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Effects of habitat structural complexity on nekton assemblages: lab and field observations in southern Louisiana

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**EFFECTS OF HABITAT STRUCTURAL COMPLEXITY ON NEKTON
ASSEMBLAGES: LAB AND FIELD OBSERVATIONS IN SOUTHERN
LOUISIANA**

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Renewable Natural Resources

by
Austin T. Humphries
B.S., University of Vermont, 2006
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ABSTRACT

Greater structural complexity is often associated with more diverse and abundant species assemblages. Biogenic reefs formed by the eastern oyster (*Crassostrea virginica*) are structurally complex in nature and have been recognized for their potential habitat value in estuarine systems along the Atlantic and Gulf of Mexico coasts. To determine how the structural complexity of newly created oyster reefs may influence the abundance and distribution of species, three objectives were established. First, to examine spatial and temporal patterns of nekton use at newly created oyster reefs, as well as the impact of wave exposure, six paired oyster reef and mud-bottom treatments at low and medium wave energy shorelines were sampled quarterly, from June 2009 to March 2010, at Caillou (Sister) Lake, Louisiana, using gill nets, seine, and substrate trays. Transient species showed seasonal shifts with no evidence of habitat preference. Resident species were consistently more abundant at oyster reefs than mud-bottom treatments. There were no patterns in nekton use that could be directly attributed to wave exposure. Second, to determine how changes within the structural complexity of newly created oyster reefs may influence nekton use, oyster reef treatments of various complexities were created and sampled using a drop sampler. The presence of oyster reefs per se was the most important factor determining nekton assemblages; newly created oyster reefs provided habitat for nekton assemblages, but there was little difference between reef treatments. Lastly, to determine how oyster reefs mediate predator foraging success, treatments of various complexities were created and trials executed in a laboratory setting using wild red drum (*Scianops ocellatus*) and grass shrimp (*Palaemonetes pugio*). Foraging success was negatively correlated to the structural complexity of oyster reefs, indicating there may be a point above which increased complexity no longer increases the refuge value of the reef. These results show that oyster reefs may support a

high abundance and diversity of resident nekton, but that after structure is introduced, further increasing structural complexity does not automatically increase species abundance and diversity, or the amount of refugia provided.

CHAPTER 1. INTRODUCTION

Ecologists have long recognized that the structural complexity of a habitat is a vital characteristic influencing population biology and species interactions (Bell et al. 1991), perhaps because it may directly control the distribution and abundance of associated species by providing necessary resources (Lenihan 1999). For example, structural complexity is positively correlated with abundance, diversity, and biomass of associated species in coral reefs (Luckhurst and Luckhurst 1978, Tuya et al. 2009), forest tree canopies (MacArthur and MacArthur 1961), vegetated freshwater systems (Diehl 1992), shallow and soft bottom marine systems (Orth et al. 1984, Hixon and Menge 1991, Talman et al. 2004). The paradigm that complex habitats beget more abundant and diverse species assemblages may be explained by the interaction of a variety of interconnected biotic and abiotic processes within ecological systems. Habitat structure may provide substrate for colonization (Underwood and Denley 1984), refuges from competition and predation (Huffaker 1958), and alter physical variables, which have subsequent biological effects (Belsky et al. 1989). These mechanisms may effectively increase the quality and quantity of resources available to organisms, and thus, allow potentially competing species to coexist (Beukers and Jones 1997).

Eastern oysters (*Crassostrea virginica*; hereafter oyster) historically formed extensive, 3-dimensional reef networks in estuarine systems along the southeastern Atlantic and northern Gulf of Mexico (GOM) (Kirby 2004). Oyster reefs not only have the ability to sequester carbon (Hargis and Haven 1999), protect fringing shorelines (Meyer et al. 1997, Piazza et al. 2005), and provide important filtration services (Dame 1996), but they also create complex, biogenic structures that serve as essential fish habitat (Coen et al. 1999, Peterson et al. 2003). Mechanisms underlying this habitat enhancement may be a direct result of increased structural

complexity (Breitburg 1999); oyster reefs introduce spatial heterogeneity to the environment that can provide increased spawning substrate (Lehnert and Allen 2002), spatial refuge from predation (Grabowski 2004), and greater forage availability. Once ubiquitous features of the estuarine landscape, oysters are important ecological engineers (Jones et al. 1994), and despite the enhanced survival and increased production of ecologically and economically important organisms (Sogard 1997, Stunz et al. 2002), oysters have not been well-managed historically for ecological support (Beck et al. 2009).

Successful management of oyster reefs is likely to improve with a better understanding of how physical structure might influence biological communities. To determine how the structural complexity of newly created oyster reefs influence the abundance and distribution of species, I established three objectives. The first objective was to examine spatial and temporal patterns of nekton use at newly created oyster reefs through time, and determine the relative influence of wave exposure in mediating nekton assemblages. A large-scale field experiment was conducted to address this objective and is presented in Chapter 2. The second objective was to investigate a mechanism that may influence nekton assemblages at newly created oyster reefs, specifically, whether the degree of variations in structural complexity influence nekton use. Using a quantitative sampling technique, a small-scale manipulative field experiment was conducted and is presented in Chapter 3. The third objective was to determine if predation may be a mechanism mediating species demographics at newly created oyster reefs with variations in structural complexity. Wild red drum (*Sciaenops ocellatus*) and grass shrimp (*Palaemonetes pugio*) were used in a laboratory experiment presented in Chapter 4. Understanding nekton assemblage

patterns at oyster reefs and identifying mechanisms that influence habitat value can help determine the role newly created reefs may provide and inform the design of oyster restoration and creation projects.

CHAPTER 2. SPATIAL AND TEMPORAL PATTERNS OF NEKTON USE AND THE INFLUENCE OF WAVE EXPOSURE AT NEWLY CREATED OYSTER REEFS IN A SOUTHERN LOUISIANA ESTUARY

Introduction

Estuaries may contain a diverse assemblage of biogenic structures that introduce heterogeneity to the surrounding landscape. Seagrass beds, mangroves, and shellfish reefs supply structure that may support a variety of functions for nekton (e.g., refuge, nursery, forage, and spawning habitat), and thus promote a high abundance and diversity of estuarine species (Heck and Thoman 1981, Baltz et al. 1993, Peterson et al. 2003). For example, it has been estimated that each 10 m² of restored oyster reef in the southeast United States supports an additional yield of 2.6 kg yr⁻¹ of fish and large mobile crustaceans (Peterson et al. 2003); oyster reefs are essential habitat for estuarine nekton (Coen et al. 1999, Peterson et al. 2000, Stunz et al. 2010). With destructive harvest practices, introduction of diseases, and an overall reduction in water quality (Rothschild et al. 1994), oyster reefs are in decline globally (Kirby 2004). Although the Gulf of Mexico (GOM) is generally considered to have healthy reefs, efforts to conserve, restore, and create this habitat are beginning, and it is therefore appropriate to examine the functional support newly created reefs can provide.

Oysters create biogenic structure that plays an important role in the life history of many organisms. Besides providing important filtration services (Dame 1996) and carbon sequestration (Hargis and Haven 1999), oysters create complex structures that support an abundance of resident nekton (Bahr and Lanier 1981, Breitburg 1999, Luckenbach et al. 2005, Stunz et al. 2010). Mechanisms underlying this enhancement may be a direct result of structural complexity; complex structures can increase the number of diverse habitats and allow for potentially competing organisms to coexist by providing additional spawning substrate (Lehnert

and Allen 2002), spatial refuge from predation (Hixon 1998, Grabowski 2004), and greater forage availability. Because oyster reefs provide a lasting structure, they provide habitat for a temporally diverse assemblage of organisms in the estuaries through different seasons (Shervette and Gelwick 2008). Despite the enhanced survival and increased production of ecologically and economically important organisms on oyster reefs (Stunz et al. 2002), historically reefs have not been well-managed for ecological support (Beck et al. 2009).

The importance of wave exposure in shaping species assemblages in marine environments has long been recognized (Lewis 1964, McQuaid and Branch 1985, Menge 1991), but little is known about its significance in structuring nekton assemblages at oyster reefs in shallow estuarine environments. Oyster reef assemblages are often evaluated in comparison with different habitat types such as seagrass beds, salt marsh, or unstructured soft-bottom (e.g., Eggleston et al. 1998, Minello et al. 2003, Plunket and La Peyre 2005, Stunz et al. 2010), with relatively little attention on the influence of variations in the degree of wave exposure. Sustainable, healthy oyster reefs require an accumulation of accreting shell to compensate for sedimentation and degradation (Mann and Powell 2007, Schulte et al. 2009), as well as global sea-level rise and subsidence. Because an accumulation of shell is dependent upon rates of larval settlement (Breitburg et al. 1995) and delivery of food material and sediment (Sanford et al. 1994), hydrodynamics may directly impact the life history of oysters (Lenihan 1999), and thus, associated nekton assemblages.

This study investigated nekton assemblages and use of newly created oyster reefs over time in Caillou (Sister) Lake, Louisiana, and examined the relative influence of wave exposure in mediating community structure. The objectives of this study were to, (1) characterize and quantify species abundance, diversity, and biomass of nekton at and around newly created oyster

reefs (constructed from unaggregated shell), as well as mud-bottom habitat, through time, and (2) examine relationships among wave exposure and nekton communities (at oyster reef and mud-bottom treatments) to identify patterns of habitat use. Understanding nekton use patterns at newly created oyster reefs and surrounding mud-bottom habitat can help define the habitat role of oysters and the reefs they create.

Materials and Methods

Study Site

The study was conducted at Caillou (Sister) Lake, located in Terrebonne Parish, Louisiana (29°14' 11.09 N, 90°55' 16.48 W) (Fig. 1). Sister Lake is primarily an open water, brackish system with a mean tidal range of 0.3 ± 0.03 m (1 SE) (National Geodetic Vertical Datum). Water levels are driven primarily by wind events; dominant winds are typically from the southeast, except during the winter when northerly winds accompany cold fronts. Fetch distance can be quite large (> 7.5 km) and daily mean (± 1 SE) water temperature, salinity, and water level in the study area between 1997 and 2009 were $23.5 \pm 1.9^{\circ}\text{C}$, 12.0 ± 2.8 , and 0.33 ± 0.03 m, respectively (LDWF/USGS 07381349—Caillou Lake southwest of Dulac, LA, U.S.A.). Sister Lake has served as a state public oyster seed reservation since 1940, and oyster beds are abundant within the system.

Experimental Reef Placement and Deployment

In March 2009, three study sites were chosen within Sister Lake (Fig. 2). Within each study site, paired shorelines were identified as having either ‘low’ or ‘medium’ wave exposure. Energy classification was based on shoreline orientation, prevailing winds, and fetch distances,

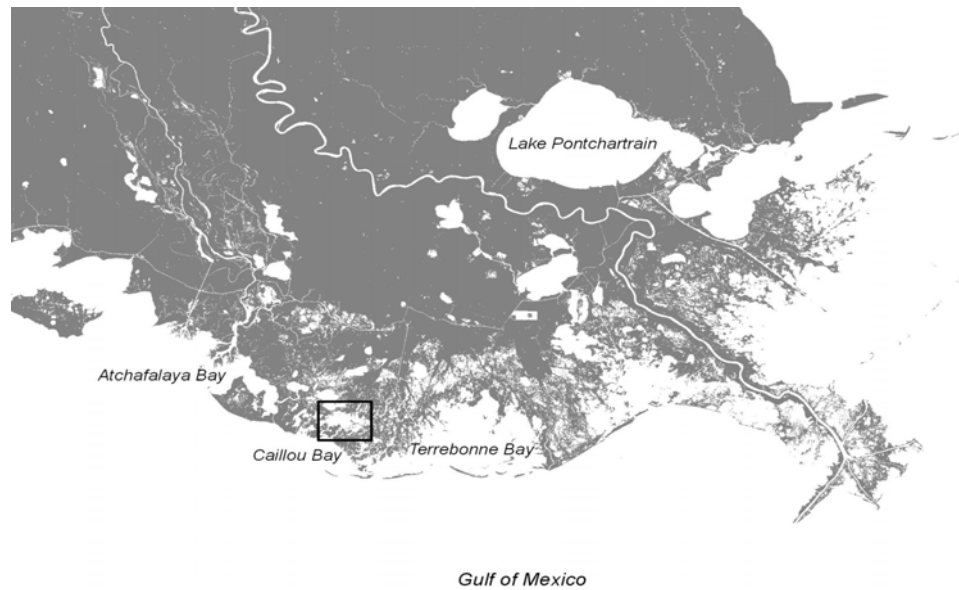


Fig. 1. Study site, Caillou (Sister) Lake, located in Terrebonne Parish, Louisiana, USA.

using methods similar to La Peyre and Birdsong (2008). At each shoreline, 25 m sections of oyster reef and mud-bottom treatment were selected with a minimum of 50 m between selected treatments (3 study sites x 2 shorelines x 2 treatments). Each treatment was delineated with PVC poles anchored in the sediment. Oyster reefs (25 x 1 x 0.7 m) were constructed in March 2009 with 17.5 m³ of shucked, unaggregated oyster shell using methods similar to Meyer et al. (1997) and Piazza et al. (2005). All reefs were placed as close to the shoreline as possible (5 - 10 m) and are subtidal. Plastic substrate trays (63 x 52 x 11 cm) lined with 0.5 mm mesh screening were placed in each oyster reef and at mud-bottom treatments ([6 oyster reefs + 6 mud-bottom treatments] x 3 substrate trays x 4 dates = 144 trays). Substrate in the trays matched that of the reef (oyster shell) or reference (mud-bottom) treatment.

Sampling Procedure

Water quality variables were taken concurrent with nekton sampling (June, August, December 2009, and March 2010) at each site. At each site, a YSI model 556 Multiprobe (YSI



Fig. 2. Shorelines (low [L] and medium [M] energy) established for sampling at Caillou (Sister) Lake. Nekton sampling occurred in June, August, and December 2009, and March 2010.

Inc., Yellow Springs, OH, U.S.A.) was used to determine temperature ($^{\circ}\text{C}$), salinity, and dissolved oxygen (mg l^{-1}). Although not always concurrent with sampling of nekton, turbidity was quantified by collecting monthly water samples at each treatment, placed on ice, and returned to the laboratory for analysis of total particulate matter (mg l^{-1}) using standard methods for the examination of water and wastewater (Taras 1971). Meteorological conditions of wind direction (degrees) and speed (m s^{-1}) during this study were downloaded from a continuous data recorder (LDWF/USGS 07381349—Caillou Lake southwest of Dulac, LA, U.S.A.).

To characterize nekton assemblages, we used a combination of sampling gears including gill nets, bag seine, and plastic substrate trays (Fig. 3). At each treatment, a gill net (50 x 1.75 m with 5, 7, 10, 12, 14 cm monofilament sections) was first deployed to form a semicircular

enclosure with the shoreline. Gill nets sampled larger transient fish that may be using the reef as foraging habitat. A bag seine (5 x 2 m with 3 mm square delta mesh) was then swept parallel to the shoreline, over mud-bottom, for a distance of 25 m. One sweep each was executed on either side of the treatment (reef or mud-bottom) and dragged to the shore where collected nekton were removed and placed in labeled bags on ice for identification in the laboratory. The bag seine sampled smaller transient species in areas adjacent to the treatment. Therefore, the same habitat type was seined in both treatments (mud-bottom). Instead of direct comparisons of species over mud-bottom and oyster reefs, comparisons using the bag seine were actually made between mud-bottom adjacent to created oyster reefs and mud-bottom with no adjacent reef (mud-bottom treatment). This examines the effect of nearby reef on mud-bottom species assemblages. Plastic substrate trays (n=3) at oyster reef treatments were randomly sampled, without replacement, by quickly lifting the trays and placing the contents in mesh bags (3 mm square delta mesh). Trays sampled resident species living within the oyster reef itself. Not all substrate trays were recovered for sampling due to logistical difficulties; a total of 90 substrate trays were sampled (June = 22, August = 29, December = 25, March = 14). Substrate tray contents were rinsed to remove excess sediment by sieving tray contents on site, and placing contents in labeled bags on ice. After substrate tray removal, substitute cultch was used to fill the hole flush with the reef surface. Substrate trays at reference treatments (mud-bottom) were anchored in the sediment using PVC poles and sampled with replacement. The gill net was then removed and all nekton were identified, weighed to the nearest 1 g (wet weight), and total length measured to the nearest 1 cm before being released on site.

In the laboratory, nekton from seine and substrate tray samples were identified to species or the lowest feasible taxon. Individuals of a species in each sample were weighed to the nearest

0.1 g (wet weight) and measured to the nearest centimeter of total length for fishes and shrimps, or carapace width (CW) for crabs. Thirty individuals were randomly subsampled to obtain lengths and weights of individuals from abundant species ($n > 30$).

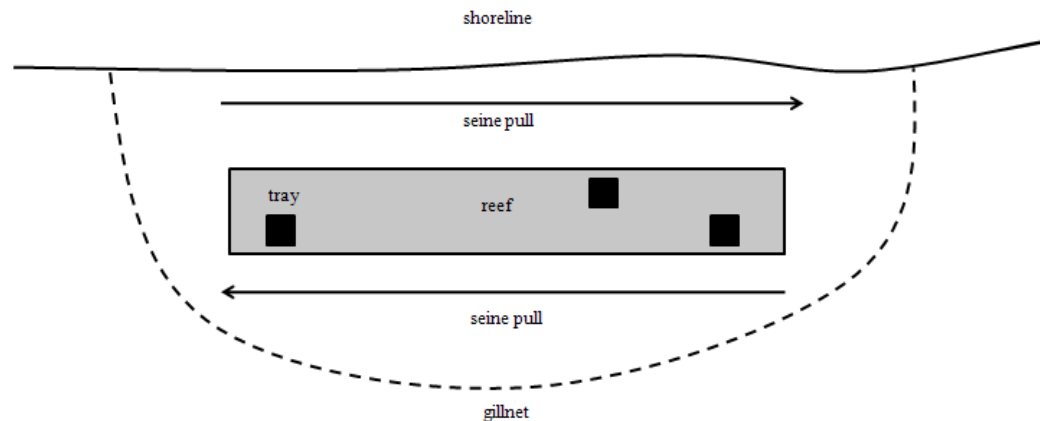


Fig. 3. Nekton sampling design at oyster reef treatments. Gill net (50 m) was set and seine pulls (25 m) were made in front of and behind the oyster reef, emptying contents between pulls. Substrate trays (63 x 52 x 11 cm) were then pulled and gill net removed.

Statistical Analyses

Multivariate analysis of variance (MANOVA) (SAS version 9.1; SAS Institute, Inc., Cary, NC, U.S.A., 2002) was used to test whether water quality variables (temperature, salinity, dissolved oxygen, turbidity), compared simultaneously, differed among sites and between wave exposure (low and medium energy) or treatment (reef and mud-bottom). Wind speed and direction were used to calculate an index of exposure and this was used to validate wave energy level within sites and used in subsequent analyses (as the 'exposure' variable in Canonical Correspondence Analysis below). Comparisons of least squared means, using a one-way analysis of variance (ANOVA), followed by Tukey's Studentised Range tests, were conducted for any significant ($p < 0.05$) MANOVA models (data are reported as mean \pm 1 SE unless indicated differently).

MANOVA was used to test whether abundance (catch per unit effort; CPUE), species diversity (Shannon diversity index; H'), or biomass, compared simultaneously, differed among sites or sample date, or between wave exposure (low and medium energy) or treatment (reef and mud-bottom). The Shannon diversity index is a common ecological measurement of biodiversity (Shannon 1948). Analyses were performed on the entire data set (all gear types), then by individual gear type. To check for homogeneity of variance, we assessed homoscedasticity by inspection of the residuals and no transformations were necessary. All values were tested 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 CPUE and biomass data. Simpson's diversity index (D), which measures the probability that two individuals randomly selected from a sample will belong to the same species (Simpson 1949), and species richness (number of species present) were not used as they were highly correlated with H' ($p < 0.01$).

ANOVA was used to test whether resident and transient species differed among sites or sample date, or between wave exposure (low and medium energy) or treatment (reef and mud-bottom). Resident species were defined as those dependent on oyster reefs as their primary habitat and spend their entire life in the estuary (e.g. *Hypsoblennius ionthas*, *Gobiosoma bosc*) (Breitburg 1999, Peterson et al. 2003). Transient species were defined as those that may spawn offshore and use the estuarine habitat as nursery areas (e.g. *Leiostomus xanthurus*, *Sciaenops ocellatus*) (Baltz et al 1993).

To compare nekton assemblages among dates and between wave exposure and treatments, a two-way crossed analysis of similarity (ANOSIM) was performed on a reduced, raw species abundance matrix using PRIMER statistical software (version 6.1.9; Clark and

Warwick 2001). The reduced species abundance matrix contained only species whose abundance accounted for more than 3% of the total catch (Gauch 1982). Next, similarity percentages analysis (SIMPER) was conducted on the raw species abundance matrix to determine which species contributed the most to the similarities or dissimilarities. The analyses were performed on the entire data set (all gear types), then by individual gear type, comparing sample date, wave exposure, and treatment.

Canonical Correspondence Analysis (CCA) (CANOCO version 4.5; ter Braak and Smilauer 2002) was used on the same reduced species abundance matrix used in PRIMER to relate nekton assemblage structure to environmental variables (temperature, salinity, wave exposure, and a dummy variable for “REEF” treatment). As in PRIMER, CCA analyses were first performed on the entire data set (all gear types), then by individual gear types. CCA is a direct-gradient analysis that relates community variation patterns to environmental variation. All canonical axes were tested for significance with 499 Monte Carlo simulations on the full model.

Results

Environmental Variables

Water temperature varied seasonally and daily temperature ranged between 2 and 34 °C (mean \pm 1 SE; 22.0 ± 0.4) throughout the 12 mo sampling period, with highest temperatures in August and lowest in December (Table 1). Daily salinity ranged from 0 to 23 (mean \pm 1 SE; 8.6 ± 0.3) and was highest in August and lowest in June. Dissolved oxygen ranged between 4 and 11 mg l⁻¹ at shorelines and was highest in December and lowest in August. Turbidity varied seasonally and ranged between 12 and 252 mg l⁻¹ and was highest at all shorelines in December and lowest in August. MANOVA detected no significant ($p < 0.05$) differences in environmental variables among sites, or between shorelines or treatments.

Table 1. Environmental variables (mean \pm 1 SE) collected at June, August, December 2009, and March 2010 sample dates at Sister Lake, Terrebonne Parish, Louisiana. Mean temperature ($^{\circ}\text{C}$), salinity, and dissolved oxygen (mg l^{-1}) recorded using a YSI Model 556 multiprobe, and turbidity (ml l^{-1}) collected and presented as total particulate matter. There were no significant differences ($p < 0.05$) between wave exposure (low and medium energy) or treatments (reef and mud bottom).

	June	Aug	Dec	Mar
Temperature ($^{\circ}\text{C}$)	27.9 (0.4)	29.4 (0.4)	14.7 (0.4)	17.4 (0.2)
Salinity	5.9 (0.6)	11.2 (0.9)	7.8 (0.1)	7.6 (0.6)
DO (mg l^{-1})	7.9 (0.3)	6.9 (0.4)	9.2 (0.3)	8.1 (0.1)
Turbidity (TSS)	83.6 (4.1)	23.7 (1.8)	99.3 (24.7)	26.5 (5.1)

Species Abundance, Diversity, and Biomass

A total of 9,133 individuals from 44 species and 30 families were collected in 32 gill nets, 96 seine hauls, and 90 substrate trays over the course of four sampling events from June 2009 to March 2010 (Table 2).

MANOVA indicated that, CPUE, H' , and biomass did not differ significantly among sites. In one-way ANOVAs, CPUE differed significantly by date and treatment, with March 2010 CPUE greater than June, August or December 2009 (CPUE, $F_{3,40} = 8.95$, $p < 0.001$), and oyster reef CPUE greater than mud-bottom (CPUE, $F_{1,40} = 6.93$, $p = 0.012$) (Table 3; Fig. 4). CPUE did not differ significantly by wave exposure, although H' differed significantly by date (H' , $F_{3,39} = 10.03$, $p < 0.001$), wave exposure (H' , $F_{1,39} = 5.66$, $p = 0.023$), and reef (H' , $F_{1,39} = 29.54$, $p < 0.001$) (Table 3; Fig. 5). H' was significantly greater at oyster reefs (1.8 ± 0.1), and March 2010 H' (1.0 ± 0.1) was significantly lower than all other dates. Low wave exposure shorelines had significantly greater H' than medium wave exposure shorelines (1.7 ± 0.1 and 1.4 ± 0.1 , respectively). No significant results were detected when using biomass as the response variable.

One-way ANOVAs indicated that gill net CPUE and H' were not significantly different between wave exposures, but were significantly greater at oyster reefs than mud-bottom (CPUE, $F_{1,43} = 6.95$, $p = 0.011$; H' , $F_{1,43} = 4.85$, $p = 0.033$) (Table 3; Fig. 4). Gill net biomass was not significantly different between wave exposures or treatments. Date had a significant effect on gill net H' ($F_{3,44} = 4.41$, $p = 0.009$) with lower H' for the March 2010 sample date (Fig. 5). Date did not have a significant effect on gill net CPUE or biomass. Sheepshead (*Archosargus probatocephalus*), gulf menhaden (*Brevoortia patronus*), striped mullet (*Mugil cephalus*), and black drum (*Pogonias cromis*) accounted for 69% of the total gill net catch and occurred in the majority of gill net samples.

One-way ANOVAs indicated that seine CPUE, H' , and biomass were not significantly different between wave exposures or treatments (Table 3; Fig. 4). Date had a significant effect on seine CPUE ($F_{3,44} = 18.37$, $p < 0.001$) and H' ($F_{3,44} = 5.37$, $p = 0.003$), but not biomass; there was lower CPUE at the August 2009 sample date and higher CPUE at the March 2010 sample date, and higher H' at the June 2009 sample date (Fig. 5). Bay anchovy (*Anchoa mitchilli*), gulf menhaden, and grass shrimp (*Palaemonetes pugio*) accounted for over 80% of the total seine catch and occurred in the majority of seine samples.

One-way ANOVAs indicated that substrate tray CPUE, H' , and biomass were not significantly different between wave exposure, but were all significantly greater at oyster reefs than mud-bottom (CPUE, $F_{1,88} = 49.65$, $p < 0.0001$; H' , $F_{1,85.2} = 52.01$, $p < 0.0001$; biomass, $F_{1,85.7} = 70.01$, $p < 0.0001$) (Table 3; Fig. 4). Date did not have a significant effect on CPUE, but did on H' ($F_{3,86} = 5.37$, $p = 0.002$) with lower H' for the March 2010 sample date (Fig. 5). Atlantic mud crab (*Panopeus herbstii*) and naked goby (*Gobiosoma bosc*) accounted for over 70% of the total substrate tray catch and occurred in the majority of substrate tray samples.

Resident species (see Table 2 for individuals) CPUE and H' did not differ by wave exposure as indicated by a one-way ANOVA, but CPUE was significantly greater at oyster reefs than mud-bottom (CPUE, $F_{1,43} = 11.53$, $p = 0.001$) (Table 3). Transient species (see Table 2 for individuals) CPUE and H' did not differ by wave exposure or treatment. Date did not have a significant effect on overall resident or transient CPUE or H' . Biomass was excluded from analyses because it was highly correlated with CPUE ($p < 0.001$) when species were grouped into resident or transient assemblages.

Nekton Assemblages

The CCA for the entire data set (all gear types) with temperature as a proxy for season indicated a strong relationship between nekton assemblages and environmental variables (Table 4). The first axis accounted for 54 % of the variance and was correlated with season (TEMP; $r = 0.90$) and treatment (REEF; $r = 0.51$) (Fig. 6). Species associated with warmer temperatures, or June and August 2009 sample dates, included Atlantic croaker (for all species codes, see Table 2; MU), naked goby (GB), skilletfish (GS), hardhead catfish (AF), and brown shrimp (FA). Species associated with cooler temperatures, or December 2009 and March 2010 sample dates, included spot (LX) and gulf menhaden (BP). SIMPER analysis corroborated these groupings, indicating that naked goby and brown shrimp were more abundant at warmer temperatures and spot and gulf menhaden at cooler temperatures (ANOSIM; $r = 0.272$, $p = 0.001$; 83 % different). Species associated with oyster reefs included Atlantic mud crab (PH), freckled blenny (HI), and bay anchovy (AM), whereas species associated with mud-bottom included spot, gulf menhaden, and grass shrimp. SIMPER also supported these groupings (ANOSIM: $r = 0.178$, $p = 0.002$; 78 % different). The second axis accounted for 28 % of the variance and was negatively correlated with wave exposure ($r = -0.73$). Bay anchovy was associated with more exposed (medium

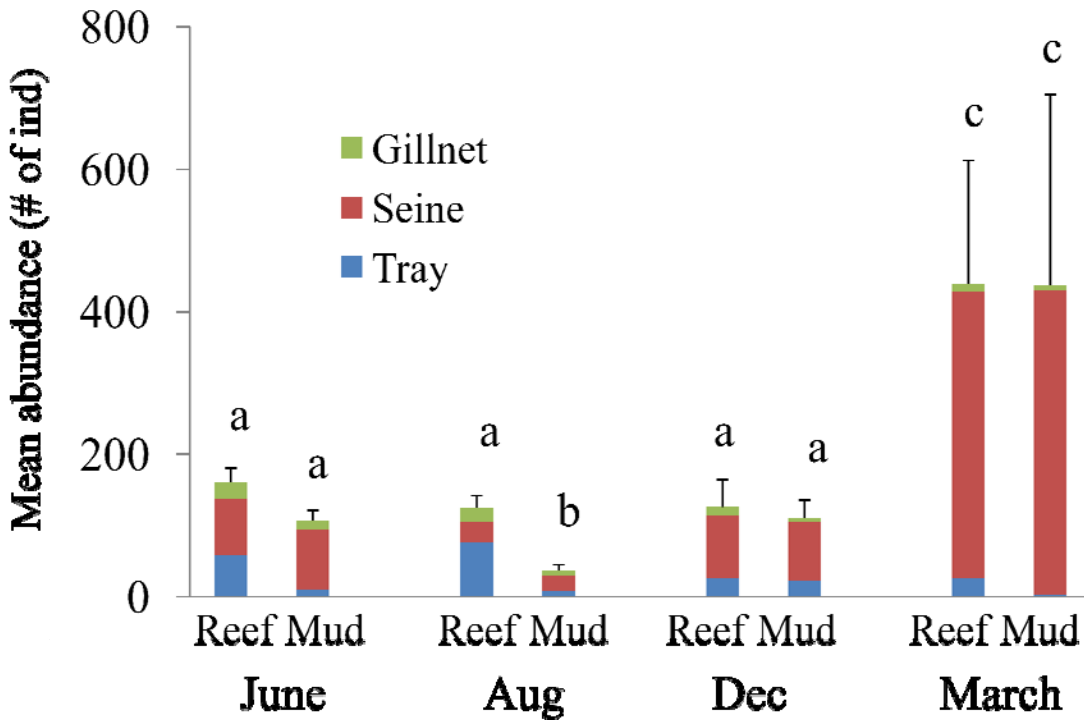


Fig. 4. Mean abundance (# of ind \pm 1 SE) by sample date (June, August, December 2009, and March 2010) of all species collected at oyster reef and mud-bottom treatments at gill net ($n = 48$), seine ($n = 48$) and substrate trays ($n = 90$). Treatments with different letters resulted in significant differences (one-way ANOVA, $p > 0.05$).

energy) shorelines, but assemblages were not significantly different based on ANOSIM and SIMPER analyses.

The CCA of the gill net catch indicated a relationship between nekton assemblages and environmental variables (Table 4). The first axis accounted for 68 % of the variance and was negatively correlated with season (TEMP; $r = -0.96$) (Fig. 7). Hardhead catfish, Atlantic croaker, and Gulf menhaden were associated with warmer temperatures, in June and August 2009, and

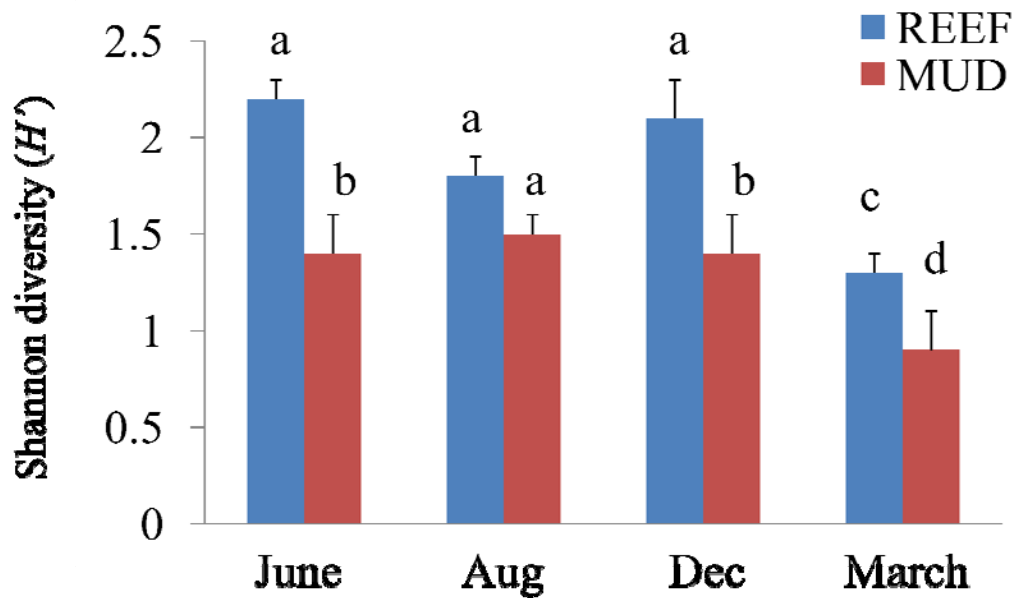


Fig. 5. Mean Shannon diversity ($H' \pm 1$ SE) by sample date (June, August, December 2009, and March 2010) of all species collected at oyster reef and mud-bottom treatments. Means were computed from 6 samples at each treatment per sample date. Bars with different letters resulted in significant differences (one-way ANOVA, $p > 0.05$).

sheepshead (AP) and red drum (SO) were associated with cooler temperatures. SIMPER analyses corroborated these groupings (ANOSIM; $r = 0.236$, $p = 0.001$; > 74 % different). The second axis accounted for 25 % of the variance and was correlated with salinity ($r = 0.88$). No species was strongly correlated with salinity.

The CCA of the seine catch indicated a relationship between nekton assemblages and environmental variables (Table 4). The first axis accounted for 46 % of the variance and was correlated with season (TEMP; $r = 0.86$) (Fig. 8). Brown shrimp were associated with warmer temperatures. SIMPER analyses indicated that bay anchovy had the most influence on dissimilarities among seasons (ANOSIM; $r = 0.269$, $p = 0.001$; > 87 % different). The second axis accounted for 37 % of the variance and was correlated with wave exposure ($r = -0.71$).

Table 2. Total catch and mean catch per unit effort (± 1 SE) for all gear types, by species for June, August, December 2009 and March 2010 sample dates at oyster reef and mud-bottom treatments in Sister Lake, Terrebonne Parish, Louisiana. Means calculated from a total of 186 samples (gill net = 48, seine = 48, tray = 90). Species classifications based on Baltz et al (1993), Breitburg (1999), and Peterson et al. (2003).

Species	Code	Classification	Mud bottom				Oyster reef				Total
			Medium energy		Low energy		Medium energy		Low energy		N
			N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	
<i>Brevoortia patronus</i>	BP	trans	1629	67.9 (60.5)	74	3.0 (1.5)	106	4.4 (2.7)	875	36.4 (30.2)	2684
<i>Anchoa mitchilli</i>	AM	trans	637	19.9 (16.6)	129	10.4 (3.2)	1254	104.5 (90.2)	355	29.6 (13.4)	2375
<i>Palaemonetes pugio</i>	PP	res	197	12.1 (6.1)	381	26.3 (10.7)	276	20.8 (12.7)	280	20.8 (9.1)	1134
<i>Panopeus herbstii</i>	PH	res	17	2.1 (0.7)	5	0.6 (0.6)	365	45.6 (6.7)	298	26.9 (5.1)	685
<i>Leiostomus xanthurus</i>	LX	trans	33	2.8 (1.9)	205	17.1 (10.6)	68	5.7 (3.7)	100	8.3 (5.8)	406
<i>Farfantepenaeus aztecus</i>	FA	trans	67	5.6 (4.4)	95	7.9 (4.0)	19	1.1 (0.7)	100	8.3 (3.6)	281
<i>Gobiosoma bosc</i>	GB	res	10	0.4 (0.3)	18	0.5 (0.3)	113	3.5 (1.7)	67	0.5 (0.3)	208
<i>Mugil cephalus</i>	MC	trans	81	3.4 (2.6)	37	1.4 (0.4)	39	1.6 (0.6)	39	1.6 (1.0)	196
<i>Micropogonias undulatus</i>	MU	trans	6	0.3 (0.1)	71	3.0 (4.2)	18	0.8 (0.4)	81	3.4 (2.8)	176
<i>Bairdiella chrysoura</i>	BC	trans	37	3.1 (1.7)	46	3.8 (2.8)	36	1.5 (3.1)	17	1.4 (1.4)	136
<i>Pogonias cromis</i>	PC	trans	23	1.9 (0.8)	23	1.8 (0.6)	20	1.7 (0.5)	54	4.5 (1.5)	120
<i>Gobiesox strumosus</i>	GS	res	3	0.4 (0.3)	0		60	7.5 (1.6)	49	4.5 (2.3)	112
<i>Menidia beryllina</i>	MB	res	22	1.8 (0.9)	47	3.9 (2.4)	18	1.5 (0.6)	13	1.1 (0.6)	100
<i>Callinectes sapidus</i>	CS	trans	16	0.5 (0.3)	22	0.6 (0.3)	30	0.9 (0.8)	16	0.5 (0.2)	84
<i>Archosargus probatocephalus</i>	AP	trans	20	1.7 (1.1)	8	0.7 (0.4)	24	2.0 (1.1)	25	2.1 (0.8)	77
<i>Arius felis</i>	AF	trans	4	0.3 (0.2)	19	1.6 (0.9)	9	0.8 (0.3)	29	2.4 (1.4)	61
<i>Penaeus setiferus</i>	PS	trans	6	0.5 (0.3)	32	2.7 (1.7)	17	1.4 (1.3)	5	0.4 (0.3)	60
<i>Hypsoblennius ionthas</i>	HI	res	0		0		26	3.3 (1.3)	11	1.0 (0.5)	37
<i>Sciaenops ocellatus</i>	SO	trans	3	0.3 (0.1)	7	0.6 (0.2)	7	0.6 (0.3)	19	1.5 (0.9)	36
<i>Myrophis punctatus</i>	MP	res	1	0.1 (0.1)	0		15	1.9 (0.9)	15	1.4 (0.7)	31
<i>Paralichthys lethostigma</i>	PL	trans	4	0.3 (0.3)	4	0.2 (0.1)	9	0.7 (0.3)	3	0.1 (0.1)	20
<i>Cynoscion nebulosus</i>	CN	trans	2	0.1 (0.1)	7	0.3 (0.2)	2	0.1 (0.1)	5	0.4 (0.2)	16
<i>Fundulus grandis</i>	FG	res	5	0.4 (0.3)	3	0.3 (0.3)	7	0.6 (0.6)	1	0.1 (0.1)	16
<i>Anchoa hepsetus</i>	AHP	trans	0		14	1.2 (0.9)	1	0.1 (0.1)	0		15

Table 2 continued.

Species	Code	Classification	Mud bottom				Oyster reef				Total
			Medium energy		Low energy		Medium energy		Low energy		N
			N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	
<i>Elops saurus</i>	ES	trans	2	0.2 (0.1)	0		1	0.1 (0.1)	6	0.3 (0.2)	9
<i>Rhithropanopeus harrisii</i>	RH	res	0		0		8	0.9 (0.6)	0		8
<i>Alosa chrysochloris</i>	AC	trans	0		0		7	0.6 (0.7)	0		7
<i>Lucania parva</i>	LP	res	0		0		1	0.1 (0.1)	5	0.4 (0.4)	6
<i>Opsanus beta</i>	OB	res	0		0		2	0.3 (0.1)	4	0.4 (0.2)	6
<i>Adinia xenica</i>	AX	res	0		0		4	0.3 (0.4)	0		4
<i>Bagre marinus</i>	BM	trans	0		3	0.3 (0.2)	1	0.1 (0.1)	0		4
<i>Cyprinodon variegates</i>	CV	res	0		2	0.2 (0.2)	2	0.2 (0.2)	0		4
<i>Carcharhinus leucas</i>	CL	trans	0		0		1	0.1 (0.1)	2	0.2 (0.1)	3
<i>Eucinostomus argenteus</i>	EA	trans	0		2	0.2 (0.2)	0		0		2
<i>Fundulus pulvereus</i>	FP	res	0		0		2	0.2 (0.2)	0		2
<i>Fundulus majalis</i>	FM	res	0		0		2	0.2 (0.1)	0		2
<i>Lagodon rhomboides</i>	LR	trans	1	0.1 (0.1)	1	0.1 (0.1)	0		0		2
<i>Synodus foetens</i>	SF	trans	0		1	0.1 (0.1)	0		1	0.1 (0.1)	2
<i>Alpheus heterochaelis</i>	AH	res	0		0		1	0.1 (0.1)	0		1
<i>Chaetodipterus faber</i>	CF	trans	0		0		0		1	0.1 (0.1)	1
<i>Chasmodes bosquianus</i>	CB	res	0		0		0		1	0.1 (0.1)	1
<i>Cynoscion arenarius</i>	CA	trans	0		0		1	0.1 (0.1)	0		1
<i>Dasyatis sabina</i>	DS	trans	1	0.1 (0.1)	0		0		0		1
<i>Lutjanus griseus</i>	LG	trans	0		0		0		1	0.1 (0.1)	1

Table 3. Results of ANOVA testing for significant differences in abundance (catch per unit effort, CPUE; # ind), species diversity (H'), and biomass (g), for all gear types, by sample date (June, August, and December 2009 and March 2010), shoreline (low and medium energy), and treatment (reef and mud bottom). See Table 2 for species composition of residents and transients. Mean values (± 1 SE) are presented; * $p < 0.05$.

	Sample date				Shoreline		Treatment	
	June 09	Aug 09	Dec 09	Mar 10	Low energy	Medium energy	Oyster reef	Mud bottom
All gear types (n = 186)								
Abundance (CPUE)	130.7 (15.0)	79.8 (16.1)	117.8 (21.9)	435.8 (152.1)*	156.8 (35.4)	225.3 (78.6)	211.5 (49.8)*	170.5 (70.8)*
Diversity (H')	1.8 (0.1)	1.6 (0.1)	1.7 (0.2)	1.0 (0.1)*	1.7 (0.1)	1.4 (0.1)	1.8 (0.1)*	1.3 (0.1)*
Biomass (kg)	7.9 (3.3)	3.3 (0.7)	8.3 (1.8)	6.9 (2.1)	8.6 (2.0)	4.6 (0.8)	8.6 (1.9)	7.9 (1.0)
Gillnet (n = 48)								
Abundance (CPUE)	17.8 (5.7)	13.8 (4.1)	8.3 (1.8)	8.3 (2.1)	14.5 (3.5)	9.6 (1.5)	16.5 (3.4)*	7.7 (1.4)*
Diversity (H')	1.8 (0.2)	1.9 (0.2)	1.4 (0.2)	1.0 (0.2)*	1.7 (0.1)	1.4 (0.2)	1.7 (0.1)*	1.3 (0.2)*
Biomass (g)	7821 (7274)	3187 (650)	8257 (1831)	6737 (2121)	8483 (1964)	4518 (828)	8503 (1877)	4498 (1007)
Seine (n = 48)								
Abundance (CPUE)	82.1 (8.9)	24.8 (8.3)*	85.8 (20.3)	415.6 (151.4)*	118.5 (35.8)	185.7 (79.3)	149.2 (51.6)	154.9 (70.8)
Diversity (H')	2.3 (0.2)*	1.1 (0.2)	1.9 (0.3)	1.7 (0.2)	1.9 (0.1)	1.5 (0.2)	1.6 (0.2)	1.9 (0.1)
Biomass (g)	80.1 (15.2)	108.3 (61.4)	34.9 (7.3)	109.6 (26.1)	79.1 (16.3)	87.3 (30.7)	98.7 (31.4)	67.7 (14.3)
Substrate trays (n = 90)								
Abundance (CPUE)	16.8 (2.6)	17.0 (3.3)	11.4 (2.1)	10.2 (2.6)	13.6 (1.7)	15.0 (2.2)	19.0 (1.7)*	6.0 (1.7)*
Diversity (H')	0.8 (0.1)	1.1 (0.1)	1.1 (0.1)	0.3 (0.1)*	0.9 (0.1)	0.9 (0.1)	1.2 (0.1)*	0.4 (0.1)*
Biomass (g)	7.5 (1.5)	22.1 (4.8)	12.2 (3.7)	6.7 (1.7)	11.9 (2.8)	14.7 (2.8)	19.4 (2.8)*	2.5 (0.5)*
Nekton type (n = 186)								
Residents (CPUE)	49.0 (8.9)	51.2 (14.2)	60.3 (17.2)	28.9 (9.4)	48.8 (7.5)	45.9 (10.7)	67.0 (9.9)*	27.7 (6.1)*
Transients (CPUE)	51.4 (8.3)	20.3 (4.8)	31.5 (12.1)	228.0 (132.8)	37.5 (7.7)	128.1 (68.2)	73.3 (34.0)	92.4 (61.1)

Bay anchovy was associated with more exposed shorelines (medium energy). SIMPER analysis was not significant for exposure.

The CCA of the substrate tray catch indicated a relationship between nekton assemblage and environmental variables (Table 4). The first axis accounted for 83 % of the variance and was negatively correlated with treatment (REEF; $r = -0.96$) and season (TEMP; $r = -0.63$) (Fig. 9). Atlantic mud crab, skilletfish, naked goby, and freckled blenny were associated with oyster reefs and warmer temperatures. SIMPER analysis corroborated these groupings, indicating Atlantic mud crab and skilletfish were more abundant at oyster reefs (ANOSIM; $r = 0.612$, $p = 0.001$; 90 % different). The second axis accounted for only 11 % of the variance and was correlated with season (TEMP; $r = 0.72$). Skilletfish, naked goby, and freckled blenny were associated with warmer temperatures. SIMPER analysis was not significant for season.

Table 4. Canonical correspondence analysis results of nekton assemblage structure and environmental variables. Presented are total inertia, eigenvalue, and the significance of all canonical axes (p-value) of 499 Monte Carlo permutations of the full model. Species contributing less than 3 % of total catch, by gear type, were excluded from analysis.

	Total inertia	Eigenvalue	Significance of all canonical axes
All gear types	2.695	0.375	0.002
Gillnet	1.856	0.279	0.002
Seine	2.260	0.273	0.002
Substrate trays	1.735	0.557	0.002

Discussion

Although there were very few significant effects on transient species assemblages directly attributable to the presence of oyster reefs, reefs appeared to benefit resident species as they supported greater numbers of resident species as compared to mud-bottom. Since the reefs were newly created using clean disarticulated shell piles, this finding suggests that the presence

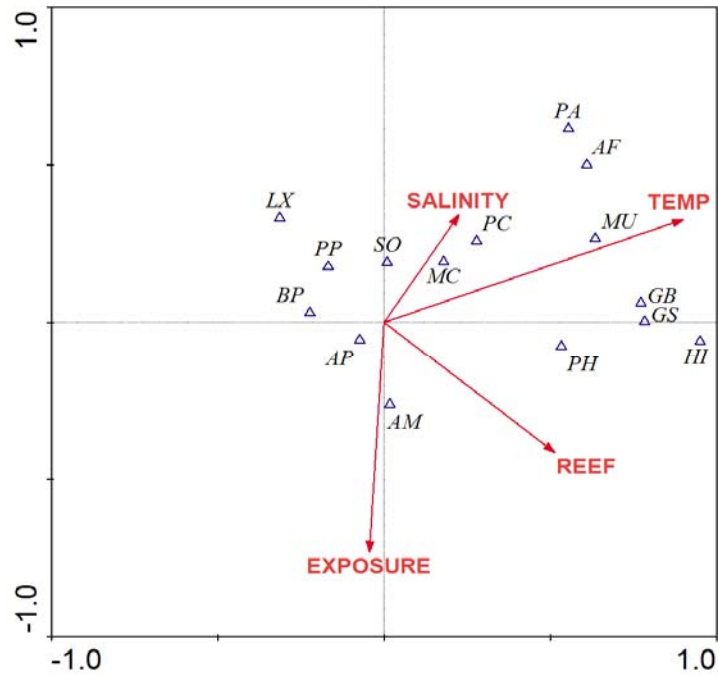


Fig. 6. Association of nekton species and environmental characteristics from a canonical correspondence analysis for the entire data set (all gear types combined). Species codes are listed in Table 2.

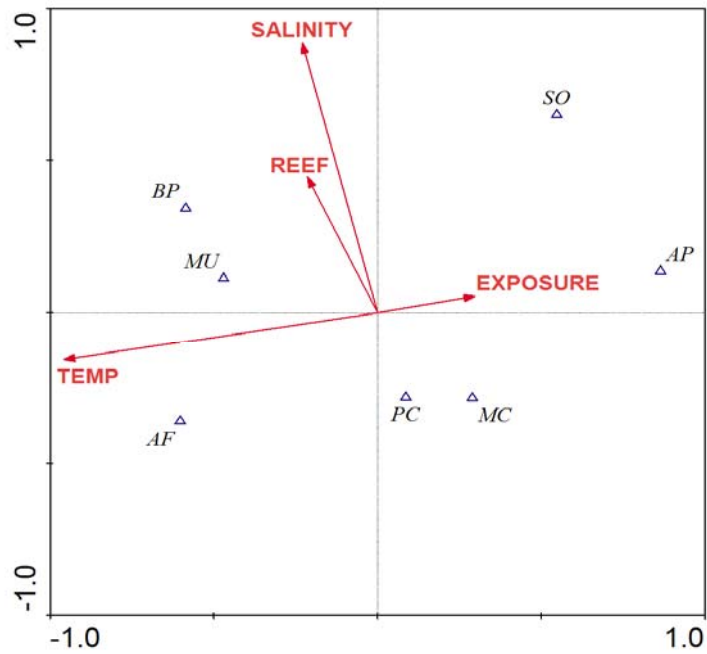


Fig. 7. Association of nekton species and environmental characteristics from a canonical correspondence analysis for gill net catch. Species codes are listed in Table 2.

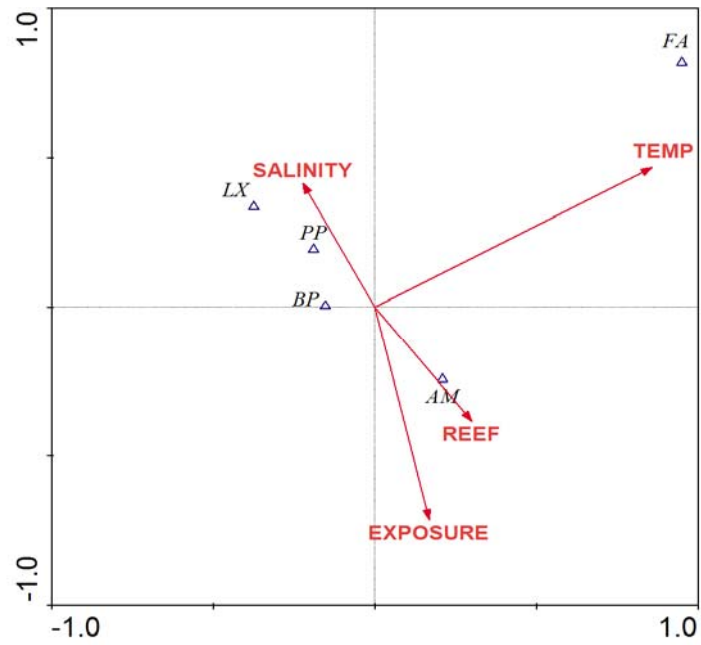


Fig. 8. Association of nekton species and environmental characteristics from a canonical correspondence analysis for seine catch. Species codes are listed in Table 2.

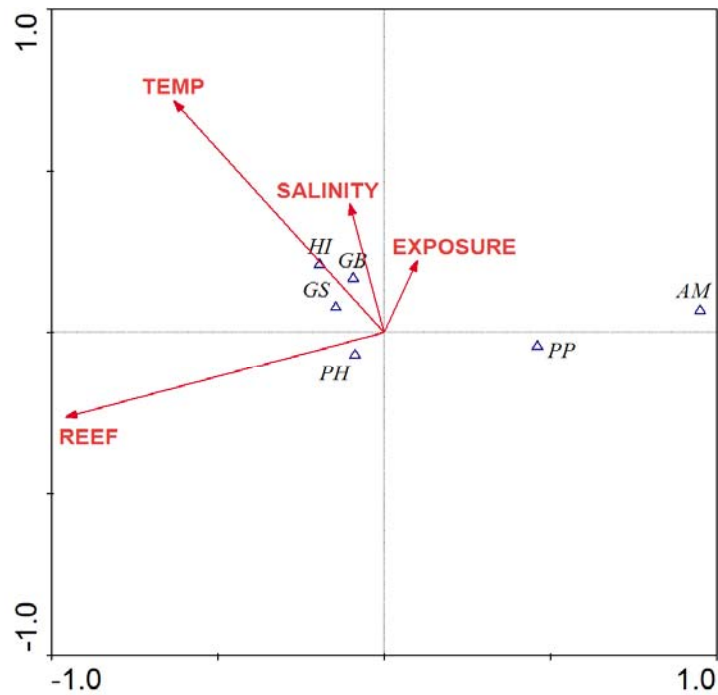


Fig. 9. Association of nekton species and environmental characteristics from a canonical correspondence analysis for substrate tray catch. Species codes are listed in Table 2.

of shell structure per se, and not the provision of food or other resources, provides valuable habitat to resident species; this finding is interesting from a theoretical stand point as it suggests that for resident species, a reefs primary value may result purely from its structure. That said, it is unclear without further sampling of these communities how the resident and transient communities will respond over time as the reef recruits and grows oysters, building the reef in size and complexity. At a minimum however, this one year of field data suggests that shell reefs provide some type of valuable habitat (possibly refuge) for resident species, and secondly, suggests to managers that reef creation with the goal of supporting resident species may not require complicated engineering.

Species assemblages were consistently more abundant and diverse on and around oyster reefs than at mud-bottom treatments. Forty-two of the 44 species identified in our study were collected near oyster reefs as compared to 30 over mud-bottom treatments. The occurrence and prevalence of resident species appeared to be directly related to the presence of oyster reefs, with greater than 70 % of residents occurring at reef treatments. For example, the Atlantic mud crab and skillettfish were two of the most abundant species found at oyster reefs. The mud crab is a predator on oysters and other mollusks (Dame and Patten 1981) and skillettfish is a marsh resident in the northern GOM (Baltz et al. 1993) whose diet consists primarily of small crustaceans and are attracted to dead oysters (Boschung and Mayden 2004). Other studies have also documented the dominance of these species in oyster habitat (e.g., Wells 1961, Zimmerman et al. 1989, Glancy et al. 2003).

The three most abundant species in our study were bay anchovy, gulf menhaden, and grass shrimp. These species were extremely abundant and showed no significant habitat preference; they are ubiquitous throughout northern GOM estuaries and similar results have been

reported (e.g., Baltz et al. 1993, Stunz et al. 2010). These species were also not caught with any regularity in the experiment in Chapter 3, but this may be due to the relatively small area sampled using the drop sampler (1 m²). Interestingly, intermediate size predators showed little evidence for habitat preference even though higher abundances of resident species occupied oyster reefs. This may result from a trade-off between attraction to foods and predation risk, where, although foods were more abundant at oyster reefs, so was the potential predation pressure.

When developing a sampling design, one of the most important decisions is gear selection (Rozas and Minello 1997). Some species may have been underrepresented in the total catch because of our inability to directly sample on the oyster reefs (e.g., bag seine). There have been restraints from gear limitations for sampling at oyster reefs (but see Zimmerman et al. 1989, Stunz et al. 2010) and the use of other sampling techniques (e.g., drop sampler, lift nets, SCUBA) were not logistically feasible for the reefs in this study. For example, lifts nets are arguably the most successful technique for quantitatively sampling oyster reefs (Tolley and Volety 2005), but require predictable receding tides at intertidal reefs. In the northern GOM, meteorological events often dominate astronomical tides (Rozas 1995) and therefore make lift nets difficult to use.

Spatial Variation and Nekton Use

Oyster reefs supported higher abundances and more diverse resident assemblages, but transient assemblages were less influenced by the presence of reefs. While direct comparisons between studies might be complicated by differences in sampling techniques (Rozas and Minello 1997), our results agree with similar findings in different systems where oyster reefs increased resident organisms living within the shell matrix (e.g., Zimmerman et al. 1989, Breitburg 1999,

Lehnert and Allen 2002, Glancy et al. 2003, Shervette and Gelwick 2008, Stunz et al. 2010), but transient communities were not significantly affected (e.g., Harding and Mann 1999, 2001, Dame et al. 2002, Grabowski et al. 2005, Luckenbach et al. 2005). Even though the evidence has been equivocal, many of these studies still attribute oyster reefs with enhancements in the production of non-resident fishes and large mobile crustaceans (Geraldi et al. 2009). Further research is necessary in verifying the overall importance of oyster reefs for transient assemblages.

Determining the appropriate spatial scale at which to evaluate ecological processes is critical, and thus, the surrounding landscape may exert strong control on communities and mediate species assemblages (Turner 1989). For example, while oyster reefs have been shown to increase the abundance of juvenile fishes when placed in areas surrounded by mud flats, they may not have a significant impact when placed in areas adjacent to salt marsh or seagrass meadows (Grabowski et al. 2005). Also, the addition of oyster reefs may not significantly increase the abundance or biomass of mobile fishes and crustaceans in tidal creeks surrounded by salt marsh (Geraldi et al. 2009). Grabowski et al. (2005) and Geraldi et al. (2005) both cite the possibility of functional redundancy of nearby biogenic habitats. Oyster reefs in this study were placed as close (5 -10 m) to the shoreline (salt marsh) as possible while still maintaining a primarily subtidal position. As previously described, the seine was pulled directly over mud-bottom habitat adjacent to oyster reefs, or at treatments without reefs, and therefore may have effectively been sampling marsh edge habitat. Very few differences existed between combined abundances at oyster reefs and mud-bottom treatments for the seine catch; although reefs increased the overall abundance of resident nekton, they may be functionally redundant with the surrounding salt marsh edge in providing additional habitat for non-resident species. In fact,

nekton abundance and diversity have been shown to be similarly high between oyster reefs and vegetated marsh edge (Shervette and Gelwick 2008). The surrounding habitat and treatment location within the estuary may explain some of the temporal and spatial differences observed in species assemblages.

The methods of oyster reef creation may influence the habitat complexity in an area and thus have community-level impacts. Inconsistencies in methods across systems and investigators may complicate direct comparisons. The oyster reefs in this study were created using unaggregated shells, piled upon one another. This method is similar to the simple or low complexity reefs created by others (e.g., Grabowski 2004, Grabowski and Powers 2004, Grabowski et al. 2008). Shell orientation can affect the availability of refugia and that fish species may show a high affinity for vertically oriented oyster shell as compared to horizontally oriented shell (Soniati et al. 2004). Thus, our methods could have effectively created lower habitat complexity than vertically oriented shell (or an aggregated shell matrix) that is typically associated with healthy oyster reefs. With less diversity, the amount of available refugia or spawning substrate may be limited. Trophic cascades have been shown to be influenced by the habitat complexity created by reefs constructed from unaggregated shell versus aggregated oyster clusters (Grabowski and Kimbro 2005). While there may be indirect effects attributable to reef creation methods, it has also been shown that assemblages did not differ significantly between unaggregated oyster shell reefs as compared to live, aggregated oyster clusters (Tolley and Volety 2005). This may indicate the amount of niche space available is not significantly different between reef creation methods.

Research comparing exposed and sheltered sites of rocky intertidal environments has shown that species assemblages can be largely controlled by the degree of wave exposure (e.g.,

McQuaid and Branch 1985, Menge 1991, Blanchette et al. 2009), but research in estuaries have shown the impact of wave energy to be negligible (Selleslagh et al. 2008). Shorelines in this study were characterized using a measure of exposure derived from wind speed and direction, as well as fetch, at the time of sampling. For no sample date did our analysis detect a significant difference in nekton assemblages between wave exposures (low and medium energy). The positioning of our reefs within the water column may be a reason why this result might differ from those in other systems (i.e. rocky intertidal). Because the reefs were subtidal for the majority of the sampling period, waves passed over the crest and were dissipated by the surrounding salt marsh. Although the wave energy created variable subsurface conditions, this wave energy may not have created the gradient necessary to directly impact nekton use at reefs. Delineating the degree of wave exposure for this experiment may be very different from that of rocky intertidal systems because of the shallow gradient inherent to a Louisiana estuary; Louisiana has a low tidal amplitude and when splitting the wave exposure into categories (low and medium energy), the context is much different in comparison to many rocky intertidal systems. We may not have gotten the range and frequency of wind speeds needed to create significant, consistent differences in wave exposure. The average wind speed was 3.4 m s^{-1} and below 5.4 m s^{-1} for over 90 % of the sampling period; only in the winter did prolonged periods of wind exceed speeds of 5.4 m s^{-1} . The relatively small differences and shallow gradient between the degree of wave exposure may be why we, or Selleslagh et al. (2008), did not see significant nekton assemblage differences.

Temporal Variation in Nekton Community

Nekton assemblage structure likely develops over time in newly constructed oyster reefs. Oyster recruitment may affect the quantity and quality of available niche space and habitat for

nekton (Breitbart et al. 1995). Changes in the structural complexity of oyster reefs has been shown to influence a variety of biological processes, and may be driven by temporal patterns linked to larval supply and recruitment (Lenihan 1999). It is possible there has not been time for our oyster reefs to have significant recruitment and colonization of oysters/shell, and thus, significantly increase the structural complexity within the reef. The oyster reefs were only beginning to recruit new oysters and accumulate shell; first year data on oyster recruitment and growth indicates not only significant growth of oysters over the one year time period, but significant differences in survival and growth by site (Casas et al. unpubl data).

Estuaries experience seasonal fluctuations in physical conditions (Shenker and Dean 1979) and differences in nekton use patterns may be related to observed differences in environmental variables (Kneib 1984, Baltz et al. 1993, Akin et al. 2003). Although CCA analyses indicated species-specific temporal shifts, overall resident and transient abundance did not differ significantly by season. Due to the relatively small sample size per season, the inherent high variability of the system and ecological data, as well as variability due to gear characteristics (e.g., gill net, seine), the variance in the data is likely too large to detect significant statistical differences. Ecological data have been shown to be inherently variable because much of it is field-based with different sampling techniques (Hilborn and Mangel 1997). Weak environmental-community effects may be caused by variations in species-specific responses, life history characteristics, and temporal variability of species performance, which reflects environmental variability (Adler et al. 2009).

Life history characteristics may be more important than the presence of oyster reefs in determining transient species usage patterns, whereas residents may depend more on the structure of oyster reefs for year-round habitat. Timing of recruitment has been documented as

an important factor mediating temporal changes in fish and invertebrate assemblages (Heck and Thoman 1984, Akin et al. 2003). The March 2010 catch contained high abundances of juvenile gulf menhaden and bay anchovy, but few other species were present (lowest diversity of all sampling dates); samples contained only a few, but abundant schooling/ubiquitous species, possibly because they were highly aggregated. Resident assemblages showed some temporal stability and were consistently more abundant and diverse at oyster reefs than mud-bottom. This demonstrates the habitat value that oyster reefs may provide resident species throughout the year.

Summary

Oyster reefs have been called essential fish habitat due to support they provide to resident and transient fish (Breitburg and Miller 1998), despite the fact that shellfish reefs remain notoriously difficult to sample in a consistent manner. In this study, the combined use of gill nets, seines and substrate trays provides a comparison of nekton assemblages and abundances in areas on and immediately adjacent to oyster reefs, and on mud-bottom habitat that is not adjacent to oyster reefs. The overall nekton community showed temporal shifts correlated with season (temperature) and was rarely significantly influenced by treatment type (oyster reef and mud-bottom) within each season. Transients fluctuated temporally, and the addition of oyster reefs did not appear to influence their habitat preference; seasonal shifts related to species-specific life history characteristics may be more important in determining usage patterns for transient species than the presence of oyster reefs. Resident nekton were consistently more abundant at oyster reefs than mud-bottom throughout the sampling period, indicating a possible habitat preference regardless of season. The findings from this study indicate that the disarticulated shell piles immediately (3 months post-creation) provided preferred habitat to resident nekton species. While this increased use of habitat by resident species may be due to structure per se, it may also

be an indirect result of the structure altering the hydrodynamics in the vicinity of the reef, which could affect food resources and the physicochemical environment (Dame and Patten 1981, Dame et al. 1984).

In recent years, concern over declining extent of these shellfish reefs has led to extensive efforts to create and enhance existing reefs (Beck et al. 2009, Coen and Luckenbach 2000). Many different approaches have been used to create reefs ranging from the use of limestone rocks, to clam shell, oyster shell, to various bio-engineered products, all at varying costs. While this study using created reefs of disarticulated shell found immediate recruitment of resident nekton, it is unclear without comparative studies how the use of these created reefs compares to either well-established living, growing reefs, or to other reefs created with different techniques, materials and complexities. One difficulty with shellfish reef work, particularly in areas of turbid water, is the issue of developing and finding a consistent and reliable sampling technique. For example, while the use of trays, seines and gill nets in this study did provide a fairly complete view of overall community usage, it would be difficult to replicate this sampling scheme at many other reefs either due to the fact that they are too large to encircle with a gill net, too deep to seine, or bio-engineered in a manner that substrate trays could not be built into them. Regardless of future comparisons, these data do suggest that shell reefs provide valuable habitat for resident species, likely by providing refuge. What is less clear, is whether over time as the reefs build and becoming increasingly complex, do they provide support for greater numbers of resident nekton by providing greater refuge space, and/or do they attract greater numbers of transient species? The following chapters attempt to answer these questions.

CHAPTER 3. THE EFFECT OF VARIATIONS IN STRUCTURAL COMPLEXITY ON NEKTON ASSEMBLAGES AT CREATED OYSTER REEFS IN CAILLOU (SISTER) LAKE, LOUISIANA

Introduction

A fundamental aim in ecology is to better understand how the abundance and distribution of species are organized and regulated (Paine 1966). Variations in abiotic and biotic factors may influence species interactions and community assemblages (Lenihan 1999, Grabowski et al. 2008). 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 and more diverse communities than structurally simple ones (Luckhurst and Luckhurst 1978, Diehl 1992). Consequently, the structural morphology of a habitat has the potential to influence its value and dictate community assemblages by altering resource availability and predation risk (Hixon and Menge 1991).

A variety of ecological theories have been suggested to explain demographic patterns at structurally complex habitats (e.g. MacArthur and MacArthur 1961, Hicks 1980, Christensen and Persson 1993, Gratwicke and Speight 2005). Biogenic reefs formed by the eastern oyster (*Crassostrea virginica*; hereafter oyster) have been recognized for their ability to create biogenic structure (Jones et al. 1994) and support large populations of resident organisms (Brietburg 1999, Tolley and Volety 2005, Shervette and Gelwick 2008, Stunz et al. 2010). 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, this habitat may allow for the coexistence of potentially competing species within a structurally complex environment (Beukers and Jones 1997). Organisms may

use structure provided by oyster reefs for a number of reasons (e.g. spawning substrate, nursery, refugia, foraging, attachment space). It is unclear, however, whether nekton abundance and diversity are linearly related to complexity, or if a point exists at which effective niche space is no longer limiting and the quantity of structure becomes redundant in supporting higher populations and more diverse assemblages.

Oysters provide significant structure in shallow marine ecosystems worldwide, yet are often underrepresented in studies of estuarine 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). Although 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), only one (Eggleston et al. 1998) of the 64 sources they reviewed 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 contribute to nekton use (e.g. Harding and Mann 2001, Plunket and La Peyre 2005, Shervette and Gelwick 2008, Geraldi et al. 2009, Stunz et al. 2010 but see Lenihan et al. 2001, Soniat et al. 2004, Tolley and Volety 2005).

The objective of this study was to investigate whether the presence of structure or variations within the structural complexity of created oyster reefs influence associated nekton assemblages. Using a quantitative sampling technique, we examined fish and decapod crustacean abundance and diversity at mud-bottom treatments and oyster reefs of two/varying complexities constructed from unaggregated shell. We predicted an increase in species

abundance and diversity at oyster reefs and as reef structural complexity (i.e. shell density) increased.

Materials and Methods

Study Site

The study was conducted along the northern shore of Caillou (Sister) Lake, located in Terrebonne Parish, Louisiana (29°15'N, 90°55'W) (Fig. 1). Sister Lake is a typical brackish system with water depths ranging from 1 to 3 m. It is primarily an open water, brackish system with a mean tidal range of 0.3 ± 0.03 m (1 SE) (National Geodetic Vertical Datum). Dominant winds are typically from the southeast, except for during the winter when northerly winds accompany cold fronts. Mean (± 1 SE) water temperature, salinity, and water level in the study area between 1997 and 2009 were 23.5 ± 1.9 °C, 12.0 ± 2.8 , and 0.33 ± 0.03 m, respectively (LDWF/USGS 07381349—Caillou Lake southwest of Dulac, LA, U.S.A.). Sister Lake has served as a state public oyster seed reservation since 1940, and oyster beds are abundant within the system.

Experimental Reef Construction

Treatments (0.7 m²) were created by varying the density of clean, unaggregated oyster shell and placing them in cylindrical cage structures (1" diameter chicken wire), with the top left open. The cages were used to enable the simulation of three-dimensional reefs using unaggregated shell and prevent destruction or movement of reefs in the field. Four treatments were tested (volume, vertical relief): (1) mud-bottom, no cage (0 L, 0 cm; hereafter MUD), (2) mud-bottom, with cage (0 L, 0 cm; hereafter CAGE), (3) low oyster shell density (3 L, approx. 5 cm; hereafter LOW), and (4) high oyster shell density (8 L, approx. 20 cm; hereafter HIGH).

CAGE was created to determine if the structure of the cages themselves had an effect on nekton communities. PVC poles ($n = 3$) were set at the edges of each treatment to locate plots for sampling. In July 2009, two 225 m sampling shorelines were chosen for the placement of treatments in Sister Lake (Fig. 10). At each sampling shoreline, treatments were randomly placed 15 m apart and 25 m from the shoreline vegetation (5 MUD + 5 CAGE + 10 LOW + 10 HIGH). Deployment of experimental oyster reefs occurred on July 13 and 14, 2009.

Sampling Procedure

On October 26-28, 2009, fishes and decapod crustaceans were quantitatively sampled using a 1-m² drop sampler (Zimmerman et al. 1989). Treatments were sampled in random order. Adjacent treatments were never sampled consecutively to avoid disturbing them prior to sampling. Water clarity was measured using a sechi disc, water depth measurements were taken in triplicate, and a YSI model 556 Multiprobe (YSI Inc., Yellow Springs, OH, U.S.A.) 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 and used a 5-mm mesh sieve to remove organisms on site. Samples were placed on ice and returned to the laboratory for processing. In the laboratory, organisms were separated from detritus and identified to the lowest feasible taxon. Individuals of a species in each sample were weighed to the nearest 0.1 g (wet weight) to determine biomass. Total length of fishes and shrimps and carapace width (CW) of crabs were measured to the nearest millimeter.



Fig. 10. Sampling shorelines (October 2009) in Caillou (Sister) Lake, Terrebonne Parish, Louisiana, USA.

Statistical Analyses

Multivariate analysis of variance (MANOVA) (SAS Institute, Inc., Cary, NC, U.S.A.) was used to test whether water quality variables (secchi, temperature, salinity, dissolved oxygen) and site characteristics (water depth), compared simultaneously, differed between sampling shoreline or among treatments (MUD, CAGE, LOW, HIGH).

Comparisons of least squared means using a one-way analysis of variance (ANOVA), followed by Tukey's Studentised Range tests, were used to test for differences in nekton abundance (ind. m⁻²) and diversity (Shannon diversity index [H']) among treatments (MUD, CAGE, LOW, HIGH), blocking on sampling shoreline. A one-way ANOVA was also used to test for differences in fish (see Table 2 for species) and decapod crustacean (see Table 2 for species) abundance and diversity (H') among treatments, blocking on sampling shoreline. To

check for homogeneity of variance, we assessed homoscedasticity by inspection of the residuals and no transformations were necessary. All values were tested for normality using Shapiro-Wilk's *W* test to satisfy the assumptions of the statistical analyses and no transformations were necessary. Simpson's diversity index (*D*) and species richness were not used as they were highly correlated with *H'* ($p < 0.01$). Biomass (g) was not used as it was highly correlated with abundance ($p < 0.001$).

To examine the overall similarity of nekton assemblages at each treatment, cluster analysis and multidimensional scaling (MDS) were performed. Both methods were performed on a reduced, raw species abundance matrix using PRIMER statistical software (version 6.1.9; Clarke and Warwick 2001). Only species whose abundance accounted for more than 3% of the total catch were used for community analyses (Gauch 1982). Dendrograms were constructed to display cluster analysis, using hierarchical agglomerative clustering with group averaging. MDS analysis was displayed using 2-dimensional ordination. To test for differences in the similarity of nekton assemblages at each treatment, a one-way analysis of similarity (ANOSIM) was performed. Similarity percentage (SIMPER) analysis was also conducted to determine the species that contributed the most to the similarities or dissimilarities among treatments.

Results

Environmental Variables

Water temperature and salinity ranged from 17.8 to 20.4 °C and 9.8 to 13.4, respectively during sampling (Oct 26-28, 2009) (Table 5). Dissolved oxygen ranged from 6.21 to 8.87 mg l⁻¹, secchi depth from 36 to 63 cm, water level from 0.83 to 1.35 m. MANOVA detected no significant ($p < 0.05$) interactions in environmental variables between sampling shorelines or among treatments.

Table 5. Environmental variables at treatments (n = 30) during sampling in October 2009. Mean temperature (°C), salinity, and dissolved oxygen (mg l⁻¹) recorded using a YSI Model 556 multiprobe, and secchi depth (cm), water depth (m). MANOVA detected no significant (p < 0.05) interactions between sampling shorelines or among treatments (MUD, CAGE, LOW, HIGH). Mean values ± 1 SE are presented.

	Mean (± 1 SE)
Temperature (°C)	19.13 (0.12)
Salinity	11.39 (0.26)
Dissolved oxygen (ml l ⁻¹)	7.64 (0.13)
Secchi depth (cm)	49.89 (1.28)
Water depth (m)	1.13 (0.03)

Nekton Assemblages

We collected a total of 551 individuals (188 fishes and 363 decapod crustaceans) representing 23 species (17 fishes and 6 decapod crustacean) and a total biomass of 8375 g wet weight (6941 and 1434 g for fishes and decapod crustaceans, respectively) (Table 6). Across all treatments, decapod crustaceans outnumbered fishes and accounted for 65.9 % of individuals caught. Fish biomass accounted for 82.9 % of the total biomass, although, without sheepshead (*Archosargus probatocephalus*), fishes only accounted for 32.9 % of the total biomass. Although sheepshead were excluded from our multivariate analyses, they were only collected at oyster reefs (LOW, HIGH). 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 3 % of the total fish catch. The only fish present across all treatments was the naked goby. The only species absent from oyster reefs were striped mullet and southern flounder (*Paralichthys lethostigma*). Atlantic mud crab (*Panopeus herbstii*) and

white shrimp (*Litopenaeus setiferus*) accounted for 64.2 % of all decapod crustaceans and were the only crustacean species found across all treatments. Other invertebrate species contributing to the catch included bigclaw snapping shrimp (*Alpheus heterochaetis*), blue crab (*Callinectes sapidus*), and brown shrimp (*Farfantepenaeus aztecus*); no other species of decapod crustacean accounted for more than 3 % of the total decapod crustacean catch.

One-way ANOVAs determined total nekton ($F_{3, 26} = 17.41$, $p < 0.0001$), fish ($F_{3, 26} = 11.75$, $p < 0.0001$) and decapod crustacean ($F_{3, 26} = 10.75$, $p < 0.0001$) abundances (ind. m⁻²) differed significantly between oyster reefs (LOW + HIGH) and mud-bottom (MUD + CAGE), with higher abundances at the reefs (Table 7; Fig. 11). However, there were no significant differences in densities between oyster reefs (LOW vs. HIGH) or between mud-bottom treatments (MUD vs. CAGE).

Total nekton diversity (H') was significantly lower at MUD ($F_{3, 26} = 15.69$, $p < 0.0001$) than the other three treatments (CAGE, LOW, HIGH), which did not differ from one another (Table 7; Fig. 12). Fish diversity was significantly higher at oyster reefs than mud-bottom ($F_{3, 26} = 19.36$, $p < 0.0001$). In contrast, decapod crustacean diversity differed only between MUD and LOW treatments ($F_{3, 26} = 3.46$, $p = 0.0295$).

Multivariate analysis revealed differences in nekton assemblages between oyster reefs and mud-bottom, with LOW and HIGH treatments grouping more discretely than MUD and CAGE (Fig. 13). ANOSIM indicated that assemblages were significantly different from one another ($r = 0.416$, $p < 0.001$) and that both oyster reef treatments were significantly different from MUD and CAGE ($r = 0.406$, $p < 0.001$), but not from one another ($r = 0.061$, $p = 0.127$). SIMPER analysis indicated that the species composition of LOW and HIGH treatments were 69.56 % and 75.78 % different, respectively, than the CAGE treatment. These differences were

driven by the presence of snapping shrimp, mud crabs, and white shrimp at the oyster reefs. Species composition at oyster reefs was also 84.69 % and 89.64 % different, respectively, compared to MUD treatments. These differences were driven largely by the presence of snapping shrimp and mud and blue crabs at the oyster reefs. Oyster reefs differed from one another by 53.59 % with significantly greater densities of blue crabs at LOW treatments and significantly greater densities of snapping shrimp at HIGH treatments.

Discussion

Experimental shell reefs created over mud-bottom habitats clearly resulted in increased abundance and diversity of nekton. At the same time, the results demonstrated that while there may be an increase in species abundance and diversity at newly created oyster reefs, there may not be a continued increase in abundance and diversity as structural complexity increases. This underscores the potential role of biogenic structure and habitat complexity in influencing estuarine communities. Furthermore, as only resident species seem to increase in abundance at these newly created clean structures, the data suggest that these structures may be serving initially largely as refuge.

Overall, oyster reefs had a higher abundance of fishes and decapod crustaceans than mud-bottom treatments (MUD + CAGE), and this pattern was relatively consistent among species. Some exceptions to the pattern included grass shrimp and striped mullet, which had highest densities over mud-bottom. Benthic invertebrate species such as Atlantic mud crab, snapping shrimp, white shrimp, and blue crab generally had significantly higher densities at oyster reefs than in mud-bottom habitat. Interestingly, snapping shrimp were one of the most abundant invertebrate species at oyster reefs in this study, but were only rarely associated with oyster reefs in Chapter 2. Similar to results reported in Chapter 2, fishes such as freckled blenny, naked

Table 6. Mean abundance (ind. m⁻² ± one SE) and biomass (g), by species, collected at all treatments (n = 30) in Sister Lake, Terrebonne Parish, Louisiana.

Functional group	Species	Mud bottom		Cage structure		Low oyster density		High oyster density		Total	Total
		Mean (SE)	Biomass (g)	Mean (SE)	Biomass (g)	Mean (SE)	Biomass (g)	Mean (SE)	Biomass (g)	N	Biomass (g)
Fish	<i>Archosargus probatocephalus</i>	0		0		0.18 (0.12)	2595.4	0.3 (0.15)	3640	5	6235.4
	<i>Bairdiella chrysoura</i>	0		0		1 (0.33)	19.77	0.5 (0.22)	10.99	16	30.76
	<i>Bathygobius soporator</i>	0		0		0.09 (0.09)	7.82	0.1 (0.1)	11.7	2	19.52
	<i>Citharichthys spilopterus</i>	0		0		0		0.1 (0.1)	0.15	1	0.15
	<i>Ctenogobius boleosoma</i>	0		0		0		0.1 (0.1)	0.39	1	0.39
	<i>Cyprinodon variegatus</i>	0		0		0.36 (0.15)	11.25	0.3 (0.15)	11.11	7	22.36
	<i>Gobiesox strumosus</i>	0		0		1.27 (0.38)	26.63	1.8 (0.55)	40.06	32	66.69
	<i>Gobiosoma boleosoma</i>	0		0		0.18 (0.12)	0.47	0.1 (0.1)	0.22	3	0.69
	<i>Gobiosoma bosc</i>	0.33 (0.21)	1.5	0.4 (0.24)	1.22	1 (0.33)	5.94	2.5 (1.08)	10.87	40	19.53
	<i>Hypsoblennius ionthas</i>	0		0.4 (0.24)	10.93	1.36 (0.64)	71.63	2.5 (0.79)	96.68	42	179.24
	<i>Lutjanus griseus</i>	0		0.2 (0.2)	5.4	0.18 (0.18)	26.35	0.7 (0.21)	32.97	10	64.72
	<i>Microgobius gulosus</i>	0		0.2 (0.2)	0.3	0.36 (0.36)	1.29	0.3 (0.15)	0.98	8	2.57
	<i>Mugil cephalus</i>	1.33 (1.15)	158.97	0		0		0		8	158.97
	<i>Myrophis punctatus</i>	0		0		0.09 (0.09)	1.59	0.2 (0.13)	2.45	3	4.04
	<i>Opsanus beta</i>	0		0		0.09 (0.09)	5.34	0.3 (0.15)	17.88	4	23.22
	<i>Paralichthys lethostigma</i>	0		0.2 (0.2)	100.84	0		0		1	100.84
	<i>Symphurus plagiusa</i>	0		0		0.27 (0.19)	6.21	0.2 (0.2)	5.32	5	11.53
Decapod crustaceans	<i>Alpheus heterochaetis</i>	0		0		1.45 (0.47)	20.53	4.2 (0.83)	51.78	58	72.31
	<i>Callinectes sapidus</i>	0.33 (0.21)	36.73	1 (.45)	287.25	2.72 (0.7)	447.88	0.8 (0.51)	10.46	45	782.32
	<i>Litopenaeus setiferus</i>	0.83 (0.65)	6.44	1.6 (1.12)	9.62	5 (2.02)	64.02	3.6 (1.33)	39.69	104	119.77
	<i>Palaemonetes pugio</i>	1.17 (0.48)	1.69	0.4 (0.24)	0.22	0.18 (0.18)	0.48	0		11	2.39
	<i>Panopeus herbstii</i>	0.17 (0.17)	8.67	0.4 (0.24)	2.75	4.36 (1.54)	111.99	7.8 (1.83)	276.24	129	399.65
	<i>Farfantepenaeus aztecus</i>	0		1.6 (1.36)	25.92	0.55 (0.37)	21.98	0.2 (0.2)	10.38	16	58.28

Table 7. Results of ANOVA testing for significant differences in mean species abundance (ind. $m^{-2} \pm$ one SE) and diversity (H') for all species, fishes and decapod crustaceans by treatment type (MUD, $n = 5$; CAGE, $n = 5$; LOW, $n = 10$; HIGH, $n = 10$). Mean values \pm one SE are presented. * $p < 0.05$.

	All		Fishes		Decapod crustaceans	
	Abundance (ind m^{-2})	Diversity (H')	Abundance (ind m^{-2})	Diversity (H')	Abundance (ind m^{-2})	Diversity (H')
Mud bottom	4.2 (2.9)	0.9 (0.2)*	1.7 (1.3)	0.1 (0.1)	2.5 (2.3)	0.4 (0.2)
Cage structure	6.4 (3.1)	1.7 (0.2)*	1.4 (1.4)	0.4 (0.2)	5 (2.5)	1.1 (0.2)*
Low oyster density	20.6 (2.1)*	2.3 (0.1)*	6.3 (0.9)*	1.6 (0.2)*	14.3 (1.7)*	1.3 (0.2)*
High oyster density	26.3 (2.2)*	2.4 (0.1)*	9.7 (1.0)*	1.8 (0.2)*	16.6 (1.8)*	1.2 (0.2)*

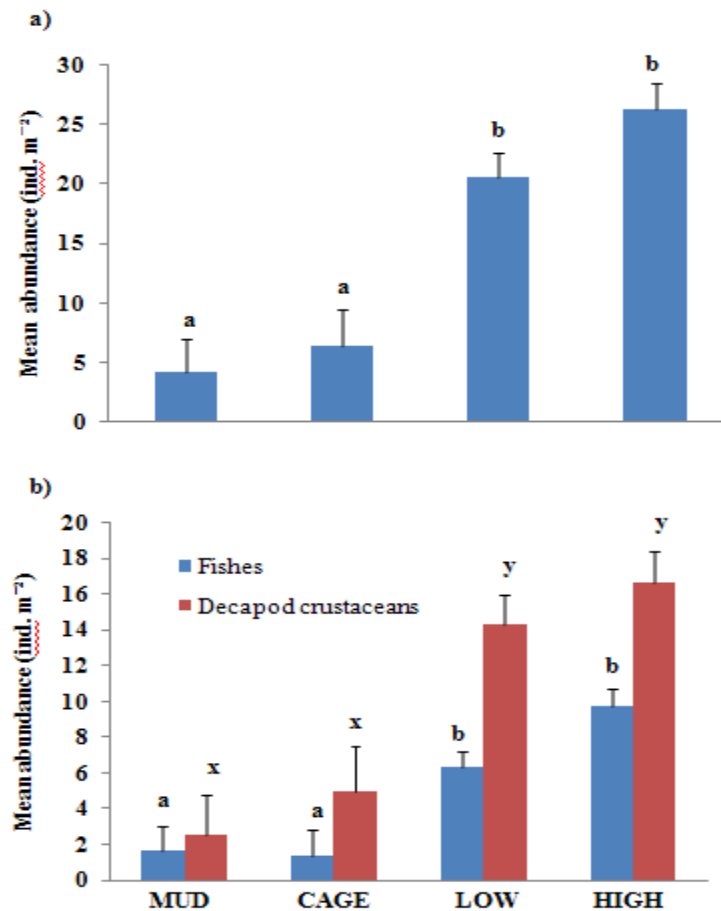


Fig. 11. Mean abundance (ind. m^{-2}) of (a) all species, and (b) fishes and decapod crustaceans collected across all treatments ($n = 30$). Error bars represent one standard error of the mean. Separate 1-way ANOVAs were used to determine significant ($p < 0.05$) differences between treatments for all organisms. Treatments with different letters resulted in significant differences.

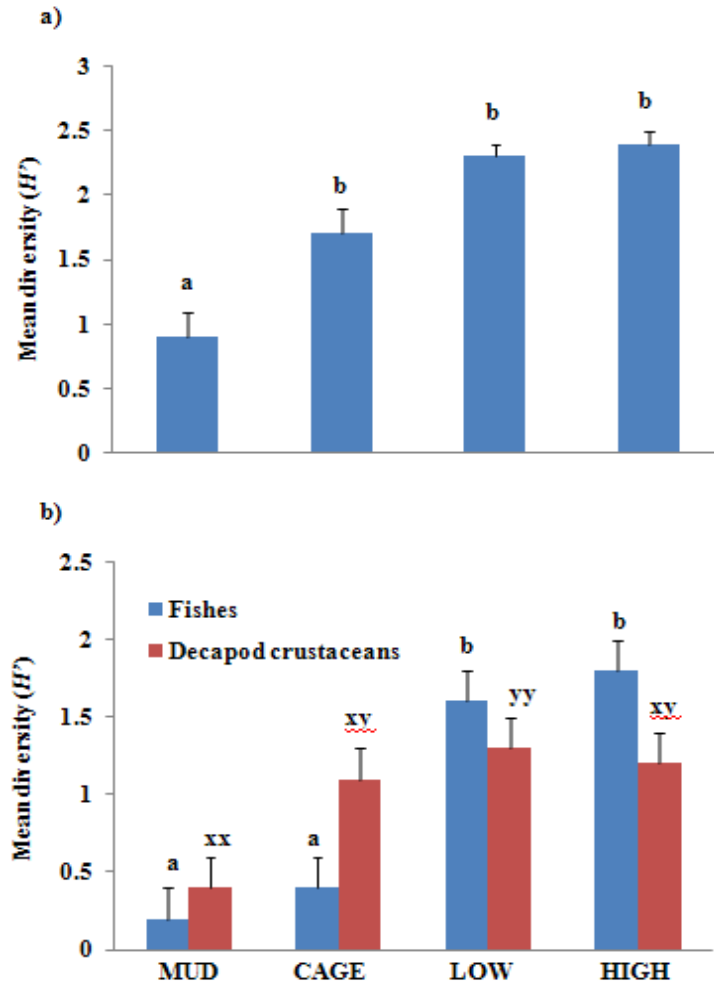
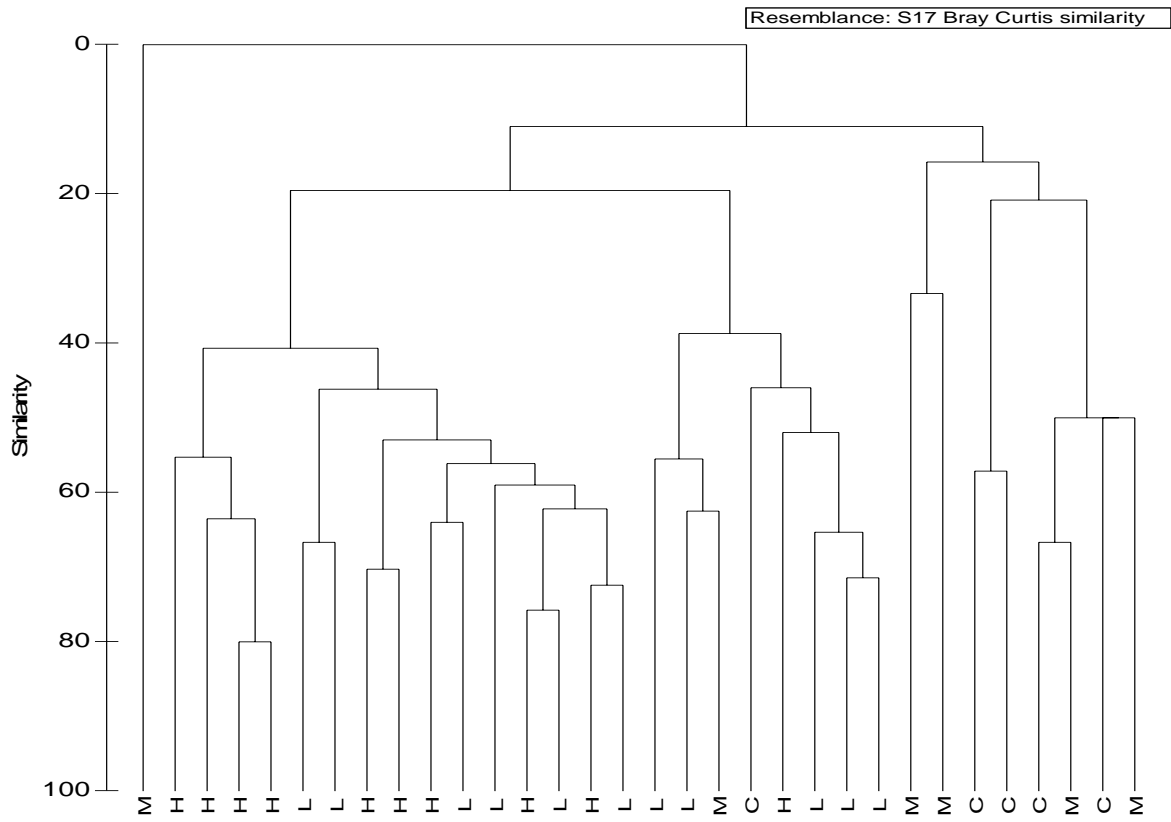


Fig. 12. Mean Shannon diversity (H') of (a) all species and (b) fishes and decapod crustaceans collected across all treatments ($n = 30$). Error bars represent one standard error of the mean. Separate 1-way ANOVAs were used to determine significant ($p < 0.05$) differences between treatments for all organisms. Treatments with different letters resulted in significant differences.

goby, and skillettfish had highest mean densities at oyster reefs. The MDS and cluster analyses indicated that assemblages at oyster reefs were different than those at mud-bottom, but very similar to one another regardless of complexity. The high nekton densities we observed for many species at oyster reefs indicate that the value reefs may provide and similar results have been reported in the northern GOM (Shervette and Gelwick 2008, Stunz et al. 2010).

a)



b)

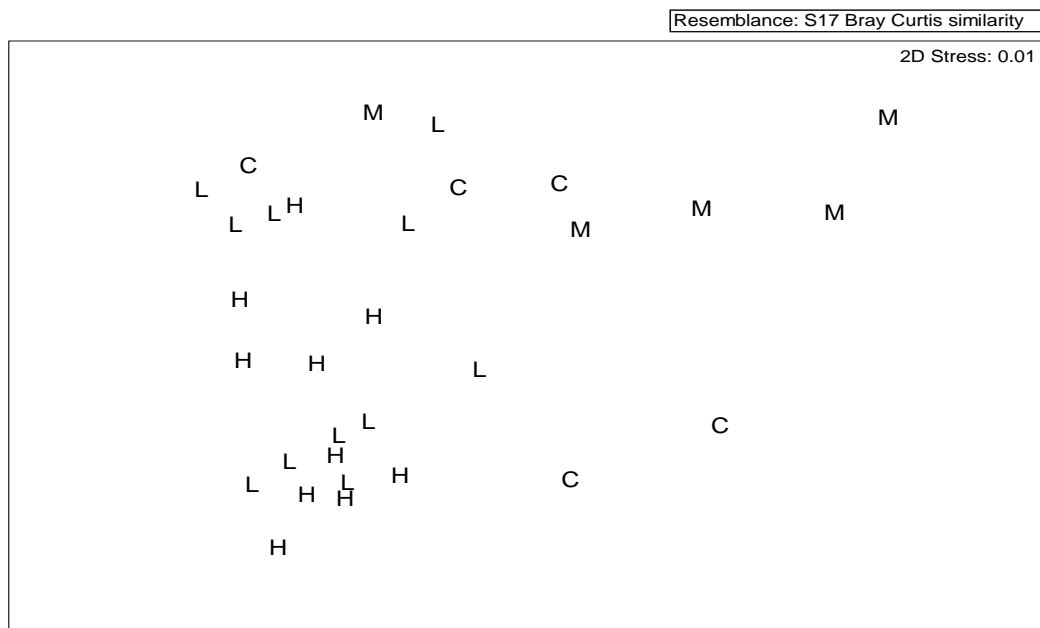


Fig. 13. Results of (a) cluster analysis (Bray-Curtis similarity index) on oyster reef assemblage abundance data from MUD (M), CAGE (C), LOW (L), and HIGH (H), and (b) MDS ordination of same data.

The presence of biogenic structure *per se* seems to be the most important factor determining species abundance and diversity, and therefore fails to support the common assumption that by increasing structural complexity, and thus habitable surface area, species abundance and diversity increases linearly (Gunnill 1982, Gee and Warwick 1994). While this assumption is widely supported in estuarine literature (e.g. seagrass patches with variable blade densities; Orth and Heck 1980, Diehl 1988, 1992, Wyda et al. 2002), it has not previously been explicitly tested in shellfish reefs to our knowledge. The lack of agreement of our result with findings in other estuarine communities could be due to several explanations. One, altering the structural complexity of oyster reefs has been shown to influence a variety of biological processes through time (Lenihan 1999); it is possible, given the short period of time that the created reefs were allowed to soak and recruit sessile organisms was not long enough to influence other biological processes that could affect nekton use patterns on the reefs (e.g. trophic cascades; Grabowski et al. 2008). It is also possible that the construction of our reefs did not create a wide range of usable habitats. By creating reefs from unaggregated shell, we may have failed to create the desired range of niche spaces available to nekton (i.e. unaggregated shells were packed too tightly for the interior of the reef to be utilized by resident nekton at high oyster shell treatments). Also, edge effects or habitat heterogeneity of structured habitats at larger spatial scales may have influenced species demographics. Proximity of habitat to other habitat types within the estuary can influence distribution patterns (Grabowski et al. 2005).

Predation can have significant effects on community assemblages and has been shown to be influenced by structural complexity (e.g. Nelson 1979, Hixon and Menge 1991, Warfe and Barmuta 2004). It is unclear whether structural complexity increases prey survivorship by providing more refuge areas (Heck and Thoman 1981, Beukers and Jones 1997) or increases

predator foraging efficiency by reducing inter- and intraspecific interactions among predators (Finke and Denno 2002, Grabowski and Powers 2004, Grabowski et al. 2008). Regardless of the methods by which density-regulation may be achieved, in this study, the presence of structure seemingly provided more refugia for fishes and decapod crustaceans as evidenced by greater abundances of organisms. This may have also created areas with increased predator foraging efficiency as compared to areas with no structure (mud-bottom). More complex reefs may in fact provide greater refuge space as compared to the low complexity reefs, but may also increase predator foraging efficiency by aggregating greater numbers of prey together. The interaction of these processes could explain the lack of significant differences in nekton assemblages between oyster reef treatments.

The creation of oyster reefs may contribute to increased species abundance and diversity in estuarine systems; newly created oyster reefs appear to support a diverse and spatially distinct nekton community. But, further increasing the structural complexity of reefs may not automatically result in greater abundances and diversity of organisms. The absence of a direct relationship between structural complexity and community demographics could be the result of a number of biotic and abiotic interactions, including limited food rates, competition among resident species for space and food, or increased predation by transients. It is possible that density dependent effects limit continued increases in resident species abundances. In the following chapter, we examined whether increased habitat complexity may provide better refuge from predator species.

CHAPTER 4. STRUCTURAL COMPLEXITY OF CREATED OYSTER REEFS DETERMINE THE FORAGING SUCCESS OF RED DRUM (*SCIAENOPS OCELLATUS*) ON GRASS SHRIMP (*PALAEMONETES PUGIO*)

Introduction

One of the most intensively studied subjects in ecology is how predators organize communities (Gause and Witt 1935, Nelson 1979, Menge 2000). Predation can have significant direct and indirect effects on biotic communities in both terrestrial (Wilcove 1985) and aquatic (Paine 1966) environments. In its broadest sense, predation is any interaction that results in the flow of energy from one organism to another (Sih 1982). The effects of predation are prey mortality or an alteration in the behavior of prey, such as habitat use, time of activity, diet and foraging mode (Carpenter et al. 1985). Consequently, these behaviors determine prey encounter rates with predators, competitors, and food (Hixon and Beets 1993). Prey can reduce the risk of mortality from predation by avoiding encounters, or escaping from an encounter (Sih 1987). Structural complexity provides opportunity for prey to avoid predation and seek refuge (Hixon and Menge 1991, Lenihan et al. 2001).

A common assumption is that structure acts as a physical impedance to predator foraging success by creating a variety of refugia where predators cannot physically reach prey (McCoy and Bell 1991). This structure can cause a reduction in the contact time and encounter rates between predators and their prey, as well as degrade efficiency and capture success (Diehl 1992, Nestlerode 2007). In accordance with optimal foraging theory, such impedance is believed to cause shifts in resource utilization strategies, and thus, have community-level impacts (Pyke et al. 1977). In previous research, Nelson (1979) proposed that a step function with two thresholds was an appropriate description of the apparent non-linear correlation. Nelson's model was

supported by numerous subsequent studies (e.g. Heck and Thoman 1981, Savino and Stein 1982, Adams et al. 2004), but has recently been brought into question because of the possibility of variations in encounter rates across treatments (Matilla et al. 2008, Canion and Heck 2009). Regardless of whether thresholds actually exist, and subsequently, where they might occur, predator foraging success and structural complexity have traditionally been shown to be negatively correlated and non-linear (Stoner 1982, Jordan et al. 1996, Hovel and Lipcius 2001).

Mollusks provide significant biogenic structure in shallow marine ecosystems worldwide, and in the northern Gulf of Mexico (GOM), the eastern oyster (*Crassostrea virginica*, hereafter oyster) introduces structural complexity and heterogeneity into benthic environments. A once ubiquitous feature of the estuarine landscape (Kirby 2004), oysters are important ecological engineers (Jones et al. 1994) that provide services such as water filtration and nutrient removal (Dame 1996, Jackson et al. 2001), shoreline protection (Meyer et al. 1997, Piazza et al. 2005), and serve as important biogenic habitat for benthic invertebrates (Wells 1961, Zimmerman et al. 1989) as well as fishes and mobile crustaceans (Breitburg 1999, Lenihan et al. 2001). Reefs may enhance fish production by providing spatial refuges, thereby increasing survival as well as subsidizing growth of individuals (Peterson et al. 2003). Oyster reefs can also have a strong influence on nekton assemblages by altering trophic interactions of predators and their associated prey (Lenihan 1999, Grabowski et al. 2008). While there is a large body of evidence examining the role of seagrass meadows and salt marshes in providing nursery and refuge habitat (e.g. see reviews by Heck et al. 2003, Minello et al. 2003), there is less evidence explicitly examining habitat created by shellfish (but see Lenihan et al. 2001, Grabowski 2004, Grabowski and Powers 2004, Grabowski and Kimbro 2005, Grabowski et al. 2008); clearly, as Heck and others

(2003) highlight, there is a need to better understand the role of other equally dominant habitats (i.e. oyster reefs) in estuarine systems.

The objective of this study was to investigate the relationship between the structural complexity of oyster reefs and foraging success of a common predator and prey from the northern Gulf of Mexico (GOM). Using a controlled laboratory experiment, we tested the effects of four levels of oyster reef complexity on the foraging success of wild red drum (*Sciaenops ocellatus*) on grass shrimp (*Palaemonetes pugio*). We predicted a decrease in foraging success as oyster reef complexity increased.

Materials and methods

Experimental Predator

The red drum is a common, estuarine-dependent species in the western Atlantic Ocean from Massachusetts to Veracruz, Mexico, but obtains its greatest abundance in the northern GOM (Pattillo et al. 1997). Larvae are transported and distributed into estuaries via currents and tides, where they settle and remain through the juvenile stage (Holt et al. 1983). Red drum are opportunistic feeders throughout all life stages (Boothby and Avault 1971) and use mechanoreception acting as the primary foraging behavior and vision secondary (Liao and Chang 2003). Scharf and Schlicht (2000) reported that the size and composition of prey consumed by red drum remained relatively constant with increasing body size. Shrimp species (e.g. *Litopenaeus setiferus*, *Palaemonetes pugio*, *Penaeus aztecus*) constitutes the bulk of red drum diet during some months (Boothby and Avault 1971).

Experimental Prey

Shrimp belonging to the genus *Palaemonetes* are among the most abundant and ecologically dominant species in coastal estuaries of the southeastern U.S. (Leight et al. 2005). The grass shrimp is uniquely adapted to highly stressed tidal environments and represent a vital link in the energy transfer of tidal marsh ecosystems, both as potential prey items and as benthic detritivores (Welsh 1975, Kneib 1985, Zimmerman et al. 1989). Grass shrimp may reflect diel predation risks and are therefore more active and abundant at night (Clark et al. 2003). In the presence of predators, grass shrimp select oyster-shell pyramids over seagrass and shallow water habitats (Eggleston et al. 1999).

Collection and Maintenance of Experimental Species

All red drum used in experiments were captured at Rockefeller State Wildlife Refuge in Grand Chenier, Louisiana, using hook and line. Red drum used in experiments were 28 to 35 cm total length (mean = 31.1 ± 3.2 cm). Grass shrimp were collected along marsh edges at Caillou (Sister) Lake in Terrebonne Parish, Louisiana, or at Cypremort Point State Park in St. Mary Parish, Louisiana, using a seine (5 x 2 m bag seine composed of 3 mm square delta mesh). Experimental grass shrimp ranged in size from 20 to 35 mm total length (mean = 28.0 ± 4.1 mm). Fish and shrimp were transported to a laboratory at Louisiana State University AgCenter and held in cylindrical, recirculating fiberglass tanks (350 L), equipped with bio-filters (AST Bead Filter, Aquaculture Systems Technologies, LLC., New Orleans, Louisiana) for 2 weeks before trials were initiated (Coen et al. 1981). Salinity was maintained between 13 and 17 and temperature between 18 and 22 °C. Ammonia and oxygen concentrations in the water were measured daily (0.10 ± 0.05 ppm and 9.27 ± 1.13 mg L⁻¹, respectively). Fluorescent lights (40W) were placed above the holding tanks and a 12:12 hr light-dark regime was maintained

throughout the experiment. Individual red drum were kept in isolation in separate tanks while grass shrimp were grouped together in two tanks. Red drum were fed frozen *Penaeid* shrimp, and grass shrimp were fed wet cat food. All trials for the experiment occurred between February 15 and March 4, 2009.

Experimental Mesocosms

All trials were conducted in 2 recirculating, rectangular fiberglass tanks (length x width x height; 180 x 90 x 40 cm) located side by side, in a room adjacent to the holding tanks. The bottom of each experimental tank was left bare water depth was maintained at 35 cm. Water quality characteristics (salinity, temperature, dissolved oxygen) were measured before and after each trial using a YSI model 556 Multiprobe (YSI Inc., Yellow Springs, OH, U.S.A.) and ammonia concentration was measured using Hach Master Test Kit (Hach Company, Loveland, CO, U.S.A.). Fluorescent lights (40 W) were placed above the experimental tanks and a 12:12 hr light-dark regime was maintained throughout the experiment. A clear plexiglass cover was placed on top of each experimental tank to prevent escape by either species. Structural complexity was created using clean, unaggregated oyster shells (volume, vertical relief): (1) control (0 L, 0 cm), (2) low (2 L, < 5 cm), (3) medium (3 L, 10 – 15 cm), and (4) high (5 L, > 20 cm). Each experimental reef (45 x 60 cm) covered approximately 20% of the tank bottom, with the remainder of the tank bare (Fig. 14). Reefs were constructed by piling unaggregated shell. Oyster reefs were simulated by stacking unaggregated shells over the prescribed area using the excess shells to build an elevated reef-like structure. Pilot runs involving both predator and prey indicated there were no so-called corner effects (Coen et al. 1981) where prey may be able to hide from predators by aggregating in the corners of the tank, thereby eliminating the need to have the corners of the rectangular tank rounded with plastic.

Experimental Trials

All treatments were replicated 5 times (4 treatments x 5 replicates). Treatments were assigned randomly to experimental tanks and days. Each trial was run for 24 hr and consisted of first partitioning the tank (separating the reef area) with a barrier. All filter siphons and air hoses were removed prior to the initiation of a trial to ensure that shrimp would not use these as “substrates.” For each trial, randomly selected shrimp ($n = 40$) were added to the side of the tank with the reef and one randomly selected red drum (starved for 48 hr) was added to the other side. The same procedure was used for control trials with no reef. Predators were randomly selected and used more than once, but never in consecutive trials. Pilot runs indicated that 40 shrimp would avoid predator satiation in the allotted interaction time (Humphries unpub. data). Initial observations indicated that red drum needed time to acclimate to their new surroundings (> 1 hr; Humphries pers. obs.); organisms were allowed 2 hr to acclimate before removing the barrier and the trial allowed interactions for 22 hr. After each trial was complete, the red drum was removed followed by the oyster shell. Remaining shrimp were then quantified and removed, and water quality (salinity, temperature, dissolved oxygen, ammonia) measured.

Statistical Analyses

All data were tested for normality and homogeneity of variance; no transformations were necessary (Shapiro-Wilk's $W = 0.95$). Comparisons of least squared means, using a one-way analysis of variance (ANOVA; proc mixed), followed by Tukey's Studentised Range tests were run with oyster shell density, day, tank, and fish as factors, and predator foraging success (% eaten) as the response variable (SAS Institute, Inc., Cary, NC, U.S.A.; version 9.1). Day, tank,

and fish were included as randomized block factors and the model was independent of order.

Data are reported as mean \pm 1 SE unless indicated differently.

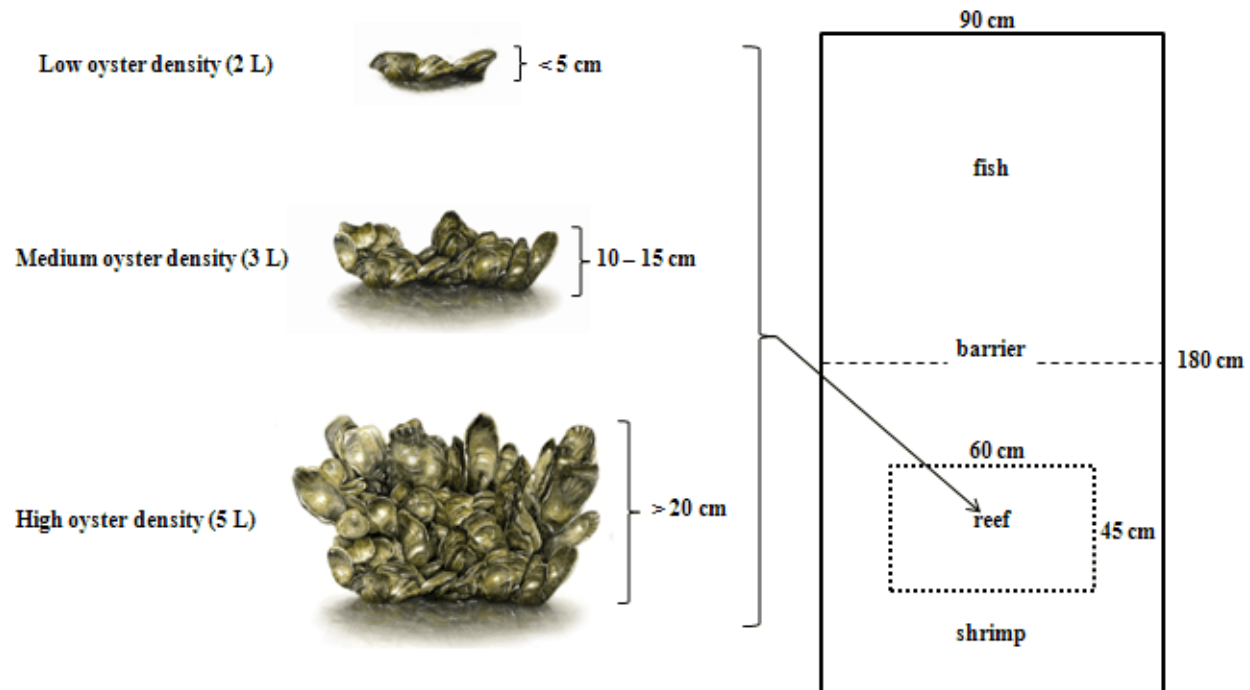


Fig. 14. Design of experimental setup for oyster reefs of variable structural complexities. Reef treatments were constructed from unaggregated oyster shell.

Results

The foraging success (% eaten) of red drum on grass shrimp differed significantly among treatments ($F_{3, 13} = 102.4$, $p < 0.0001$) (Fig. 15). The highest foraging success was in the control treatment (95.5 ± 3.9 %), which was significantly higher ($p < 0.0001$) than other oyster reef treatments. Of the reef treatments, low complexity reefs had significantly higher foraging success (28.5 ± 2.9 %) than medium (15.5 ± 2.5 %) or high complexity reefs (10.5 ± 3.2 %), but medium and high did not differ significantly.

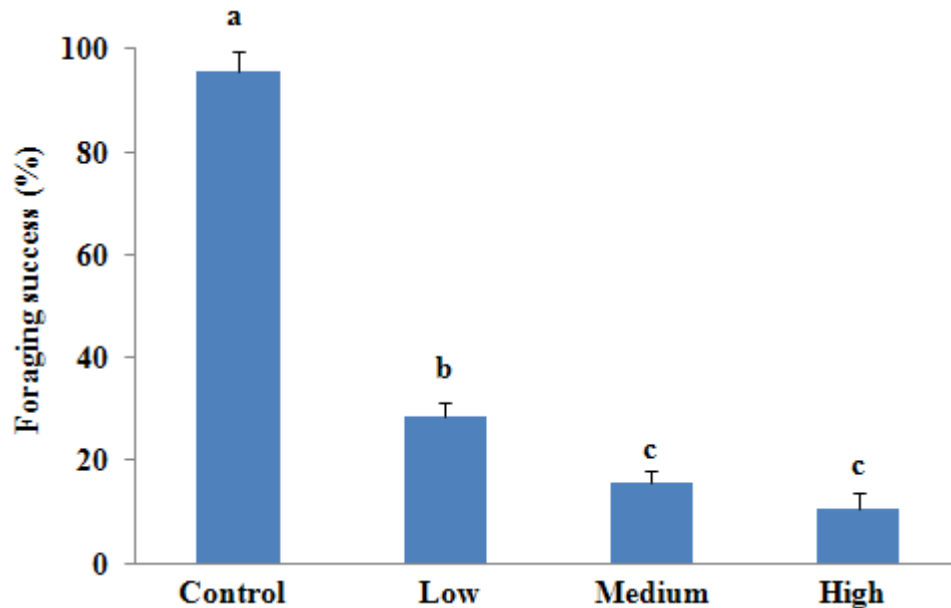


Fig. 15. Foraging success (%; mean \pm 1 SE) of red drum on grass shrimp by structural complexity, denoted by oyster shell density ($n = 20$). Treatments with different letters were significantly different ($p < 0.05$).

Discussion

Foraging success of red drum was affected by the presence of an oyster reef and its structural complexity, but there may be a point above which increased complexity no longer significantly increases the refuge value of the reef. Essentially, the presence of oyster reefs provides refuge for prey species and this refuge value does not necessarily continue to increase as reef complexity, as measured by shell density, increases.

This study agrees with previous hypotheses that predators may impact prey populations in structurally complex environments, but the relationship may include a point(s) of diminishing returns (Nelson 1979, Heck and Thoman 1981, Savino and Stein 1982, Adams et al. 2004); predator foraging success decreased from control to low oyster shell treatment, and from low to medium treatments, with no difference between the medium and high oyster shell treatments.

The actual availability of refugia or the methods by which experimental reefs were created may complicate comparisons among studies (e.g., methods in Lenihan 1999, Soniat et al. 2004, Grabowski et al. 2008); our ability to accurately define and quantify structural complexity from a fish's point of view remains limited. Soniat et al. (2004) showed that shell orientation could affect the availability of refugia on oyster reefs; fish species showed a high affinity for vertically oriented oyster shell, as compared to horizontally oriented shell that they used as nesting sites and refuge. Other studies (e.g. Grabowski 2004, Grabowski and Powers 2004, Grabowski et al. 2008) used aggregated oyster clusters to create reefs mimicking those in the wild and demonstrated that habitat structural complexity had a significant impact on assemblages and trophic interactions. Although Tolley and Volety (2005) show that nekton communities did not differ significantly from articulated, clean oyster shell reefs to live, aggregated oyster clusters, the fact that our reefs were constructed with unaggregated oyster shell may not have generated/simulated the range of complexities desired. It is possible the grass shrimp could utilize only the reef surface because the shells were too tightly packed in the interior of the reef. Future experiments should take into consideration these variations in reef creation techniques to account for possible habitat differences mediating refuge creation.

The arrangement of spaces in a reef complex may also influence encounter rates between predators and prey. A constant ratio of predators to prey across all treatments has been recommended to avoid confounding the effects of variable encounter rates and structural complexity, (Matilla et al. 2008, Canion and Heck 2009. Recently, attempts to control encounter rates, Matilla et al. (2008) and Canion and Heck (2009) completed studies in seagrass beds where they increased the number of both predators and prey with seagrass density to reflect natural abundances observed in the field. These studies showed that when controlling for both

predator and prey density, the only differences in predation rate were between unvegetated and seagrass treatments; increased seagrass density (i.e. structural complexity) failed to decrease predator foraging success. This result differs from many other predator-prey study findings (i.e. this study, Nelson 1979, Heck and Thoman 1981, Crowder and Cooper 1982, Jordan et al. 1996, Adams et al. 2004) that show lower foraging success at complex structures. However, this approach assumes that predator and prey abundances increase similarly with structural complexity. Species encounter rates may thus reflect not just the structural complexity of the habitat, but also the density of both the prey and predator; patterns of encounter rates may vary uniquely for different predator-prey combinations and their different responses to changing structural complexity in the system being tested.

To reflect what occurs in nature, determining appropriate patterns of species encounter rates should/must to take into account the response of both predator and prey species to increased structural complexity. For example, while the abundance of resident species living within the shell matrix of oyster reefs increases with reef area or structural complexity (Breitburg 1999, Coen and Luckenbach 2000, Grabowski et al. 2005), the abundance of transient species does not always increase (Harding and Mann 1999, 2001, Grabowski et al. 2005, Allen et al. 2007). This may suggest that studies on predator foraging success over increasingly complex oyster reef structure should maintain constant predator densities (assuming transient species), while increasing densities of prey (assuming resident species). Thus, the decreased foraging success that we documented at higher complexities (in this study) may be more a result of density-dependent processes and should be accounted for in future studies by incorporating increasing prey densities as a factor.

Structure may influence interactions by providing refuge and affecting predator-prey dynamics within a community. This study demonstrated that created oyster reefs play a role in affecting trophic relationships through predator-prey interactions. It also indicated there may be a point at which additional structural complexity becomes redundant in providing significantly more refugia for prey. Interestingly, our field experiment (Chapter 3) showed a similar pattern, with increased abundances of resident species with the addition of shell reefs, but no increased abundance of nekton with increased shell density. Combined, both results suggest that either our treatments were not providing actual increased refuge space or complexity from the fish perspective, or that density-dependent effects may limit the actual abundance of resident species that may co-exist within a set area, regardless of structural complexity.

CHAPTER 5. CONCLUSIONS

Oyster reefs have been called essential fish habitat due to support they provide to resident and transient fish (Breitburg and Miller 1998). This research was designed to better understand the influence of habitat structure and complexity on the abundance and distribution of species at newly created oyster reefs, as well as determine mechanisms that may contribute to variations in species assemblages. Overall results from the three studies, summarized below, demonstrate that shell reefs provide valuable habitat for resident nekton species, and that the complexity of the reef may influence the refuge function of the reef. Furthermore, combined results from field and lab studies also indicate that the structure per se, provides valuable habitat, regardless of complexity. Given that this work was completed on recently created reefs, these findings also indicate that post-creation, the presence of increased structure, may immediately enhance valuable habitat for nekton and the findings underscore the potential role of biogenic structure and habitat complexity in influencing estuarine communities.

The first experiment (Chapter 2) examined nekton assemblages at newly created oyster reefs and mud-bottom habitat, as well as wave exposure, to characterize spatial and temporal patterns of nekton use. Transient species appeared to show no habitat preference and were seasonally abundant. Resident species appeared to be less affected by season and were consistently more abundant at and around oyster reefs than mud-bottom treatments. No pattern in nekton use could be directly attributed to wave exposure.

While there were very few significant effects on transient species assemblages directly attributable to the presence of oyster reefs, reefs appeared to benefit resident species as they supported greater numbers of resident species as compared to mud-bottom. Since the reefs were newly created using clean disarticulated shell piles, this finding suggests that the presence of

shell structure per se, and not the provision of food or other resources, provides valuable habitat to resident species; this finding is interesting from a theoretical stand point as it suggests that for resident species, a reefs primary value may result purely from its structure. That said, it is unclear without further sampling of these communities how the resident and transient communities will respond over time as the reef recruits and grows oysters, building the reef in size and complexity.

The second experiment (Chapter 3) examined the relationship between the presence and structural complexity of created oyster reefs and nekton assemblages. The presence of structure, regardless of complexity, appeared to be the most important factor determining assemblages at newly created reefs. The lack of a direct relationship between habitat complexity and species abundance and diversity could be the result of a number of biotic and abiotic interactions including available niche space and habitat setting. The creation of oyster reefs may contribute to increased species abundance and diversity, but further increasing the structural complexity may not result in higher abundances and more diverse assemblages.

The absence of a direct relationship between structural complexity and community demographics in the field experiment could be the result of a number of biotic and abiotic interactions, including limited food rates, competition among resident species for space and food, or increased predation by transients. It is possible that density dependent effects limit continued increases in resident species abundances.

The third experiment (Chapter 4) examined the refuge value of oyster reefs by investigating how variations in structural complexity influence predator-prey interactions. Predator foraging success decreased as structural complexity increased; there may be a point at

which increasing the structural complexity becomes redundant in providing more refuge for organisms and no longer increases the refuge value of the oyster reef.

Combined, the lab and field data all support the contention that structural complexity of a habitat is a vital mechanism influencing population biology and species interactions (Bell et al. 1991). Specifically, the two field studies clearly demonstrated that resident nekton species quickly congregated to the complex habitat created by oyster reefs with greater numbers of resident species found at the created oyster reefs. Furthermore, the lab study clearly demonstrated that increasing complexity of the habitats provides greater refuge for prey species, demonstrating how structural complexity may affect trophic relationships through predator-prey interactions, thus affecting populations and community dynamics. At the same time, both the lab and the experimental field project suggested that there is a threshold of complexity at which the effects of increased complexity are no longer simple to measure through changes in species abundances, or increased refuge value.

The management of oyster reefs may affect the extent to which reefs provide habitat for nekton, and thus influence community and local estuarine populations. If the results of these experiments were to hold true on different spatial and temporal scales, managers could (1) create oyster reefs that provide immediate habitat of value, (2) create oyster reefs using methods that do not require sophisticated or complicated designs. Chapters 2 and 3 demonstrate that newly created oyster reefs provide significant habitat for fish and invertebrate species (e.g., freckled blenny, naked goby, Atlantic mud crab, bigclaw snapping shrimp), and Chapter 4 demonstrates that created oyster reefs may provide refugia for prey. These results suggest that managers may create simple oyster reefs with very little vertical relief (structural complexity) as nekton habitat. Although, because healthy oyster reefs require an accumulation of accreting shell to keep up

with sedimentation and relative sea-level rise, managers cannot ignore other factors influenced by structural complexity (e.g., disease, larval recruitment, survivorship, growth). Conclusions from this research suggest that the presence of newly created oyster reefs may increase the abundance and diversity of resident nekton, but further/infinately increasing the structural complexity does not automatically increase nekton use or the refuge value of the reef.

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VITA

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