

# The effects of intertidal oyster reef habitat characteristics on faunal utilization

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**ABSTRACT:** The presence, abundance, and distribution of organisms within a landscape are highly dependent on the composition, quality, and configuration of habitat patches. Intertidal oyster *Crassostrea virginica* reefs provide a structured habitat for many organisms; however, declining oyster populations have induced reef fragmentation and loss. Over 2 years (2011–2012), we evaluated naturally occurring fringing and patch intertidal oyster reefs in southeastern North Carolina, USA, to determine how varied reef type, size, and distance from edge to interior influenced the associated benthic macrofauna and mobile nekton. In addition, the effects of size and edge vs. interior were examined on constructed intertidal reefs at 2 different locations. On the natural reefs, species richness of benthic macrofauna and mobile nekton were significantly increased on fringing reefs. Benthic macrofauna richness significantly decreased on large natural reefs, whereas mobile nekton richness significantly increased off of large reefs. Further, associated benthic macrofauna richness significantly decreased along the reef edge, whereas mobile nekton diversity increased along the reef/open bottom interface. Species richness and densities for benthic macrofauna increased with created reef size, while there was greater species richness and diversity and dissimilar communities for mobile nekton along constructed reef edges. Habitat specificity may influence utilization for mobile nekton, as resident organisms with limited vagility had a stronger response to habitat characteristics. Thus, utilization of intertidal oyster reefs can be highly structured by habitat characteristics on many scales, and should be considered when examining species interactions, ecosystem management, and future restoration efforts.

**KEY WORDS:** Habitat characteristics · Habitat heterogeneity · Patch size · Edge effects · Mobile nekton · Benthic macrofauna · Habitat fragmentation · Habitat restoration · Oyster reefs · *Crassostrea virginica*

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## INTRODUCTION

Landscape heterogeneity is influenced by abundance, variety, configuration and complexity of habitat patches (Wedding et al. 2011). Species distributions within heterogeneous landscapes can be influenced by the spatial arrangement of habitat types, in which habitat utilization is a result of physical processes, resource availability, and predation risk (Gonzalez et al. 1998, Ewers & Didham 2006).

Along with this inter-patch heterogeneity, habitat patches often exhibit internal heterogeneity (Wiens et al. 1993) because the edge and interior of a habitat patch can be ecologically unique microhabitats that often dictate species utilization (Murcia 1995, Ries et al. 2004). Finally, both inter- and intra-patch heterogeneity may be increased through habitat loss and fragmentation, which can further impact species distributions, interactions, and assemblages within the landscape (Andren 1994, Fagan 2002).

Within the marine environment, habitats created by organisms such as corals, seagrasses, and oysters all support diverse communities. These habitat types exhibit inter- and intra-patch heterogeneity and have also experienced high levels of degradation and fragmentation, which all can influence the associated communities (Jones et al. 1994, Coleman & Williams 2002). Within these habitat types, a species' utilization and response to an increasingly heterogeneous landscape may be highly dependent on the species' life history. For many sessile organisms, or organisms that have little movement between habitat patches after settlement, inter-patch processes are mainly responsible for recruitment to habitat patches (Fagan 2002). However, after settlement or colonization of a habitat patch, these species with limited or no movement are highly influenced by intra-patch processes. Rather than depending on the connectivity and configuration of a landscape for dispersal and recruitment to a habitat patch, mobile species may utilize a matrix of habitat patches (Leibold et al. 2004). The greater vagility of these mobile species increases their ability to survive disturbances and rapidly colonize disturbed habitat patches (Thomas 2000); thus, they may be less affected by some intra-patch characteristics. Therefore, habitat patches that experience fluxes of organisms, due to their active movement within a landscape, may have altered local and regional processes and community structure (France & Duffy 2006, Muneeppeerakul et al. 2008).

The eastern oyster *Crassostrea virginica* is an important estuarine organism that creates 3-dimensional reef structure which provides habitat for epifauna, crabs, shrimp, and transient and resident fish in habitats that would otherwise be unstructured (Coen & Luckenbach 2000, Lehnert & Allen 2002, Peterson et al. 2003). Along the Atlantic coast of the United States, oysters predominately exist as either subtidal or intertidal reefs, and differences in tidal fluctuations between these 2 reef types can influence the community dynamics by impacting faunal utilization, encounter patterns, and time spent feeding on a reef (Lehnert & Allen 2002, Brown et al. 2008, Byers et al. 2015). Within the intertidal zone, oysters form fringing reefs, which are parallel to *Spartina alterniflora* marshes, or patch reefs, which are completely surrounded by open bottom habitat (McCormick-Ray 2005, Smyth et al. 2015). Within our study system in southeastern North Carolina, oyster densities varied between these 2 reef types: greater densities exist on patch reefs compared to fringing reefs (Smyth et al. 2015, Hanke et al. 2017). These 2 reef types also differ in tidal exchange because fringing reefs have a

single encounter edge for an incoming tide, while the entire patch reef edge is an encounter area. Additionally, mobile organisms might perceive these 2 habitat types differently, as fringing oyster reefs can function as a corridor habitat into the saltmarsh, whereas patch reefs congregate nekton in areas that would otherwise be open bottom (Micheli & Peterson 1999, Grabowski et al. 2005).

The decline of oyster populations over the last century due to multiple natural and anthropogenic forces has fragmented intertidal reefs from large expansive reefs into smaller isolated reefs (Lenihan & Peterson 1998, Coen & Luckenbach 2000, Beck et al. 2011). With the increased relative amount of reef edge due to fragmentation, oyster populations are at a greater disadvantage because the edges have the least amount of structural complexity and a greater predation risk (Macreadie et al. 2012, Hanke et al. 2017). Therefore, the amount of edge may influence how associated reef fauna and mobile nekton perceive and utilize the habitat (Griffitt et al. 1999). Furthermore, increased structural reef complexity towards the interior of the reef could impact species utilization, interactions, and even community function (Grabowski 2004, Grabowski & Powers 2004). Oyster densities on intertidal reefs in southeastern North Carolina are also affected by other habitat characteristics of reef size and distance from reef edge (Hanke et al. 2017). Reef size influences naturally occurring intertidal reef oyster densities, as intermediate sized reefs have greater densities (Hanke et al. 2017), and the response of organisms that utilize oyster reefs is also influenced by size; however, this can be highly variable and species specific (Eggleston et al. 1998, 1999, Harwell et al. 2011). Further, the interior of intertidal reefs can have greater oyster densities (Hanke et al. 2017), but the spatial distribution or organismal utilization based on edge to interior microhabitats is less known.

Artificial oyster reefs have been constructed to regain lost critical habitat and ecosystem services (Meyer et al. 1997, Meyer & Townsend 2000, Coen et al. 2007). Creating substrate for oysters to colonize and initiate reef formation also facilitates the colonization and utilization by other reef-associated organisms, and provides structured habitat for mobile nekton. The community structure of created reefs can be highly dependent on the restoration setting, because the habitat characteristics can directly influence utilization of the reef by mobile and resident fauna (Grabowski et al. 2005, Gregalis et al. 2009, Hadley et al. 2010, Harwell et al. 2011). While many studies have assessed the establishment of communities on

created oyster reefs (e.g. Meyer & Townsend 2000, Coen & Luckenbach 2000, Grabowski et al. 2005), little is known about the community and species-specific responses to the spatial context of natural or created reefs (Eggleston et al. 1998, Harwell et al. 2011, McCormick-Ray 2005). For example, in a 2011 review of seascape ecology studies from major coastal biogenic ecosystems, Boström et al. (2011) identified only 2% of seascape ecology studies utilizing oyster reefs as a study system, which indicates that oyster reefs (in particular with regards to the context to the landscape) are a comparatively rarely studied coastal habitat. Therefore, the objective of this study was to understand the community and species-specific response within a varied landscape by (1) determining how different reef types, reef sizes, and distances from edge to interior influenced the associated benthic macrofauna and mobile nekton on naturally occurring intertidal oyster reefs and (2) determining how different reef sizes, distances from reef edge to interior, and amount of edge vs. interior influenced the associated benthic macrofauna and mobile nekton on created intertidal oyster reefs.

## MATERIALS AND METHODS

We employed large-scale observational and experimental methods. The influence of habitat characteristics on oyster *Crassostrea virginica* population dynamics and on associated communities were assessed (1) on a suite of natural fringing and patch oyster reefs (Hanke 2014), and (2) on replicate sets of created reefs of 3 different sizes in 2 different locations (Hanke 2014). All reefs were in southeastern North Carolina.

### Study sites

#### Natural reefs

Natural fringing and patch intertidal oyster reefs (n = 22) were sampled in Hewletts Creek, Howe Creek, and Masonboro Sound near Wilmington, North Carolina, USA (Table 1). Reefs were selected from these tidal creeks because they have a similar tidal range (~1.1 m) and salinity regime, are comprised of mainly sandy substrates, and are closed to legal oyster harvesting (Dame et al. 2000, Cressman et al. 2003, Mallin et al. 2007). Fringing reefs were selected based on similar shape, proximity to a *Spartina alterniflora* marsh, a well-defined transition between the reef and open bottom, and similar tidal range. Patch reefs were

Table 1. The natural reefs (n = 22) utilized in the study by reef type and size

Reef size	Reef type	
	Fringing	Patch
Small	4	3
Medium	4	5
Large	3	3

all completely surrounded by open bottom habitat (no vegetation or other structured habitat), had a regular circular or oblong shape, and were also of similar tidal range. For both patch and fringing oyster reefs, 3 size classes of reefs were selected based on the distance from the edge to interior of the reef: small (3 m distance to center), medium (5 to 8 m distance to center), and large (14 to 17 m distance to center). These distances from edge to interior were selected because they represented the small, medium, and large sizes of oyster reefs naturally found within the tidal creeks of southeastern North Carolina, based on initial surveys and previous studies (Hanke 2014).

#### Created reefs

Dead loose oyster shell was used to create intertidal reefs at Jones Island and Permuda Island, along the southeastern North Carolina coast, during the summer of 2010. At each location, 3 replicate sets of oyster reefs were constructed by placing the loose oyster shell approximately 0.2 m deep on sandy substrate in areas without any submerged aquatic vegetation (SAV). Each replicate set of reefs comprised 3 reefs of varying sizes: 10 × 10 m, 5 × 10 m, and 1 × 10 m (with the long axis parallel to the shore), for a total of 9 reefs at each location. All reefs were created approximately 2 m from the shoreline, with a minimum of 3 m between each reef, and each set had a 10 m long control open bottom plot (no reef or other structured habitat).

### Sampling methods

#### Associated benthic macrofauna

The associated benthic macrofauna community was sampled at low tide with a 0.04 m<sup>2</sup> quadrat in the fall (October to November) and in the spring (May to June) over 2 yr (2011 to 2012). For each quadrat collected from the natural and created reefs, all of the

shell within the quadrat (included culm in quadrat if >50% was along the edge) was removed down to the sediment and returned to the lab. At the lab, all of the oyster culms, which are connected clusters of upright oysters, and shell, were cleaned of mud and debris on a 2 mm sieve screen, and all associated macrofauna were removed and preserved in 70% alcohol. All shrimp, crabs, and bivalves were identified to species and counted and measured (carapace width for crabs, post-orbital head length for shrimp, and shell height for bivalves). Polychaetes were identified down to family, and any other fauna found within the shell matrix were identified, as far as taxonomically feasible, then enumerated and measured.

Each natural reef was used as a replicate, and for all sized reefs, one quadrat was deployed 1 m away from the edge of the reef, and one 3 m away. For the medium (5 to 8 m) and large (14 to 17 m) reefs, 1 additional quadrat was sampled at the most interior distance on the reef.

On the created reefs at Jones Island and Permuda, the 1 × 10 m plots were sampled with 3 quadrats along the length of the reefs: one in each corner and one in the middle of the reef, all 0.25 m from the edge. On the 5 × 10 m and 10 × 10 m plots, 3 quadrats were sampled 0.25 m from the lower edge, and 3 quadrats were sampled 0.25 m from the upper edge of the reef, one in each corner and one in the middle. The interiors of the 5 × 10 m and 10 × 10 m plots were sampled with 1 quadrat in the geometric center of the reef and another 2 quadrats 0.5 m on either side.

### Mobile nekton

Mobile nekton utilizing intertidal oyster reefs were sampled with Breder traps (Breder 1960). Breder traps are clear acrylic boxes (31 × 15 × 16 cm), which have been successfully used to passively sample juvenile fish and mobile crustaceans on oyster reefs (Griffitt et al. 1999, Harwell et al. 2011). Sampling was conducted in the spring (February to March) of 2012, summers (June to August) of 2011 and 2012, and the falls (October to November) of 2011 and 2012. Traps were deployed at low tide and left on the reef for 2 h after reef submergence. On all natural reefs, 3 traps were deployed off the reef, 1 m from the edge, and on the reef, 1 m and 3 m from the edge. On the medium (5–8 m) and large (14–17 m) reefs, an additional 3 traps were deployed at the most interior distance on the reef.

On the created reefs, traps were deployed on the open bottom, 1 m off the reefs along the lower edge

and upper (near shore) edge. On the 1 × 10 m plots, 3 traps were deployed on the reef: one in each corner and one in the middle of the reef, all 0.5 m from the edge. For the 5 × 10 and 10 × 10 plots, 3 traps were placed on the reef, 1 m from the lower and upper edge: one in each corner and one in the middle of the reef. The interior of these plots was sampled with 1 trap placed in the geometric center of the reef with 2 additional traps on either side.

For each set of 3 traps deployed on all reefs, the direction of the trap was alternated with the first and third trap facing open water, with the direction alternated each sampling event. All organisms were identified, enumerated, measured to the nearest millimeter (standard length for fish, carapace width for crabs, and post-orbital head length for shrimp), and released. If field identification and verification was not possible, organisms were returned to the lab for identification and measurements.

On the natural reefs, a 6.1 m seine net was also used to determine if mobile nekton utilizing the reef-open substrate interface was influenced by reef size. Seines on the natural fringing reefs were pulled along the lower edge of the reef and along the channel side for the patch reefs. The seine tows were standardized to 10 m tows for all reefs and replicated for all large reefs to account for potential patchiness with the large habitat, with individual reefs serving as replicates. Sampling was conducted 3 times a year in 2012: early spring (February to March), late spring (May to June), and fall (October to November). All organisms were identified, enumerated, measured, and released. If field identification and verification was not possible, organisms were returned to the lab for identification and measurements.

### Statistical analysis

Data were analyzed using SAS Version 9.2 software (SAS Institute). Prior to analysis, all data were checked for the assumptions of homogeneity of variance (Levene's test), and if the variance tests failed, the data were transformed ( $\log(x+1)$ ) prior to analysis. All significant ANOVA results ( $p < 0.05$ ) were analyzed with Student-Newman-Keuls (SNK) post hoc tests.

Species richness and species diversity (Shannon-Weiner index) were log transformed, and a 4-way ANOVA tested for differences in season, reef type, reef size, and distance from edge to interior for the reef associated and mobile nekton communities on the natural reefs. On the created reefs, a 3-way

ANOVA on log-transformed data tested for differences in species richness and diversity with season, reef size, and edge vs. interior as main effects. The densities and organism size (if applicable) were analyzed with a 4-way ANOVA to test for differences by season, reef type, reef size, and distance from the reef edge on the natural reefs, and a 3-way ANOVA on the created reefs used season, reef size, and edge vs. interior as main effects. However, due to significant interactions with all of the dominant mobile nekton species by season, a subsequent 3-way ANOVA determined differences by season with reef type, reef size, and distance from the edge as main effects on the natural reefs, and a 2-way ANOVA by season with reef size and edge vs. interior for mobile nekton at Jones Island. Abundances of mobile nekton collected off the natural reefs with seines were analyzed with a 3-way ANOVA to determine the effects of season, reef size, and reef type.

Analysis of similarity (ANOSIM) in the Primer statistical package (Primer 6 and Permanova+) was used to determine if the assemblages of the reef associated and mobile nekton communities on the natural reefs differed statistically among reef type, reef size, and distance from to interior. ANOSIM analyses were also used to test for community differences on the created reefs based on differing reef sizes and distances from edge to interior. For the mobile nekton community ANOSIM analysis, the created reefs control plots were not included in analysis for edge vs. interior on reef. For each habitat factor, the data were square root transformed, and levels of similarity were compared with a 1-way pairwise ANOSIM (999 permutations).

## RESULTS

### Natural reefs

#### Associated benthic macrofauna

On the natural *Crassostrea virginica* reefs, a total of 33 different taxa were observed, and 8 species composed >1% of total abundance as *Brachidontes exustus*, nereid polychaetes, *Boonea impressa*, *Panopeus herbstii*, *Geukensia demissa*, *Eurypanopeus depressus*, *Loxothylacus panopaei*, and *Crepidula fornicata* comprised 94.7% of the total abundance (Hanke 2014).

Reef type significantly ( $F_{1,81} = 14.420$ ,  $p = 0.0003$ ) influenced species richness: richness was greater on fringing reefs compared to patch reefs (Table 2);

Table 2. Species richness and species diversity for the habitat characteristics examined on the natural reefs for the associated benthic macrofauna and the mobile nekton community. Data are mean  $\pm$  SE. When significant differences were found with ANOVA (**bold values**), post-hoc differences (Student-Newman-Keuls method) are presented in decreasing means

	Reef type		Reef size			Distance from edge			
	Fringing	Patch	Small	Medium	Large	1 m off	1 m	3 m	Center
<b>Richness</b>									
Associated macrofauna	<b>8.56 <math>\pm</math> 0.32<sup>A</sup></b>	<b>6.38 <math>\pm</math> 0.41<sup>B</sup></b>	<b>8.12 <math>\pm</math> 0.46<sup>A</sup></b>	<b>7.91 <math>\pm</math> 0.52<sup>A</sup></b>	<b>6.00 <math>\pm</math> 0.45<sup>B</sup></b>	<b>6.46 <math>\pm</math> 0.46<sup>B</sup></b>	<b>7.43 <math>\pm</math> 0.45<sup>A</sup></b>	<b>7.75 <math>\pm</math> 0.59<sup>A</sup></b>	
Mobile nekton	<b>2.67 <math>\pm</math> 0.22<sup>A</sup></b>	<b>2.15 <math>\pm</math> 0.16<sup>B</sup></b>	2.45 $\pm$ 0.29	2.32 $\pm$ 0.22	2.33 $\pm$ 0.20	2.63 $\pm$ 0.33	2.65 $\pm$ 0.23	2.20 $\pm$ 0.22	1.87 $\pm$ 0.25
<b>Diversity</b>									
Associated macrofauna	0.61 $\pm$ 0.03	0.68 $\pm$ 0.02	0.65 $\pm$ 0.03	0.64 $\pm$ 0.04	0.66 $\pm$ 0.04	0.70 $\pm$ 0.02	0.64 $\pm$ 0.03	0.59 $\pm$ 0.06	
Mobile nekton	0.26 $\pm$ 0.02	0.19 $\pm$ 0.02	0.22 $\pm$ 0.02	0.20 $\pm$ 0.02	0.24 $\pm$ 0.02	<b>0.24 <math>\pm</math> 0.03<sup>AB</sup></b>	<b>0.27 <math>\pm</math> 0.03<sup>A</sup></b>	<b>0.21 <math>\pm</math> 0.03<sup>AB</sup></b>	<b>0.15 <math>\pm</math> 0.03<sup>B</sup></b>

however, there was no significant difference between reef types for species diversity ( $F_{1,81} = 2.46$ ,  $p = 0.10$ ). There were no significant differences between fringing and patch reefs in the abundances of the dominant species, but the mean size of *B. exustus* was significantly greater on fringing reefs ( $F_{1,179} = 10.85$ ,  $p < 0.0001$ ) compared to patch reefs.

Large natural reefs had significantly lower species richness ( $F_{2,81} = 5.92$ ,  $p = 0.004$ ) compared to medium and small reefs (Table 2). Further, reef size had limited effect on the densities and sizes of the dominant fauna on the natural reefs, as only season and reef size ( $F_{2,204} = 3.55$ ,  $p = 0.03$ ) had a significant interactive effect for *Boonea impressa* density, with significantly greater densities ( $F_{1,70} = 5.28$ ,  $p = 0.02$ ) on small reefs compared to large reefs in the spring. Reef size significantly ( $F_{2,179} = 7.32$ ,  $p = 0.0009$ ) influenced the size of *B. impressa*, with a greater mean size on small reefs compared to medium reefs. Additionally, *B. exustus* had a significantly smaller size ( $F_{2,179} = 9.42$ ,  $p < 0.0001$ ) on small reefs compared to large and medium sized reefs.

Based on the distances from the reef edge, species richness was significantly lower ( $F_{2,81} = 4.83$ ,  $p = 0.04$ ) at the 1 m location compared to the 3 m and center locations (Table 2), but there were no significant differences for species diversity ( $F_{2,81} = 2.19$ ,  $p = 0.13$ ). For the dominant species of the associated benthic macrofauna, *B. exustus* ( $F_{2,228} = 4.20$ ,  $p = 0.01$ ), *E. depressus* ( $F_{2,228} = 10.20$ ,  $p < 0.0001$ ), and *P. herbstii* ( $F_{2,228} = 3.66$ ,  $p = 0.02$ ) all had significantly lower densities along the edge (Fig. 1), whereas densities of *G. demissa* were significantly ( $F_{2,228} = 9.01$ ,  $p = 0.0002$ ) greater at the reef interior (Fig. 1). Finally, the natural reefs indicated no differences in community structure between reef types, reef sizes, and distance from reef edge (Table 3).

### Mobile nekton

From the natural reefs, 29 different taxa were collected and *Fundulus heteroclitus*, *Lagodon rhomboides*, and *Leistomus xanthurus* composed 91.6% of the catch (Hanke 2014). For species richness, there was a significant interaction of season and reef type ( $F_{2,140} = 4.75$ ,  $p = 0.01$ ): species diversity was significantly greater ( $F_{1,59} = 13.92$ ,  $p = 0.0004$ ) on fringing reefs compared to patch reefs in the summer. The dominant species on the natural reefs, *Fundulus heteroclitus*, demonstrated preferential utilization between reef types given that during the spring ( $F_{1,58} = 5.53$ ,  $p = 0.02$ ) and summer ( $F_{1,140} = 4.35$ ,  $p = 0.04$ ),

abundances were greater on fringing reefs compared to patch reefs. Utilization for *L. rhomboides* varied by reef type and reef size ( $F_{2,140} = 4.15$ ,  $p = 0.02$ ) during the summer: utilization of patch reefs was significantly greater ( $F_{2,79} = 6.33$ ,  $p = 0.0042$ ) on the large reefs compared to medium and small reefs. The mean

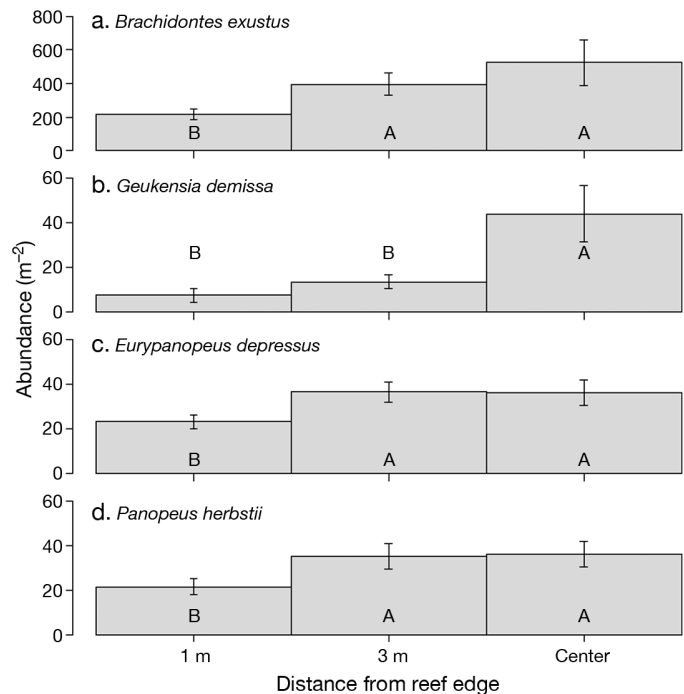


Fig. 1. Mean ( $\pm 1$  SE) abundance of dominant species that had a significant edge to interior distribution on the natural reefs, which were (a) *Brachidontes exustus*, (b) *Geukensia demissa*, (c) *Eurypanopeus depressus*, and (d) *Panopeus herbstii*. Letters represent results from SNK post-hoc tests, and those that do not share a common letter are significantly different ( $p < 0.05$ )

Table 3. ANOSIM tests and the significant 1-way pairwise comparisons for natural reef habitat characteristics for the associated benthic macrofauna and mobile nekton communities. Significant values ( $p < 0.05$ ) in **bold**

	Global R	Significance
<b>Associated benthic macrofauna</b>		
Reef type	-0.014	0.76
Reef size	-0.016	0.637
Distance from edge	0.043	0.063
<b>Mobile nekton</b>		
Reef type	0.021	0.079
Reef size	-0.021	0.753
Distance from edge	0.054	<b>0.007</b>
1 m off vs. 1 m	0.069	<b>0.023</b>
1 m off vs. 3 m	0.067	<b>0.002</b>
1 m off vs. center	0.108	<b>0.002</b>

size of *L. xanthurus* was significantly greater on patch reefs during the spring ( $F_{1,38} = 4.35$ ,  $p = 0.04$ ), but during the summer, the mean size was significantly ( $F_{1,9} = 31.28$ ,  $p = 0.0003$ ) greater on fringing reefs. In addition, mobile nekton species richness ( $F_{2,65} = 0.14$ ,  $p = 0.70$ ) or diversity ( $F_{2,65} = 0.35$ ,  $p = 0.55$ ) collected adjacent to the reef with a seine net were not significantly influenced by reef type.

Natural reef size had no significant effect on species richness ( $F_{2,123} = 0.31$ ,  $p = 0.73$ ) or species diversity ( $F_{2,140} = 1.38$ ,  $p = 0.25$ ) (Table 2) and only had significant effects on the abundance and size of the dominant transient species. In the spring, *L. rhomboides* abundance was significantly greater ( $F_{2,58} = 9.28$ ,  $p = 0.0003$ ) on the natural large and medium sized reefs compared to the small reefs, although the mean size of *L. rhomboides* was significantly larger ( $F_{2,32} = 3.74$ ,  $p = 0.03$ ) on the small reefs compared to the medium or large reefs. Only species richness was significantly ( $F_{2,60} = 4.16$ ,  $p = 0.02$ ) influenced by reef size for mobile nekton collected adjacent to the reefs with seine nets: richness from the large sized reefs was greater than the medium sized reefs (Table 4).

Distance from the reef edge did not significantly influence species richness ( $F_{3,140} = 1.33$ ,  $p = 0.26$ ), but species diversity was significantly ( $F_{3,140} = 3.01$ ,  $p = 0.03$ ) lower at the reef interior compared to the edge (1 m on the reef) (Table 2). Utilization of edge and interior microhabitats for the dominant species tended to differ between resident and transient species. The dominant resident species, *F. heteroclitus*, had a significantly greater ( $F_{3,140} = 10.26$ ,  $p < 0.0001$ ) utilization of the reef interior during the fall. Conversely, the dominant transient species tended to have preferential utilization of the reef edge/open bottom interface, as *L. rhomboides* had significantly ( $F_{3,58} = 6.69$ ,  $p = 0.0005$ ) greater abundances during the spring along the reef edge interface (1 m on the reef and 1 m off the reef) compared to the 3 m or center locations. Reef utilization for *L. xanthurus* demonstrated an affinity for the reef edge, with significantly greater edge utilization compared to interior locations during the spring ( $F_{3,58} = 5.36$ ,  $p = 0.002$ ) and fall ( $F_{3,140} = 10.26$ ,  $p < 0.0001$ ).

There was no significant difference for community similarity for mobile nekton ( $p > 0.05$ ) for reef type and reef size based on the global R, but there were dissimilar communities ( $p < 0.01$ ) based on distance from the reef edge (Table 3). Pair-wise analyses indicated this pattern was driven by differences from 1 m off the reef, because this location was significantly different ( $p < 0.05$ ) from all locations on the reef (Table 3).

## Created reefs

### Associated benthic macrofauna

On the created reefs at Permuda Island, a total of 30 different taxa were collected, and *Boonea impressa*, *Brachidontes exustus*, *Eurypanopeus depressus*, capitellid polychaetes, eucinid polychaetes, nereid polychaetes, terebellid polychaetes, and *Crepidula fornicata* accounted for 88.73% of the total abundance (Hanke 2014). From the created reefs at Jones Island, a total of 37 different taxa were collected, and *B. exustus*, *Boonea impressa*, *E. depressus*, nereid polychaetes, *Geukensia demissa*, *Ilyanassa obsoleta*, *Panopeus herbstii*, terebellid polychaetes, *Urosalpinx cinerea*, and *C. fornicata* composed 97.1% of the total abundance (Hanke 2014).

Reef size significantly impacted species richness at Jones Island ( $F_{2,16} = 8.86$ ,  $p = 0.01$ ), with lower richness on the smallest (1 × 10 m) plots (Table 5), but no significant reef size effect ( $F_{2,16} = 4.53$ ,  $p = 0.05$ ) at Permuda Island (Table 5). Reef size had no significant effect on species diversity for the created reefs at Jones ( $F_{2,16} = 0.90$ ,  $p = 0.42$ ) or Permuda Islands ( $F_{2,16} = 0.23$ ,  $p = 0.31$ ) (Table 5). There were reef size effects for densities of the dominant fauna on the created reefs, which varied between Permuda and Jones Islands. At Permuda Island, the densities increased with increasing reef size for *B. exustus* ( $F_{2,56} = 3.59$ ,  $p = 0.03$ ; Fig. 2a), *C. fornicata* ( $F_{2,37} = 4.09$ ,  $p = 0.02$ ; Fig. 2b), and *E. depressus* ( $F_{2,56} = 4.96$ ,  $p = 0.01$ ; Fig. 2c). However, at Jones Island, there was a significant reef size effect for *B. exustus* ( $F_{2,47} =$

Table 4. Species richness and species diversity for the habitat characteristics examined on the natural reefs for the mobile nekton community off the reef, collected with a seine net. Data are mean ± SE. When significant differences were found with ANOVA (**bold** values), post-hoc differences (SNK) are presented in decreasing means

	Spring	Summer	Fall	Fringing	Patch	Small	Medium	Large
Richness	<b>3.63</b> <b>3.63<sup>A</sup></b>	<b>2.27 ± 0.31<sup>B</sup></b>	<b>0.81 ± 0.20<sup>C</sup></b>	2.24 ± 0.33	2.06 ± 0.27	<b>2.34 ± 0.42<sup>AB</sup></b>	<b>1.63 ± 0.26<sup>B</sup></b>	<b>2.83 ± 0.45<sup>A</sup></b>
Diversity	<b>0.26 ± 0.04<sup>A</sup></b>	<b>0.17 ± 0.04<sup>B</sup></b>	<b>0.06 ± 0.03<sup>C</sup></b>	0.18 ± 0.03	0.15 ± 0.03	0.18 ± 0.05	0.12 ± 0.03	0.21 ± 0.04

Table 5. Species richness and species diversity values for the landscape factors examined on the created reefs at Permuda and Jones Islands for the associated benthic macrofauna and the mobile nekton community. Data are mean  $\pm$  SE. When significant differences were found with ANOVA (**bold values**), post-hoc differences (SNK) are presented in decreasing means

	Reef size				Distance from edge				
	1 $\times$ 10 m	5 $\times$ 10 m	10 $\times$ 10 m	Control	Lower edge off	Lower edge	Center	Upper edge	Upper edge off
<b>Permuda</b>									
Richness									
Associated macrofauna	6.25 $\pm$ 2.13	8.11 $\pm$ 0.84	9.55 $\pm$ 0.69						
Mobile nekton	1.80 $\pm$ 0.24	1.74 $\pm$ 0.15	1.67 $\pm$ 0.16	1.75 $\pm$ 0.26	1.67 $\pm$ 0.19	7.74 $\pm$ 1.31	9.00 $\pm$ 1.36	8.66 $\pm$ 0.69	1.91 $\pm$ 0.21
Diversity									
Associated macrofauna	0.60 $\pm$ 0.21	0.77 $\pm$ 0.05	0.84 $\pm$ 0.03			0.70 $\pm$ 0.12)	0.78 $\pm$ 0.08	0.82 $\pm$ 0.04	
Mobile nekton	0.20 $\pm$ 0.03	0.16 $\pm$ 0.02	0.15 $\pm$ 0.02	0.20 $\pm$ 0.04	<b>0.18 <math>\pm</math> 0.03<sup>AB</sup></b>	<b>0.17 <math>\pm</math> 0.03<sup>AB</sup></b>	<b>0.12 <math>\pm</math> 0.03<sup>B</sup></b>	<b>0.16 <math>\pm</math> 0.03<sup>AB</sup></b>	<b>0.21 <math>\pm</math> 0.03<sup>A</sup></b>
<b>Jones</b>									
Richness									
Associated macrofauna	<b>4.66 <math>\pm</math> 1.76<sup>B</sup></b>	<b>9.88 <math>\pm</math> 0.44<sup>A</sup></b>	<b>9.88 <math>\pm</math> 0.90<sup>A</sup></b>	2.93 $\pm$ 0.54	2.44 $\pm$ 0.47	8.00 $\pm$ 1.31	11.00 $\pm$ 0.44	9.00 $\pm$ 0.51	3.92 $\pm$ 0.50
Mobile nekton	3.77 $\pm$ 0.52	3.03 $\pm$ 0.50	2.76 $\pm$ 0.36			2.25 $\pm$ 0.65	2.80 $\pm$ 0.43	3.44 $\pm$ 0.60	
Diversity									
Associated macrofauna	0.63 $\pm$ 0.09	0.72 $\pm$ 0.05	0.79 $\pm$ 0.10	0.30 $\pm$ 0.05	<b>0.24 <math>\pm</math> 0.04<sup>BC</sup></b>	0.77 $\pm$ 0.09	0.71 $\pm$ 0.08	0.72 $\pm$ 0.08	
Mobile nekton	0.38 $\pm$ 0.04	0.28 $\pm$ 0.04	0.28 $\pm$ 0.03			<b>0.21 <math>\pm</math> 0.05<sup>C</sup></b>	<b>0.29 <math>\pm</math> 0.03<sup>ABC</sup></b>	<b>0.36 <math>\pm</math> 0.05<sup>AB</sup></b>	<b>0.38 <math>\pm</math> 0.04<sup>A</sup></b>

3.82,  $p = 0.02$ ; Fig. 2d), *B. impressa* ( $F_{2,55} = 4.55$ ,  $p = 0.01$ ; Fig. 2e) and *G. demissa* ( $F_{2,14} = 6.11$ ,  $p = 0.02$ ; Fig. 2f), with the 5  $\times$  10 m sized reefs having the greatest densities.

Differences between edge and interior locations on the reef did not impact either richness (Jones:  $F_{2,16} = 0.43$ ,  $p = 0.65$ , Permuda:  $F_{2,16} = 1.66$ ,  $p = 0.25$ ) or diversity (Jones:  $F_{2,16} = 0.43$ ,  $p = 0.66$ , Permuda:  $F_{2,16} = 1.4$ ,  $p = 0.37$ ) for the created reefs (Table 5). For the dominant species, the only significant edge to interior pattern on the created reefs was for *C. formicata* at Jones Island, with significantly ( $F_{2,37} = 4.09$ ,  $p = 0.02$ ) lower densities along the lower reef edge compared to the reef center or upper edge.

Permuda Island had similar reef-associated communities based on reef size and distance from the edge (Table 6). Jones Island had similar communities for reef edge vs. interior, but there were dissimilar communities based on reef size ( $p < 0.001$ ) as all subsequent pair-wise tests for reef size were significantly different (Table 6).

#### Mobile nekton

At Permuda Island, 29 different taxa were collected, and *Fundulus heteroclitus*, *Lagodon rhomboides*, *Leiostomus xanthurus*, *Paleomonetes pugio*, and *Paralichthys dentatus* composed 93.1% of the catch (Hanke 2014). At Jones Island, 24 taxa were observed, and *F. heteroclitus*, *Illyanassa obsoleta*, *L. rhomboides*, *L. xanthurus*, *P. pugio*, and *Paleomonetes vulgaris* composed 95.1% of the total abundance (Hanke 2014).

Reef size did not significantly influence species richness (Jones:  $F_{3,82} = 0.92$ ,  $p = 0.43$ , Permuda:  $F_{3,82} = 0.68$ ,  $p = 0.56$ ) or species diversity (Jones:  $F_{3,81} = 0.88$ ,  $p = 0.45$ , Permuda:  $F_{3,82} = 1.54$ ,  $p = 0.20$ ) for the created reefs (Table 5). On the created reefs at Permuda Island, *P. dentatus* had significantly ( $F_{3,75} = 11.09$ ,  $p < 0.0001$ ) greater abundances on both the open bottom control and the 1  $\times$  10 m sized reefs compared to the 5  $\times$  10 m and 10  $\times$  10 m sized reefs. In terms of size, the created reefs at Jones Island had significantly ( $F_{3,31} = 6.74$ ,  $p = 0.001$ ) larger *L. rhomboides* on the open bottom control plots compared to the 3 sizes of created reefs.

There was no significant edge to interior effect on species richness at Jones ( $F_{4,82} = 0.92$ ,  $p = 0.43$ ) or Permuda ( $F_{4,82} = 1.21$ ,  $p = 0.31$ ) Islands. However, there was a significant ( $F_{4,82} = 2.62$ ,  $p = 0.04$ ) edge and interior effect on species diversity at Jones Island, with the greatest diversity off the upper reef edge and the



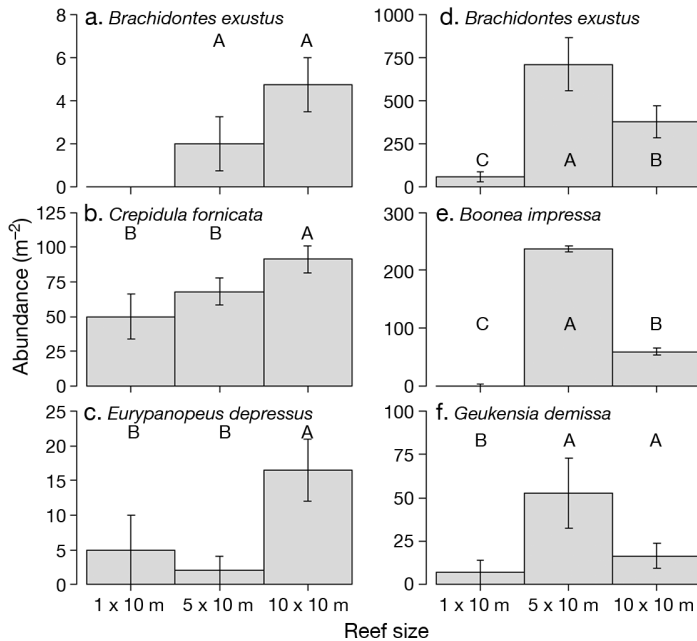


Fig. 2. Mean ( $\pm 1$  SE) density for dominant reef-associated species that had a significant reef size effect on the created reefs at Permuda Island: (a) *Brachidontes exustus*, (b) *Crepidula fornicata*, and (c) *Eurypanopeus depressus*. At Jones Island, the species that had a significant reef size effect were (d) *Brachidontes exustus*, (e) *Boonea impressa*, and (f) *Geukensia demissa*. Letters represent results from SNK post-hoc tests, and those that do not share a common letter are significantly different ( $p < 0.05$ )

Table 6. Results of ANOSIM tests and the significant 1-way pairwise comparisons for the habitat characteristics of the created reefs at Jones and Permuda Islands for the associated benthic macrofauna and mobile nekton communities. Significant values ( $p < 0.05$ ) in **bold**

	Global R	Significance
<b>Associated benthic macrofauna</b>		
Jones Island		
Reef size	0.2	0.001
10 x 10 m vs. 1 x 10 m	0.386	<b>0.004</b>
10 x 10 m vs. 5 x 10 m	0.043	<b>0.015</b>
1 x 10 m vs. 5 x 10 m	0.53	<b>0.01</b>
Edge vs. Interior	0.004	0.415
Permuda Island		
Reef size	0.023	0.26
Edge vs. Interior	-0.029	0.835
<b>Mobile nekton</b>		
Jones Island		
Reef size	-0.0006	0.50
Edge vs. Interior	0.095	<b>0.036</b>
Upper edge off vs. Lower edge	0.248	<b>0.019</b>
Upper edge off vs. Lower edge off	0.328	<b>0.001</b>
Permuda Island		
Reef size	0.078	0.06
Edge vs. Interior	0.042	0.186

lowest along the lower edge of the reef edge (Table 5). At Permuda Island, diversity was significantly ( $F_{4,82} = 2.60$ ,  $p = 0.03$ ) lower at the reef interior compared to the upper reef edge (Table 5).

Reef utilization for dominant species, based on edge vs. interior, also varied for estuarine resident and transient species. Similar to the natural reefs, *L. xanthurus* had significantly greater edge utilization of the created reefs at Permuda Island during the spring ( $F_{4,75} = 5.36$ ,  $p = 0.002$ ), with abundances greatest in open bottom off the lower reef edge. Further, the greatest mean size ( $F_{4,28} = 2.92$ ,  $p = 0.03$ ) of *L. xanthurus* was found off the reef along the lower and upper reef edges, and the lowest mean sizes were found on the reefs. In contrast, *F. heteroclitus* had a significantly greater abundance off the upper reef edge and along the upper reef edge at Permuda during the spring, and at Jones Island, there was also a preferential utilization ( $F_{4,210} = 2.89$ ,  $p = 0.002$ ) off the upper reef edge and the reef interior.

There were no differences in community similarity for the mobile nekton for the created reefs at Permuda Island based on reef size or reef edge vs. interior (Table 6). The created reefs at Jones Island had no differences in the mobile nekton community for reef size, but there was a significant difference ( $p < 0.05$ ) based on edge vs. interior locations (Table 6). There were differences between the location off the upper reef edge and on/off the lower reef edge (Table 6).

## DISCUSSION

Intertidal oyster *Crassostrea virginica* populations on natural and created reefs were strongly influenced by habitat factors in terms of reef type, reef size, and distance from edge to interior (Hanke et al. 2017), and this study demonstrated that reef-associated organisms also respond to these habitat characteristics. Previous terrestrial and marine studies have highlighted that the response to a changing landscape is often species-specific (Murcia 1995, Ries et al. 2004, Johnson & Heck 2006), and numerous species-specific responses to the heterogeneous intertidal oyster reef habitat were observed, generally linked with habitat specificity or mobility. Species that tended to have limited or no movement among habitat patches after initial recruitment had a stronger response to reef type, habitat

patch size, and distance from edge to interior habitat, which may be a result of post-settlement processes. However, mobile nekton with increased vagility, such as *Lagodon rhomboides*, tended to utilize reefs as habitat patches within the matrix of the estuarine environment and appeared less responsive to habitat characteristics. Therefore, these results further suggest that the consequences of habitat fragmentation to communities in the marine environment are temporal-, location-, and highly species-specific (Johnson & Heck 2006).

The inherent differences between the spatial locations of reefs may result in a tradeoff for oyster populations and habitat function. While fringing reefs had significantly lower densities of oysters than patch reefs (Hanke et al. 2017), the fringing reefs had greater species richness for both associated benthic macrofauna and the mobile nekton communities. Greater richness on fringing reefs may be due to the facultative marsh species utilizing the reefs as a corridor (Micheli & Peterson 1999), along with the *Spartina* marsh providing another highly structured habitat type via increased areal structural complexity. Therefore, the fringing reefs may have lower oyster densities due to the increased number of species utilizing this habitat as foraging grounds. In contrast, patch reefs supported greater oyster densities (Hanke et al. 2017) but lower community richness. Previously, Grabowski et al. (2005) found patch reefs with higher juvenile fish abundances, which they attributed to both greater resource availability and isolation of the habitat patch. Within the context of the landscape, patch reefs may provide habitat for a smaller number of species, potentially decreasing some predation pressure on oysters and thus enabling greater numbers of a few species to utilize this habitat type. In addition to differences in oyster production and habitat provisions, these 2 reef types may also provide different ecosystem services based on landscape context, such as water filtration (zu Ermgassen et al. 2013), energy dissipation, and stabilization for sediments (Meyer et al. 1997), and further research is needed to understand these differences for other ecosystem services (Kremen 2005, Coen et al. 2007) and environmental conditions.

Utilization of patch and fringing reefs may also be influenced by the life history strategies of mobile nekton. For example, *Fundulus heteroclitus* are an estuarine resident with limited vagility and preferentially utilize *Spartina* marsh habitats (Kneib 1984, Meyer & Posey 2009). This species had a significantly greater utilization of fringing reefs during the spring and summer. This difference could be attributed to

the obligate utilization of marsh habitats as spawning grounds and as a nursery habitat; therefore, during peak reproductive periods, *F. heteroclitus* utilizes fringing reefs along marshes as a corridor habitat (Micheli & Peterson 1999). A transient species with greater vagility, *L. rhomboides* are ubiquitous within many estuarine habitat types and may be attracted to the structure from large patch reefs within an open mudflat (Potthoff & Allen 2003, Meyer & Posey 2014). The difference in reef type utilization between *F. heteroclitus* and *L. rhomboides* further highlights the difference in how resident and transient species may perceive the estuarine landscape (Meyer & Posey 2009). Conversely, dominant associated benthic macrofauna showed no differences in abundances between the 2 reef types; however, the sizes of the scorched mussels *Brachidontes exustus* were larger on fringing reefs compared to patch reefs. This difference suggests that these mussels have greater survivorship and growth on the fringing reefs compared to the patch reefs, as crabs that prey on mussels preferentially choose smaller mussels (Eggleston 1990, Hadley et al. 2010).

The associated benthic macrofauna demonstrated different patterns for habitat patch size between Permuda and Jones Island, indicating location-specific processes in landscape patterns. Densities of the dominant fauna at Permuda Island increased significantly with increasing reef size, which follows the expectations of the island biogeography theory (MacArthur & Wilson 1967). However, at Jones Island, densities of the dominant macrofauna and oysters were greatest on the intermediate sized reefs (Hanke 2014). Increased mussel densities are often correlated with increased oyster densities (Hadley et al. 2010), and at Jones Island, both the scorched mussel *B. exustus* and the ribbed mussel *Geukensia demissa* had greater densities on the intermediate sized reefs, which had the greatest oyster densities (Hanke 2014). Additionally, *Boonea impressa*, which is an ectosymbiont on oysters (Wilson et al. 1991), also had greater densities on the intermediate sized reefs, which suggests that *B. impressa* may have large-scale spatial distributions in addition to small-scale distributions (Powell et al. 1987). Furthermore, the species richness and densities of the dominant fauna at Jones Island were significantly lower on the smallest reefs. These reefs had significantly lower oyster densities, reef cover, and complexity (Hanke et al. 2017), which decreases the available habitat for the reef-associated fauna. The lower oyster densities on the 1 × 10 m sized reefs had limited reef structure under high sedimentation rates (M. Hanke pers.

obs.), which further limited the available habitat and potentially the survivorship of fauna. While this further suggests that species richness will decline as a habitat becomes fragmented (Gonzalez et al. 1998), other experimental studies have shown declines in species richness are highly variable (Johnson & Heck 2006, Reed & Hovel 2006, Ewers & Didham 2006). The decline in the associated benthic macrofauna species richness on the large natural reefs provides further evidence for this high variability and suggests there could also be an upper patch size threshold for declines in species richness.

The sizes of oyster reefs examined in this study appeared to have limited influence on the composition and structure of the mobile nekton community. The lack of community response for the mobile nekton on the reef might be attributed to the sampling gear: Breder traps passively sample a select size class of mobile organisms close to the reef matrix, and seines could not sample larger fish over the reef. However, Harwell et al. (2011) found large mobile nekton communities had a limited response to reef size, which is often attributed to the reefs not being large enough to detect a response (Grabowski et al. 2005). Yet in this study, the largest size possible of naturally occurring intertidal reefs was utilized, and there were no significant responses, with the exception of significantly greater species richness for mobile nekton collected off the reef with seines. This increased richness may be a result of mobile species being attracted to larger habitat patches that have more edge habitat. Mobile nekton communities utilizing different sized patches of seagrass beds were also shown to have very inconsistent and limited community responses, and the patterns for habitat patch size were species-specific (Johnson & Heck 2006, Smith et al. 2010). This also seems to be the case on intertidal oyster reefs, as the mobile nekton community was not significantly affected by reef size but did have species-specific responses. For example, in the spring, when *L. rhomboides* were the smallest, abundances were greatest on medium sized fringing reefs and large patch reefs. *L. rhomboides* have also been shown to use large fragmented reefs more than small fragmented reefs (Harwell et al. 2011).

Naturally occurring intertidal oyster reefs have lower shell cover and reef complexity along the reef edge (Hanke 2014), and associated benthic macrofauna species richness was significantly lower along the reef edge. The lower reef cover and complexity along the reef edge may reduce the persistence of species along the edge by limiting the amount of

complex habitat and increasing the risk of predation. The dominant reef-associated fauna had lower densities along the reef edge, which further highlights the need to understand species-specific responses in order to understand future habitat loss and fragmentation. Two of these species were mussels, *B. exustus* and *G. demissa*, which are common prey species on intertidal oyster reefs (Grabowski & Powers 2004, Hadley et al. 2010). The significant decrease in mussel density along the reef edge could be a result of lower settlement due to limited substrate availability (Hanke 2014) or from increased predation by higher trophic predators, such as blue crabs *Callinectes sapidus*. The mussel densities may have been enhanced towards the reef interior due to the greater reef complexity towards the interior (Hanke 2014), which provides greater interstitial space for mussels to inhabit and limits predation pressure (Soniati et al. 2004). Additionally, the 2 dominant species of xanthid crabs (*Panopeus herbstii* and *Eurypanopeus depressus*) had significantly lower densities along the reef edge. This response to edge habitat may be attributed to greater predation pressure, such as from blue crabs feeding along the reef edge (Macreadie et al. 2012). This response may also be a relic of the reef structure, as abundances of *P. herbstii* have been shown to have a positive association with flat shell cover on the reef and *E. depressus* have been shown to have a positive association with oyster shell culms (Meyer 1994), and reef cover and complexity was significantly lower along the reef edge (Hanke et al. 2017).

Edge interfaces are important microhabitat in many marine systems (e.g. Bowden et al. 2001, Stunz et al. 2002), and the edge of intertidal oyster reefs provide an important habitat for mobile nekton. Greater species diversity and dissimilar communities along the reef edge compared to more interior locations suggests that edge and interior locations may function as different microhabitats. Habitat edges can often act as barriers (Fagan et al. 1999), and on intertidal reefs, the edge may be functioning as a barrier by limiting movement of some species into the reef interior. This limitation can concentrate nekton along the reef edge open bottom interface and potentially increase predatory interactions. For example, blue crabs preferentially feed along the reef edge and have limited movement onto reefs with an interior (Macreadie et al. 2012). Additionally, the concentration of mobile nekton may decrease abundances of infaunal organisms along the reef edges, as decreased infaunal abundances have been a result of predation along edges

of marshes (Whaley & Minello 2002) and other hard bottom habitats (Posey & Ambrose 1994). Utilization of edge and interior microhabitats appeared to differ based on life history, as differences were between estuarine residents and transient species. The estuarine resident, *F. heteroclitus*, had significantly greater utilization of the reef interior during the fall, which may be a result of movement into the interior with an incoming tide to avoid predators. Conversely, the estuarine transient, *Leiostomus xanthurus*, demonstrated preferential utilization for the interface between the open bottom and reef edge on the natural reefs, and most organisms are likely utilizing the reef edge for both refuge and as a foraging habitat, where they are feeding on benthic invertebrates (O'Neil & Weinstein 1987).

Loss and fragmentation of oyster reefs has increased over the last century due to declining oyster populations (Beck et al. 2011), and this study illustrates how fragmentation could impact the function of reefs as habitat. As naturally occurring reefs continue to degrade and fragment, reef size will decline, and the proportion of edge to interior will increase. This may confound population declines of the associated benthic macrofauna and resident estuarine fishes. One outcome of this work indicates the importance of habitat characteristics when managing naturally occurring or restoring intertidal reefs, as different reef characteristics may provide alternative habitat quality and ecosystem services, which suggests the necessity of determining specific *a priori* goals within the context of the landscape. For example, on the natural and created reefs, the open bottom reef edge interface was an important habitat for the mobile nekton, but the associated benthic macrofauna had lower richness on the edge of natural reefs and no significant response on the created reefs. In contrast, utilization of varied sized reefs for benthic macrofauna tended to follow oyster densities, because the upper and lower reef sizes tended to limit the benthic macrofauna densities and communities. Therefore, management of natural reefs and restoration of intertidal oyster reefs should have definitive objectives, which incorporate all of the costs and benefits of different habitat characteristics, within the context of the landscape, to optimize ecological benefits.

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