ABSTRACT

Title of Document: COMPARISONS OF MACROFAUNA ASSEMBLAGES ON RESTORED AND NON-RESTORED OYSTER REEFS IN MESOHALINE REGIONS OF CHESAPEAKE BAY IN MARYLAND

William S. Rodney, Masters of Science, 2007

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Recently restored oyster sanctuary reefs in Maryland allowed for a unique opportunity to observe the abundance and species composition of macrofauna assemblages on unexploited reefs with high concentrations of mature oysters and undisturbed reef architecture. These observations provided insights on the potential changes to reef dwelling macrofauna communities and various reef ecological functions resulting from reef restoration. I sampled macrofauna at four restored oyster sanctuary reefs and adjacent non-restored plots located outside sanctuary boundaries. I then compared the effects of study site location and habitat quality (restored vs. non-restored) on macrofaunal density using thirteen response variables. Motile macrofauna density was an order of magnitude higher on restored reefs and sessile macrofauna density was two orders of magnitude higher on restored reefs. Two out of four functional feeding groups: suspension

feeders and carnivore/omnivores, were more abundant on restored plots. Results indicate that restoration improved reef ecological structure and function.

# COMPARISONS OF MACROFAUNA ASSEMBLAGES ON RESTORED AND NON-RESTORED OYSTER REEFS IN MESOHALINE REGIONS OF CHESAPEAKE BAY IN MARYLAND

By

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# Dedication

This work is dedicated to the memory of my father, William Stanley Rodney Sr., who instilled in me an appreciation of science at an early age.

# Acknowledgements

I am deeply grateful to my parents, Flora Anne and William Stanley Rodney Sr. for urging me to return to graduate school and for emotional and financial support during the lean years that ensued. I also would like to thank my wife Kristin for suffering through the unpredictable slings and arrows of the graduate student existence. I am also grateful to my faculty advisor, Dr Kennedy T. Paynter for giving me the opportunity to pursue this most interesting research program. Drs David Secor, Ronald Klauda and Roger Newell reviewed early drafts of the resulting manuscript and provided advice that resulted in a much improved document. Dr. Sandra Shumway and two anonymous reviewers also provided valuable input on a later draft of the manuscript. Dr. Denise Breitburg offered advice on sampling methods. Jake Goodwin and Tim Koles provided logistical support. Claire Goldschmidt, Valerie Hagan, Stephanie Stottel, Ellison Alldredge, and numerous others provided field, lab and sample processing help. I also thank Wonderbread, Inc. for donation of trays. Finally, I wish to thank the Oyster Recovery Partnership, the Army Corps of Engineers, and Maryland Department of Natural Resources for financial support.

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## Chapter 1: Introduction

*Background Information*

Large complex reefs created by eastern oysters (*Crassostrea virginica*) were once a prominent feature of the Chesapeake Bay ecosystem. Explorers reported that the Bay's oyster reefs were so large that they posed a hazard to ship navigation (Wharton 1957). By the early 20th century, overfishing and habitat degradation had decimated the Bay's oyster population. In the mid 20th century two diseases, MSX and Dermo, further reduced the Bay's struggling oyster population (Kennedy 1996). These insults have nearly eliminated the Bay's oyster population, and likely had a profound effect on the ecological functions once provided by oyster reefs and on the diverse macrofauna assemblages that the reefs supported. Unfortunately there are few data on Chesapeake Bay oyster reef fauna prior to the mid 1900s**.**

Maryland's recent oyster restoration effort provides a unique opportunity to observe the composition of macrofaunal assemblages on unharvested reefs with high concentrations of mature oysters and undisturbed reef architecture. Therefore, they may be used to assess the ecological roles of oyster reefs and reef dwelling macrofauna. It might then be possible to estimate the ecological benefits of large scale oyster reef restoration. There is currently great interest in restoring oysters in Chesapeake Bay. The Chesapeake 2000 agreement includes a stated goal of restoring oysters to 10 times the 1994 baseline level by 2010 (USEPA 2000). The Magnuson-Stevens Act includes a stated goal to protect, enhance and restore all "essential fish habitats" defined as "waters and substrate necessary to fish for spawning, breeding,

feeding, and/or growth to maturity". Fish were defined as "finfish, mollusks, crustaceans, and all other forms of marine animal and plant life other than marine mammals and birds" (USDOC 1997).

*Theoretical Basis for OysterRestoration*

Reasons for restoring oysters rest on certain theories about the ecological functions of oyster reefs. These functions include: (1) water filtration and regulation of water column phytoplankton dynamics, (2) enhanced nitrogen cycling between the benthic and pelagic system components, (3) enhanced recruitment, growth, and survival of oyster populations, (4) nursery and predation refuge habitat for a diverse community of invertebrates and small fishes, and (5) foraging habitat for transient piscivorous and benthivorous fishes.

*Oyster Reef Ecological Functions*

The theoretical basis for the first ecological function, that of water filtration and regulation of water column phytoplankton dynamics, comes from studies of introduced filter feeding bivalves in other systems (Cloern 1982, Cohen et al. 1984, Dame et al. 1992, Roditi et al. 1996) and from modeling studies (Cerco and Noel 2007, Ulanowicz & Tuttle 1991, Newell 1988). Theoretical support for the second function, enhanced benthic pelagic coupling, comes from studies of individual oysters (Srna & Baggaley 1976), mussel beds (Nixon et al. 1971, Asmus & Asmus 1991), and oyster reefs in other systems (Boucher & Boucher-Rodoni 1988). These studies illustrate how phytoplankton consumed by filter feeding bivalves is remineralized and released as ammonium. This ammonium may then be available for reuse by phytoplankton resulting in higher rates of nitrogen cycling (Newell et al. 2004, Dame et al. 1992).

The theory that oyster reef restoration can enhance recruitment, growth, and survival of oyster populations has been supported by studies of created oyster reefs in the Virginia portion of Chesapeake Bay. These studies have shown that concentrating many large oysters in a small area may increase fertilization efficiency (Pavlos & Paynter In Review) and that placement of restoration sites in semi-enclosed "trap" estuaries may retain oyster larvae near the site until they are competent to settle (Southworth & Mann 1998). Also, by providing clean shell in a spatially complex arrangement with many interstitial refugia, predation mortality on new recruited oysters may be reduced (O'beirn et al. 2000).

Several studies have described the diverse communities of macroinvertebrates and small fish that oyster reefs support (Wells 1961, Dame 1979, Zimmerman et al. 1989, Wenner et al. 1996, Meyer and Townsend 2000). However, most of these studies were conducted on intertidal reefs in polyhaline areas of the Southeastern and Gulf Coast regions. Similarly, several studies have demonstrated high finfish diversity and abundance over oyster reef habitats (Arve 1960, Bass & Guillory 1979, Zimmerman et al. 1989, Wenner et al. 1996, Luckenbach et al. 1997, Harding and Mann 1999, Harding and Mann 2000, Lehnert and Allen 2002). But again, most of these studies were either conducted on intertidal reefs in polyhaline areas of the Southeastern and Gulf Coast regions, or in the polyhaline zone of the Virginia portion of Chesapeake Bay, and on reefs that were not composed of densely packed, large oysters. The paucity of information on the faunal assemblages utilizing Maryland's mesohaline subtidal oyster reef habitats is not a trivial matter since disease mortality of oysters is

much higher in the Virginia portion of Chesapeake Bay and Maryland's waters therefore have better potential for successful long term oyster reef restoration.

*Study Goals and Objectives*

This study was primarily concerned with quantifying the differences in benthic macrofaunal community composition between restored and unrestored plots on oyster bars. Specifically, I set out to compare the macrofaunal assemblages of restored and degraded subtidal mesohaline oyster reef habitats in Maryland. My goal was to assess whether reef restoration may result in (1) increased diversity and/or abundance of benthic macrofauna, (2) improved foraging habitat for transient piscivorous and benthivorous fish, and (3) increased transfer of energy to higher trophic levels. I interpreted my findings in terms of the magnitude of macrobenthic community enhancement due to reef restoration.

# Chapter 2: Materials and Methods

*Study Sites*

Benthic macrofauna assemblages were sampled at four oyster sanctuary reefs in the mesohaline region of Chesapeake Bay: Chinks Point, Neal Addition, Spaniard Point and Howell Point. Each site was located in a different Chesapeake Bay subestuary: the Severn, Patuxent, Chester and Choptank Rivers respectively. For each restored (treatment) site a nearby paired unrestored (control) site was also sampled. "Restored" reefs were defined as areas having been restored with fresh oyster shell and topped with a layer of shell that was seeded with live juvenile oysters. Sanctuaries were protected from oyster harvesting activities and were allowed to develop for four to five years prior to sampling. These reefs had high densities of adult oysters (mean of 173 oysters $m^{-2}$) embedded in a thick matrix of living and dead oysters and oyster shell. These areas were established by a large scale experimental oyster restoration program designed to recreate healthy oyster reef habitats in numerous areas where oyster reefs existed prior to historical degradation. Unrestored reefs were defined as areas located on the same historic oyster bars, according to Maryland Department of Natural Resources maps (Smith 1997), as the restored plots but not restored with new shell or oyster seed and not protected from oyster harvesting. Unrestored plots typically contained dead oyster shells buried beneath up to several centimeters of silt. Unrestored sites were between 0.16 and 0.8 km from their paired treatment sites and were located at about the same water depth. Criteria for my site definitions were verified visually for each sampling location by SCUBA divers. Water quality information for my four study sites was obtained from the Maryland Department of Natural Resources Water Quality Monitoring Program.

Water temperature ranged from 0.9 ˚C to 28.8 ˚C with a mean of 22.3 ˚C. Salinity ranged from 5.3 psu to 18.5 psu with a mean of 10.3 psu. Dissolved oxygen ranged from 0.2 mg $L^{-1}$ to 13.0 mg $L^{-1}$ with a mean of 5.9 mg $L^{-1}$. Details on site locations and environmental characteristics are provided in Appendix 2 and in Smith (1997).

*Sampling Procedures*

Sampling units were plastic bakery trays (50 x 58 x 10 cm) lined with fiberglass window screen, and randomly assigned to sites and treatments. Nylon ropes of randomly assigned length (≥ 2 m) linked the trays together and were attached to nearby permanent buoy anchors or anchor screws. SCUBA divers excavated holes in the bottom substrate and placed this material into the trays. These trays were then inserted into the holes created by excavation. Because my goal was to compare conditions on high quality undisturbed oyster reefs to the degraded conditions that currently prevail, trays at treatment sites were filled with the best available substrate at the site. This included clumps of live oysters and articulated shells of recently deceased oysters (henceforth referred to as "boxes"). Care was taken to transfer clumps of restored reef materials into trays with as little disturbance as possible and to place the reef materials in the trays without changing the original orientation of the oysters relative to flow direction or the vertical dimension. Trays were allowed a minimum of 6 weeks colonization time. During tray retrieval, caps were placed over the trays by SCUBA divers. Caps were then secured with elastic cords. The trays were then lifted aboard a boat where trays and their contents were placed in plastic bags and taken to shore for field processing.

Trays were placed upright on a sieving apparatus that consisted of two sieves with large (1.6 cm2 ) and small (1 mm2 ) mesh stacked on a special sieving platform. All visible motile organisms were removed and placed in jars containing 70% ethanol.

Clumps of oysters, single oysters and all loose shells were dunked and agitated in buckets of water to dislodge cryptic organisms. Buckets were then poured through a sieve (1 mm2 mesh size) and organisms collected were preserved in 70% ethanol. Trays were then inverted onto the large sieve and gently rinsed with ambient bay water (Organisms attached to the trays were not included in the samples in order to minimize any tray effect). Materials retained on the large sieve were gently rinsed and all live organisms were collected. Remaining materials on the large sieve were placed in plastic bags for further processing in the laboratory. Once cleared, the large sieve was removed and any visible organisms retained on the small sieve were collected. Any materials remaining on the small sieve were retained in 70% ethanol for further processing. Organisms collected in the field and from preserved samples were identified, enumerated and weighed in the lab. High abundances of amphipods and polychaetes from Howell Point plots made it necessary to subsample these collections. Abundances for these species were estimated using simple random sampling without replacement (Thompson 2002).

*Habitat Characteristics*

Data was collected for three measures of physical habitat quality: an index of surface complexity, the number of oysters per sample, and the number of oyster "boxes" per sample. The surface complexity index was calculated for each sample by taking a plastic coated copper wire and, starting at one side of the tray, forcing the wire down into the spaces between shells until the wire reached the other end of the tray. The wire was then removed, straightened and measured. The measurement was then divided by the straight line length of the tray to give a dimensionless index of surface roughness. This method, adapted from the sinuosity index used in freshwater stream ecology (Allan 1995), returns a value of 1 for a flat surface and grows larger as

surface complexity increases. Three measurements were taken from each tray. Since oysters provide the physical substrate for the reef community, the density of oysters is a direct measure of habitat quality. Therefore, I counted all live oysters in each sample. I also counted the number of intact shells of recently deceased oysters in each sample. These intact shells, called "boxes", provide nesting sites and shelter for several species of resident fishes and xanthid crabs and are therefore considered to be an important component of reef habitat quality. Physical habitat data was not collected from the Neal Addition site because of equipment malfunction.

*Fouling Community*

All dominant fouling organisms were counted in samples from the Neal Addition site. In subsequent samples, due to logistical constraints, abundances of the dominant fouling organisms (*Ishadium recurvum*, *Balanus* sp., and *Diadumene leucolena*) were estimated by subsampling using the methods described above. Colonial and/or encrusting organisms such as bryozoans and hydroids were recorded as being present or absent. Fouling community data was not included in analyses of faunal density between restored and unrestored plots because these organisms are sessile and thus obligate hard substrate dwellers. Differences in abundance of fouling organisms between restored and unrestored plots were large, and in my opinion, did not warrant statistical analysis. Fouling community data was used in comparisons of functional feeding group densities and mean number of macrofauna species per sample and was included in my species list (Table 1).

*Macrofauna Group Density Comparisons*

I compared the effects of study site and habitat quality (restored vs. unrestored) on macrofauna density using eight response variables. Three of these eight response

variables were broadly inclusive groups including: (1) total free living macrofauna; (2) epifaunal organisms; and (3) infaunal organisms. The other five response variables were groups of taxonomically related organisms: (1) xanthid crabs; (2) polychaetes; (3) clams; (4) amphipods; and (5) demersal fish. Only free living organisms were used for density comparisons because these organisms could, in theory, move between habitat types and are thus capable of demonstrating habitat preferences. I defined "free living macrofauna" as any species that regulates its position on or in the substrate. Free living organisms included xanthid crabs, amphipods, errant polychaetes, demersal fish, clams, gastropods, isopods, caridean shrimp, nemerteans, and flatworms. I defined "epifaunal organisms" as any species that lives part of the time on the upper surface of the substrate. Epifaunal organisms included xanthid crabs, amphipods, demersal fish, gastropods, isopods, caridean shrimp, and flatworms. "Infaunal organisms" were defined as any species that lives most of its life below the upper surface of the substrate. Infaunal organisms included polychaetes, nemerteans, and clams. Counts of organisms per sample were converted to density (organisms $m^{-2}$) by dividing counts by the area of the settlement trays (0.28 $m^2$).

The differences between treatments to each response variable were analyzed using a 2-way ANOVA model in a randomized complete block design. Sites were treated as random blocks and treatments (restored and unrestored) were treated as fixed effects. Before any analyses were performed, the ANOVA assumptions of homoscedasticity and normality were evaluated using Levene's test and the Shapiro-Wilkes test respectively. When either test indicated that ANOVA assumptions were violated, graphical analysis of residuals was employed to examine the distribution of the

residuals. Either a log(x +1) transformation or a square root(x) + 0.5 transformation was used to correct for heteroscedasticity.

When variability in faunal density attributed to site effects was not significant, differences in density attributed to treatments were compared using data pooled among sites ($\alpha = 0.05$). In certain cases, single species that were numerically dominant within groups were analyzed separately to determine if life history differences among species confounded the results of the group analysis.

*Functional Feeding Group Density Comparisons*

Organisms were aggregated into functional feeding groups in order to asses the community level effects of restoration on ecosystem structure and function. I used a modified version of the USEPA Chesapeake Bay Program's classification system (Ranasinghe et al. 1994) to assign functional feeding groups to specific taxa. In some cases functional feeding group membership was determined from other published sources. Five functional feeding groups were used in my analysis. These groups were: Deep deposit feeders, surface deposit feeders, suspension feeders, carnivore/omnivores, and carnivores. "Deep deposit feeders" are those organisms that feed on biodeposits below the sediment surface. "Surface deposit feeders" are organisms that feed on biodeposits at the sediment-water interface. "Suspension feeders" are organisms that filter plankton from the overlying water column. "Carnivore/omnivores" feed on other organisms but may also ingest significant amounts of non-living materials (biodeposits) either intentionally or while foraging for live prey. Differences in functional feeding group densities between restored and unrestored plots were compared using the same statistical procedures used for the faunal groups.

# Chapter 3: Results

*Physical Habitat Quality*

Structural heterogeneity, as measured by my surface complexity index, was much greater on restored plots compared to unrestored control plots. Mean surface complexity index values were 1.84 (SEM = 0.15) versus 1.15 (SEM = 0.05) for restored and unrestored plots respectively. Mean oyster density on restored plots was 173 oysters $m^{-2}$ (SEM = +/- 25.52). Mean density of oyster boxes on restored plots was 70.63 boxes $m^{-2}$ (SEM = +/- 9.99). Oysters and oyster boxes were absent from samples of unrestored plots.

*Description of Macrofuana Assemblages*

I collected more than 19,000 free living macrofaunal organisms during the course of this study. Of these, 70% were collected from restored plots. If I were to include sessile or "fouling" organisms (barnacles, mussels, anemones and tunicates) in the total, then more than 40,000 organisms were collected with 86% from restored plots (Table 1). Thirty five species from 12 taxonomic groups were represented in my samples. Five taxonomic groups accounted for more than 95% of all organisms: xanthid crabs (Xanthidae), polychaete worms (Polychaeta), clams (Bivalvia), amphipods (Amphipoda), and demersal fish (Teleostei). The other seven groups included portunid crabs (Portunidae), caridean shrimp (Caridea), isopods (Isopoda),

| Latin Name | Common Name | Totals | |
|---|---|---|---|
| **Fish** | | **Restored** | **Non-restored** |
| *Gobiosoma bosci* | Naked Goby | 452 | 113 |
| *Opsanus tau* | Oyster Toadfish | 6 | 0 |
| *Chasmoides bosquianus* | Striped Blenny | 19 | 0 |
| **Mud Crabs** | | | |
| *Panopeus herbstii* | Black-clawed Mud Crab | 484 | 12 |
| *Eurypanopeus depressus* | Flat Mud Crab | 316 | 4 |
| *Rhithropanopeus harrisii* | White-fingered Mud Crab | 917 | 432 |
| **Grass Shrimp** | | | |
| *Palaemonetes pugio* | Grass Shrimp | 205 | 17 |
| **Amphipods** | | | |
| *Gammarus tigrinus* | Scud | 329 | 8 |
| *Gammarus mucronatus* | Spined-back Scud | 88 | 6 |
| *Corophium lacustre* | Slender Tube Builder | 1,230 | 1,018 |
| *Leptocheirus plumulosus* | Common Burrower | 0 | 641 |
| *Melita nitida* | Scud | 4,464 | 24 |
| **Clams** | | | |
| *Mya arenaria* | Soft Shell Clam | 431 | 410 |
| *Macoma* Sp. | Hard Clam | 450 | 542 |
| *Gemma gemma* | Gem Clam | 0 | 7 |
| *Mulinia lateralis* | Little Surf Clam | 0 | 63 |
| **Polychaetes** | | | |
| *Nereis succinea* | Common Clam Worm | 4,226 | 1,562 |
| *Steblospio benedicti* | | 0 | 2 |
| *Heteromastis filiformis* | Capitelid Thread Worm | 2 | 50 |
| *Arabella iricolor* | Opal Worm | 0 | 5 |
| *Pectinaria gouldii* | Trumpet Worm | 14 | 445 |
| **Other Motile Taxa** | | | |
| *Stylochus ellipticus* | Oyster Flatworm | 10 | 3 |
| *Micrura leidyi* | Red Ribbon Worm | 0 | 4 |
| *Calinectes sapidus* | Blue Crab | 0 | 1 |
| *Urosalpinx cinerea* | Oyster Drill | 0 | 4 |
| *Cyathura polita* | Slender Isopod | 0 | 1 |
| Unidentified snail | Snail | 3 | 1 |
| *Idotea* Sp. | Isopod | 6 | 11 |
| *Edotea* Sp. | Isopod | 1 | 0 |
| **Total Motile Organisms** | | 13,653 | 5,386 |
| **Fouling Organisms** | | | |
| *Mogula manhatenensis* | Sea Squirt | 179 | 45 |
| *Ishadium recurvum* | Recurved Mussel | 11,456 | 52 |
| *Balanus* Sp. | Barnacle | 11,129 | 339 |
| *Diadumene leucolena* | White Anenome | 259 | 83 |
| *Garveia franciscana* | Rope Grass | Present | Present |
| *Membranipora* Sp. | Encrusting Bryozoan | Present | Present |
| **Total Fouling Organisms** | | 23,023 | 519 |
| **Total Macrofauna** | | 36,676 | 5,905 |

Table 1. Cumulative macrofauna collected on restored and non-restored portions of four historic Maryland natural oyster bars. Totals represent fauna collected from a cumulative area of approximately 3.5 $m^{-2}$.

nemerteans (Nemertea), flatworms (Platyhelminthes), gastropods (Gastropoda), and cnidarians (Scyphozoa). These seven groups were sparsely represented in the samples and combined they made up less than five percent of all organisms. Free living macrofauna were more than twice as abundant on restored habitats compared to unrestored habitats (Table 1).

More than 23,000 fouling organisms were collected with 97% coming from restored plots. Fouling organisms were two orders of magnitude more abundant in restored plots compared to unrestored plots. The dominant fouling organisms were the recurved mussel (*Ishadium recurvum*) and balanoid barnacles (*Balanus* sp.). The white anemone (*Diadumene leucolena*) was also common. Colonies of encrusting bryozoans (Membranipora sp.) and hydroids (mostly *Garveia franciscana*) were extremely abundant on all restored plots but only occasionally observed in unrestored plots. Abundance of free living macrofauna and fouling organisms combined was an order of magnitude higher on restored plots compared to unrestored plots (Table 1). The average number of species per sample was significantly higher on restored plots (14.9) compared to unrestored plots (12.0 ) (paired t test, $p < 0.05$).

*Macrofauna Group Density Comparisons*

The density of free living macrofaunal organisms (log (x + 1) transformed) was more than twice as high on restored plots compared to non-restored plots (Figure 1.A.; $F = 35.45$, $p < 0.0001$). Epifaunal organisms were also found at more than twice the density in restored plots compared to non-restored plots ($F = 50.77$, $p < 0.0001$). No differences in infaunal density (square root (x) + 0.5 transformed) between restored

and non-restored plots were detected (F = 2.29, p = 0.1469). Amphipods were the most abundant taxonomic group in my samples and made up 41% of all organisms.

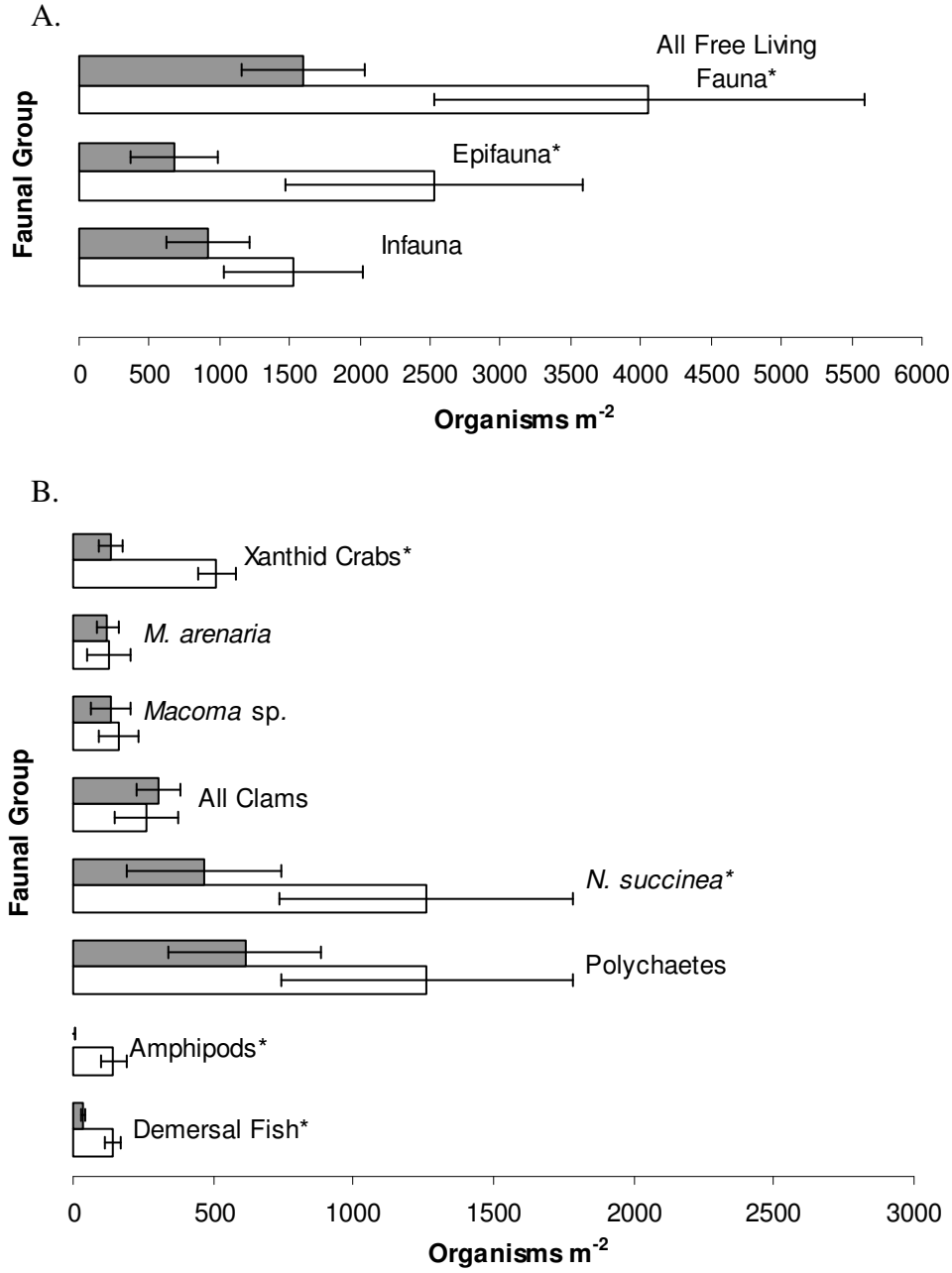


Fig. 1. Comparisons of mean faunal densities in restored (white bars) and non-restored (gray bars) plots for 3 broadly inclusive functional groups (A), and 8 taxonomic groups (B). Error bars represent +/- 1 SEM. Asterisks following group titles indicate statistically significant differences ($\alpha = 0.05$). Amphipod data for Howell Point is not included

A total of 7,808 amphipods representing four genera in four families of the Suborder Gammaridea were collected. These four genera were *Melita* (Melitidae), *Corophium*

(Corophiidae), *Leptocheirus* (Aoridae), and *Gammarus* (Gammaridae) made up 57.5%, 28.8%, 8.2%, and 5.5% of all amphipods respectively. 2 way ANOVA revealed a strong effect of Site on amphipod density ($F = 7.12$, $p = 0.0021$). Comparisons of least square means identified the Howell Point site as the source of this variability. Amphipod density was extremely high in both restored and non-restored plots at Howell Point compared to the other sites (Figure 2.B). Between sample variability in amphipod density was also extremely high in both restored and non-restored plots at Howell Point. For these reasons, I treated Howell Point as an outlier with respect to amphipod density. When Howell Point was excluded from the analysis, no significant differences in amphipod density were found among sites ($F = 1.75$, $p = 0.2103$). Amphipod density was 20 times higher in restored plots compared to non-restored plots ($F = 10.59$, $p = 0.0058$) (Figure 1.B). There was no difference in amphipod density between restored and non-restored plots from Howell Point (Figure 2.B).

Polychaetes were the second most abundant taxonomic group in my samples and accounted for 33% of all organisms. Two species dominated the counts, *Nereis succinea* and *Pectinaria gouldii*, which made up 91% and 7% of all polychaetes respectively. Three other polychaete genera, *Heteromastus*, *Arabella*, and *Streblospio* were present in small numbers. Polychaete densities were on average twice as abundant on restored plots compared to non-restored plots ($F = 6.64$, $p = 0.0185$). The two dominant polychaete species were clearly associated with different treatments. The tube building polychaete *Pectinaria gouldii* was found exclusively at

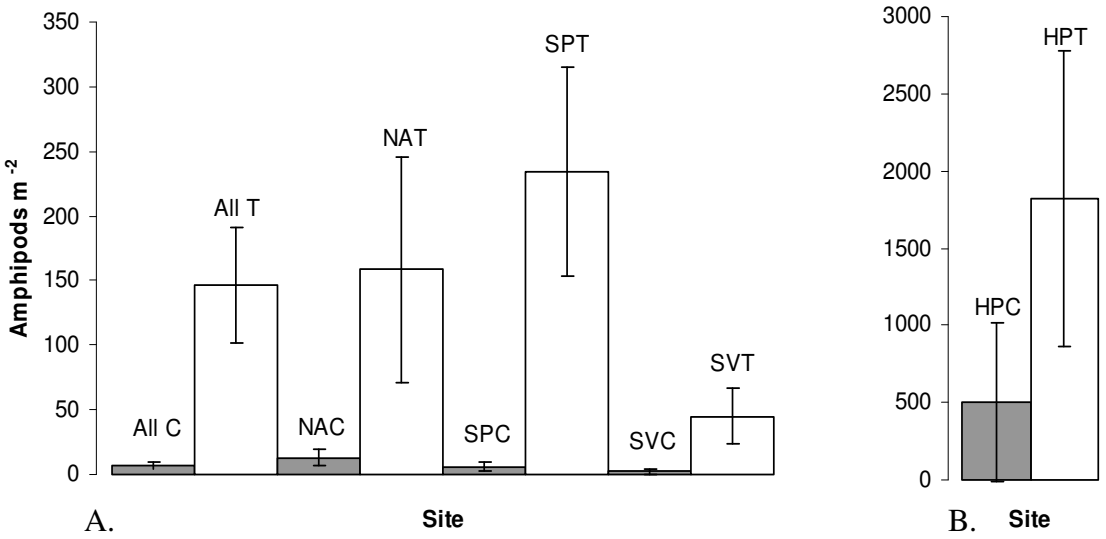


Fig. 2. Mean amphipod density for (A) all sites combined (All), Neal Addition (NA), Spaniard Point (SP), Severn (SV) and (B) Howell Point (HP). Site labels ending with 'C' (grey bars) are control (non-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/- 1 SEM. See text for significance.

the Neal Addition site and was found in greater densities in the non-restored plots at that site ($F = 14.74$, $p = 0.0185$). The errant polychaete, *Nereis succinea*, was the most abundant polychaete in my samples. Density of *N. succinea* (log (x + 1) transformed) was significantly higher in restored plots compared to non-restored plots ($F = 24.2$, $p < 0.0001$, Figure 2).

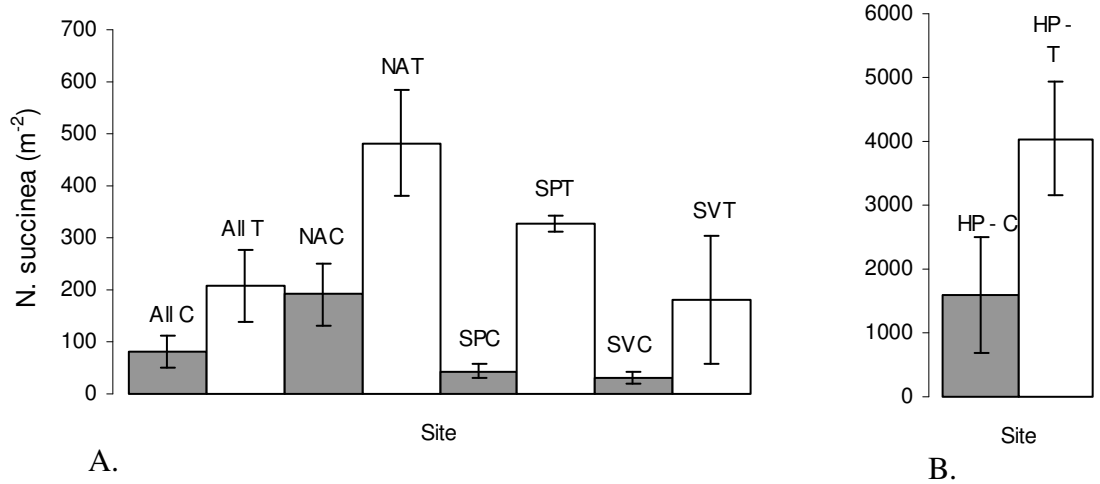


Fig 3. Mean *N. succinea* density for (A) all sites (Howell Point not included) combined (All), Neal Addition (NA), Spaniard Point (SP), and Severn (SV); and (B) Howell Point (HP). Site labels ending with 'C' (grey bars) are control (un-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/- 1 SEM See text for significance.

Xanthid crabs (mud crabs) were the third most abundant organisms in my samples and made up 11% of all individuals collected. Three species were represented, *Rhithropanopeus harrisi*, *Panopeus herbstii*, and *Eurypanopeus depressus*, which made up 62%, 22%, and 15% of all mud crabs respectively.

Mud crab density (square root (x) + 0.5 transformed) was not significantly different when compared among sites (2-way ANOVA; $F = 0.0$, $p > 0.99$). Mud crab density was more than four times higher in restored plots compared to non-restored plots (2-way ANOVA; $F = 85.64$, $p < 0.0001$) (Figure 1.B).

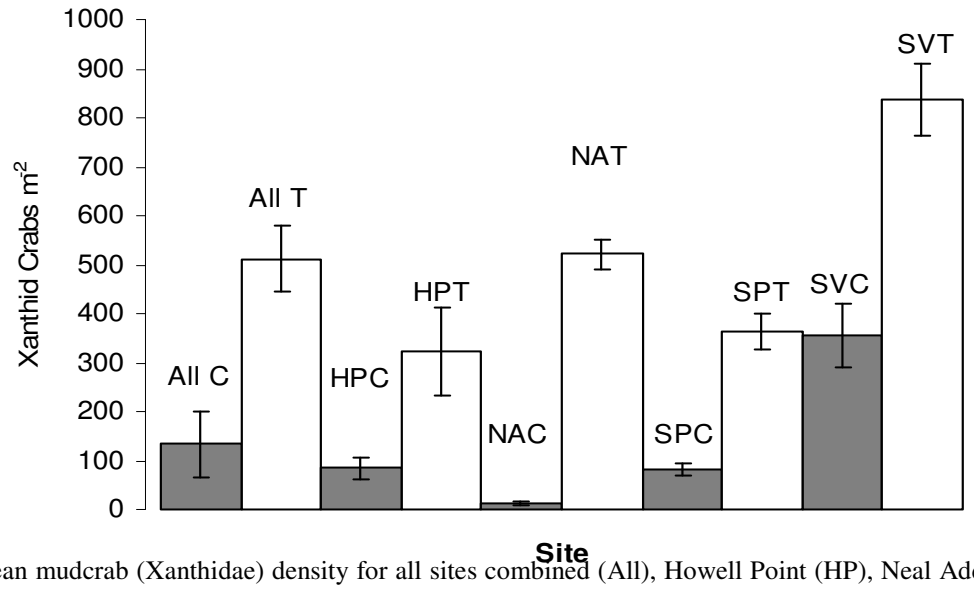


Fig 4. Mean mudcrab (Xanthidae) density for all sites combined (All), Howell Point (HP), Neal Addition (NA), Spaniard Point (SP), and Severn (SV). Site labels ending with 'C' (grey bars) are control (un-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/- 1 SEM See text for significance.

Clams were the fourth most abundant group of organisms in my samples and made up 10% of all organisms. I collected 1,903 clams representing four genera in four families. Of these four genera, three were identified to the species level: *Mya arenaria* (Myacidae), *Mulinia lateralis* (Mactridae), and *Gemma gemma* (Veneridae). The fourth genus, *Macoma* sp. (Tellinidae), was probably dominated by the Baltic

clam (*M. balthica*). A close congener, *M. mitchelli*, may have also have been present but time constraints limited my ability to distinguish the species. Although both species occur in the study region, average density of the *M. balthica* is typically an order of magnitude greater than that of *M. mitchelli* in the mesohaline region of Chesapeake Bay (Gerritsen et al. 1994). Clams collections were dominated by *Macoma* sp. (52%) and *Mya arenaria* (44%). *Mulinia lateralis* and *Gemma gemma* were collected in small numbers. Tests of homoscedasticity and normality revealed that clam density data were not normally distributed. Graphical analysis did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, it was decided that densities of the two dominant clam species should be analyzed separately.

*Macoma* sp. densities did not satisfy tests of ANOVA assumptions. Tests of homoscedasticity and normality revealed that hard clam density data were not normally distributed. Graphical analysis did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, the nonparametric Wilcoxon rank sums test was used as an alternative method. No significant differences in *Macoma* sp. densities on restored versus non-restored plots were detected (Figure 1.B).

The Soft Clam (*Mya arenaria*) was the second most abundant clam species in my samples. Tests of homoscedasticity and normality revealed that soft clam density data were not normally distributed. Visual inspection did not suggest any particular pattern to the data and various transformations did not satisfy the normality assumption. Therefore, the nonparametric Wilcoxon rank sums test was used as an alternative

method. When treatments were compared using pooled data, densities of *M. arenaria* were significantly different on restored plots versus non-restored plots (t approximation, $p < 0.05$)(Figure 1.B).

Demersal fish were the fifth most abundant faunal group in my samples and made up 3% of all organisms. One species, the naked goby (*Gobiosoma bosc*), made up more than 95% of all demersal fish collected. Other species present in the samples included striped blennies (*Chasmoides bosquianus*) and oyster toadfish (*Opsanus tau*). Mean density of demersal fish (log(x +1) transformed) was not significantly higher in comparisons among sites ($F = 0.00$, $p > 0.99$). However, demersal fish density was four times higher in restored plots compared to non-restored plots ($F = 32.56$, $p < 0.0001$) (Figures 1.B & 4).

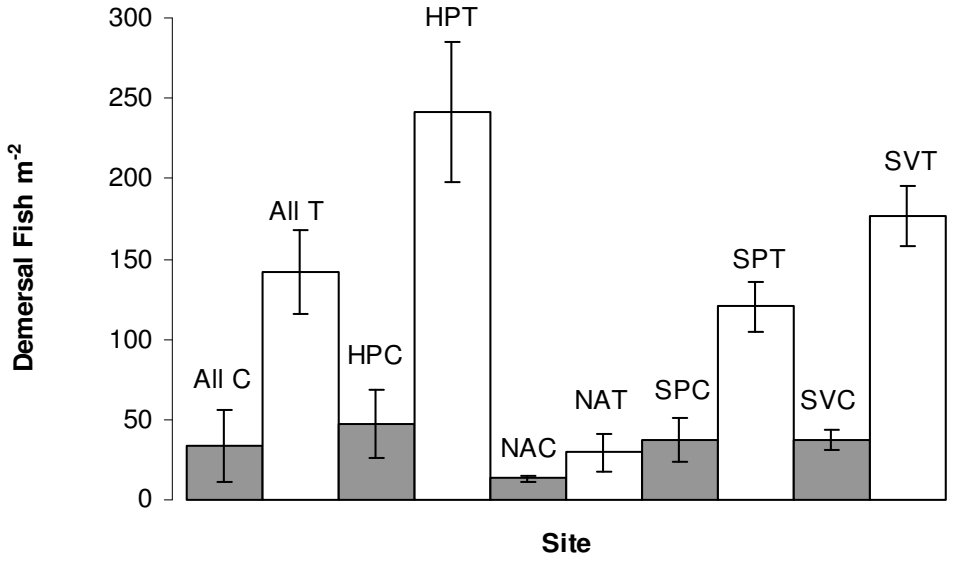


Fig 5. Mean demersal fish density for all sites combined (All), Howell Point (HP), Neal Addition (NA), Spaniard Point (SP), and Severn (SV). Site labels ending with 'C' (grey bars) are control (un-restored) sites and sites ending with 'T' (white bars) are treatment (restored) sites. Error bars represent +/- 1 SEM See text for significance.

*Functional Feeding Group Density Comparisons*

Analysis of functional feeding groups indicated that restored reef creation resulted in a more complex trophic structure and increased energy sequestered in higher trophic levels. Two of the four functional feeding groups were found in significantly higher densities on restored plots. Only one group, deep deposit feeders, was found in higher densities on non-restored plots (Figure 5). Deep deposit feeders were absent from samples from restored plots and occurred only sporadically in samples from non-restored plots. Mean density of deep deposit feeders on non-restored plots was 2.5 organisms m-2. Data for deep deposit feeders did not satisfy ANOVA assumptions of normality and homoscedasticity so differences in density between habitats were assessed using the nonparametric Wilcoxon rank sums test. The difference in deep deposit feeder density between the two habitats was statistically significant (t approximation, $p < 0.05$). There was no difference in density of surface deposit feeders between restored and non-restored plots ($F = 0.98$, $p > 0.05$). Density of suspension feeders was an order of magnitude greater on restored plots compared to non-restored plots ($F = 127.5$, $p < 0.0001$). Mussels (*I. recurvum*), barnacles (*Balanus* sp.), and soft shell clams (*M. arenaria*) were the numerically dominant suspension feeders and accounted for 46.5%, 46.4% and 3.4% of all suspension feeders respectively. Carnivore/omnivore density was twice as high on restored plots ($F = 34.29$, $p < 0.0001$) compared to unrestored plots.

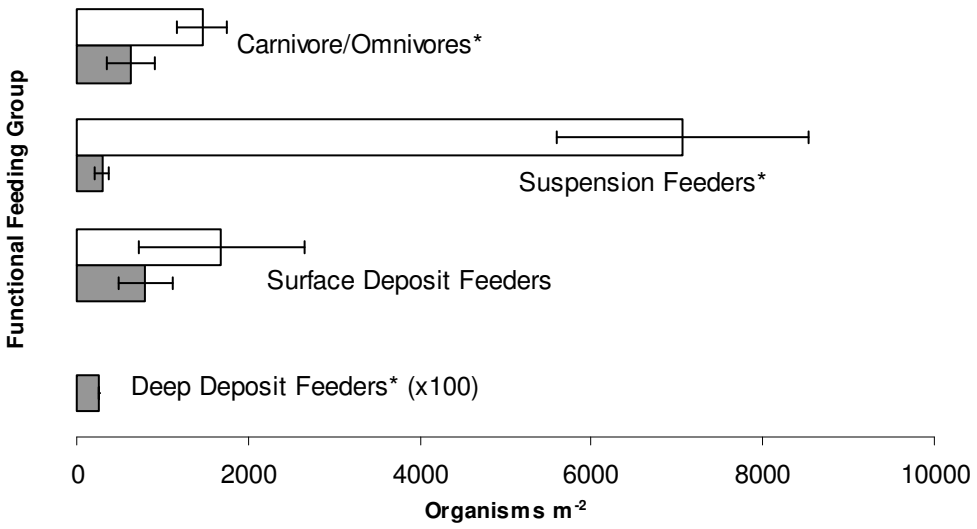


Fig 5. Mean density of four macrofauna functional feeding groups. Grey bars are organisms from control (un-restored) sites and white bars represent organisms collected from treatment (restored) sites. Error bars represent +/- 1 SEM. See text for significance.

# Chapter 4: Discussion

My primary goal was to assess habitat value of structurally complex, undisturbed oyster reef habitat in the mesohaline portion of Chesapeake Bay. To do this I compared benthic faunal assemblages on mature, undisturbed, restored reefs (4 to 5 yrs old) to those on non-restored oyster reefs. Restored reefs exhibited greater structural complexity than non-restored reefs due to the presence of large numbers of live oysters and oyster boxes. Provision of habitat for a diverse community of benthic macrofauna is an important ecological function of oyster reefs. Undisturbed oyster reefs, naturally settled or restored, are comprised of hundreds of oysters $m^{-2}$ most of which are oriented vertically from the bottom. This orientation and the structurally complex surface it creates provide a unique habitat to benthic organisms. The loss of this habitat through the destructive effects of fishing gear, and subsequent high rates of oyster mortality due to oyster disease has resulted in the loss of tens of thousands of acres of valuable benthic habitat in Chesapeake Bay.

My results show reef restoration can restore reef community structure to a certain degree. I found that the mean number of macrofauna species per sample was greater on restored plots compared to non-restored plots. Total macrofauna abundance (free living + fouling organisms) was an order of magnitude higher on restored plots, free living macrofauna were twice as abundant on restored plots and fouling organisms were two orders of magnitude more abundant on restored plots. Also, three out of the five dominant taxonomic groups were much more abundant on restored plots. Mean amphipod density was 20 times higher on restored plots and densities of xanthid crabs and demersal fish were both four times greater on restored plots. Furthermore, closer

examination of infaunal community composition revealed that the numerically dominant polychaetes species (*Nereis succinea*) was also significantly more abundant on restored reef habitats. Since many of the species that benefited from reef restoration are also important fish prey items, restoration clearly has the potential to increase the fish habitat value of the Bay's degraded oyster bars. By providing high quality habitat to a variety of ecologically important species, several other aspects of reef ecological function may be greatly improved, thus further increasing the intrinsic value of reef systems in terms of ecosystem services.

Analysis of functional feeding groups indicated that reef restoration improved two important reef ecological functions: increased grazing rates (water filtration) and subsequent transfer of energy from the plankton community to the benthos, and increased transfer of energy to the higher trophic levels of the reef community. The high density of suspension feeders on restored reefs clearly indicates that the water filtration/plankton grazing function of the reef system was restored. The vertical orientation, high oyster densities, and the ample hard substrate for other suspension feeders combine to maximize the density of suspension feeders per unit of benthic surface area. The loss of suspension feeding due to destruction of oyster reef cannot be replaced by the establishment of benthic infaunal suspension feeders in the same amount of space (Newell and Ott 1999) and the ability of dense assemblages of suspension feeding organisms to influence phytoplankton dynamics has been demonstrated in several systems for several species (Cloern 1982, Cohen et al. 1984, Newell 1988, Dame et al. 1992, Roditi et al. 1996,). Such effects have also been predicted in modeling studies (Ulanowicz & Tuttle 1991, Newell 1988, Newell 2004, Newell et al. 2004). Restoration of large populations of *C. virginica* may not be able

to reverse the effects of cultural eutrophication in Chesapeake Bay's deep waters. However, restoration of oyster populations, and their associated suspension feeding epifaunal, may be capable of having significant positive effects on the Bay's shallow water habitats by reducing chlorophyll concentrations, enhancing denitrification, and enhancing submerged macrophyte biomass (Cerco and Noel 2007).

The higher densities of carnivore/omnivores that we observed on restored reefs is consistent with a scenario whereby energy is removed from the water column by suspension feeders and transferred to the benthic subsystem in the form of feces and psuedofeces. These biodeposits, in turn, are grazed by surface deposit feeders that are then preyed upon by carnivore/omnivores. Since the latter two categories are the highest trophic levels of the reef resident community, the net effect is a transfer of energy to higher trophic levels. The loss of dense suspension feeders from reef systems results in a simplified food web and a trophic bottleneck wherein energy from the plankton community is largely prevented from reaching the carnivore/omnivore component of the reef system. Such trophic bottlenecks have been predicted by modeling studies (Ulanowicz & Tuttle 1991, Newell 1988) and have been implicated as a cause of decreased fish biomass production in polluted lakes (Sherwood et al. 2002).

Another important oyster reef ecological function may be that of providing foraging grounds for predatory fishes thus facilitating the transfer of energy from the benthos to higher trophic levels. Peterson et al. (2003) synthesized several studies of fish utilization of restored oyster reefs to estimate that restoration of 10 $m^2$ of reef in the Southeast United States results in an additional 2.57 kg $10m^{-2}$ $year^{-1}$ of fish biomass.

This relationship was derived from studies of reefs in the Southeast United States and may need to be adjusted to better fit my study area. However, my results suggest that reef restoration has the potential to increase the biomass of prey items available to fish predators. Many of the organisms that were significantly more abundant on restored reefs are also known to be important food items for several commercially and recreationally important finfish species. In mesohaline areas of Chesapeake Bay, these fishes include several species of the drum family (Sciaenidae) such as Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and weakfish (*Cynoscion regalis*); and two members of the temperate bass family: white perch (*Morone americana*) and striped bass (*Morone saxatilus*). Diets of adult spot, croaker, and white perch are primarily composed of benthic prey such as polychaetes, mollusks, small crustaceans, and small demersal fish (Homer and Boynton 1978, Chao and Musick 1977). Benthic prey also make up a large proportion of juvenile weakfish and striped bass diets (Stickney et al. 1975, Gardinier and Hoff 1982, Hartman and Brandt 1995) but these species become increasingly piscivorous as they grow larger.

In the past several decades, commercial catches of all of these species have declined in Chesapeake Bay (Murdy et al 1997). The destruction of oyster reefs has not received serious consideration as a contributing factor in these fisheries declines. However, modeling studies generally support a scenario where loss of benthic biomass production results in less biomass transferred up to fish predators. Szyrmer and Ulanowicz (1987) demonstrated how one can calculate the degree of importance to a species' diet for every other species in a given system through both direct and indirect pathways. When this method was applied to the seasonal trophic dynamics of

the Chesapeake mesohaline system, all of the aforementioned fish species, with the exception of striped bass, were found to depend heavily on the benthos as their energy source. Another estuarine fish predator, the bluefish (*Pomatomus saltatrix*), was also found to be strongly linked to the benthos. Baird and Ulanowicz (1989) proposed that the current dominance of deposit feeders in the Chesapeake Bay benthos is a relatively recent phenomena and that the loss of dense communities of suspension feeders has likely caused a "trophic restructuring" in the estuary. A modeling study that compared the trophic functioning of three mid-Atlantic estuaries found that Chesapeake Bay was less efficient at producing carnivorous fish than both Delaware and Narragansett bays. Carnivorous fish in Chesapeake Bay relied more heavily on benthic deposit feeders than did their counterparts in the other two systems which relied more heavily on pelagic primary producers and parabenthic shrimp (Monaco and Ulanowicz 1997).

Another function of oyster reefs is to provide nursery habitat for juvenile fish (Breitburg 1991, Breitburg et al. 1995, Breitburg 1999, Coen et al. 1999, Lehnert and Allen 2002). My results suggest that Maryland's restored reefs have ample prey for juvenile fish. However, my sites, though spatially complex, may have been in water too deep to afford juvenile fish much refuge from large predatory fish. The nursery habitat function of restored oyster reefs might be maximized by locating reefs in shallow (<2 m deep) waters where large fish predators are less abundant. This is especially true if reefs are located in areas where other refuge habitats (e.g., seagrass beds and tidal marshes) are scarce or absent (Grabowski 2002). Shallow water oyster reefs, when located adjacent to deeper waters, can also provide alternative foraging habitats for fish and crabs that are displaced by anoxia/hypoxia below the pycnocline

(Lenihan et al. 2001). This function can be optimized by designing reefs for maximum habitat complexity (Grabowski 2004). Results of my study suggest that it may be possible to design reefs to maximize benthic primary and secondary production. This may facilitate recruitment of amphipods, polychaetes, and other species as I observed on my Howell Point plots.

Comparisons of my results with other published studies are complicated by differences in location, faunal groupings, sampling methods, and other factors. My results are, however, qualitatively comparable to studies of oyster reef macrofauna in Chesapeake Bay and other systems. Walters and Coen (2006) collected a total of 59 taxa from natural and constructed intertidal oyster reefs in tidal creeks around Charleston, South Carolina. Their study employed a suite of analytical approaches including two analyses of taxa abundance: multivariate analysis of variance (MANOVA) and expected species compositional similarity (ECOSIM), and two analyses of taxa similarity: a nonparametric analysis of compositional similarity (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA). They sought to evaluate the influence of level of taxonomic identification and level of taxa reduction on these 4 tests' ability to identify convergence in macrofauna community compositional similarity between natural and constructed reefs over 4 and 7 year intervals.

Their study differed from mine in a number of important ways. Walters and Coen (2006) used average Bray-Curtis dissimilarity as their response variable whereas I used various taxa abundance measures. The control reefs in their study system were natural intertidal reefs that supported high densities of oysters and still retained

significant vertical reef structure. Such reefs are extremely rare in the mesohaline regions of Chesapeake Bay. The unrestored subtidal reefs that I sampled lacked significant concentrations of live oysters and although dead shell was abundant, it was mostly covered with a layer of fine sediments. Walters and Coen's treatment reefs were also fundamentally different from those of my study in that their treatment reefs were constructed in places where no prior reefs had existed. The treatment reefs in my study were restored plots located on existing degraded oyster reefs. Walter's and Coen's (2006) study also utilized data from samples collected in January between 1996 and 2001 and sought to investigate if macrofauna assemblage structure on constructed reefs over time might eventually became similar to that of natural reefs. My study, with data collected in one summer, had no temporal dimension but rather gave a snap shot comparison of macrofauna assemblages on restored reefs of similar age (4-5 years post restoration) to assemblages on adjacent unrestored reefs.

Walters and Coen (2006) addressed an important question in restoration ecology: what is the best method to assess if macrofauna assemblage structure on constructed (or restored) reefs eventually becomes similar to assemblages on natural reefs? The overall result of their study was that most tests failed to detect any significant convergence in macrofauna assemblage structural similarity after 7 years. Their MANOVA results indicated either no difference of significant difference in macrofauna structure between reef types depending on level of taxa identification and/or data reduction. The MANOVA results were likely compromised by difficulties in satisfying assumptions of multivariate heteroscedasticity. Ecosim results found no compelling evidence of convergence but this approach may suffer from significant design limitations. ECOSIM does not calculate a Bray-Curtis dissimilarity score.

Rather it calculates its own index of co-occurrence patterns in the raw data matrix and compares this index with the same index as generated by random resorting of the data. This approach may not be well suited for detecting compositional similarity among different treatments. ANOSIM results indicated that assemblage structural dissimilarity did not decrease after 4 or 7 years compared to data from about one year post reef creation. As with ECOSIM, this approach suffered from design limitations and from an inability to generate enough permutations to analyze data sets with relatively small sample sizes resulting from data reduction methods. With one exception, all test results for PERMANOVA indicated that macrofauna assemblage structure on created reefs did not converge in similarity with assemblages on natural reefs after 7 years. The exception was for a data set that had been reduced to only 5 taxa by using principal components analysis to identify which species were accounting for the majority of variation in macrofauna assemblage dissimilarity.

The overall lesson of Walters and Coen's study was that success in detecting convergence in assemblage structure between created and natural reefs is highly dependant on the statistical test employed and the degree of taxonomic identification and data reduction applied. Although no compelling evidence for convergence between reef types was found, this study did identify the PERMANOVA approach as being the least constrained by design limitations and small sample sizes. However, more intriguing questions of whether assemblage compositional similarity is even a reasonable restoration goal or necessary for restoration of ecological function remain to be answered.

Boudreaux et al. (2006) collected 76 species of macrofauna from intertidal polyhaline oyster reefs in Mosquito Lagoon, Florida using lift nets. Their study goal was to compare back biodiversity of back reef areas on reefs impacted by recreational boating pressures to similar areas on unimpacted control reefs. Of their 76 species, 25 were sessile organisms and 51 were motile. They found no difference in biodiversity between the impacted and control reefs. Boudreaux et al.'s (2006) list of motile species included at least 6 fish species that could be described as "transient" reef users (e.g., not full time reef residents). If these species were subtracted from their list, their reefs would still support nearly double the number of species that I observed. This higher species richness is likely a result of their study area's higher salinity and of being located in the transition zone between the Carolinian and Caribbean zoogeographic provinces.

Plunket and La Peyre (2005) sampled shell and mud bottom habitats on a leased oyster bed in Barataria Bay, Louisiana. With trays of similar design (0.31$m^2$ Plunket & La Peyre vs. 0.28$m^2$ this study), they collected 16 species of fish and invertebrates from both habitat types. Although many species were collected on both bottom types, there were two fish species (striped blenny *Chasmoides bosquianus* and crested blenny *Hypleurochilus geminatus*) and one invertebrate (porcelain crab *Petrolisthes* sp.) that were unique to oyster shell samples. Similarly, two fish species (mangrove snapper *Lutjanus griseus* and speckled worm eel *Myrophis punctatus*), and one invertebrate (brown shrimp *Penaeus aztecus*) that were unique to mud samples. Plunket and La Peyre's (2005) study observed some similar patterns to this study. Both studies found higher densities of resident fish on oyster shell bottom compared to adjacent structurally simple habitats. Both studies also found higher densities of

xanthid crabs on shell bottoms compared to adjacent structurally simple habitats. Other reef resident taxa that were found in higher densities in shell habitats in both studies include grass shrimp (*Palaemonetes pugio*) and the hooked mussel (*Ishchadium recurvum*). Only one species common to both studies, the dwarf surf clam (*Mulinina lateralis*) was found in higher densities in unstructured/unrestored habitats in both studies. Of Plunket and La Peyre's (2005) 10 fish and 9 invertebrate taxa, 8 fish and 4 invertebrate taxa were not collected in the course of this study. This difference is largely reflective of differences in biogeography between the two studies. Other factors, such as salinity, gear type, level of effort, and season may also have contributed to this variability. More information on potentially important differences between these two studies and others is given in Appendix 1.

Luckenbach et al. (2005) reported the results two parallel oyster reef habitat restoration studies, one in the Rappahannock River (a subestuary of Chesapeake Bay) and the other in Inlet Creek, South Carolina (a tributary of Charleston Harbor). In both locations, sites were restored by planting fresh shell and allowing natural recruitment to populate the reefs. The purpose of this paper was not to compare restored reef macrofauna assemblages to other habitat types but rather to examine the relationship between oyster abundance and various macrofauna assemblage metrics. Nevertheless, there are some interesting parallels between Luckenbach et al. (2005) and this study.

For the Rappahannock River, Luckenbach et al. (2005) only reported results for restored habitats (although his description of unrestored reefs as "all but disappeared" is qualitatively similar to my unrestored sites). Therefore, I will compare only results

from my restored sites to those of the Rappahannock River. Furthermore, since my restored sites were sampled r 4 to 5 years post restoration, and Luckenbach et al (2005) sampled at 1, 1.25 and 2 years post restoration, I will compare my results only to their second year data so as to minimize any temporal/succesional differences between the two studies. Finally, Luckenbach et al. (2005) did not report the number of species collected for their Rappahanock River study so comparisons will be limited to reef community metrics that are common to both the Rappahanock River and my study.

Oysters recruited naturally to the Rappahannock restored reefs and reached a density of about 250 oysters $m^{-2}$ after two years. Mean oyster density at my restored sites was 82.1 oysters $m^{-2}$ (± 16.6 SEM). Luckenbach et al. (2005) reported epifaunal densities of between 800 and 1000 organisms $m^{-2}$ whereas I observed a mean epifaunal density of 3,797.3 organisms $m^{-2}$ (± 1561.7 SEM). My greater epifaunal densities are likely conservative because I only included motile epifaunal and classified sessile organisms separately as the "fouling" community. Also, Luckenbach et al. included, as epifauna, several bivalve species that I classified as infauna. These bivalve species (*Macoma sp., Mulinia lateralis, Mya arenaria*) are usually found buried within the upper sediment layer. However, it is possible that larvae of these species may recruit to sedimentary microhabitats within the reef matrix and then grow up to be incorporated in outer layers of the reef matrix. This would make them, arguably, "facultative" epifauna. Luckenbach et al. (2005) reported xanthid crab densities of about 1,600 crabs $m^{-2}$ whereas I observed a mean xanthid crab density of 511.0 crabs $m^{-2}$ (± 66.5 SEM).

Mean barnacle (Balanus spp.) density on Luckenbach et al.'s (2005) restored sites was about 8,000 barnacles $m^{-2}$ compared to 3,312.3 (±1408.9 SEM) barnacles $m^{-2}$ for this study. Interestingly, Luckenbach et al. observed a ~600 barnacle $m^{-2}$ decline between summer 2001 and summer 2002. My lower barnacle density could be a result of a longer post restoration interval before being sampled. Other potentially important factors include my broader spatial separation between sites, differences in predation intensity between the two studies, differences in anthropogenic stressors between the studies, or just random variation. Important commonalities between these two studies are that both were done in mesohaline portions of Chesapeake Bay tributaries and both studies sampled in summer 2002. Important differences between the two studies include restoration methodologies, sampling techniques, post restoration sampling interval and location within the Chesapeake Bay system.

The second study reported in Luckenbach et al. (2005), conducted in Inlet Creek, South Carolina, compared macrofaunal densities on constructed reefs to adjacent natural reefs. They sampled annually over a five year period ending in January 2001. As with the Rappahanock River results, I will compare only their final year's results to mys. However, in this case the post restoration/reef creation interval is similar between studies. Also, both studies compare restored/created reefs to adjacent control reefs although the natural control reefs of Luckenbach et al. (2005) are fundamentally different from my degraded control reefs. The authors reported 87 species of reef resident macrofauna compared to my 35 species but they did not compare species richness between reef types. In the Inlet Creek system, oyster densities on created reefs were consistently lower than on natural reefs. This is completely opposite of my results reflecting the difference between the degraded natural reef sites in my study

versus the healthy natural control reefs in their study. Luckenbach et al (2005) also observe higher epifaunal density on his natural reefs compared to created reefs. Again, my results were to the opposite. However, epifaunal density on Luckenbach et al.'s created reefs was of a similar magnitude as my restored reefs. Final xanthid crab densities on created and natural reefs were similar in the Inlet Creek study and were much lower(~80%) compared to my restored sites. Interestingly, Luckenbach et al. (2005) observed nearly identical trends in densities of the large xanthid crab *Panopeus herbstii* between habitat types over the course of their study. I observed much greater *P. herbstii* densities on restored sites compared to unrestored sites. Qualitative differences between control sites likely contribute to these contrasting results, suggesting that *P. herbstii* requires healthy oyster reef habitat in order to thrive. Luckenbach et al.'s (2005) reported positive correlation between *P. herbstii* abundance and oyster height ($r = 0.722$, $p = 0.028$) also supports this hypothesis.

Lenihan et al. (2001) sampled macrofauna on natural reefs, restored reefs and sand bottom in the Neuse River estuary, North Carolina. They collected 15 species of amphipods, decapods, molluscs and resident fishes from restored and natural reefs combined and only three species from sand bottom. They did not report density of total macrofauna or the mean number of species on restored versus natural reefs. Also, their species list did not include any annelids. The methods of Lenihan et al. (2001) differed from mines in that they used defaunated oyster shells in 0.25 $m^2$ "traps" that were deployed for seven days whereas my 0.28 $m^2$ trays were filled on-site with benthic materials containing organisms at ambient densities and deployed for at least six weeks. Therefore, the data describe a very early successional community made up of animals that recently immigrated or recruited to their traps

whereas my data describe populations that more closely resemble a mature, undisturbed community.

Meyer and Townsend (2000) reported mean numbers of species of 17.3 and 9.6 for restored and natural reef habitats respectively on intertidal salt marsh edge reefs in coastal North Carolina. These results are similar to my mean numbers of species per sample. However, Meyer and Townsend (2000) did not report any annelids in their samples and only reported densities for four macroinvertebrate species. Zimmerman et al. (1989) compared winter and summer densities of infauna and epifauna on natural oyster reef, salt marsh and mud bottom habitats in West Bay, Texas. They found 63 macrofaunal species on natural oyster reefs in winter compared to 59 in summer. Macrofaunal densities for oyster reefs and salt marshes were similar (~430 versus ~375 organisms $m^{-2}$ respectively) and both were significantly greater than macrofaunal densities for mud bottom habitats (~100 organisms $m^{-2}$) (these densities are converted from organisms · 0.785 $m^{-2}$ to organisms $m^{-2}$ and averaged across seasons). Bahr & Lanier (1981) combined the results of three earlier studies (Dame 1979, Bahr 1974, and Lehman 1974) to report a total of 42 species for natural intertidal reefs in the southeastern United States. Dame (1979) found 37 species and densities ranging from 2,476 to 4,077 organisms $m^{-2}$ on natural intertidal reefs in South Carolina. Bahr (1974) reported 42 species and a mean density of 3,800 organisms $m^{-2}$ on natural intertidal reefs near Sapelo Island, Georgia. Similarly, Lehman (1974) reported 31 species and a mean faunal density of about 6,200 organisms $m^{-2}$ from Crystal River, Florida. Frey (1946) reported 41 species of free living epifaunal and infaunal organisms from natural reefs in the Potomac River, Maryland. These results are similar to my 35 species and mean densities of 4,057 and

1,596 organisms $m^{-2}$ on restored and non-restored sites respectively. Wells (1961) reported 284 species from reefs in the Newport River, North Carolina. Wells' study sampled five reefs located along a salinity/intertidal-subtidal gradient. When the mean number of species per collection was plotted against salinity, a steep drop (from 30 species to 16 species) was observed between 24 mg $l^{-1}$and 19 mg $l^{-1}$. This decline in species richness with decreasing salinity is similar to that observed for soft bottom benthic fauna in Chesapeake Bay (Boesch 1972) and probably accounts for much of the lower species counts in my study relative to Wells (1961).

My study differed from the 13 studies mentioned above in several important respects. I sampled mesohaline, subtidal reefs with high densities of mature oysters. Frey (1946) and Luckenbach et al.'s (2005) Rappahannock River study were the only other studies we found that matched these conditions. However, Frey sampled natural reefs only and only reported presence/absence data for reef organisms (not to mention a time span of more than five decades between the two studies) whereas Luckenbach et al. sampled only restored sites and only reported results for selected reef macrofauna assemblage metrics. Three other studies (Walters and Coen 2006, Lenihan et al 2001, Meyer & Townsend 2000) compared restored reefs to natural reefs and two studies (Luckenbach et al's 2005 Inlet Creek study, and Walters and Coen 2006) compared created reefs to relatively unimpacted natural reefs. One study (Plunket and La Peyre 2005) compared a commercially fished oyster lease located in a subtidal mesohaline system to adjacent soft bottom habitats.

With the exception of Frey (1946), Plunket and La Peyre (2005) and Luckenbach et al.'s (2005) Rappahannock River study, all of the aforementioned studies were

located in higher salinity areas than this study. With respect to zoogeography, two of these studies (Meyer & Townsend 2000, Lenihan et al 2001) were located in coastal North Carolina near the boundary between the Virginian and Carolinian biogeographic provinces (Cerrame-Vivas & Gray 1966, Engle & Summers 1999) while the Carolinian fauna were firmly represented in Plunket and La Peyre ( 2005) Walters and Coen (2006) and Luckenbach et al's (2005) Inlet Creek study. The influence of the more subtropical Carolinian fauna is quite evident in the species lists of these studies. These salinity and biogeographic differences also mean that organisms in these three locations were subjected to a different suite of fish and invertebrate predators than my location. These three studies also used different restoration methods than this study. In Maryland, where natural oyster reproduction is unpredictable, reefs are topped with a layer of shell that is seeded with juvenile oysters in the hatchery. In Virginia, North Carolina and South Carolina, where oyster spatfall is more predictable, reefs are created by depositing unseeded shell on a site and letting oysters recruit naturally. The remaining seven studies (Wells 1961, Bahr 1974, Lehman 1974, Dame 1979, Bahr & Lanier 1981, Zimmerman et al. 1989, and Boudreaux et al. 2006) were all conducted on natural reefs, in different tidal and salinity zones and were located either in or near different biogeographic provinces compared to my study. Yet in spite of these many differences, a general pattern is evident. Oyster reefs typically support between 33 and 63 macrofaunal species at densities ranging from around 300 to around 6,000 organisms $m^{-2}$. Oyster reef macrofauna assemblages typically have high densities of xanthid crabs, demersal fish, amphipods, annelids and various sessile suspension feeding organisms. A summary of the 13 studies reviewed above is included in Appendix I.

# Chapter 5: Conclusions

The restored oyster reefs I sampled clearly supported higher densities of benthic organisms than their degraded "non-restored" counterparts. Analysis of faunal groups indicated that reef community structure was enhanced by reef restoration. Analysis of functional feeding groups indicted that two important ecological functions, water filtration and transfer of energy to higher trophic levels (e.g., predators/omnivores) were also enhanced. These results have important implications for resource management. Since many of the benthic species that benefited from restoration are also important fish prey items, reef restoration clearly has the potential to increase the fish habitat value of the Bay's degraded oyster bars. By locating oyster restoration projects in shallow, well mixed areas that are not prone to anoxia/hypoxia, restored oyster reefs may be useful in mitigating the adverse effects of eutrophication on benthic macrofauna and the fish, decapod and avian predators that rely upon them for food. These shallow water reefs may also provide valuable predation refuge habitats for commercially and recreationally important fish and decapod species. This is especially true for areas where sea grasses and other structured habitats are scarce. The high densities of oysters and other suspension feeders that I observed on restored plots indicates that reef restoration will facilitate water filtration and regulation of phytoplankton dynamics. Through biodeposition, energy from plankton removed from the water column by suspension feeders is transferred to the benthic subsystem. Thus an important linkage between the benthic and pelagic system components has been restored, further increasing the intrinsic value of restored

oyster reefs in terms of ecosystem services. Therefore, it is important to view oyster restoration as fitting into a larger framework of holistic ecosystem management rather than as just a means of increasing oyster fisheries production. The ongoing effort to restore oyster reef habitats in Maryland offers many opportunities for ecological insights. This is fortunate because many questions, both applied and theoretical, remain to be answered. Understanding the pathways and magnitudes of trophic energy flows through these systems will require carefully designed manipulative experiments. Many other questions regarding the relative importance of competitive versus facilitative interactions, predation, resource partitioning, and possible indirect effects also beg to be explored.

# Appendices

Appendix 1: Summary of selected published studies of oyster reef macrofauna assemblages (ND = no data, NA = not applicable).

| Study # | Author | Year | Location | Natural or Created (time since created?) | Compared to: |
|---|---|---|---|---|---|
| 1 | This Study | 2004 | Chesapeake Bay MD | Created (4-5 y.o.) | Natural (degraded) |
| 2 | Boudreaux et al | 2006 | Mosquito Lagoon FL | Natural (unimpacted) | Natural (impacted) |
| 3 | Walters & Coen | 2006 | Toler's Cove & Inlet Creek SC | Created (6 y.o.) | Natural |
| 4 | Luckenbach et al. | 2005 | Rapahannock River VA | Restored | NA |
| 5 | Luckenbach et al. | 2005 | Inlet Creek SC | Restored ("experimental") | Natural |
| 6 | Plunket & La Peyre | 2005 | Barataria Bay LA | Commercial Oyster Lease | Mud |
| 7 | Grabowski | 2002 | Back Sound NC | Created (1 - 3 y.o.) | Created (height x depth) |
| 8 | Lenihan et al | 2001 | Neuse River NC | Created (6 - 7 y.o.) | Natural & Sand |
| 9 | Meyer & Townsend | 2000 | Coastal NC | Created (2 y.o.) | Natural |
| 10 | Zimmerman et al. | 1989 | West Bay TX | Natural | salt marsh & mud bottom |
| 11 | Bahr & Lanier | 1981 | SE USA | Natural | NA |
| 12 | Dame* | 1979 | North Inlet SC | Natural | NA |
| 13 | Bahr* | 1974 | Sapelo Island GA | Natural | NA |
| 14 | Lehman* | 1974 | Crysal River FL | Natural | NA |
| 15 | Wells | 1961 | Beaufort NC | Natural | NA |
| 16 | Frey | 1946 | Potomac River MD | Natural | NA |

| Study # | Tidal Regime | Salinity | Biogeographic Province | # Species | Density (org.s/$m^2$) | Gear → Mesh |
|---|---|---|---|---|---|---|
| 1 | Subtidal | Mesohaline | Virginian | Total: 33 ($14.9_{\bar{y}created}$ vs. $12_{\bar{y}natural}$) | ~$4000_{\bar{y}created}$ vs.$1500_{\bar{y}natural}$ | 0.28 $m^2$ trays → 1 mm |
| 2 | Intertidal | Polyhaline | Carolinian/Carribean | Total: 76 | ~65 (± ~8) | 1.0 $m^2$ lift nets → (see notes) |
| 3 | Intertidal | Polyhaline | Carolinian | ND | 59 | 0.14 $m^2$ trays → 1.3 mm |
| 4 | Subtidal | Mesohaline | Virginian | ND | ~900 | 0.5 $m^2$ quadrat |
| 5 | Intertidal | Polyhaline | Carolinian | 87 | ~1,200 | 0.143 $m^2$ trays → 1.3 mm |
| 6 | Subtidal | Mesohaline | Carolinian | Total: 19 ($16_{shell}$ vs. $16_{mud}$) | ~$46_{shell}$ vs. $56_{mud}$ | 0.31 $m^2$ trays → 0.5 mm |
| 7 | Intertidal | Eu-Polyhaline | Carolinian/Virginian | ND | ~$2500_{(created)}$ vs. ~$400_{(control)}$ | 0.25 $m^2$ plots → 1 mm |
| 8 | Subtidal | Euhaline | Carolinian/Virginian | 15 on oyster reefs vs. 3 on sand | ~300 $_{Ocracoke(natural)}$ vs, ~433 $_{(\bar{y}created)}$ vs. ~186 $_{Neuse\ River(sand)}$ | 0.25 $m^2$ traps → 1 mm |
| 9 | Intertidal | Euhaline | Carolinian/Virginian | Total: 33 ($17_{\bar{y}created}$ vs. $10_{\bar{y}natural}$ (N=3)) | ND | 0.25 $m^2$ quadrat → 1mm |
| 10 | Intertidal | Euhaline-high meso. | Carolinian/Carribean | $63_{(winter)}$ vs. $59_{(summer)}$ | ~$500_{(winter)}$ vs.~$300_{(summer)}$ | 78.5 $cm^2$ core → 0.5 mm |
| 11 | Intertidal | Euhaline | Carolinian | 42 | *3,300-38,000 | * |

| Study # | Tidal Regime | Salinity | Biogeographic Province | # Species | Density (org.s/$m^2$) | Gear → Mesh |
|---|---|---|---|---|---|---|
| 12 | Intertidal | Euhaline | Carolinian | 37 | 3,300 | 0.25 $m^2$ quadrat → 1 mm |
| 13 | Intertidal | Euhaline | Carolinian | 42 | 3,800 | 0.5 mm |
| 14 | Intertidal | Euhaline | Carolinian/Carribean | 31 | 6,200 | ? |
| 15 | Inter-Sub Gradient | Eu-Meso. Gradient | Carolinian/Virginian | 303 | ND | None |
| 16 | Subtidal | High Meso. - Low Meso. Gradient | Virginian | 43 | ND | None |

| Study # | Notes |
|---|---|
| 1 | Species total is a minimum, some snails and barnacles not identified to species. Densities are for free living epifaunal and infaunal organisms only (no fouling organisms). Gear soak time ≥ 6 weeks. |
| 2 | No difference in species richness or density of organisms between reef types. Mesh sizes: 3.2 cm diameteron sides, 0.2 cm diameter on bottom. |
| 3 | Data on species richness between treatments not provided. Data reported is units of % Dissimilarity using Bray Curtis index. Same data set as Luckenbach et al. 2005's Inlet Creek study but for entire period 1996 – 1998. |
| 4 | Data on various faunal metrics correlated with oyster abundance metrics. |
| 5 | Natural "control" reefs in SC were not degraded like in Chesapeake Bay and species diversity and total faunal abundance on experimental reefs were always less than on natural controls. |
| 6 | Trays filled with single layer of shell, probably not comparable to lease that was clutched for over 50 years. Some fish species were not resident species. |
| 7 | 1. control = pooled saltmarsh points, fringes (w/SAV) and sand/mud. 2. Faunal groups: Gastropods, Bivalves, Decapods, Other Arthropods. No poly.s or demersal fish and "Bivalves" may include fouling mussels and infaunal clams. |
| 8 | Densities = ~300 Ocracoke(natural) vs, ~287 West Bay(restored) vs. ~ 579 Neuse River(restored) vs. ~186 Neuse River(sand). No polychaetes. |
| 9 | Authors found that created reefs were quickly colonized and developed assemblages similar to natural but w/ more spp and higher densities. |
| 10 | density of macro.s: 0yster Reef > Salt Marsh > Mud (oysters and marsh not sig.diff.) for both seasons but sig. habitat x season interactions. |
| 11 | (*from 3 studies below marked "*") |
| 12 | Density is median not mean. |
| 13 | |
| 14 | Total: 33 ($17_{\tilde{y}created}$ vs. $10_{\tilde{y}natural}$ (N=3)) |
| 15 | 1. Total spp = 303 but ranged from $220_{euryhaline}$ to $56_{highmeso}$ with means of $\tilde{y} = 67_{euryhaline}$ to $\tilde{y} = 16_{highmesohaline}$. 2. Includes many fowling and other non-macro spp) |
| 16 | 1. Used dredge sampling. 2. I excluded fouling org.s and plants. |

Appendix 2.A
Sampling site locations with information on depth, length of deployment and season recovered. Maps depicting the historical reef systems where these sites were located can be found in Smith (1997).

| Site | River | Latitude | Longitude | Depth (m) | Days Deployed | Season Recovered |
|---|---|---|---|---|---|---|
| Chinks Point | Severn | 38° 57.403' N | 076° 27.111'W | 6 | 55 | Summer |
| Neal Addition | Patuxent | 38° 22.560' N | 076° 31.484'W | 5 | 37 | Spring |
| Howell Point | Choptank | 38° 37.402' N | 076° 07.200'W | 2 | 72 | Fall |
| Spaniard Point | Chester | 39° 05.500' N | 076° 09.307'W | 2.5 | 63 | Summer |

Appendix 2.B
Water quality data summarized from Maryland DNR Water Quality Monitoring Program sites near my sampling sites and specific for each site's period of deployment. Severn River data is from real time monitoring data over the study period. All other data is from monthly data collected between 1985 and 2002. Parameter means and ranges are specific for the deployment period for each site.

| River | Statistic | DO (mg $L^{-1}$) | Salinity (ppt) | T (°C) |
|---|---|---|---|---|
| Severn: | | | | |
| | Mean: | 7.2 | 5.7 | 25.6 |
| | Minimum: | 0.8 | 5.3 | 18.9 |
| | Maximum: | 13.0 | 6.3 | 28.7 |
| Patuxent: | | | | |
| | Mean: | 8.1 | 13.2 | 13.4 |
| | Minimum: | 0.4 | 5.4 | 0.9 |
| | Maximum: | 12.3 | 18.5 | 28.0 |
| Choptank: | | | | |
| | Mean: | 6.1 | 13.2 | 23.5 |
| | Minimum: | 1.3 | 7.5 | 15.3 |
| | Maximum: | 9.8 | 18.2 | 28.8 |
| Chester: | | | | |
| | Mean: | 2.3 | 9.3 | 26.6 |
| | Minimum: | 0.2 | 5.3 | 21.6 |
| | Maximum: | 6.0 | 13.0 | 28.4 |

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