Effects of Shoreline Development and Oyster Reefs on Benthic Communities in Lynnhaven, Virginia

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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DEDICATION

This thesis is dedicated to my grandfather, Charles Robert Peters, who would take me fishing and never make me put the worm on the hook. He was a great man, and a wonderful grandpa, who always believed that I could do anything I put my mind to. I miss him and love him very much.

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ABSTRACT

Shoreline hardening and construction of restoration oyster reefs are occurring at rapid rates throughout Chesapeake Bay and little research has been conducted to determine whether installment of a hardened shoreline and oyster reef placement has an effect on the surrounding benthic infaunal communities. I investigated the effects of shoreline development and oyster reefs on benthic communities in Lynnhaven, Virginia.

Throughout Lynnhaven, I determined the effects of shoreline type (natural marsh, oyster reef, rip-rap and bulkhead), sediment grain size, Total Organic Carbon/Total Nitrogen (TOC/TN) of the sediment, and predation (caging study) on density, biomass, and diversity of benthic infauna. An information-theoretic approach using Akaike's Information Criterion (AIC) was used. Of the variables measured, shoreline type was the best predictor of benthic infaunal density (highest density at oyster reefs and lowest at bulkheads), while sediment composition (grain size and TOC/TN) and predators were the best predictors of biomass and diversity. Lynnhaven is a polyhaline, shallow, semi-enclosed, natural marsh-dominated system with high overall productivity, which could be masking any small-scale disturbances due to shoreline hardening at the sites.

A Before-After-Control-Impact (BACI) study was completed at two sites (Eastern Branch and Linkhorn Bay) in Lynnhaven to examine the benthos before and after placement of oyster reefs. Replicate samples for benthic infauna, sediment grain size, and sediment TOC/TN were taken before and one year after reef placement. Based on the AIC analysis, oyster reefs had a positive effect on infaunal density at the Linkhorn Bay site after one year, mainly attributed to an influx of the bivalve *Gemma gemma*. The density increase occurred even with a decrease in polychaete density. There was no change in infaunal biomass or diversity at this site. At the Eastern Branch site, there was no effect of oyster reefs on density, biomass, or diversity.

To characterize the benthos prior to reef placement, benthic samples were collected at two sites (Eastern Branch and Linkhorn Bay) in Lynnhaven. Four reef types (oyster shell, rip-rap, concrete modules, and reef ball) were deployed at both sites. Oyster production values for existing oyster reefs were used to estimate expected oyster production on each reef type. Biomass estimates and published P:B ratios for each taxa were used to calculate secondary production for benthic infauna and oysters. Lost benthic production due to each reef type at both sites was compared to estimated oyster production on each reef type to determine if each reef compensated for benthic production lost by placing the reefs on top of the benthos. Oyster production on oyster shell and reef ball reefs compensated for benthic production lost due to placement of the reefs at both sites. Oyster productivity on rip-rap and concrete module reefs did not compensate for lost benthic production at the highly productive Eastern Branch site, and barely compensated for lost benthos at the lower productivity Linkhorn Bay site.

The preservation of natural marsh and use of the proper types of oyster reefs could help maintain the high productivity of both the benthic community and the Lynnhaven system itself.

Effects of Shoreline Development and Oyster Reefs on Benthic Communities in Lynnhaven, Virginia

GENERAL INTRODUCTION

In this thesis I investigated the effects of shoreline development and oyster reefs on associated benthic communities using three separate studies in Lynnhaven, Virginia. My objective in Chapter 1 was to determine the effects of shoreline type (natural marsh, oyster reef, rip-rap and bulkhead), sediment grain size, sedimentary Total Organic Carbon (TOC) and Total Nitrogen (TN), and predation on the density, biomass, and diversity of benthic infauna. This was accomplished through the use of benthic suction sampling and cores, along with predator trawls, and a predator-exclusion caging study. An information theoretic approach was used and allowed me to determine what parameters best predicted the differences observed in the benthic community among the sites in Lynnhaven.

Chapter 2 examined the effects that placement of oyster reefs had on the composition of the surrounding benthic infaunal community at two sites within Lynnhaven. A Before-After, Control-Impact (BACI) sampling design was used at each site to determine if there would be a positive, negative, or negligible effect of the oyster reefs on the surrounding benthic infaunal density, biomass, and diversity, or a change in the sedimentary TOC/TN and grain size of the sediment after one year.

In Chapter 3, I determined if estimated oyster production on four types of restoration oyster reefs would compensate for the amount of benthic production lost by placing the oyster reefs on top of the benthos at two sites in Lynnhaven. I used actual biomass values for benthic infauna at the two sites and estimated oyster production values along with published production to biomass ratios (P:B) for each taxa to calculate and compare secondary production of the benthic infauna and oysters.

Shoreline type was the best predictor of benthic infaunal density in Lynnhaven with oyster reef shorelines having the highest associated benthic densities and bulkhead shorelines having the lowest. Oyster reefs had a slightly positive to negligible effect on the surrounding infauna and sediment and oyster production on certain types of oyster reefs compensated for the lost benthic production due to placing the reefs on top of the benthos. Given these results, landowners in Lynnhaven should be encouraged to protect their shoreline from erosion through the use of living shorelines (i.e., natural marsh) including oyster reefs, since these habitats can have positive effects on adjacent benthos.

CHAPTER 1

Effects of Shoreline Development on Benthic Communities in Lynnhaven, Virginia

ABSTRACT

Coastlines in Chesapeake Bay are being altered through the process of shoreline hardening and the placement of oyster reefs in intertidal areas. These alterations to the shoreline could have a direct effect on the adjacent benthic infaunal communities. A study was completed throughout Lynnhaven, Virginia, to determine the effects of shoreline type (natural marsh, oyster reef, rip-rap and bulkhead), sediment grain size, sediment Total Organic Carbon (TOC) and Total Nitrogen (TN), and predation on the density, biomass, and diversity of benthic infauna. An information-theoretic approach using Akaike's Information Criterion (AIC) was used to determine a model that best fit the data. Based on the models, shoreline type was the best predictor of benthic infaunal density (oyster reef highest benthic density and bulkhead the lowest), while sediment composition (grain size and TOC/TN of the sediment) and predators were the best predictors of biomass and diversity of the variables measured. I believe this difference in the best predictors of the response variables was due to the ecological features of the Lynnhaven system. Lynnhaven is a unique system with many qualities (i.e., large percentage of natural marsh shoreline) that cause high overall benthic density, biomass, and productivity, which is masking small-scale disturbances due to shoreline hardening. This study helped support the use of oyster reefs as an alternative to hardened shoreline since the highest benthic density was associated with oyster reef shorelines. However, conversion of the shoreline throughout Lynnhaven to a hardened shoreline may result in an overall decrease in the benthic community. A balance between natural and hardened shorelines must be maintained to keep highly productive systems such as Lynnhaven from becoming negatively affected by anthropogenic influences.

INTRODUCTION

Vital natural marsh habitats are being altered or destroyed daily through the anthropogenic process of shoreline hardening. De Jonge et al. (2002) projected that, by 2012, over 75% of the United States' population will live within 75 kilometers of the coast. The Chesapeake Bay watershed alone has experienced a tripling in its population in the last century and this population continues to grow, with hundreds of new people moving into the watershed each day (Boesch & Greer 2003). As people buy land and build homes along the coast, they 'harden' the shoreline to prevent loss of their land to the sea. Shoreline 'hardening' consists of the removal of natural marsh and placement of rip-rap (large rocks) or bulkhead (a seawall constructed of metal, wood, concrete, or plastic) along a shoreline to stabilize it against erosion. According to the Virginia Coastal Zone Management Program, from 1993-2002 approximately 230 miles of new, hard erosion protection measures were installed in Virginia alone. Oyster reefs are also being used for erosion control by placing oyster shells along the shores as "living shorelines". Shoreline alteration (e.g., shoreline hardening and oyster reef placement) is occurring at a rapid rate and this study investigates whether the loss of natural marsh and installment of an altered shoreline has an effect on the associated benthic infaunal community.

Natural Marsh and Benthos Relationships

There are thousands of miles of tidal marsh habitat within Chesapeake Bay, and adjacent to these shorelines are important infaunal communities located in the shallow sub-tidal sand and mud habitats (Seitz et al. 2006). These ecosystems provide critical functions that are important to the health of the Bay. Tidal marshes are capable of trapping and assimilating nutrients and, thus, become major nutrient sinks, which help buffer against the effects of eutrophication (Kemp et al. 2005). Natural marsh shoreline can act as an important food source for deposit-feeding infauna, providing carbon from marsh materials (Currin et al. 1995, Peterson et al., in prep). These nearshore habitats also act as nurseries and "Effective Juvenile Habitat" (Dahlgren et al. 2006) by providing food and protection from predation for ecologically and commercially important juvenile fishes and decapod crustaceans (Hines & Ruiz 1995, Beck et al. 2001, Whaley & Minello 2002, Minello et al. 2003, Heck et al. 2003). Natural marshes also can stabilize surrounding sediments and buffer the shoreline against erosion by dissipating incoming wave energy. These nearshore areas are particularly susceptible to anthropogenic stressors because they serve as an interface between terrestrial and open-water environments (Goforth & Carman 2005).

Infaunal communities serve critical ecosystem functions such as nutrient cycling (Diaz & Schaffner 1990) and provide essential food for predators including the blue crab *Callinectes sapidus* and benthic feeding fish such as spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus* (Virnstein 1977, Diaz & Schaffner 1990, Hines et al. 1990). For example, clams can compose up to 50% of the blue crab diet (Hines et al. 1990). Benthic communities can be driven by bottom-up (i.e., sediment grain size, salinity, recruitment, food availability) or top-down controls (i.e., predators) (Sanders 1958, Virnstein 1977, Posey et al. 1995, Seitz & Lipcius 2001). Estimates of the benthic community are often used to indicate environmental health because benthic organisms are relatively sedentary, have relatively long life spans, and are commercially and ecologically important (Dauer 1993).

Large-Scale Anthropogenic Effects

Large-scale urbanization in a watershed can negatively affect water bodies. Watersheds associated with high urban land use can be characterized by aquatic biotic communities with lower species diversity, less trophic complexity, altered food webs, altered community composition, and reduced habitat diversity (Dauer et al. 2000, Holland et al. 2004, Bremner et al. 2005, Kemp et al. 2005, King et al. 2005, Thrush et al. 2005). Distribution of biota in estuaries is influenced by both natural and anthropogenic factors. For example, blue crabs within Chesapeake Bay were found in low abundances in subestuaries with predominantly developed and agricultural land use (King et al. 2005). Increased urbanization within the Chesapeake Bay watershed has a negative effect on the benthic community and this effect can be seen when as little as 12% of the watershed is developed (Dauer et al. 2000, Bilkovic et al. 2006). Shoreline development along freshwater lakes and streams is associated with areas of high urbanization and leads to low habitat heterogeneity that has a negative impact on fish abundance and diversity (Eadie & Keast 1984, Scheuerell & Schindler 2004, Goforth & Carman 2005).

Small-Scale Anthropogenic Effects

Smaller-spatial-scale studies completed for various aquatic species show a negative effect of altered shorelines when compared with natural shorelines. However, little work has examined the direct effects of shoreline development on adjacent infaunal benthic communities. Fish and crustaceans had decreased abundance and diversity associated with altered shorelines when compared to natural marsh (Jennings et al. 1999, Hendon et al. 2000, Peterson et al. 2000, Carroll 2002, Seitz et al. 2006). In addition, shoreline armoring decreases abundance and taxa richness of benthic infauna invertebrate and insect assemblages in the supratidal zone of Puget Sound (Sobocinski 2003). Among sites within seven German lowland lakes, eulittoral species richness and abundance was lowest associated with bulkheads, but communities adjacent to rip-rap did not differ significantly from those adjacent to natural shorelines, and all but one collected littoral macroinvertebrate group decreased with increasing proportion of shoreline development (Brauns et al. 2007). Macrozoobenthic richness, diversity, and density were low associated with artificial interfaces (i.e., bulkhead) when compared with natural interfaces in Lake Geneva, Switzerland (Bänziger 1995). In Korea, construction of a seawall caused the sediment grain size adjacent to the wall to become significantly coarser, which resulted in a shift in dominance of abundant species from deposit- to filter-feeders (Ahn & Choi 1998). Along the east coast of the United States, species richness, diversity, and biomass of benthic infauna were lowest immediately adjacent to wooden bulkhead as compared to un-bulkheaded reference sites due to chemicals leaching from the wooden bulkhead (Weis et al. 1998). Nekton assemblages in the James River system of Chesapeake Bay were more diverse along natural marsh and rip-rap shorelines as opposed to bulkhead shorelines (Bilkovic & Roggero 2008). Abundance and diversity of both infauna and predators (i.e., blue crabs), in the York and Lafayette River systems of Chesapeake Bay, were decreased in association with bulkhead as compared to natural marsh or rip-rap shorelines (Seitz et al. 2006).

A variety of patterns have been discovered associated with benthic infaunal communities surrounding artificial reefs. Increased benthic abundances near reef edges (Davis et al. 1982), decreased benthic abundances near reef edges (Ambrose & Anderson 1990), as well as no change in the benthic community (Langlois et al. 2006) have been associated with reefs. Numerous physical and biological processes have been proposed to explain these benthic changes, and therefore, it is hard to predict the effect of an oyster reef on the adjacent benthos.

The Study

I chose to do this study in a highly developed, shallow system within Chesapeake Bay because previous studies have not focused on the effects shoreline development would have in this type of system. This study took place in the Lynnhaven River system, the southern-most system in Chesapeake Bay, located within the City of Virginia Beach, Virginia. Lynnhaven consists of four main water bodies (Broad Bay, Linkhorn Bay, the Eastern Branch and the Western Branch of the Lynnhaven River), is ~67 square miles in area, and has a total of ~150 miles of shoreline. This system was chosen because the Lynnhaven watershed is highly altered with ~ 72% of the watershed developed as residential, commercial, or industrial property. Low benthic density and diversity in Linkhorn Bay is believed to result from urban development and urbanization of the shoreline (Tourtellotte & Dauer 1983).

The objective of this study is to determine the relative influence of several variables on the density, biomass, and diversity of benthic infaunal organisms (e.g., bivalves and polychaetes) associated with four shoreline types (natural marsh, oyster shell reef, rip-rap, and bulkhead) in Lynnhaven, Virginia. I included oyster reefs as a shoreline type and examined the effects of oyster reefs on the benthic community as compared to the other three shoreline types. Main drivers of benthic density, biomass, and diversity in Chesapeake Bay, besides shoreline type, are sediment composition (i.e., grain size and Total Organic Carbon [TOC] and Total Nitrogen [TN]) (Boesch 1977, Snelgrove & Butman 1994), and number of predators (Virnstein 1977, Dauer et al. 1982, Hines et al. 1990), which were also measured at each site to determine which of these variables had a greater affect on the benthos. A predator-exclusion caging study was conducted at a subset of sites to examine changes in predation across shoreline types (Virnstein 1977, Holland et al. 1980, Dauer et al. 1982b, Seitz 1996).

MATERIALS AND METHODS

Site Selection

Twenty-nine shoreline sites were randomly selected throughout the Lynnhaven system (Fig. 1). The shoreline types were 1) natural marsh, 2) oyster shell reef, 3) rip-rap, or 4) bulkhead. All sampling sites were required to meet the following criteria prior to sampling: (1) the shoreline must consist of at least 50 consecutive meters (m) of a shoreline type, (2) the shoreline must consist of only one shoreline type (i.e., bulkhead with natural marsh along the water line was not sampled), (3) bulkheads could not be wooden (due to the potential for chemical leaching; Weis et al. 1998), and (4) water depth could not exceed ~1.2 m (maximum depth allowable to complete suction sampling). Sites that met the criteria were each assigned a number and a random-number generator was used to select eight replicates for each of three shoreline types (natural marsh, rip-rap, and bulkhead shorelines; oyster reef described below). Eight replicates of each site were found to be a sufficient number to observe an effect between shoreline types (Seitz et al. 2006). Five intertidal restored oyster shell reefs were sampled since these were the only reefs in the system that met the criteria.

Physical Parameters

At each site, water quality was assessed by measuring physical and chemical variables including water temperature, salinity, and dissolved oxygen (DO) using a YSI meter. A benthic habitat assessment also was performed at each site by determining sediment grain size using standard wet sieving and pipetting (Folk 1974) and by completing a Carbon, Hydrogen, Nitrogen (CHN) analysis of the sediment. Sediment grain-size analysis was completed for each of the sites and was reported in percent sand/gravel content of the sample. These samples were taken in association with benthic macrofauna samples (described below) using a 2.5-centimeter (cm)-diameter surface-sediment core.

Benthic Sampling

All samples for the shoreline-development study were collected during July and August 2006. Benthic samples were taken once at a randomly selected location at each of the 29 shoreline sites. Samples were taken ~4 m from the edge of the shoreline. Benthic samples included a suction sample and a small core sample. A suction apparatus was used to collect larger benthic organisms, which involved the removal of sediment within a cylinder of 0.11 m^2 surface area to ~40 cm depth (Eggleston et al. 1992). Sampling to this depth in the sediment ensures an accurate estimation of densities of deep-dwelling, large bivalves that are sparsely distributed (Hines & Comtois 1985). The sediment and infauna were collected in a 1-millimeter (mm) mesh bag and sieved on a 1-mm mesh screen. A 10-cm diameter core, used to remove sediment to a 15-cm depth, was taken in association with the suction sample. This sample was sieved through a 500-micron sieve to collect smaller organisms in the community. Both the suction samples and small core samples were taken back to the lab and frozen until they were processed. The 10-cm core samples were not processed for this project; however, they can be used in the future to further examine patterns observed from the suction samples. Suction samples were sorted and the animals removed and identified to the lowest possible taxonomic level (usually species). Shell length of each bivalve from each sample was measured. Three of the samples were sub-sampled due to the large size of the sample. Each sample was homogenized and a random fraction was taken (sub-sample) and sorted. The Shannon-Wiener diversity index (H') (Krebs 1989, Gray 2000), which integrates species richness and evenness, was calculated to obtain diversity using Primer v.6.1.6. software (Clarke & Warwick 2001).

Biomass estimates for all organisms were calculated using ash-free dry weight (AFDW). Polychaetes, crustaceans, and shucked bivalves were dried to a constant weight and ashed in a muffle furnace at 550°C for six hours to obtain ash weight. Regressions of shell length (SL) to AFDW were used for abundant bivalve species (*Macoma balthica* and *Tagelus plebeius*) to estimate biomass from size. Clams were selected throughout the entire range of sizes collected (27 clams ranging from 7.8 to 36.5 mm SL for *M. balthica* and 25 clams ranging from 4.2 to 75.2 mm SL for *T. plebeius*) for input into the regression. The best-fit equations were the following single, three-parameter models:

$$\textit{M. balthica}: \text{AFDW} = -0.0861 + 0.0427e^{0.0651*\text{SL}} \quad (r^2 = 0.97)$$

$$\textit{T. plebeius}: \text{AFDW} = -0.3222 + 0.2237e^{0.0261*\text{SL}} \quad (r^2 = 0.93)$$

Mercenaria mercenaria were collected in both the shoreline-development study and the caging study; however, they were not included in the density, biomass, or diversity calculations. This was because *M. mercenaria* were not appropriately sampled via our sampling method (suction sampling of 0.11 m^2 surface area) because of the sparse distribution of the adult clams; past stock studies of *M. mercenaria* have used patent tongs that sample one square meter of bottom to adequately determine the density and distribution of the species (Mann et al. 2005).

Predator Sampling

A 2 m-wide, 4.9 m-long otter-trawl net, with a 3/8 inch inner mesh size, was used to sample along 50 m of shoreline at each of the 29 shoreline sites in August 2006. The trawl net was pulled behind the boat at a constant speed at each site. Predators were identified to species and measured to the nearest millimeter (total length) and released. This sampling was completed in accordance with an approved Institutional Animal Care and Use Committee (IACUC) permit (#IACUC-2006-10-31-4471).

Caging Study

To determine the amount of predation occurring on the benthos at each shoreline type, four of the eight sites sampled for each of the three shoreline types along with four of the five oyster shell reef sites were used in the predator-exclusion caging study (16 sites total). The sites with the highest densities of polychaetes or bivalves, based on a cursory count obtained from the suction sample, were used in the caging study. At each site, one 50 cm x 50 cm plot of sediment was caged ~4 m from the shoreline near the location of the initial suction sample. Cages were constructed of a 1-cm galvanized hardware mesh. The cages were 8 cm in depth and were pushed 4 cm into the sediment to ensure solid placement while minimizing the obstruction of water flow. The cages remained in place for approximately four months (July/August-November 2006), at which time the cages were removed and at each site the area within the cage (“caged” sample) and an area approximately one meter from the cage (“adjacent” sample) were sampled by suction with the 0.11 m^2 cylinder to a depth of ~40 cm (as described above). Samples were taken back to the lab and sorted; however, only bivalves were identified and measured for this study. Caged versus adjacent samples were compared to determine the amount of predation that occurred at each site over the time frame (Virnstein 1977).

Statistical Analyses

Shoreline type (natural marsh, oyster reef, rip-rap, and bulkhead), TOC and TN of the sediment, sediment grain size, and number of predators were hypothesized to have a potential effect on the response variables density, biomass, and diversity (H') of the benthos in Lynnhaven and were used as variables to establish a set of seven models to describe these effects. Each model represented a different combination of variables (Table 1) that could describe differences observed in the response variables among the sites. Grain size and TOC/TN of the sediment were highly inversely correlated (Fig. 2) and were therefore combined into one variable (Sediment Variable) to be used in the models. All variables were categorical, except number of predators, which was continuous. The parameter estimates for the models were derived using least squares regression analysis. From this analysis, coefficients of differences and associated confidences in the parameters were estimated. An information-theoretic approach using Akaike's Information Criterion (AIC) with a second-order bias correction (AICc) for low sample size was used to determine the best model from the model set for each of the three response variables (Burnham & Anderson 2002, Anderson 2008). AICc values were calculated for each model using the following equation:

$$\mathrm{AICc} = \mathrm{n} * \ln(\sigma^2) + 2\mathrm{K}\left[\frac{\mathrm{n}}{\mathrm{n}-\mathrm{K}-1}\right]$$

where ln (σ^2) is equal to the residual sum of squares (RSS) divided by the sample size (n) and K is the number of estimable parameters in a model. To rank the different models, ΔAICc was calculated for each model as follows:

$$\Delta \mathrm{AICc} = \mathrm{AICc}_i - \mathrm{AICc}_{min}$$

where AICc_i are the values for each of the i models and AICc_{min} is the lowest AICc value of all the models. The best model has a ΔAICc = 0. Model probabilities or weights (w_i) for each model estimate the probability that a particular model is the best model given the data and the model set. Model probabilities are calculated as:

$$\mathbf{w_1} = \frac{\exp\left(-\frac{1}{2}\Delta i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta r\right)}$$

Models with a probability ≥ 0.10 in a model set were also considered likely models along with the best model. If a parameter was included in more than one of the likely models it was considered a good predictor for that response variable and my confidence in the parameter was determined.

For the caging study, a multiple regression approach was used to determine the difference in predation of adult bivalves for the four shoreline types. The difference in adult bivalve density and biomass between the cage and adjacent sample (adjacent sample subtracted from the cage sample) at each site was used in the analysis. Juvenile bivalves were removed from the analysis because a large recruitment event occurred during the experiment and I did not want to measure the effects of a cage structure on recruitment (Virnstein 1977, Hines et al. 1990, Dauer et al. 1982b). Patterns for total bivalves, however, reflected those of adults ($r^2 = 81.3\%$).

RESULTS

Physical Parameters

Temperatures of the sites ranged from 26.1°C to 32.0°C, salinities from 20.9 to 23.6, and DO from 4.1 mg l^{-1} to 7.7 mg l^{-1}. For the sediment grain-size analysis, 20 sites were classified as sand with an average sand/gravel content of 95.53% (standard error [SE] = ± 0.54), eight were classified as mud with an average sand/gravel content of 5.07% (SE = ± 1.96), and one was classified as sandy mud (54.26% sand/gravel content). The TOC and TN of the sediment were inversely correlated with percent sand/gravel content of the sediment samples (Fig. 2). Sand samples had an average TOC value of 0.17% (SE = ± 0.05) TOC of the dry sediment sample, while mud samples averaged 1.70% (SE = ± 0.06). Total Nitrogen in the sand samples averaged 0.02% (SE = ± 0.004) TN of the dry sediment sample, where as mud averaged 0.16% (SE = ± 0.007). The sandy mud sample's TOC and TN values fell within the same range as the mud samples.

Benthic Sampling

I collected a total of 36 benthic infaunal species at the 29 sites throughout the Lynnhaven system (Table 2). Nine species of bivalves were collected in the shoreline development study, with *Aligena elevata* (47% of total bivalves), *Macoma balthica* (22%), and *Tagelus plebeius* (10%) being the numerically dominant species. In the caging study, nine species of bivalves also were collected with *A. elevata* (46%), *M. mitchelli* (18%), *M. balthica* (12%), and *T. plebeius* (12%) being the numerically dominant species. Seventeen species of polychaetes, two isopod species, and five species of amphipods were also collected in the shoreline-development study. Numerically dominant polychaetes in the shoreline-development study were *Clymenella torquata* (34% of the total polychaetes), *Neanthes succinea* (23%), *Leitoscoloplos* spp. (14%), and Capitellidae (12%).

In the shoreline development study, bivalves accounted for 80% of the overall biomass with *T. plebeius* contributing 59% of the total bivalve biomass, *M. balthica* 27%, and *Ensis directus* 13%. Polychaetes accounted for 19% of the overall benthic biomass. Bivalves that contributed most to the biomass in the caging study were *T. plebeius* (64% of the total bivalve biomass) and *M. balthica* (30%). None of the above biomass totals included *Mercenaria mercenaria* due to inefficient sampling of this bivalve (see Materials and Methods).

Predator Sampling

Fifteen species of fish and crabs were collected in the trawls taken at the 29 sites (Table 3). The dominant benthic predators were the blue crab *Callinectes sapidus* and spot *Leiostomus xanthurus*. Blue crabs accounted for 48% and spot accounted for 20% of the total predators collected.

Statistical Analyses

Density

Shoreline type influences benthic infaunal density (Fig. 3a). This was supported by the AICc model selection for density (Table 4), which indicated that the model including the shoreline variables only (g_4) was the strongest model with probability = 0.53 (adjusted r^2 = 26.4%). The oyster reef shoreline had the highest associated benthic density, followed by rip-rap, natural marsh, and bulkhead, respectively. I had high confidence (~98%) that oyster reef shorelines had twice the benthic infaunal density adjacent to them when compared with natural marsh shorelines (natural marsh: mean = 41.25, SE = 10.03 [coefficient of difference = 43.95, SE = 16.17]). However, my confidence was low (60% - 65%) that there was a difference in density between the natural marsh, rip-rap (coefficient of difference = 12.87, SE = 14.18), and bulkhead (coefficient of difference = -12.37, SE = 14.18) shorelines due to high variability. Model g_3, which included shoreline parameters as well as number of predators, was also a likely model (probability = 0.19); however, I had low confidence in the predator parameter (coefficient of difference = 1.68, SE = 1.70) due to high variability. Approximately the same number of predators occurred across the four shoreline types (Fig. 3b). Finally, model g_2, including shoreline type and the sediment variable, was also a likely model with probability = 0.11; however, I had low confidence in the sediment parameter as well (coefficient of difference = 3.68, SE = 13.44) due to high variability. I can therefore conclude that the shoreline types are the best variables to use to predict benthic infaunal density since the shoreline variables were included in all three likely models.

<u>Biomass</u>

Shoreline type did not influence biomass of benthic infauna substantially (Fig. 3c). This was supported by the AICc model for biomass (Table 5), where the strongest model included the sediment variable only (g_6) with probability = 0.40 (adjusted r^2 = 0%). Sand sites had higher benthic biomass (mean = 1.73, SE = 0.44) when compared to mud sites (mean = 1.16, SE = 0.66). While I had high confidence (90% - 95%) in the means for both sand and mud sites, I had low confidence (~55%) that there was a difference between the two types of sites (coefficient of difference = 0.57, SE = 0.79) due to high variability. Another strong model was model g_7, which included number of predators only, with probability = 0.31. I had low confidence (<50%) in the predator parameter for this model (coefficient of difference = -0.02, SE = 0.12). In addition, both models g_4 (shoreline parameters only [probability = 0.13]) and g_5 (sediment variable and number of predators [probability = 0.10]) could also be likely models. Shoreline type was not considered a good predictor since it only occurred in one of the four top models. To predict biomass of the benthic infauna, the sediment variable and number of predators were the best predictors since at least one of the variables occurred in three of the four top models, though I had low confidence in the predator variable.

Diversity

Shoreline type did not influence Shannon-Wiener diversity (H') of the benthic infauna (Fig. 3d). This was supported by the AICc model selection for diversity (Table 6). There were two outliers (one outlier for bulkhead, and one for oyster reef) in the data that were removed before analysis. The model trend for diversity followed closely with that of biomass, with the strongest model including only the sediment variable (g_6) with probability = 0.59 (adjusted r^2 = 12.9%). I had high confidence (95%) in the mean diversity for both sand (mean = 1.66, SE = 0.08) and mud (mean = 1.35, SE = 0.12) sites, and I had high confidence (96%) that sand sites had higher benthic diversity than mud sites (coefficient of difference = 0.31, SE = 0.14). Model g_7, including number of predators only with probability = 0.19, was also a likely model. I had high confidence

(~85%) that the number of predators was affecting the diversity of the benthos at each site (coefficient of difference = -0.03, SE = 0.02), though the effect was quite small. Model g_5, including the sediment variable and number of predators with probability = 0.18, was also a likely model, though, while I still had high confidence (~85%) in the sediment variable (coefficient of difference = 0.26, SE = 0.16), I had low confidence (<50%) in the predator variable (coefficient of difference = -0.01, SE = 0.02) due to high variability. Benthic infaunal diversity (H') in Lynnhaven can thus be best predicted using the sediment variable followed by the number of predators though the predictive power of the model is low (adjusted r^2 = 12.9%).

Caging Study

In analyzing the results from the caging study, I wanted to determine if shoreline type had an effect on predation by looking at the difference between the cage and adjacent samples for adult bivalve density and biomass. There was an increase in adult bivalve density inside the cage versus adjacent to the cage for each shoreline type. Predation had the largest effect on density at the rip-rap shoreline followed by oyster reef, bulkhead, and natural marsh shorelines, respectively. However, I had low confidence (~50% - 70%) that the amount of predation was different between natural marsh (mean = 2.00, SE = 8.09), rip-rap (coefficient of difference = 12.75, SE = 11.44), oyster reef (coefficient of difference = 10.75, SE = 11.44), and bulkhead (coefficient of difference = 9.75, SE = 11.44) shorelines.

There was an increase in adult bivalve biomass inside the cages versus adjacent to the cages for all shoreline types (Fig. 4). Predation had the largest effect on biomass at the oyster reef shoreline followed by bulkhead, rip-rap, and natural marsh shorelines, respectively. I had high confidence (~85%) that there was greater predation at the oyster reef shorelines than the natural marsh shorelines (natural marsh: mean = 0.03, SE = 0.53 [coefficient of difference = 1.18, SE = 0.75]). However, I had low confidence (<50%) that the amount of predation was different between natural marsh, bulkhead (coefficient of difference = 0.49, SE = 0.75), and rip-rap (coefficient of difference = 0.44, SE = 0.75) shorelines.

DISCUSSION

While shoreline development influences the density of the benthic community, sediment composition (grain size and TOC/TN of the sediment) and predators are better predictors of the biomass and diversity of the benthos. Physical variables (i.e., temperature, salinity, and DO) remained virtually constant across the 29 sites throughout Lynnhaven and therefore no further analysis was conducted on this data.

The dominant bivalve species in Lynnhaven, *Macoma* spp. and *Tagelus plebeius*, not only contributed to the density of the benthos, but also contributed the most to the biomass found at each site. This high contribution of bivalves to numbers and biomass of the infauna has been seen in other areas of Chesapeake Bay (Hines & Comtois 1985, Seitz et al. 2006). The bivalve *Aligena elevata* contributed significantly to the overall density; however, this small bivalve (≤ 6.1 mm) did not play a significant part in the overall biomass. *Aligena elevata* lives commensally with *Clymenella torquata*, the numerically dominant polychaete in the study (Sanders et al. 1962, Gage 1968). High densities and numerous species of polychaetes also were found and contributed ~20% of the overall biomass. Polychaete biomass contribution at each site varied from 1.5% to 100% of the total biomass. This high contribution of the polychaetes to the overall biomass has been recorded in other areas of Chesapeake Bay, especially in polyhaline areas (Boesch 1977, Dauer et al. 1987, Diaz & Schaffner 1990). Benthic infaunal species found in my study are similar to those found in past studies of Lynnhaven (Dauer et al. 1979, Dauer et al. 1982a, Dauer et al. 1982b, Tourtellotte & Dauer 1983) and are common in other shallow-water systems found throughout Chesapeake Bay (Holland 1985, Dauer et al. 1987, Diaz & Schaffner 1990, Seitz et al. 2006). The top benthic predators in the system were spot and blue crab, both of which are dominant benthic predators throughout Chesapeake Bay (Virnstein 1977, Hines et al. 1990).

While the AICc analysis was completed for density, biomass, and diversity of the benthos, the adjusted r^2 values for the regressions of even the best models were low, implying that the models created did not predict the response variables well. This could mean that other variables, not measured as a part of this study, would be better predictors.

Benthic Density

Based on the AICc analysis, of the variables measured, shoreline type was the best predictor of benthic infaunal density in Lynnhaven. Of the total benthic infaunal density in this study, polychaetes made up anywhere from 48% to 100% of the total density at a site. Oyster reefs had the highest mean density of adjacent benthos, while rip-rap had a higher density than natural marsh shoreline, but natural marsh had a higher benthic density than bulkhead shoreline. Due to high variability, in all shoreline types except natural marsh, the benthic densities associated with natural marsh, rip-rap, and bulkhead shorelines were comparable, but densities at bulkhead shorelines were the lowest, as has been seen in previous studies (Bänziger 1995, Seitz et al. 2006, Brauns et al. 2007, Seitz & Lawless 2008).

Increased densities at the oyster-reef sites may be an artifact of the dominant sediment at those sites. The five oyster-reef sites and seven of the eight rip-rap sites were sand sites, while only three natural marsh sites and five bulkhead sites were sand. Sand sediment tends to support higher benthic densities and biomass than mud (Boesch 1973, Boesch 1977, Dauer et al. 1979, Diaz & Schaffner 1990, Ricciardi & Bourget 1999, Seitz et al. 2006); therefore, mean densities of sand-dominated oyster-reef and rip-rap habitats would be expected to be higher than those of the natural marsh and bulkhead habitats that included more mud sites. The distribution of sand and mud sites among the different shoreline types was an artifact of the random sample design used to select the sites. Sediment type was not considered a priori before site selection. Additionally, all the oyster reef sites were restored oyster shell reefs, which are typically constructed in sand areas rather than mud areas to prevent sedimentation of the reefs (Lenihan 1999).

Along with shoreline type, sediment composition and number of predators were also identified as predictors of benthic density; however, these variables did not have a large effect on density due to high variability. Based on the results of the caging study, I concluded that while predation had an effect on adult bivalve density at all the shoreline types, the effect of predation on bivalve density among the shoreline types did not differ.

Shoreline development decreases the benthic infaunal density associated with hardened shorelines (Sobocinski 2003, Bilkovic et al. 2006, Seitz et al. 2006, Brauns et al. 2007, Seitz & Lawless 2008). The alteration of pristine marsh habitat via bulkheading or stabilization by rip-rap significantly reduces the relative abundance and diversity of the majority of the abundant taxa in the adjacent shallow zones (Hendon et al. 2000, Peterson et al. 2000, Seitz et al. 2006). Alteration of the shoreline could change the hydrodynamics impeding settlement of some benthic organisms (i.e., a low-energy environment may be transformed into one of moderate energy due to reflection of the waves from the bulkhead shoreline [Odum 1970, Ahn & Choi 1998]) and the input of carbon from the natural marsh to the benthos could be reduced where shorelines are hardened (Seitz & Lawless 2008).

Benthic Biomass and Diversity

Shoreline development did not have an influence on benthic infaunal biomass or diversity in Lynnhaven and both response variables were best predicted by sediment composition and predation. Unfortunately, because sediment grain size and TOC/TN of the sediment were highly correlated, these two variables could not be teased apart to determine if one was having a greater effect on the benthos than the other. Benthic infaunal distribution, abundance, and diversity are commonly associated with sediment type, as mentioned above, and also TOC/TN of the sediment (Sanders 1958, Gray 1974, Lopez & Levinton 1987, Snelgrove & Butman 1994, Seitz & Lipcius 2001).

Predation can also strongly affect the density, biomass, and diversity of the benthic infaunal community (Virnstein 1977, Eadie & Keast 1984, Diaz & Schaffner 1990, Hines et al. 1990, Seitz & Lipcius 2001, Seitz et al. 2003). Based on the caging study, I concluded that, while predation had an effect on adult bivalve biomass at all shoreline types, it had a greater effect on the biomass at the oyster-reef shorelines compared with natural marsh shorelines, but did not differ among the natural marsh, rip-rap, and bulkhead shorelines. A reason for increased predation associated with oyster reefs could be that the placement of sub-tidal (Lenihan et al. 2001) and inter-tidal (Grabowski et al. 2005) oyster reefs augmented the abundance of adult and juvenile fish and mobile crustaceans. This augmentation could be due to the reef acting as a structural refuge for benthic predators or to an increase in prey resources (Micheli & Peterson 1999). An increase of epibenthic predators on the reef could increase predation on the benthos around the reef. Higher densities of benthic infauna and predation were associated with the reefs, which could mean bottom-up control is occurring around the oyster reefs and, therefore, more predators would be attracted to these habitats (Seitz & Lipcius 2001, Seitz et al. 2003).

The Lynnhaven System

Density of the benthos was affected by shoreline type, but biomass and diversity were not. How can abundance of the benthos be affected by shoreline development, but not have an effect on biomass and diversity? I believe this is due to the bathymetry, hydrodynamics, and productivity of the Lynnhaven system. Samples collected throughout Lynnhaven had a high average density (~445 ind./m^2), biomass (~14 g/m^2), and diversity (~7 species/m^2) of the benthic community.

The Lynnhaven system is very productive for many reasons. There is no riverine input into Lynnhaven; therefore, the system from the mouth to the far reaches of each branch is entirely polyhaline (Neilson 1976). Benthic infaunal density, biomass, diversity, and productivity are higher in polyhaline regions (Remane & Schlieper 1971, Möller et al. 1985, Diaz & Schaffner 1990, Dauer 1993). The Lynnhaven system is also very shallow, with the average depth of the system at mean low water being ~2.5 m (Dauer et al. 1979). Shallow-water systems can exhibit higher density, biomass, and diversity of infaunal benthos than deeper-water systems (Seitz et al. 2003, Seitz et al. 2006). The Lynnhaven system is also semi-enclosed with only one area of major input and output of water located at the northern end of the system. This allows for a high residence time in the system that gives recruits, from within and outside the system, a substantial amount of time to settle within the system before potentially being exported (H.V. Wang, pers. comm.). Moreover, ~ 78.4% of the shoreline in Lynnhaven has natural marsh associated with it, 11.2% of the shoreline is developed with bulkhead only, and 5.2% of the shoreline is developed with only rip-rap (P.G. Ross, pers. comm.). It is hypothesized that the large percentage of unaltered natural marsh areas are subsidizing the adjacent developed shorelines with nutrients and benthic infaunal recruits. Therefore, altered shorelines (i.e., rip-rap) in the Lynnhaven system were not as negatively influenced by development as in other highly developed systems with large expanses of hardened shoreline and fewer natural marsh habitats to subsidize the developed shorelines (Schmude et al. 1998, Hendon et al. 2000, King et al. 2005, Seitz et al. 2006, Brauns et al. 2007, Seitz & Lawless 2008).

Lynnhaven is a polyhaline, shallow, semi-enclosed, natural marsh-dominated system where the benthic community is driven by bottom-up control. This serves to explain why the system has an overall high productivity and why the altered shorelines in Lynnhaven were comparable to the natural shorelines (though bulkhead had the lowest associated benthic density) and no substantial effect was seen on the biomass and diversity of the benthos. The high productivity of the Lynnhaven system appears to be masking small-scale effects of shoreline hardening on the benthos. Another study comparing fish communities within Lynnhaven also noted that extreme variability in physical and chemical features in the highly dynamic Lynnhaven system may be driving influences structuring fish communities and may obscure responses to anthropogenic impacts (Bilkovic et al. 2007).

Though shoreline development influences benthic density, sediment composition, and predators appear to be stronger drivers of benthic biomass and diversity in Lynnhaven instead of shoreline development. Additional shoreline hardening, however, could have an effect on the Lynnhaven system. The balance of estuarine ecosystems can be affected by habitat alterations from direct effects, such as habitat loss, affecting multiple species, and indirect effects, such as lowered abundances of certain trophic-link-species (i.e., benthic infauna), that would affect both lower and higher levels of the food web (Hendon et al. 2000). Odum (1970) warned that cumulative impacts and environmental alterations of the estuarine environment, such as bulkheading, may cause serious damage on a long-term basis and influence estuarine productivity and sustainability. For instance, a decrease in the benthic community would have a direct result on benthic predators since prey density can be directly related to predator density (i.e., bottom-up control) (Posey et al. 1995, Seitz et al. 2003, King et al. 2005, Seitz et al. 2006). Fluctuations in abundances of infaunal clams can be attributed to annual fluctuations of blue crab abundances (Hines et al. 1990, Micheli 1997). Predators may be concentrating in habitats with elevated prey densities (i.e., natural marsh) and have diminished abundances in habitats associated with bulkhead where infaunal densities are reduced (Seitz et al. 2006). In this case, an increase in the percentage of hardened shoreline within a system could lead to a decrease in natural resources, including commercially important species such as the blue crab (Hines & Ruiz 1995).

Conversion of the shoreline throughout the Lynnhaven system to a hardened shoreline type may result in an overall decrease in the benthic community because less natural marsh would be available to supplement altered shorelines (Jennings et al. 1999, Seitz & Lawless 2008). In Chesapeake Bay, within the more heavily impacted Lafayette River system (<50% of shoreline is natural marsh), the infauna adjacent to rip-rap displayed the depauperate conditions exhibited by bulkhead whereas in the less developed York River system (~86% of shoreline is natural marsh) infauna near rip-rap displayed the higher abundance and diversity characteristics of natural marsh (Seitz et al. 2006, Seitz & Lawless 2008). Natural marsh shoreline could be subsidizing rip-rap shoreline with allocthonous inputs of nutrients and benthic recruits and, therefore, rip-rap shorelines would not be as negatively influenced by development as those in a more heavily developed system with decreased amounts of natural marsh shoreline and increased amounts of hardened shoreline (Heck et al. 2003). As shorelines become hardened, the heterogeneity of the shorelines throughout a system decreases, and with a decrease in shoreline heterogeneity also comes a decrease in resource and species diversity (Eadie & Keast 1984, Schmude et al. 1998). Studies need to be completed to determine what percentage of natural marsh must exist within a system to supplement hardened shorelines. As little as 10% developed shoreline within a watershed can have a negative effect on macrobenthic communities (Bilkovic et al. 2006).

Managers must take all these factors into account when deciding whether to allow the replacement of a natural shoreline with a hardened shoreline. This study helped support the use of oyster reef as an alternative to bulkhead or rip-rap shoreline since the highest benthic density was associated with oyster reef shorelines. With increasing urbanization of the Lynnhaven watershed taking place every day, the high productivity of the benthic community in the system could be maintained if preservation of much of the remaining natural marsh shoreline, and potential use of oyster reef shoreline, is made a priority.

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Table 1. Models used in the AIC analysis for density, biomass, and diversity (H') of the benthic infaunal community. K = number of parameters in each model. The sediment (Sed.) variable represents both the grain size and TOC/TN of the sediment since these two factors were highly correlated and the predator (Pred.) variable represents the number of predators collected at each site. If a β is located in a column then that variable was included in that model.

			Variables				
		α	x_1	x_2	x_3	x_4	x_5
Model	K	**Constant - Natural Marsh (NM)**	**Bulkhead (B)**	**Rip-Rap (RR)**	**Oyster Reef (OR)**	**Sed.**	**Pred.**
g_1	7	α	β_1	β_2	β_3	β_4	β_5
g_2	6	α	β_1	β_2	β_3	β_4	
g_3	6	α	β_1	β_2	β_3		β_5
g_4	5	α	β_1	β_2	β_3		
g_5	4	α				β_4	β_5
g_6	3	α				β_4	
g_7	3	α					β_5

Table 2. Total number of bivalves, polychaetes, and crustaceans collected in benthic samples (0.11 m^2) in 2006 at the 29 shoreline-development sites in Lynnhaven, VA, and the adult bivalves collected in the 16 caging-study sites.

Species Name	Number Collected- Shoreline Development (Total)	Number Collected- Caging Study (Adults)
BIVALVES		
Aligena elevata	149	237
Cyrtopleura costata	0	1
Dosina discus	1	0
Ensis directus	18	1
Gemma gemma	11	38
Macoma balthica	70	60
M. mitchelli	12	92
M. tenta	0	5
Mercenaria mercenaria	12	10
Mulinia lateralis	9	10
Tagelus plebeius	33	59
Total Bivalves	**315**	**513**
POLYCHAETES		
Arabella iricolor	1	
Arenicola cristata	3	
Capitellidae	127	
Clymenella torquata	362	
Drilonereis longa	41	
Eteone heteropoda	4	
Euclymene zonalis	14	
Glycera americana	3	
G. dibranchiata	65	
Glycinde solitaria	20	
Leitoscoloplos spp.	146	
Lumbrineria fragilis	4	
Neanthes succinea	251	
Nephtys squamosa	2	
Opheliidae	1	
Scoloplos rubra	7	
Spionidae	25	
Total Polychaetes	**1076**	
CRUSTACEANS		
Ampithoe longimana	2	
Cyathura polita	12	
Cymadusa compta	7	

Table 2. Cont.

Species Name	**Number Collected- Shoreline Development (Total)**	**Number Collected- Caging Study (Adults)**
CRUSTACEANS		
Erichsonella attenuata	1	
Mysidaceae	1	
Neohaustorius biarticulatus	1	
Unknown Amphipod(a)	1	
Unknown Amphipod (b)	4	
Total Crustaceans	**29**	

Table 3. Total number of benthic predators (fish [F] and crabs [C]) collected in trawls at the 29 sites throughout Lynnhaven, VA.

Species Name	Common Name	Number Collected
Leiostomus xanthurus (F)	Spot	19
Lagodon rhomboides (F)	Pinfish	1
Mugil cephalus (F)	Striped mullet	7
Paralychthys dentatus (F)	Summer flounder	1
Micropogonias undulatus (F)	Atlantic croaker	2
Opsanus tau (F)	Oyster toadfish	1
Orthopristis chrysoptera (F)	Pigfish	2
Dorosoma cepedianum (F)	Gizzard Shad	8
Trinectes maculatus (F)	Hogchoker	3
Sciaenops ocellatus (F)	Red drum	1
Eucinostomus argenteus (F)	Spotfin mojarra	2
Fundulus heteroclitus (F)	Mummichog	1
Symphurus plagiusa (F)	Blackcheek tonguefish	1
Sphoeroides maculatus (F)	Northern puffer	1
Callinectes sapidus (C)	Blue crab	47
TOTAL FISH		**50**
TOTAL CRABS		**47**
TOTAL PREDATORS		**97**

Table 4. Results of the AICc analysis for benthic infaunal density in Lynnhaven, VA. Models are listed in order from best to worst. Variables included in the model are listed in parentheses under each model. The four shoreline type variables are represented by "ST". The sediment (Sed.) variable represents both the grain size and TOC/TN of the sediment since these two factors were highly correlated and the predator (Pred.) variable represents the number of predators collected at each site. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_4 *(ST)*	5	-94.85	202.31	0	**0.5349**
g_3 *(ST+Pred.)*	6	-94.27	204.35	2.04	**0.1924**
g_2 *(ST+Sed.)*	6	-94.80	205.43	3.12	**0.1124**
g_6 *(Sed.)*	3	-99.97	206.89	4.59	0.0540
g_1 *(ST+Sed.+Pred.)*	7	-93.79	206.92	4.61	0.0533
g_5 *(Sed.+Pred.)*	4	-99.18	208.03	5.73	0.0305
g_7 *(Pred.)*	3	-100.84	208.65	6.34	0.0225

Table 5. Results of the AICc analysis for benthic infaunal biomass in Lynnhaven, VA. Models are listed in order from best to worst. Variables included in the model are listed in parentheses under each model. The four shoreline type variables are represented by "ST". The sediment (Sed.) variable represents both the grain size and TOC/TN of the sediment since these two factors were highly correlated and the predator (Pred.) variable represents the number of predators collected at each site. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_6 *(Sed.)*	3	-18.56	44.09	0	**0.4002**
g_7 *(Pred.)*	3	-18.82	44.60	0.51	**0.3093**
g_4 *(ST)*	5	-16.87	46.36	2.26	**0.1292**
g_5 *(Sed.+Pred.)*	4	-18.55	46.77	2.68	**0.1048**
g_2 *(ST+Sed.)*	6	-16.87	49.56	5.47	0.0260
g_3 *(ST+Pred.)*	6	-16.87	49.56	5.47	0.0260
g_1 *(ST+Sed.+Pred.)*	7	-16.87	53.07	8.98	0.0045

Table 6. Results of the AICc analysis for benthic infaunal Shannon-Wiener (H') diversity in Lynnhaven, VA. Models are listed in order from best to worst. Variables included in the model are listed in parentheses under each model. The four shoreline type variables are represented by "ST". The sediment (Sed.) variable represents both the grain size and TOC/TN of the sediment since these two factors were highly correlated and the predator (Pred.) variable represents the number of predators collected at each site. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_6 *(Sed.)*	3	30.63	-54.22	0	**0.5881**
g_7 *(Pred.)*	3	29.50	-51.96	2.26	**0.1903**
g_5 *(Sed.+Pred.)*	4	30.86	-51.90	2.31	**0.1850**
g_4 *(ST)*	5	29.71	-46.57	7.65	0.0128
g_2 *(ST+Sed.)*	6	31.29	-46.38	7.84	0.0117
g_3 *(ST+Pred.)*	6	31.08	-45.96	8.26	0.0095
g_1 *(ST+Sed.+Pred.)*	7	31.65	-43.41	10.80	0.0027

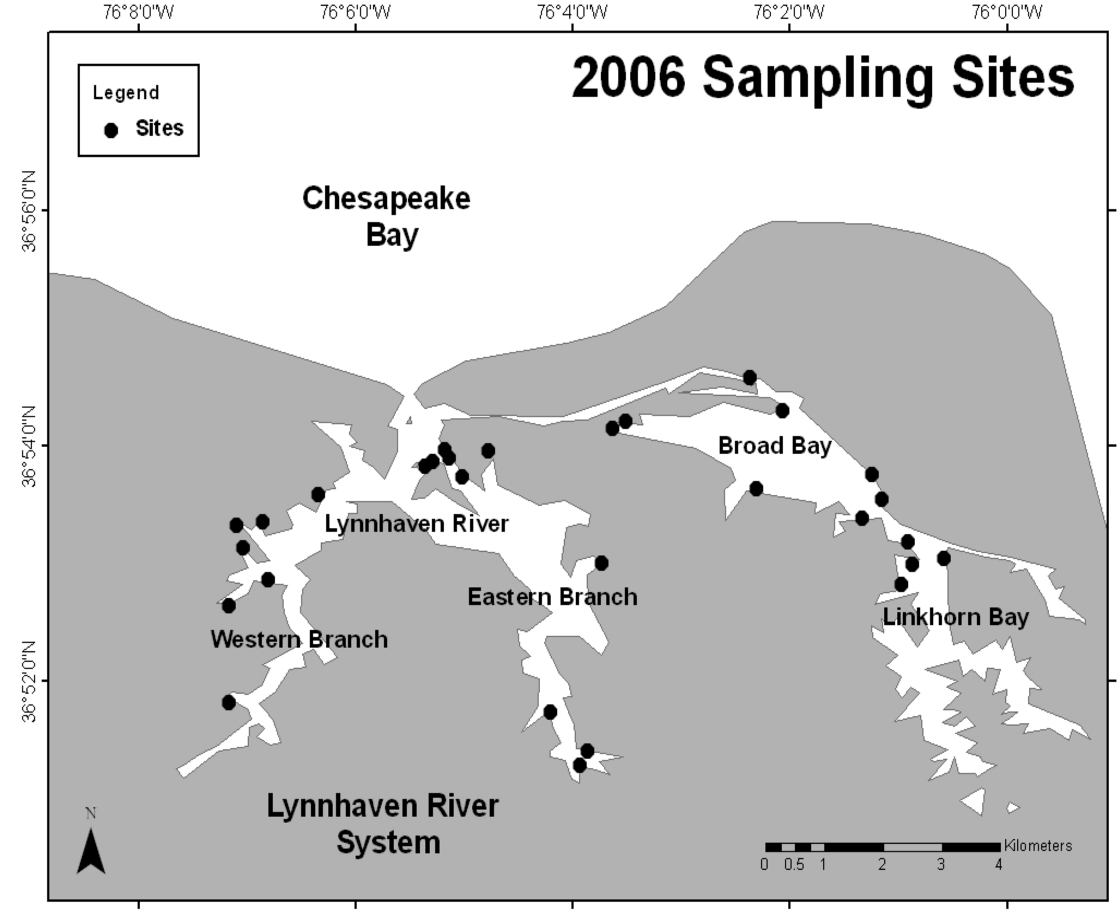

Figure 1. Location of the 29 benthic-sampling sites distributed throughout Lynnhaven, VA.

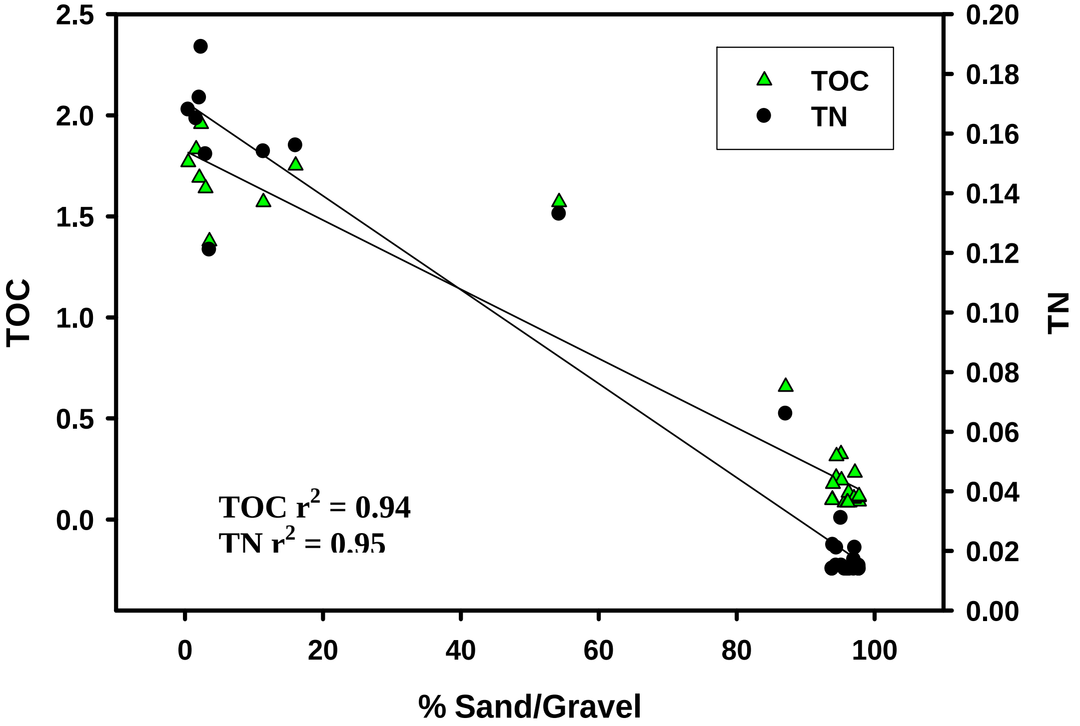

Figure 2. Regression of percent sand/gravel content of the sediment versus Total Organic Carbon (TOC) and Total Nitrogen (TN) content of the sediment in Lynnhaven, VA.

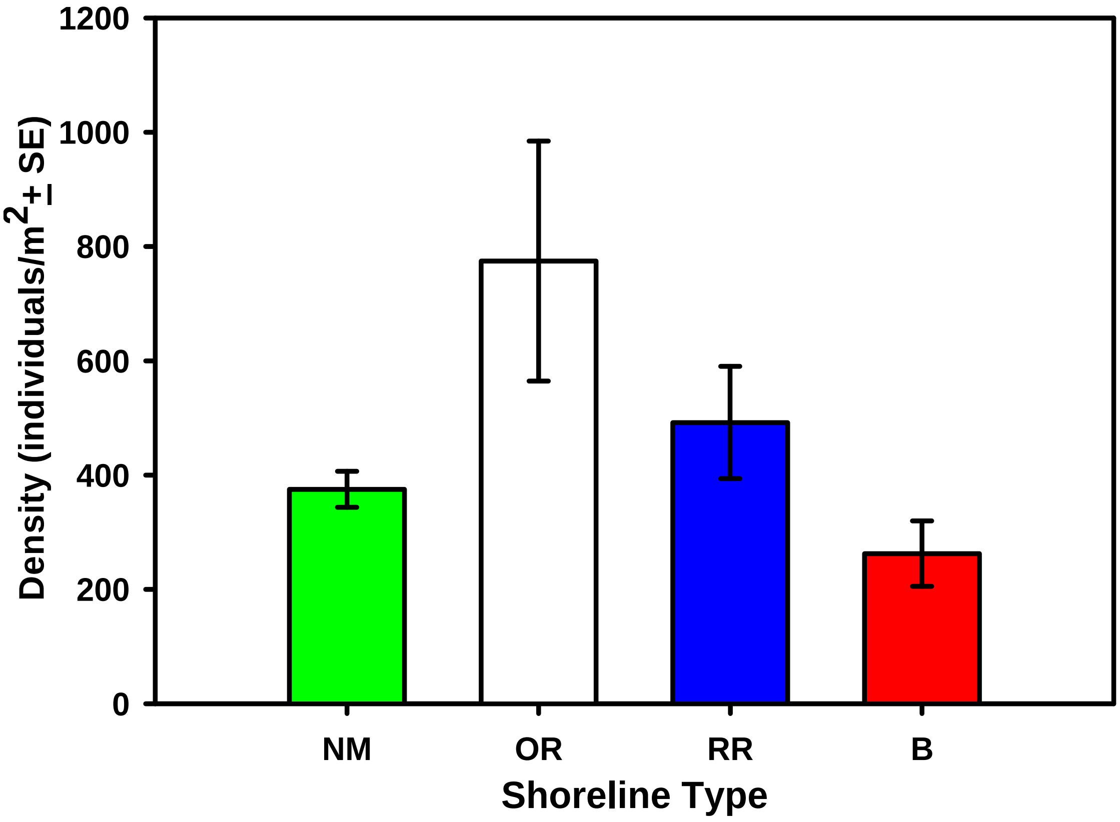

Figure 3a. Mean density (± SE) of the total benthic infaunal community adjacent to “Natural Marsh” (NM), “Oyster Reef” (OR), “Rip-Rap” (RR), and “Bulkhead” (B) shorelines in Lynnhaven, VA.

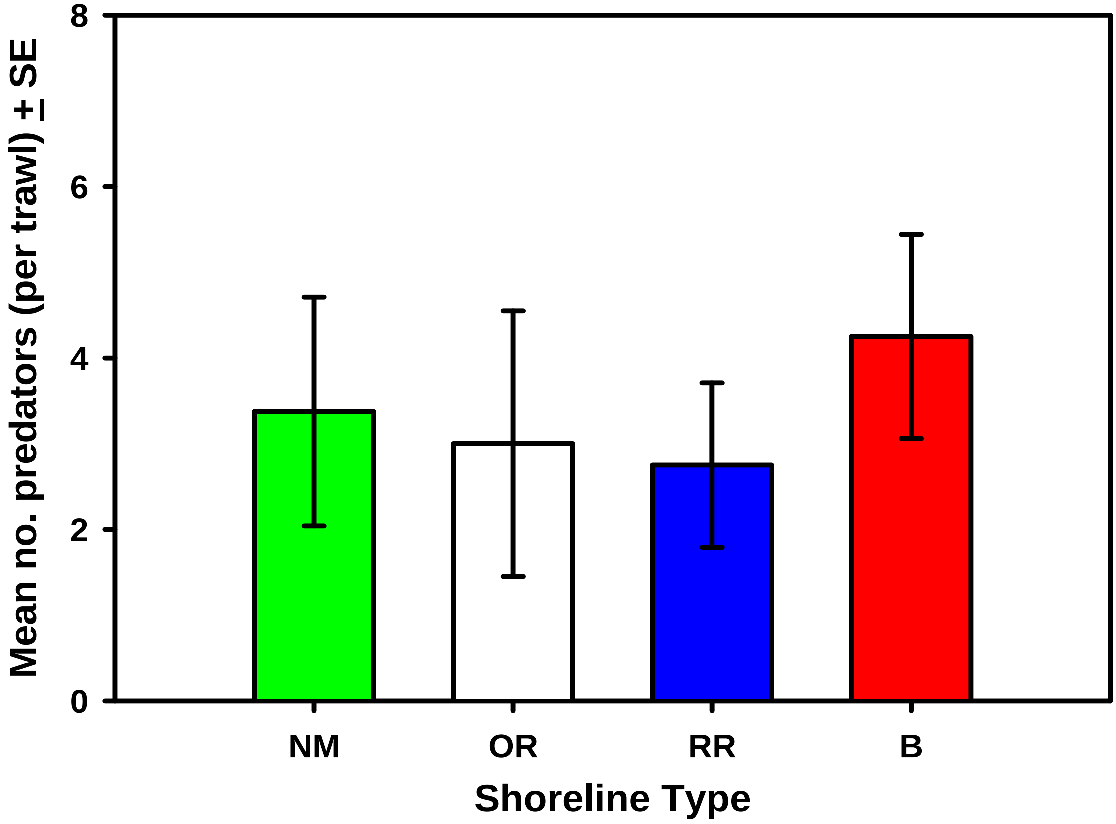

Figure 3b. Mean number (±SE) of benthic predators adjacent to "Natural Marsh" (NM), "Oyster Reef" (OR), "Rip-Rap" (RR), and "Bulkhead" (B) shorelines in Lynnhaven, VA.

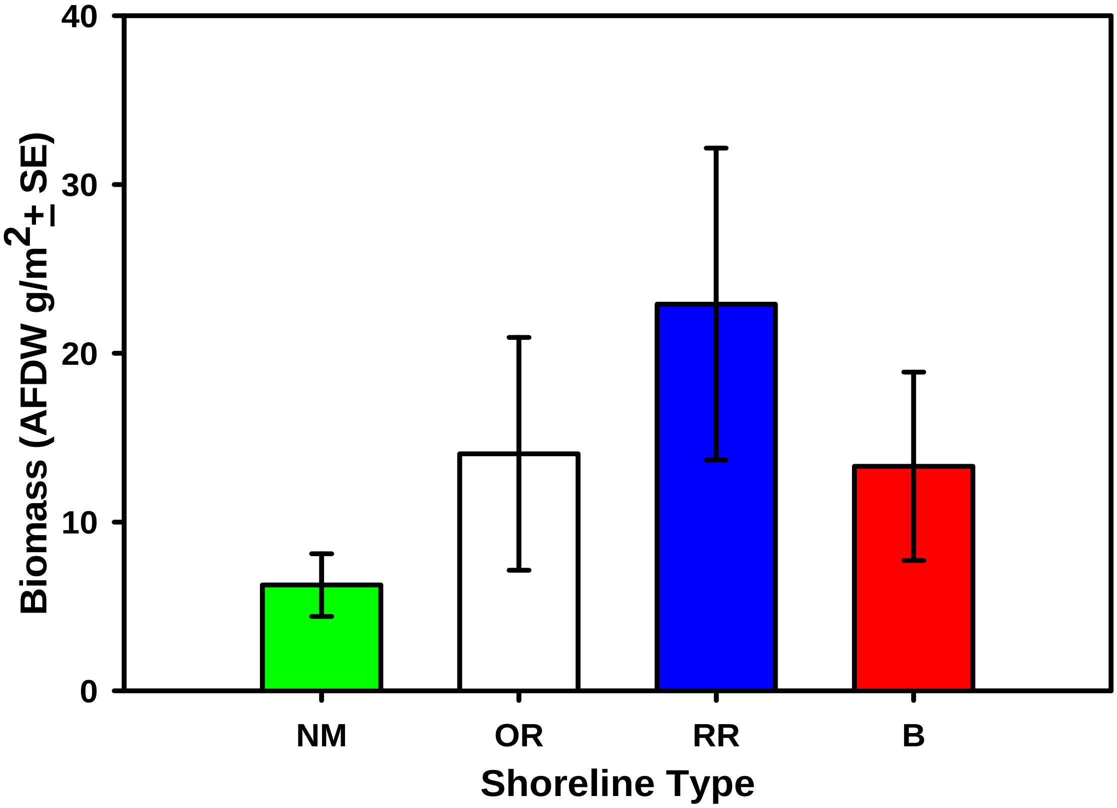

Figure 3c. Mean biomass (±SE) of the total benthic infaunal community adjacent to "Natural Marsh" (NM), "Oyster Reef" (OR), "Rip-Rap" (RR), and "Bulkhead" (B) shorelines in Lynnhaven, VA.

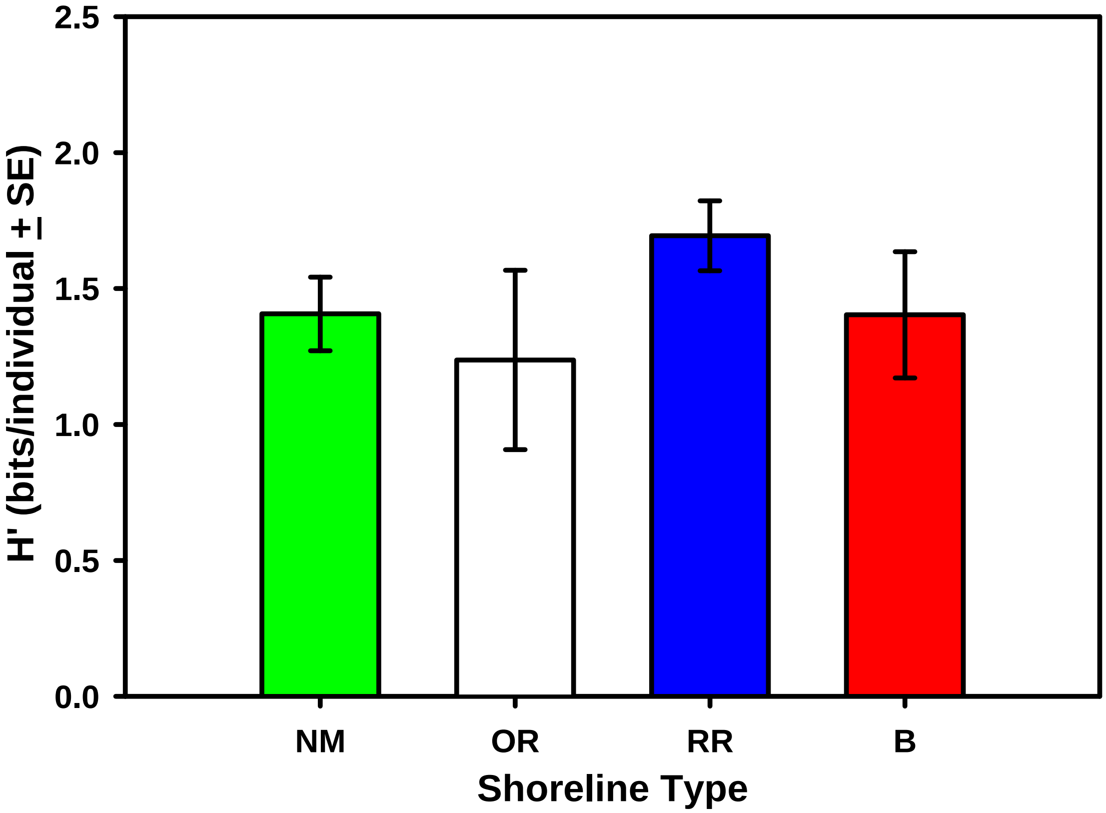

Figure 3d. Shannon-Wiener diversity (±SE) of the total benthic infaunal community adjacent to "Natural Marsh" (NM), "Oyster Reef" (OR), "Rip-Rap" (RR), and "Bulkhead" (B) shorelines in Lynnhaven, VA.

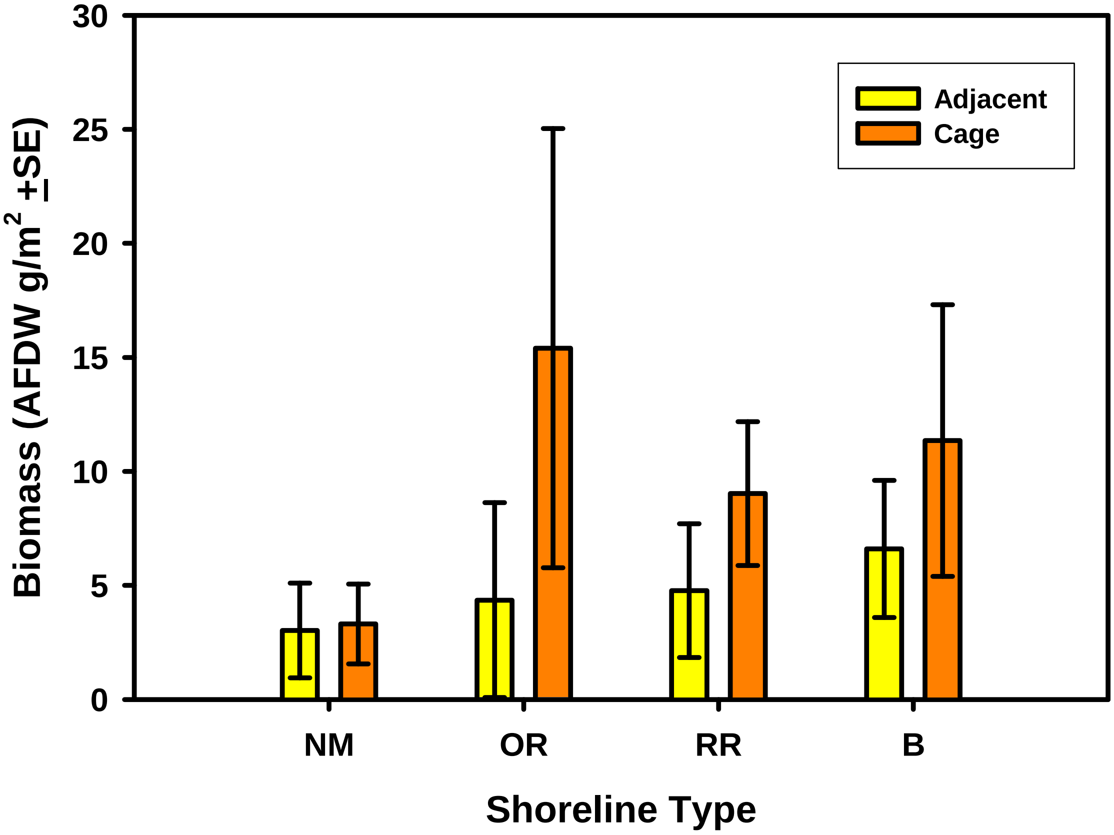

Figure 4. Mean biomass (±SE) of adult bivalves found in cages vs. adjacent to the cages associated with "Natural Marsh" (NM), "Oyster Reef" (OR), "Rip-Rap" (RR), and "Bulkhead" (B) shorelines in the predator exclusion caging study completed in Lynnhaven, VA.

CHAPTER 2

Benthic Infaunal Community Responses to Oyster Reefs in Lynnhaven, Virginia

ABSTRACT

Little work has focused on the effects of oyster reefs on the surrounding benthic infauna, which is surprising considering that oyster reef restoration involves placing an oyster reef on top of benthic infauna to enhance oyster production. The benthic community is dynamic and diverse; thus, it is hard to predict the effect the oyster reefs will have. The placement of an oyster reef could have a negative effect (e.g., due to increased predation) or a positive effect (e.g., due to increased oyster fecal pellet deposition acting as food for the benthos) on surrounding benthic infauna. A survey was completed at two locations (Eastern Branch and Linkhorn Bay) in Lynnhaven, Virginia, to examine the benthic community before and after the placement of living-shoreline oyster reefs in intertidal areas. The experiment was designed as a Before-After, Control-Impact (BACI) study with one treatment and two control sites at each of the two reef locations. Replicate samples for benthic infauna, sediment grain size, and Total Organic Carbon/Total Nitrogen of the sediment were taken before and one year after the placement of the oyster reefs. Oyster reefs had a positive effect on benthic infaunal density at the Linkhorn Bay site after one year, mainly attributed to the appearance of the bivalve *Gemma gemma*. This overall increase in density occurred even with a decrease in polychaete density at the site. There was, however, no change in benthic infaunal biomass or diversity (H' and species richness) and no effect on the surrounding sediment at this site. After one year at the Eastern Branch site, there was no effect of the oyster reefs on density, biomass, or diversity (H') of the benthos, with the exception of an increase in species richness at the reef site, and no effect on the surrounding sediment.

INTRODUCTION

Oyster restoration efforts, such as replacing lost oyster habitat with oyster reefs, are taking place throughout the Chesapeake Bay. Vast oyster shell reefs once were prominent in Chesapeake Bay (Jackson et al. 2001); however, over the last 100 years the population of this ecologically and commercially important species has been drastically reduced due to over-harvesting, disease, pollution, and loss of habitat (Rothschild et al. 1994). One way in which this loss is being counteracted in Chesapeake Bay is through oyster reef restoration, which mainly involves the inter-tidal and sub-tidal placement of various oyster reef-types on top of the seabed.

Another community that oyster reef restoration potentially affects is the benthic infaunal community. Benthic infaunal communities serve critical ecosystem functions such as nutrient cycling (Diaz & Schaffner 1990) and provide essential food for predators including the blue crab *Callinectes sapidus* and benthic feeding fish such as spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus* (Virnstein 1977, Diaz & Schaffner 1990, Hines et al. 1990).

Studies have been completed looking at the effects of various types of natural and artificial reefs (i.e., large rocks, scrap metal, tires, oil platforms, concrete modules, PVC pipe, sunken sea vessels) on the surrounding benthic community (Davis et al. 1982, Grant et al. 1982, Ambrose & Anderson 1990, Foster et al. 1994, Posey & Ambrose 1994, Culter & Truitt 1997, Barros et al. 2001, Danovaro et al. 2002, Fabi et al. 2002, Langlois et al. 2005, Langlois et al. 2006, Wilding 2006). The artificial reefs in these studies were deployed to either enhance fish abundances (i.e., fisheries management tools) or as a mitigation tool to replace habitat losses caused by human impacts (Ambrose & Anderson 1990, Fabi et al. 2002). These studies compared benthic samples taken at various distances from the reef edge. A variety of benthic patterns have been discovered associated with distance from the reef edge, and various studies have observed different patterns for different size classes of infauna in different sediment types. Increased abundances near reef edges (Davis et al. 1982, Ambrose & Anderson 1990, Foster et al. 1994, Culter & Truitt 1997, Barros et al. 2001, Langlois et al. 2005), decreased abundances near reef edges (Davis et al. 1982, Ambrose & Anderson 1990, Posey & Ambrose 1994, Barros et al. 2001, Langlois et al. 2005, Wilding 2006), as well as no change in the benthic community (Davis et al. 1982, Ambrose & Anderson 1990, Barros et al. 2001, Danovaro et al. 2002, Fabi et al. 2002, Langlois et al. 2006, Wilding 2006) have been associated with reefs. Numerous physical and biological processes have been proposed to explain these changes in the surrounding reef benthos. Little work, however, has focused on the effects of oyster reefs on the surrounding benthos, which is surprising considering that oyster reef restoration involves placing an oyster reef on top of benthic infauna to enhance oyster production. Based on past studies, many hypotheses can be developed regarding the effects these new structures could have on surrounding benthos.

Negative Reef Effects

The placement of an oyster reef could have a negative effect on surrounding benthic infauna. Placement of sub-tidal (Lenihan et al. 2001) and inter-tidal (Grabowski et al. 2005) oyster reefs in areas which previously lacked habitats (i.e., mud flats) augmented the abundance of adult and juvenile fish and mobile crustaceans (Peterson et al. 2003). This augmentation could be due to the reef acting as a structural refuge for benthic predators or to an increase in prey resources (Micheli & Peterson 1999). An increase of epibenthic predators on the reef could increase predation on the benthos around the reef, thus decreasing the abundance of the surrounding benthic community (Lindquist et al. 1994, Langlois et al. 2005, Watts & Weissburg 2008). Severe predation on the benthos could also decrease benthic diversity by reducing population densities of all species (Virnstein 1977). Surrounding benthic communities also could experience a halo effect (Ogden et al. 1973), in which predators deplete the surrounding benthos to a point where the risk of their own predation outweighs resource availability (Shulman 1985, Posey & Ambrose 1994, Micheli & Peterson 1999, Grabowski et al. 2005).

Another potential negative effect could be on the surrounding benthic infaunal filter feeders due to competition with the oysters. Oysters filter large volumes of water (Newell 1988); therefore, oysters on the reefs may filter food sources (i.e., phytoplankton) from the water column before the food reaches the benthos, reducing food availability and causing a decrease in the surrounding benthic infauna. Competition, however, is difficult to prove and little evidence exists for it in soft-sediment systems (Lenihan & Micheli 2001).

Current patterns around the reefs could also be altered causing sediment erosion and thus scouring around the base of the reefs (Davis et al. 1982, Grant et al. 1982, Foster et al. 1994). The increased current velocity and subsequent scouring could remove smaller adjacent infauna having an effect on the density and biomass of organisms surrounding the reefs.

Positive Reef Effects

The physical structure of oyster reefs and associated changes in hydrodynamics (Baynes & Szmant 1989) could have positive effects due to increased abundances of the surrounding benthos. Increased water flow (i.e., higher current velocities) in the areas around the oyster reefs could augment settlement rates of the benthic recruits due to enhanced larval supply (Lenihan 1999, Grabowski et al. 2005). At certain areas around oyster reefs the velocity of the current decreases (Lenihan 1999) and would allow particle deposition (i.e., larval settlement, food deposition) to occur (Virnstein 1977, Butman et al. 1988, Grabowski & Powers 2004). This potential increase in larval supply, larval settlement, and food deposition could have a positive effect on the surrounding benthos.

Another effect of the oyster reef structures could be on sediment grain size around the reef. As mentioned previously, currents can increase or decrease in velocity around the reef depending on the hydrodynamics in the area of reef placement (Baynes & Szmant 1989, Lenihan 1999). This could lead to enhanced sediment deposition on and around the reef changing the composition of the sediment (i.e., mean grain size). Increased currents around the reef could cause greater movement of fine sediments leaving coarser sediment behind and thus increase the sediment grain size around the reef (Davis et al. 1982, Ambrose & Anderson 1990, Barros et al. 2001). Also, shells from oysters, barnacles, mussels, and other fouling biota on the reefs could modify the surrounding sediments (Davis et al. 1982, Culter & Truitt 1997, Barros et al. 2001). A change in the sediment around the reef could cause a shift in the benthic community between filter-feeding and deposit-feeding infauna (Ahn & Choi 1998).

Positive effects of the reefs on surrounding benthos could include an increase in the surrounding benthic diversity. Low-level predation could reduce the density of dominant species, which would allow the density and diversity of competitively inferior species to increase (Paine 1966, Virnstein 1977, Posey & Hines 1991).

Another positive effect would occur if oysters on the reef and the surrounding benthos act as alternative prey for predators (Schmitt 1987, Wennhage 2000, Wong et al. 2005). The oysters could either alleviate predation pressure on the benthos, thus, no change or an increase in the abundance of the surrounding benthos would be observed. Alternatively, the benthic community may alleviate predation pressure on the adjacent oyster reef by acting as an alternative prey to juvenile oysters and thus the benthos would experience a decrease in abundance in the vicinity of the oyster reefs.

Oysters on the reefs could enhance the food supply of the benthos through oyster biodeposition (Frankenberg & Smith 1967). Fecal pellets of oysters can contain between 4% - 12% organic carbon (Haven & Morales-Alamo 1966) that can enrich an environment with up to 80% organic carbon (Sornin 1983). Entrapment of organic materials (i.e., plankton), along with reef-associated activities and deaths of reef organisms, could result in an increase in organic matter of the sediments around the reefs (Davis et al. 1982, Ambrose & Anderson 1990, Steimle et al. 2002, Wilding 2006). This supplement of organic carbon could increase the density of the surrounding benthos.

Oyster reefs support a diverse community of epifaunal and infaunal benthic species (Bahr & Lanier 1981, Nestlerode 2004). Many of the same species can be found on an oyster reef and in the sediment around it. The addition of oyster reefs could promote settlement of these species not only on the oyster reefs, but also around them, causing an increase in benthic infaunal density (Dauer et al. 1982).

Effect of Reef Location

The spatial proximity of an oyster reef to other habitats (i.e., salt marshes) can influence the density and community structure of benthic invertebrates (Micheli & Peterson 1999, Grabowski et al. 2005). Restored oyster reefs located adjacent to salt marshes and seagrass beds had decreased diversity and density of associated macroinvertebrates than reefs spatially separated from vegetation (Micheli & Peterson 1999); the salt marshes and seagrass beds acted as corridors facilitating the access of blue crabs to oyster reefs and enhancing blue crab predation associated with the reefs. Oyster reefs only significantly increased juvenile fish abundance when reefs were placed on isolated mudflats rather than adjacent to seagrass beds and salt marshes (Grabowski et al. 2005). The lack of structure on mudflats, as opposed to the already available structure of seagrass beds and salt marshes, and thus a lack of refuge from predation, may have contributed to the increased utilization of mudflat reefs by juvenile fish; however, there was a decrease in use by blue crabs since no corridor was available to protect them from predation (Grabowski et al. 2005). These studies show how predation on surrounding benthos could be affected by the proximity of a reef to an adjacent habitat.

The Study

This study took place in conjunction with another study that was completed at the same two sites. The concurrent study is looking at the settlement and survival rates of oysters on four reef types (oyster shell, rip-rap, reef ball, and concrete module). Each of these four reef types were placed in triplicate in a row parallel to shore and were located in the low intertidal zone at each site. I collected one set of benthic samples prior to the placement of the reefs at the replicate locations (Haroun et al. 1994, Wilding & Sayer 2002) and collected a second set of samples roughly one year after reef deployment. One main difference between this study and previous studies is that previous studies compared samples taken at various distances from natural and artificial reef edges to determine an effect of the reefs on the surrounding benthos, where as this study compares benthic samples before and after oyster reef placement to determine what effect, if any, the reefs had on the benthic infauna of the areas.

The objective of this study was to determine if the placement of oyster reefs would change the composition of the surrounding benthic infaunal community at two sites within Lynnhaven Bay, Virginia. A Before-After, Control-Impact (BACI) sampling design was used at each site to determine if there would be a positive, negative, or negligible effect of the oyster reefs on the surrounding benthic infaunal density, biomass, and diversity, as well as a change in the Total Organic Carbon (TOC)/Total Nitrogen (TN) and grain size of the sediment after one year. My hypothesis was that the placement of oyster reefs would change the composition of the surrounding benthic community when compared with the benthic community present prior to the placement of the oyster reefs; however, whether the effect of the oyster reefs on the benthic community would be positive or negative could not be predicted because evidence exists that supports both theories.

MATERIALS AND METHODS

This study took place in the Lynnhaven River system, the southern-most system in Chesapeake Bay, located in the City of Virginia Beach, Virginia. Lynnhaven consists of four main water bodies (Broad Bay, Linkhorn Bay, and the Eastern Branch and the Western Branch of the Lynnhaven River), is ~67 square miles in area, and has ~150 miles of shoreline. This study was completed at two sites in Lynnhaven (one in Linkhorn Bay and one in the Eastern Branch) that were pre-determined by the concurrent study (Fig. 1).

A Before-After, Control-Impact (BACI) sampling design was used (Schroeter et al. 1993, Gotelli & Ellison 2004). Twelve sample locations were randomly selected at each site. Prior to reef deployment, four locations were randomly sampled in the footprint of the oyster reefs (~23 m^2) (impact area), and four locations were sampled at randomly selected distances on either side of the reef area (control areas). The pre-reef samples (i.e., before samples) were taken in June/mid-July 2006, and the oyster reefs were deployed in late July 2006. Samples were taken approximately one year after deployment (June/July 2007) (i.e., after samples) and were collected on the seaward side of the reefs immediately adjacent to the pre-reef samples (within ~1 m). Sampling one meter from the reef edge has captured reef effects on the surrounding benthos in past studies (Davis et al. 1982, Ambrose & Anderson 1990, Barros et al. 2001, Fabi et al. 2002, Langlois et al. 2005, Wilding 2006).

Physical Parameters

A benthic habitat assessment also was performed for each of the pre- and post-reef sample locations at each site by determining sediment grain size (using standard wet sieving and pipetting) (Folk 1974) and by completing a Carbon, Hydrogen, Nitrogen (CHN) analysis of the sediment. These samples were taken in association with benthic macrofauna samples (described below) using a 2.5-centimeter (cm)-diameter surface-sediment core. Due to cost limitations, only two of the four samples taken at the reef and two of the four samples taken on either side of the reef (six samples total pre-reef and six samples post-reef) were randomly selected and analyzed for sediment grain size and TOC and TN. Sediment grain-size analysis was completed and reported in percent sand/gravel content of the sample.

Benthic Sampling

Benthic samples included a suction sample and a small core sample at each sample location. A suction apparatus was used to collect larger benthic organisms, which involved the removal of sediment within a cylinder of 0.11 m^2 surface area to ~40 cm depth (Eggleston et al. 1992). Sampling to this depth in the sediment ensures an accurate estimation of densities of deep-dwelling, large bivalves that are sparsely distributed (Hines & Comtois 1985). The sediment and infauna were collected in a 1 millimeter (mm) mesh bag and sieved on a 1 mm mesh screen. A 10-cm diameter core, used to remove sediment to 15 cm depth, was taken in association with each suction sample. This sample was sieved through a 500 micron sieve to collect smaller organisms in the community. Both the suction samples and small core samples were taken back to the lab and frozen until they were processed. The 10 cm core samples were not processed for this project; however, they can be used in the future to further examine patterns observed from the suction samples. Suction samples were sorted and the animals removed and identified to the lowest possible taxonomic level (usually species). Shell length of each bivalve from each sample was measured. Twelve of the samples from the Linkhorn Bay site were sub-sampled due to their large size. Each sample was homogenized and a random fraction was taken (sub-sample), and sorted. The Shannon-Wiener diversity index (H') (Krebs 1989, Gray 2000), which integrates species richness and evenness, was calculated using Primer v.6.1.6. software (Clarke & Warwick 2001).

Biomass estimates for all organisms were calculated using ash-free dry weight (AFDW). Polychaetes, crustaceans, and shucked bivalves (except *Macoma balthica* and *Tagelus plebeius* -- see below) were dried to a constant weight and ashed in a muffle furnace at 550°C for six hours to obtain ash weight. Regressions of shell length (SL) to AFDW were used for abundant bivalve species (*M. balthica* and *T. plebeius*) to estimate biomass from size. Clams were selected throughout the entire range of sizes collected from a previous study (Chapter 1) completed in Lynnhaven (27 clams ranging from 7.8 to 36.5 mm SL for *M. balthica* and 25 clams ranging from 4.2 to 75.2 mm SL for *T. plebeius*) for input into a regression. The best-fit equations were the following single, three-parameter models:

$$\textit{M. balthica}\text{: AFDW} = -0.0861 + 0.0427e^{0.0651*SL} \quad (r^2 = 0.97)$$

$$\textit{T. plebeius}\text{: AFDW} = -0.3222 + 0.2237e^{0.0261*SL} \quad (r^2 = 0.93)$$

Mercenaria mercenaria were collected at the Linkhorn Bay site; however, they were not included in the density, biomass, or diversity calculations. This was because *M. mercenaria* are not appropriately sampled via our sampling method (suction sampling of 0.11 m^2 surface area) due to the sparse distribution of the adult clams; past studies of *M.*

mercenaria stocks have used patent tongs that sample one square meter of bottom to adequately determine the density and distribution of the species (Mann et al. 2005).

Predator Sampling

A 2 m-wide, 4.9 m-long otter-trawl net, with a 3/8 inch inner mesh size, was used to sample along 50 m of shoreline at each of the two reef sites. The trawl net was pulled behind the boat at a constant speed at each site. Predators were identified to species and measured to the nearest millimeter (total length) and released. This sampling was completed in accordance with an approved Institutional Animal Care and Use Committee (IACUC) permit (#IACUC-2006-10-31-4471). A trawl was completed at each site before and after reef deployment.

Statistical Analyses

The control (samples on either side of the reef area) vs. impact (reef area samples) and site (Eastern Branch vs. Linkhorn Bay) factors were analyzed to determine if the placement of the reefs had an effect on the measured response variables. Measured response variables included density, biomass, and diversity (H' and species richness) of the benthos and grain size and TOC/TN of the sediment. Differences between pre- and post-reef samples (pre-reef samples subtracted from post-reef samples) at each sampling location for each response variable at each site were used to run the models. The impact/control and site variables (categorical variables) were used to establish a set of four models to describe the effects on the response variables from pre- to post-reef. Each model represented a different combination of variables (Table 1) that could describe differences observed in the response variables among the samples. The amount of TOC and TN followed the same pattern in relation to sediment grain size (Fig. 2); therefore, only TOC was analyzed. Model parameter estimates were derived using least squares regression and analysis of variance (ANOVA) models. From this analysis, coefficients of differences and associated confidences in the parameters were estimated. An information -theoretic approach using Akaike's Information Criterion (AIC) with a second-order bias correction (AICc) for low sample size was used to determine the best model from the model set for each of the response variables (Burnham & Anderson 2002, Anderson 2008). AICc values were calculated for each model using the following equation:

$$AICc = n * \ln(\sigma^2) + \ 2K\left[\frac{n}{n\ - K - 1}\right]$$

where ln (σ^2) is equal to the residual sum of squares (RSS) divided by the sample size (n) and K is the number of estimable parameters in a model. To rank the different models, ΔAICc was calculated for each model as follows:

$$\Delta AICc = AICc_i - AICc_{min}$$

where $AICc_i$ are the values for each of the i models and $AICc_{min}$ is the lowest AICc value of all the models. The best model has a ΔAICc = 0. Model probabilities or weights (w_i) for each model estimate the probability that a particular model is the best model given the data and the model set. Model probabilities were calculated as:

$$w_i \ = \frac{\exp(-{}^{1}/{}_{2}\,\Delta_i)}{\sum_{r=1}^{R}(-{}^{1}/{}_{2}\Delta_r)}$$

Models with a probability ≥ 0.10 in a model set were also considered likely models. If a parameter was included in more than one of the likely models it was considered a good predictor for that response variable and my confidence in the parameter was determined.

RESULTS

Eastern Branch

In June 2006, the temperature of the site was ~24.5°C (M. Sisson, pers. comm.) and the salinity was 22.1. Average sand/gravel composition at the Eastern Branch site for the pre-reef samples was 23.31% (standard error [SE] = ± 4.84) and for the post-reef was 4.88% (SE = ± 0.91), classifying the site as mud. The TOC average of the pre-reef samples was 1.49% (SE = ± 0.38) of the dry sediment sample and the post-reef average was 1.45% (SE = ± 0.11). Total Nitrogen averages were 0.11% (SE = ± 0.02) of the dry sediment sample for the pre-reef samples and 0.14% (SE = ± 0.005) for the post-reef samples.

I collected a total of 17 benthic infaunal species at the Eastern Branch site in the pre- and post-reef samples (Table 2). Five species of bivalves were collected at the site, with *Macoma balthica* being the numerically dominant species in the pre- and post-reef samples (99% of total bivalve density in pre-reef samples and 90% in post-reef samples). *Macoma mitchelli* also contributed 8% to the total bivalve density in the post-reef samples but were not present in the pre-reef samples. Bivalves accounted for a higher percentage of the overall benthic density in the pre-reef samples than in the post-reef samples (Fig. 3a & 3b). Five species of polychaetes, two isopod species, four species of amphipods, and several mysids were also collected at the site. Numerically dominant polychaetes were *Leitoscoloplos* spp. (53% of total polychaete density in pre-reef samples and 69% in post-reef), *Neanthes succinea* (29% pre-reef and 17% post-reef), and Capitellidae (17% pre-reef and 9% post-reef). The percentage of polychaetes contributing to total benthic density decreased from pre- to post-reef samples; however, the percentage of crustaceans increased (Fig. 3a & 3b).

Bivalves accounted for 98% of the total benthic biomass for both the pre- and post-reef samples. *Macoma balthica* contributed 98% of the total biomass for the pre-reef samples and 89% for the post-reef samples. *Tagelus plebeius* were not collected in the pre-reef samples but contributed 5% to the total biomass in the post-reef samples. Polychaetes accounted for 2% of the overall biomass for the pre-reef samples and 0.10% for the post-reef samples. Crustaceans had a negligible contribution to the overall benthic biomass of the pre-reef samples and contributed 1.90% to the overall biomass of the post-reef samples.

Predators collected in the pre-reef trawl consisted of 13 blue crabs *Callinectes sapidus*, two hogchoker *Trinectes maculatus*, and one spot *Leiostomus xanthurus*. In the post-reef trawl, the only predators collected were 34 juvenile spot (< 12.6 cm total fish length).

Linkhorn Bay

In July 2006, the temperature at the site was ~30.0°C (M. Sisson, pers. comm.) and the salinity was 17.5. Average sand/gravel composition at the Linkhorn Bay site for the pre-reef samples was 97.68% (SE = ± 0.61) and for the post-reef was 97.53% (SE = ± 0.37), classifying the site as sand. The TOC average of the pre-reef samples was 0.21% (SE = ± 0.06) of the dry sediment sample and the post-reef average was 0.23% (SE = ± 0.08). Total Nitrogen averages were 0.02% (SE = ± 0.002) of the dry sediment sample for the pre-reef samples and 0.02% (SE = ± 0.006) for the post-reef samples.

I collected a total of 21 benthic infaunal species at the Linkhorn Bay site in the pre- and post-reef samples (Table 3). Eight species of bivalves were collected at the site, and similar to the Eastern Branch site, *M. balthica* was the numerically dominant species in the pre-reef samples (66% of total bivalve density in pre-reef samples) followed by *T. plebeius* (18%) and *M. mitchelli* (14%). *Gemma gemma* was the numerically dominant species in the post-reef samples (92% of total bivalve density in post-reef samples), followed by *M. balthica* (5%). There was a large increase in bivalve density from pre- to post-reef samples (Fig. 4a & 4b). Ten species of polychaetes, one isopod species, and two species of amphipods were also collected at the site. Numerically dominant polychaetes in the pre-reef samples were *N. succinea* (58% of total pre-reef polychaete density), Capitellidae (32%), and *Leitoscoloplos* spp. (5%). The numerically dominant species in the post-reef samples was also *N. succinea* (74% of total post-reef polychaete density), followed by *Arenicola cristata* (9%) and Capitellidae (7%). There was a large decrease in polychaete density from pre- to post-reef samples and a small increase in crustacean density (Fig. 4a & 4b).

Bivalves accounted for 92% of the total benthic biomass for both the pre- and post-reef samples. *Tagelus plebeius* contributed 87% of the total benthic biomass for the pre-reef samples with *M. balthica* contributing 4%. For the post-reef samples, *T. plebeius* contributed 42% of the total benthic biomass, *Mya arenaria* contributed 28%, *Ensis directus* contributed 16%, and *M. balthica* contributed 4%. Polychaetes accounted for 8% of the overall benthic biomass for both the pre- and post-reef samples. Crustaceans did not contribute to the overall biomass of the pre-or post-reef samples.

Predators collected in the pre-reef trawl consisted of five blue crabs, four croaker *Micropogonias undulatus*, and four spot. In the post-reef trawl, the only predator collected was one croaker.

Statistical Analyses

Density

Oyster reefs had an effect on surrounding benthic infaunal density, depending on the site (Fig. 5). In the AICc model selection for density (Table 4), the model including the impact/control variable only (g_4) was the strongest model with probability = 0.36 (adjusted r^2 = 5.16%). There was a mean increase in benthic density from pre- to post-reef for both impact (i.e., adjacent to the reefs) (mean = 52.25, SE = 14.93) and control samples (mean = 24.81, SE = 10.56). I had high confidence (~85%) that the increase in the impact samples was twice that of the control samples (coefficient of difference = 27.44, SE = 18.29). Three other models, model g_1 (site and impact/control variables with an interaction [Site*Impact/Control], probability = 0.30), model g_3 (site variable only, probability = 0.19), and model g_2 (impact/control variable only, probability = 0.15) were also likely models. Since all models were likely, this suggests that the effect of impact/control varied by site, necessitating a separate analysis by site.

At the Eastern Branch site, there was an increase in benthic density in both the control (mean = 27.50, SE = 11.40) and impact samples (mean = 20.00, SE = 16.18) (Fig. 5); however, while my confidence was high (95%) for the increase in the control samples, it was low for the impact samples due to high variability. My confidence was also low

(<5 0%) that there was a difference in the increase in density between the control and impact samples at this site (coefficient of difference = -7.50, SE = 19.80).

At the Linkhorn Bay site, there was an increase in benthic density in both the impact and control samples and though my confidence was low for the increase in the control samples (mean = 22.13, SE = 15.94) due to high variability, it was high (95%) for the increase in the impact samples (mean = 84.50, SE = 22.54) (Fig. 5). There was high confidence (95%) that the increase in density in the impact samples was greater than the increase in the control samples (coefficient of difference = 62.38, SE = 27.61).

I also compared the density of individual groups and species from pre- to post-reef samples at the Linkhorn Bay site to determine what could be driving the density pattern at the site. The average increase of *G. gemma* in the impact samples was higher than the increase in the control samples. *Gemma gemma* increased in both the control (mean = 58.25, SE = 13.22) and impact samples (mean = 92.00, SE = 18.69), and my confidence in these increases was high (95%). I also had confidence (80% - 85%) in the difference in this increase between control and impact samples (coefficient of difference = 33.75, SE = 22.90). *Macoma balthica* increased in the control samples (mean = 0.50, SE = 1.66) and decreased in the impact samples (mean = -1.50, SE = 2.34); however, my confidence in these changes was low due to high variability; thus, my confidence that the reef had an effect on *M. balthica* was low as well. Total polychaete density decreased in both the control (mean = -36.00, SE = 7.23) and impact samples (mean = -14.75, SE = 10.22); however, while my confidence in this decrease was high (95%) for the control samples, it was low for the impact samples due to high variability. I had high confidence (85% - 90%) that there was a greater decrease in the control than impact samples (coefficient of difference = 21.25, SE = 12.52). Total crustacean density decreased in the control samples (mean = -1.00, SE = 4.04) and increased in the impact samples (mean = 8.00, SE = 5.71); however, my confidence that the reef had an effect on the crustaceans was low due to high variability.

Biomass

Oyster reefs did not influence the surrounding benthic infaunal biomass (Fig. 6). In the AICc model selection for biomass (Table 5), the strongest model included the impact/control variable only (g_4) with probability = 0.53 (adjusted $r^2 = 1.10\%$). There was a mean decrease in benthic biomass for both impact and control samples from pre- to post-reef across the sites; however, the decrease was greater in impact than control samples. Other likely models were model g_3 (site variable only, probability = 0.30) and model g_2 (impact/control and site variables with no interaction, probability = 0.14). To predict biomass of the surrounding benthic infauna, the impact/control variable was the best variable to use; however, my confidence in the decrease in biomass from pre- to post-reef in the impact (mean = -1.01, SE = 0.69) and control samples (mean = -0.07, SE = 0.49) at each site was low due to high variability. Therefore, my confidence that there was a difference in this decrease between the control and impact samples was low as well (~75% confident, [coefficient of difference = 0.95, SE = 0.85]).

Diversity

The oyster reefs did not influence the surrounding benthic infaunal diversity (Fig. 7), as was supported by the AICc model selection for diversity (H') (Table 6). The strongest model included only the site variable (g_3) with probability = 0.74 (adjusted r^2 =

42.10%). There was a mean decrease in benthic diversity at the Linkhorn Bay site but an increase in benthic diversity at the Eastern Branch site from pre- to post-reef. Model $g_{2,}$ including the site and impact/control variables with no interaction, had a probability = 0.18 and was also considered a likely model. I had high confidence (95%) in the site parameter for both sites (Linkhorn Bay: mean = -0.36, SE = 0.11; Eastern Branch: mean = 0.32, SE = 0.11) and high confidence (99%) that the change in diversity between the two sites was different (coefficient of difference = 0.68, SE = 0.16). However, I had low confidence (< 50%) in the impact/control parameter (coefficient of difference = -0.05, SE = 0.18) due to high variability. I therefore concluded that the reefs were not having an effect on the diversity of the surrounding benthic infauna and that diversity is best predicted using the site variable only.

An AICc analysis also was completed for benthic species richness (i.e., number of species) (Table 7). The strongest model included only the site variable (g_3) with probability = 0.45 (adjusted r^2 = 29.00%). There was a mean decrease in benthic species richness at the Linkhorn Bay site, but a mean increase in benthic species richness at the Eastern Branch site from pre- to post-reef. Model g_2, including the site and impact/control variables with no interaction (probability = 0.42), and model g_1, including the site and impact/control variables with an interaction (probability = 0.12), were also considered likely models. I had high confidence (95%) in the increase in species richness from pre- to post-reef for the Eastern Branch site (mean = 2.42, SE = 0.57) and low confidence in the decrease at the Linkhorn Bay site (mean = -0.17, SE = 0.57) due to high variability. There was also high confidence (85% - 90%) in the impact/control parameter (mean = 1.31, SE = 0.82). Since three of the models were likely, including the model with the interaction term, this suggests that the effect of impact/control varied by site, necessitating a separate analysis by site.

At the Linkhorn Bay site, there was an increase in benthic species richness in the impact samples (mean = 0.25, SE = 1.06) and a decrease in the control samples (mean = -0.38, SE = 0.75) from pre- to post-reef; however, my confidence in these changes was low due to high variability. The impact/control model for the difference in species richness at the Eastern Branch site from pre- to post-reef showed an increase in benthic species richness in both the impact (mean = 3.75, SE = 0.84) and control samples (mean = 1.75, SE = 0.59), and my confidence was high (95%) for the increase in both. There was high confidence (90% - 95%) that the increase in species richness in the impact samples was higher than the increase in the control samples (coefficient of difference = 2.00, SE = 1.03).

I compared species richness of individual groups from pre- to post-reef samples at the Eastern Branch site to determine what could be driving the increase in species richness. Total clam richness increased in both the control (mean = 0.88, SE = 0.27) and impact samples (mean = 1.75, SE = 0.38), and I had high confidence (90% - 95%) that the increase was higher in the impact than control samples (coefficient of difference = 0.88, SE = 0.46). I had low confidence in the changes in both the control and impact samples for total polychaete and total crustacean richness due to high variability.

Sediment Composition

Oyster reefs did not influence the surrounding sediment grain size (Fig. 8), as suggested by the AICc model selection for sediment grain size (Table 8). The strongest model included only the site variable (g_3) with probability = 0.91 (adjusted r^2 = 57.60%). There was a mean decrease in percent sand/gravel of the sediment at both sites from pre- to post-reef; however, the decrease was greater at the Eastern Branch site. To predict the change in percent sand/gravel composition of the sediment, the site variable was the best variable to use; however, my confidence in the estimate of the change in the sediment was high (95%) at the Eastern Branch site (mean = -18.43, SE = 3.24) and low at the Linkhorn Bay site (mean = -0.15, SE = 3.24) due to high variability. Since the impact/control variable was a poor predictor in the models, I concluded that the reefs were not having an effect on the surrounding sediment grain size.

Oyster reefs did not influence the surrounding TOC of the sediment (Fig. 9). The AICc model selection for the TOC of the sediment (Table 9), indicated the strongest model included only the impact/control variable (g_4) with probability = 0.70 (adjusted r^2 = 9.20%). There was a mean decrease of TOC in the impact samples across the sites, but a slight increase in the control samples from pre- to post-reef. Another likely model was model g_3, which included the site variable only with probability = 0.22. To predict the change in TOC of the sediment, impact/control was the best variable to use; however, my confidence in the decrease in the TOC of the sediment from pre-to post-reef in the impact samples (mean = -0.41, SE = 0.34) and increase in the control samples (mean = 0.19, SE = 0.24) was low due to high variability.

DISCUSSION

Placement of oyster reefs on the seabed had an effect on the surrounding benthic infaunal density, depending on the site. There was no change in density at the Eastern Branch site, and an increase at the Linkhorn Bay site. However, the oyster reefs did not have an effect on the surrounding benthic infaunal biomass or Shannon-Wiener diversity (H') after one year. At the Eastern Branch site, there was an increase in species richness, while at the Linkhorn Bay site there was no change after one year. There was also no effect of the oyster reefs on TOC/TN or grain size of the surrounding sediment after one year. It should be noted that there was good settlement and survival of the oysters located on the reefs at both sites (R.P. Burke, pers. comm.).

The Eastern Branch site was a muddy site, at which the shoreline adjacent to the reefs was rip-rap (i.e., large rocks) with natural marsh along the water line. *Macoma balthica* (a facultative suspension and deposit-feeder) was one of the dominant species driving densities and contributed most of the biomass in both the pre- and post-reef samples. *Leitoscoloplos* spp., *Neanthes succinea*, and Capitellidae were the dominant polychaetes in the pre- and post-reef samples and were the other main drivers of benthic density; however, these polychaetes contributed little to the overall biomass.

The Linkhorn Bay site was a sandy site, at which the shoreline adjacent to the oyster reefs was natural marsh. *Macoma balthica* was the dominant bivalve in the pre-reef samples; however, it was surpassed in dominance by *Gemma gemma* in the post-reef samples. *Gemma gemma* are small (adults ~5 mm) suspension-feeding bivalves that brood their young and are found patchily distributed in sandy habitats (Sellmer 1967, Weinberg 1985, Commito et al. 1995). The bivalve *Tagelus plebeius* was the main contributor to the overall biomass of both the pre- and post-reef samples. *Neanthes succinea* and Capitellidae were the dominant polychaetes in the pre- and post-reef samples and were the main drivers of benthic density in the pre-reef samples with their numbers dropping drastically in the post-reef samples. Polychaetes contributed little to the overall biomass.

At the Eastern Branch site, there was an average decrease in the sand/gravel and TOC of the sediment, but there was not a difference in this decrease between the impact and control samples due to high variability. This means that the decrease in sand/gravel and TOC of the sediment occurred across the entire site. At the Linkhorn Bay site, there was a slight average decrease in the sand/gravel content of the sediment and a slight increase in the TOC of the sediment, but variability among the samples was high. Surrounding grain size and TOC of the sediment were not affected by the oyster reefs at either site. Also, no increase was noted in the amount of shell debris located in the post-reef samples.

Oyster reefs did not have an effect on the surrounding benthic infaunal density at the Eastern Branch site after one year. There was an average increase in density in both the impact and control samples; however, the density did not differ between the control and impact samples. Oyster reefs did have an effect on the surrounding benthic density at the Linkhorn Bay site after one year. There was an average increase in total infaunal density from pre- to post-reef in both the control and impact samples; however, the density increase in the impact samples was four times greater than the increase in the control samples. This density increase was due to an increase in *G. gemma* and a decrease in the total polychaete density.

No *G. gemma* were collected in the pre-reef samples, but 834 individual *G. gemma* were collected in the post-reef samples. The increase in the impact samples of *G. gemma* was almost twice the increase of *G. gemma* in the control samples. There was no substantial change in density of the other bivalve species at the site from pre- to post-reef. The increase in *G. gemma* associated with the reefs could not be attributed to an increase in biodeposition from the oysters (Davis et al. 1982, Ambrose & Anderson 1990, Steimle et al. 2002, Wilding 2006) because there was not a significant increase in TOC in the sediments surrounding the oyster reefs. Our samples, however, represent a snapshot in time and would not indicate fluctuations of TOC or TN occurring in the sediment previous to my sampling.

Both juvenile and adult *G. gemma* are transported passively through currents and wave action and would be effected by a change in the hydrodynamics of an area due to reef placement (Sellmer 1967). The changing hydrodynamics that occur around reefs help to enhance larval supply and allow for the deposition of passive particles (Butman et al. 1988, Lenihan 1999, Grabowski et al. 2005). Emergent structures, such as oyster reefs, may enhance densities of infauna by baffling water, which allows for particle deposition, and subsequently enhances the settlement of larvae and post-larvae (Grabowski & Powers 2004). *G. gemma* transported to the reef area, and their subsequent deposition as passive particles due to the baffling of water by the reefs, could account for the higher densities in association with the oyster reefs. High rates of post-larval supply and dispersal of *G. gemma* could have quickly homogenized infaunal abundances over wide areas at this site (Commito et al. 1995).

Various reasons why no *G. gemma* were collected in 2006 were theorized. There may not have been the high rate of post-larval supply and dispersal in 2006 that could have occurred in 2007, or *G. gemma* could have experienced a population crash in 2006 (Weinberg 1985). Also, due to the patchy nature of *G. gemma* (Sellmer 1967), our sampling in 2006 potentially did not capture the population that existed there at the time.

Another potential theory for the greater increase in *G. gemma* surrounding the oyster reefs could be the juvenile oysters on the reef acting as alternative prey. After the placement of the oyster reefs, predators of both *G. gemma* and juvenile oysters (i.e., mud crabs) may have shifted their efforts from the *G. gemma* in the sediment to the juvenile oysters on the reefs, thus alleviating *G. gemma* from this predation pressure (Sellmer 1967, Bisker & Castagna 1987, Glancy et al. 2003, Nestlerode 2004, Newell et al. 2007).

The site also experienced a large decrease in polychaetes, one of which was *N. succinea*, an omnivorous species that could eat *G. gemma* (Rasmussen 1973, Fauchald & Jumars 1979, Kravitz 1983). A decrease in *N. succinea* at the site could have allowed for better survival of *G. gemma* in 2007 than in 2006 when *N. succinea* was more abundant.

As mentioned above, a decrease also occurred in polychaete density at the Linkhorn Bay site in both the control and impact samples. Though there was an overall decrease in polychaetes across the site, there was less of a decrease associated with the oyster reefs (almost half that of the control samples). The two polychaete taxa that decreased the most were *N. succinea* (~60% decrease across the site) and Capitellidae (~93% decrease).

The drastic decrease across the entire site possibly could be attributed to system-wide occurrences. In fall 2006, Tropical Storm Ernesto and two Nor'easter storm systems impacted Lynnhaven. These storms could have caused large disturbances at the site causing a decrease in polychaetes. A decrease in nutrient input into the system could have also affected the polychaetes. Capitellidae are deposit-feeders that rely on nutrients (i.e., organics [carbon and nitrogen]) in the sediment for nourishment (Fauchald & Jumars 1979). If there was a decrease in organic input into the system (i.e. draught conditions in spring 2007 would cause less nutrient run-off from land) Capitellidae would receive less nutrients and thus decrease in abundance. A large decrease in sediment nutrients in early 2007 would not have been captured by our sediment sampling if the system returned to normal by summer time. Both species also could have had a system-wide decrease in recruitment success that could have resulted in lower densities (Pettibone 1963). Predators of polychaetes (i.e., benthic feeding fish) could have had an increase in numbers throughout the system resulting in higher predation at the site thus decreasing polychaete numbers (Posey & Ambrose 1994, Langlois et al. 2005). Based on the predator trawls completed, I was not able to determine if the number of predators at the site increased. The small size of the oyster reefs at the site could have limited my ability to detect whether highly mobile predator fish species utilized the oyster reefs (Grabowski et al. 2005). Larger reefs or more reef habitat may be needed to influence adult predatory fish abundances (Lenihan et al. 2001, Grabowski et al. 2005).

This large decrease in polychaete density at the site also could be due to the mobility of *N. succinea* and Capitellidae. Both taxa can leave the sediment and swim freely through the water (Pettibone 1963, Rasmussen 1973, Diaz & Schaffner 1990, Rouse & Pleijel 2001) and both have been found on oyster reefs (Wells 1961, Pettibone 1963, Larsen 1974, Nestlerode 2004). *Neanthes succinea* and Capitellidae could have left the surrounding sediment and moved to the reefs at the site. The interstitial spaces of the reefs provide crevices for refuge from numerous predators and can accumulate food via biodeposition from oysters and other organisms on the reefs (Larsen 1974, Bahr & Lanier 1981, Nestlerode 2004, Grabowski et al. 2005).

The decrease in polychaetes was much greater in the control than impact samples. It should be noted that there were less polychaetes in the impact samples (~27 polychaetes per sample) than the control samples (~50 polychaetes per sample) before reef placement. Therefore, there would be less polychaetes that could be affected in the reef area as opposed to the control areas. Also, the reefs at this site were located adjacent to natural marsh, which can act as a corridor for predators, resulting in an increase in predation associated with the reefs (Micheli & Peterson 1999, Grabowski et al. 2005). This could explain some of the decrease in density at the reef site. Competition between the oysters and polychaetes was not likely since there was no significant change in the TOC/TN of the sediment around the reefs.

Factors that caused the polychaete decrease in the control samples did not appear to have as great of an effect on the samples associated with the oyster reefs. In addition, the reefs may have helped to enhance the surrounding polychaete population. As mentioned for the *G. gemma*, the reef structures themselves can increase larval supply and subsequent deposition of larvae, thus potentially enhancing polychaete densities around the reefs, which could help compensate for the large polychaete decrease (Butman et al. 1988, Lenihan 1999, Grabowski et al. 2005). Also, juvenile oysters on the reef could be acting as alternative prey for polychaetes, as well as *G. gemma*. Predators such as the blue crab feed on both polychaetes and oysters (Eggleston 1990, Hines et al. 1990).

Thus, oyster reefs would alleviate predation pressure on the polychaetes around the reefs, but such protection would not be afforded to the polychaetes in the control areas.

A small average decrease in biomass at the Eastern Branch and Linkhorn Bay sites occurred though there was no appreciable difference in these decreases in benthic biomass between the impact and control samples at either site due to high variability among samples. The large influx of *G. gemma* to the Linkhorn Bay site did not cause an increase in biomass due to the small size of *G. gemma* at the site (< 2.6 mm).

Finally, an average increase in diversity and species richness was observed at the Eastern Branch site from pre- to post-reef. There was no difference between the control and impact samples for diversity (H'); however, the increase in species richness in the impact samples was higher than that in the control samples. The driver of this increase in species richness was an increase in bivalve richness at the site. At the Linkhorn Bay site, an average decrease in diversity (H') and species richness occurred. There was no difference in this decrease between the control and impact samples for both diversity (H') and species richness. The overall changes in diversity (H') (both sites) and species richness (Linkhorn Bay site) occurred across the entire site in both areas and were not affected by the oyster reefs.

In the AICc analysis for density and biomass of the benthos, the adjusted r^2 values for the regression of even the best models were low, which suggests that the models created did not predict these response variables well. This low correlation could mean other variables, not measured as a part of this study, would be better predictors of the difference in density and biomass between the pre-and post-reef samples. High variability also was seen among the samples at the two sites, and past studies have found macrofaunal benthic assemblages inhabiting sediments close to reefs (1 m) were more variable than those living farther away (> 5 m); this great variability is a result of a combination of several biological and physical factors (Barros et al. 2001).

Oyster reefs had a positive effect on benthic infaunal density at the Linkhorn Bay site, mainly attributed to the appearance of *G. gemma*, which mostly likely increased due to enhanced larval supply and deposition in association with the reefs. This overall increase in density occurred even with a decrease in polychaete density because the reefs may have helped to compensate for this decrease through enhancement of polychaete recruits or by alleviating predation on polychaetes surrounding the reefs by supplying alternative prey. There was, however, no change in benthic infaunal biomass or diversity (H' and species richness) at this site. At the Eastern Branch site, there was no effect of the oyster reefs on density, biomass, or Shannon-Wiener diversity (H'), with the exception of an increase in species richness at the reef site. Recall that the reefs in this study had only been in place for one year prior to the post-reef sampling, and it could take longer than one year before a major effect of the reefs is seen on the surrounding benthos (Wilding 2006). Additional sampling of these sites is planned to determine if the trends seen after one year continue.

It is important from a management perspective to understand the effects of oyster reefs on the surrounding benthos (Davis et al 1982). If negative effects of the reefs on the benthos are discovered, then managers would need to analyze the benthic community before reef placement to determine what long term effects the reefs could have on the benthos. Our study was done on a small-scale and effects of these small reefs were observed, therefore, it is hypothesized that as the size of the reefs increased so would the effect, positive or negative, the reefs would have on the surrounding benthos (Davis et al. 1982, Grant et al. 1982, Lenihan et al. 2001, Grabowski et al. 2005, Langlois et al. 2006). However, positive or negligible effects of the reefs on the surrounding benthos, as seen in this study, could help support oyster reef restoration because such restoration could enhance not only the oyster community, but the benthic community as well.

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Table 1. Models used in the AIC analysis for density, biomass, diversity (H'), and species richness of the benthic infaunal community and for grain size and TOC of the sediment at two sites in Lynnhaven, VA. K = number of parameters in each model. The site variable represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable x_3 represents the interaction term between the Site and Impact/Control variables. If a β is located in a column then that variable was included in that model.

			Variables		
		α	x_1	x_2	x_3
Model	K	**constant**	**Site**	**Impact/Control**	**Site*Impact/Control**
g_1	5	α	β_1	β_2	β_3
g_2	4	α	β_1	β_2	
g_3	3	α	β_1		
g_4	3	α		β_2	

Table 2. Total number of bivalves, polychaetes, and crustaceans collected in 12 benthic samples (0.11 m^2) taken in 2006 (pre-reef) and 2007 (post-reef) at the Eastern Branch site in Lynnhaven, VA.

Species Name	**Eastern Branch- Pre-Reef**	**Eastern Branch- Post-Reef**
BIVALVES		
Control		
Gemma gemma	0	0
Macoma balthica	168	240
M. mitchelli	0	21
Mulinia lateralis	4	0
Tagelus plebeius	0	3
Total Bivalves	**172**	**264**
Impact		
Gemma gemma	0	1
M. balthica	135	124
M. mitchelli	0	13
Mulinia lateralis	0	0
Tagelus plebeius	0	2
Total Bivalves	**135**	**140**
POLYCHAETES		
Control		
Capitellidae	32	29
Eteone heteropoda	2	2
Glycinde solitaria	1	11
Leitoscoloplos spp.	121	170
Neanthes succinea	55	61
Total Polychaetes	**211**	**273**
Impact		
Capitellidae	24	8
Eteone heteropoda	0	2
Glycinde solitaria	1	3
Leitoscoloplos spp.	52	101
Neanthes succinea	39	6
Total Polychaetes	**116**	**120**
CRUSTACEANS		
Control		
Caprella penantis	1	0
Cyathura polita	16	75
Edotea triloba	1	1

Table 2. Cont.

Species Name	**Eastern Branch-Pre-Reef**	**Eastern Branch-Post-Reef**
CRUSTACEANS		
Control		
Gammarus mucronatus	1	0
Leptocheirus plumulosus	1	50
Melita nitida	0	0
Mysidaceae	41	1
Total Crustaceans	**61**	**127**
Impact		
Caprella penantis	0	0
Cyathura polita	5	61
Edotea triloba	0	1
Gammarus mucronatus	0	0
Leptocheirus plumulosus	0	20
Melita nitida	2	0
Mysidaceae	5	1
Total Crustaceans	**12**	**83**

Table 3. Total number of bivalves, polychaetes, and crustaceans collected in 12 benthic samples (0.11 m^2) taken in 2006 (pre-reef) and 2007 (post-reef) at the Linkhorn Bay site in Lynnhaven, VA.

Species Name	Linkhorn Bay-Pre-Reef	Linkhorn Bay-Post-Reef
BIVALVES		
Control		
Ensis directus	0	4
Gemma gemma	0	466
Macoma balthica	27	31
M. mitchelli	7	5
Mercenaria mercenaria	1	0
Mulinia lateralis	0	2
Mya arenaria	1	1
Tagelus plebeius	5	4
Total Bivalves	**41**	**513**
Impact		
Ensis directus	0	3
Gemma gemma	0	368
M. balthica	21	15
M. mitchelli	3	1
Mercenaria mercenaria	0	0
Mulinia lateralis	0	0
Mya arenaria	0	1
Tagelus plebeius	8	9
Total Bivalves	**32**	**397**
POLYCHAETES		
Control		
Arenicola cristata	6	14
Capitellidae	130	11
Clymenella torquata	0	1
Drilonereis longa	2	1
Eteone heteropoda	9	0
Glycera americana	0	2
Glycinde solitaria	0	6
Leitoscoloplos spp.	22	2
Neanthes succinea	232	77
Spionidae	1	0
Total Polychaetes	**402**	**114**

Table 3. Cont.

Species Name	Linkhorn Bay- Pre-Reef	Linkhorn Bay- Post-Reef
POLYCHAETES		
Impact		
Arenicola cristata	0	1
Capitellidae	32	0
Clymenella torquata	0	0
Drilonereis longa	1	3
Eteone heteropoda	7	0
Glycera americana	0	1
Glycinde solitaria	0	0
Leitoscoloplos spp.	2	0
Neanthes succinea	64	42
Spionidae	0	0
Total Polychaetes	**106**	**47**
CRUSTACEANS		
Control		
Ampithoe longimana	0	0
Cymadusa compta	0	12
Erichsonella attenuata	20	0
Total Crustaceans	**20**	**12**
Impact		
Ampithoe longimana	0	16
Cymadusa compta	0	16
Erichsonella attenuata	0	0
Total Crustaceans	**0**	**32**

Table 4. Results of the AICc analysis for benthic infaunal density in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**$\triangle$AICc**	**w_i**
g_4 *(IC)*	3	-88.79	184.78	0	**0.3552**
g_1 *(Site+IC+Site*IC)*	5	-85.89	185.10	0.32	**0.3022**
g_3 *(Site)*	3	-89.41	186.03	1.25	**0.1906**
g_2 *(Site+IC)*	4	-88.19	186.48	1.70	**0.1520**

Table 5. Results of the AICc analysis for benthic infaunal biomass in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_4 *(IC)*	3	-15.10	37.40	0	**0.5326**
g_3 *(Site)*	3	-15.67	38.54	1.14	**0.3012**
g_2 *(Site+IC)*	4	-15.00	40.11	2.71	**0.1371**
g_1 *(Site+IC+Site*IC)*	5	-14.94	43.21	5.81	0.0291

Table 6. Results of the AICc analysis for benthic infaunal Shannon-Wiener (H') diversity in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_3 *(Site)*	3	23.16	-39.11	0	**0.7392**
g_2 *(Site+IC)*	4	23.21	-36.32	2.79	**0.1828**
g_1 *(Site+IC+Site*IC)*	5	23.96	-34.60	4.51	0.0774
g_4 *(IC)*	3	16.09	-24.99	14.12	0.0006

Table 7. Results of the AICc analysis for benthic infaunal species richness in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	**K**	**log ($\mathcal{L}$)**	**AICc**	**△AICc**	**w_i**
g_3 *(Site)*	3	-15.12	37.43	0	**0.4481**
g_2 *(Site+IC)*	4	-13.74	37.58	0.15	**0.4165**
g_1 *(Site+IC+Site*IC)*	5	-13.33	39.99	2.56	**0.1247**
g_4 *(IC)*	3	-18.85	44.90	7.47	0.0107

Table 8. Results of the AICc analysis for sediment grain size in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	K	log ($\mathcal{L}$)	AICc	△AICc	w_i
g_3 *(Site)*	3	-23.76	56.52	0	**0.9066**
g_2 *(Site+IC)*	4	-23.76	61.23	4.71	0.0860
g_1 *(Site+IC+Site*IC)*	5	-23.58	67.15	10.63	0.0045
g_4 *(IC)*	3	-29.48	67.95	11.43	0.0030

Table 9. Results of the AICc analysis for TOC of the sediment in Lynnhaven, VA. Variables included in each model are listed in parentheses under each model. The site variable (Site) represents whether the samples were taken at the Eastern Branch or Linkhorn Bay site and the Impact/Control variable (IC) represents whether the samples were taken in the impact (reef area) or control areas at each site. Variable Site*IC represents the interaction term between the Site and Impact/Control variables. log ($\mathcal{L}$) = log likelihood. Bolded numbers in the w_i column represent the top models in the set.

Models	K	log ($\mathcal{L}$)	AICc	△AICc	w_i
g_4 *(IC)*	3	5.87	-2.75	0	**0.6983**
g_3 *(Site)*	3	4.74	-0.47	2.27	**0.2239**
g_2 *(Site+IC)*	4	5.89	1.94	4.69	0.0670
g_1 *(Site+IC+Site*IC)*	5	7.20	5.60	8.35	0.0107

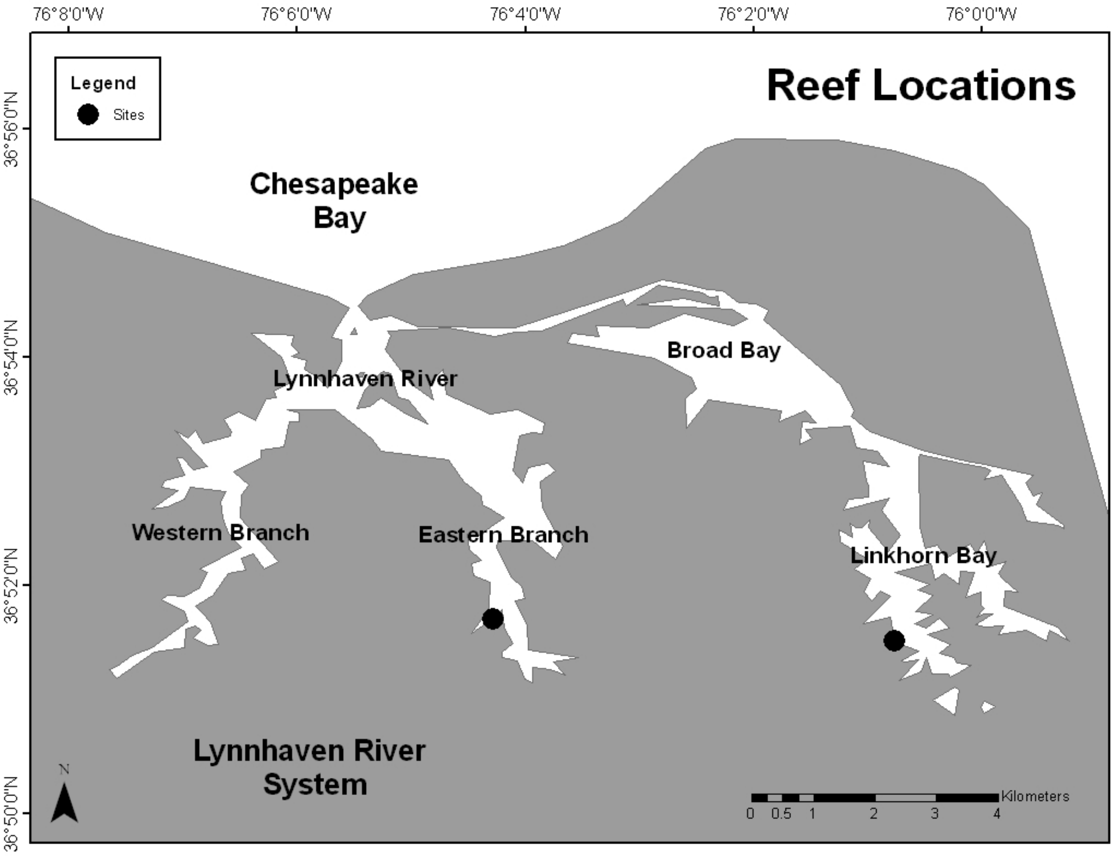

Figure 1. Locations of the Eastern Branch and Linkhorn Bay sites located in Lynnhaven, VA.

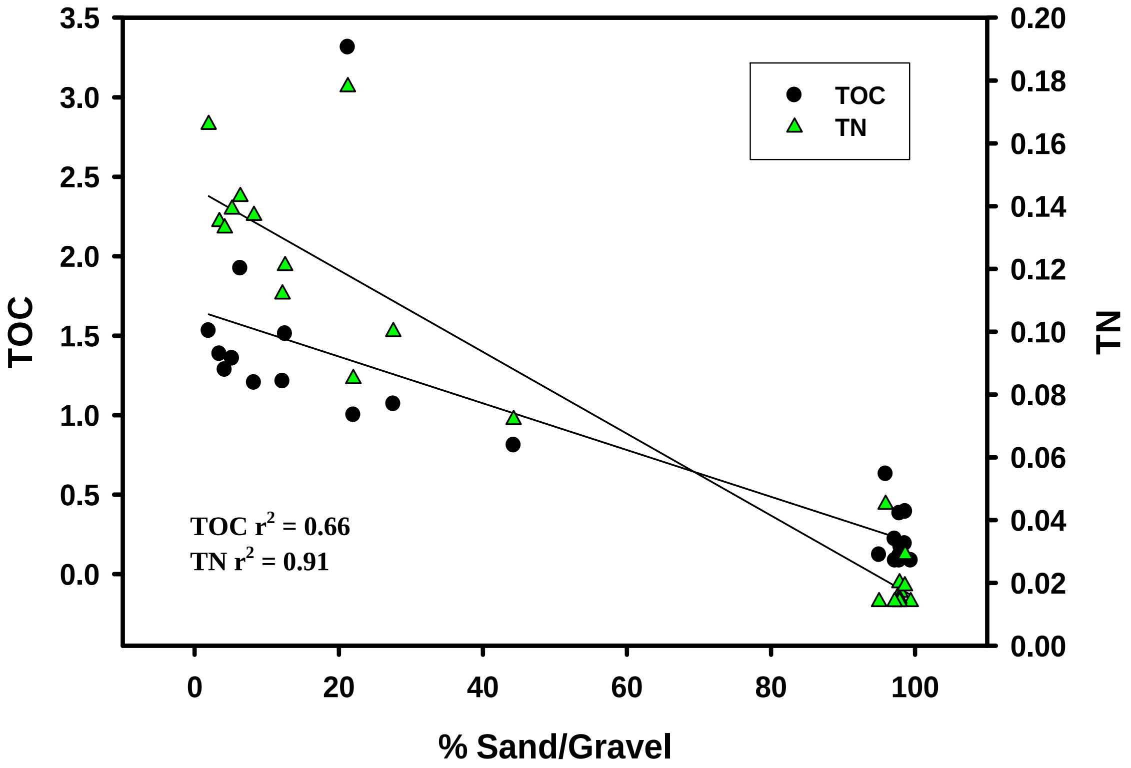

Figure 2. Regression of percent sand/gravel of the sediment versus Total Organic Carbon (TOC) and Total Nitrogen (TN) of the sediment.

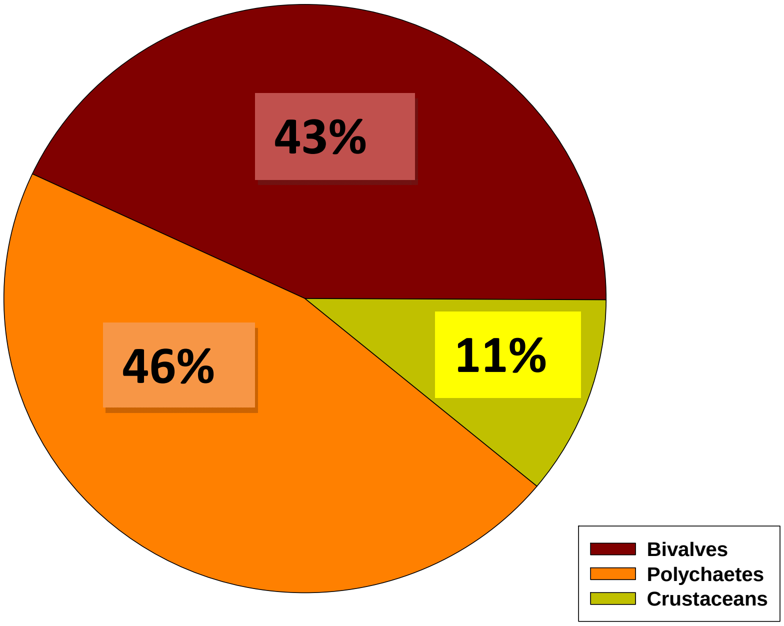

Figure 3a. Percent contribution of the bivalves, polychaetes, and crustaceans to the overall benthic infaunal density in the pre-reef samples at the Eastern Branch site.

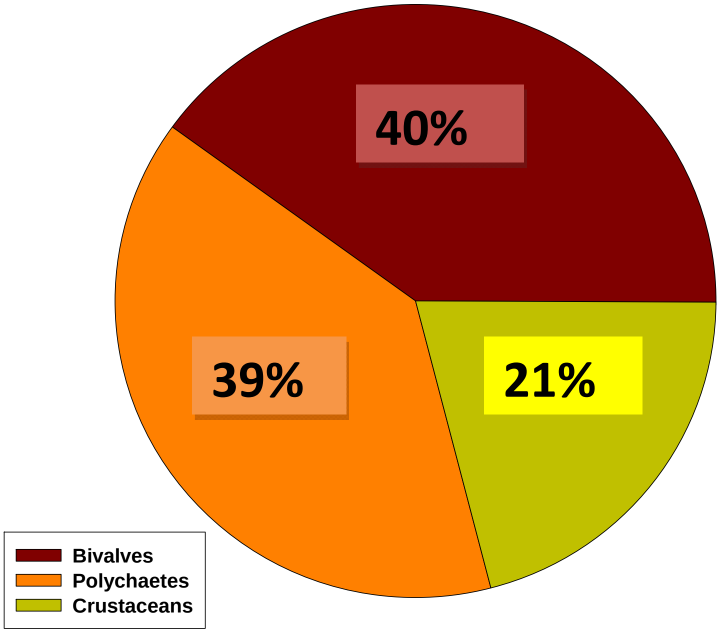

Figure 3b. Percent contribution of the bivalves, polychaetes, and crustaceans to the overall benthic infaunal density in the post-reef samples at the Eastern Branch site.

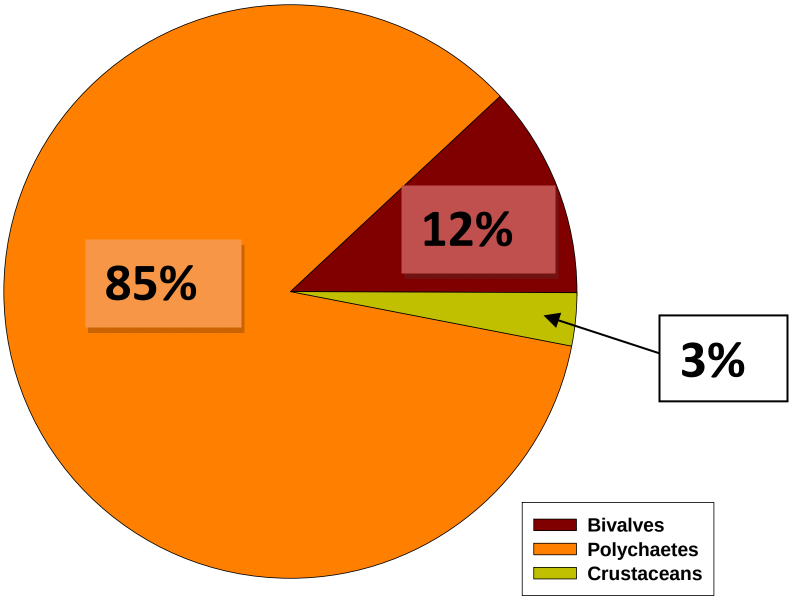

Figure 4a. Percent contribution of the bivalves, polychaetes, and crustaceans to the overall benthic infaunal density in the pre-reef samples at the Linkhorn Bay site.

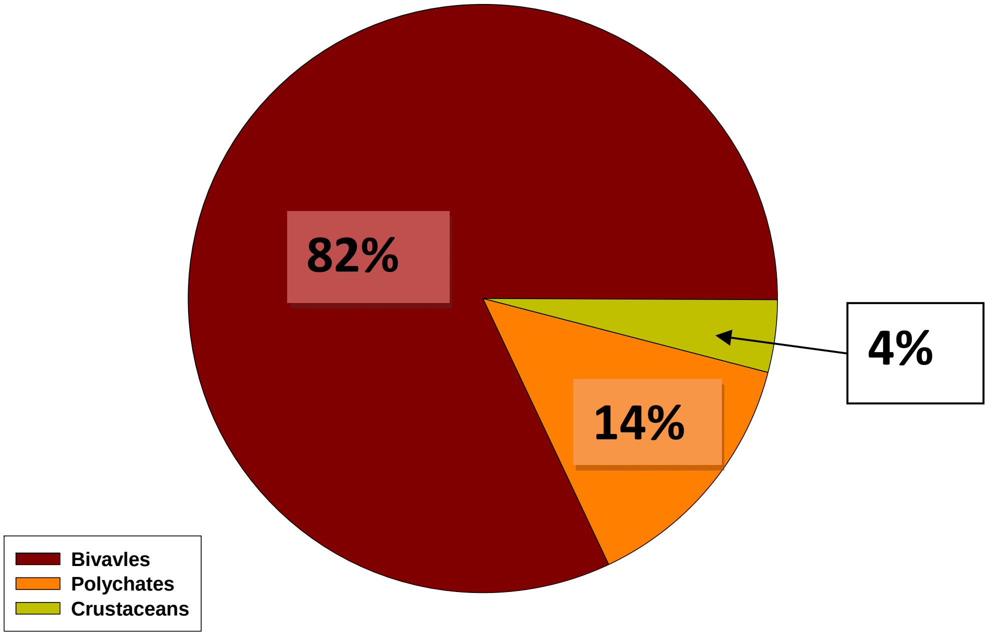

Figure 4b. Percent contribution of the bivalves, polychaetes, and crustaceans to the overall benthic infaunal density in the post-reef samples at the Linkhorn Bay site.

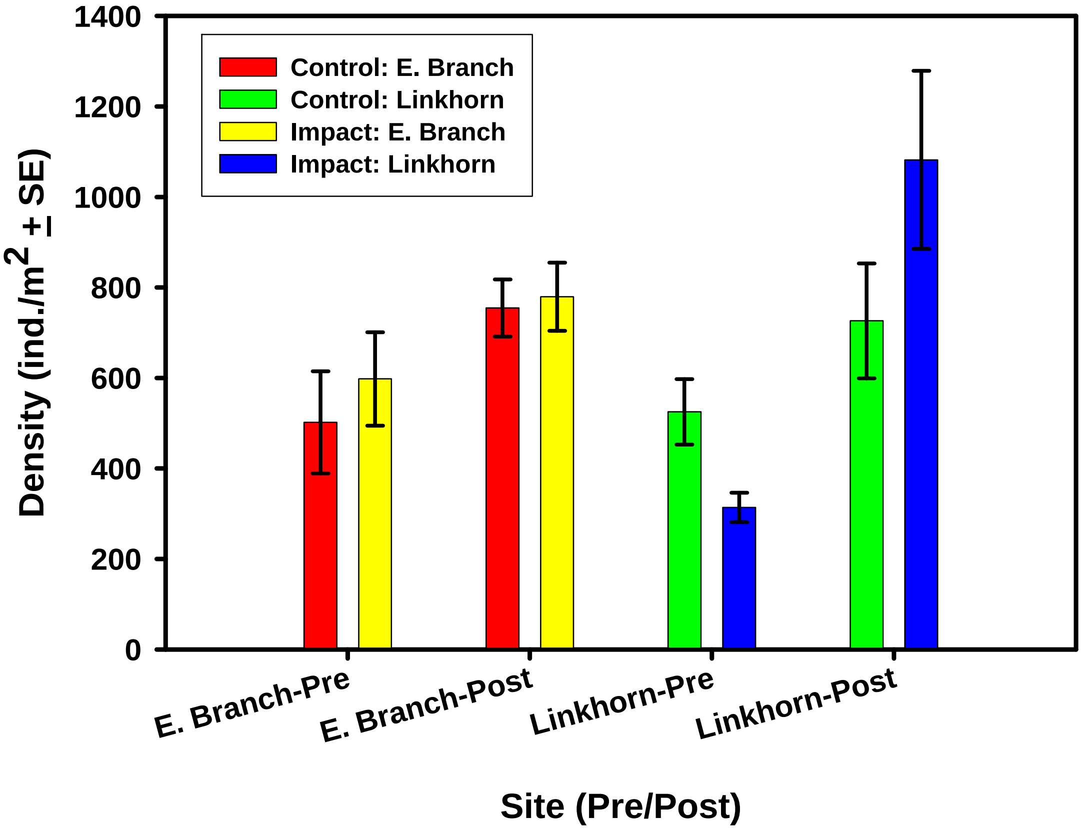

Figure 5. Mean density (± SE) of the total benthic infaunal community in the pre- and post-reef samples separated into impact and control samples at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites in Lynnhaven, VA.

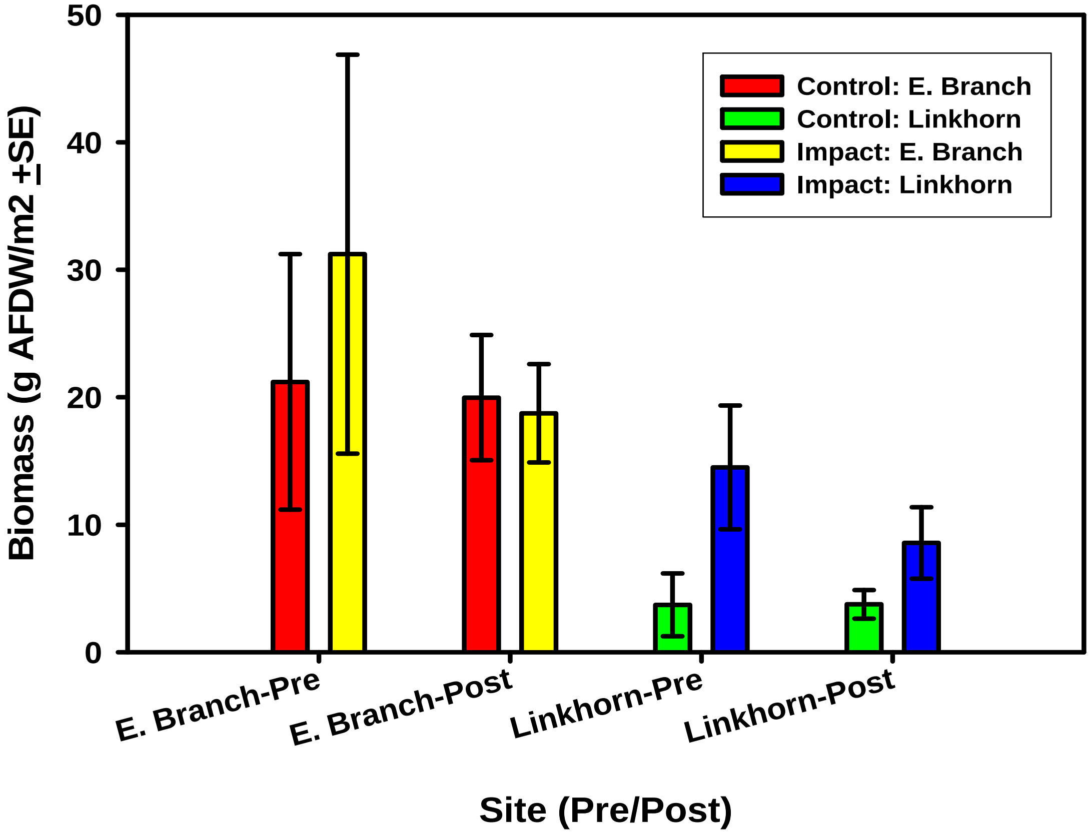

Figure 6. Mean biomass (±SE) of the total benthic infaunal community in the pre- and post-reef samples separated into impact and control samples at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites in Lynnhaven, VA.

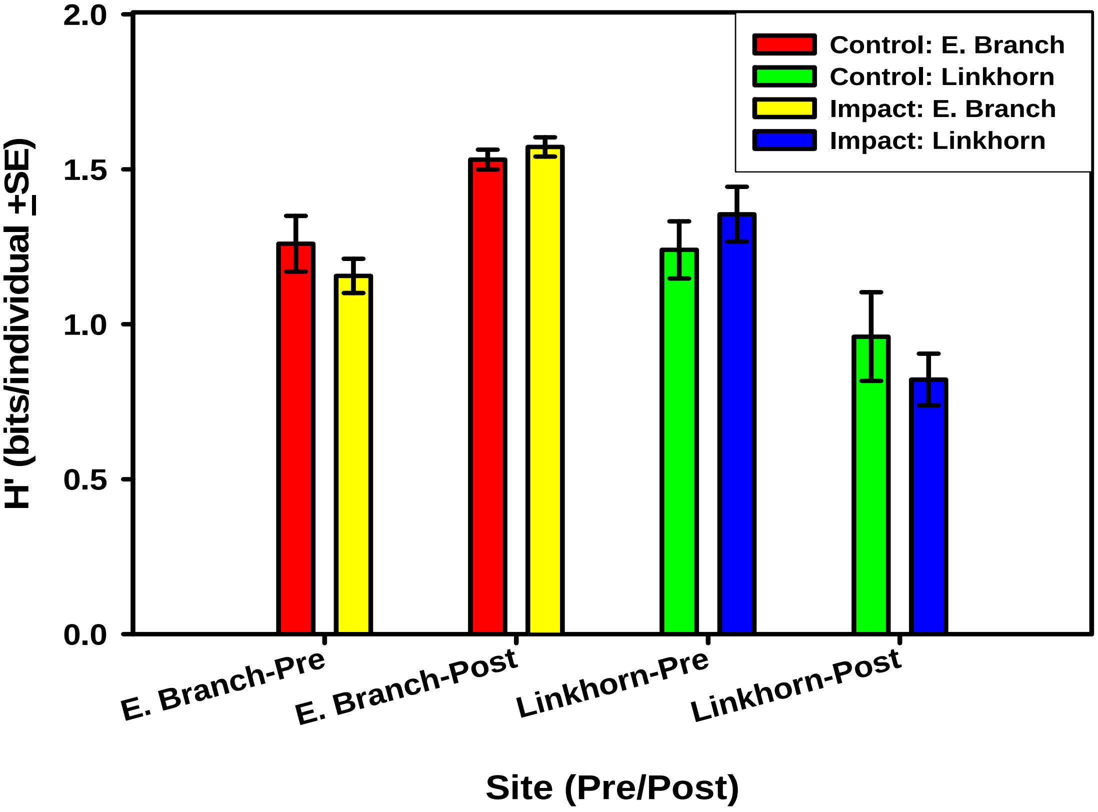

Figure 7. Mean Shannon-Wiener diversity (H') (±SE) of the total benthic infaunal community in the pre- and post-reef samples separated into impact and control samples at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites in Lynnhaven, VA.

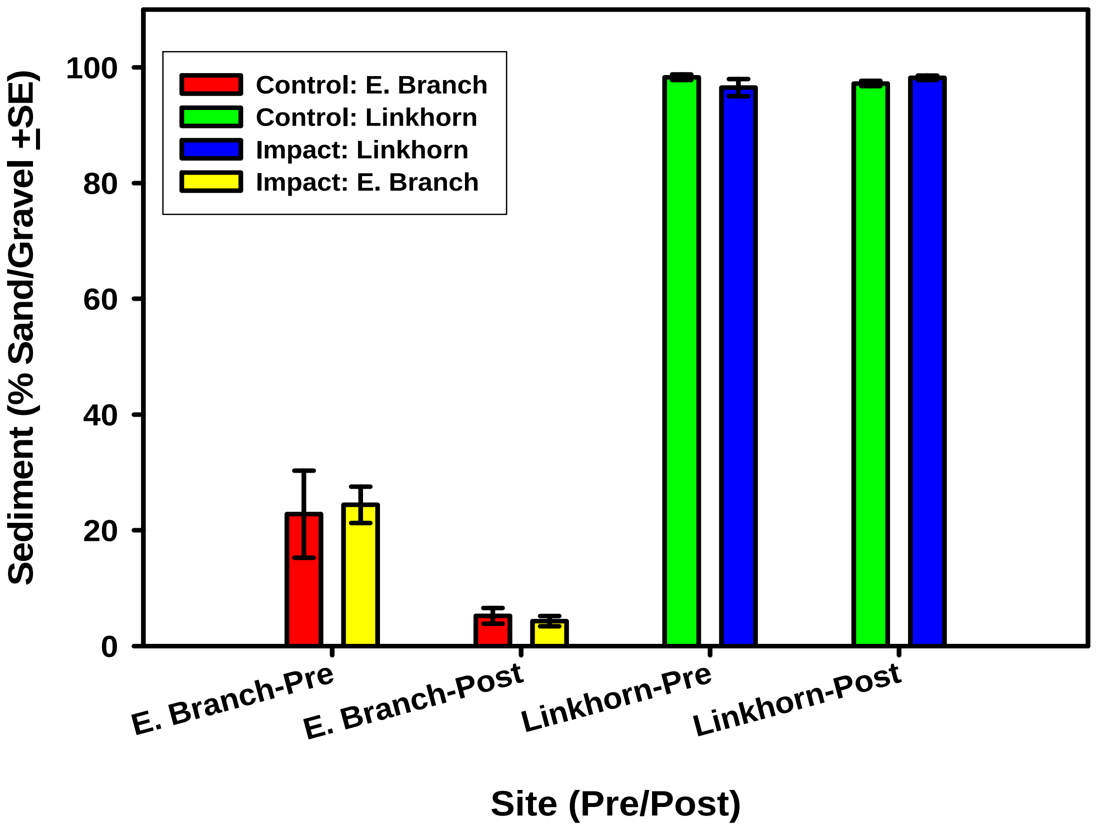

Figure 8. Mean percent sand/gravel of the sediment (±SE) in the pre- and post-reef samples separated into impact and control samples at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites in Lynnhaven, VA.

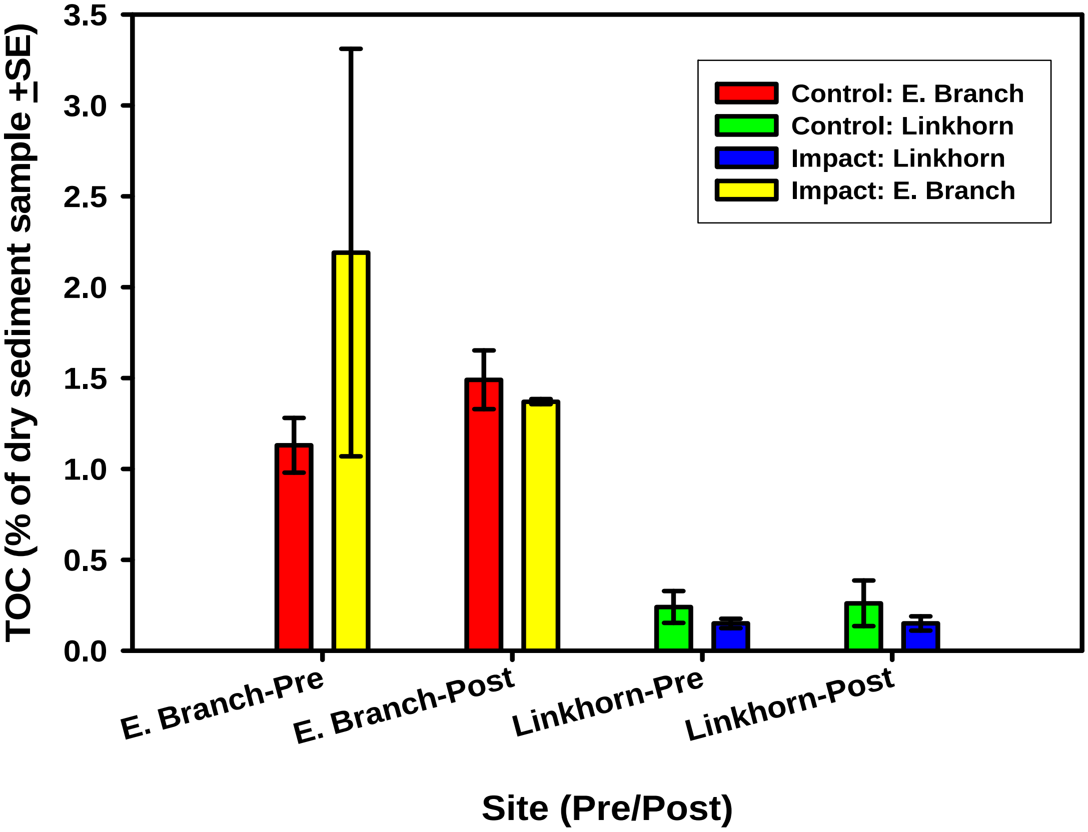

Figure 9. Mean Total Organic Carbon (TOC) of the sediment (±SE) in the pre- and post-reef samples separated into impact and control samples at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites in Lynnhaven, VA.

CHAPTER 3

Habitat Trade-Off Considerations between Oyster Reefs and Associated Benthic Infauna in Lynnhaven, Virginia

ABSTRACT

Restoration projects involving the Eastern oyster, *Crassostrea virginica*, are underway throughout the Chesapeake Bay. The placement of oyster reefs upon the seabed requires covering existing benthic infaunal communities. My study compared the productivity of lost benthic communities to the productivity of oysters on four oyster reef types. Macrobenthic suction samples were collected in the footprint of the reefs, prior to reef placement, at two sites in Lynnhaven, Virginia. One site (Eastern Branch) was very productive and had twice the benthic biomass and secondary production than did the second site (Linkhorn Bay). Four reef types (oyster shell, rip-rap, concrete modules, and reef ball) were deployed at both sites in late July 2006, and their full productivity would not be quantifiable for some time. Hence, I used oyster production values for existing established oyster reefs to estimate expected production of the oysters on the four reef types. Biomass estimates and published P:B ratios for each taxa were used to calculate secondary production for the benthic infauna and oysters. The lost benthic production due to each reef type at both sites was then compared to the estimated oyster production on each reef type to determine whether each of the four reef types compensated for the benthic production lost by placing the reef on top of the benthos. Production of oysters on oyster shell and reef ball reefs compensated for the amount of benthic production lost due to placing the reefs on top of the benthos at both sites. The oyster productivity on rip-rap reefs and concrete module reefs, however, did not compensate for lost benthic production at the Eastern Branch site where benthic productivity was high, and just barely compensated for the benthos at the Linkhorn Bay site, which had lower benthic productivity. Managers must consider the habitat trade-offs between oyster reefs and the associated productive benthic communities that are lost during oyster restoration.

INTRODUCTION

The population of the Eastern oyster, *Crassostrea virginica*, has been in drastic decline since the early 20th century, and landings throughout Chesapeake Bay are at historical lows (Rothschild et al. 1994, Jackson et al. 2001, Nestlerode 2004). This decrease has led to oyster reef restoration efforts at several locations throughout the Bay (Breitburg et al. 2000, Mann 2000). However, there is a trade-off when oyster reef restoration occurs because the creation of a reef involves the destruction of benthic infauna underneath the oyster reef (Ambrose & Anderson 1990). Benthic infaunal communities serve critical ecosystem functions such as nutrient cycling (Diaz & Schaffner 1990), filtering of the water column (Jackson et al. 2001), and providing essential food for commercially important predators including the blue crab *Callinectes sapidus* and benthic-feeding fish such as spot *Leiostomus xanthurus* and Atlantic croaker *Micropogonias undulatus* (Virnstein 1977, Hines et al. 1990, Seitz et al. 2003). Benthic communities in intertidal and shallow subtidal flats are highly productive and have comparable production values to salt marshes and seagrass beds (Peterson et al., in prep.)

Oyster reef placement on top of a benthic community is a type of compensatory restoration that involves the replacement of one currently existing functioning habitat by another (e.g., habitat substitution; Foster et al. 1994, Fonseca et al. 2000, Peterson et al., in prep). If organisms are going to be destroyed in the name of restoration, then the restored organisms should compensate for the loss due to the reef's placement on top of the benthos (Peterson & Kneib 2003). Benthic losses not only include the biomass killed but also the loss associated with the production that would have been expected had the benthic infauna been able to live their natural life spans (Peterson et al. 2003).

Secondary production is the rate of change in biomass of a population per unit of time and area and is a comparative parameter that can be applied as an estimate of ecological quality of different habitats with different species, life histories, and growth rates (Burton et al. 2002, Nestlerode 2004, Cusson & Bourget 2005, Peterson et al., in prep). To estimate the loss and potential gain in production between benthic and oyster reef habitats, biomass production for each habitat can be calculated and secondary production can serve as a proxy for ecosystem services (Diaz & Schaffner 1990, Edgar 1990, Fonseca et al. 2000, Burton et al. 2002, Steimle et al. 2002, French McCay & Rowe 2003, Peterson & Lipcius 2003, Nestlerode 2004, Peterson et al., in prep). Estimates of the annual loss of secondary producers in the benthos can be compared to estimates of annual secondary production of the oyster reefs by obtaining total macrobenthic biomass for the benthos and oyster biomass for oyster reefs along with published annual production to biomass (P:B) ratios for each taxa (Banse & Mosher 1980, Diaz & Schaffner 1990, Burton et al. 2002, Steimle et al. 2002, Cusson & Bourget 2005, Peterson et al., in prep). Only oyster secondary production was used to determine the success of the different oyster restoration reef types since the purpose of these reefs was to enhance oyster production.

Oyster reef restoration may include the use of various substrate types. Many restoration reefs are constructed of oyster shell to mimic the natural reefs that once existed. Oyster shell, though, is becoming a limiting resource and other substrates are being tested to determine if they would be suitable habitats for oysters (Nestlerode et al. 2002, Nestlerode 2004, Lipcius & Burke 2006). Different substrates and their construction will affect the amount of oyster settlement and thus the amount of oyster production on each reef type. A concurrent study at VIMS is using four types of experimental oyster reefs (oyster shell, rip-rap, concrete module, and reef ball) at two sites within Lynnhaven, Virginia, to compare the settlement and survival rates of oysters on these four reef types (R. Lipcius, pers. comm.).

My study examines the benthos in association with this oyster reef restoration at the same two sites as the concurrent study. I will conduct benthic sampling in the area of the reefs' footprint prior to the deployment of the four reef types to characterize the benthic community at each site and compare the infaunal benthic production to an estimate of oyster production on the oyster reefs. The objective of my study is to determine if estimated oyster production on four types of oyster reefs will compensate for the amount of benthic production lost by placing the oyster reefs on top of the benthos at two sites in Lynnhaven, VA.

MATERIALS AND METHODS

This study took place in the Lynnhaven River system, the southern-most system in Chesapeake Bay, located within the City of Virginia Beach, Virginia. Lynnhaven consists of four main water bodies (Broad Bay, Linkhorn Bay, and the Eastern and the Western Branch of the Lynnhaven River), is ~67 square miles in area, and has a total of ~150 miles of shoreline. The study was completed at two sites in the Lynnhaven system (one in Linkhorn Bay and one in the Eastern Branch) that were pre-determined by the concurrent study (Fig. 1).

Prior to the reefs' deployment, four sample locations were randomly sampled in the footprint of the future location of the oyster reefs (~23 m^2) at each site. The samples were taken in June/mid-July 2006, and the oyster reefs were deployed in late July 2006. Four reef types (oyster shell, rip-rap, concrete module, and reef ball) were placed in triplicate in a row parallel to shore and were located in the low intertidal zone at each site (Fig. 2). Oyster shell reefs consisted of oyster shells piled on top of each other in a mound. Rip-rap reefs consisted of large rocks placed on top of one another in a mound. A concrete module consisted of two concrete squares (each ~0.31 m^2) stacked on top of each other with space between the squares and holes within the squares to provide for good water flow and to maximize the area for oyster settlement. Two concrete modules (each consisting of two concrete squares) were placed on top of a square concrete base, which was then placed on the seabed, to prevent the modules from sinking into the sediment. A reef ball reef consisted of a hollow concrete sphere with a flat top and bottom that had holes throughout to allow for good water flow and maximize the surface area for oysters to settle. The concrete reef ball had oyster shells embedded throughout the surface to help enhance oyster settlement.

Physical Parameters

A benthic habitat assessment was performed for each of the sample locations at both sites by determining sediment grain size (using standard wet sieving and pipetting) (Folk 1974) and by completing a Carbon, Hydrogen, Nitrogen (CHN) analysis of the sediment. Two of the four samples taken were randomly selected and analyzed for sediment grain size and Total Organic Carbon (TOC) and Total Nitrogen (TN). Sediment grain-size analysis was completed and reported in percent sand/gravel content. These samples were taken in association with benthic macrofauna samples (described below) using a 2.5-centimeter (cm)-diameter surface-sediment core.

Benthic Sampling

Benthic samples included a suction sample and a small core sample at each sample location. A suction apparatus was used to collect larger benthic organisms, which involved the removal of sediment within a cylinder of 0.11 m^2 surface area to 40 cm depth (Eggleston et al. 1992). Sampling to this depth in the sediment ensures an accurate estimation of densities of deep-dwelling, large bivalves that are sparsely distributed (Hines & Comtois 1985). The sediment and infauna were collected in a 1 millimeter (mm) mesh bag and sieved on a 1 mm mesh screen. A 10-cm diameter core, used to remove sediment to 15 cm depth, was taken in association with the suction sample. This sample was sieved through a 500 micron sieve to collect smaller organisms in the community. Both the suction and small core samples were taken back to the lab and frozen until they were processed. The 10 cm core samples were not processed for this project; however, they can be used in the future to further examine patterns observed from the suction samples. Suction samples were sorted and the animals removed and identified to the lowest possible taxonomic level (usually species). Shell length of each bivalve from each sample was measured.

Biomass estimates for all organisms were calculated using ash-free dry weight (AFDW). Polychaetes, crustaceans, and shucked bivalves (except *Macoma balthica* and *Tagelus plebeius* -- see below) were dried to a constant weight and ashed in a muffle furnace at 550°C for six hours to obtain ash weight. Regressions of shell length (SL) to AFDW were used for abundant bivalve species (*M. balthica* and *T. plebeius*) to estimate biomass from size. Clams were selected throughout the entire range of sizes collected from a previous study (Chapter 1) completed in Lynnhaven (27 clams ranging from 7.8 to 36.5 mm SL for *M. balthica* and 25 clams ranging from 4.2 to 75.2 mm SL for *T. plebeius*) for input into a regression. The best-fit equations were the following single, three-parameter models:

M. balthica: $\mathrm{AFDW} = -0.0861 + 0.0427e^{0.0651*\mathrm{SL}}$ ($r^2 = 0.97$)

T. plebeius: $\mathrm{AFDW} = -0.3222 + 0.2237e^{0.0261*\mathrm{SL}}$ ($r^2 = 0.93$)

Statistical Analyses

The first step in determining production values for the benthos lost at the two sites was to calculate the total infaunal biomass in grams (g) AFDW m^{-2}. Average biomass of the infaunal community was obtained from the four benthic suction samples taken in the area of the reefs. Infaunal biomass for each taxonomic group at each site was multiplied by the appropriate published P:B ratio (bivalve P:B = 2.9, polychaete P:B = 4.9, and crustacean P:B = 5.7; Baird & Ulanowicz 1989, Diaz & Schaffner 1990) to obtain the production of the benthos in g AFDW m^{-2}/yr. The production numbers were then multiplied by the area of benthos lost per reef type at each site to obtain total production lost (g AFDW/yr).

The same process was followed to obtain production values for the predicted oyster abundance on each reef type. Since oysters did not have sufficient time to settle on the new reefs prior to the completion of this study, oyster biomass values (g AFDW m^{-2}) were estimated from previous studies researching the same established reef types within the Lynnhaven system (oyster shell – Luckenbach & Ross, in prep, rip-rap – Burke, in prep) and the Chesapeake Bay (concrete module – Lipcius & Burke 2006). Little work has been conducted on reef balls, therefore, to establish an oyster production (biomass) number, 90% of the concrete module reef oyster production value was used, since a majority of the reef ball was concrete, and was added to 10% of the oyster shell reef oyster production value, since oyster shells were embedded in the reef ball. The oyster biomass numbers were multiplied by the published P:B ratio (2.4) for oysters (Dame 1972, Bahr & Lanier 1981) to obtain the production of oysters on each reef type (g AFDW m^{-2}/yr). Oyster production values for each reef type were then multiplied by the area available for oyster settlement per reef type to obtain the total oyster production value for each reef type (g AFDW/yr).

Oyster biomass estimates (g AFDW m^{-2}) for oyster shell and rip-rap reefs were recorded as three-dimensional estimates. The number of oysters present in a 1 m^2 column of the reef was estimated from counts that started from the surface of the reef and preceded down into the reef until no further live oysters were found (Coen & Luckenbach 2000, Luckenbach & Ross, in prep, Burke, in prep). Since oyster biomass estimates were reported in this manner for oyster shell and rip-rap reefs, the estimates were multiplied by the footprint of these reefs as opposed to the actual surface area available for settlement (as was done for concrete modules and reef balls) to obtain total oyster production values for each reef type.

Finally, the amount of benthic production lost at each site for each reef type was compared to the amount of oyster production estimated for each reef type to determine if the oyster production on each reef type would compensate for the amount of benthic production lost by placing that reef over the benthos (*sensu* Peterson et al., in prep).

RESULTS

Eastern Branch

The Eastern Branch site was a muddy site with temperatures in June 2006 of ~24.5°C (M. Sisson, pers. comm.) and salinity ~22.1. Average sand/gravel composition at the Eastern Branch site was 24.41% (standard error [SE] = ± 3.15), classifying the site as mud. The average TOC of the samples was 2.19% (SE = ± 1.12) of the dry sediment sample and the average TN was 0.14% (SE = ± 0.04).

I collected a total of eight benthic infaunal species at the Eastern Branch site in the four samples collected in the reef footprint (Table 1). *Macoma balthica* was the only bivalve species collected. Four species of polychaetes, one isopod species, one species of amphipod, and mysids were also collected at the site. Numerically dominant polychaetes were *Leitoscoloplos* spp. (45% of total polychaete density), *Neanthes succinea* (34%), and Capitellidae (21%).

Macoma balthica accounted for 98% of the total benthic biomass. Polychaetes accounted for approximately 2% of the overall biomass, and crustaceans contributed less than 1% to the overall benthic biomass.

Linkhorn Bay

The Linkhorn Bay site was a sandy site with temperatures in July 2006 of ~30.0°C (M. Sisson, pers. comm.) and salinity ~17.5. Average sand/gravel composition at the Linkhorn Bay site was 96.48% (SE = ± 1.48), classifying the site as sand. The average TOC of the samples was 0.15% (SE = ± 0.03) of the dry sediment sample and the average TN was 0.02% (SE = ± 0.001).

I collected a total of eight benthic infaunal species at the Linkhorn Bay site in the four samples collected in the reef footprint (Table 1). Three species of bivalves were collected at the site, and, similar to the Eastern Branch site, *M. balthica* was the numerically dominant species (66% of total bivalve density) followed by *Tagelus plebeius* (25%) and *M. mitchelli* (9%). Five species of polychaetes and zero crustacean species were collected at the site. Numerically dominant polychaetes were *N. succinea* (60% of total polychaete density), Capitellidae (30%), and *Eteone heteropoda* (7%).

Bivalves accounted for 98% of the total benthic biomass. *Tagelus plebeius* contributed approximately 96% of the total benthic biomass with *M. balthica* contributing 2%. Polychaetes accounted for 2% of the overall benthic biomass, and there were no crustaceans to contribute to the biomass.

Secondary Production

For each sample, the total biomass (g AFDW m^{-2}) of the bivalves, polychaetes, and crustaceans (Table 2) were multiplied by their respective P:B ratios and the average production of the four samples for each taxonomic group was calculated for both sites (Fig. 3). The average total infaunal community production for the Eastern Branch site was 91.92 (SE = ± 45.15) g AFDW m^{-2}/yr and for the Linkhorn Bay site was 42.68 (SE = ± 14.20) g AFDW m^{-2}/yr. Benthic production values for each site were then multiplied by the area of seabed covered by each reef type (i.e., footprint of the reef [Table 3]) to determine the amount of benthos lost (g AFDW/yr) per reef type at each site.

Biomass estimates of the oysters on each reef type (Table 3) were multiplied by the P:B ratio for oysters, resulting in the production of oysters (g AFDW m^{-2}/yr) on each reef type (Fig. 4). These production estimates were multiplied by the area available for oyster settlement for each reef type (Table 3) to obtain the total amount of oyster production (g AFDW/yr) on each reef type. It was assumed that 100% of the area available for settlement was occupied by live oysters.

The amount of benthic production lost due to each reef type at each site was then compared to the estimated oyster production for each reef type (Fig. 5) to determine if the oyster production on each reef type compensated for the amount of benthic production lost by placing that reef on top of the benthos. Estimated oyster production on the oyster shell and reef ball reefs was higher than the amount of benthic production lost at each site due to these reefs. The estimated oyster production on the rip-rap reefs and the concrete module reefs with bases was higher than the amount of benthic production lost due to these reefs at the Linkhorn Bay site; however, the estimated oyster production on these two reef types was lower than the amount of benthic production lost at the more productive Eastern Branch site.

DISCUSSION

The Eastern Branch site had twice the benthic biomass and secondary production than did the Linkhorn Bay site. At the Eastern Branch site, *Macoma balthica* was one of the dominant species that drove densities and contributed most of the biomass. *Leitoscoloplos* spp., *Neanthes succinea*, and Capitellidae were the dominant polychaetes and the other main drivers of benthic density; however, these species contributed little to the overall biomass. At the Linkhorn Bay site, *Macoma balthica* was the dominant bivalve, though *Tagelus plebeius* was the main contributor to the overall total biomass. *Neanthes succinea* and Capitellidae were the dominant polychaetes and the main drivers of benthic density at this site; however, they contributed little to the overall biomass. Crustaceans contributed very little to the overall biomass at the Eastern Branch site and were not present in samples at the Linkhorn Bay site.

Of the four reef types, oyster shell reefs had the highest estimated oyster secondary production, followed by reef ball, concrete modules, and rip-rap reefs. Production of oysters on oyster shell and reef ball reefs compensated for the amount of benthic production lost due to placing the reefs on top of the benthos at both sites; however, the oysters on the rip-rap reefs and concrete module reefs with bases did not compensate for lost benthic production at the Eastern Branch site where benthic productivity was high, and they just barely compensated for the benthos at the Linkhorn Bay site, which had lower benthic productivity.

Oyster shell reefs were estimated to have the highest oyster productivity of the four reef types, and predominately have had higher oyster settlement and survival when compared with alternative reef types in the Chesapeake Bay (O’Beirn et al. 1999, Nestlerode et al. 2002, Nestlerode 2004, Burke, in prep). High oyster productivity on the oyster shell reefs more than compensated for the benthic production lost due to the oyster shell reefs at both sites.

Reef ball reefs covered the least amount of benthic bottom compared to the other four reef types; therefore, less oyster production was needed to compensate for this lost benthos. Reef ball reefs covered 40% less bottom than oyster shell and rip-rap reefs and almost four times less bottom than the concrete module reefs with bases. It was estimated that reef ball reefs would have the second highest oyster production of the four reef types, mainly due to the 10% of the oyster production that was attributed to the oyster shell embedded in the concrete of the reef ball structure (recall that oyster production on reef balls was estimated as 90% of concrete module reef oyster production plus 10% oyster shell reef oyster production). Oysters on the reef ball reefs more than compensated for the benthic production lost at both sites due to the small amount of bottom area covered and the high oyster productivity estimated on the reef ball.

Rip-rap reefs had the lowest amount of estimated oyster production of the four reef types and only compensated for the benthic production lost at the Linkhorn Bay site. Both oyster shell and rip-rap reefs covered the same amount of benthic bottom; however, the low oyster production on the rip-rap reefs did not compensate for the high benthic production at the Eastern Branch site.

Concrete module reefs with bases had the third highest estimated oyster production and, similar to the rip-rap reefs, only compensated for the benthic production lost at the Linkhorn Bay site (with lower benthic productivity). The concrete module reefs with bases covered the largest amount of benthic bottom due to the ~1.49 m^2

concrete base that was placed over the benthos prior to the placement of the concrete modules on top. A concrete base was necessary to prevent the concrete modules from sinking into the sediment. Oyster production on the concrete modules did not compensate for the amount of benthic production lost at the Eastern Branch site by placing the concrete base on top of the benthos because the benthic infauna at this site included many large, productive bivalves. If the concrete base had not been placed on top of the benthos then the two concrete modules at each site would have covered ~0.64 m^2 bottom area (compared to the ~1.49 m^2 covered by the base), similar to the bottom covered by the oyster shell and rip-rap reefs. Oyster production on the concrete modules without the bases would have easily compensated for the lost benthic production at lower productivity Linkhorn Bay site and would have just barely compensated at the higher productivity Eastern Branch site.

When estimating the amount of oyster production for each reef type, it was assumed that 100% of the area available for oyster settlement on the four reef types was occupied by live oysters. This is clearly an over-estimation, as the oyster settlement on a reef depends on many physical and biological factors (Wells 1961, Bisker & Castagna 1987, Eggleston 1990, Lenihan 1999, Mann 2000, Peterson & Associates 2003, Nestlerode 2004, Newell et al. 2007). In spite of this, even if the oyster shell and reef ball reefs in this study only had half the amount of oyster settlement estimated, they still would have compensated for the amount of benthic production lost at both sites. However, even at 100% oyster settlement, the rip-rap reefs and concrete module reefs with bases would not have compensated for the amount of benthic production lost at the more productive Eastern Branch site. And, while I stated previously that the oyster production on the rip-rap reefs and concrete module reefs with bases did compensate for the amount of lost benthic production at the Linkhorn Bay site, this would only hold true if at least ~78% of the area available for settlement on the rip-rap reefs and at least ~90% of the area available for settlement on the concrete modules with bases were occupied by live oysters. These percentages are still high, therefore, based on these values, the rip-rap reefs and concrete modules reefs with bases likely would not have compensated for lost benthic production at either site. If bases had not been placed out prior to deployment of the concrete modules, the oysters on the concrete modules would have compensated for lost benthic production at the Linkhorn Bay site, but at least ~83% of the area available for oyster settlement on the concrete modules without bases would need to be occupied by live oysters to compensate for lost benthos at the Eastern Branch site.

There are various methods for calculating production estimates (Thayer et al. 1973, Waters & Crawford 1973, Morin et al. 1987, Baird & Ulanowicz 1989, Diaz & Schaffner 1990) many of which are labor-intensive and restricted to estimating single-species rather than community production (Nestlerode 2004). As an alternative to the P:B ratio method (used in this study), the Edgar method uses ash-free dry weight and temperature in an equation for estimating daily macrobenthic secondary production (Edgar 1990). Temperature values, however, were not available from the sources from which the oyster biomasses were obtained, and therefore this method could not be used in this study. Because I was able to obtain published P:B ratios for benthos and oysters in Chesapeake Bay and since this method has been used reliably in previous studies, the use of P:B ratios to calculate secondary production was most appropriate for this study (Banse & Mosher 1980, Diaz & Schaffner 1990, Burton et al. 2002, Steimle et al. 2002, Cusson & Bourget 2005, Peterson et al., in prep). Once actual oyster biomass estimates and temperatures are obtained from the four reef types at the sites (Burke, in prep), production estimates from the Edgar method could be used and the results compared to those obtained herein using P:B ratios.

It is well recognized that oyster reefs house additional organisms besides oysters (Wells 1961, Larsen 1974, Nestlerode 2004). Meiobenthos was not included in my production estimates for either the oyster reefs or the benthic infauna. Additionally, no other macrobenthos besides oysters were included in the production estimates for the oyster reefs. The main reason for this is while additional macrobenthic production estimates could be obtained from the literature for oyster shell reefs (Wells 1961, Larsen 1974, Nestlerode 2004), no estimates were available for the other three reef types. Additional macro- and meiobenthic production of the reefs and meiobenthic production of the infauna would of course increase the total production of both habitats; however, oysters alone can account for up to 80% of the respiration (and thus production) of macro-invertebrates on an oyster shell reef (Bahr 1974, Bahr & Lanier 1981) and, therefore, would be representative of the total macrobenthic production. For total macrobenthic production of an oyster shell reef, an additional 20% macrobenthic production would need to be added to the 80% oyster production. In this study, oyster secondary production was used as a currency (since the purpose of these reefs was to enhance oyster production) to determine the success of the different reef types in replacing the lost infaunal macrobenthic secondary production (Peterson et al. 2003, Peterson & Lipcius 2003).

Reefs have been used to mitigate benthic loss; however, careful consideration of the size and construction of the reefs is important to be sure they will compensate for the lost benthos. Artificial concrete reefs were deployed in Delaware Bay to mitigate for the destruction of soft-bottom habitat dredged in the Bay (Foster et al. 1994, Burton et al. 2002, Steimle et al. 2002). The artificial reefs, dominated by mussels and invasive bivalves, compensated for infauna lost due to reef placement, with the footprint of the reef being ~10% of the total reef surface area (Foster et al. 1994). Reef epifauna of these same reefs were found to have higher productivity by 1-2 orders of magnitude than that of local infauna, though there was large variability in enhancement of the reef epifauna due to potential annual recruitment variability of different taxa (Steimle et al. 2002). Finally, these reefs had improved benthic secondary production per unit area compared to the lost benthic habitat. However, the reefs did not compensate for the total lost annual benthic secondary production of the destroyed benthos because not enough reef surface area was created to mitigate for the total area of subtidal habitat dredged for which the reefs were suppose to compensate (Burton et al. 2002).

Oyster reefs provide very different habitats from the benthic habitats that existed before their placement (Steimle et al. 2002). Shallow sand and mud areas have high habitat values due to productive benthic communities (Seitz et al. 2006, Peterson et al., in prep). This study was completed to show the importance of habitat trade-off considerations between oyster reefs and the associated benthic communities. Oysters on two of the four reef types used for oyster restoration did not compensate for lost benthic secondary production due to placement of the oyster reefs on top of productive infaunal communities. Calculations of the benefits of oyster restoration, which involves substituting a structured habitat (i.e., oyster reefs) for a shallow benthic habitat, must include deductions for the lost services from the unstructured benthic habitat area that will be destroyed (Peterson et al., in prep). Consideration needs to be given to the direct role this lost benthic habitat plays in the marine ecosystem and the use of production estimates as proxies for important ecosystem functions can be used to accomplish this (French McCay & Rowe 2003). Productive infaunal communities must not be abandoned in the name of oyster restoration; therefore, managers must ensure that production on restored oyster reefs offsets the loss of these valuable benthic infaunal habitats.

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Table 1. Total number of bivalves, polychaetes, and crustaceans collected in four benthic samples (0.11 m^2) taken in the area of the reefs at the Eastern Branch and Linkhorn Bay sites in Lynnhaven, VA.

Species Name	Eastern Branch	Linkhorn Bay
BIVALVES		
Macoma balthica	135	21
M. mitchelli	0	3
Tagelus plebeius	0	8
Total Bivalves	**135**	**32**
POLYCHAETES		
Capitellidae	24	32
Drilonereis longa	0	1
Eteone heteropoda	0	7
Glycinde solitaria	1	0
Leitoscoloplos spp.	52	2
Neanthes succinea	39	64
Total Polychaetes	**116**	**106**
CRUSTACEANS		
Cyathura polita	5	0
Melita nitida	2	0
Mysidaceae	5	0
Total Crustaceans	**12**	**0**
Total Benthos	**263**	**138**

Table 2. Mean (±SE) biomass (g AFDW m^{-2}) of the bivalves, polychaetes, and crustaceans collected in four samples in the footprint of the reefs at the Eastern Branch and Linkhorn Bay sites in Lynnhaven, VA.

Site	**Bivalves**	**Polychaetes**	**Crustaceans**
Eastern Branch	30.54 (± 15.78)	0.62 (± 0.28)	0.06 (± 0.04)
Linkhorn Bay	14.15 (± 4.79)	0.34 (± 0.07)	0.00

Table 3. Area (m^2) of seabed covered (i.e., footprint of the reef) by each of four reef types, estimated biomass (g AFDW m^{-2}) of oysters and area (m^2) available for oyster settlement on each of four reef types in Lynnhaven, VA (Lipcius & Burke 2006, Burke, in prep, Luckenbach & Ross, in prep).

Reef Type	Reef Footprint	Oyster Biomass	Settlement Area
Oyster Shell	0.66	152.50	0.66
Rip-Rap	0.66	22.70	0.66
Concrete Module	1.49	6.86	4.28
Reef Ball	0.40	21.42	2.40

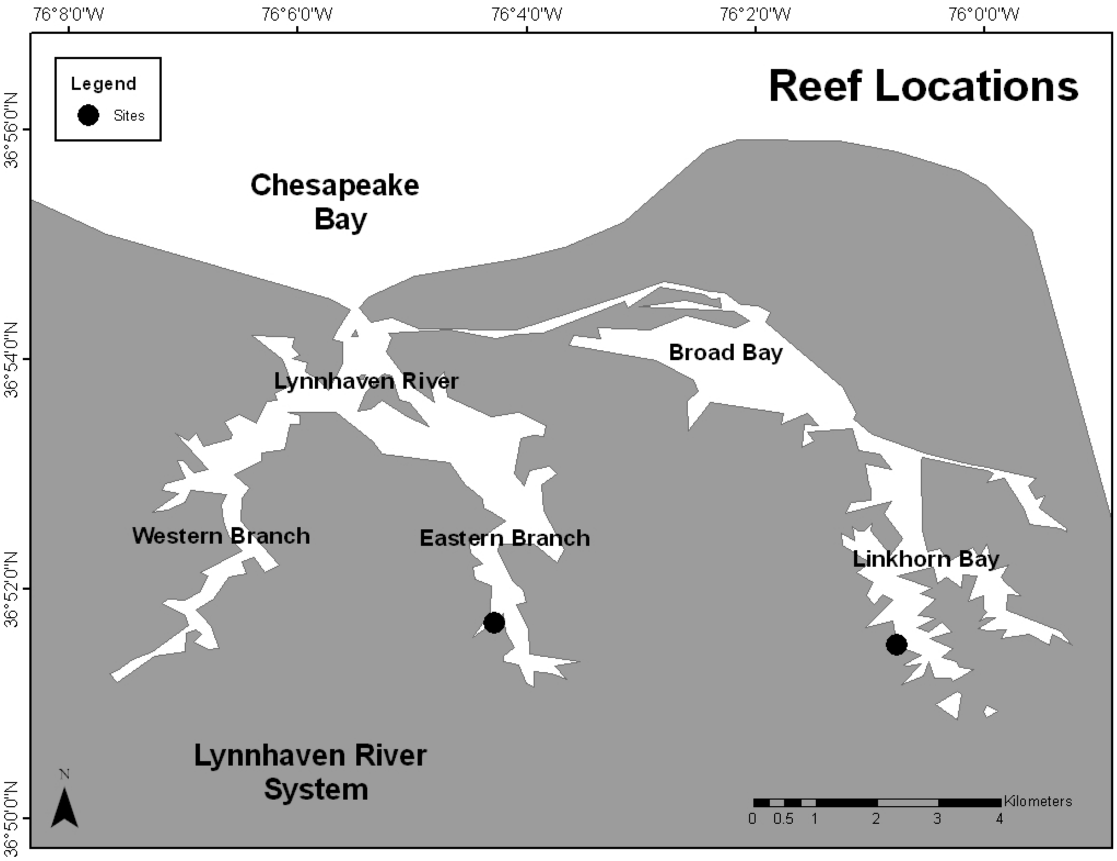

Figure 1. Locations of the Eastern Branch and Linkhorn Bay sites located in Lynnhaven, VA.

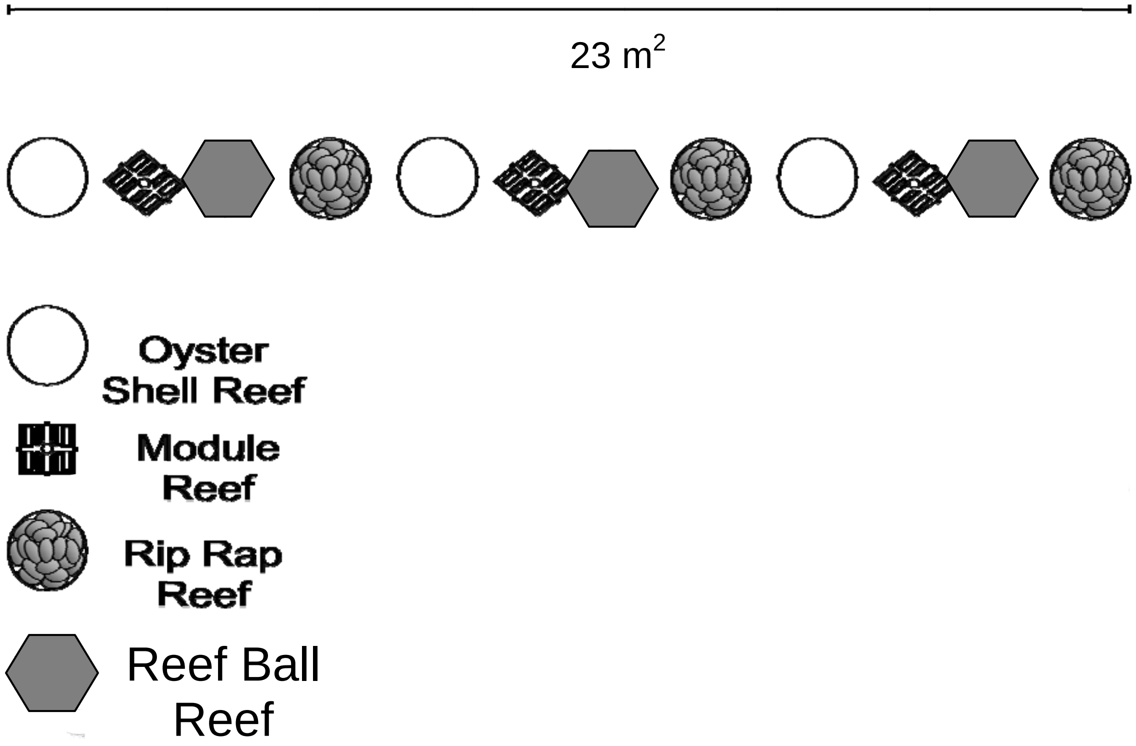

Figure 2. Layout of four reef types located in a 23 m^2 footprint at the Eastern Branch and Linkhorn Bay sites in Lynnhaven, VA.

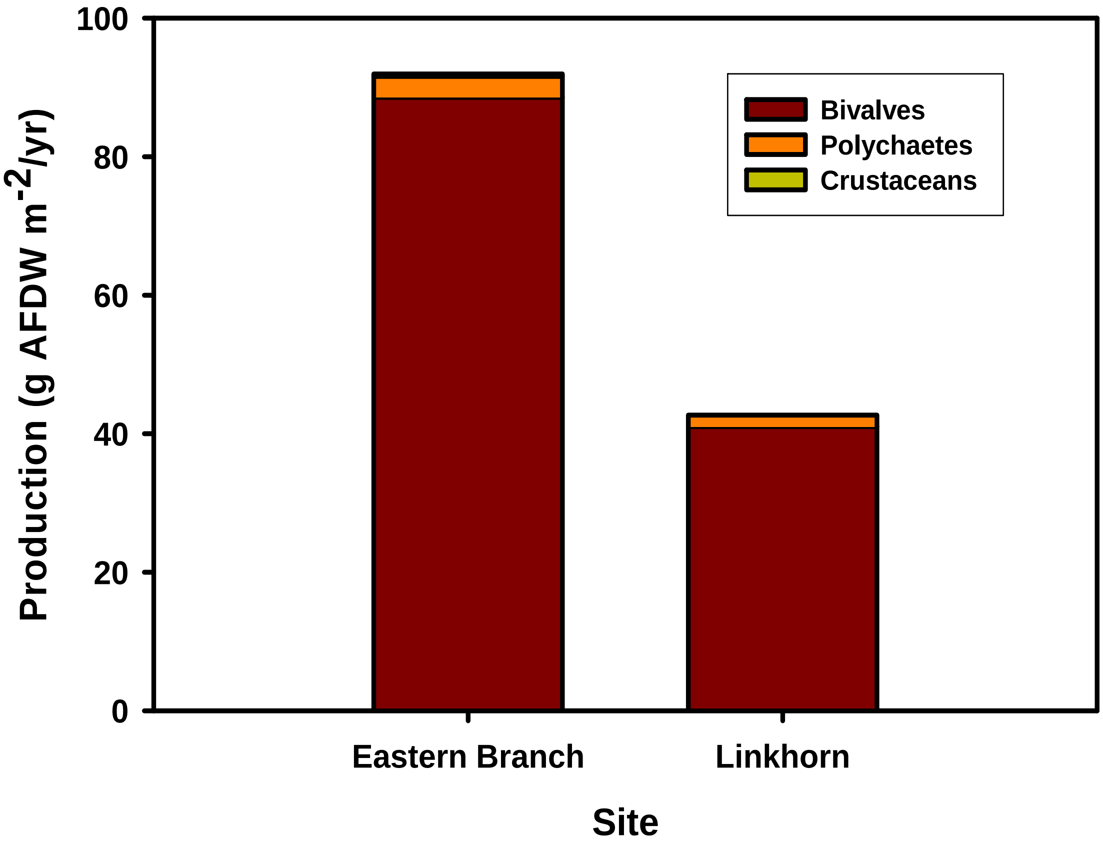

Figure 3. Average production (m^2) of bivalves, polychaetes, and crustaceans collected in four benthic samples taken in the area of the reefs at the Eastern Branch and Linkhorn Bay sites in Lynnhaven, VA.

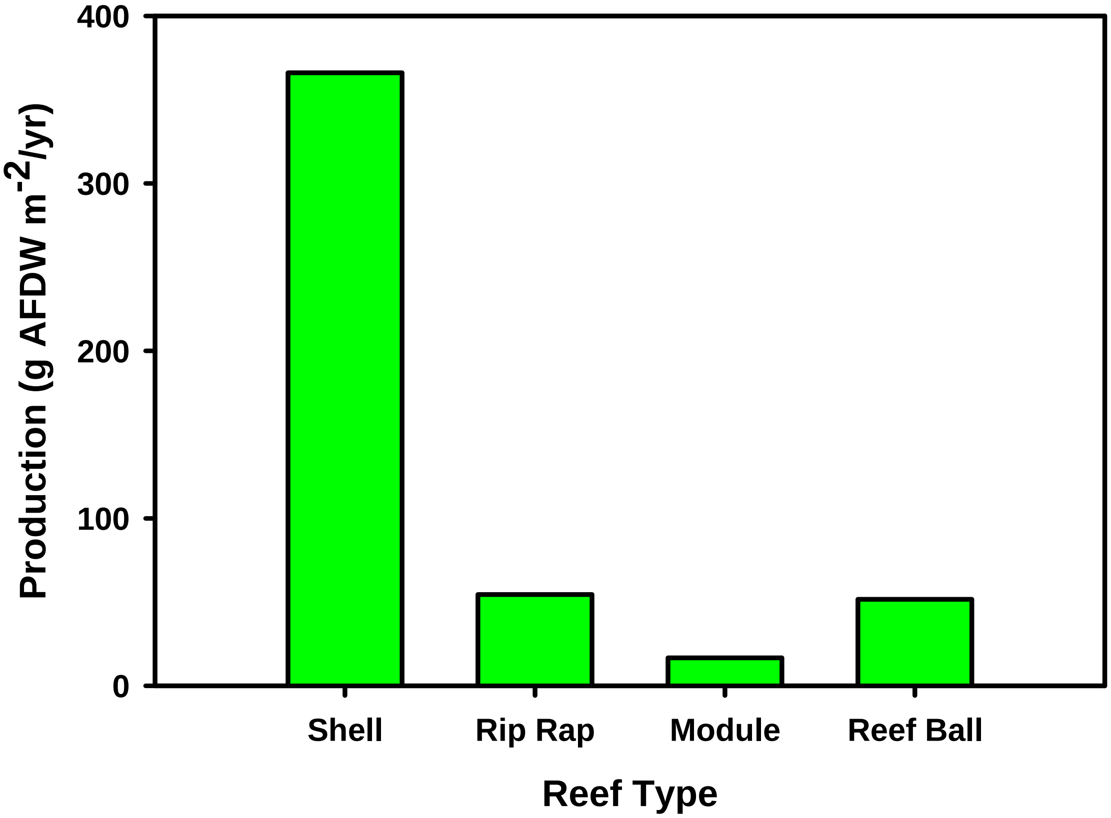

Figure 4. Average production estimates of oysters per m^2 on each of four reef types in Lynnhaven, VA.

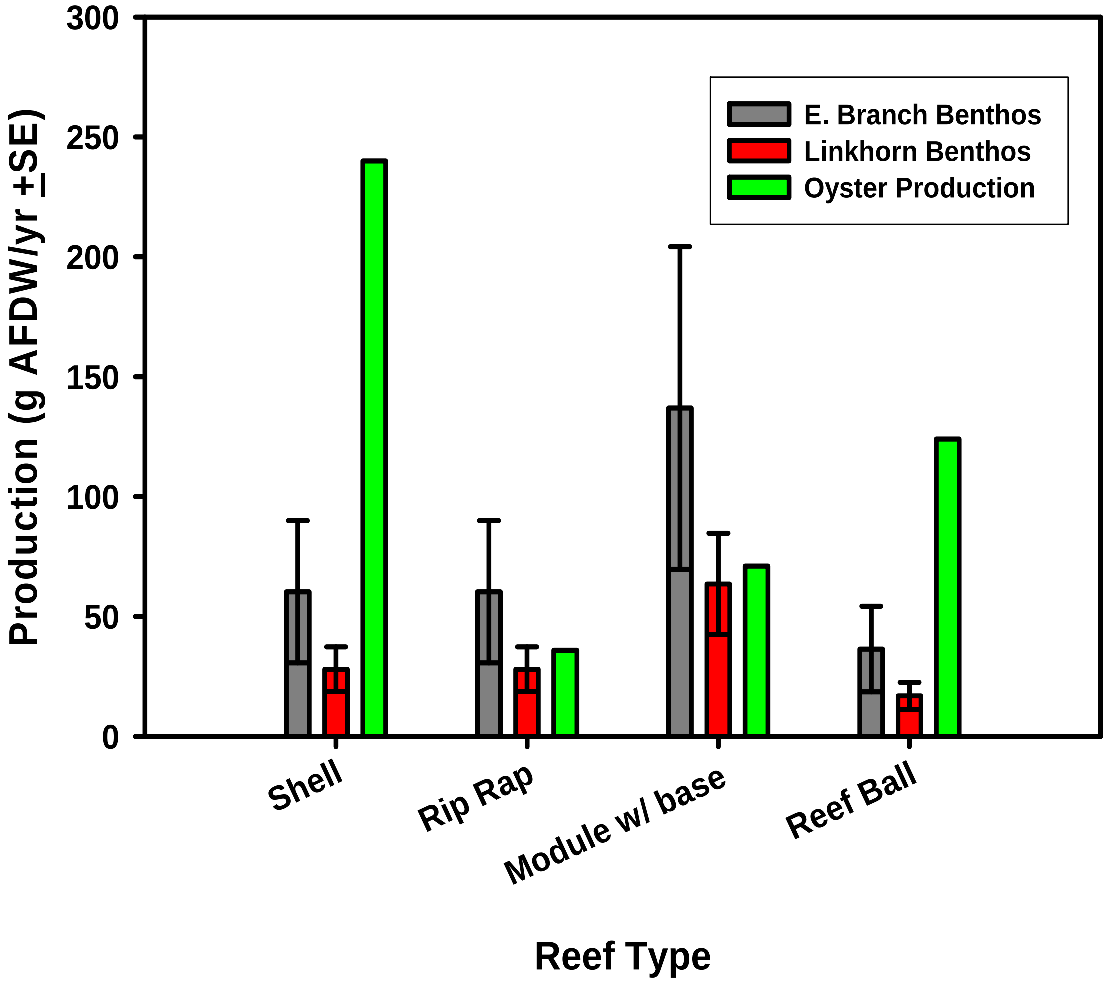

Figure 5. Amount of benthic production lost (+SE) at the Eastern Branch (E. Branch) and Linkhorn Bay (Linkhorn) sites for each reef type compared to the amount of total estimated oyster production for each reef type in Lynnhaven, VA.

CONCLUSIONS

The objective of this study was to determine what effects shoreline development and oyster reefs had on associated benthic infauna in Lynnhaven, Virginia. Both the hardening of shorelines and the construction of restoration oyster reefs are occurring rapidly in Chesapeake Bay. The effects of these structures on the adjacent benthic communities need to be quantified to help managers make decisions about replacement of natural shorelines with hardened shorelines and to aid in the determination of the appropriate type of oyster reef for a specific area.

As shown in Chapter 1, shoreline type was the best predictor of benthic infaunal density (oyster reef had the highest benthic density and bulkhead the lowest), while sediment composition (grain size and TOC/TN of the sediment) and predators were the best predictors of biomass and diversity. Interestingly, density of the benthos was affected by shoreline type, but biomass and diversity were not. This was attributed to the highly productive nature of the Lynnhaven system. Lynnhaven is a polyhaline, shallow, semi-enclosed, natural marsh-dominated system, which serves to explain why the system has an overall high productivity and why the altered shorelines in Lynnhaven were comparable to the natural shorelines (though bulkhead had the lowest associated benthic density) and no substantial effect was seen on the biomass and diversity of the benthos. The high productivity of Lynnhaven appears to be masking small-scale effects of shoreline hardening on the benthos.

In the Chapter 1 study, there was high density of benthic infauna associated with oyster shell reef shorelines. This led to the study in Chapter 2, to determine what effects oyster reefs had on the surrounding benthic community. Benthic infauna was sampled before and after the placement of restoration oyster reefs at two sites in Lynnhaven. There was a slightly positive effect of oyster reefs at one site on the surrounding benthos and no effect of the reefs at the other site after one year. Since the Lynnhaven system is highly productive, the small effects of these reefs on the surrounding benthos may not have been readily apparent and it may take longer than one year before the full effects of the reefs on the benthos can be observed.

The placement of restoration oyster reefs in the highly productive Lynnhaven system means productive benthic communities are destroyed when the oyster reefs are constructed. Results from Chapter 3 showed that oyster production on only two (oyster shell and reef ball) of four types (rip-rap and concrete modules) of restoration oyster reefs compensated for the benthic production lost due to the reefs being placed at the two sites in Lynnhaven.

The high productivity of the Lynnhaven system played an important part in the results of all three chapters. My results highlight that managers must still use caution when making decisions about the placement of hardened shorelines and oyster reefs in the Lynnhaven or any other system. Each system is unique and these structures could have different effects in different systems. With increasing urbanization of the Lynnhaven watershed taking place daily, the high productivity of the system needs to be maintained, and preservation of much of the remaining natural shoreline needs to be made a priority. Maintaining existing natural marsh shorelines and the use of certain types of oyster reefs as “living shorelines” in various areas throughout Lynnhaven could help promote not only the recovery of the oyster population but also help maintain the high productivity of the benthic community and the rest of the Lynnhaven system.

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