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

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ABSTRACT

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

1. Introduction

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

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

Oyster reefs provide significant structure in shallow marine ecosystems worldwide, yet are often underrepresented in studies of estuarine nekton community and population dynamics as compared to other biogenic structures (e.g., seagrass meadows, salt marshes, mangroves, coral reefs) (see review in Minello et al., 2003). For example, Heck et al. (2003) concluded that very few differences exist in the abundance, growth, or survival of associated nekton assemblages when comparing seagrass meadows to other biogenic structures (i.e., oyster or cobble reefs, macroalgal beds). In their review, however, only one (Eggleston et al., 1998) of the sixty-four cited references explicitly included oyster reefs. Studies that focus on community assemblages at oyster reefs often compare reefs to other biogenic structures or mud-bottom, ignoring possible structural differences within reefs that may influence nekton use (e.g., Geraldi et al., 2009; Harding and Mann, 2001; Plunket and La Peyre, 2005; Shervette and Gelwick, 2008; Stunz et al., 2001, 2002, 2010; but see Tolley and Volety, 2005). An exception is Soniat et al. (2004), who reported that

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shell orientation affects the availability of refugia, and fish species may show a higher affinity for vertically- rather than horizontally-oriented oyster shell.

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

2. Materials and methods

2.1. Study site

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

2.2. Experimental reef construction

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

2.3. Field sampling

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

2.4. Statistical analyses

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

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

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

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