INFLUENCE OF STRUCTURAL COMPLEXITY AND LOCATION ON THE HABITAT VALUE OF RESTORED OYSTER REEFS

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Master of Science

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Melissa Karp

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APPROVAL SHEET

This thesis is submitted in partial fulfilment of

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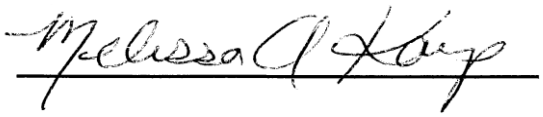

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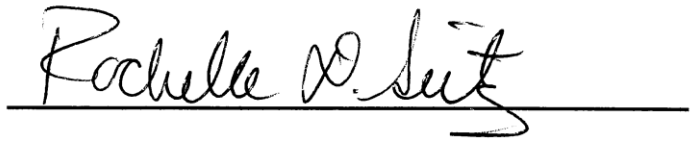

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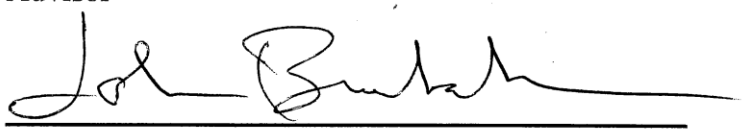

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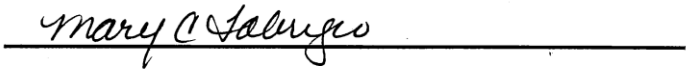

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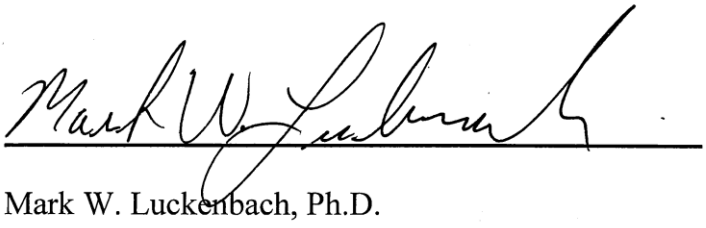

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DEDICATION

I would like to dedicate this thesis in loving memory of my Grandmom, Margaret B. Andersen (1922-2016). Though she may not have completely understood exactly what my project was about, she always let me know how proud she was of me, and how excited she was that I was doing what I loved. I love you Grandmom, and you will always be with me.

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THESIS ABSTRACT

In the Chesapeake Bay, < 1% of the historic oyster population remains, and efforts have been increasing to restore oysters and the services they provide. Building reefs that successfully provide ecosystem services–especially habitat and foraging grounds–may require different restoration techniques than those previously used, and success may depend on reef morphology (complexity), location, and environmental conditions. Salinity and habitat complexity are two important factors that may interact to effect benthic communities and predator-prey interactions on restored reefs. The goals of this project were: (1) Characterize the benthic communities on restored oyster reefs in lower Chesapeake Bay, and (2) examine the effects of structural complexity and salinity on benthic communities and predator-prey interactions. A two-year field survey of restored reefs was carried out in four rivers in lower Chesapeake Bay to characterize faunal communities on restored reefs and to quantify the effect of reef complexity on faunal communities. A laboratory mesocosm experiment was conducted to examine the effect of reef complexity on predator foraging. In total, 61 macrofaunal species were identified among all samples, and restored reefs supported on average, 6,169 org/m^2 and 67.88 g-AFDW/m^2. There were significant differences in the community composition and diversity among the rivers, and salinity was the environmental factor that best explained the observed differences in species composition across the rivers. Salinity and rugosity (i.e., structural complexity) both positively affected diversity, while salinity negatively affected macrofaunal abundance and biomass. Oyster density and rugosity positively affected macrofaunal biomass, and oyster density positively affected mud crab, polychaete, and mussel densities. In the mesocosm experiment, predator foraging, measured by proportion and number of prey consumed, was significantly reduced in the presence of oyster shell structure. However, predators were able to consume more prey when prey density was increased, even in the presence of oyster shell structure. These results combine to enhance our understanding of the benefits of increased habitat complexity for both prey and predators on restored oyster reefs. Increasing complexity worked to increase the abundance, biomass, and diversity of organisms inhabiting restored reefs, and even though predator consumption was reduced in the presence of structure compared to non-structured habitat, predators were able to consume more prey individuals when prey density was increased. Therefore, increasing the structure of oyster reef habitat may benefit prey species by providing refuge habitat, and benefit predators by providing an increased abundance of available prey items.

HABITAT VALUE OF RESTORED OYSTER REEFS

GENERAL INTRODUCTION

In this thesis, I investigated the effects of location and structural complexity of restored oyster reefs on the species composition of reef residents and predator-prey interactions. This research addressed several of the gaps in our understanding of oyster reef community structure, and specifically it addresses the importance of habitat complexity and salinity in structuring benthic communities and affecting ecosystem function.

The research is separated into two parts. Chapter 1 details a two-year field survey of restored reefs that was designed to: (1) quantify species diversity, density, and biomass on restored oyster reefs in Virginia tributaries of the lower Chesapeake Bay; and (2) examine the effects of structural complexity and salinity on benthic organism abundance, biomass, and species composition. This was accomplished through the use of benthic settling trays embedded in restored oyster reefs in four different tributaries in lower Chesapeake Bay. The trays were collected and sorted to remove all organisms, which were later identified, weighed and burned to obtain species-specific biomasses. Ordination, general linear models, and ANOVA analyses were used and allowed me to determine the structural and environmental parameters that were most important in affecting community structure on these restored reefs.

Chapter 2 examines the combined effects of oyster reef habitat complexity and prey density on predator-prey interactions and potential trophic transfer off of oyster reefs of differing complexity. A mesocosm experiment was conducted in which three levels of habitat complexity (none, low, high) was crossed with three levels of prey density (low, medium, high). Two-way Analysis of Variance was used to determine the effects of

altering prey density and habitat complexity on predator foraging success. The goal of this experiment was to determine the potential value of increasing oyster reef habitat complexity for foraging transient predators, such as striped bass.

CHAPTER 1

FAUNAL COMMUNITIES ON RESTORED OYSTER REEFS: THE EFFECTS OF HABITAT COMPLEXITY AND ENVIRONMENTAL CONDITIONS

ABSTRACT

Many marine benthic habitats are generated by the presence of either a single or a few habitat-modifying species, which often provide crucial habitat for other species. Oysters are an example of such a habitat-forming species. Unfortunately, wild oyster populations and their habitat have suffered >85% global loss, and in Chesapeake Bay, only 1% of the historic oyster population remains. In response, there have been increasing efforts to restore oysters and the services they provide. Determining the importance of these habitats, and the environmental and structural characteristics that affect species utilization of these habitats, is a crucial next step for successful restoration. In a field survey, benthic settling trays were embedded into restored reefs, varying in their structural complexity, in four rivers in Chesapeake Bay. Trays were retrieved after 7 weeks, sorted through, and species identified and weighed to obtain species diversity, abundance, and biomass. In total, 61 macrofaunal species inhabited restored oyster reefs across all the samples. The mean macrofaunal biomass supported by these restored reefs was 67.88 g-AFDW/m^2, and mean macrofaunal density was 6,169 ind/m^2. There were significant differences in species composition both in terms of abundance and biomass of organisms among the rivers, and salinity was the environmental parameter that best explained patterns in species composition. Salinity and rugosity (i.e., structural complexity) had significant and positive effects on macrofaunal diversity, while oyster density and rugosity had significant positive effects on macrofaunal biomass on restored reefs. Oyster density also had a significant positive effect on polychaete, mussel, and mud crab densities. These results suggest that restored oyster reefs have the potential to be highly productive habitats in Chesapeake Bay, and that their benthic communities depend on the density of live oysters and salinity. Ultimately, the results from this project will aid resource managers in developing more effective restoration strategies to construct reefs that provide both quality habitat and rich foraging opportunities for a diversity of marine organisms.

INTRODUCTION

Many marine benthic habitats are generated by the presence of either a single or a few habitat-modifying species, which often provide crucial habitat for other species (Bruno et al. 2003). Examples of these habitat-forming species include corals, seagrass, saltmarsh plants, mangroves, and oysters (Jones et al. 1994, Bruno et al. 2003). The structural complexity and habitat architecture provided by these species have profound effects on abundance and diversity of organisms (Alvares-Filip et al. 2011). Unfortunately, many of these biogenic habitats have been declining worldwide. For instance, seagrass (Waycott et al. 2009), salt marshes, mangroves, and coral reefs (Millennial Ecosystem Assessment 2005) have all suffered an estimated 20-30% global loss. Oyster reefs, which have only recently been recognized for providing critical habitat, are currently one of the most rapidly deteriorating habitats in the world, having suffered an estimated 85% global loss (Beck et al. 2011).

In Chesapeake Bay, once the largest producer of oysters in the United States (Haven et al. 1978), the oyster population was recently classified to be in 'poor condition' by Beck et al. (2011), with only 1% of the historic oyster population remaining. This dramatic decline is a result of a combination of stressors experienced by the oyster population over the last century, including destructive harvesting, overfishing, declining water quality (Rothschild et al. 1994), and increased prevalence of diseases (MSX and DERMO) in the 1950s and 80s (Carnegie and Burreson 2011). This decline has had both negative economic and ecological impacts in the Chesapeake region.

Restoration has occurred for several decades now, with substantial state and federal funds contributing to these efforts with limited success (Brumbaugh et al. 2010;

Beck et al. 2011). The main focus of these early restoration efforts has been to increase oyster biomass to maintain the oyster fishery. Recently, oyster reefs have been recognized as providing a suite of ecosystem services, or 'benefits to humans' beyond their direct economic value. These services include water filtration (Grizzle et al. 2008), sequestration of carbon (Peterson and Lipcius 2003), stabilization of intertidal and benthic habitats, de-nitrification (Kellogg et al. 2013), provision of habitat and foraging grounds for benthic invertebrates and fish, and enhanced benthic-pelagic coupling through facilitation of energy from the benthos to higher trophic levels (Dame 1979; Harding and Mann 2001; Peterson et al. 2003; Plunket and La Peyre 2005; Rodney and Paynter 2006). In recognition of these services, there has been a recent shift in management objectives to manage and restore oyster reefs for their ecosystem services, especially their value as productive habitats (Brumbaugh et al. 2010; Beck et al. 2011).

To date, however, success of restoration efforts is frequently judged based on either abundance of market sized (> 75 mm shell height) oysters or fishery landings data, neither of which may truly reflect the successful restoration of important ecosystem services (Luckenbach et al. 2005). Many of these services, particularly provision of habitat and foraging grounds, have not been adequately quantified in lower Chesapeake Bay. Collection of quantitative data to illustrate the role of restored oyster reefs as habitat for benthic invertebrates and fish, and identification of the factors that influence its value as habitat, are crucial next steps for successful restoration.

Two important factors with the potential to influence the success of restoration efforts in Chesapeake Bay are reef architecture (complexity) and environmental conditions (Dame 1979; Bruno et al. 2003; Peterson et al. 2003). One key environmental

factor controlling the distribution of fauna in the aquatic environment is salinity (Wells 1961). As one moves along a salinity gradient in an estuary and the water becomes fresher, certain marine species that cannot tolerate the decline in salinity are eliminated, but are not replaced by freshwater organisms. Thus, there is a notable decline in species diversity as salinity declines, until one enters the freshwater environment. This is a particularly important factor in relation to site selection for oyster reefs, as oysters and their associated fauna may respond differently to salinity. Despite its importance as a factor shaping faunal communities, salinity's effects on oyster reef communities have been addressed by only a few studies (see Wells, 1961; Tolley et al. 2005).

Habitat complexity, or the amount, density, or configuration of structural elements in a habitat, is another factor influencing the abundance, diversity, and distribution of organisms (Tews et al. 2004). It has been widely hypothesized that complex habitats will sustain more diverse and dense macrofaunal communities compared to simple habitats, a concept known as the "habitat heterogeneity hypothesis" (Diehl 1992; Tews et al. 2004). The hypothesis was originally proposed by examining complex terrestrial habitats, but has also been applied to various aquatic habitats as well, such as coral reefs (Alvarez-Filip 2011), freshwater benthos (Diehl 1992), and freshwater macrophytes (Crowder and Cooper 1982).

Oyster reef habitats only recently have been examined for patterns with respect to habitat complexity. Oysters are important ecosystem engineers providing hard 3-dimensional structure and modifying the environment in ways that facilitate not only their own growth and survival but that of many other species as well (Jones et al. 1994). Previous studies suggest that the topography, morphology, and spatial extent of these

reefs can affect the recruitment, abundance, and diversity of reef inhabitants. In Louisiana, oyster reefs supported significantly greater diversity and abundance compared to surrounding non-structured, less-complex mud and sand habitats (Plunket and La Peyre 2005). There were similar results on Florida oyster reefs (Tolley and Volety 2005), and restored oyster reefs in Maryland tributaries had greater structural complexity and supported significantly greater diversity of organisms compared to non-restored reefs (Rodney and Paynter 2006).

These previous studies compared abundance and diversity of organisms between structured and non-structured environments; however, how organisms respond to changes in habitat complexity within a specific structured habitat is not well understood, with studies yielding somewhat conflicting results. This is particularly the case with oyster reef habitats. For instance in Mobile Bay, Alabama, reef height, a measure of reef complexity, had no significant impact on species diversity. Reef height did have a significant effect on species abundance, with more organisms collected on low-relief reefs (Gregalis et al. 2009). In contrast, on New Zealand oyster reefs, species diversity and abundance both increased with increasing reef height and surface complexity (Cranfield et al. 2003).

Quantifying species utilization of restored oyster reefs and determining the relationship between oyster reef architectural complexity and environmental conditions, and species utilization of restored reefs is needed to better evaluate and improve restoration success (Luckenbach et al. 2005).

The current study addressed several of the gaps in our understanding of oyster reef community structure, and specifically it addressed the importance of habitat complexity and environmental conditions (especially salinity) in structuring benthic communities. This study was designed to characterize the macrofaunal community of

sub-tidally restored oyster reefs in the Virginia portion of Chesapeake Bay. The specific objectives of this study were to (1) quantify species diversity, density, and biomass on restored oyster reefs in the lower Chesapeake Bay; and (2) determine the relationship between the structural complexity and salinity of reefs, and the macrofaunal density, biomass, and composition on those reefs. I hypothesized that restored oyster reefs would provide habitat for a diversity of benthic organisms, that diversity would increase with increasing salinity, and that habitat complexity would positively affect both diversity and macrofaunal abundance.

METHODS

Sampling Locations

Field sampling took place during the summers of 2014 and 2015 on previously restored oyster reefs in four rivers in lower Chesapeake Bay – the Great Wicomico, Lynnhaven, Piankatank, and Lafayette (Figure 1). Reefs sampled in this study were part of previous large-scale restoration efforts carried out by the Army Corps of Engineers and Virginia Marine Resources Commission, and reefs were of different ages and sizes. The reefs in the Piankatank (Figure 2a) were the oldest, originally restored in 1993-1995, and have been reseeded several times since then. In the Great Wicomico River (Figure 2b), reefs were restored in 2003-2004, and in the Lynnhaven River (Figure 2c), reefs were restored in 2008-2009. Restoration in the Lafayette River (Figure 2d) began in 1998 with reseeding efforts occurring since then.

During the 2014 sampling, restored oyster reefs were sampled in the Lynnhaven and Great Wicomico Rivers, and in 2015 sampling occurred in the Lynnhaven,

Piankatank, and Lafayette rivers. In each river, four previously restored reefs were selected using Army Corps of Engineers and Virginia Marine Resource Commission maps of the reefs. These maps provided information regarding relief (surrogate for complexity) of the reefs and oyster abundance and were used to ensure that the reefs selected were representative of the variability in architecture of the reefs in each river. Exceptions to the above occurred in the Lynnhaven River in 2014 when instead of four individual reefs, two large reefs were selected, and each was then separated into a high- and a low-relief section. In 2015, four individual reefs were sampled in the Lynnhaven River, two of which were the same reefs sampled in 2014. Additionally, in the Lafayette only two restored reefs could be sampled due to lack of additional restoration reefs in that river; however, the Lafayette has relict natural reefs. Therefore, in addition to the two restored reefs I also sampled two relict natural reefs in the Lafayette River. There were no significant differences in terms of reef characteristics (number of oysters, oyster volume, and rugosity) or macrofaunal abundance and biomass between the relict and restored reefs, and therefore they were treated as the same for further analysis.

Field Sampling: Tray Deployment and Retrieval

On each reef, or reef section (Lynnhaven 2014 sampling), four replicate benthic sampling trays (0.122 m^2 x 15 cm deep, 1.0 mm mesh liner) were embedded into the reef matrix by divers, for a total of 16 trays per river per year. Divers excavated a hole in the reef in which to place the tray flush with the rest of the reef and, following from previous studies, care was taken to place the excavated reef material into the tray with as little disturbance as possible to maintain the orientation and vertical dimensions of the reef

matrix (Plunket and La Peyre 2005; Rodney and Paynter 2006). Trays were left for a 7-week colonization period to collect resident macrofauna. Measurements of temperature, salinity, and dissolved oxygen (DO) (using a handheld YSI model 85, Professional Plus), as well as depth (using a weighted tape measurer) were taken at the location of each tray, both during deployment and retrieval of the trays. Surface complexity (rugosity) of the material in each tray that was successfully retrieved was measured immediately after being brought onto the boat using the 'chain-link' method (Rodney and Paynter 2006). Two measurements were taken at 90 degree angles of each other, and averaged to obtain an average rugosity for each tray. A chain with 1.5cm long links was used for the rugosity measurements. All material in the tray was then transferred into Ziploc bags and placed on ice for transport to the lab where they were stored in -6 ^{o}F freezers until lab processing could take place. Tray deployment took place from May 21-23 in 2014 and May 20th, 22nd, and 27th in 2015. Retrieval of the trays occurred July 8th and 9th in 2014 and July 9th, 10th, and 16th in 2015.

Laboratory Processing

Samples were thawed and rinsed over a 1 mm sieve prior to sorting. During sorting, all organisms were removed and stored in vials with 75% ethanol until identification and biomass measurements could be carried out. Organisms were identified to the lowest taxonomic level possible (usually species). Encrusting algae and bryozoans were not quantified in this study. Species-specific biomass was obtained by first drying organisms in an oven at 65 ^{o}C for at least 24-hrs and weighing them, and then burning them in a muffle furnace at 550 ^{o}C for 6-hrs to obtain ash weight. Biomass was calculated

by subtracting ash weight from the dry weight to obtain ash-free dry weight (AFDW). In addition to removing organisms from each sample, the oyster material was also sorted into several categories: live single oysters, live clumped oysters, and dead shell hash. The volume of each category was then measured using water displacement, and each live oyster was measured (length) (see appendix I for size distribution of oysters on each reef), and burned to obtain biomass measurements. These measurements served as additional metrics of reef complexity.

Statistical Analysis

Community structure metrics such as density, diversity, evenness, richness, and biomass, were calculated for each sample and compared among rivers using nested Analysis of Variance (ANOVA), using the 'proc mixed' procedure in SAS vs 9.3 statistical software with a type 3 methods of moment's estimation, river as a fixed factor, and reef nested within river as a random factor in the model. Post-hoc pairwise comparisons were made on least-squared means with a Tukey-Kramer adjustment when significant differences among rivers were found. Prior to analysis, data were evaluated for meeting the assumptions of normality and homoscedasticity using the Shapiro-Wilk's and Levene's Test, respectively. If those tests indicated non-normality or heteroscedasticity, visual inspection of residuals and QQ-plots was carried out to further assess the need for transformation. When necessary, data were transformed to correct for heteroscedasticity and large deviations from normality using a square-root (x) transformation. Significant differences were present with an alpha < 0.05.

The PRIMER-6 statistical package (Clarke and Gorley 2001) was used to analyze the community composition data. For this analysis, the species abundance-by-sample matrix was square-root transformed (to down-weight the importance of abundant taxa), and the Bray-Curtis index was used to construct the similarity matrix which was then used to create the non-metric multidimensional scaling (nMDS) ordination plot (Clarke and Warwick 2001). Stress values are shown on the nMDS plots and are a measure of goodness of fit of the ordination. Values < 0.2 indicate a useful 2-dimentional picture, though caution should be taken for values at the upper end of this range (Clarke 1993; Clarke and Warwick 2001). Analysis of similarity (ANOSIM) was used to test for significant differences in macrofaunal assemblages among the 4 rivers. The test statistic for this analysis is the R statistic, which is calculated using the following equation,

$$R = (r_B - r_W)/(\frac{M}{2})$$

$$M = n(n-1)/2$$

where r_W is the average of all rank similarities, from the Bray-Curtis similarity matrix, among replicates within a river, and r_B is the average of all rank similarities from all pairs of replicates between different rivers. An R = 1 indicates complete separation between two groups, while R = 0 indicates no separation (or difference) between groups. Similarity Percentages (SIMPER) analysis was used to identify the species contributing the most to the average dissimilarity between rivers. Species that are good discriminators between rivers are defined as those where the average dissimilarity divided by the standard deviation is greater than 1.5 (i.e. Diss/Sd > 1.5), indicating that they consistently contribute to the dissimilarity (Clarke 1993). BioEnv analysis was used to identify the subset of environmental variables (water quality and reef structure) that best explained

the pattern in the community composition data, both in terms of abundance and biomass (Clarke and Ainsworth 1993).

Multiple linear regression analysis was carried out using the 'proc glm' procedure in SAS vs. 9.3 to determine the effect of oyster reef habitat complexity (i.e. oyster density, total volume of oyster material, rugosity) and salinity, on macrofaunal density, biomass, and diversity. Additional models were fit for the densities of the four main taxonomic groups within the reef community: mussels (*Ischadium recurvum*), mud crabs, polychaetes, and resident fish. Factors were considered to be significant predictors in the model at the alpha < 0.05 significance level. To remove potential problems arising from multicollinearity, Type II tolerances for the various predictors were determined. Tolerances of < 0.1 indicated the presence of multicollinearity, and one of the variables was then removed from the model. Partial regression plots were created for significant or marginally significant predictors in the models. These plots show the true relationship between the response variable, Y, and one of the predictors in the model by holding all other predictors constant.

RESULTS

Environmental and Structural Parameters

The average salinity, dissolved oxygen, and temperature differed among the rivers (Table 1). Mean salinity was lowest in the Great Wicomico River, and increased moving southward, being the highest in the Lynnhaven River during 2015 (Table 1; Figure 3a). Mean salinity was significantly different between all rivers except the Lynnhaven during 2014 and the Lafayette ($p = 0.25$). Mean dissolved oxygen was significantly lower in the

Lynnhaven in 2014 compared to the Great Wicomico and Piankatank Rivers ($p = 0.007$ and $p = 0.045$ respectively) (Table 1; Figure 3b). Dissolved oxygen was never recorded below hypoxic levels (< 4 mg-O_2/L) in any river during the sampling periods. Mean temperature was greater in the Lynnhaven in 2015 compared to the Piankatank ($p = 0.04$) and Great Wicomico Rivers ($p = 0.0496$); however, the greatest difference in the mean temperature was only 1.6 ^{o}C, and probably not biologically meaningful (Table 1; Figure 3c). There was no significant difference in mean depth of the reefs among the rivers ($F = 3.03$, $p = 0.052$).

Mean total oyster volume (live and dead combined), live oyster density (#oysters/m^2), and rugosity also significantly differed among the rivers (Table 1; Figure 4). Mean total oyster volume was significantly greater in the Great Wicomico and Lynnhaven in 2015 compared to the Lafayette river ($p = 0.001$ and $p = 0.012$, respectively), but did not differ among the other rivers. Mean live oyster density tended to be greater in the Great Wicomico and Piankatank rivers compared to the Lafayette and Lynnhaven; however, significant differences were found only between the Great Wicomico and the Lafayette ($p = 0.019$). Mean rugosity was significantly greater in the Lynnhaven during 2014 compared to 2015 ($p = 0.0081$), and in the Piankatank compared to the Great Wicomico and Lynnhaven during 2014 ($p = 0.039$ and $p = 0.0055$).

Description of Resident Species

In total, 41,402 organisms from 61 macrobenthic species were collected in the 55 ($n = 25$ in 2014, $n = 30$ in 2015) benthic settling trays that were successfully retrieved across all four rivers (Table 2). Of those species, 30 were found in the Great Wicomico,

31 in the Piankatank, 41 in the Lafayette, and 44 in the Lynnhaven, and 13 were commonly found in all four rivers (Table 2). Five species were unique to the Lynnhaven River (*Lepidametria commensalis, Glycera dibranchiatta*, *Guekensia demissa*, *Seila adamsi*, and *Leitoscoloplos* sp.), six species were unique to the Lafayette river (*Anachis* sp., *Astyris rosacea*, *Anomia simplex*, *Triphora nigrocincta*, *Anadara transversa,* and *Synidotea laevidorsalis*), and one species was unique to the Great Wicomico (*Phyllodocea* sp.). Six species were found predominantly in the Lynnhaven and Lafayette rivers (*Marphysa sanguinea, Alpheus heterochaelis, Corophium* sp*., Dulchiella appendiculata, Microdeutopsus* sp*.,* and *Astyris lunata*), and three species were found only in the Great Wicomico and Piankatank Rivers (*Mulinia lateralis, Cymadusa compta,* and *Palaemonetes pugio*).

Abundance and biomass data were converted to percent composition to determine which species dominated both in terms of abundance and biomass within each river. Dominant species were defined as species which accounted for, on average, > 1% of total abundance or biomass in at least one river. In terms of abundance, 23 species met this criteria, accounting for > 95% of the total abundance in each river. These species included three mud crabs (*Eurypanopeus depressus*, *Panopeus herbstii, and Dyspanopeus sayi*), two shrimp (*Palaemonetes vulgaris,* and *Alpheus heterochaelis*), one fish (*Gobiosoma bosc*), four molluscs (*Crepidula convexa, C. plana, Astyris lunata,* and *Ischadium recurvum*), five polychaetes (*Alitta succinea, Hydroides dianthus, Marphysa sanguinea, Terebellid* sp., and *Phyllodocea* sp.), six amphipods (*Cymadusa compta, Corophium* sp*., Dulichiela appendiculata, Caprellid* sp*., Microdeutopsus gryllotalpa,* and *Melita nitida*), one tunicate species (*Molgula manhattensis*), and barnacles (*Balanus*

spp.*)*. Differences in the relative proportions of these species among the four rivers were evident (Figure 5). In the Great Wicomico and Piankatank rivers, abundance was largely dominated by the polychaete *A. succinea* which accounted for 63% and 54% of total abundance respectively (Figure 5). In the Lynnhaven and Lafayette rivers approximately the same proportion of total abundance was comprised of three species: *Mogula manhattensis, A. succinea,* and *Melita nitida*, in the Lynnhaven, and *Mogula manhattensis, A. succinea,* and *Marphysa sanguinea* in the Lafayette.

Dominant species, as determined by biomass, showed different patterns than those observed for abundance (Figure 6). Seventeen species accounted for > 1% of total biomass in at least one river, and together these species accounted for > 95% of the total biomass in each river. These species included five crabs (*Callinectes sapidus, Panopeus herbstii, E. depressus, D. sayi,* and *Pinnotheres ostreum*), two shrimp (*Palaemonetes vulgaris* and *Alpheus heterochaelis*), three fish (*Gobiosoma. bosc, Chasmodes bosquianus,* and *Opsanus tau*), three mulluscs (*Guekensia demissa, I. recurvum,* and *Mercenaria mercenaria*), two polychaete (*Alitta succinea* and *Marphysa sanguinea*), one tunicate species (*Molgula manhattensis*), and barnacles (*Balanus* spp.). Unlike with the abundance data, which was largely dominated by polychaetes and tunicates, biomass was largely dominated by crustaceans. For instance, the mud crab, *Panopeus herbstii,* accounted for between 20-40% of the total biomass in the four rivers (Figure 5). Additionally, relative contribution of the various organisms to total biomass appeared more similar across the rivers than it was for the percent composition in terms of abundance.

Community Composition: Multivariate Analysis

Species composition in terms of numerical abundance varied among the four rivers and between the Lynnhaven in 2014 and 2015, as evident in the clustering pattern in the nMDS ordination plot (Figure 7). Analysis of Similarity (ANOSIM) test confirmed that there were significant differences in the macrofaunal communities among the rivers sampled, and pairwise comparisons revealed significant separation between all pairs of rivers (Table 3). There was strong separation between the Great Wicomico River and the Lafayette ($R = 0.929$, $p = 0.001$) and the Great Wicomico and both years in the Lynnhaven River ($R = 0.989$, $p = 0.001$ and $R = 0.884$, $p = 0.001$ for 2014 and 2015 respectively). The Piankatank River also showed strong separation from the Lafayette ($R = 0.862$, $p = 0.001$) and from both years in the Lynnhaven River ($R = 0.995$, $p = 0.001$ and $R = 0.834$, $p = 0.001$ for 2014 and 2015, respectively). The Lafayette and Lynnhaven (2014 and 2015) rivers were the least different from each other ($R = 0.383$, $p = 0.001$ and $R = 0.357$, $p = 0.001$, respectively), and there was moderate separation between the Great Wicomico and Piankatank Rivers ($R = 0.579$, $p < 0.001$).

The tunicate *Molgula manhattensis* contributed the most (10.18 %) to the dissimilarity between the Lynnhaven and Lafayette rivers; however, it was not a good discriminator between the rivers (Table 4). The polychaete, *A. succinea,* contributed the most (between 16-19 %) to the dissimilarity between the two higher salinity rivers (Lynnhaven and Lafayette), and the two lower salinity rivers (Great Wicomico and Piankatank rivers) (Table 4), as it was more abundant in the latter two rivers. The amphipod *Cymadusa compta* had the greatest contribution to the dissimilarity between the Great Wicomico and Piankatank (12.62 %) and was a good discriminator between the

two rivers (Table 4). BioEnv analysis indicated that salinity was the parameter that best explained the observed pattern in the biological data (r = 0.664).

Ordination of the biomass data showed a similar grouping pattern as with the abundance data (Figure 8); however, the strength of the separation was notably less than that observed with the abundance data. ANOSIM revealed that there were significant differences in the macrofaunal communities in terms of biomass among the four rivers sampled (ANOSIM, Global R = 0.463, $p < 0.0001$). The greatest differences in community structure in terms of biomass were between the 2014 Lynnhaven communities and the Great Wicomico and Piankatank rivers (Table 5). The Lynnhaven communities were not significantly different in terms of biomass between the 2014 and 2015 sampling, and there was only weak separation, as indicated by the low R values (Table 5), between the Lafayette and Lynnhaven (both years).

In contrast to differences in communities in terms of abundance, crustaceans and mulluscs contributed the most to differences in communities in terms of biomass. *Panopeus herbstii* contributed the most to the dissimilarity between the Great Wicomico, and the Lafayette and Lynnhaven Rivers; however it was not a good discriminator in either case (Table 6). *E. depressus* contributed the most to the dissimilarity between the Piankatank and Lynnhaven rivers, while *I. recurvum* contributed the most to the dissimilarity between the Piankatank and Lafayette Rivers (Table 6). Similar to the community composition in terms of abundance, BioEnv analysis revealed that the salinity was the environmental parameter that best explained the variation in macrofaunal biomass among rivers (r = 0.341).

Macrofaunal Abundance, Biomass, and Diversity

The restored oyster reefs sampled in this study supported on average 6,169 organisms per m^2, and there were differences in the mean density among the rivers (Table 7). The mean organism density was 2-3x greater on restored reefs in the Piankatank and Great Wicomico Rivers compared to the Lafayette and Lynnhaven rivers (Table 7; Figure 9a). Mean organism density (square-root transformed) was greater in the Piankatank compared to the Lafayette ($p = 0.0017$) and Lynnhaven samples in 2014 and 2015 ($p = 0.0128$ and $p=0.0006$ respectively), and greater in the Great Wicomico compared to the Lynnhaven in 2015 ($p = 0.0187$). The average total macrofaunal biomass supported by these restored reefs was 67.88 g-AFDW/m^2, and although biomass tended to be greater in the Great Wicomico and Piankatank rivers compared to the other rivers, this difference was not significant ($F=3.16$, $p=0.0507$) (Table 7).

There was also an effect of river on Shannon-Wiener ($H^{'}$) Diversity and Pielou's Evenness. Diversity and evenness were significantly greater in the Lafayette and Lynnhaven (both years) Rivers compared to the Great Wicomico (Table 7; Figure 10a, b). The Lafayette and Lynnhaven (2015 sampling) Rivers also had greater diversity and evenness compared to the Piankatank River (Table 7; Figure 10a, b). Species richness was significantly greater in the Lafayette River compared to the Piankatank ($p = 0.0453$) and Great Wicomico ($p = 0.0015$) Rivers, but no other significant differences were present.

Multiple Linear Regression: Habitat Complexity and Salinity

Three oyster reef complexity parameters (total oyster volume (L/m^2), oyster density (ind/m^2), and rugosity) and one environmental parameter (salinity) were included as predictors in the models of macrofaunal density, biomass, and diversity. I chose to include these factors in the models because they have been previously proposed to impact macrofaunal abundance and diversity and are easy to measure in the field with minimal amount of destruction of the reef habitat. Additionally, there were no issues with multicollinearity for these variables. Organism density ($individuals/m^2$) and biomass ($g\text{-}AFDW/m^2$) were both square-root transformed to meet the assumptions of normality and homogeneity of variance.

The model results for organism density indicated that all three reef complexity measures (total oyster volume, rugosity, and oyster density ($\#oys/m^2$) positively influenced macrofaunal density; however, none were significant in the model. Oyster density and rugosity, however, were marginally significant predictors in the model ($p = 0.08$ and $p = 0.067$ respectively; Figure 11a, b). In the taxonomic-level models oyster density was a significant and positive predictor of mud crab, polychaete, and *I. recurvum* density (Figure 14b, c, f), and rugosity was a significant and positive predictor of mud crab and *I. recurvum* density (Figure 14 d, e). Total oyster volume was a significant and positive factor in the model of fish density (Figure 14a). Salinity significantly and negatively influenced mussel, fish, polychaete, and total macrofaunal densities (Figure 11c), and (Table 8).

Rugosity, total oyster volume, and oyster density also positively affected macrofaunal biomass; however, only rugosity and oyster density were significant factors in the model (Table 8, Figure 12a, b). Salinity also negatively influenced macrofaunal

biomass, and was significant in the model (Table 8; Figure 11c). Salinity and rugosity were both positive and significant factors affecting diversity (Table 8, Figure 13a, b).

DISCUSSION

The primary goal of this study was to characterize the macrofaunal communities of restored oyster reefs in the lower Chesapeake Bay, and determine what factors influence their value as habitat. Restored reefs provided habitat that supported an abundance and diversity of benthic macrofaunal organisms. The macrofaunal communities that developed on the restored reefs sampled differed among the rivers, with differences being largely associated with differences in salinity across the rivers. Reef structural complexity was an important driver of macrofaunal density, biomass, and diversity, with increases in habitat complexity increasing all three responses.

Resident Fauna

Several studies have described the habitat value of oyster reefs and the enhancement of macrofaunal density and diversity in these habitats compared to soft sediment unstructured habitats (Plunket and La Peyre 2005, Rodney and Paynter 2006, Grabowski et al. 2005). However, my study is one of the few studies that describes the entire macrofaunal community associated with restored oyster reefs, as well as quantify the biomass of this community. Additionally, to my knowledge, this study is one of the most extensive studies of restored oyster reefs in regards to both the size of the reefs sampled and the geographic range over which reefs were sampled (four different rivers).

In this study, restored oyster reefs supported diverse, abundant, and productive macrofaunal communities. Sixty-one macrofaunal species were found in total on the restored oyster reefs sampled. This total, and the numbers within each river (Table 1), are consistent with other studies and fall within the range of species (33-63) that was compiled by Rodney and Paynter (2006) from a literature review of several previous studies conducted along the Gulf and Atlantic coasts of the United States. The average density, 6,169 orgs/m^2, reported in my study, is also consistent with the range of 300-6,000 orgs/m^2 reported by Rodney and Paynter (2006). Therefore, this study provides further evidence that there is some consistency in the community structure and common organisms found on oyster reefs across various regions. There are a limited number of studies that have quantified the biomass of the entire macrofaunal assemblage on oyster reefs making direct comparisons difficult. One study I was able to find that reported entire community biomass was conducted in Louisiana, and oyster reefs in that system supported on average 50g-AFDW/m^2 of resident fish and invertebrates (Humphries et al. 2015). The value is consistent with the range of biomass found across the four rivers sampled in the current study. Comparisons between the range of biomass reported in my study (43.61 – 90.62 g-AFDW) to that of other habitats present in the Bay such as seagrass (11.7 – 47.2 g-AFDW/m^2) (Edgar 1990), and unstructured soft sediments (7-25 g-AFDW/m^2) (Lovall et al., in review, Lawless and Seitz 2014) suggests that macrofaunal biomass on restored oyster reefs may be greater than either of those habitats in Chesapeake Bay. However, future studies should be conducted that directly compare the biomass and abundance of the entire macrofaunal community among oyster reef, seagrass, and soft-sediment benthic habitats.

The macrofaunal assemblages described in this study were similar to those described in previous studies both in Chesapeake Bay and elsewhere along the US Atlantic and Gulf Coasts. Polychaetes were the most abundant taxa in this study, accounting for 49.48% of the total number of organisms identified, with *Alitta succinea*, making up 90% of the polychaetes collected. Amphipods were the second most abundant taxa (15.57%), followed by decapod crustaceans (shrimp and crabs) (12.71%). These results are similar to those reported in Rodney and Paynter (2006), which found Amphipods to be the most abundant group (41%), followed by Polychaetes (33%), and Xanthid crabs (11%). Consistent with my study, *A. succinea* was also found in every sample at every site by Rodney and Paynter (2006), and made up 91% of total polychaete abundance.

Almost all of the species that were numerical and/or biomass dominants in this study were also reported in previous studies of oyster reef habitats at high abundances (Breitburg 1999, Coen et al. 1999, Meyer and Townsend 2000, Tolley et al. 2005, Rodney and Paynter 2006). For instance, the mud crab, *E. depressus*, was a dominant crustacean found on North Carolina (Meyer 1994), Maryland (Rodney and Paynter 2006), and Florida (Glancy et al. 2003, Tolley et al. 2005) oyster reefs. In the current study *E. depressus* was the second most dominant crustacean, and most abundant mud crab species. Many of the organisms found in high abundance and biomass in this, and previous studies, are prey organisms readily found in the diets of transient fish such as striped bass, weakfish, and white perch which are recreationally and commercially important (Harding and Mann 2001). This study therefore provides further evidence for

the potential role restored oyster reefs can play in enhancing fisheries yields in the Chesapeake Bay by supporting an abundance of benthic prey organisms.

Habitat Complexity

Habitat complexity (as measured by number of oysters and rugosity) was positively associated with total macrofaunal biomass, densities of major taxonomic groups, and diversity. The positive relationships are consistent with several previous studies (Luckenbach et al. 2005, Tolley et al. 2005, Berquist et al. 2006, Colden 2015, Margiotta et al. 2016). Mud crabs, such as *P. herbstii* and *E. depressus*, prefer habitats of increased structural complexity (Day and Lawton 1988), and increase in density with increasing rugosity and live oyster density on intertidal oyster reefs (Margiotta et al. 2016). The positive association between complexity and mud crab density observed in the current and previous studies could be attributed to increased surface complexity and provision of refuges provided by live oysters resulting in decreased predation risk (Crowder and Cooper 1982, Warfe and Barmuta 2004, Humphries et al. 2011a) and increased habitat availability. The positive affect of oysters on mussel (*I. recurvum*) density has also been documented previously (Hadley et al. 2010, Colden 2015). This is likely a result of reduced flow over oyster reefs with increased live oyster abundance, which is conducive to settlement (Soniat et al. 2004), combined with increased refuge from predation for newly settled mussels. Fish density in the current study was positively affected by total oyster volume, but not live oyster density or rugosity. This could be a reflection of the way in which resident fish utilize oyster reefs. Resident fish, such as gobies and blennies, utilize empty, still-articulated oyster shells (i.e. oyster boxes) in

which to lay their eggs and as refuge from predation (Crabtree and Middaugh 1982). Therefore, total oyster volume may better capture the amount of this structural element within an oyster reef compared with live oyster density or rugosity.

However, there are also several studies that found contrasting results and did not find positive relationships between overall macrofaunal abundance and oyster metrics (Hadley et al. 2010, Humphries et al. 2011b). For instance, Humphries et al. (2011b) saw an increased abundance and biomass of nekton on experimental oyster reefs compared to mud bottoms, but failed to see a further increase in abundance or biomass with greater structural complexity within the oyster reef habitats. This could largely be because these were small experimental reefs that did not have live oysters on them, and therefore may have lacked the complexity of the living oyster reefs sampled in the current study. Additionally, live oyster density and rugosity, but not oyster shell volume, were significant or marginally significant predictors in the models of macrofaunal biomass and abundance, suggesting that in order to see an increase in biomass and abundance there needs to be more live oysters, not simply oyster shell material. This further supports the observation that live oysters, and their vertically growing orientation, are important to increasing the habitat complexity within an oyster reef.

The increase in diversity with increasing rugosity observed is also consistent with previous studies (Gratwicke and Speight 2005, Rodney and Paynter 2006), providing further evidence to support the 'habitat heterogeneity hypothesis' (Tews et al. 2004). One explanation for this positive relationship is that increasing habitat complexity increases niche diversification and amount of habitable area, which allows resource partitioning

and coexistence of different species, leading to increased diversity in more complex habitats (Heck and Welston 1977; Tews et al. 2004).

Previous measures of restoration success included the abundance of market-sized oysters (> 75 mm SH) and oyster biomass. In this study, abundance of live oysters, regardless of their size, was a significant predictor of macrofaunal biomass. This suggests that restored oyster reefs can provide valuable habitat and support productive macrofaunal communities even in the earlier stages of reef development before an abundant market sized oyster population has been established. Luckenbach et al. (2005) and Hadley et al. (2010) also found no indication that an abundance of market-sized oysters was necessary for supporting an abundant and diverse macrofaunal community. Additionally, measuring oyster size and biomass is a destructive and time-consuming process that often requires the permanent removal of oysters from a reef. The results of the current study indicate that those methods may not be necessary and that the number of live oysters and/or rugosity are good indicators of habitat value. Counting oysters or measuring rugosity can be done in the field and the oysters could then be returned to the reef making it a less time-consuming and less-destructive process.

Location (Salinity) Effects

Although several species were found in all four rivers (Table 1), many species were found only in certain of the rivers sampled, resulting in significant differences in the species assemblages and diversity on restored oyster reefs among the four rivers. The differences in oyster reef community structure, both in terms of abundance and biomass, were highly correlated to salinity (BioEnv; Figure 8 and 9), and salinity was a significant

and positive predictor of diversity in the multiple linear regression model. This is consistent with several other studies conducted in different geographical areas, such as China, North Carolina, and Florida, which also showed changes in overall community structure and diversity along a salinity gradient (Wells 1961, Tolley et al. 2005, Berquist et al. 2006, Shervette and Gelwick 2008, Quan et al. 2012). This current study is one of the first to sample restored oyster reefs across a broad salinity gradient within Chesapeake Bay, and provides further evidence of the importance of salinity in structuring marine communities.

Wells (1961) concluded that "salinity seems to be the single most important factor limiting the upstream progression of some oyster reef associates". My results are consistent with this, as there were 16 species (Table 2) that were observed only in the higher salinity Lafayette or Lynnhaven Rivers. Those rivers had significantly greater diversity and evenness compared to the lower salinity Great Wicomico and Piankatank Rivers. It is presumed that species found only in the higher salinity rivers are those that are more marine oriented, have evolved narrower salinity tolerances, and are not able to survive as well in the brackish waters of the middle and upper estuary (Vernberg and Vernberg 1972). In addition to having greater salinity, these two rivers are also closer to the mouth of the estuary and therefore may have greater access to the larval supply of those species, which could be a contributing factor to the increased diversity observed in those rivers.

Total macrofaunal density, conversely, was significantly greater in the Great Wicomico and Piankatank compared to the Lynnhaven and Lafayette rivers, and salinity was a significant negative predictor of macrofaunal density in the models. This trend is

consistent with several studies that reported an inverse relationship between salinity and macrofaunal abundances (Wells 1961, Berquist et al. 2006). This also follows what might be expected based on the model proposed by Menge and Sutherland (1987). They proposed that the importance of predation and competition increases with decreasing environmental stress. In the estuarine environment, environmental stress decreases closer towards the mouth, where the salinity does not fluctuate as much compared to the more brackish waters of the middle and upper estuary. This allows for increased diversity of organisms, thus more competition between those organisms, and increased importance of predation. This increased role of predation and competition works to keep the abundance of dominant organisms low. In my study, *A. succinea* was a dominant oyster reef organism, but was significantly more abundant in the two lower-salinity rivers compared to the higher salinity waters. Additionally, as shown in the SIMPER analysis, *A. succinea* contributed the most to the percent dissimilarity between the lower-salinity Piankatank and Great Wicomico Rivers, and the higher-salinity Lafayette and Lynnhaven Rivers. *A. succinea* is a cosmopolitan species, with a wide salinity tolerance, but in the high salinity waters, *A. succinea* may be prevented from booming in abundance due to increased competition with other polychaetes species, particularly *Marphysa sanguinea,* which are not present at the lower salinities.

In those studies and the current study, oyster density was also greater in the lower-salinity waters (Tolley et al. 2005, Berquist et al. 2006). This pattern could be attributed to increased susceptibility and exposure of oysters to diseases (MSX and DERMO) and predation in higher salinity waters (Haven et al. 1978, Tolley et al. 2005, Berquist et al. 2006). For instance, stenohaline oyster predators, such as the oyster drill

(*Urosalpinx cinerea*), tend to be restricted to higher salinity environments (> 15 psu) (Manzi 1970). Oyster drills were not particularly common in this study, but when they were encountered they were in the Lafayette River where salinity averaged 21.44 psu.

Aside from salinity, differences in overall water quality among the rivers could also play a role in explaining the differences in community structure between the rivers. In this study, only DO, salinity, temperature, and depth were measured, but it is possible that other environmental variables not measured such as total suspended sediments (TSS), chl-*a*, and/or turbidity, and temporal fluctuations in salinity and/or DO not captured in the sampling, could also be important. Two filter feeders were significantly more abundant in the Great Wicomico and Piankatank Rivers compared to the Lafayette and Lynnhaven Rivers: *I. recurvum,* and barnacles (*Balanus* spp.). The Piankatank and Great Wicomico rivers had much clearer water (personal observations) throughout the sampling periods compared to the Lafayette and Lynnhaven rivers. This may be because the Lynnhaven and Lafayette Rivers are surrounded by more urban development compared to the other two rivers. Barnacles and mussels may experience increased clogging of their gills in the more turbid waters of the Lynnhaven and Lafayette, which may not pose a problem in the other two rivers allowing for larger populations sizes. Conversely, the tunicate, *Molgula manhattensis* was found in greater abundance in the Lafayette and Lynnhaven rivers compared to the Great Wicomico and Piankatank Rivers. Tunicates are fouling organisms that can often tolerate poorer water quality (Lippson and Lippson 2006), and therefore may be able to survive and compete better in the Lafayette and Lynnhaven Rivers.

CONCLUSIONS

An important ecological service of oyster reefs is the provision of habitat for a diversity of macrobenthic organisms that utilize the crevices within the shell matrix for habitat, refuge, and foraging grounds. The three-dimensional structure of oyster reefs that provide this habitat is largely created by the vertical orientation and clumping together of live oysters. Unfortunately, overharvesting, disease, and poor water quality have all contributed to significant declines in oyster populations and subsequent loss of this valuable habitat. Increasing efforts have been carried out over the last decade to restore oysters and the various services they provide. Restored oyster reefs in the lower Chesapeake Bay sampled in this study clearly provided habitat that supported diverse and abundant benthic prey communities; however, these restored reefs developed distinct communities in the four rives sampled. The results from this study provide evidence that the macrofaunal communities on restored oyster reefs vary with the salinity gradient. Although community composition and diversity were related to differences in salinity, my results suggest that the density and biomass of reef organisms were positively affected by increased habitat complexity, particularly density of live oysters and reef rugosity. Species diversity was also positively influenced by habitat complexity as measured by rugosity. The results from this study emphasize that the location and design of restoration efforts can have a significant impact on oyster reef community development. In terms of macrofaunal density, biomass, and diversity, my results suggest that increasing oyster reef complexity by increasing live oyster density, total oyster volume, and/or surface rugosity, would potentially increase macrofaunal density, biomass, and diversity within a given system. Therefore, future restoration efforts aimed

at restoring habitat and refuge value of oyster reefs, should take a more local, tributary approach, and be designed in a way which will increase oyster recruitment and survival, and therefore the habitat complexity of the reef. Potential methods to accomplish this would be to seed reefs with spat-on-shell and hard substrates, such as concrete or rock rubble and shells, which would initiate growth of live oysters and provide settlement substrate. This approach may be more costly than the common, simpler approach of dumping shells onto reefs, but may increase the likelihood of success.

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Table 1: **Summary of mean environmental and structural variables,** reported as mean (SE), of the reefs sampled in each of the four rivers. Environmental parameters are calculated as the average of measurements taken during deployment and retrieval of sampling trays using a YSI, for only those sites where trays were successfully retrieved. Samples sizes were n=15 in the Great Wicomico, n= 11 in the Piankatank and Lafayette, n=10 in the Lynnhaven during 2014, and n=8 during 2015. Test statistics and p-values are from nested ANOVA analysis, unless otherwise indicated

Variables	Rivers					F statistic	p-value
	Great Wicomico	Piankatank	Lafayette	Lynnhaven 2014	Lynnhaven 2015		
Dissolved Oxygen (mg O2/L)	7.13 (0.11)	6.63 (0.20)	6.26 (0.23)	5.16 (0.17)	6.26 (0.25)	4.77	0.0137
Salinity (psu)	13.76 (0.09)	17.75 (0.13)	21.44 (0.12)	22.40 (0.12)	24.69 (0.12)	258.88	< 0.0001
Temperature (C)	24.75 (0.22)	24.61 (0.05)	25.68 (0.11)	25.69 (0.12)	26.28 (0.45)	4.1	0.023
Depth (ft)	10.31 (0.57)	7.20 (0.53)	7.61 (0.24)	8.21 (0.53)	7.81 (0.62)	3.03	0.052
Number of Oysters (ind/m2) *	422.95 (54.73)	377.79 (85.97)	153.50 (38.92)	225.41 (26.36)	225.41 (52.46)	4.6	0.0156
Total Oyster Volume	4.92 (0.36)	3.81 (0.33)	2.87 (0.22)	4.49 (0.21)	3.67 (0.34)	8.13	0.0016
Rugosity	1.34 (0.046)	1.60 (0.060)	1.39 (0.071)	1.22 (0.045)	1.63 (0.122)	7.34	0.0026

* F-statistic and p-value comes from nested ANOVA on square-root transformed data, while untransformed raw means are reported.

Table 2: Complete species Lists, *with the total number collected and mean density as number per m2 of all organisms collected in each of the four rivers. The total number of each species collected overall and relative abundance (Percent %) of each species is also provided.*

			Great Wicomico		Piankatank		Lafayette		Lynnhaven	
Common name (scientific name)	**Total Number**	**Percent (%)**	Total #	density (ind/m2)	Total #	density (ind/m2)	Total #	density (ind/m2)	Total #	density (ind/m2)
Sea grape (*Molgula manhattensis)*	3811	9.21	93	50.82	618	460.51	1087	809.99	2013	916.67
POLYCHEATES										
Common clam worm (*Alitta succinea*)	18439	44.54	8389	4584.15	8057	6003.73	804	599.11	1189	541.44
Red-gilled marphysa or Rock Worm (*Marphysa sanguinea*)	1009	2.44	0	0	0	0	545	406.11	464	211.29
Limy tubeworm (*Hydroides dianthus*)	732	1.77	6	3.28	257	191.51	224	166.92	245	111.57
Phyllocidea worm	152	0.37	152	83.06	0	0	0	0	0	0
Terebellid spp.	113	0.27	0	0	0	0	0	0	113	51.46
Feather duster worm (*Demonax mirocpthalmus*)	27	0.07	0	0	0	0	0	0	27	12.30
Opal worm (*Arabella iricolor)*	8	0.02	0	0	0	0	3	2.24	5	2.28
Commensal scaleworm (*Lepidametria commensalis*)	3	0.01	0	0	0	0	2	1.49	1	0.46
Common blood worm (*Glycera dibranchiatta*)	2	0.00	0	0	0	0	0	0	2	0.91
Leitoscopolos spp.	1	0.00	0	0	0	0	0	0	1	0.46
FISH										
Naked Goby (*Gobiosoma bosci*)	1698	4.10	732	400	246	183.31	226	168.41	493	224.50
Oyster Toad Fish (*Opsanus tau*)	67	0.16	9	4.37	22	16.39	11	8.20	25	11.38
Skilletfish (*Gobiosox strumosa*)	56	0.14	22	12.02	30	22.35	0	0	4	1.82
Striped blenny (*Chasmodus bosquianus*)	16	0.04	3	1.64	11	8.20	0	0	2	0.91
Feather blenny (*Hypsoblennius hentz)*	2	0.00	1	0.55	0	0	1	0.75	0	0
Dusky pipefish (*Syngnathus floridae*)	1	0.00	0	0	0	0	0	0	1	0.46
AMPHIPODS and ISOPODS										
Melita nitida	3671	8.87	300	163.93	2414	1798.81	117	87.18	840	382.51
Cymadusa compta	2114	5.11	264	144.26	1841	1371.83	0	0	9	4.10
Corophium sp.	200	0.48	0	0	0	0	108	80.48	92	41.89
Caprellid sp.	151	0.36	0	0	93	69.30	14	10.43	44	20.04
Microdeutopsus sp	121	0.29	0	0	0	0	37	27.57	84	38.25
Dulichiela appendiculata	120	0.29	0	0	0	0	8	5.96	112	51.00
Erichsonella attenuata	44	0.11	0	0	41	30.55	3	2.24	0	0
Gammaraus mucronatus	16	0.04	5	2.73	10	7.45	1	0.75	0	0
Synidotea laevidorsalis	9	0.02	0	0	0	0	9	6.71	0	0
Idotea baltica	1	0.00	0	0	0	0	0	0	1	0.46

Table 2 continued...

Common name (scientific name)	Total Number	Percent (%)	Great Wicomico Total #	Great Wicomico density (ind/m2)	Piankatank Total #	Piankatank density (ind/m2)	Lafayette Total #	Lafayette density (ind/m2)	Lynnhaven Total #	Lynnhaven density (ind/m2)
DECAPOD CRUSTACEANS										
Barnacle (Balanus sp.)	3355	8.10	2944	1608.74	275	204.92	40	29.81	96	43.72
Flatbacked mudcrab (*Eurypanopeus depressus*)	865	2.09	226	123.50	518	385.99	53	39.49	68	30.97
Common grass shrimp (*Palaemonetes vulgaris*)	463	1.12	58	31.69	88	65.57	94	70.04	223	101.55
Atlantic mud crab (*Panopeus herbstii*)	200	0.48	50	27.32	15	11.18	31	23.10	104	47.36
Big-clawed snapping shrimp (*Alpheus heterochaelis*)	140	0.34	8	4.37	0	0	27	20.12	105	47.81
Palaemonetes spp.	108	0.26	22	12.02	10	7.45	29	21.61	47	21.40
Equal-clawed mud crab (*Dyspanopeus sayi*)	79	0.19	1	0.55	0	0	14	10.43	64	29.14
Oyster peacrab (*Pinnotheres ostreum*)	35	0.08	2	1.09	5	3.73	25	18.63	3	0.91
Daggerblade grass shrimp (*Palaemonetes pugio*)	7	0.02	2	1.09	5	3.73	0	0	0	0
Palaemonetes intermedius	6	0.01	3	1.64	2	1.49	0	0	1	0.46
Blue crab (*Calinectes sapidus*)	2	0.00	1	0.55	0	0	0	0	1	0.46
BIVALVES										
Hooked mussel (*Ischadium recurvum*)	1425	3.44	565	308.74	723	538.75	112	83.46	25	11.38
Baltic clam (*Macoma balthica*)	34	0.08	18	8.74	3	2.24	8	5.96	5	2.28
Dwarf surf clam (*Mulinia lateralis*)	28	0.07	27	14.75	1	0.75	0	0	0	0
Common jingle shell (*Anomia simplex*)	9	0.02	0	0	0	0	8	5.96	1	0.46
Hard Clam (*Mercenaria mercenaria*)	9	0.02	0	0	1	0.75	3	2.24	5	2.28
Mitchell macoma (*Macoma mitchelli*)	6	0.01	0	0	0	0	4	2.98	2	0.91
Soft-shelled clam (*Mya arenaria*)	6	0.01	5	2.73	1	0.75	0	0	0	0
Glassy lyonsia (*Lyonsia hyalina*)	6	0.01	0	0	1	0.75	1	0.75	4	1.37
Transverse ark (*Anadara transversa*)	3	0.01	0	0	0	0	3	2.24	0	0
Atlantic paper mussel (*Amygdalum papyrium*)	2	0.00	1	0.55	1	0.75	0	0	0	0
Stout razor clam (*Tagelus plebius*)	1	0.00	1	0.55	0	0	0	0	0	0
Ribbed mussel (*Guekensia demissa*)	1	0.00	0	0	0	0	0	0	1	0.46

Table 2 continued...

Common name (scientific name)	Total Number	Percent (%)	Great Wicomico Total #	Great Wicomico density (ind/m2)	Piankatank Total #	Piankatank density (ind/m2)	Lafayette Total #	Lafayette density (ind/m2)	Lynnhaven Total #	Lynnhaven density (ind/m2)
GASTROPODS										
Convex slippershell (*Crepidula convexa*)	1047	2.53	0	0	215	160.21	127	94.63	705	321.04
Lunar dovesnail (*Astyris lunata*)	570	1.38	0	0	0	0.00	560	417.29	10	4.55
Eastern white slippershell (*Crepidula plana*)	312	0.75	0	0	162	120.72	23	17.14	127	57.83
Anachis snail spp.	23	0.06	0	0	0	0	23	17.14	0	0
Unidentified snail sp.	22	0.05	0	0	11	8.20	11	8.20	0	0
Rosy northern dovesnail (*Astyris rosacea*)	21	0.05	0	0	0	0	21	15.65	0	0
Nassarius vibex	22	0.05	5	2.73	11	8.20	3	2.24	3	1.37
Eastern or Atlanic Oyster drill (*Urosalpinx cinerea*)	6	0.01	0	0	0	0	6	4.47	0	0
Black-lined triphora (*Triphora nigrocincta*)	3	0.01	0	0	0	0	3	2.24	0	0
Adam's miniature cerith (*Seila adamsi*)	1	0.00	0	0	0	0	0	0	1	0.46
Mudsnail (*Ilynassa obsoleta*)	1	0.00	0	0	0	0	0	0	1	0.46
TOTAL ORGANSIMS	41402									
NUMBER OF SPECIES	61		30		31		41		44	

Table 3: Results of ANOSIM analysis for differences in community composition in terms of abundance.

Global Test	**R statistic**	**Sig level**
Global R	0.75	0.001
Groups: Pairwise Tests		
Great Wicomico, Lafayette	0.929	0.001
Great Wicomico, Lynnhaven15	0.884	0.001
Great Wicomico, Lynnhaven14	0.989	0.001
Great Wicomico, Piankatank	0.579	0.001
Lafayette, Lynnhaven15	0.357	0.001
Lafayette, Lynnhaven14	0.383	0.001
Lafayette, Piankatank	0.862	0.001
Lynnhaven15, Lynnhaven14	0.391	0.001
Lynnhaven15, Piankatank	0.834	0.001
Lynnhaven14, Piankatank	0.995	0.001

Table 4: Results of SIMPER analysis for differences in species composition in terms of abundance.

Groups Great Wicomico & Lafayette Average dissimilarity = 63.42						
	Group Great Wicomico	Group Lafayette				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	22.85	8.11	10.76	2.05	16.96	16.96
Barnacles	11.04	1.47	6.68	1.32	10.53	27.49
M_manhattensis	2.09	9.28	5.28	1.95	8.33	35.82
M_sanguinea	0	6.48	4.85	2.11	7.65	43.47
A_lunata	0	4.76	3.18	1.01	5.01	48.48
I_recurvum	5.5	2.33	2.7	1.42	4.26	52.74

Groups Great Wicomico & Lynnhaven15 Average dissimilarity = 64.75						
	Group Great Wicomico	Group Lynnhaven15				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	22.85	8.17	12.07	1.85	18.64	18.64
Barnacles	11.04	1.16	7.59	1.31	11.72	30.36
M_sanguinea	0	5.25	3.91	2.09	6.04	36.4
I_recurvum	5.5	0.65	3.84	1.79	5.94	42.34
P_vulgaris	1.33	4.57	2.81	1.65	4.34	46.68
G_bosci	6.87	4.15	2.7	0.95	4.16	50.84

Groups Lafayette & Lynnhaven15 Average dissimilarity = 49.29						
	Group Lafayette	Group Lynnhaven15				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
M_manhattensis	9.28	3.15	5.68	1.41	11.53	11.53
A_lunata	4.76	0.6	3.31	0.93	6.72	18.25
M_sanguinea	6.48	5.25	2.95	0.89	5.99	24.24
A_succinea	8.11	8.17	2.76	1.27	5.6	29.83
Melita nitida	2.9	4.27	2.59	1.55	5.26	35.09
P_vulgaris	2.34	4.57	2.51	1.53	5.09	40.18

Table 4 continued….

Groups Great Wicomico & Lynnhaven14 Average dissimilarity = 62.38						
	Group Great Wicomico	Group Lynnhaven14				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	22.85	7.52	10.68	2.72	17.13	17.13
M_manhattensis	2.09	12.73	7.73	2.53	12.4	29.52
Barnacles	11.04	2.11	6.24	1.31	10	39.53
C_convexa	0	5.61	3.86	1.12	6.19	45.72
I_recurvum	5.5	0.64	3.38	1.98	5.42	51.14
Melita nitida	4.26	6.9	3.2	1.39	5.13	56.27

Groups Lafayette & Lynnhaven14 Average dissimilarity = 43.63						
	Group Lafayette	Group Lynnhaven14				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
M_manhattensis	9.28	12.73	3.74	1.08	8.57	8.57
Melita nitida	2.9	6.9	3.71	1.21	8.51	17.07
C_convexa	3.05	5.61	3.26	1.19	7.48	24.55
A_lunata	4.76	0	3.17	1.02	7.26	31.81
M_sanguinea	6.48	3.79	2.6	1.32	5.96	37.77
A_succinea	8.11	7.52	2.03	1.5	4.66	42.42

Groups Lynnhaven15 & Lynnhaven14 Average dissimilarity = 49.71						
	Group Lynnhaven15	Group Lynnhaven14				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
M_manhattensis	3.15	12.73	8.24	1.65	16.57	16.57
Melita nitida	4.27	6.9	4.35	1.11	8.75	25.32
C_convexa	1.67	5.61	3.82	1.04	7.69	33.01
P_vulgaris	4.57	0.98	2.9	2.33	5.84	38.85
M_sanguinea	5.25	3.79	2.37	1.27	4.76	43.61
A_succinea	8.17	7.52	2.17	1.15	4.37	47.99

Table 4 continued….

Groups Great Wicomico & Piankatank
Average dissimilarity = 42.12

	Group Great Wicomico	Group Piankatank				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Cymadusa compta	3.27	12.38	5.31	2.2	12.62	12.62
Melita nitida	4.26	12.18	4.67	1.12	11.09	23.71
A_succinea	22.85	26.38	4.56	1.18	10.82	34.53
Barnacles	11.04	4.75	4.47	1.24	10.6	45.14
M_manhattensis	2.09	7.17	2.93	2.08	6.97	52.1
H_dianthus	0.34	4.48	2.39	2.27	5.68	57.79

Groups Lafayette & Piankatank
Average dissimilarity = 59.00

	Group Lafayette	Group Piankatank				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	8.11	26.38	10.9	2.45	18.47	18.47
Cymadusa compta	0	12.38	7.19	3.93	12.18	30.65
Melita nitida	2.9	12.18	5.31	1.19	9	39.65
M_sanguinea	6.48	0	3.92	2.17	6.65	46.29
I_recurvum	2.33	7.34	3.09	1.65	5.24	51.53
E_depressus	1.8	6.6	2.85	2.12	4.83	56.37

Groups Lynnhaven15 & Piankatank
Average dissimilarity = 63.45

	Group Lynnhaven15	Group Piankatank				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	8.17	26.38	11.87	2.2	18.7	18.7
Cymadusa compta	0.22	12.38	7.68	3.35	12.1	30.81
Melita nitida	4.27	12.18	5.7	1.19	8.99	39.8
I_recurvum	0.65	7.34	4.13	2.02	6.51	46.31
M_sanguinea	5.25	0	3.17	2.08	5	51.31
E_depressus	1.86	6.6	3.06	1.96	4.82	56.13

Table 4 continued….

Groups Lynnhaven14 & Piankatank Average dissimilarity = 57.36						
	Group Lynnhaven14	Group Piankatank				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
A_succinea	7.52	26.38	10.92	3.21	19.04	19.04
Cymadusa compta	0.27	12.38	6.93	4	12.08	31.12
Melita nitida	6.9	12.18	4.7	1.37	8.19	39.31
I_recurvum	0.64	7.34	3.76	2.14	6.56	45.87
M_manhattensis	12.73	7.17	3.54	1.37	6.18	52.05
C_convexa	5.61	2.56	3	1.23	5.24	57.28

Table 5: Results of ANOSIM analysis for differences in species composition in terms of Biomass.

Global Test	**R statistic**	**Sig level**
Global R	0.463	0.001
Groups: Pairwise Tests		
Great Wicomico, Lafayette	0.619	0.001
Great Wicomico, Lynnhaven15	0.581	0.001
Great Wicomico, Lynnhaven14	0.681	0.001
Great Wicomico, Piankatank	0.291	0.001
Lafayette, Lynnhaven15	0.163	0.039
Lafayette, Lynnhaven14	0.259	0.003
Lafayette, Piankatank	0.498	0.001
Lynnhaven15, Lynnhaven14	0.096	0.053
Lynnhaven15, Piankatank	0.535	0.001
Lynnhaven14, Piankatank	0.684	0.001

Table 6: Results of SIMPER analysis identifying the species which contribute the most to differences in species composition in terms of biomass

Groups Great Wicomico & Lafayette
Average dissimilarity = 56.94

Species	Group Great Wicomico Av.Abund	Group Lafayette Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.93	1.19	7.58	1.36	13.32	13.32
Ischadium recurvum	1.28	0.96	7.52	1.58	13.2	26.52
Eurypanopeus depressus	0.98	0.52	4.23	1.39	7.43	33.95
Marphysa sanguinea	0	0.6	3.94	1.91	6.92	40.87
Alitta succinea	0.85	0.31	3.56	1.89	6.25	47.12
Molgula manhattensis	0.19	0.68	3.24	1.72	5.69	52.81

Groups Great Wicomico & Lynnhaven15
Average dissimilarity = 56.35

Species	Group Great Wicomico Av.Abund	Group Lynnhaven15 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.93	1.29	9.57	1.17	16.99	16.99
Ischadium recurvum	1.28	0.17	7.8	1.48	13.85	30.84
Eurypanopeus depressus	0.98	0.47	4.84	1.3	8.59	39.43
Alitta succinea	0.85	0.28	4.17	2.15	7.4	46.83
G. bosci	0.99	0.74	3.67	1.09	6.51	53.33
Alpheus heterochaelis	0.15	0.5	3.51	1.11	6.23	59.56

Groups Lafayette & Lynnhaven15
Average dissimilarity = 51.39

Species	Group Lafayette Av.Abund	Group Lynnhaven15 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ischadium recurvum	0.96	0.17	6.53	0.93	12.72	12.72
Panopeus herbstii	1.19	1.29	5.86	1.33	11.41	24.13
O. tau	0.47	0.12	3.33	0.84	6.48	30.61
Molgula manhattensis	0.68	0.34	3.28	1.33	6.39	37
Alpheus heterochaelis	0.39	0.5	3.01	1.09	5.85	42.85
Eurypanopeus depressus	0.52	0.47	2.92	1.23	5.69	48.54

Table 6 continued….

Groups Great Wicomico & Lynnhaven14
Average dissimilarity = 56.03

Species	Group Great Wicomico Av.Abund	Group Lynnhaven14 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.93	1.41	8.86	1.33	15.81	15.81
Ischadium recurvum	1.28	0.19	7.96	1.55	14.2	30.01
Eurypanopeus depressus	0.98	0.34	5.25	1.58	9.38	39.39
Molgula manhattensis	0.19	0.65	3.49	1.23	6.23	45.62
Alitta succinea	0.85	0.4	3.46	1.98	6.17	51.79
Alpheus heterochaelis	0.15	0.49	3.17	1.5	5.65	57.45

Groups Lafayette & Lynnhaven14
Average dissimilarity = 50.88

Species	Group Lafayette Av.Abund	Group Lynnhaven14 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ischadium recurvum	0.96	0.19	6.62	0.95	13.02	13.02
Panopeus herbstii	1.19	1.41	5.1	1.3	10.03	23.05
O. tau	0.47	0.06	3.32	0.79	6.53	29.58
Marphysa sanguinea	0.6	0.24	3.18	1.52	6.25	35.84
Molgula manhattensis	0.68	0.65	3.05	1.3	6	41.84
Eurypanopeus depressus	0.52	0.34	2.87	1.24	5.64	47.49

Groups Lynnhaven15 & Lynnhaven14
Average dissimilarity = 48.78

Species	Group Lynnhaven15 Av.Abund	Group Lynnhaven14 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.29	1.41	7.88	1.13	16.15	16.15
Molgula manhattensis	0.34	0.65	3.87	1.14	7.94	24.09
Alpheus heterochaelis	0.5	0.49	3.44	1.14	7.06	31.15
Palaemontes vulgaris	0.5	0.17	3.11	1.65	6.37	37.51
G. bosci	0.74	0.58	3.08	1.12	6.31	43.82
Eurypanopeus depressus	0.47	0.34	2.7	1.31	5.53	49.36

Table 6 continued….

Groups Great Wicomico & Piankatank
Average dissimilarity = 43.98

Species	Group Great Wicomico Av.Abund	Group Piankatank Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.93	1.07	8.3	1.41	18.88	18.88
Ischadium recurvum	1.28	1.08	5.2	1.2	11.82	30.7
Eurypanopeus depressus	0.98	1.41	3.84	1.23	8.72	39.42
Molgula manhattensis	0.19	0.71	3.1	1.63	7.05	46.48
O. tau	0.1	0.52	2.97	0.67	6.76	53.24
G. bosci	0.99	1	2.23	1.2	5.07	58.3

Groups Lafayette & Piankatank
Average dissimilarity = 54.22

Species	Group Lafayette Av.Abund	Group Piankatank Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ischadium recurvum	0.96	1.08	6.65	1.46	12.26	12.26
Eurypanopeus depressus	0.52	1.41	5.65	1.65	10.42	22.69
Panopeus herbstii	1.19	1.07	4.4	1.44	8.12	30.81
O. tau	0.47	0.52	4.17	0.95	7.7	38.51
Marphysa sanguinea	0.6	0	3.73	1.85	6.88	45.39
G. bosci	0.63	1	2.75	1.41	5.07	50.46

Groups Lynnhaven15 & Piankatank
Average dissimilarity = 56.60

Species	Group Lynnhaven15 Av.Abund	Group Piankatank Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Panopeus herbstii	1.29	1.07	6.76	1.39	11.95	11.95
Eurypanopeus depressus	0.47	1.41	6.62	1.64	11.69	23.64
Ischadium recurvum	0.17	1.08	6.17	1.36	10.91	34.55
G. bosci	0.74	1	3.78	1.24	6.67	41.22
Alpheus heterochaelis	0.5	0	3.66	1.1	6.46	47.68
Molgula manhattensis	0.34	0.71	3.14	1.34	5.56	53.24

Table 6 continued….

Groups Lynnhaven14 & Piankatank
Average dissimilarity = 56.79

Species	Group Lynnhaven14 Av.Abund	Group Piankatank Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Eurypanopeus depressus	0.34	1.41	7.19	2.07	12.66	12.66
Panopeus herbstii	1.41	1.07	6.39	1.46	11.25	23.91
Ischadium recurvum	0.19	1.08	6.3	1.41	11.09	34.99
Alpheus heterochaelis	0.49	0	3.39	1.65	5.97	40.97
O. tau	0.06	0.52	3.28	0.67	5.78	46.75
G. bosci	0.58	1	3.14	1.69	5.53	52.28

Table 7: **Summary of community metrics**, reported as mean (SE) for each river. F- and p-values are from one-way nested ANOVA analysis.

Variables	Rivers						
	Great Wicomico	Piankatank	Lafayette	Lynnhaven 2014	Lynnhaven 2015	F-test	p-value
Density (orgs/m2)*	7602.19 (1129.71)	1690.02 (1444.76	3300.3 (512.80)	4158.20 (396.15)	2350.41 (504.88)	11.06	0.0004
Biomass (g-AFDW/m2)*	90.63 (13.72)	81.28 (13.92)	63.16 (8.82)	44.71 (6.60)	42.25 (9.01)	3.18	0.05
H' diversity	1.21 (0.053)	1.52 (0.097)	2.09 (0.088)	1.90 (0.080)	2.15 (0.17)	18.27	< 0.0001
Pielou's Evenness	0.467 (0.020)	0.544 (0.035)	0.685 (0.022)	0.660 (0.021)	0.764 (0.032)	14.22	0.0001
Richness	13.8 (0.78)	16.36 (0.41)	21.54 (1.45)	17.90 (0.89)	17.38 (2.07)	6.79	0.0035

* F-statistic and p-value comes from nested ANOVA on square-root transformed data, while Raw means are reported.

Table 8: **Results of multiple linear regression analysis for macrofaunal density, biomass, and diversity.**

Dependent Variables	Intercept			Oyster Density (oys/m2)			Total Oyster Volume			Rugosity			Salinity			R^2
	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value	
Macrofaunal Density	65.16	22.7	0.006	0.0382	0.021	0.0809	0.4466	0.37	0.2351	24.1	12.8	0.067	-2.73	0.83	0.002*	0.54
Macrofaunal Biomass	4.466	1.94	0.0258	0.0043	0.0018	0.0223*	0.0426	0.032	0.187	2.497	1.1	0.0278*	-0.149	0.072	0.0424*	0.56
H' Diversity	-0.44	0.32	0.1709	-0.0004	0.0003	0.1975	-0.002	0.005	0.6727	0.629	0.18	0.001*	0.0748	0.012	< 0.0001*	0.68
Fish Density	19.5	4.1	<0.0001	0.0013	0.0039	0.7348	0.145	0.067	0.0356*	-0.14	2.33	0.952	-0.447	0.151	0.0048*	0.41
Polychaete Density	81.54	15.5	<0.0001	0.0525	0.0147	0.0008*	-0.137	0.254	0.5933	12.96	8.78	0.1463	-3.18	0.57	<0.0001*	0.7
Mud Crab Density	1.49	4.94	0.764	0.0124	0.0047	0.0107*	-0.058	0.081	0.4761	9.19	2.8	0.0019*	-0.24	0.182	0.1934	0.5
I. recurvum Density	15.15	7.36	0.0447	0.0159	0.007	0.0267*	-0.029	0.121	0.8127	11.71	4.17	0.0071*	-1.3	0.27	<0.0001*	0.62

* indicates significant factor in the model

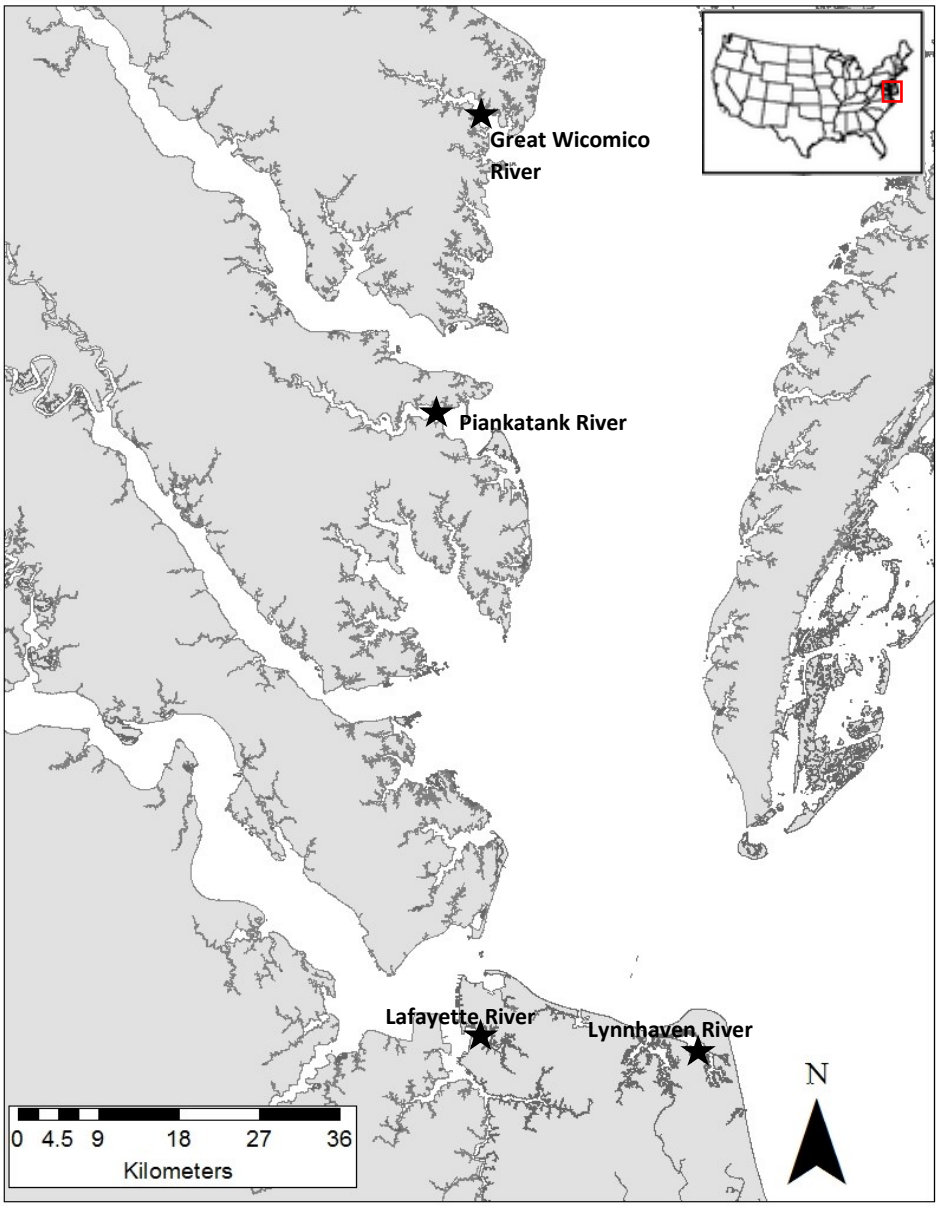


Figure 1: **Map of the Virginia portion of Chesapeake Bay**, with stars indicating the locations of the four rivers in which restored oyster reefs were sampled. Map created by Katie Knick and printed with permission.

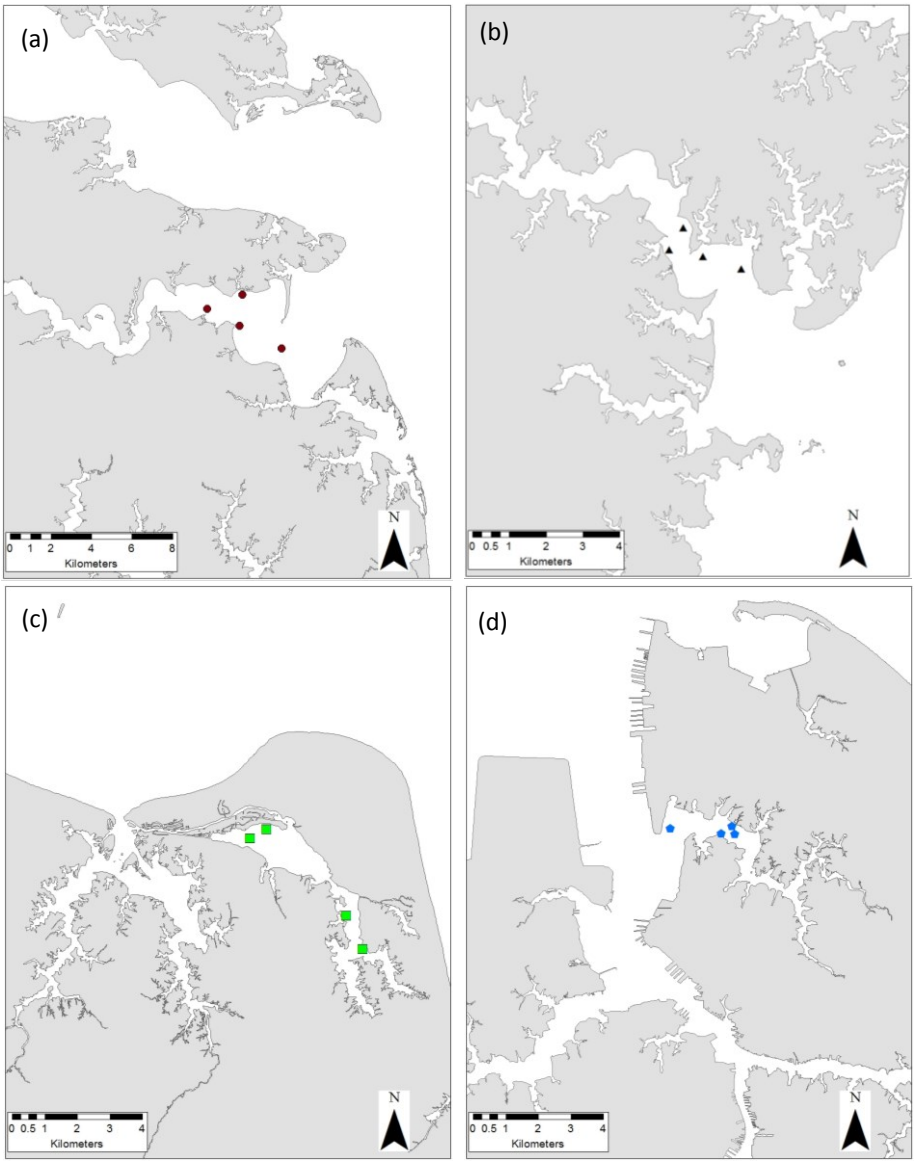


Figure 2: **Maps of the locations of the reefs sampled in each of the four rivers**: (a) Piankatank (37.51137, -76.3327), (b) Great Wicomico (37.82708, -76.2989), (c) Lynnhaven (36.90469, -76.0413), (d) Lafayette (36.90546, -76.3191). Points indicate locations of each reef sampled, and GPS coordinates are for reef closet to the mouth of each river. Maps created by Katie Knick and printed with permission.

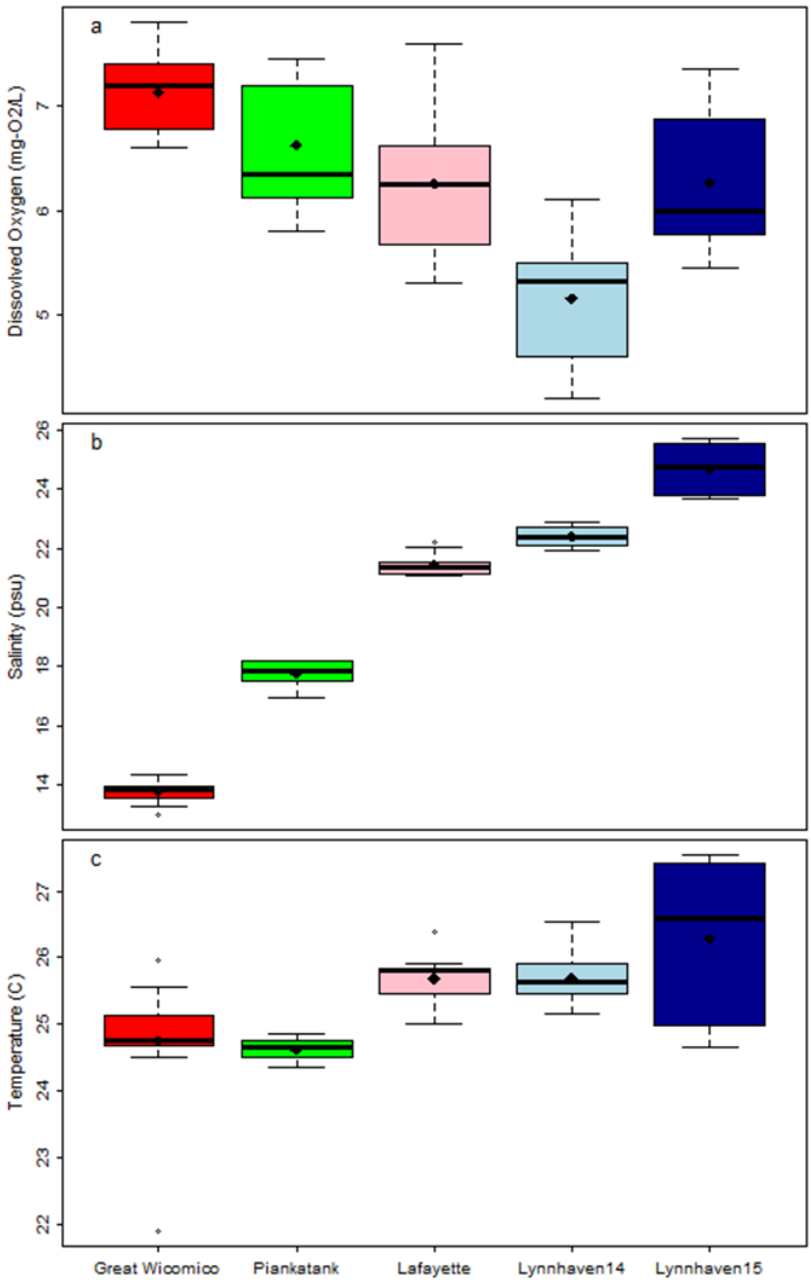


***Figure 3: Boxplots of the d*istribution of water quality parameters by river.** (a) Dissolved oxygen, (b) salinity, (c) temperature. These boxplots display the full range of variation (represented by the tails), the likely range of variation (Interquartile range, represented by the central box), and the typical value or median (represented by the horizontal black line within the central box. The large dark points represent the mean values.

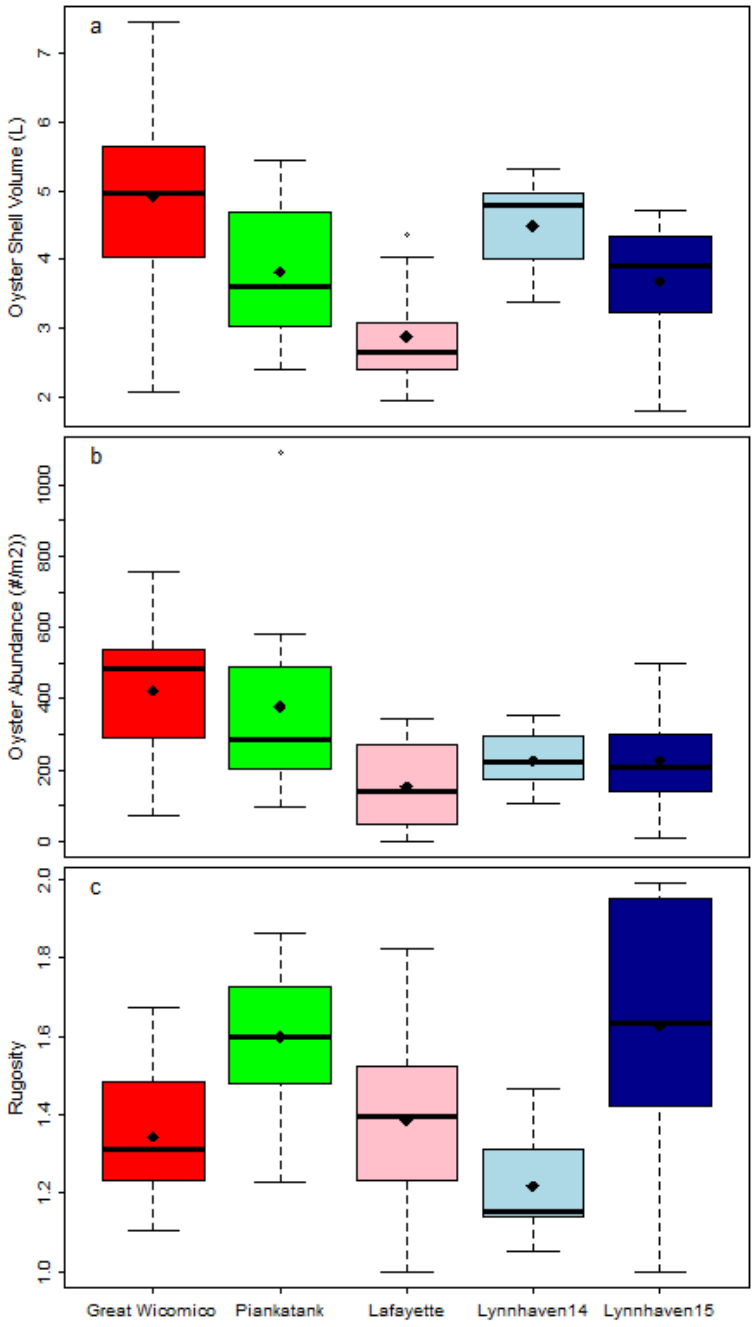


Figure 4: **Boxplots showing the distribution of habitat complexity measurements by river.** (a) Total Oyster Volume, (b) oyster abundance (# oysters/tray), and (c) rugosity taken using the chain-link method. See figure 3 for description of boxplots.

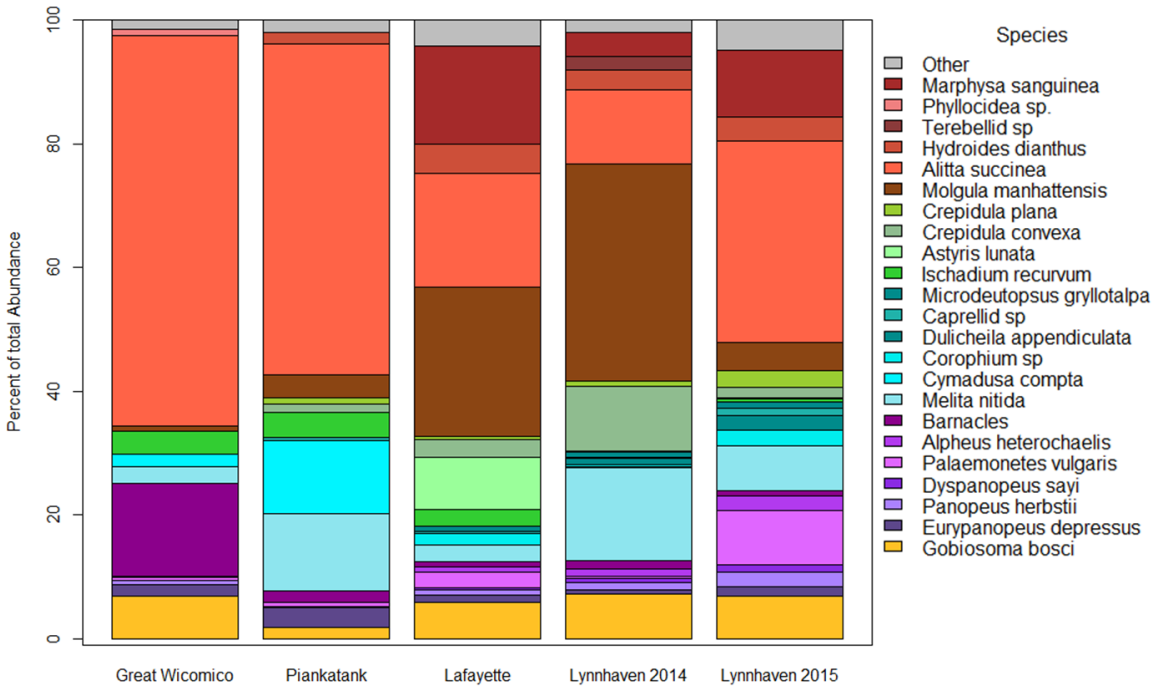


Figure 5: **Proportion of average total abundance** in each river attributed to the numerically dominant species which account for on average >1% of the total abundance in at least one of the rivers. "Other" represents the remaining organisms not listed in the legend.

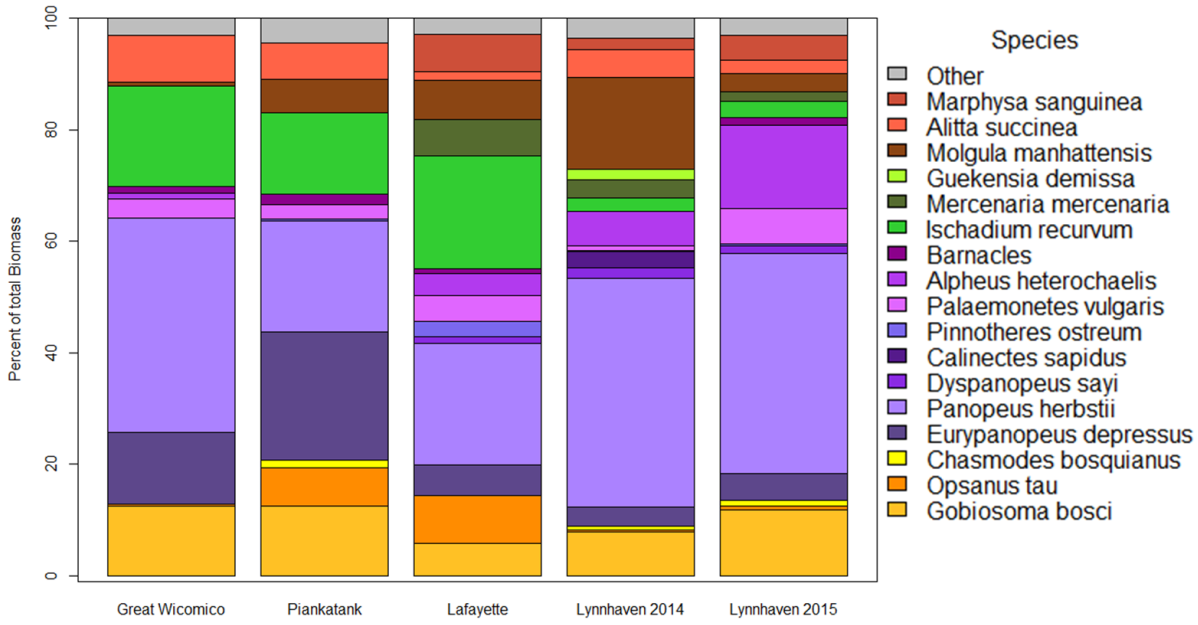


Figure 6: **Proportion of average total biomass** in each river attributed to the biomass dominant species which account for on average >1% of the total biomass in at least one of the rivers. "Other" represents the remaining organisms not listed in the legend.

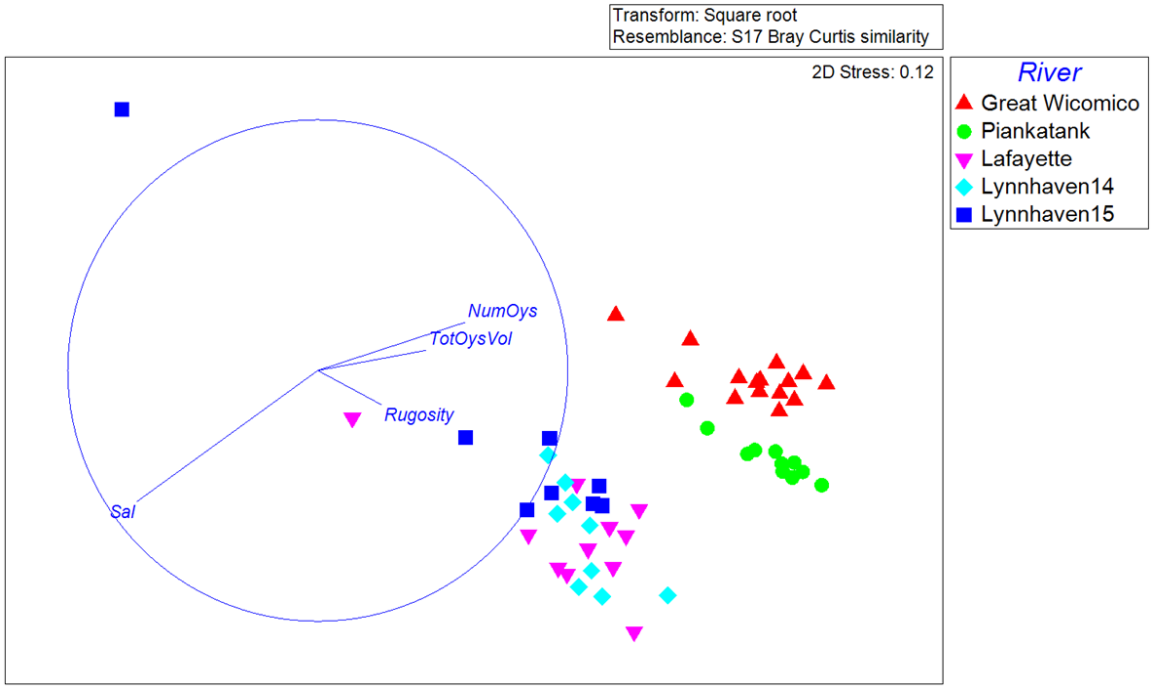


Figure 7: **Non-metric multidimensional scaling plot** for square-root transformed abundances of associated fauna in the four rivers. The blue circle illustrates the direction and strength of the correlations between the environmental and structural parameters and the observed clumping pattern in the biological data. The longer the line the stronger the correlation. This indicates that salinity is the environmental parameter which is most highly correlated with the pattern in the biological data.

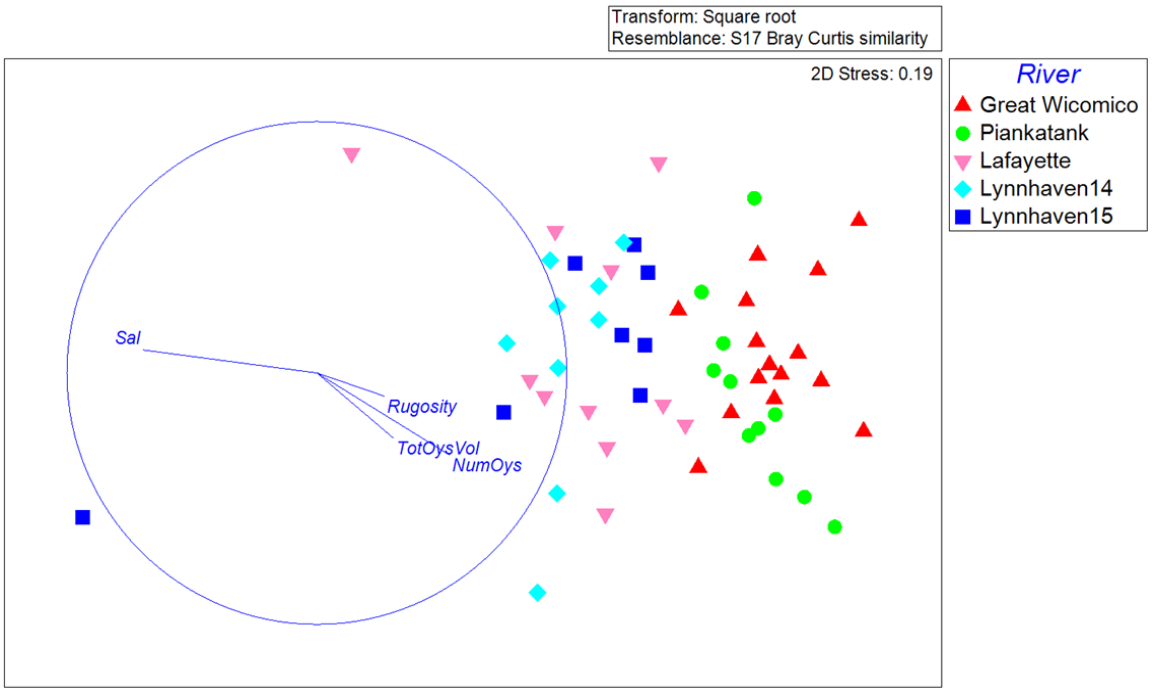


***Figure 8*: Non-metric multidimensional scaling plot** for square-root transformed biomass of associated fauna in the four rivers. The blue circle illustrates the direction and strength of the correlations between the environmental and structural parameters and the observed clumping pattern in the biological data. The longer the line the stronger the correlation.

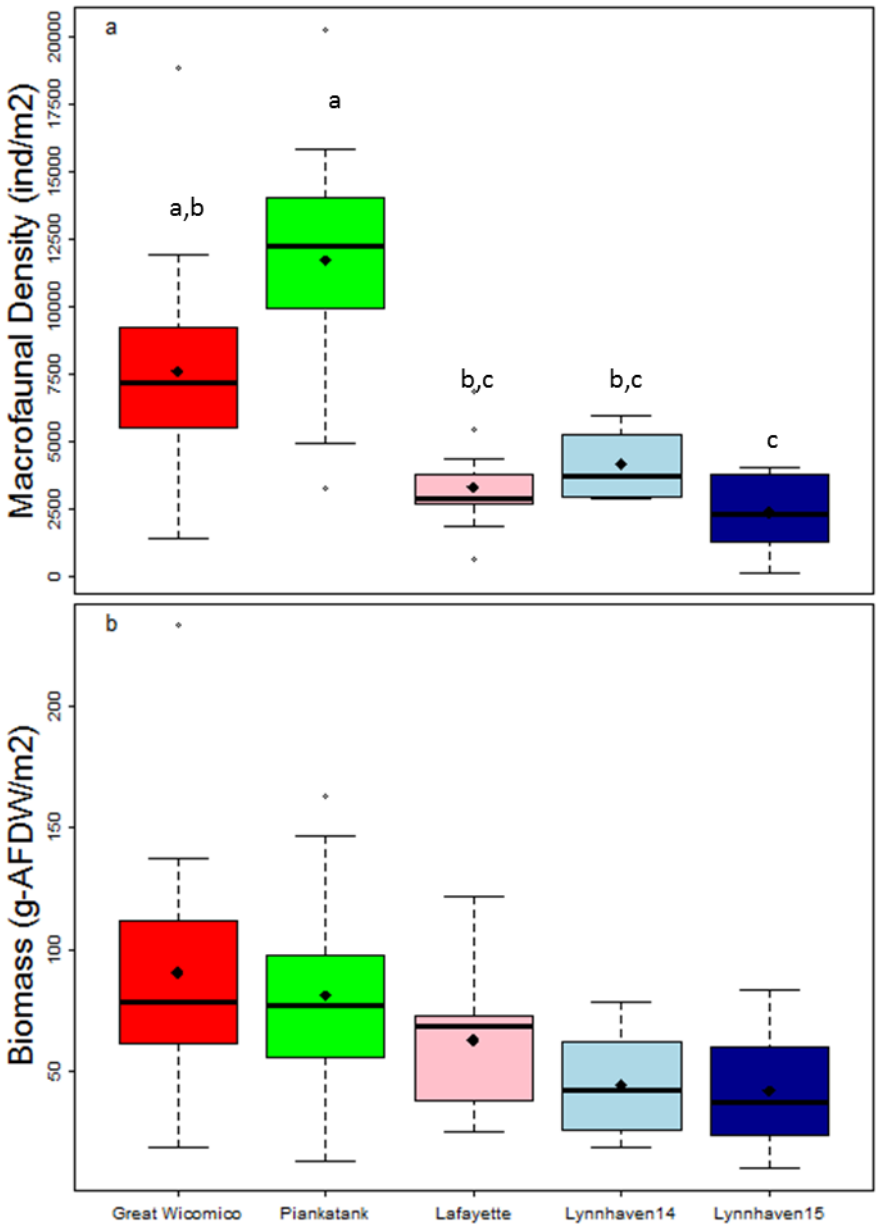


Figure 9: Boxplots of distribution of macrofaunal (a) abundance and (b) biomass by river. Sample size is n=15 for Great Wicomico, n=11 for Piankatank and Lafayette, n=10 for Lynnhaven14, and n=8 for Lynnhaven15. Letters indicate significant differences.

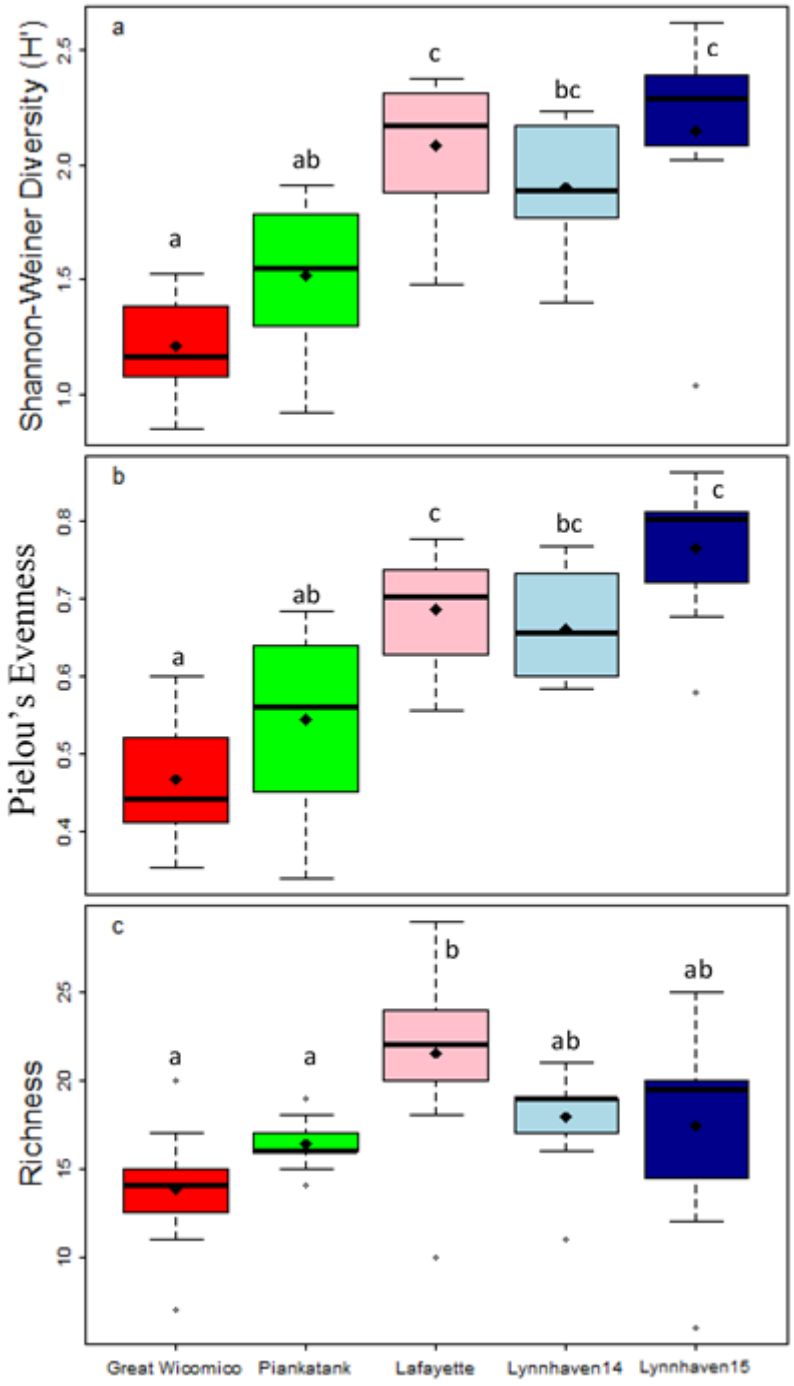


Figure 10: Boxplots of community structure metrics by river. (a) Shannon-Weiner diversity, (b) Pielou's Evenness, and (c) Species Richness. Significant differences are indicated by the different letters.

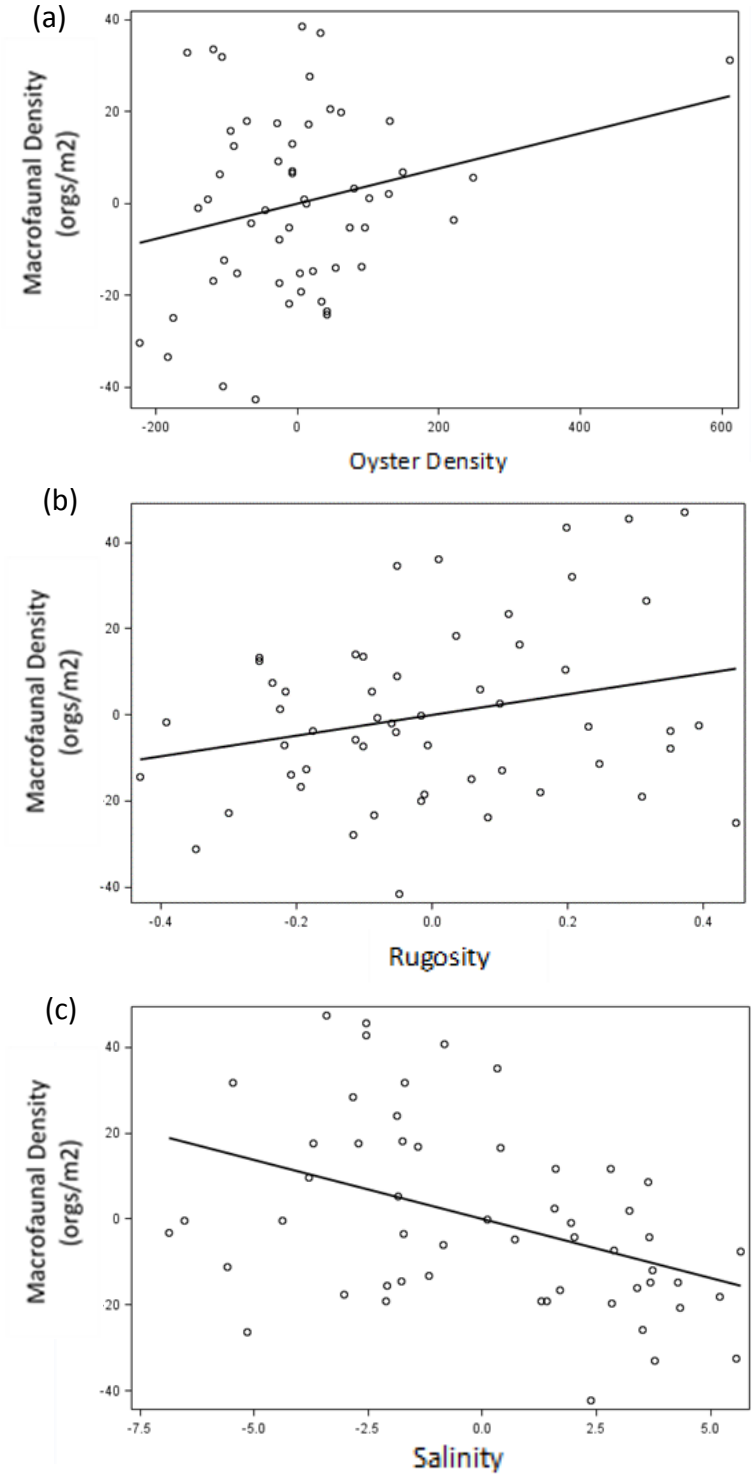


Figure 11: **Partial regression plots showing the relationship between square-root transformed macrofaunal density (orgs/m^2) and (a) oyster density (# oysters/m^2), and (b) rugosity, and (c) salinity.** The partial regression plot shows the true relationship between a predictor in the model and the response variable, by holding all other predictors constant. The y-axis is the residuals from a model of macrofaunal density versus all other predictors except the one of interest, and the x-axis is the residuals from a model of the predictor of interest (indicated by the x-axis label) versus all other predictors.

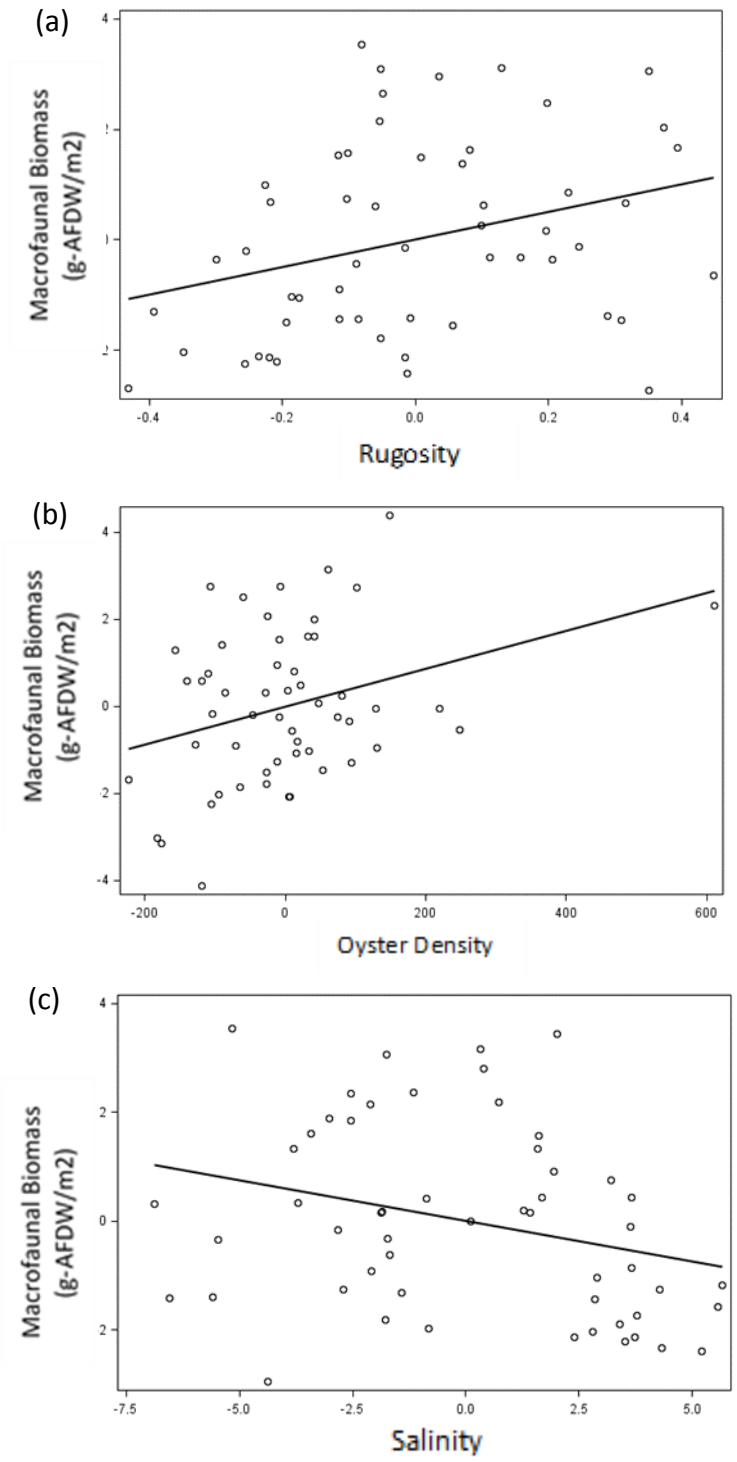


Figure 12: **Partial regression plots showing the relationship between square-root transformed macrofaunal biomass (g-AFDW/m²) and (a) rugosity, (b) oyster density (# oysters/m²), (c) salinity.** See figure 11 for description of partial regression plots.

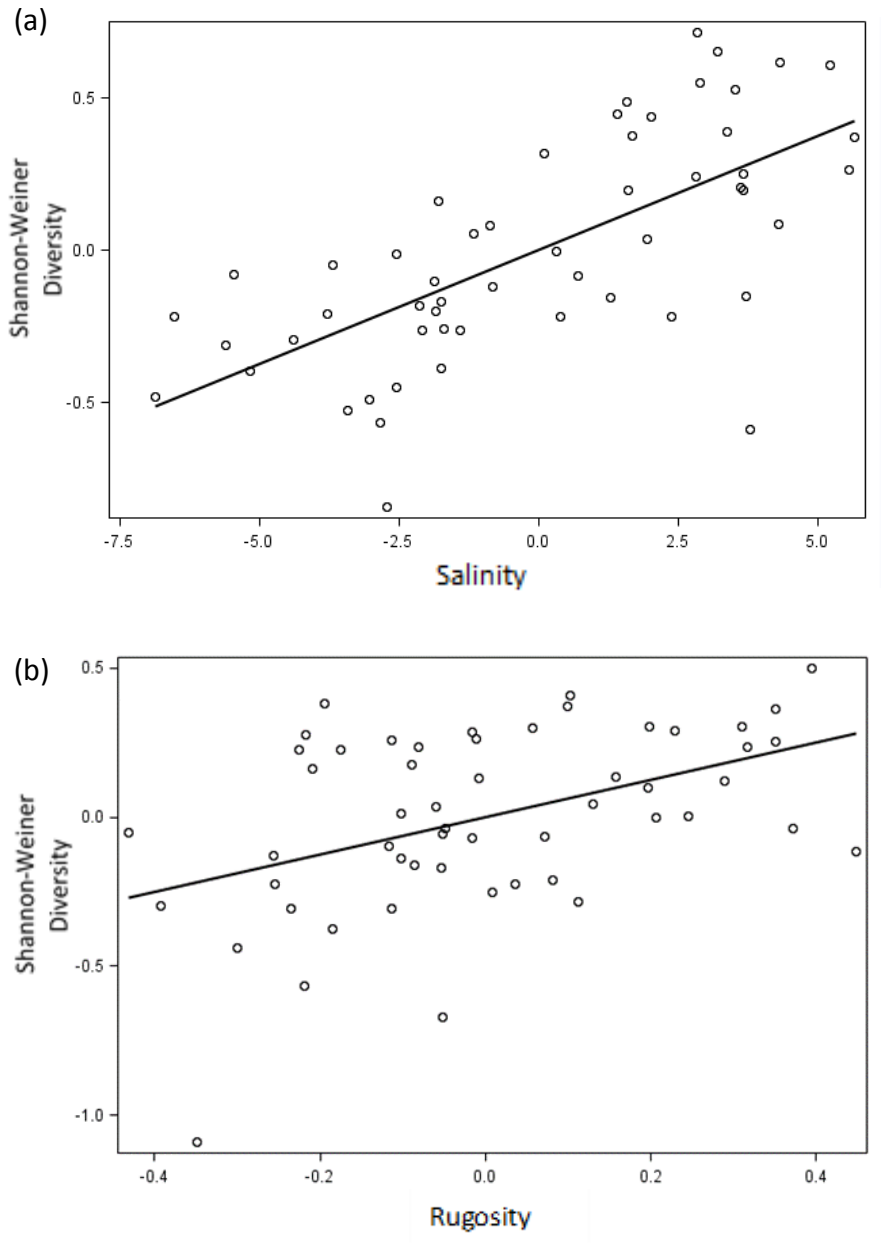


Figure 13: **Partial regression plots showing the relationship between Shannon-Weiner Diversity and (a) salinity, and (b) rugosity.** See figure 11 for description of partial regression plots.

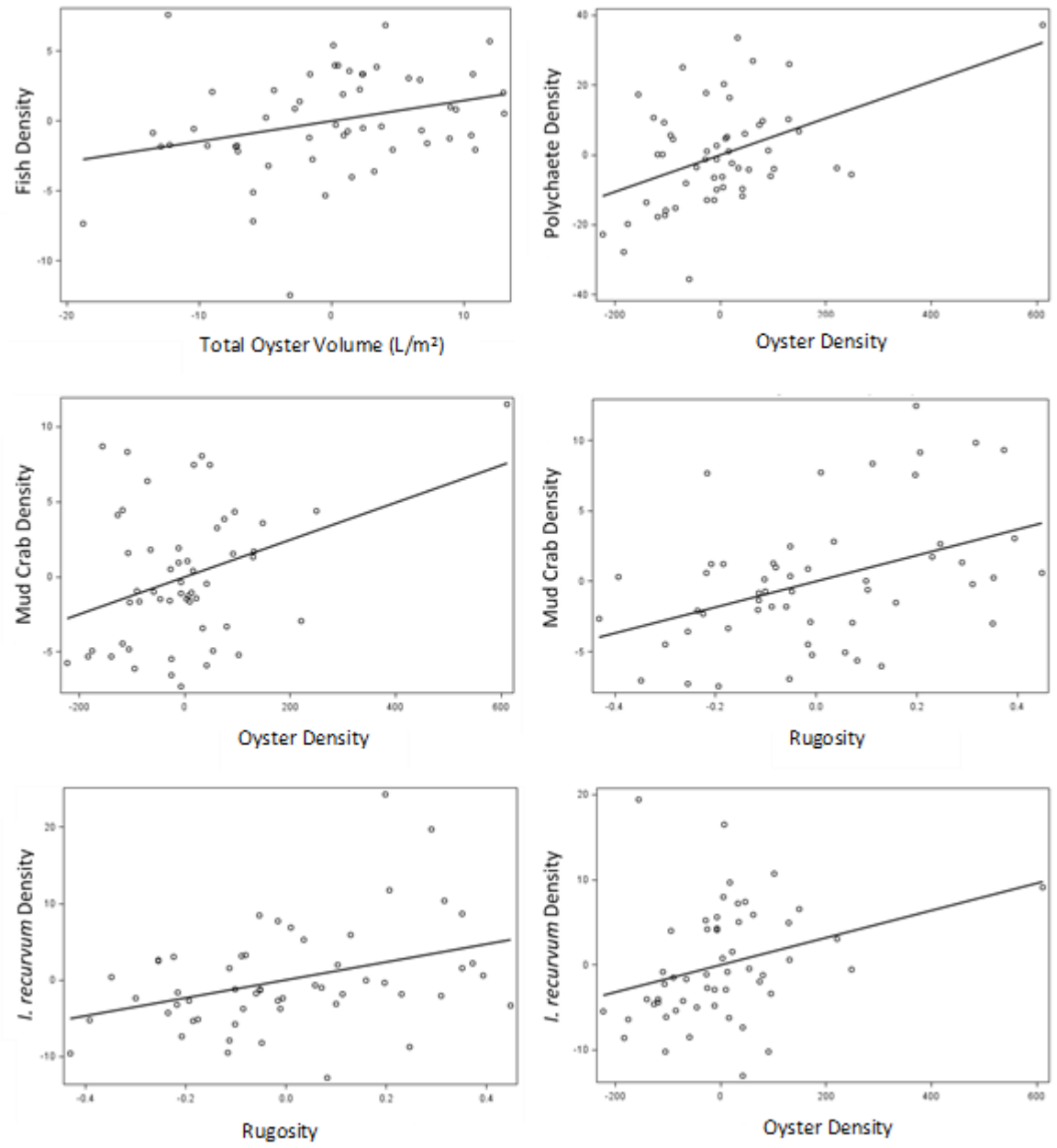
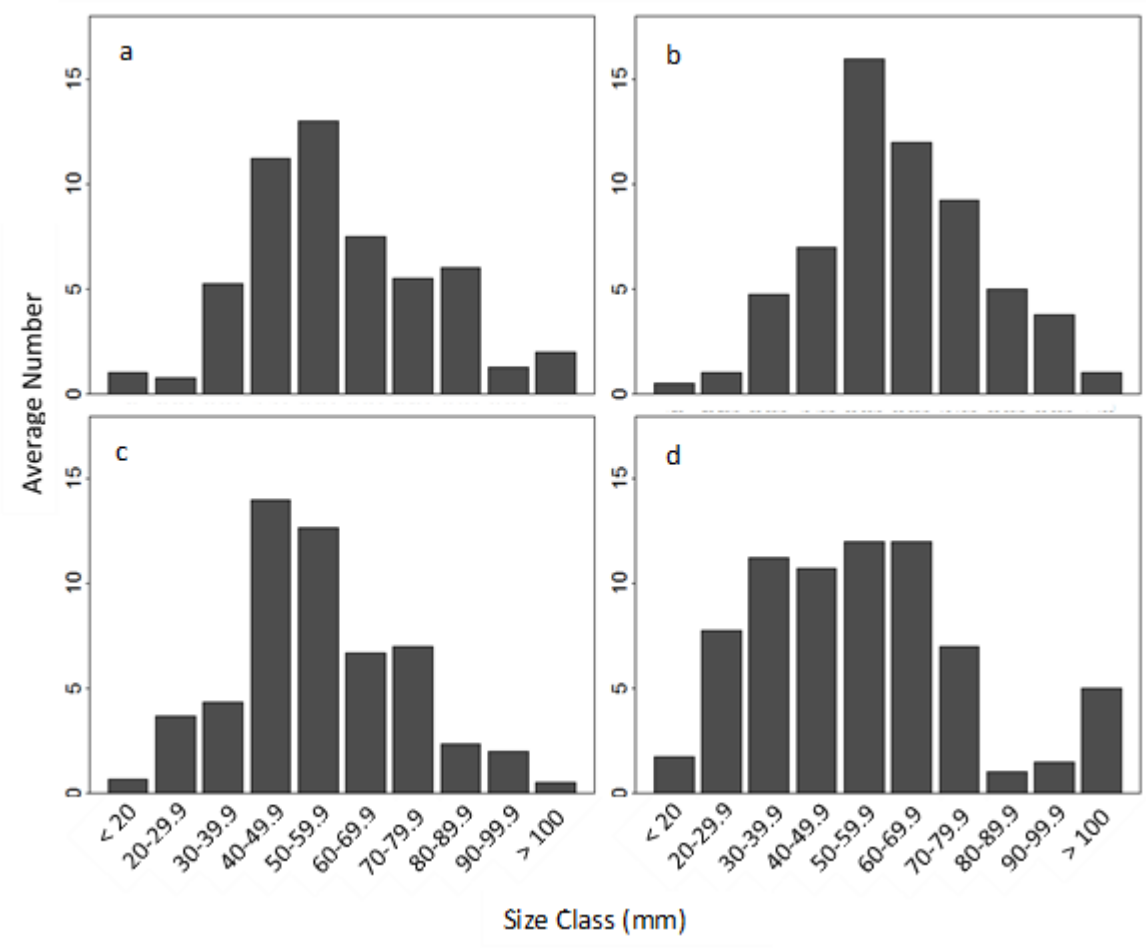
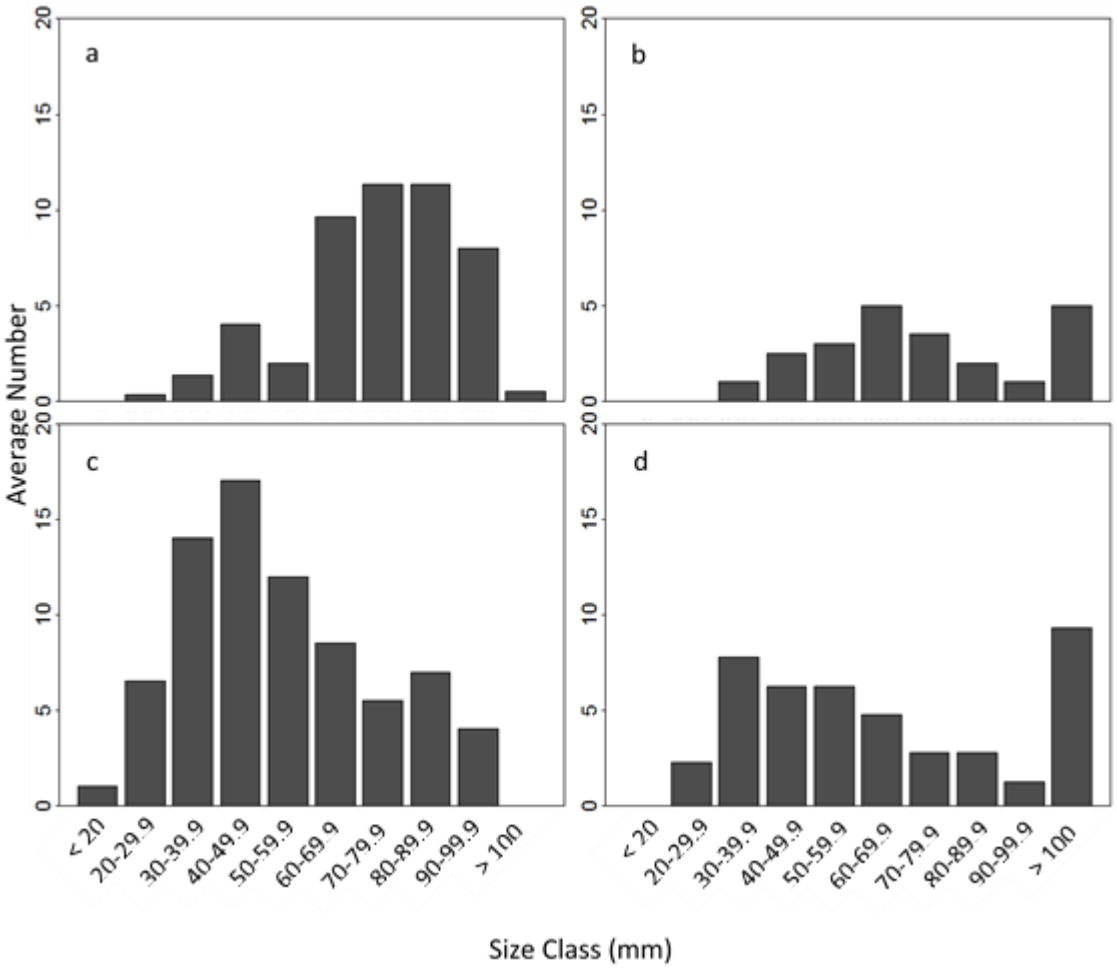


Figure 14: **Partial regression plots showing relationship between densities of major taxonomic groups and significant predictors in the models.** (a) Fish density, (b) polychaete density, (c) and (d) mud crab density, and (e) and (f) mussel (*I. recurvum*) density. See figure 11 for description of partial regression plots.

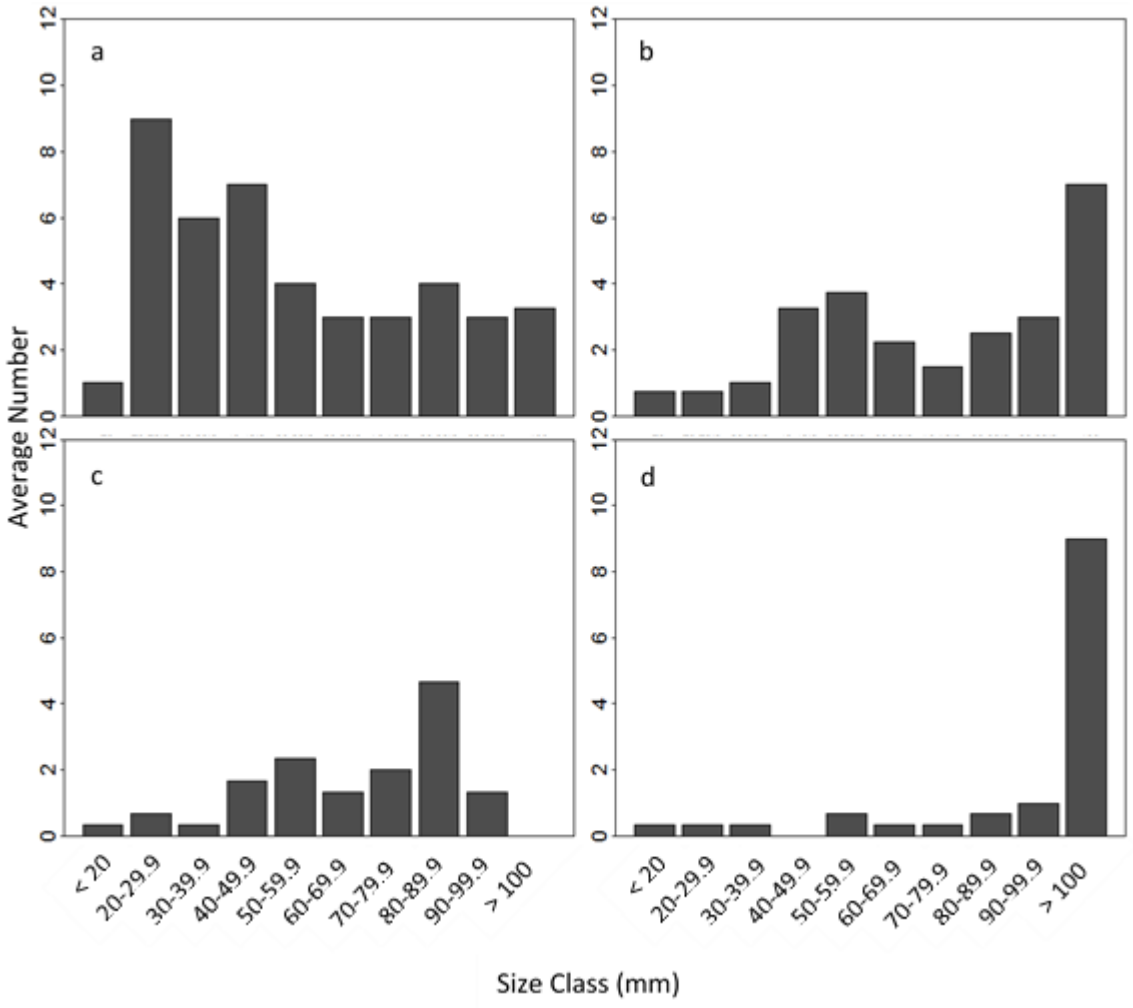
APPENDIX I



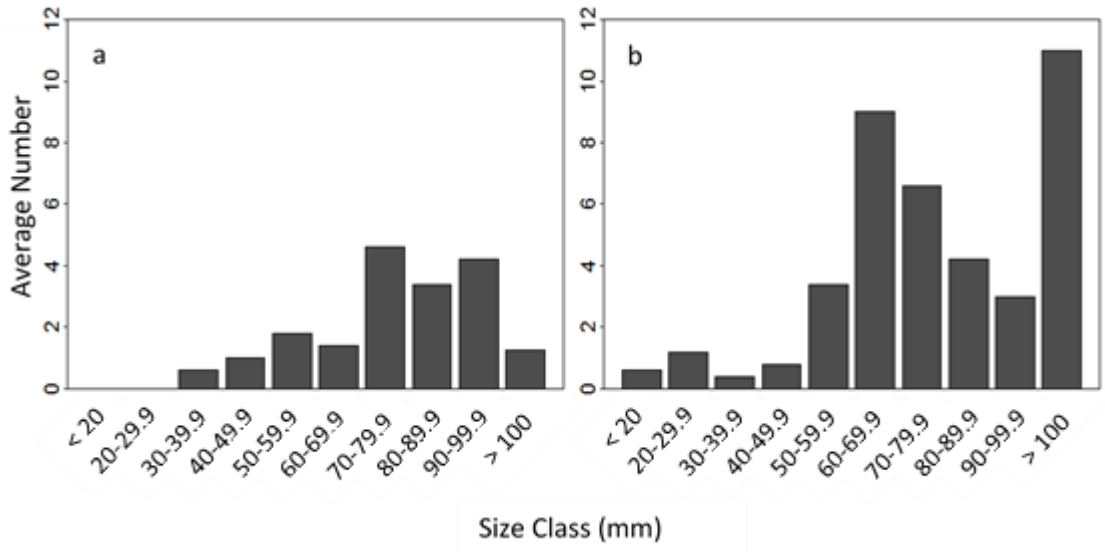
Supplemental Figure 1: **Oyster size distribution for the four reefs sampled in the Great Wicomico River.** (a) Reef 11, (b) Reef 13, (c) Reef 16, (d) Reef 9. The average number (y-axis) is the number of oysters in each size class averaged across the replicate trays from each reef.



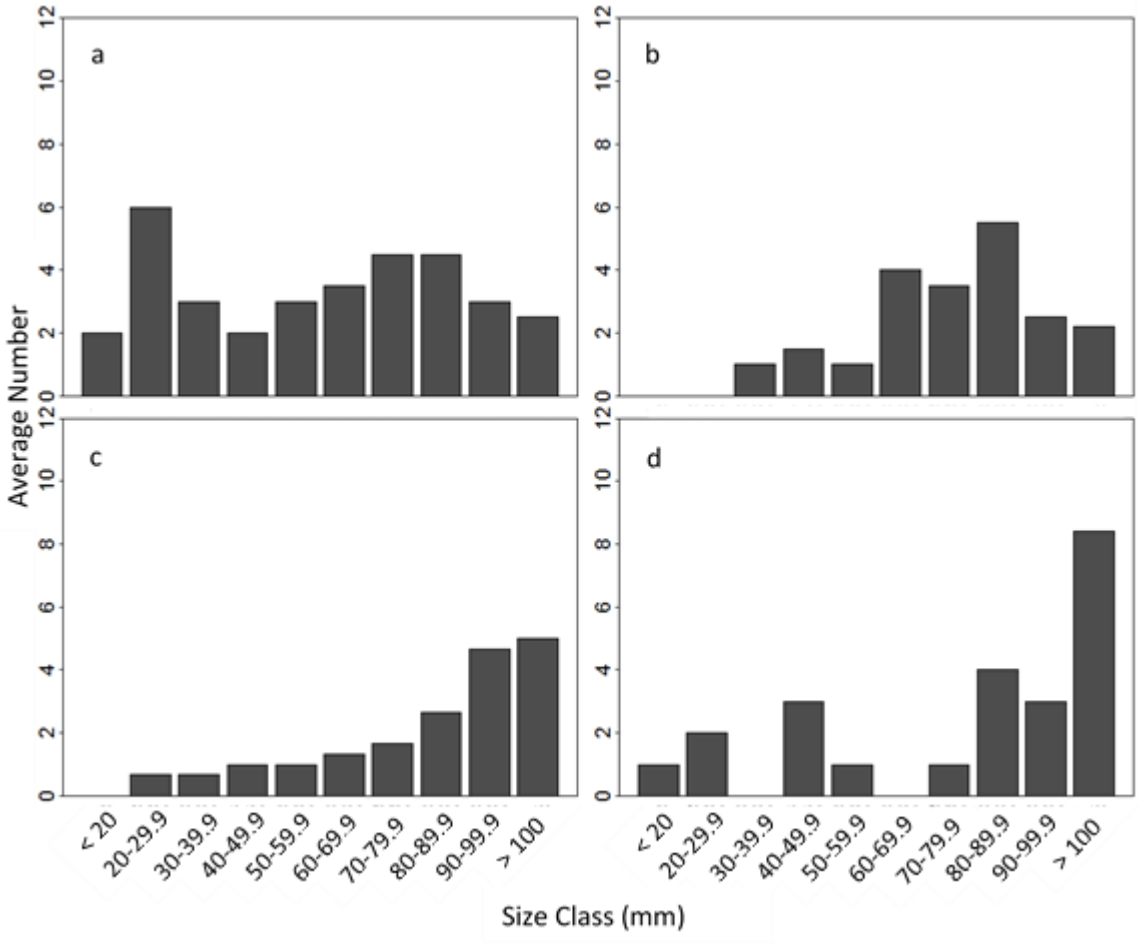
Supplemental Figure 2: **Oyster size distribution for the four reefs sampled in the Piankatank River.** (a) Burton Point, (b) Iron Point, (c) Palace Bar, (d) Bland Point. The average number (y-axis) is the number of oysters in each size class averaged across the replicate trays from each reef.



Supplemental Figure 3: **Oyster size distribution for the four reefs sampled in the Lafayette River.** (a) Relict Reef 1, (b) Relict Reef 5, (c) Restored Reef 1, (d) Restored Reef 2. The average number (y-axis) is the number of oysters in each size class averaged across the replicate trays from each reef.



Supplemental Figure 4: **Oyster size distribution for the two reefs sampled in the Lynnhaven River sampled in 2014.** (a) Linkhorn Bay 1, (b) Broad Bay 1. The average number (y-axis) is the number of oysters in each size class averaged across the replicate trays from each reef.



Supplemental Figure 5: **Oyster size distribution for the four reefs sampled in the Lynnhaven River sampled in 2015.** (a) Linkhorn Bay 1, (b) Broad Bay 1. The average number (y-axis) is the number of oysters in each size class averaged across the replicate trays from each reef.

CHAPTER 2

OYSTER REEF HABITAT COMPLEXITY AND PREY DENSITY AFFECT PREDATOR-PREY INTERACTIONS

ABSTRACT

Species diversity and abundance are often positively correlated with habitat complexity in many natural systems, and this positive relationship can be attributed to structured habitats providing refuge from predation. In fact, fish prey capture efficiencies are significantly reduced with increasing habitat complexity. Understanding how altering structural complexity within a habitat affects both predators and their prey is increasingly important today as many biogenic habitats are being degraded worldwide and efforts are being undertaken to restore their structure and function. This is especially true for oyster reefs, which are among the most endangered habitats in the world. The current assumption in oyster reef restoration is that increasing the habitat complexity of constructed reefs will result in increased prey abundance that will be readily available for upper trophic levels of commercially and recreationally important finfish. This assumption ignores the potential negative effects that structural complexity has on the foraging success of predators. In this study, I conducted a mesocosm experiment to examine the effects of both increased prey density and habitat complexity on predator foraging within an oyster reef habitat. The predator was the striped bass (*Morone saxitilis*), a common oyster reef transient predator, and the prey was the grass shrimp (*Palaemonetes* spp.), a common oyster reef resident. Predator foraging efficiency was significantly reduced in the presence of oyster shell material. Increasing prey density did not have an effect on the proportion of prey consumed, but it did increase the actual numbers of prey the consumed. Therefore, increasing structural complexity of oyster reef habitat has the potential to increase the amount of food available to upper trophic levels.

INTRODUCTION

The structural complexity of a habitat is an important environmental factor that plays a role in structuring marine communities and altering predator-prey interactions. Habitat structure has been defined as any biotic or abiotic physical structure in space, while habitat structural complexity refers to the morphological characteristics within a structure itself or the heterogeneity in the arrangement of objects in space (Bell et al. 1991). The benefits of structurally complex habitats to small benthic organisms and juveniles of larger pelagic species have been well documented (Crowder and Cooper 1982, Stuntz and Minello 2001). Structurally complex habitats, such as seagrass beds, coral reefs, and oyster reefs, often support higher diversity and abundance of macrofaunal prey compared to less-structured habitats (Crowder and Cooper 1982, Tews et al. 2004, Plunket and La Peyre 2005, Rodney and Paynter 2006). Species diversity and abundance positively correlate with increasing habitat complexity in many natural systems (Chapter 1; Tews et al. 2004). This positive correlation between habitat structural complexity and prey abundance is commonly attributed to structured habitats providing refuge from predation in the form of nooks and crannies, or interstructural spaces (Scharf et al. 2006), which can impede predator mobility and visibility, increase search and handling times, and decrease encounter rates, which contribute to enhanced prey survival (Crowder and Cooper 1982, Buekers and Jones 1997, Grabowski 2004). Several researchers have observed significantly reduced fish prey capture efficiencies with increasing habitat complexity (Diehl 1992, Scharf et al. 2006).

Most previous studies examining predator-prey interactions within structured habitats have focused on the benefits of increasing structure for the prey organism, and

the negative effects of structure on the predator's foraging (Crowder and Cooper 1982; Scharf et al. 2006; Grabowski 2004; Humphries et al. 2011). However, most of these previous studies that found a negative effect of increasing structure on predator foraging, were conducted using constant prey density across all complexity treatments (but see Matilla et al. 2008, Canion et al 2009, Humphries et al. 2011). Predator-prey interactions are frequently density-dependent, where a predator's per capita prey consumption (i.e. functional response) increases with prey density to a point. These experiments were therefore not mirroring the natural settings where prey density increases with increasing habitat complexity, and predator-prey encounter rates are expected to remain relatively constant across habitat complexity treatments (Canion et al. 2009). Several studies suggest that predator foraging efficiencies may be maximized at intermediate or high levels of habitat complexity, presumably due to increased prey densities (Crowder and Cooper 1982, Winfield 1986).

Understanding how altering structural complexity within a habitat affects both predators and their prey is increasingly important today as many biogenic habitats are being degraded worldwide and efforts are being undertaken to restore their structure and function. This is especially true for oyster reefs, which were once prominent features in estuarine landscapes, but are now among the most endangered habitats in the world, having suffered an estimated 85% global loss (Beck et al. 2011). In Chesapeake Bay, the situation is even more severe as < 1% of the historic oyster (*Crassotrea virginica*) population remains (Rothchild et al. 2004). The goals of current restoration efforts now extend beyond simply increasing oyster biomass to also restoring some of the various ecosystem functions provided by these reefs, such as habitat and foraging grounds.

Oyster reefs, are important ecosystem engineers (Jones et al. 1994), modifying, maintaining and creating habitat in estuarine ecosystems, which facilitates the abundance of other organisms. These reefs have been found to support dense assemblages of fish, crabs, shrimp, and polychaetes which are common prey items for fish species of commercial and recreational importance (Chapter 1 this Thesis; Wells 1961, Coen et al. 1999, Harding and Mann 2001, Rodney and Paynter 2004), including tautog, weakfish, and striped bass. Several of these predatory fish utilize oyster reef habitats in the Chesapeake Bay for feeding and nursery habitats (Harding and Mann 2001). Juvenile striped bass, 1-2 years of age, for instance, are found in greater abundance on oyster reefs compared to sand bottoms, and have a diet that reflects this distribution pattern consisting of common oyster reef fauna such as naked goby (*Gobiosoma* bosc) and shrimp (*Palaemonetes* spp.) (Harding and Mann 2003). As a result, several studies have proposed that services such as fish production may be enhanced by restored oyster reefs that provide habitat for diverse and abundant benthic prey communities that serve as food resources for upper trophic levels of fish and shellfish (Peterson et al. 2003, Grabowski et al. 2012).

Peterson et al. (2003) estimated that 10 m^2 of restored oyster reefs would enhance fish production by 2.5 kg. However, this estimate does not consider the structural complexity of that 10m^2 of oyster reef, and therefore does not take into account the potential negative effects that structural complexity may have on the foraging success of some predators. Therefore the value of more highly structured reefs for foraging fish remains unclear, and the relationship between increased structure, prey abundance, and trophic transfer off of the reefs may not be as straightforward as suggested. The

combined effects of varying prey densities and structural complexity on predator foraging on oyster reefs needs to be examined to provide insight into the potential value of restoring structured oyster reef habitat for both predators and their prey.

In this study, I conducted a mesocosm experiment to examine the effects of both increased prey density and habitat complexity on predator foraging within an oyster reef habitat. The predator used in this experiment was the striped bass (*Morone saxatilis*), which is both recreationally and commercially harvested in Chesapeake Bay and coastal waters of the eastern United States. Striped bass are apex predators that are commonly found in estuarine and coastal waters along the Atlantic and Pacific coasts of the United States (Murdy et al. 1997). They utilize estuaries, including Chesapeake Bay tributaries, for spawning, nursery, and feeding grounds during several life stages, and forage on oyster reefs (Harding and Mann 2001, Harding and Mann 2003). When striped bass were collected around oyster reefs, grass shrimp were frequently found in their stomachs (Harding and Mann 2003). The prey species used in this experiment was the grass shrimp (*Paleamonetes* spp.), which are among the most abundant organisms in estuarine waters of southeastern United States, and are found in greater abundance on oyster reefs compared to mud bottoms (Plunket and La Peyre 2005). Grass shrimp play an important role in energy transfer as they are detritivores that eat debris on oyster reefs, and serve as prey for upper trophic levels, passing energy up the food chain (Harding and Mann 2003).

The objective of this mesocosm experiment was to determine how reef complexity (three levels: none, low, and high) and prey density (low, medium, and high) interact to affect predator foraging efficiency. The aim of this study was to determine

whether increased prey density, similar to that observed on more complex oyster reefs, might counteract the negative effect of increased habitat complexity on predator foraging efficiency. I hypothesized that number and proportion of prey consumed would decrease with structural complexity, but would increase with prey density irrespective of the amount of structure present.

METHODS

Organism Collection and Maintenance

Striped bass were obtained from a hatchery and maintained in a flow-through system for two years prior to being used in this experiment. Prior to the start of the experiment, nine striped bass, of approximately 20-cm total length, were randomly selected from this population and transferred to cylindrical tanks with a flow-through system using York River water. These fish were then weaned off of fish food pellets and trained to eat live shrimp, and to eat when not in a school. Shrimp were caught from marsh edges along the York River and from the Virginia Institute of Marine Science's boat basin using a dip net. Shrimp were maintained in a large aquarium with ambient temperature and constant air bubbling. Water in the aquaria was frequently changed and shrimp were supplied with fresh *Ulva* algae as a food source.

Experimental design

This study was conducted in January 2016, in a randomized block design with one replicate per treatment per block and four replicate blocks through time, with time as the blocking factor. For each trial, treatments were randomly assigned to 12 cylindrical

mesocosm tanks (0.87 m diameter and 0.59 m height) housed in the Seawater Laboratory at VIMS. Nine treatments resulted from crossing oyster reef complexity (none, low, high) and prey density (low [10 shrimp (7.69 shrimp/liter of oyster shell)], medium [20 shrimp (15.39 shrimp/liter of oyster shell)], high [50 shrimp (38.46 shrimp/liter of oyster)]), with one predator (striped bass) per tank. The shrimp densities used are consistent with those observed on restored oyster reefs (see Chapter 1). Three predator-free controls, one for each prey density, were also included for each block and were used to determine if there was any background shrimp mortality that was not due to the predator. The tank bottom was left bare, with no oyster reef complexity, for each predator-free control.

Predators were starved for 48 hrs. prior to the start of each trial and the water temperature in each tank was gradually increased to 14 degrees Celsius by pumping in heated water from a holding tank. The day before each trial, the experimental oyster reefs were created in the appropriate tanks to allow the predator time to acclimate to the presence of the structure. For the 'no-complexity' treatment, the bottom of the tank was left bare. For the 'low-complexity' treatment, 1.3 L of oyster shell halves were placed on the bottom, covering about one-quarter of the tank (Figure 1A). For the 'high-complexity' treatment, 1 L of live oyster clumps (which extended vertically into the tank), collected from natural oyster reefs, was placed on the bottom and surrounded with 0.3 L of shell halves, again covering about one-quarter of the tank bottom (Figure 1B).

Experiments began between 9 am and 10 am by first placing a mesh barrier across the tank to separate the striped bass from the portion of the tank with the constructed oyster reef. The designated number of shrimp was then added to the designated treatment tank on the side with the oyster reef and no predator, or in the case of the no complexity

treatment, without the predator. The shrimp were given approximately 30 seconds to acclimate and find refuge, before the barrier was removed allowing the striped bass to forage freely. This was shown in a pilot study to be enough time for the shrimp to acclimate and find the oyster shell structure within the tanks. After 24 hrs., the striped bass was removed from each tank, the oyster shell was removed, and the remaining shrimp were removed and counted. The striped bass was then returned to tanks and fed live shrimp for 2 days before the entire process was started again for the next trial.

Statistical Analysis

All data were tested for normality using Shapiro-Wilks test, and homogeneity of variance using Levene's Test, and data were transformed as necessary to meet the assumptions of ANOVA; mortality data were arcsine square-root transformed and number of shrimp eaten was $\log_{10}$ transformed. Two-way Analysis of Variance (two-way ANOVA), followed by pairwise comparisons with a Bonferroni adjustment, was conducted to examine the effect of prey density and oyster reef habitat complexity on both the proportion and the number of prey consumed.

RESULTS

Survival of *Palaemonetes* spp. prey was 100% in the predator-free controls and therefore I attributed experimental mortality during the trials to predation by striped bass. Oyster reef complexity had a significant effect on prey mortality (i.e., proportion of prey eaten, arcsine square-root transformed) (Two-way ANOVA, $p < 0.0001$), with mortality being greater in the no-complexity treatment compared to either the high- or low-

complexity treatments. There was no difference in prey mortality between the high- (i.e. live oyster clumps and shell halves) and low- (i.e. dead shell halves) complexity treatments. The proportion of prey consumed ranged from 26 to 94 %, and was significantly greater in the no-complexity treatments (77-94 %) compared to the low- (26-33 %) or high-complexity (30-50 %) treatments ($p < 0.0001$) (Table 1; Figure 2). Prey density did not have a significant effect on prey mortality (Two-way ANOVA, $p = 0.59$), and there was no significant interaction between complexity and prey density ($p=0.6858$).

In contrast with effects of density and complexity on prey proportional mortality, both initial prey density and habitat complexity had significant effects on number of shrimp eaten (log transformed) ($F = 26.36$, $p < 0.001$ and $F = 15.52$, $p < 0.0001$, respectively) (Figure 3), and there was no significant interaction between complexity and prey density ($F = 0.6391$, $p = 0.6392$). The number of shrimp eaten was greater in the high-density (50 shrimp) treatment compared to both the low- (10 shrimp) and medium-density (20 shrimp) treatments ($p = 0.0016$ and $p = 0.027$, respectively), but did not differ between the low- and medium-density treatments ($p = 0.11$). The number of shrimp eaten was also significantly greater in the no-complexity treatment compared to the low-complexity ($p = 0.0054$) and high-complexity ($p = 0.033$) treatments, but did not differ between the high- and low-complexity treatments ($p = 0.39$). Additionally, there was no significant effect of block (four replicates for each treatment were done at different times) on either the proportion of shrimp consumed or the raw number of shrimp eaten ($p = 0.48$ and $p = 0.43$, respectively).

DISCUSSION

Predator foraging efficiency, both in terms of proportion and number of shrimp consumed, was significantly reduced in the presence of complex oyster reef habitat as hypothesized, but only to a certain point. Increasing the complexity of the experimental oyster reefs from dead shell to live three-dimensional clusters did not result in a further reduction in foraging efficiency. Contrary to my hypothesis, increasing prey density did not counteract this decline in foraging efficiency with habitat complexity. These results are consistent with other studies (Crowder and Cooper 1982, Matilla et al. 2008, Canion et al. 2009, Humphries et al. 2011) and provide further evidence to suggest that predator foraging efficiency is significantly reduced in the presence of any habitat structure and irrespective of prey density. Possible explanations for the reduction in foraging efficiency observed in this study could be increased search times with increased structural complexity due to increased surface area in which to locate prey, or reduced mobility of the predator due to the physical structure impeding movement (Crowder and Cooper 1982). Complexity can also lower the probability of successful attack and capture upon encountering prey if the prey can hide within the protective spaces within the habitat (Ryre 1988, Scharf et al. 2006). Almost all shrimp remaining at the end of each trial for the oyster shell treatments were found within or under the shell structure.

There was no difference between the high- and low-complexity treatments in this study both in regards to number of prey eaten and proportion of prey consumed. One reason for this could be that the method used to increase the structural complexity (i.e. adding a set volume of live oyster clumps) may not be a measure of habitat complexity that is beneficial to or perceived by the shrimp. Both the dead shell and an equal volume

of live clumps may provide the same refuge benefits to the shrimp. It is possible that increasing complexity by another means, for example by increasing the total volume of shell material, may have resulted in increased complexity that would be beneficial to the shrimp and may have allowed for detection of differences between complexity treatments. Also, using different prey species may have resulted in a different outcome as a result of different behaviors and refuge utilization (Scharf et al. 2006, Humphries et al. 2011). For instance, oyster reef fish residents, such as the naked goby (*Gobiosoma bosc*) or blennies have high affinity to vertically structured oyster shells, which they often use for refuge and nesting sites (Soniat et al. 2004). Therefore, using a fish as prey may have resulted in different outcome. Shrimp can burrow under the dead shells and thus that habitat may be just as good a refuge as the three-dimensional structure of oyster clumps, while fish may not be able to use the dead shell structure as effectively and therefore may benefit more from the presence of oyster clumps.

Contrary to what I hypothesized, increasing prey density did not counteract the negative effect of increased structure on predator foraging efficiency in terms of the proportion of prey consumed. The proportion of prey consumed did not change with increasing prey densities for any level of habitat complexity. This result is consistent with Humphries et al. (2011) who also did not find a significant effect of increasing prey density on the percent survival of prey. One explanation is that the prey densities used in this experiment were not high enough to fully saturate the refuge spaces available in the experimental habitats, allowing ample space within the structure for all prey to hide from predators. However, this may not be the only explanation at work here. If this were the case, then I would expect to see lower, if not zero, mortality at the lower prey densities.

Therefore, another explanation for the equal percent mortality among the prey densities may be a result of individual prey "personalities". There may be a certain proportion of individuals within the prey population that are more daring or 'bold' (Wolf and Weissing 2012) and may venture out of the safety of the structure more often. Those 'bold' individuals are then the ones that are consumed by the waiting predators. This could explain why the number of prey eaten increased with prey density, but the proportion remained the same for all density treatments for each level of complexity.

Although my experiment generally agrees with the theory that the presence of habitat structure decreases predator foraging efficiency, increasing prey survivorship, it is important to note that this mesocosm experiment was simplified with one predator and one prey species, and caution should be taken in generalizing these results to more-complex ecosystems. There are potential interactions between multiple predators or prey in the natural environment that are not represented in this experimental mesocosm. Multiple predators of either the same or different species could interact with each other in ways that could either increase (facilitation) or decrease their consumption of prey, and habitat complexity can influence these multi-predator interactions (Warfe and Barmuta 2004, Grabowski et al. 2008). Different predators have different foraging behaviors that could alter how habitat complexity impacts their foraging. For instance, habitat complexity reduced foraging efficiency to a much lesser extent for ambush predators, such as summer flounder, compared with active predators, such as the sea robin (Sharfe et al. 2006). In addition, some predators may be able to shift foraging tactics in the presence of structure, which may allow them to continue catching high levels of prey, while other predator species may not be able to switch modes and therefore experience

reduced prey capture (Michael and Adams 2008). In my study, it appears that striped bass did not exhibit this plasticity and did not switch foraging strategy in the presence of structure, as evidence by the significant reduction in number and proportion of prey consumed when foraging in oyster shell habitats. Predators, especially generalist predators, such as striped bass, could also exhibit prey switching behavior when multiple prey species are available, and fish could target either the most readily available species or their preferred prey species (Hughes and Grabowski 2006). Therefore, to more realistically model the natural environment, future studies should include multiple prey and predator interactions.

Even though the proportion of prey consumed did not change with increased prey density, the actual number of prey that were eaten did change. In this study, significantly more prey were consumed in the highest prey density treatment compared to the medium- and low-density treatments, regardless of the habitat complexity. Despite differences in our objectives, similar results were found by Huang et al. (2016), who investigated the effect of habitat complexity and prey density on the foraging success of an invasive predator (red swamp crayfish) on a native prey within a vegetative habitat. In their study increasing habitat complexity (i.e. plant density) also significantly reduced predator foraging success, while increasing prey density significantly increased the amount of prey consumed. Previous studies, such as Humphries et al. (2011), recognized the potential effects prey density might have on predator foraging success, but they scaled prey density with complexity, which did not enable the testing of these two factors independently. Both this current study, and Huang et al. (2016) build upon previous studies as ours were

designed to test the two main factors, prey density and habitat complexity, independently and to test for interaction effects.

The increase in per capita prey consumption at high prey densities is consistent with functional response theory. When one considers this in combination with the observation that organism abundance and biomass are often positively associated with habitat complexity (Tews et al. 2004), my results suggest that predators may be able to take advantage of increased prey density associated with oyster reefs despite the reduction in predator foraging efficiency in these habitats relative to bare sediment habitat. That is to say that the number of prey consumed by a predator, and therefore the amount of energy transferred up the food chain, may increase with the increased prey density on more complex reefs. Therefore, medium- and high-complexity oyster reefs may be beneficial to both the prey and predators, as they provide refuge from predation for the prey, as well as enhanced prey resources available to the predator compared to lower-complexity environments. Also, in this mesocosm experiment, oyster shells worked just as well as live oyster clumps as refuge from predation for shrimp. This was somewhat surprising based on the results of Chapter 1 of this thesis where density of several taxa and total macrofaunal biomass increased with live oyster density. This could be, in part, because the total biomass included numerous types of organisms, which, like the specific taxa whose densities were modeled in Chapter 1, may utilize the oyster habitat differently than grass shrimp. Therefore, in future restoration efforts it may be most beneficial to have a combination of both live and dead shell material. Increasing the diversity of refuge space types available in the oyster reef habitat could lead to increases in the diversity and abundance of prey organisms available to upper trophic levels.

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Table 1: Summary of results showing complexity treatment, number of prey added, mean number of prey removed (i.e. eaten by the predator), and mean proportion consumed.

Oyster Reef Complexity Treatment	Prey Added	Number Prey Removed	Proportion consumed
None	10	7.67	0.77
None	20	18.67	0.93
None	50	47	0.94
Low	10	3.33	0.33
Low	20	5.33	0.26
Low	50	15	0.3
High	10	5	0.5
High	20	6.67	0.33
High	50	15	0.3

A).

B).

Figure 1: **Images of mesocosm tank set up, showing** (A) low habitat complexity, with 1.3-L shell halves, and (B) high habitat complexity, with 1.0-L live oyster clumps with 0.3-L shell halves.

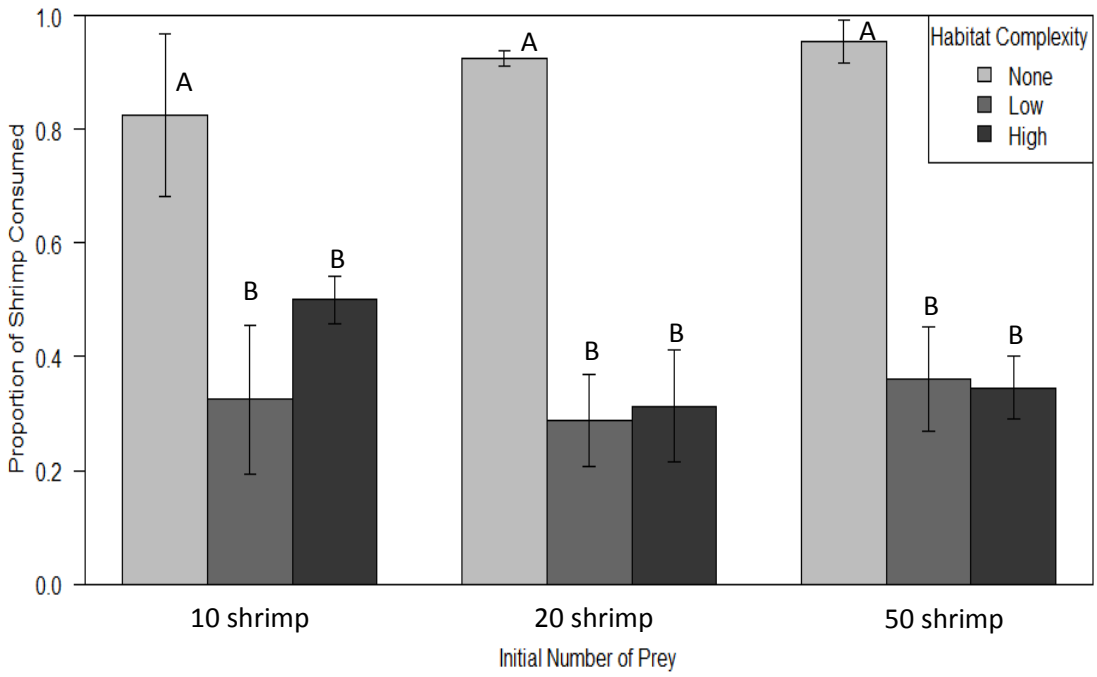

Figure 2: **Proportion of prey consumed by complexity and prey density.** Vertical bars represent the mean proportion of shrimp eaten (± 1 standard error) from the n=4 trials. Two-way ANOVA revealed that oyster reef complexity, but not prey density, had a significant effect on the proportion of shrimp consumed ($p<0.0001$). Significant differences are indicated by the different letters.

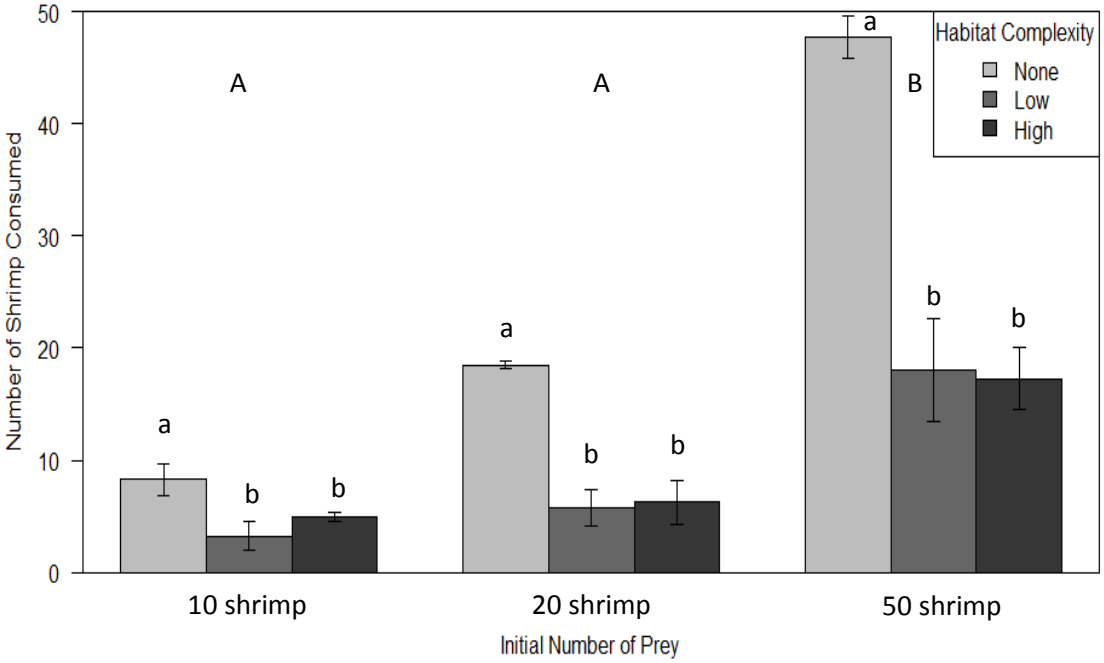

Figure 3: **Number of shrimp consumed by complexity and prey density.** Vertical bars represent the mean number of shrimp eaten (± 1 standard error) from the n=4 trials. Two-way ANOVA revealed that oyster reef complexity, and prey density, had significant effects on the number of shrimp consumed ($p<0.0001$). Significant differences are indicated by different letters. Upper case letters indicate significant differences between prey-density treatments, and lower case letters indicate differences between habitat complexity treatments.

THESIS CONCLUSIONS

The objectives of this study were to quantify the value of restored oyster reefs in the lower Chesapeake as both habitat and foraging grounds, and determine what environmental and structural parameters affect that value. Oyster reef habitat has been declining worldwide and in the Chesapeake, and a substantial amount of financial and technical resources having recently gone to restoring this habitat. Quantifying the value of these habitats for both transient fish and reef organisms is important to help managers to justify continued restoration efforts, and guide managers when making decisions about where and how best to restore oyster reefs in the Bay.

As shown in Chapter 1, restored oyster reefs in Chesapeake Bay supported diverse and abundant macrofaunal communities, which differed across the salinity gradient. Reef rugosity and salinity were significant positive factors predicting diversity, while salinity was a significant negative factor predicting macrofaunal abundance. Oyster density was a significant positive factor predicting mud crab, polychaete, and mussel densities, rugosity was also a significant positive factor predicting mud crab and mussel densities, while total oyster volume was a significant positive factor predicting fish density. Oyster density and rugosity were significant positive predictors of macrofaunal biomass. The positive relationship between reef complexity (rugosity, oyster density, and total oyster volume) and the macrofaunal diversity, abundance, and biomass, is consistent with previous studies conducted in different systems, and is attributed to the fact that structured habitats provide refuge from predation in for forms of nooks and crannies which interfere with predator mobility and visibility.

In Chapter 1, densities of several taxa increased with increasing structural complexity of the reef habitat. Chapter 2 was conducted to determine how the increased prey density observed in more-complex reef habitats might affect the value of complex oyster reefs as foraging grounds for transient predatory fish. This was done by conducting a controlled laboratory mesocosm experiment, with striped bass as the predator and grass shrimp as prey. Three levels of habitat complexity (none, oyster shell halves (low complexity), and oyster clumps (high complexity)) were crossed with three prey densities (low (10 shrimp), medium (20 shrimp) and high (50 shrimp)). Consumption of shrimp by the striped bass, both in terms of proportion and numbers consumed, was significantly reduced in the presence of oyster shell material (either low or high complexity), but did not vary between the high- and low-complexity treatments. Prey density did not have an effect on the proportion of prey consumed, but the striped bass were able to eat more individual shrimp as prey density increased, even in the high-complexity treatments.

My results from Chapter 1 and Chapter 2 highlight the important role that restored oyster reefs play in providing both habitat for benthic organisms, and rich foraging grounds for transient predators in the Chesapeake Bay. Restoration efforts should be furthered to ensure the continued presence of this diverse habitat in the Bay ecosystem. Future efforts should take into account both the location and design of restoration reefs, as both salinity and structural complexity were shown to affect macrofaunal diversity, abundance, and biomass of resident organisms.

VITA

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Born on July 18th, 1991, in Berwyn, PA, a suburb of Philadelphia, and graduated from Conestoga High School in 2009. She graduated *summa cum laude* from Tufts University, outside of Boston, with a Bachelor of Science in Biology and Environmental Science in 2013. Prior to graduating from Tufts, she conducted an independent project while studying abroad in Ecuador, evaluating the success of an artificial nest-box program in la Reserva Tapichalaca in southeast Ecuador. She enrolled in the Master of Science program at the Virginia Institute of Marine Science, The College of William and Mary, School of Marine Science, in fall 2013 with Dr. Rochelle Seitz.