosc* at oyster reefs compared to the other treatments.

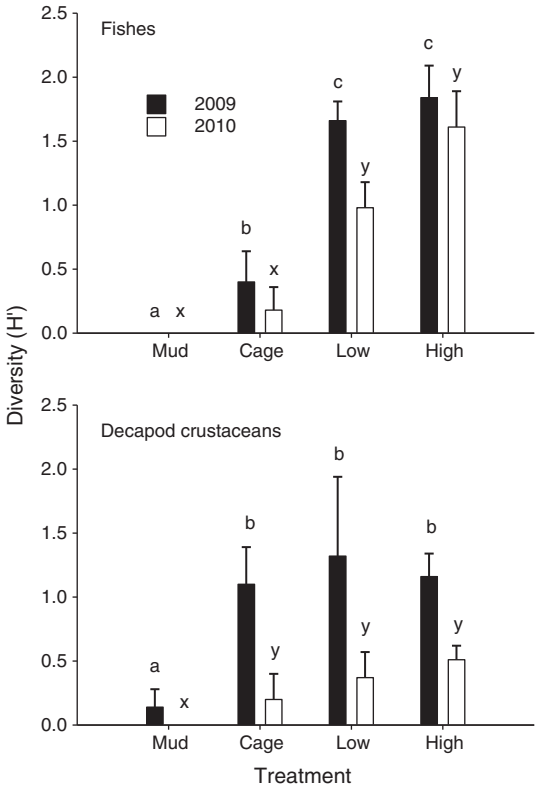

Fig. 2. Mean species Shannon diversity (±1 standard error) for fishes and decapod crustaceans by treatment type for 2009 and 2010. Means and SEs were computed from 5 MUD, 5 CAGE, 10 LOW, and 10 HIGH treatment samples each year, except only 4 MUD samples in 2010. Different letters indicate significant differences in treatments.

4. Discussion

Nekton abundance, biomass and diversity all increased at experimental oyster reefs as compared to mud-bottom, but failed to increase with greater structural complexity (i.e., shell volume, reef height).

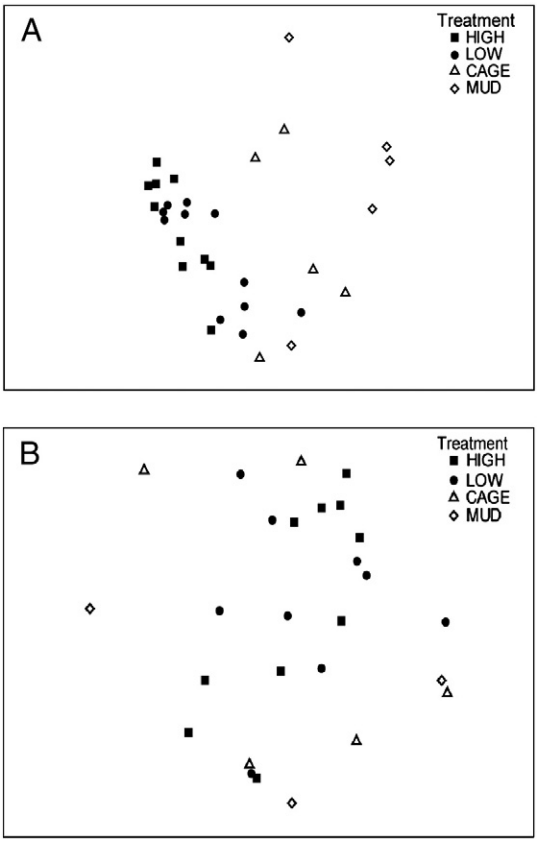

Fig. 3. Results of MDS ordination of species abundance (ind m^{-2}) in, (A) 2009 and (B) 2010.

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Similarly, nekton assemblages were distinct between treatments with (reef) and without (mud and cage control) structure, indicating that the structural reefs supported not only greater abundances, but also different assemblages of species. Our results document the value of constructed oyster reefs in creating immediate nekton habitat and providing enhanced habitat value as compared to non-vegetated mud bottom. Furthermore, these results suggest that the presence of structure per se is more important than the actual degree of structural complexity.

The higher nekton density we observed at our experimental oyster reefs indicates the high habitat value subtidal oyster reefs provide in the northern Gulf of Mexico, and this result is consistent with other studies from the region (Plunket and La Peyre, 2005; Shervette and Gelwick, 2008; Soniat et al., 2004; Stunz et al., 2010; Tolley and Volety, 2005). In our study, the highest fish density was associated with the high volume reefs (10.0 ± 1.4 ind m^{-2}). This density is similar to the mean density (10.7 ± 1.1 ind m^{-2}) reported by Stunz et al. (2010), who used gear identical to ours to sample subtidal, created oyster reefs in Galveston Bay, TX, and the mean density (13.9 ± 1.6 ind m^{-2}) from Plunket and La Peyre (2005), who used trays to sample subtidal oyster leases in Barataria Bay, LA. In all cases, despite differences in reef origin (natural, created), method of creation, or sampling gear, fish densities were comparable.

Unlike those for fishes, densities of decapod crustaceans reported in the literature vary widely. Our study documented decapod crustacean densities that were relatively low (16.6 ± 1.9 ind m^{-2} mean for HIGH treatment) in comparison to a similar study using experimental reefs in Galveston Bay (41.8 ± 2.7 ind m^{-2}; Stunz et al., 2010). Stunz et al. (2010), however, created 0.50 m^2 reefs using 57 L of live, local oysters, whereas our HIGH reefs were created with a relatively miniscule 8 L of cultched clean shell over a 0.45 m^2 area. Thus, the available structure and interstitial spaces available in our reefs were only 7–14% of that provided by the reefs used by Stunz et al. (2010). Both our study and Stunz et al. (2010) documented much higher decapod crustacean densities than a study using a modified epibenthic sled to sample existing subtidal reefs (2.23 ± 1.0 ind m^{-2}; Robillard et al., 2010), but lower densities than studies using modified trays to sample over created cultch reefs (86.3 ± 7.3 ind m^{-2}; Humphries, 2010), existing harvested reefs (168.4 ± 16.1 ind m^{-2}; Plunket and La Peyre, 2005) and unharvested reefs (245.6 ± 4.2 ind m^{-2}; Beck, unpublished data) in Louisiana. While catch efficiency of drop samplers has been estimated at greater than 96% (Rozas and Minello, 1997; Stunz et al., 2010), the catch efficiency of trays has not been documented. Trays have been used extensively to sample the resident and benthic community of reefs (e.g., Breitburg, 1999; Gregalis et al., 2009; Lehnert and Allen, 2002; Lenihan et al., 2001; Plunket and La Peyre, 2005), and nekton densities reported from these studies are equal to or greater than those reported from studies employing drop samplers. The relatively high nekton densities collected by trays provide evidence for the validity of their use in reef studies. These elevated densities may be, at least in part, a response to the structure created by the tray itself; however, this potential artifact may be remedied by embedding the trays in the substrate. This possible tray effect, however, has yet to be explicitly tested. In our study, the cage structure did not appear to affect the overall densities of organisms, but did affect the nekton diversity. The large range of decapod crustacean densities documented from various oyster reefs indicates that decapod crustacean density may be influenced by factors other than sampling gear type, including reef characteristics (created, natural, complexity) or reef location (biophysical environment, adjacent habitat).

In our study, the presence of biogenic structure seems to be the most important factor determining species abundance and diversity, and our results fail to support the common assumption that any increase in structural complexity, and thus habitable surface area, translates into increased species abundance and diversity (Coull and Wells, 1983; Fretter and Manly, 1977; Gibbons, 1988; Morse et al., 1985). While this assumption is widely supported in the estuarine literature (e.g., seagrass patches with variable blade densities; Diehl, 1988, 1992; Orth and Heck, 1980; Wyda et al., 2002), it has not been tested using shell reefs as substrate. Oyster reef size, age, substrate type, and height may all affect nekton, and in particular, decapod crustacean use of created and existing reefs. We may have created the simplest and smallest artificial reefs possible using piles of clean unaggregated oyster shell. Consequently, these reefs may have lacked the complexity of living oyster reefs, had a high edge: area ratio, and relatively low vertical relief (5–20 cm). Our experimental design may have also failed to incorporate a great enough difference in complexity between reef treatments (4 L versus 8 L of clean cultched shell) and consequently failed to rigorously test the hypothesis that greater structural complexity begets greater species abundance and diversity. Lastly, our use of relatively simple reef treatments could explain the lower densities in our study than those from the more complex reefs used by Stunz et al. (2010). Despite these potential criticisms, we believe that our study provides an opportunity to begin to understand how structure and structural complexity may influence function within oyster reefs.

In addition to site-specific reef complexity, adjacent habitat or the size of the reef may further influence decapod crustacean densities. Although using small, simple reefs can be extremely valuable for testing hypotheses, it is quite possible that this approach, while documenting the high value of the reef structure itself, underestimates the total value of the oyster reefs by creating small reef "islands" surrounded by mud-bottom. Numerous studies in different estuarine habitats have demonstrated the importance of location in determining nekton densities and assemblages (Grabowski et al., 2005; Gregalis et al., 2009; Irlandi and Crawford, 1997; Lehnert and Allen, 2002; Micheli and Peterson, 1999; Robblee and Zieman, 1984; Rozas and Minello, 2006; Rozas and Odum, 1987). For example, Irlandi and Crawford (1997) demonstrated higher abundances of pinfish in seagrass beds adjacent to marsh than seagrass beds adjacent to non-vegetated bottom. Gregalis et al. (2009), examining constructed oyster reefs of different designs and located at three different sites, concluded that nekton response to site differences may be due to biophysical characteristics of each reef location and less a response to individual reef differences. We sampled half of the reefs 4 months following construction and did not sample the other half until a year later. Because half of the reefs were sampled and destroyed in the first year, the reefs that remained were spaced farther apart. It is possible, given the size of our reefs and the increased amount of space among treatments during the second year, that the location of the reef "islands" may have influenced our results by limiting recruitment. We believe, however, that reef spacing is unlikely to have confounded our experiment because the reefs were initially spaced relatively far apart (15 m) at deployment.

In the 16 month study, we failed to detect an increase in nekton abundance or assemblage structure over time; the only temporal changes evident involved reductions from 2009 to 2010 in abundance, diversity and biomass, and these changes were more pronounced in the oyster reef than mud-bottom treatments. These changes are likely associated with the sinking of, or sedimentation over, the experimental reefs, and a lack of reef development (i.e., reef building organisms) over time. The lack of change in nekton assemblages, or increase in nekton density, at our experimental reefs between sampling events suggest that the reefs are only attracting organisms, or that conditions are preventing the reefs from developing through recruitment and growth of oysters and other sessile fauna (Peterson et al., 2003; Powers et al., 2003). For example, in Mobile Bay, AL, Gregalis et al. (2009) found that reef community structure failed to change after 2 years, and suggested that local environmental conditions may be preventing the reefs from developing. Our experimental reefs failed to develop a live oyster or attached faunal

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community, and, in fact, the 2010 samples showed a slight decline in reef volume from 2009 when the experiment was initiated, which may indicate a loss of shell or reef burial through sedimentation. The lack of recruitment to our experimental reefs by oyster spat may be due to an unusually low spat set recorded for 2010 in coastal Louisiana, and within Sister Lake in particular, where our sites were located (Casas-Liste, unpublished data). Some of these temporal changes, however, may be related to timing of the sampling events (e.g., weather conditions). For example, *L. setiferus* was completely absent in 2010, even though this species was relatively abundant in 2009. Although the water temperature had rebounded by the time we collected samples in 2010, this sampling event was preceded by the passage of a strong cold front and a sharp decline in water temperature from 30 to 19 °C (LDWF/USGS data recorder 07381349 — Caillou Lake southwest of Dulac, LA, USA). This sudden drop in temperature likely caused juvenile white shrimp to migrate out of our shallow study area and into deeper inshore waters or offshore (Knudsen et al., 1996; Lindner and Anderson, 1956; Rogers and Herke, 1985).

Although our study corroborates other work documenting that the presence of structure provided by oyster reefs supports relatively high nekton populations and thus may be increasing refugia, this and other studies fail to identify the mechanism by which added structural complexity affects community assemblages. While increased structural complexity is often highlighted as a benefit to resident nekton communities by providing more refugia and reducing predation (Hixon and Menge, 1991; Nelson, 1979; Warfe and Barmuta, 2004), it remains unclear whether this structural complexity increases prey survivorship by providing more refuge areas (Beukers and Jones, 1997; Heck and Thoman, 1981) or increases predator foraging efficiency by reducing inter- and intraspecific competition among predators (Finke and Denno, 2002; Grabowski et al., 2008; Grabowski and Powers, 2004). However, if structure decreases the visibility of predators (Rilov et al., 2007; Underwood, 1982) or obstructs their movements (van de Koppel et al. 1996), predator foraging efficiency may be negatively affected. Regardless of the methods by which density regulation may be achieved, the presence of structure in our study seemingly provided additional refugia for most fishes and decapod crustaceans as evidenced by greater abundances of resident organisms. At the same time, the relatively high abundance of nekton on the reefs may also have created areas with increased predator densities and/or foraging efficiency; while more complex reefs may in fact provide greater refugia than low complexity reefs, structurally complex reefs may also act to increase predator foraging efficiency by aggregating their prey. The interaction of these processes could explain the lack of significant differences in nekton assemblages between oyster reef treatments. However, because our sampling technique (drop sampler) and design are unable to detect such changes in transient predator species and their behavior, we may only speculate on causal relationships.

Our results show that oyster reefs contribute to increased species abundance, biomass, and diversity in estuarine systems. While the estimates of nekton densities we documented on our experimental reefs are likely conservative, our findings are similar to those of many previous studies that used more complex reefs and different reef materials (Gregalis et al., 2009; Lehnert and Allen, 2002; Shervette and Gelwick, 2008; Steimle and Zetlin, 2000; Stunz et al., 2010; Szedlmayer and Howe, 1997; Tolley and Volety, 2005). Newly constructed oyster reefs appear to provide immediate nekton habitat and support a diverse and spatially distinct community. Increasing the structural complexity of reefs, however, may not necessarily result in a greater abundance, biomass, or diversity of organisms. Biotic and abiotic interactions among local spatial characteristics of reefs and adjacent habitat, substrate morphology, competition among resident species, and increased predation by transients may obscure responses to structural complexity by the nekton community. It is possible that density-dependent effects limit the populations of resident nekton assemblages at oyster reefs that vary in complexity. Future studies should consider these factors as well as differences in reef design and construction techniques to improve the sustainability of this valuable estuarine habitat.

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References

Beukers, J.S., Jones, G.P., 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia 114, 50–59.
Breitburg, D., 1999. Are 3-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community. Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Williamsburg, VA, pp. 238–249.
Christensen, B., Persson, L., 1993. Species-specific antipredatory behaviors — effects on prey choice in different habitats. Behav. Ecol. Sociobiol. 32, 1–9.
Clarke, K., Warwick, R., 2001. Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd Edition. PRIMER-E, Plymouth, UK. 172 pp.
Coull, B.C., Wells, J., 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64, 1599–1609.
Dean, R.L., Connell, J.H., 1987. Marine invertebrates in an algal succession: mechanisms linking habitat complexity with diversity. J. Exp. Mar. Biol. Ecol. 109, 249–273.
Diehl, S., 1988. Foraging efficiency of 3 freshwater fishes — effects of structural complexity and light. Oikos 53, 207–214.
Diehl, S., 1992. Fish predation and benthic community structure — the role of omnivory and habitat complexity. Ecology 73, 1646–1661.
Eggleston, D.B., Etherington, L.L., Elis, W.E., 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. J. Exp. Mar. Biol. Ecol. 223, 111–132.
Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology 83, 643–652.
Fretter, V., Manly, R., 1977. Algal associations of *Tricolia pullus*, *Lacuna vincta* and *Cerithiopsis tubercularis* (gastropoda) with special reference to the settlement of their larvae. J. Mar. Biol. Assoc. U. K. 57, 999–1017.
Gauch, H., 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, NY. 294 pp.
Geraldi, N.R., Powers, S.P., Heck, K.L., Cebrian, J., 2009. Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. Mar. Ecol. Prog. Ser. 389, 171–180.
Gibbons, M., 1988. The impact of sediment accumulations, relative habitat complexity and elevation on rocky shore meiofauna. J. Exp. Mar. Biol. Ecol. 122, 225–241.
Grabowski, J.H., Hughes, A.R., Kimbro, D.L., 2008. Habitat complexity influences cascading effects of multiple predators. Ecology 89, 3413–3422.
Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86, 1926–1935.
Grabowski, J.H., Powers, S.P., 2004. Habitat complexity mitigates trophic transfer on oyster reefs. Mar. Ecol. Prog. Ser. 277, 291–295.
Gratwicke, B., Speight, M.R., 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Mar. Ecol. Prog. Ser. 292, 301–310.
Gregalis, K.C., Johnson, M.W., Powers, S.P., 2009. Restored oyster reef location and design affect responses of resident and transient fish, crab, and shellfish species in Mobile Bay, Alabama. Trans. Am. Fish. Soc. 138, 314–327.
Harding, J.M., Mann, R., 2001. Oyster reefs as fish habitat: opportunistic use of restored reefs by transient fishes. J. Shellfish. Res. 20, 951–959.
Heck, K.L., Thoman, T.A., 1981. Experiments on predator–prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53, 125–134.
Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136.
Hicks, G.R., 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J. Exp. Mar. Biol. Ecol. 44, 157–192.
Hixon, M.A., Menge, B.A., 1991. Species diversity — prey refuges modify the interactive effects of predation and competition. Theor. Popul. Biol. 39, 178–200.
Humphries AT (2010) Effects of habitat structural complexity on nekton assemblages: lab and field observations in southern Louisiana. Master's thesis, Louisiana State University, Baton Rouge, Louisiana.

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Irlandi, E., Crawford, M., 1997. Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. Oecologia 110, 222–230.
Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.
Knudsen, E.E., Rogers, B.D., Paille, R.F., Herke, W.H., Geaghan, J.P., 1996. Juvenile white shrimp growth, mortality, and emigration in weired and unweired Louisiana marsh ponds. North Am. J. Fish. Manage. 16, 640–652.
Van De Koppel, J., Huisman, J., Van Der Wal, R., Olff, H., 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. Ecology 77, 736–745.
Lehnert, R.L., Allen, D.M., 2002. Nekton use of subtidal oyster shell habitat in a southeastern US estuary. Estuaries 25, 1015–1024.
Lenihan, H.S., 1999. Physical–biological coupling on oyster reefs: how habitat structure influences individual performance. Ecol. Monogr. 69, 251–275.
Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol. Appl. 11, 764–782.
Lindner, M.J., Anderson, W.W., 1956. Growth, migrations, spawning, and size distribution of shrimp *Penaeus setiferus*. Fish. Bull. 56, 553–645.
Luckhurst, B.E., Luckhurst, K., 1978. Analysis of influence of substrate variables on coral-reef fish communities. Mar. Biol. 49, 317–323.
Macarthur, R., Macarthur, J.W., 1961. On bird species-diversity. Ecology 42, 594–598.
Macarthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100, 603–609.
Micheli, F., Peterson, C.H., 1999. Estuarine vegetated habitats as corridors for predator movements. Conserv. Biol. 13, 869–881.
Minello, T.J., Able, K.W., Weinstein, M.P., Hays, C.G., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar. Ecol. Prog. Ser. 246, 39–59.
Morse, D., Lawton, J., Dodson, M., Williamson, M., 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature 314, 731–733.
Nelson, W.G., 1979. Experimental studies of selective predation on amphipods — consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38, 225–245.
Orth, R.J., Heck, K.L., 1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bay. Estuaries 3, 278–288.
Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264, 249–264.
Plunket, J., La Peyre, M.K., 2005. Oyster beds as fish and macroinvertebrate habitat in Barataria Bay, Louisiana. Bull. Mar. Sci. 77, 155–164.
Powers, S.P., Grabowski, J.H., Peterson, C.H., Lindberg, W.J., 2003. Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios. Mar. Ecol. Prog. Ser. 264, 265–277.
Reames, R., Williams, A., 1984. Mud crabs of the *Panopeus herbstii* complex in Alabama, USA. Fish. Bull. 81, 885–890.
Rilov, G., Figueira, W.F., Lyman, S.J., Crowder, L.B., 2007. Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. Mar. Ecol. Prog. Ser. 329, 225–238.
Robblee, M.B., Zieman, J.C., 1984. Diel variation in the fish fauna of a tropical seagrass feeding ground. Bull. Mar. Sci. 34, 335–345.
Robillard, M.R., Stunz, G.W., Simons, J., 2010. Relative value of deep subtidal oyster reefs to other estuarine habitat types using a novel sampling method. J. Shellfish. Res. 29, 291–302.
Rogers, B.D., Herke, W.H., 1985. Estuarine-dependent fish and crustacean movements and weir management. In: Bryan, C.F., Zwank, P.J., Chabreck, R.H. (Eds.), Proceedings of the Fourth Coastal Marsh and Estuary Management Symposium. Louisiana Cooperative Fishery Research Unit, Louisiana State University Agriculture Center, Baton Rouge, LA, pp. 201–219.
Rozas, L.P., Minello, T.J., 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. Estuaries and Coasts 20, 199–213.
Rozas, L.P., Minello, T.J., 2006. Nekton use of *Vallisneria americana* Michx. (wild celery) beds and adjacent habitats in coastal Louisiana. Estuaries and Coasts 29, 297–310.
Rozas, L.P., Odum, W.E., 1987. Use of tidal fresh-water marshes by fishes and macrofaunal crustaceans along a marsh stream-order gradient. Estuaries 10, 36–43.
Shervette, V.R., Gelwick, F., 2008. Seasonal and spatial variations in fish and macroinvertebrate communities of oyster and adjacent habitats in a Mississippi estuary. Estuaries and Coasts 31, 584–590.
Soniat, T.M., Finelli, C.M., Ruiz, J.T., 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. J. Exp. Mar. Biol. Ecol. 310, 163–182.
Steimle, F.W., Zetlin, C., 2000. Reef habitats in the middle Atlantic bight: abundance, distribution, associated biological communities, and fishery resource use. Mar. Fish. Rev. 62, 24–42.
Stunz, G.W., Levin, P.S., Minello, T.J., 2001. Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. Environ. Biol. Fishes 61, 305–313.
Stunz, G.W., Minello, T.J., Levin, P.S., 2002. A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. Estuaries 25, 76–85.
Stunz, G.W., Minello, T.J., Rozas, L.P., 2010. Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas. Mar. Ecol. Prog. Ser. 406, 147–159.
Szedlmayer, S.T., Howe, J.C., 1997. Substrate preference in age-0 red snapper, *Lutjanus campechanus*. Environ. Biol. Fishes 50, 203–207.
Tolley, S.G., Volety, A.K., 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. J. Shellfish. Res. 24, 1007–1012.
Underwood, R., 1982. Vigilance behaviour in grazing African antelopes. Behaviour 79, 81–107.
Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141, 171–178.
Wyda, J.C., Deegan, L.A., Hughes, J.E., Weaver, M.J., 2002. The response of fishes to submerged aquatic vegetation complexity in two ecoregions of the mid-Atlantic bight: Buzzards Bay and Chesapeake Bay. Estuaries 25, 86–100.
Zimmerman, R.J., Minello, T.J., Zamora, G., 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston bay salt-marsh. Fish. Bull. 82, 325–336.
Zimmerman, R.J., Minello, T.J., Zamora, G., Martinez, E., 1986. Measurements of estuarine shrimp densities applied to catch predictions. In: Landry, A.M., Kima, E.F. (Eds.), Proceedings of the Shrimp Yield Prediction Workshop. Texas A & M University Sea Grant College Program, Galveston, Texas, pp. 37–55.

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