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Evaluating restored oyster reefs in Chesapeake Bay: How habitat structure influences ecological function

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EVALUATING RESTORED OYSTER REEFS IN CHESAPEAKE BAY: HOW HABITAT STRUCTURE INFLUENCES ECOLOGICAL FUNCTION

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Presented to

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The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by

Janet Andrea Nestlerode

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

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DEDICATION

This dissertation is dedicated to the memories of Molly, a very special huma-dog, and my Grandpa, Walter Johnson, who taught me how to catch worms and fish with them, and who helped me build much of the sampling gear used in this project.

TABLE OF CONTENTS

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LIST OF TABLES

Table Page

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

LIST OF FIGURES

Figure Page

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

ABSTRACT

A shortage of shell resources for restoring reefs of the Eastern oyster, *Crassostrea virginica*, has led to widespread use of other materials as substitutes for oyster shell. The effectiveness of such alternative substrates in reef construction efforts as habitat for reef-associated fauna other than oysters is largely unresolved. For this study, I investigated the habitat value of reefs comprised of oyster shell, surf clam (*Spisula solidissima*) shell, and pelletized coal ash for benthic and nektonic communities.

Oyster recruitment, survival, and growth were monitored on reefs constructed from oyster and surf clam shell near the mouth of Chesapeake Bay, USA and in the York River. The oyster shell reef supported greater oyster growth and survival and offered the highest degree of structural complexity. On the York River subtidal clam shell reef, the quality of the substrate varied with reef elevation with large shell fragments and intact valves scattered around the reef base and small, tightly packed shell fragments paving the crest and flank of the reef mound. Oysters were more abundant and larger at the reef base and less abundant and smaller on the crest of the reef. The availability of interstitial space and appropriate settlement surfaces is hypothesized to account for the observed differences in oyster abundance across the reef systems. The patterns observed give further context to the importance of substrate selection in similar restoration activities.

Invertebrate fauna associated with oyster shell, clam shell, and pelletized coal ash reef habitats were investigated. Diversity and secondary production were greatest on the oyster shell reef. Species richness was lowest on the coal ash pellet reef due to fewer rare species; however, total community abundance was significantly greater than on the other two reef types, driven by numerical dominance of small crustaceans. Clam shell reefs showed intermediate abundance and diversity patterns but had the lowest values for secondary production. Differences in macrofaunal community metrics reflect the quantity and quality of the interstitial space afforded by the substrate material and is in part driven by the presence of living oysters that grew to form a living oyster crust on the oyster shell reef during this study.

Differences in the abundance, diversity, and community structure of nekton species collected using a remotely deployed enclosure trap between these reef substrate types. Data show distinct differences in nekton community structure across habitat types. Species richness was greatest on the oyster shell and coal ash pellet habitats. Significant differences in the presence and abundance of nekton between oyster shell and clam shell reefs were detected. Clam shell reefs were similar in species composition and abundance to a bare-sand beach habitat. These reef habitats have refuge value, as demonstrated by the transient nekton species that numerically dominated all of these habitats. The oyster shell and coal ash pellet reef served as habitat to many ecologically, commercially, and recreationally important species that use the reef habitat for food and shelter during juvenile life stages, suggesting the reef habitats may be of great importance as habitat to finfish communities.

EVALUATING RESTORED OYSTER REEFS IN CHESAPEAKE BAY: HOW HABITAT STRUCTURE INFLUENCES ECOLOGICAL FUNCTION

GENERAL INTRODUCTION

Anthropogenic alterations of estuarine environments have long been structuring coastal systems around the world. Shoreline development and land uses within the Chesapeake Bay watershed since the arrival of European settlers in 1607 have had deleterious effects on water quality and altered estuarine habitats (Hargis 1999). Increased sedimentation and nutrient inputs from extensive deforestation, urbanization of the watershed, alteration of natural flow patterns and salinity regimes, and destructive agricultural practices contribute to degraded Bay water quality. Growing coastal populations and increased demand on living marine resources apply further pressure to a stressed estuarine ecosystem.

The Eastern oyster, *Crassostrea virginica*, has fallen victim to pressures of human progress. The oyster industry thrived in Chesapeake Bay since the arrival of English colonists and peaked in the late 1800's as oyster populations began to decline (Hargis and Haven 1999). Overharvesting, disease, and changes in water quality are the explanations most often given for this decline; however, these impacts are not mutually exclusive. In fact, one impetus behind restoration of oyster populations and oyster habitat is that oysters are seen as a means to help improve poor water quality, a factor that contributed to their demise. Oysters have the capacity to strain large quantities of water through their gills as they feed, clearing the water of small particles and anything attached to the particles, in the process. This filtering function helps maintain good water quality in estuaries, where the amount of suspended particles present can otherwise be quite high (Newell and Langdon 1996).

In addition to water quality improvements, the momentum behind oyster habitat restoration in Chesapeake Bay also relates to fishery stock enhancement and restoration of the structure and function of oysters and organisms normally associated with oyster reef habitat. According to Cairns (1993), "the ultimate goal of ecological restoration is to emulate a healthy, natural, self-regulating system that is integrated into the surrounding natural landscape." Often a measure of a restoration project's success involves a comparison of the restored habitat to one in its natural state. Unfortunately, little quantitative data exist on functional aspects of oyster reef habitat in lower Chesapeake Bay. Although oyster reefs are prominent features of intertidal areas of most estuaries in the southeastern United States, there are no biogenic oyster reefs remaining in high salinity waters in Virginia that can be used to evaluate the functional role of this type of habitat.

Recent oyster reef habitat restoration efforts have resulted in the placement of substrata in several locations within Chesapeake Bay. In Virginia, replenishment programs have resulted in reef construction in the James, Great Wicomoco, Piankatank, Rappahannock, and York Rivers, Mobjack Bay and on the Seaside of the Eastern Shore. These restoration efforts include (1) the construction of reef bases to provide substrate for oyster larval settlement and (2) stock enhancement with hatchery-raised juvenile oysters to provide broodstock and accelerate the formation of living oyster reef habitats. Oysters require appropriate hard substrate for settlement and survival and typically settle upon other oysters forming complex beds that support future settlement (Kennedy and Sanford

1999). Overharvesting of oysters and relic oyster shell essentially removed much of the suitable habitat for new recruits, contributing to the decline in oyster populations.

In this dissertation I investigate the relationship between physical structure and ecological function of constructed oyster reef habitats in Chesapeake Bay. I examined benthic and nektonic community structure on reef bases of varying construction materials to evaluate reef restoration approaches using alternative base substrates. Oyster reef restoration activities in the Virginia portion of Chesapeake Bay typically involve the placement of hard substrata on the seabed to form three-dimensional mounds to serve as a base for oyster recruitment and growth. A shortage of oyster shell for creating large-scale reefs has led to widespread use of other materials, such as surf clam (*Spisula solidissima*) shell, limestone marl, pelletized coal ash, and even crushed porcelain toilets (J. Wesson, pers. com.) as a substitute for oyster shell.

In Chapter 1, I discuss the population dynamics of oysters on intertidal and subtidal reefs composed of different substrate base materials. I examine and contrast the oyster recruitment, growth, and survival at different reef elevations on a subtidal *Spissula solidissima* shell reef in lower York River and intertidal reefs constructed of *Crassostrea virginica* shell and *S. solidissima* shell near the mouth of Chesapeake Bay at Fisherman's Island.

In Chapter 2, I describe a enclosure trap seine developed to sample intertidal oyster reef habitats.

In Chapter 3, I evaluate patterns of macrobenthic community abundance, biomass, and diversity among three constructed oyster reef substrates on reefs at Fisherman's Island to determine if reef structure affects community development and function. I calculate benthic secondary productivity for macrobenthic invertebrates, which be used to assess ecological integrity in constructed oyster reef communities. Attention is paid to the relative production of the most representative and abundant taxa, also according to trophic groups, degree of mobility, and larval dispersal modes on different reef substrate types (oyster shell, surf clam shell, and pelletized coal ash).

In Chapter 4, I compare nekton use and community composition of intertidal constructed oyster reef habitats of different substrate construction materials while using a nearby bare-sand beach habitat as a proxy pre-reef-construction control to assess the importance of these oyster reefs as fish habitat.

Oyster reefs cannot be considered in isolation, as closed boxes do not exist in nature. Oyster reefs likely have vital ecological linkages with other ecosystems and the restoration of oysters to Chesapeake Bay will have implications beyond the physical reef habitat. High benthic secondary production on oyster reefs can contribute to neighboring systems. The physical structure of the reef habitat provides refuge habitat to many estuarine species. The findings reported in this dissertation provide evidence on the functional role of constructed oyster reefs habitats in Chesapeake Bay and shed light on community structure and functioning of reef and adjacent habitats.

CHAPTER 1

SETTLEMENT AND SURVIVAL OF THE OYSTER *CRASSOSTREA VIRGINICA* ON CREATED OYSTER REEF HABITATS IN CHESAPEAKE BAY

ABSTRACT

Efforts to restore the Eastern oyster, *Crassostrea virginica*, reef habitats in Chesapeake Bay typically begin with the placement of hard substrata to form three-dimensional mounds on the seabed to serve as a base for oyster recruitment and growth. A shortage of oyster shell for creating large-scale reefs has led to widespread use of other materials, such as surf clam (*Spisula solidissima*) shell, as a substitute for oyster shell. Oyster recruitment, survival, and growth were monitored on intertidal reefs constructed from oyster and surf clam shell near Fisherman's Island on a subtidal surf clam shell reef in York River. At the Fisherman's Island reefs, oyster larvae settlement occurred at similar levels on both substrate types throughout the monitoring period but higher levels of postsettlement mortality occurred on clam shell reefs. The oyster shell reef supported greater oyster growth and survival and offered the highest degree of structural complexity. On the York River subtidal clam shell reef, the quality of the substrate varied with reef elevation with large shell fragments and intact valves scattered around the reef base and small, tightly packed shell fragments paving the crest and flank of the reef mound. Oysters were more abundant and larger at the reef base and less abundant and smaller on the crest of the reef. The availability of interstitial space and appropriate settlement surfaces is hypothesized to account for the observed differences in oyster abundance across the reef systems. The patterns observed give further context to the importance of substrate selection in similar restoration activities.

INTRODUCTION

Oyster reefs serve an ecologically important role by providing the predominate natural hard substrate in the characteristically sedimentary environment of the middle Atlantic coastal plain. The three-dimensional structure of oyster reef habitat created by Eastern oyster (*Crassostrea virginica*) increases the amount of surface area for attachment and crevices for refuge of newly settled oysters, as well as numerous small invertebrates and fishes (Wells 1961; Bahr 1974; Dame 1979; Zimmerman et al. 1989). Oyster reefs, which were once a prominent feature in the Chesapeake Bay ecosystem before European colonization and intense overharvesting during the 19th and 20th centuries, have been reduced to mere footprints of their original upthrusting profile (Hargis 1999). Years of poor resource management of both live oysters and shell, mortality from diseases caused by the protistan parasites *Perkinsis marinus* ("Dermo") and *Haplosporidium nelsoni* ("MSX"), and increased sedimentation and environmental degradation have all contributed to a dramatic decline in oyster populations in Chesapeake Bay. These natural, self-renewing habitats have been effectively destroyed and are the focus of many habitat restoration efforts throughout Chesapeake Bay (Kennedy and Sanford 1999; O'Beirn et al. 2000; reviewed by MacKenzie 1996 and Mann 2000).

Efforts to restore oyster reef habitats typically begin with the placement of hard substrata on the seabed to serve as a base for oyster recruitment and growth. Over time, continued settlement and subsequent growth of generations of oysters form a continuous veneer of living oyster reef over the base substrate (Wesson et al. 1999; O'Beirn et al. 2000). Numerous studies have emphasized the importance of vertical relief of these created habitats on oyster growth and survival in altering water flow and sedimentation (Lenihan 1999), and in elevating the habitat into the intertidal zone (Bartol and Mann 1999; O'Beirn et al. 2000; Volety et al. 2000). Since the early 1990's, reefs in lower Chesapeake Bay have been commonly built as three-dimensional mounds ranging in height from approximately 0.5 to 2 m above the seabed (Wesson et al. 1999; O'Beirn et al. 2000). While many of these created reefs in lower Chesapeake Bay are in the intertidal zone, some are located in deep regions or have settled or eroded and are entirely subtidal. Whether intertidal or subtidal, the structure of these constructed hummocks is intended to offer adequate surface and interstitial heterogeneity for oyster growth and survival and for recruitment by other epifaunal species. Bartol et al. (1999) underscore the importance of interstitial space within the fabric of intertidal reefs to promote oyster survival during periods of severe solar exposure and predation. The material used to create oyster reefs should afford this architectural complexity.

The most common material used in oyster reef construction is empty *Crassostrea virginica* shell secured from local shucking operations. When piled into mounds, oyster shells form an interstitial matrix of void spaces between the shell pieces. These spaces and the shell surfaces around them provide settlement habitat, refugia from predation, and moderation of physical stress for oysters and associated colonizing fauna (Gutiérrez et al.

2003). While prior research has shown that oyster larvae prefer to settle on living or recently living shells of conspecifics (Crisp 1967, Veitch and Hidu 1971), shortages of oyster shell have prompted a search for suitable alternative substrates for reef construction.

One material commonly used as an alternative to oyster shell is surf clam (*Spisula solidissima*) shell (Wesson et al. 1999). With repeated handling associated with large-scale reef construction, *S. solidissima* shells fracture into small pieces that pack tightly together and thus provide limited surface area and interstitial space for occupation by oysters and colonizing reef fauna. Overall interstitial volume afforded by fractured *S. solidissima* shell is significantly less than that provided by oyster shell (O'Beirn et al. 2000). To date, only O'Beirn et al (2000) have examined the efficacy of the *S. solidissima* shell substrate in large-scale intertidal reef restoration efforts but similar details have not been quantified for clam shell reefs in subtidal habitats.

The objective of this project is to examine and contrast the oyster recruitment, growth, and survival at different reef elevations on a subtidal *Spissula solidissima* shell reef in lower York River and intertidal reefs constructed of *Crassostrea virginica* shell and *S. solidissima* shell near the mouth of Chesapeake Bay at Fisherman's Island. The results have relevance for the selection and placement of materials and of design strategies for oyster reef restoration. Oyster populations on the reefs at Fisherman's Island were not compared statistically with that of the Goodwin Island reef because of the confounding effects of temporal difference in reef construction and considerable dissimilarities in reef surface area and tidal and salinity regime exposure.

METHODS

Site Description

The study area included two created oyster reef sites protected from commercial harvesting in lower Chesapeake Bay. One site was situated at the mouth of the York River approximately 1 km north of Goodwin Island (a Chesapeake Bay National Estuarine Research Reserve in Virginia site, Figure 1). An oyster reef base was constructed in spring 1995 of 30,000 bushels (1057 m^3) crushed surf clam (*Spisula solidissima*) shell on a subtidal sandflat (Meisner 1995). The reef measured approximately 1350 m^2 and extended approximately 1.5 m above a seabed. At low tide the water over the subtidal reef crest was 1.5 m deep.

The other oyster reef site was located at the Fisherman's Island National Wildlife Refuge near the mouth of Chesapeake Bay at Virginia's eastern shore. During summer 1996, 11 intertidal oyster reef habitats were constructed of three substrate materials: *Crassostrea virginica* shell, *Spisula solidissima* shell, and, though not evaluated in this study, pelletized coal ash (Figure 1). The reefs range in size from 162 to 364 m^2 (O'Beirn et al. 2000). Although the Fisherman's Island and Goodwin Island reef systems were characterized by different physical (salinity, tidal range, intertidal vs. subtidal reefs, etc.) and biological (benthic and nektonic community species composition, nutrient regimes, etc.) regimes, a comparison of these reefs offered an opportunity to evaluate the use of alternative substrates in oyster reef restoration efforts and the efficacy of *S. solidissima* shell reefs under distinctly different conditions.

Oyster Sampling

Sampling of the reef to determine oyster abundance and size at Goodwin Island took place from Fall 1999 through Summer 2001. Using reference stakes permanently positioned at the reef margins, the surface of the reef was divided into a grid and coordinates were assigned to each cell of the grid. The reef was further subdivided into three depth strata - crest (1.5 m above the seabed), flank (0.8 m above the seabed), and base (0.2 m above the seabed) (Figure 2). Within each depth strata, the coordinates on the reef surface were selected randomly without replacement for each sample (once a cell was sampled, the coordinate of the area was be recorded so that sampled areas were excluded from selection at a later date). Within the cell, divers placed a square plastic frame (0.25 m x 0.25 m) on the reef surface and all substrate material within the frame was removed by hand to a depth of 10 cm (below this depth, shell and associated sediments were dark black in color and indicative of anoxic conditions) and placed in a cloth bag. Samples were transported to the laboratory in ice chests and stored in flow-through seawater tanks until processing. Samples were elutriated within 48 hours of collection over a 500μm mesh screen. Six replicate quadrat samples per sampling period were collected from each elevation strata. All live adult (oysters > 30 mm shell height), juveniles (≤ 30 mm shell height) and recently dead (with empty, paired, articulated valves with no evidence of interior fouling) oysters were counted and measured.

Similar methods were used at Fisherman's Island for assessing oyster stocks on the created intertidal reefs (described in detail in O'Beirn et al. 2000). Briefly, in May 1997, 1998, and 1999, three 0.25 m x 0.25 m quadrats were collected from each of three tidal elevations on two replicate reefs of each substrate type. The elevations were subtidal (0.25 below mean low water), low intertidal (at mean low water), and high intertidal (0.25 m above mean low water). The crests and flanks of different reefs were exposed to different tidal inundation regimes because of settling and erosion of the reefs over time (in particular, one of the oyster shell reefs) (Figure 2). Since the tidal elevation of the reef crests ranged from the high to low intertidal, the higher tidal heights from all reefs were not sampled during the entire study. Therefore, to compare oyster density by reef substrate type, analysis was restricted to the samples collected from the subtidal (reef base) and low intertidal (reef crest or flank, depending on the reef) reef elevations. All live and recently dead (with paired, articulated valves with no interior fouling) oysters were enumerated and measured to the nearest 0.1 mm.

Statistical analysis

Differences in oyster densities among reef elevations (base, flank, crest) and among sampling times (November 1999, July 2000, June 2001) at the Goodwin Island reef were assessed by two-way full-factor fixed effects model ANOVA. Separate ANOVA's were conducted for small ($\leq$30 cm shell height) and large (>30 cm shell height) live oysters and for identical categories of dead oysters to independently examine the effects of elevation and date on juvenile (small) and mature (large) oyster survival. Cochran's test was used to test for homoscedasticity of variances. When necessary, density values were log transformed [ln (x+1)] to conform to homogeneity and normality assumptions. Student-Newman-Keuls *a posteriori* tests were used to explore differences among means when significant factor and interactive effects were detected (Underwood 1997).

Differences in live oyster densities among reef elevations, substrate types, and sampling times at the Fisherman's Island reefs were assessed with separate three-way ANOVA models with year, reef type, and elevation as factors. Heteroscedastic variances were corrected with a ln(x+1) transformation.

RESULTS

Goodwin Island

Oyster densities on the Goodwin Island reef show a clear pattern relative to reef elevation at all sampling times with the base of the reef having greater oyster densities than reef crest (Figures 3 and 4). Two-way ANOVA for the effects of date and elevation revealed that only elevation on the reef influenced densities of both live and dead mature oysters (> 30 mm) (Table 1a). These oysters were significantly more abundant at the reef base compared with the flank and crest. Densities of live juvenile oysters (≤ 30 mm) were significantly affected by reef elevation, date, and their interaction ($P = 0.007$). SNK tests (Table 1b) performed to decouple the cause of the elevation x date interaction revealed: (1) during the 1999 and 2000 sampling events densities of small live oysters were greater at the flank and base than densities at the crest; (2) during the 2001 sampling period no statistically significant difference in juvenile oyster density according to reef elevation was detected although as in 1999 and 2000 densities tended to be lowest at the crest; (3) recruitment of juvenile oysters was lowest in 2000 across all elevations. Densities were greatest in 1999 and intermediate in 2001 at both the reef flank and base, but no significant differences were detected in densities these years at the reef crest (Table 1b). Densities of dead juvenile oysters (≤ 30 mm) were significantly affected by reef elevation and date. These oysters were significantly more abundant at the reef base than at the flank and crest (Table 1a).

Size frequency distributions reveal that for each of the three years (Figure 5) juvenile oysters (≤ 30 mm) numerically dominated all samples. Reef crest oysters had a unimodal population distribution each year. Flank and base reef strata exhibit bimodal size distributions in 2001. Juvenile oysters dominated all three strata throughout the sampling period with mature oysters (> 30 mm) rare. A greater proportion (albeit small) of mature oysters were collected from the reef base than from the reef flank. Dead oysters (with articulated shells) were present at each elevation each year and, although fewer in number, tended to reflect the distribution of live oysters at each elevation.

Dead oysters were examined for evidence of predation by crabs in 2000 and 2001. Predation by crabs on oysters was distinguished from other sources of mortality by the presence of chipped or cracked valve margins, puncture holes within the umbo region, crushing of the umbo region, and complete crushing of the valves. Dead oysters with such characteristics were collected from each reef elevation, but were proportionally more abundant at reef crest and flank compared with the reef base (Figure 6).

Visual comparisons of the size of surf clam (*Spisula solidissima*) shell fragments that make up the reef at different elevations were striking and led to a characterization of the reef substrate in July 2000. A subsample of atleast 50 shell fragments were randomly selected from each 0.25 m^2 reef quadrate sample and the largest dimension of each fragment was measured to the nearest millimeter. The size of clam shell fragments reflected the distribution of larger oysters and varied among elevation strata (ANOVA, $p < 0.001$). Fragments of clam shell were significantly larger at reef base compared with flank and crest. Shell fragments from the flank and crest did not differ significantly (Figure 7).

Fisherman's Island

The mean density (ln(x+1) transformed) of oysters at Fisherman's Island varied significantly according to tidal reef elevation, substrate type, and date (Table 2). There was also a significant tidal reef elevation by substrate type by date interaction. This interaction effect was due to higher densities of oysters at low intertidal reef elevations than at subtidal reef elevations of the clam and oyster shell substrates each year except in 1997 when subtidal oyster densities were greater than densities at low intertidal reef elevations on clam shell reefs (Figure 8, Table 2). Densities of oysters increased over time at the subtidal elevation of the oyster shell reefs and at the low intertidal reef elevation of the clam shell reefs. This pattern was not evident at the low intertidal reef elevation on the oyster shell reef where the density of oysters was lowest in 1998. Oyster densities remained low throughout the study at the clam shell reefs' subtidal elevation (Figure 8). None of the first order interaction effects were significant (all $p > 0.079$).

Oysters were consistently more abundant on the oyster shell than on the clam shell reef habitat. Overall abundance patterns on clam shell were similar to that found on the clam shell reef at Goodwin Island with a population dominated by small oysters and few oysters surviving to attain larger sizes (> 30 mm) (Figure 9). By May 1997, nearly one year after reef construction, oysters were notably more abundant on the oyster shell reef compared with the clam shell reef. By May 1998 and through 1999, the size distribution of oysters on the oyster shell reef was bimodal with relatively large numbers of larger live oysters, whereas a unimodal size distribution of small live oysters was found on clam shell. Recently dead oysters with articulated shells were present on both reef types all years and tended to reflect the distribution of live oysters. There appeared to be increased survival on the oyster shell habitats as the ratio of live oyster to recently dead oyster abundance was greater on the oyster shell reefs than on the clam shell reefs each year. The clam shell reefs were capped in Summer 1999 with a veneer of oyster shell because of the marked difference in oyster abundance and survival between the alternative substrate and oyster shell reefs.

DISCUSSION

This study compared the development of oyster populations on different culch materials in intertidal and subtidal settings. Reefs built in lower Chesapeake Bay for habitat restoration are 3-dimensional mounds of shell (or other substrate material) rising half a meter to as much as 2 meters above the bottom. No matter what the construction configuration, the ultimate goal of substrate placement in reef restoration is the formation of a self-renewing veneer of generations of living oysters encrusted over the core base material. The formation of this living covering is dependent on the success of the substrate material to support survival and growth of the initial cohort of oysters that recruit to the constructed reef. This substrate should provide ample convolutions and surface area to afford settlement surface and refuge for young oysters from predation and physical stress. Thus, the choice of an appropriate substrate type for use as a reef base can dictate success or failure of the developing reef assemblage.

The reef bases at Goodwin Island and Fisherman's Island developed quite different oyster populations on similar substrate materials under different physical regimes and recruitment levels. Oyster settlement on the eastern shore of Chesapeake Bay is generally greater than that of the western shore tributaries. Oyster recruitment at Fisherman's Island has been monitored since 1995 (Morales-Alamo and Mann 1996) and annual fluctuations in the magnitude of recruitment, with low records in 1996 and high records in 1997 and 1999 (Southworth et al. 2000; this study).

Oyster densities on both substrate types showed a steady increase over time at Fisherman's Island but the population on the oyster shell far exceeded that on the clam shell mound. By 1999, the single oyster shells that make up the base of the reef were encrusted by a continuous living veneer of live oysters. This veneer never formed on the clam shell mounds.

Although the York River has been characterized by low recruitment in recent years (Morales-Alamo 1996, 1997, 1998; Southworth et al. 1999, 2000, 2001), juvenile oysters recruited to the Goodwin Island reef each year. Spawning of *Crassostrea virginica* is initiated by temperature (20-25° C) (Galtsoff 1964) or salinity cues (> 10 psu) (Abbe 1986) and typically occurs between June and October in lower Chesapeake Bay (Andrews 1951). Low oyster recruitment has been prevalent in Virginia since 1991 (Southworth et al. 2000). The relatively high number of recruits observed in 1999 at the Goodwin Island reef compared with subsequent years is likely due to temporal differences in sampling events. In 1999, the reef was sampled in November, after the conclusion of the settlement period so the population reported here is inclusive of young oysters recruited to the reef during the summer of 1999. During the other two years, the reef was sampled in the summer at the beginning of reproductive activity and data reflect the oysters that survived through the previous winter as well as some of the early recruits of that year. A recruitment event of the magnitude observed in November 1999 was not observed again in 2000 or 2001, nor was it reflected in the number of small oysters observed in subsequent years.

The distribution of live oysters and the physical structure of the subtidal reef at Goodwin Island is analogous to those of natural mature subtidal oyster reefs of the Gulf Coast exhibiting the "grit principle", first mentioned by MacKenzie (1977) and discussed by Gunter (1979). Reefs of this type form barren central ridges consisting of fine dead shell grit on the reef crest and live oysters are only found along the flanks and in deeper water. Constant motion of the crest substrate from effects of wind-generated waves and currents likely abrades sessile organisms and hinders oyster larvae development. Gunter suggests that delicate larvae that set on this material are destroyed through mechanical grinding by movement of the shell. It is likely that such movement of the small shell fragment substrate at the reef crest contributed to the distribution of oysters observed on this reef.

The geometry of the reef substrate culch material and the extent of predation refuge it affords likely explain the differential survival of oysters and the observed oyster abundance patterns on different substrate materials. Decapod predators, including the blue crab, *Callinectes sapidus*, and Panopeid mud crabs (i.e., *Panopeus herbstii*, *Dyspanopeus herbstii*, *Eurypanopeus depressus*) are major predators of bivalve mollusks and can cause high levels of mortality in juvenile oyster populations (McDermott 1960, Krantz and Chamberlin1978; Seed 1980; Bisker and Castagna 1987; Eggleston 1990; reviewed by White and Wilson 1996). Fragile shells of young oysters (<15 mm shell height) are susceptible to crushing by these predators. Crabs generally chip the margins of the valve of larger oysters with their chelae to gain access to the tissue inside. The vulnerability of a given oyster to decapod predation is a function of oyster shell height and thickness, oyster growth geometry, and the site of attachment on cultch material

(Eggleston 1990). An oyster attached to the cupped depression on the nacreous surface of the cultch shell is less likely to be successfully preyed upon by crabs because the depression limits the crab's ability to reach the oyster with chelae and protects the oyster from crushing (Eggleston 1990). In laboratory experiments, larger oysters (> 30 mm shell height) were less likely to be successfully preyed upon by the blue crab *Callinectes sapidus* due to increased shell thickness compared with smaller oysters.

Substrate material with ample convolutions and interior surfaces for settlement out of direct reach of decapod predators gives young oysters a survival advantage not afforded to those that settled on less suitable substrates. A greater proportion of young oysters (≤ 30 mm shell height) from the Goodwin Island reef showed evidence of decapod predation on the crest and flank of the reef compared with those collected from the base. Areas on the reef where the substrate consists of small, tightly packed shell fragments leave young oysters that settle vulnerable to crab predation. The distribution of oysters with evidence of crab predation reflected the size distribution of clam shell fragments on the reef mound (Figures 5 and 6). Proportionately fewer dead oysters collected from the base of the reef showed evidence of crab predation and it is likely that these oysters succumbed to other sources of mortality, such as disease and flat worm predation (Ragone Calvo and Burreson 1999, 2000, 2001). Since a large proportion of the oysters collected in 1999 from the Goodwin Island reef mound were unaccounted for in 2000, it is likely that many of the young oysters from 1999 were preyed upon by crabs and crushed and were not represented in these samples. In areas where the substrate did not offer adequate shelter from predation, oyster mortality likely occurred due to decapod predation before infection could kill the oyster. Where the substrate afforded adequate refuge for young oysters from predators, oysters survived to attain larger sizes with a greater percentage of the mortality attributed to parasitic infections. Early post-settlement mortality due to a combination of predation and disease structured the oyster community on this habitat.

Of the two substrate materials evaluated, oyster shell may provide more available settlement surfaces with room to grow and adequate water flow to supply food to young oysters compared with clam shell. The importance of larval supply and habitat selection in creating the patters observed is arguable. If settlement and metamorphosis success were unequal across substrate types, surviving oysters could be expected to be more abundant on reefs with favorable larval habitats, such as demonstrated by the patterns observed on the oyster shell or larger clam shell fragments. Conversely, if oyster larval settlement and metamorphosis success were equal across all reefs, the patterns observed could be a result of differing post settlement mortality pressure on different reef types. If this post settlement mortality was the result of predation, then different reef substrates may foster predator communities imposing different pressures on newly settled oysters. The matrix of the oyster shell reef base, having larger interstitial spaces compared with clam shell, could be more accessible to fish and decapod predators. While these larger predators may not prey directly upon the small, new recruits, they may feed upon smaller predator species that would, making the reef matrix a predation refuge for young oysters (McDermott and Flower 1952). Smaller interstitial spaces, such as those of the clam shell substrate, may be limiting to larger predators but accessible to small decapods (such as juvenile panopeid crabs) and flatworms. This reef type may serve as a structural refuge for these individuals, permitting grazing on newly settled oysters. The resulting oyster population would reflect these trophic interactions with few oysters persisting on clam shell substrates. Future studies of interactions of newly settled oysters and their predators on different substrate materials may further elucidate the potential importance of habitat selection and predation processes in structuring these communities.

Although this study was not designed to examine oyster settlement and early post-settlement mortalities directly, oyster recruitment to each location on the reef was observed but oysters did not persist equally through subsequent monitoring periods. The oyster populations on the clam shell mounds at Fisherman's Island and on the flank and crest of the Goodwin Island mound were numerically dominated with small, newly-recruited individuals. Oysters from these locations never attained shell heights greater than 60 mm in any of the years sampled and few reached shell heights above 30 mm (between 0 and 25 oysters/m^2 at the Fisherman's Island clam shell mounds, 5 and 18 oysters/m^2 at the Goodwin Island reef flank, and 2 and 4 oysters/m^2 at the Goodwin Island reef crest) (Figures 4 and 8). While the oyster populations at the base of the Goodwin Island reef and on the oyster shell mounds at Fisherman's Island were also dominated by small individuals, overall densities of oysters were greater and large (older) oysters representing multiple year classes were present in the population. By May 1999, 8% (110 oysters/m^2) of the standing stock at the oyster shell reefs Fisherman's Island had attained a shell height of ≥ 60 mm and 50% (680 oysters/m^2) of the standing stock had grown to ≥ 30 mm shell height. Since large oysters generally produce more eggs than do smaller oysters (Davis and Chanley 1956; Cox and Mann 1992) and oysters can reach sexual maturity at shell heights smaller than 35 mm (Andrews 1979), this proportion of the standing stock represents a considerable number of oysters that could contribute to future reproductive events to sustain these reefs.

As efforts to restore oyster reefs become more widespread along the Atlantic coast, we learn that there is no generic model for construction and configuration of the reefs (e.g., size, shape, vertical relief, substrate type). The results of this study further affirm the importance of substrate complexity in the development of oyster populations on restored reefs reported in earlier studies (Bartol and Mann 1999; Bartol et al. 1999; O'Beirn et al. 2000), but they also highlight the importance of environment specific interactions and point to the need for an improved understanding of the mechanisms affecting the interaction between substrate characteristics and oyster recruitment and survival. Constructed reef design should account for local geophysical and biological conditions and provide shelter for oysters and associated fauna from such stressors as hypoxia, siltation, ice scour, and aquatic and avian predators.

Materials used as reef substrate should provide adequate small-scale structural complexity with ample refugia for newly settled oysters to avoid predation, whether subtidally or intertidally. An interaction was observed between the substrate material used in the construction of oyster reef habitats and the subsequent abundance of oysters on these habitats. Results from this study suggest that the interstitial space afforded by the material used to construct the reef contributes to the ability of oysters escape predation and survive. Oyster shell and large fragments of clam shell provided sufficient habitat to support and sustain a viable oyster population. The provision of large-scale vertical relief extending up in to the intertidal may not be as important in shallow (<2 m), subtidal habitats with good water quality as is the provision of proper settlement substrate. Providing high relief mounds move oyster habitat higher into the water column or intertidally may not be as important as adequate surface heterogeneity in sustaining oyster populations in systems where sedimentation and water quality are not deleterious to oysters. The results of this study should be used to reassess the types of material and reef configurations in oyster reef restoration efforts and emphasize the importance of a wise use of the limited oyster shell resource in future oyster reef restoration efforts.

ACKNOWLEDGEMENTS

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Table 1 (a): Summary of ANOVAs testing whether oyster densities (ln(x+1) transformed) at the Goodwin Island's constructed oyster reef varied as a function of position on reef (Crest (C), Flank (F), or Base(B)), and date. Multiple comparisons of the means were analyzed using Student-Newman-Keuls tests. Treatments are listed in ascending order of means and treatments not connected by a common underline differed at p = 0.05.

	Source	**df**	**Mean Square**	***F*-value**	***P*-value**	**Multiple Comparisons**
Small dead oysters (≤ 30 mm)	position on reef	2	19.400	15.19	**<0.001**	$\underline{C} < \underline{F = B}$
	date	2	8.960	7.02	**0.002**	$\underline{99} < \underline{00 = 01}$
	position on reef x date	4	3.180	2.49	0.056	
	error	45	1.280			
Large dead oysters (> 30 mm)	position on reef	2	13.203	17.54	**<0.001**	$\underline{C = F} < \underline{B}$
	date	2	0.972	1.29	0.285	
	position on reef x date	4	0.527	0.70	0.596	
	error	45	0.753			
Small live oysters (≤ 30 mm)	position on reef	2	17.790	30.42	<0.001	
	date	2	39.423	67.42	<0.001	
	position on reef x date	4	2.354	4.03	**0.007**	see Table 1b
	error	45	0.585			
Large live oysters (> 30 mm)	position on reef	2	31.020	26.97	**<0.001**	$\underline{C} < \underline{F} < \underline{B}$
	date	2	1.620	1.41	0.256	
	position on reef x date	4	0.930	0.81	0.527	
	error	45	1.150			

Table 1 (b): Results of Student-Newman-Keuls multiple comparison tests on mean small live oysters (≤ 30 mm shell height) densities. Treatments not connected by a common underline differed at $p = 0.05$.

Effect of position on reef for each year:

1999	2000	2001
$\mathbf{\underline{C} < \underline{F = B}}$	$\mathbf{\underline{C} < \underline{F = B}}$	$\mathbf{\underline{C = F = B}}$

Effect of year at each position on reef:

CREST	FLANK	BASE
$\mathbf{\underline{00} < \underline{99 = 01}}$	$\mathbf{\underline{00} < \underline{01} < \underline{99}}$	$\mathbf{\underline{00} < \underline{01} < \underline{99}}$

Table 2: Summary of ANOVA of live oyster densities (ln(x+1) transformed) from the reefs at Fisherman's Island, Virginia.

Source	**df**	**Mean Square**	**F-value**	**P-value**
elevation	1	17.381	8.97	**0.004**
substrate type	1	318.188	164.29	**<0.001**
elevation x substrate type	1	1.290	0.67	0.418
date	2	20.356	10.51	**<0.001**
elevation x date	2	5.139	2.65	0.079
substrate type x date	2	1.291	0.67	0.517
elevation x substrate type x date	2	11.447	5.91	**0.005**
error	60	1.937		

Figure 1: Location of created oyster reef study areas near Goodwin Island at the mouth of York River and near Fisherman's Island at the mouth of Chesapeake Bay.

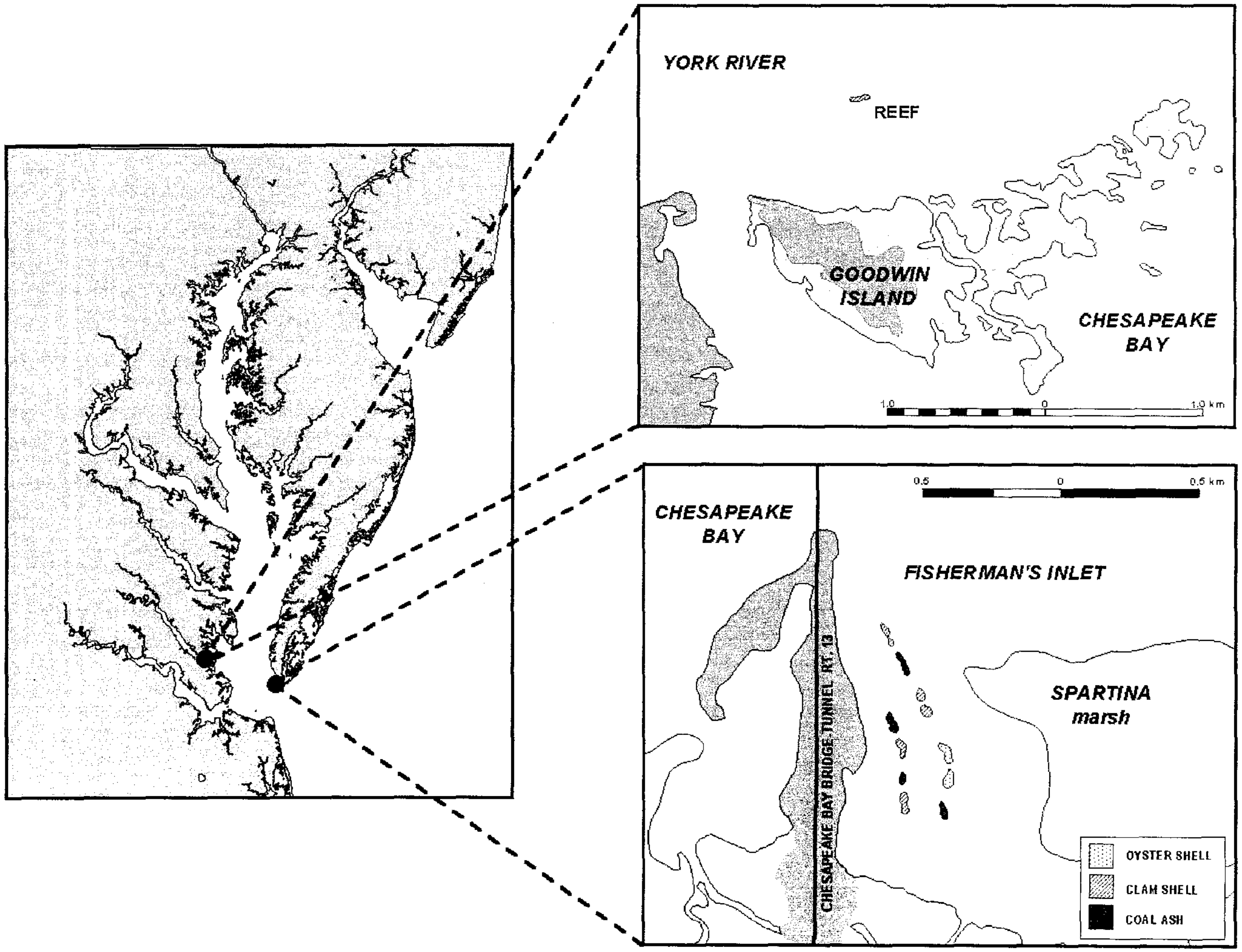
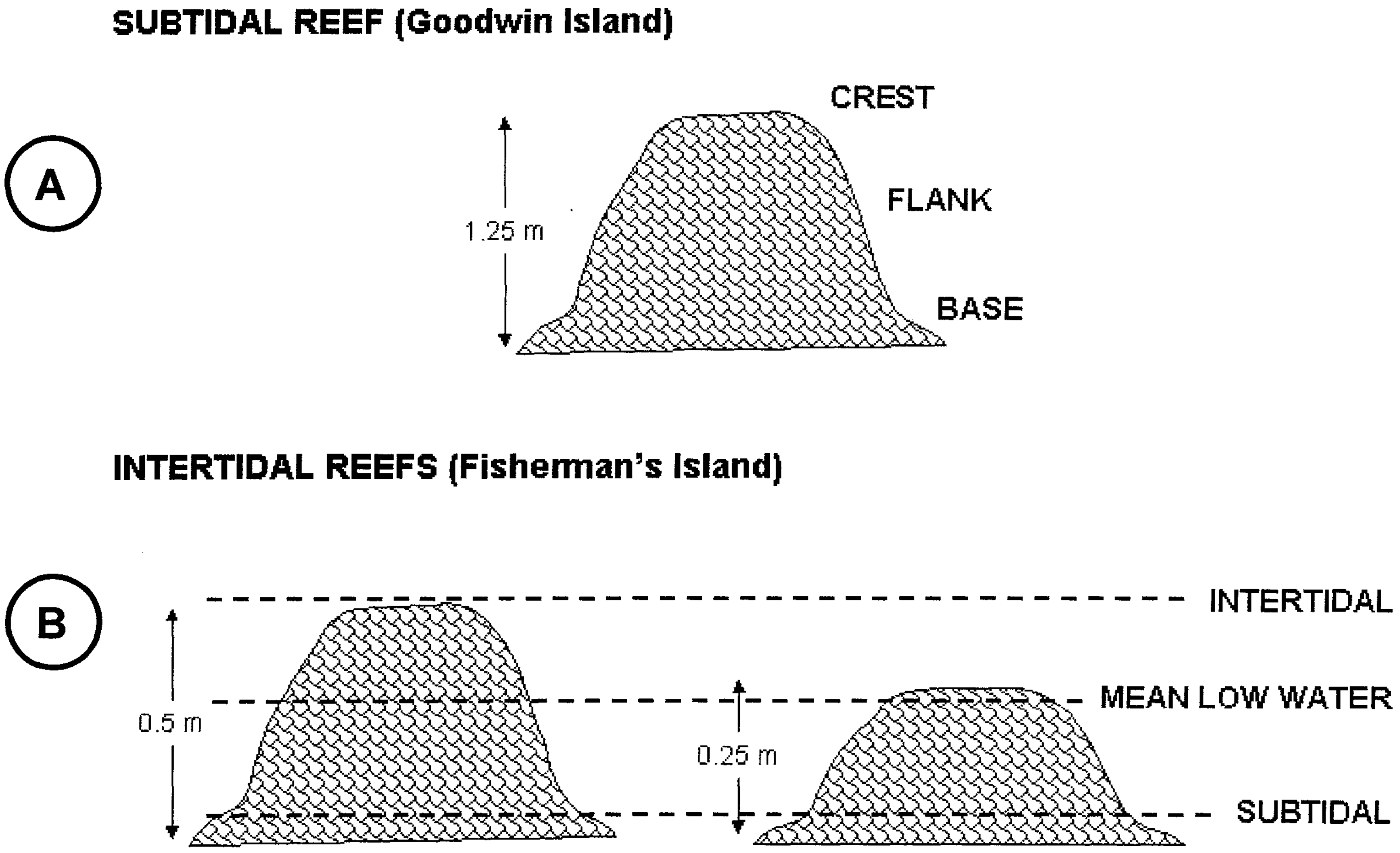

YORK RIVER
REEF
GOODWIN ISLAND
CHESAPEAKE BAY
1.0
0
1.0 km
CHESAPEAKE BAY
0.5
0
0.5 km
FISHERMAN'S INLET
CHESAPEAKE BAY BRIDGE TUNNEL RT 13
SPARTINA marsh
OYSTER SHELL
CLAM SHELL
COAL ASH

Figure 2: Sizes and shapes of constructed oyster reefs used in this study. Reefs are exaggerated vertically for this figure.

(A) The subtidal reef at Goodwin Island was constructed of surf clam shell. Samples were collected from the reef crest, flank, and base.

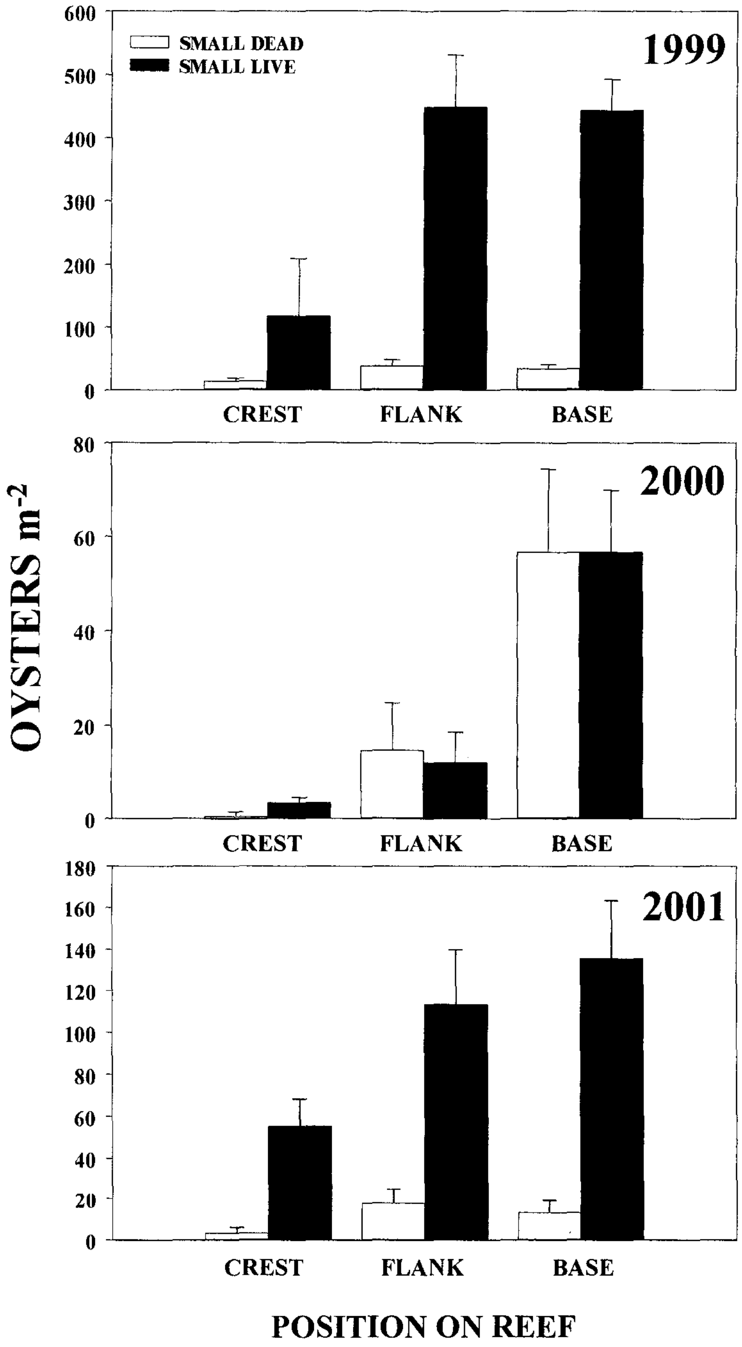
(B) The intertidal reefs at Fisherman's Island (bottom) were constructed of either surf clam or oyster shell. Regions of the reefs sampled on the intertidal reefs were based on tidal elevation rather than reef morphology. The crests and flanks of different reefs were exposed to different tidal inundation regimes over the course of the study because of settling and erosion of the reefs over time.



SUBTIDAL REEF (Goodwin Island)

INTERTIDAL REEFS (Fisherman's Island)

Figure 3: Mean density of small (≤ 30 mm shell height) live and dead oysters, *Crassostrea virginica,* at the Crest (1.5 m above the seabed), Flank (0.8 m above the seabed), and Base (0.2 m above the seabed) of the Goodwin Island created oyster reef, York River, Virginia, November 1999, July 2000, and June 2001. Bars represent mean abundance per square meter + 1 SE (n = 6).



OYSTERS m-2
600
500
400
300
200
100
0
SMALL DEAD
SMALL LIVE
1999
CREST
FLANK
BASE
80
60
40
20
0
2000
CREST
FLANK
BASE
180
160
140
120
100
80
60
40
20
0
2001
CREST
FLANK
BASE
POSITION ON REEF

Figure 4: Mean density of large (>30 mm shell height) live and dead (non-fouled, articulated oyster shells only) oysters at the Crest (1.5 m above the seabed), Flank (0.8 m above the seabed), and Base (0.2 m above the seabed) of the Goodwin Island created oyster reef, York River, Virginia in 1999, 2000, and 2001. Bars represent mean abundance per square meter +1 SE (n = 6). Separate ANOVAs and SNK a posteriori tests were used to compare densities of live and dead oysters. As there was no significant effect of sampling date, data shown are pooled from all sampling events. Letters above bars represent results of SNK *a posteriori* comparisons:

dead – a > b, live – A > B > C, $\alpha = 0.05$.

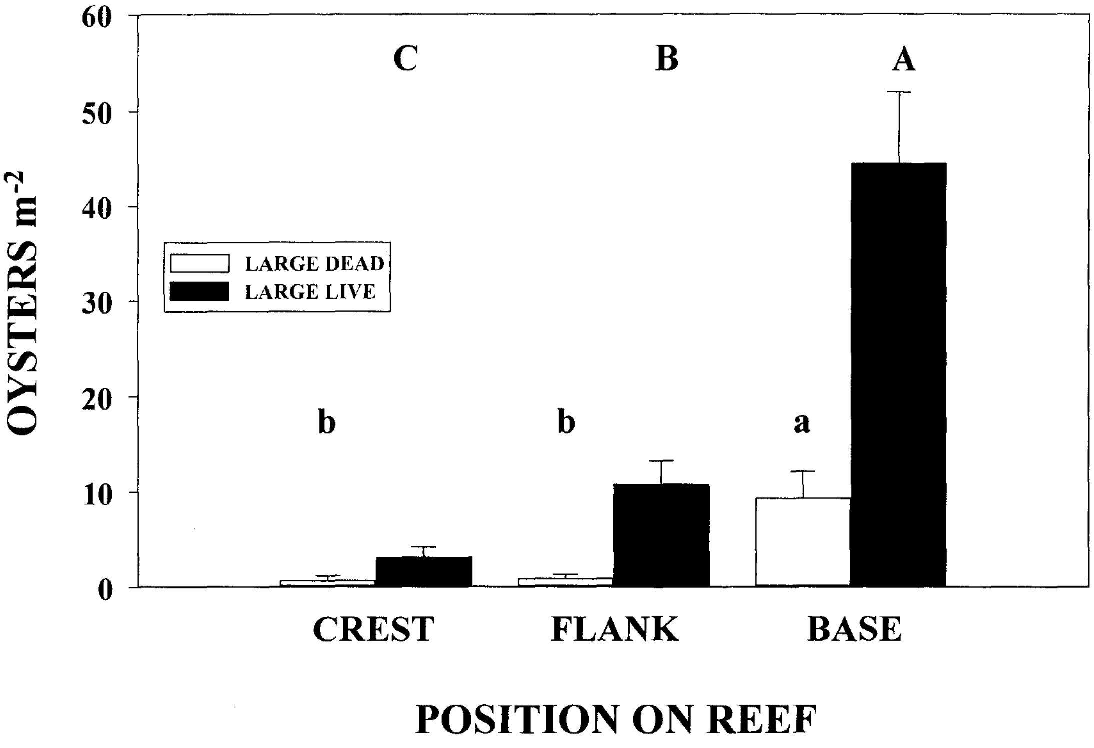

60
50
40
30
20
10
0
OYSTERS m-2
C
B
A
b
b
a
LARGE DEAD
LARGE LIVE
CREST
FLANK
BASE
POSITION ON REEF

Figure 5 Size frequency distributions for live and dead (non-fouled, empty articulated oyster shells) oysters collected from the Crest, Flank, and Base of the Goodwin Island created oyster reef, November 1999, July 2000, and June 2001. Mean oyster densities for each size class were derived from six replicate 0.25 m^2 quadrate samples collected from each reef elevation each sampling period. Omitted from this figure is one live oyster (shell height = 166 mm) collected from the reef Base in July 2000. Note the order of magnitude difference in scale of abundance between 1999 and 2000/2001.

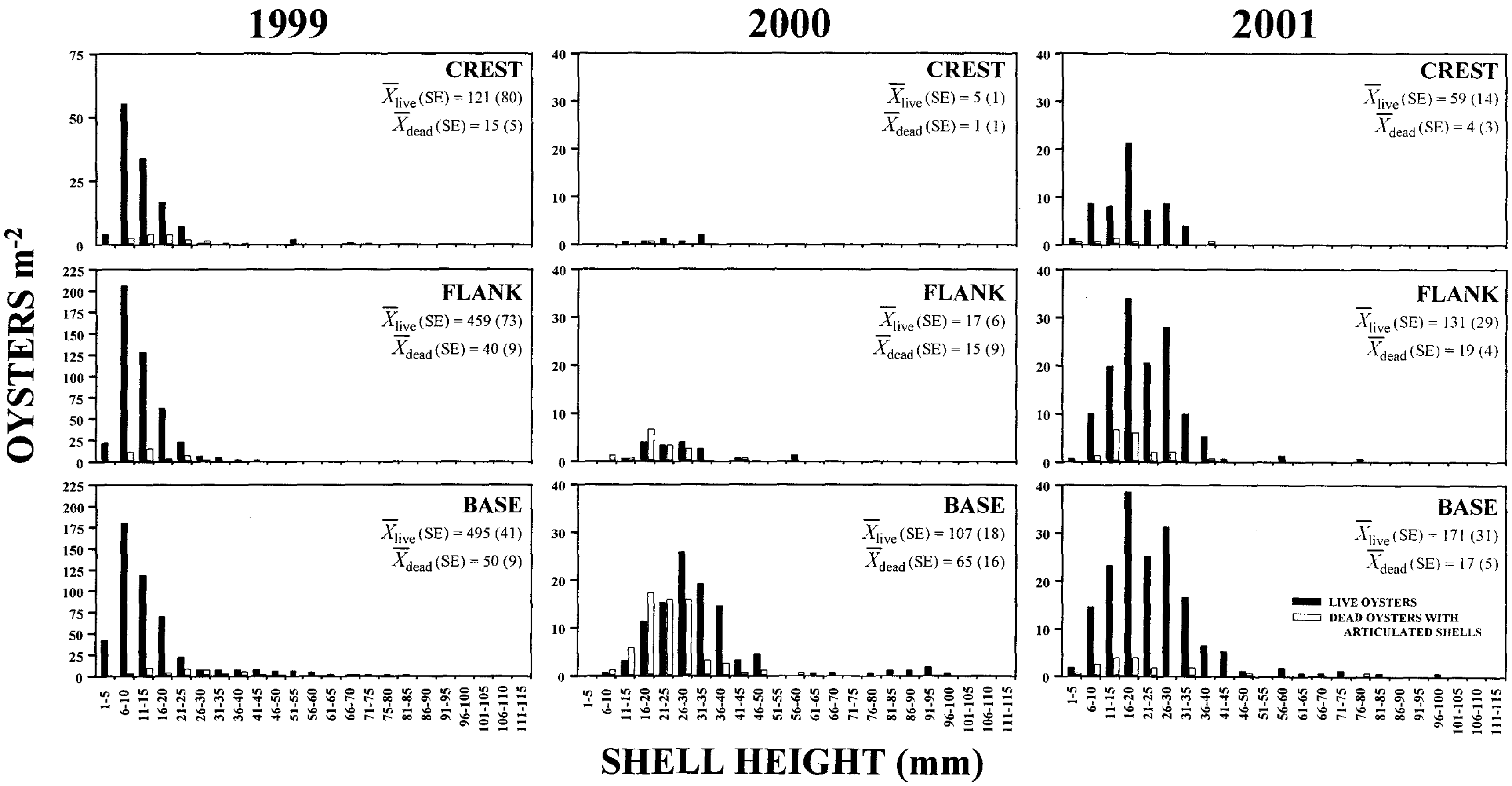

1999
2000
2001
CREST
$\overline{X}_{live}$ (SE) = 121 (80)
$\overline{X}_{dead}$ (SE) = 15 (5)
CREST
$\overline{X}_{live}$ (SE) = 5 (1)
$\overline{X}_{dead}$ (SE) = 1 (1)
CREST
$\overline{X}_{live}$ (SE) = 59 (14)
$\overline{X}_{dead}$ (SE) = 4 (3)
FLANK
$\overline{X}_{live}$ (SE) = 459 (73)
$\overline{X}_{dead}$ (SE) = 40 (9)
FLANK
$\overline{X}_{live}$ (SE) = 17 (6)
$\overline{X}_{dead}$ (SE) = 15 (9)
FLANK
$\overline{X}_{live}$ (SE) = 131 (29)
$\overline{X}_{dead}$ (SE) = 19 (4)
BASE
$\overline{X}_{live}$ (SE) = 495 (41)
$\overline{X}_{dead}$ (SE) = 50 (9)
BASE
$\overline{X}_{live}$ (SE) = 107 (18)
$\overline{X}_{dead}$ (SE) = 65 (16)
BASE
$\overline{X}_{live}$ (SE) = 171 (31)
$\overline{X}_{dead}$ (SE) = 17 (5)
LIVE OYSTERS
DEAD OYSTERS WITH ARTICULATED SHELLS
OYSTERS m^{-2}
SHELL HEIGHT (mm)
0
25
50
75
100
125
150
175
200
225
10
20
30
40
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85
86-90
91-95
96-100
101-105
106-110
111-115

Figure 6: Proportion of dead oysters with evidence of predation by crabs out of total number of dead oysters sampled in 2000 and 2001 from each position on the reef. Predation by crabs was distinguished from other mortality sources by the presence of chipped or cracked valve margins, puncture holes within the umbo region, crushing of the umbo region, and complete crushing of the valves. Numbers in parentheses above bars corresponds to total number of individuals observed.

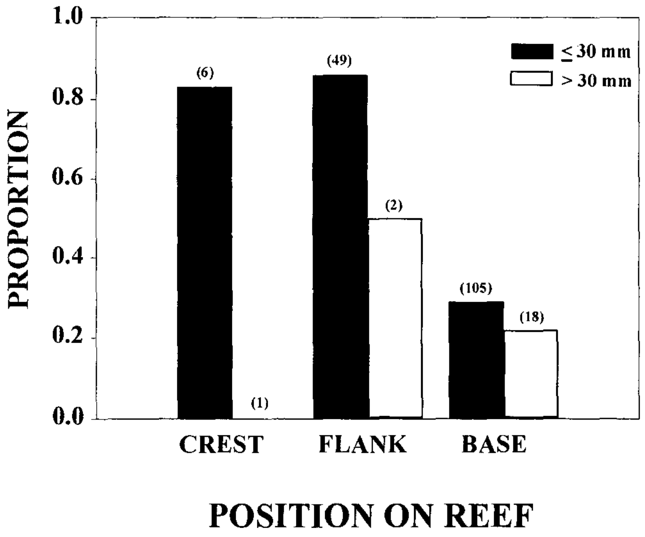

1.0
0.8
0.6
0.4
0.2
0.0
PROPORTION
(6)
(1)
(49)
(2)
(105)
(18)
■ ≤ 30 mm
☐ > 30 mm
CREST
FLANK
BASE
POSITION ON REEF

Figure 7: Size distribution patterns of surf clam shell (*Spisula solidissima*) fragments at each of three reef elevation strata: Crest (1.5 m above the seabed), Flank (0.8 m above the seabed), and Base (0.2 m above the seabed) on the Goodwin Island created oyster reef. Bars represent means + 1 SE (n = 6). Bars underlying the same line are not significantly different at α = 0.05 (SNK test).

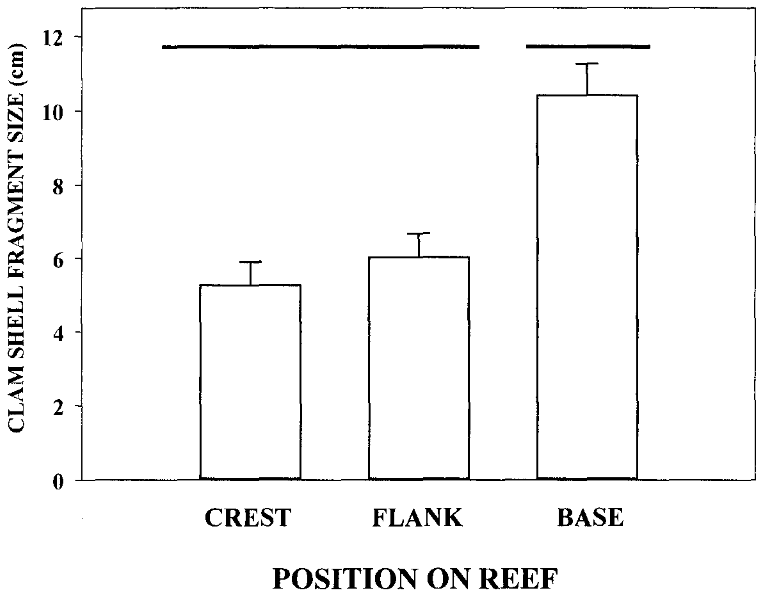

CLAM SHELL FRAGMENT SIZE (cm)
12
10
8
6
4
2
0
CREST
FLANK
BASE
POSITION ON REEF

Figure 8: Mean density of live oysters at Subtidal and Mean Low Water elevations on constructed oyster shell and clam shell intertidal reefs at Fisherman's Island, Virginia over three years. Bars represent means + 1 SE (n = 6). Numbers in parentheses in the top panel represent mean oyster abundance on clam shell substrate.

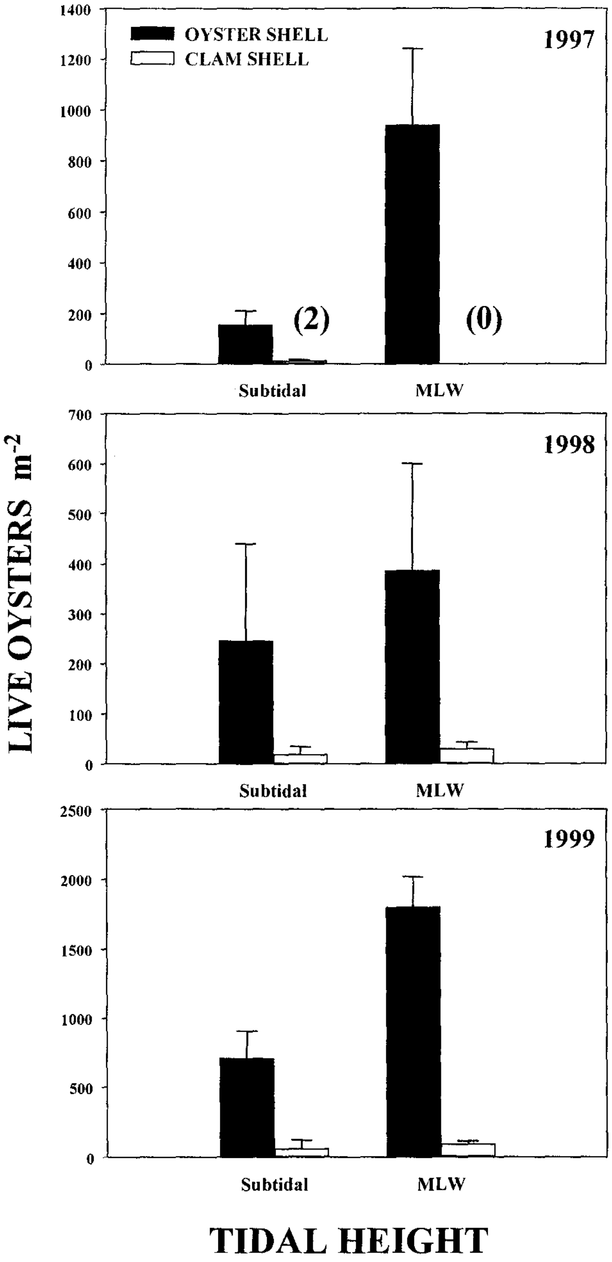
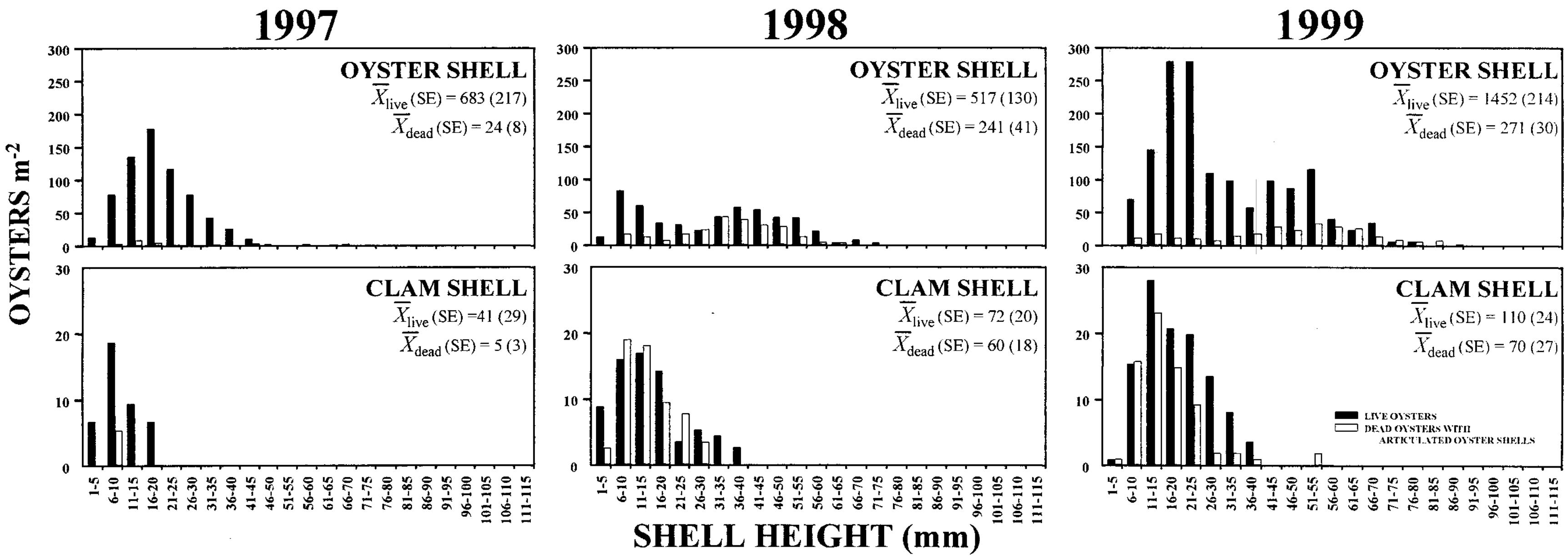

1997
1998
1999
OYSTER SHELL
CLAM SHELL
LIVE OYSTERS m-2
TIDAL HEIGHT
Subtidal
MLW
(2)
(0)
0
200
400
600
800
1000
1200
1400
100
300
500
700
500
1000
1500
2000
2500

Figure 8: Size frequency distributions for live and dead (non-fouled, empty articulated oyster shells) oysters collected from oyster shell and clam shell reef mounds at Fisherman's Island, Virginia in May 1997, 1998, and 1999. Bars represent mean oyster densities for each size class and are for all animal combined from three replicate quadrate samples (0.0625 m^2) collected from each of two clam shell reefs and one oyster shell reef at three tidal heights (0.25 m below mean low water; at mean low water; and 0.25 m above mean low water) and one oyster reef at two tidal heights (0.25 m below mean low water and at mean low water).


1997
1998
1999
OYSTERS m^{-2}
OYSTER SHELL
$\overline{X}_{live}$ (SE) = 683 (217)
$\overline{X}_{dead}$ (SE) = 24 (8)
OYSTER SHELL
$\overline{X}_{live}$ (SE) = 517 (130)
$\overline{X}_{dead}$ (SE) = 241 (41)
OYSTER SHELL
$\overline{X}_{live}$ (SE) = 1452 (214)
$\overline{X}_{dead}$ (SE) = 271 (30)
CLAM SHELL
$\overline{X}_{live}$ (SE) =41 (29)
$\overline{X}_{dead}$ (SE) = 5 (3)
CLAM SHELL
$\overline{X}_{live}$ (SE) = 72 (20)
$\overline{X}_{dead}$ (SE) = 60 (18)
CLAM SHELL
$\overline{X}_{live}$ (SE) = 110 (24)
$\overline{X}_{dead}$ (SE) = 70 (27)
LIVE OYSTERS
DEAD OYSTERS WITH ARTICULATED OYSTER SHELLS
0
50
100
150
200
250
300
0
10
20
30
1-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85
86-90
91-95
96-100
101-105
106-110
111-115
SHELL HEIGHT (mm)

CHAPTER 2

QUANTITATIVE SAMPLING OF NEKTON ASSOCIATED WITH STRUCTURED INTERTIDAL HABITATS: APPLICATION AND ASSESSMENT OF A NOVEL REMOTELY DEPLOYED ENCLOSURE TRAP

ABSTRACT

This paper describes the design and application of a remotely deployed enclosure trap used to quantitatively sample nekton associated with shallow estuarine habitats. A seine with added weight and flotation is deployed from the stern of a small, non-motorized skiff and is used in conjunction with a specially designed cod end holding box. The design of this gear permits rapid entrapment of nektonic organisms while generating minimal disturbance that may ward off target species. This capability is useful in habitats where use of a trawl is not particularly feasible because risk of snags or where rapid escaping species are not efficiently captured with a standard haul seine. This gear has value as a quantitative tool for comparative sampling of different habitat types. With minor modifications, the design could be readily adapted for use in other structured intertidal habitats such as marshes and SAV beds. The utility of the enclosure net and cod end design is demonstrated for capturing nekton on and around oyster reefs and intertidal sand flats. Tests of the recovery efficiency of this gear using mummichog *Fundulus heteroclitus* and spot *Leiostomus xanthurus* showed the remotely-deployed enclosure seine and removable cod end to be a highly reliable and effective sampling method for nekton in intertidal habitats.

INTRODUCTION

Reliable population estimates are necessary for accurate descriptions of community structure, secondary production, and trophic dynamics. Oyster reef habitats are difficult areas in which to quantitatively assess fish and macroinvertebrate populations because the nature of the reef structure hampers techniques normally employed for sampling aquatic organisms. This paper describes a remotely deployed enclosure trap used to effectively and quantitatively sample nektonic species associated with intertidal oyster reef habitats.

Much of the challenge associated with quantitative sampling of estuarine nekton on structured habitats is identifying a gear type that will collect an unbiased sample without altering the habitat (reviewed in Rozas and Minello 1997). Quantitative methods that have proved effective for sampling nekton in other structured habitats are unsuited for use on the hard, irregular, convoluted surface of an oyster reef. For example, the use of throw traps and drop rings is quite successful in intertidal and subtidal soft sediment habitats (Zimmerman et al. 1984; Chick et al. 1992), but these gear types may not seal properly along the bottom when placed over dense clusters of oysters, and permit nekton to escape underneath. Conventional methods for sampling soft-bottom habitats, such as trawls and seines, are not practical on oyster reefs because of inevitable snags or tears from oyster clusters. Furthermore, these gear types usually have low catch efficiencies

(Loesch et al. 1976; Orth and van Montfrans 1987) and, while all gear have biases and provide relative abundance estimates, some gears are more efficient for some species and show different efficiencies in different habitats. Passive sampling devices, such as flume nets (McIvor and Odum 1986) and flume weirs (Kneib 1991) rely on tidal action to capture nekton exiting a vegetated habitat on a falling tide. A variation of these passive sampling gear types was developed for use on intertidal oyster reefs in South Carolina with large (>1.5 m) tidal ranges (Wenner et al. 1996). This pop-net design requires that the enclosed habitat become fully exposed at low tide so trapped nekton are concentrated into a pit trap. For areas with smaller tidal ranges where entire oyster reefs are not fully intertidal, such as Chesapeake Bay, removal of trapped organisms from the enclosed area becomes problematic.

We have developed an enclosure net system to sample oyster reef habitats that causes minimal disturbance to the sampling area, has no permanent structures present to act as an attractant, and can be adapted for use in other habitats. Although the primary intent of this paper is to describe the design features of the enclosure trap and assess its sampling characteristics, we also provide data on species composition and abundance of fishes and decapod crustaceans collected by the gear to emphasize its effectiveness and adaptability to other intertidal habitats.

METHODS

Site Description

The study was conducted near Fisherman's Island, Virginia, U.S.A., near the mouth of Chesapeake Bay. *Spartina alterniflora* marshes and intertidal and subtidal mudflats surround this polyhaline site. Mean tidal amplitude in the study area is approximately 1.25 m. Collections were made from one of the eleven three-dimensional, intertidal oyster reef bases constructed in 1996 (described in detail in O'Beirn et al. 2000) and from an adjoining unvegetated bare-sand beach habitat. The oyster reef base was initially constructed of shucked oyster shell and, at the time of this study, supported an uninterrupted layer of naturally recruited live oysters (O'Beirn et al. 2000). The reef measures 44.2 m x 9.6 m (424.3 m^2) and is surrounded by unvegetated intertidal and subtidal mudflats. The bare-sand beach area is located 200 m northwest of the oyster reef and is characterized by a gentle continuous slope (5°) into a subtidal mudflat.

Net Design

The sampling gear consists of small skiff (126 cm x 107 cm) equipped with a net spool carrying a 30 x 1.7 m heavily weighted nylon mesh seine (3.2 mm, untreated, Figure 1). The net height of 1.7 m is sufficient to prevent the top of the net from sinking below the water surface when sampling areas up to 1 m deep in a persistent current. The flotation on the top of the net consists of 7 continuous strands of 1.3 cm foam-core polypropylene line enclosed in a 7.6 cm hem to maintain the entire length of the top of the net at the water surface. Because of strong currents and irregular bottom topography in the sampling area, this seine is designed so that the lead line is sufficiently heavy, flexible, and continuous to avoid the formation of gaps between the net and the substrate. The lead line consists of 3.5 cm (31 g) taper leads crimped 1 cm apart around a 0.5 cm diameter lead-core line and encased in a 2.5 cm hem at the bottom of the net. A 1.2 x 1.8 m sheet of 3.2 mm solid neoprene rubber is attached to the underside of the net spool and extends over the stern of the skiff and into the water to reduce noise and disturbance to the water upon deployment.

One end of the net is secured to a five-sided open-topped 3.2 mm mesh box cod end (1.2 x 1.2 x 2.4 m). This cod end has a vertical opening on one end and a conical bag on the other (Figure 2). Each side of the vertical opening of this cod end is lined with a set of 23 x 1 cm ABS plastic “Neptune Mini-Fingers” (Neptune Marine Products, Seattle, Washington) spaced 2.2 cm apart. The rows of fingers face inward, forming a 60° angle to funnel nekton into the cod end and are staggered so that each finger is spaced 0.6 cm apart to reduce escapement. To further increase removal efficiency of trapped organisms, a mesh skirt extends 1 m out from and is hinged along the bottom edge of the side of the cod end with the vertical opening. This skirt, bordered with chain to prevent escapement under the cod end, is lifted during sample removal to enclose the vertical opening in the side of the cod end along with any organisms. Upon sample collection, the entire cod end can be lifted from its support posts and out of the water. Trapped organisms are funneled down into the conical bag and removed.

The cod end is supported by and connected to the seine net with PVC connectors adapted from the design described by McIvor and Odum (1986). Each connector unit is made up of two components: a movable inner section attached to the netting and an outer sleeve fastened to a wooden post driven into the substrate (Figure 3). The inner component (hereafter, called the IC) is made up of a 1.5 m length of thick-walled (schedule 40; 480 psi) PVC pipe 1.9 cm in diameter. Each outer component or sleeve (hereafter, called OC) is made up of a 1.5 m section of 2.5 cm diameter thin-walled (200 psi) PVC pipe. A 0.5 cm and 1.0 cm wide slit is cut lengthwise in each IC and OC, respectively, using a table saw. The OC is secured to a 5 x 5 cm wooden post with flat head stainless steel wood screws. To form the IC component, the end of the net and corners of the cod end are reinforced by wrapping the net material around lengths of 6 mm line and securing in place with stainless steel hog rings. The net-wrapped line is permanently inserted into the IC so that the net extends out of the slit and forms a smooth joint that can be inserted into the OC. The resulting IC/OC junction is free of gaps or holes that may serve as potential escape routes for organisms trapped in the net.

Sampling procedure

Our sampling procedure is adapted from methods previously used to quantitatively sample intertidal vegetated (McIvor and Odum 1986, Kneib 1991) and open water estuarine habitats (Kjelson and Johnson 1974). All of these methods involve isolating a discrete area of habitat on the order of 10's of m^2 with a net and extracting the animals trapped within. We collected samples by surrounding one side of an intertidal oyster reef (or a section of bare-sand beach habitat) with the enclosure seine while using the emergent portion of the reef or beach as a barrier to fish escapement.

All samples were collected during the daylight ebb tide stage and sampling was initiated only after the crest of the reef became exposed by the falling tide. Samples were collected by surrounding one side of an intertidal reef habitat (or a section of bare-sand beach habitat) with the enclosure seine while using the emergent portion of the reef or beach as a barrier to fish escapement. The time of the tide was estimated from NOAA tide tables, and the actual time was determined by observing water current speed at the site. At least one hour before sample collection, the OC connectors on the wooden posts were put in position just down current of the sampling area. Two posts, each with 3 OC connectors (Figure 3 A), were placed at the vertical opening of the cod end. These connectors are designed to (1) accept the cod end, (2) anchor the block or enclosure seine, and (3) attach a canvas door to close off the vertical opening. Four posts, each with a single OC connector (Figure 3 B) were arranged to support each corner of the cod end. The cod end was then slid in place and a canvas door was lowered through one of the OC connectors to close the cod end and prevent entry by nekton prior to sample collection. A 3.2 mm mesh block seine (with continuous lead and float lines as described for the enclosure seine) was extended from the vertical cod end opening nearest the reef or beach and beyond the water's edge onto the reef or beach. The skiff and spool were placed adjacent to the reef (or beach) with one end of the enclosure net secured one of the OC connectors at the vertical opening of the cod end. A 5 mm diameter line was attached to the bow of the skiff and laid out in a triangle to define the area sampled and act as a pull-line (Figure 4 A). To complete the triangle and serve as a pivot point for the enclosure net path, a researcher was positioned on another boat anchored approximately 15 m away from the reef-water edge. This person remained still in position until the time of enclosure net deployment. Following this initial set-up, the other researchers waited quietly on the emergent portion of the reef (or beach) for at least 20 minutes to allow the nekton community using the habitat to return. To facilitate gear preparation and minimize site disturbance prior to sampling each day, the wooden posts to support the cod-end were left in place and removed at the end of the three-day sampling period.

Immediately prior to net deployment, the canvas door was removed from the cod end vertical opening and the researchers moved into position, creating as little disturbance as possible, to take a sample. With one researcher on the anchored boat offshore of the sampling area and another positioned on the end of the sampling area opposite the cod end (Figure 4 A), the skiff was pulled away from the cod end so that the enclosure seine, with one end staked to the vertical opening of the cod end, unreeled off the stern. The researcher positioned offshore began the enclosure net deployment by pulling the small skiff toward him or her until it reached a distance of approximately 5 m away from the shoreline. At this point, the researcher offshore released the pull line and the path of the small skiff turned in toward the researcher positioned on the shore. This researcher completed the enclosure path by pulling the small skiff upon shore and forming an enclosed area in the shape of an arc. The length of reef, the distance between the reef-water edge and the reef-mud edge, and the distance from the reef-mud edge to the circumference of the arc bordered by the net are measured to calculate the area encircled by the net. During our trials, a 10 – 15 m x 1 m section of reef habitat and approximately 25 – 40 m^2 of adjacent unvegetated mud were quietly enclosed in about 20 seconds.

Once the area was enclosed, the net was brought in toward shore to draw the captured nekton into the cod end. Starting at the end of the net furthest from the cod end, fishes and decapods were funneled into the cod end by pulling the net slack on to the reef surface while maintaining a good seal of the lead line to the bottom and reducing the area enclosed by the net (Figure 4, B). A good seal is possible despite the snagging nature of the reef surface because the net leadline was continuously weighted and could be worked in slowly over and around snags. As this area encroached on the cod end, the skirt was lifted to enclose the last 1-m sections of the enclosure and block nets. After the canvas door was dropped to seal off the cod end vertical opening, 10 sweeps were made with a 1 mm mesh dipnet in the pocket between the skirt and door to extract any remaining animals. The set of 10-sweeps was repeated until no further animals were collected by dipnet. The entire cod end was then lifted out of the water and captured organisms were funneled into the conical bag and emptied into a large bin. All collected animals were identified, counted, and measured to the nearest mm for total length (carapace width for crabs, carapace length for shrimp). Water depth (cm) at the reef edge, temperature (°C) and salinity (psu) were recorded with each sample. Samples were collected monthly from April to October 1999 over three consecutive days at neap tide preceding a full moon. The effects of Hurricane Floyd precluded sampling in September 1999.

A separate underwater video study (Nestlerode, unpublished) compared fish use of the oyster shell reef edge (the interface between the reef and mudflat) to the unvegetated subtidal mudflat immediately adjacent to the reef. Nekton activity was recorded using modified infrared security cameras placed in waterproof plexiglass housings (Cicchetti 1998b) at the reef edge and at the subtidal mudflat approximately 5 meters away from the reef edge simultaneously over the entire daylight tidal cycle for two consecutive days in August 1999. Since the video footage indicated that most fishes (>94%) are using the reef edge compared to the off-reef subtidal habitat and both of these habitats were included by the samples taken by the encircling seine gear, it is appropriate to evaluate fish use of the reef habitat in this study per linear meter of reef edge.

Efficiency Estimates

To estimate the efficiency of removing organisms from the enclosure trap, we added marked fish to the enclosed sample area, and calculated the percentage of those retrieved. We used mummichog (*Fundulus heteroclitus*) and spot (*Leistomus xanthurus*) within the size range normally captured from the habitat for these tests. Mummichogs are notoriously evasive of typical fish collection gear (seines and trawls) and their ability to swim with quick bursts of speed and rapidly change direction allows them to escape around and under seine lead lines. We observed that spot do not appear to be as evasive of seines as mummichogs and their swimming behavior typically places them higher in the water column. We chose these species for these tests because they were readily available at the sampling sites, are not demersal residents of the reef habitat, and have very different observed body shapes and swimming performances. All fish were marked by injecting neon colored acrylic craft paint (Plaid Enterprises, Inc., Norcross, Georgia) as per procedures described by Lotrich and Meredith (1974). Marks were placed subcutaneously in the musculature flanking the dorsal fin using a 26-gauge needle and a 1-cc syringe. Needles were replaced after approximately 50 fish were marked.

Five replicate removal efficiency collections were taken on each habitat type over three consecutive days in July 2000. For each efficiency trial, we released 20 marked mummichogs (mean total length = 69.1 mm) and 10 marked juvenile spot (mean total length = 109.0 mm) into the area enclosed by the net and the mean return rates were used to represent efficiency.

Five additional efficiency comparisons were conducted with each of these species for each habitat type using a 30 x 2 m haul seine with 3.2 mm mesh to compare the effectiveness of the remotely-deployed gear with a more traditional, standard, commercially available seine net. Both encircling seine and haul seine trails sampled the same area (10-15 m section of habitat edge and approximately 25 – 40 m^2 of adjacent subtidal habitat) to allow for general comparisons of the removal efficiency of each gear type. The haul seine trial involved the use of three nets. Two 10 x 2 m block nets were positioned perpendicular to the water line, spaced 15 m apart, and held in place with wooden posts (Figure 5). Two researchers positioned a haul seine between the two block seines 5 m away from the water line. A third researcher released the marked fish into the area enclosed by the three nets. The two researchers on each end of the haul seine net pulled the net shoreward while maintaining the brail poles up against the block seines and using care over the irregular bottom of the reef. A third researcher helped to pull the lead line of the net on shore and collect captured organisms from the net.

Two-way fixed factor ANOVA's were used to determine whether the percent of recaptured individuals differed between habitat type and gear. We found no evidence that variances were heterogeneous at the 5% significance level (Sokal and Rohlf 1981).

RESULTS

Despite the relatively short distance (~ 200 m) between the two habitats sampled, the nekton assemblages at the oyster reef and beach habitats of Fisherman's Island were quite different. A total of 39 species were identified from both habitats (Tables 1 and 2). Thirty-three species representing 21 fish and three decapod crustacean families were found on the oyster reef and 15 species representing nine fish and three decapod crustacean families were collected from the beach habitat. Fifteen families were found only on the oyster reef, three species were unique to the beach, and six fish families and the three decapod crustacean families were common between habitats.

Grass shrimp *Palaemonetes vulgaris* and rough silverside *Membras martinica* were most abundant and constituted 64% and 33%, respectively, of the total 17,203 individuals captured on the oyster reef from April through October 1999 (Table 1). Abundance of these species was proportionately high during each collection period. Of the remaining 3% of the total number of individuals, species composition and proportional abundance varied each month. Species richness was highest in June, July and August. Diversity (H') was greatest in samples collected in June and July. During these months, juvenile pinfish *Lagodon rhomboides*, pigfish *Orthopristus chrysoptera*, silver perch *Bairdiella chrysoura*, spot, mummichog, and rainwater killifish *Lucania parva* together made up greater than 3% of the total number of individuals collected.

Mean nekton abundance each month ranged from 42 (October) to 123 (June) individuals m^{-1} of reef edge.

Fewer individuals were collected from the beach habitat compared with samples collected during the same months from the oyster reef (ANOVA, $p<0.05$). Overall, only 15 species were collected from the beach compared with the 29 species collected from the oyster reef during July, August, and October 1999. Rough silverside, mummichog, and striped killifish *Fundulus majalis* numerically dominated the beach enclosure trap samples (Table 2). Diversity (H') was highest in July and August.

Nekton assemblages from the two habitats were assigned ecological groups based on biological data in Murdy et al. (1997), Baltz et al. (1993), Breitburg (1999), and personal observation. Species were classified into one of four categories (Tables 1 and 2): resident oyster reef species; facultative reef residents; demersal transients; and nektonic transients. Reef residents are those species that spend the majority of their life history associated with the reef structure and are dependent on the reef for feeding, shelter, and reproduction. These species, such as gobies, blennies, and oyster toadfish, feed primarily on benthic invertebrates and find shelter and nest sites among shells of live and dead oysters. Facultative reef residents are those species that use the reef habitat for food and shelter during juvenile life stages. This group includes tautog, sheepshead, pigfish, and pinfish. They feed on small crustaceans, worms, and mollusks and seek shelter among the oyster shells until they outgrow the complex matrix of spaces between the oyster shells on the surface of the reef. As adults, these species may continue to intermittently visit the reef habitat in search of food and are found associated with a variety of other habitats. Transient species, those species that may be abundant on oyster reefs but are also found in a wide range of estuarine habitats, are divided into two categories based on their behavior and favored position in the water column: demersal transients and nektonic transients. Demersal transients, such as silver perch, spot, killifish, blue crab *Callinectes sapidus*, and grass shrimp, are highly mobile and feed from the benthos. Some species within this group are found in both habitats, but were consistently more abundant in oyster reef collections. Nektonic transients, such as silversides and anchovies, are those species that are abundant in both habitats and are primarily associated with the water column. This group includes highly aggregated planktivorous species that are active swimmers and prefer surface waters.

All species collected from the beach habitat were "transients" in terms of oyster reef habitat use. No resident oyster reef or facultative species were obtained from this habitat. Although transient species numerically dominated all of the samples collected from the oyster reef, oyster reef residents and facultative residents were captured during all but one (April 1999, no facultative residents collected) sampling period.

The effect of gear type on recapture efficiencies varied between the two marked fish species, mummichog and spot (Table 3). For mummichogs, recapture efficiencies were significantly higher within the enclosure trap (80-81%) than within the haul seine (43-58%) (two-way ANOVA, $p = 0.001$). There was no effect of gear type on the recapture efficiencies of spot (64-74% for the enclosure seine and 56-74% for the haul seine, two-way ANOVA, $p>0.05$). It is also important to note that these patterns were consistent across both habitat types tested since habitat type was not significant in either analysis ($p > 0.05$).

DISCUSSION

Our enclosure net system is a modification of two types of gear commonly used to sample shallow aquatic habitats. We combined the rapid enclosure capability of an encircling seine (Kjelson and Johnson 1974) with a flume net's capacity for passive removal of captured nekton (McIvor and Odum 1986). Our adaptation provides a means for efficient, quantitative assessment of nektonic species associated with structured intertidal habitats with minimal disturbance to the area sampled.

Our enclosure net is designed to swiftly enclose a measurable area of habitat while accommodating the irregular bottom topography of the oyster reef in our sample retrieval process. Unlike a standard haul seine, our enclosure seine reduces the importance of speed in the sample recovery phase since once the area is completely enclosed, nekton cannot escape around the ends of the net. Our design incorporates gapless net connecting elements and block seines that minimize the possibility of escape around the gear. Researchers may slowly and carefully pull the net up on to the reef to decrease the size of the enclosed area, while using care to bring the lead line over the three-dimensional structure of the oyster reef habitat to reduce escapement under the lead line. Unlike flume and block nets (McIvor and Odum 1986; Thayer et al. 1987; Hettler 1989), our design has no walls or barriers (apart from the cod end) to repel or guide nekton out of or into the study area and requires little habitat modification for site preparation. Unlike lift nets (Rozas 1992; Wenner et al. 1996), the enclosure seine sample may be collected and retrieved without having to wait for the tide to fall from the enclosed area. This is particularly useful in areas, like Fisherman's Island, that do not drain completely at low tide, or have high current velocities that may pull the walls of the net under water or the bottom of the net off the substrate during periods of maximum current.

The recapture efficiency of our enclosure net system compared favorably with similar techniques used to sample other shallow (<1.5 m deep) habitats. Allen et al. (1992) estimated the catch efficiency of a haul seine in a tidal salt marsh creek to range from 7 to 91%, depending on the species, with their method having low overall efficiencies for the two species we selected for our efficiency trials: mummichog (average 27%) and spot (average 23%). Kjelson and Johnson (1974) used a longer haul seine to encircle a large area of open water and estimated average capture efficiencies of semi-demersal species, including spot, to be 47%. Both studies sampled habitats with relatively smooth bottoms having little, if any, vertical relief. Efficiencies for these gear types would likely be less for coarser substrates, such as oyster reefs, as more escapement would be expected under the seine lead line as it passes over uneven bottom topography (Parsley et al. 1989). The higher efficiency estimates for our haul seine trials (average 50% for mummichog, 65% for spot) compared with Allen et al. (1992) are likely due to our smaller mesh size (3 mm vs. 6 mm) and our use of block seines stretched perpendicular to shore at either end of the haul seine to deter escape of fishes from around the ends of the seine (Table 3).

In areas of dense emergent vegetation, such as salt marshes and mangroves, flume nets and weirs have high recovery efficiencies for transient nekton. These gear types use tidal action to passively sample large areas of vegetated areas and have proven to be quite effective in regularly flooded intertidal habitats. McIvor and Odum (1986) found that a passive flume net set adjacent to an intertidal freshwater marsh recovered an average of 73% of released mummichogs and 80% of the semi-demersal bluegill sunfish *Lepomis macrochirus*. An average of 62% of marked mummichogs and 97% of spot were recaptured with one retrieve using a flume weir from an intertidal salt marsh (Kneib 1991). Similarly, Morton (1990) recaptured between 66 and 100% of marked demersal fish species released into a mangrove area enclosed with a block net in Australia. Our enclosure net system uses a modified flume net as the cod end to take advantage of high removal efficiencies demonstrated by these gear types.

Wenner et al. (1996) used a lift net/pit trap system to sample intertidal oyster reefs in South Carolina and reports recovery efficiencies for mummichog comparable to our enclosure gear (54 to 69%). Unlike the reefs at Fisherman's Island, the South Carolina reefs are fully emergent at low tide so that the nekton may be corralled into a pit trap as the tide falls from the sampling area. Our cod end takes the place of a pit trap as a perceived refuge for the captured nekton. Vulnerability of a fish to a net is affected by how the fish reacts when it encounters the sampling gear. By giving the captured fish a perceived refuge in the cod end, we believe that we enhance the capture efficiency.

Although resident reef species such as blennies, gobies, and oyster toadfish (Breitburg 2000) were collected and are reported here, we believe that the manner we used this enclosure trap gear did not produce a quantitative sample for these taxa. When disturbed or startled, these species often exhibit a dive response and seek shelter in the substrate structure. Because our study targeted non-resident reef species, effort was not focused on inciting these organisms to leave the structure of the reef habitat. Thus, data shown in Table 1 may greatly underestimate the true abundance of these species. To remedy this omission from future sampling efforts, we suggest using a plastic garden rake to rouse the oyster reef resident species out of the substrate and herd them into the cod end. We suspect that the addition of rotenone or other toxicants to the sample area may also enhance capture efficiency of this gear type for these and other nekton species. Thayer et al. (1987) used rotenone within the enclosed area to draw fish out of the structure of mangrove roots and estimated recovery efficiencies using the block net-rotenone technique to be approximately 70%. We chose not to include the use of rotenone in our study because of the relatively small habitat being sampled, and because this project was conducted as part of an oyster reef restoration effort and we did not want to adversely affect non-targeted members of the oyster reef community.

Our enclosure net system, like all sampling devices, has limitations. The enclosure net may not work optimally under high wind conditions when there is sufficient chop on the water surface because the net does not silently deploy off the stern of the skiff. This gear type is ideally suited for use in studies comparing nekton densities among intertidal edge habitats because proper deployment and enclosure of the sampling area is dependent on an emergent barrier (i.e. intertidal reef or beach shoreline) to block the escape of nekton. Other gear types, such as drop samplers (Zimmerman et al 1984) or pop nets (Connolly 1994) with sweeping mechanisms to remove nekton from the enclosed area of water column, are better suited for sampling subtidal habitats without an emergent barrier, although the size of the area sampled is limited and may introduce biases associated with small sample sizes. Edge habitats are of interest to ecologists because they facilitate trophic transfer from the interior of the intertidal habitat to adjacent deeper waters (Thayer et al. 1987; Peterson and Turner 1994). Although we have described its use on oyster reefs, this enclosure net has also been used successfully along the erosional edge of a salt marsh (Cicchetti and Diaz 2000). With a few minor modifications (such as the addition of a block seine in place of the emergent portion of the habitat) an area of open water or SAV may be encircled and sampled using this gear.

The enclosure net system is relatively inexpensive to construct. The cost of materials to build one enclosure seine is less than $500 and one cod end is less than $80. This does not include the cost of the lumber needed to make the spool or the cost of the skiff used to deploy the net. Nets were rinsed and dried after sampling to prolong their use and small holes were repaired with a needle and tarred twine. Three people were able to set up the enclosure in less than fifteen minutes. Depending on the size of the catch and the tidal regime of a given area, multiple samples may be collected during optimal tidal levels. We were able to sample 4 different areas within the 4 hour window of optimal tide levels at Fisherman's Island.

This enclosure net system described here permits quantitative sampling of nekton associated with intertidal oyster reefs and edge habitats. Other methods used to quantify organisms associated with subtidal habitats were not suitable for the calculation of density estimates of nekton associated with the uneven and complex structure of oyster reefs. This method quantitatively samples the edge ecotone of oyster reef habitats, can be adapted for use in other habitats, and requires little habitat modification for site preparation. No permanent structures are present to act as an attractant. The gear is deployed with a minimum disturbance to target organisms, and is relatively inexpensive to construct and maintain. Information obtained from the sampling of intertidal oyster reefs aids in determining the relative value of these habitats to the ecological functioning of estuarine systems.

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Table 1: Pooled species abundance for all collections from the intertidal oyster reef at Fisherman's Island. Number (no.) is total number of specimens from 2 replicate enclosure trap collections obtained on consecutive days in April, August, and October 1999 and from 3 replicate enclosure trap collections obtained over three consecutive days in May, June, and July 1999. Total number and percentage of total catch are given for each species.

Species	April (no.)	May (no.)	June (no.)	July (no.)	Aug (no.)	Oct (no.)	grand total	% abund	rank abund
Palaemonetes vulgaris (DT)	3068	3282	1812	1914	258	672	11006	63.977	1
Membras martinica (NT)	71	557	2513	258	1658	660	5717	33.233	2
Fundulus heteroclitus (DT)	0	2	0	71	0	0	73	0.424	3
Anchoa hepsetus (NT)[a]	0	0	3	0	39	0	42	0.244	4
Lucania parva (DT)	0	0	33	4	5	0	42	0.244	4
Syngnathus fuscus (NT)	2	13	8	10	9	0	42	0.244	4
Lagodon rhomboides (F)	0	0	33	5	0	0	38	0.221	5
Orthopristus chrysoptera (F)	0	0	0	31	0	0	31	0.180	6
Hypsoblennius hentz (R)	0	1	9	9	6	2	27	0.157	7
Leiostomus xanthurus (DT)	0	0	24	3	0	0	27	0.157	7
Bairdiella chrysoura (DT)	0	0	0	24	1	0	25	0.145	8
Gobiosoma bosc (R)	2	3	10	4	3	2	24	0.140	9
Callinectes sapidus (DT)	0	0	1	12	6	0	19	0.110	10
Paralichthys dentatus (DT)	1	8	4	0	0	0	13	0.076	11
Tautoga onitis (F)	0	0	8	4	0	0	12	0.070	12
Archosargus probatocephalus (F)	0	0	0	2	7	1	10	0.058	13
Opsanus tau (R)	0	0	3	2	4	0	9	0.052	14
Hyporhamphus meeki (NT)	0	0	8	0	0	0	8	0.047	15
Gobiosoma ginsburgi (R)	0	1	0	5	0	1	7	0.041	16
Sphyreana borealis (DT)	0	0	0	6	0	0	6	0.035	17
Chasmodes bosquianus (R)	0	3	0	1	0	0	4	0.023	18
Lutjanus griseus (F)	0	0	0	0	4	0	4	0.023	18
Centropristis striata (F)	0	1	0	1	0	1	3	0.017	19
Eucinostomus argenteus (DT)	0	0	0	3	0	0	3	0.017	19
Diplodus holbrooki (F)	0	0	2	0	0	0	2	0.012	20
Eucinostomus gula (DT)	0	0	0	2	0	0	2	0.012	20
Chaetodon ocellatus (F)	0	0	0	1	0	0	1	0.006	21
Monocanthus hispidus (F)	0	0	1	0	0	0	1	0.006	21
Mycteroperca microlepis (F)	0	0	0	1	0	0	1	0.006	21
Penaeus aztecus (DT)	0	0	0	0	0	1	1	0.006	21
Sphoeroides maculatus (DT)	0	0	0	0	1	0	1	0.006	21
Syngnathus floridae (NT)	0	0	0	0	1	0	1	0.006	21
Synodus foetens (T)	0	0	0	0	1	0	1	0.006	21
Total reef resident individuals (R)	2	8	22	21	13	5	71	0.412719	
Total facultative resident individuals (F)	0	1	44	45	11	2	103	0.598733	
Total demersal transient individuals (DT)	3,071	3,305	1882	2,049	282	673	11,262	65.46533	
Total nektonic transient individuals (NT)	71	557	2,524	258	1,697	660	5,767	33.52322	
Total fish and decapods:	3,144	3,871	4,472	2,373	2,003	1,340	17,203	100.00	

[a] Ecological classification (in parentheses) based on species' dependence on oyster reef habitat and adapted from Breitburg (1999) and Baltz (1993):
R = resident oyster reef species, F = facultative oyster reef species, DT = demersal transient species; NT = nektonic transient species.

Table 2: Pooled species abundance for all collections from the bare-sand beach habitat at Fisherman's Island. Number (no.) is total number of specimens from 3 replicate enclosure trap collections obtained over three consecutive days in July 1999 and from 2 replicate enclosure trap collections obtained on consecutive days in August and October 1999.

Species	**July (no.)**	**Aug (no.)**	**Oct (no.)**	**grand total**	**% abund**	**rank abund**
Membras martinica (NT)	308	208	294	810	38.190	1
Fundulus heteroclitus (DT)	761	4	0	765	36.068	2
Fundulus majalis (DT)	388	92	5	485	22.867	3
Callinectes sapidus (DT)	0	12	8	20	0.943	4
Lucania parva (DT)	7	2	0	9	0.424	5
Palaemonetes vulgaris (DT)	2	3	2	7	0.330	6
Eucinostomus gula (DT)	0	0	6	6	0.283	7
Leiostomus xanthurus (DT)	5	0	0	5	0.236	8
Cyprinodon variegatus (DT)	4	0	0	4	0.189	9
Anchoa michelli (NT)[a]	2	0	0	2	0.094	10
Mugil curema (NT)	0	2	0	2	0.094	10
Penaeus aztecus (DT)	0	0	2	2	0.094	10
Symphurus plagiusa (DT)	0	2	0	2	0.094	10
Paralichthys dentatus (DT)	1	0	0	1	0.047	11
Selene vomer (NT)	1	0	0	1	0.047	11
Total reef resident individuals (R)	0	0	0	0	0	
Total facultative resident individuals (F)	0	0	0	0	0	
Total demersal transient individuals (DT)	1,168	115	23	1,306	61.575	
Total nektonic transient individuals (NT)	311	210	294	815	38.425	
Total fish and decapods	1,479	325	317	2,121	100	

[a] Ecological classification (in parentheses) based on species' dependence on oyster reef habitat and adapted from Breitburg (1999) and Baltz (1993):
R = resident oyster reef species, F = facultative oyster reef species, DT = demersal transient species; NT = nektonic transient species.

Table 3: Efficiency estimates for enclosure and haul seines on oyster reef and bare-sand beach habitats.

gear	**habitat**	**species**	**size range TL-mm**	**N tests**	**total organisms**	**efficiency $\bar{X}$ ± 1 SE**
enclosure seine	oyster reef	mummichog	51 – 92	5	100	0.81 ± 0.10
enclosure seine	oyster reef	spot	84 - 160	5	61	0.64 ± 0.11
enclosure seine	beach	mummichog	32 – 93	5	100	0.80 ± 0.04
enclosure seine	beach	spot	89 – 150	5	50	0.74 ± 0.09
haul seine	oyster reef	mummichog	50 – 82	5	100	0.43 ± 0.03
haul seine	oyster reef	spot	85 - 110	5	50	0.74 ± 0.08
haul seine	beach	mummichog	53 – 80	5	100	0.58 ± 0.10
haul seine	beach	spot	75 - 130	5	50	0.56 ± 0.12

Figure 1: Photograph of spooled enclosure seine on small skiff used to deploy net around sampling area. A sheet of hard neoprene rubber is attached to the bottom of the spool and extends over the stern of the skiff to reduce splashing of the net on the surface of the water as the net unwinds from the spool.

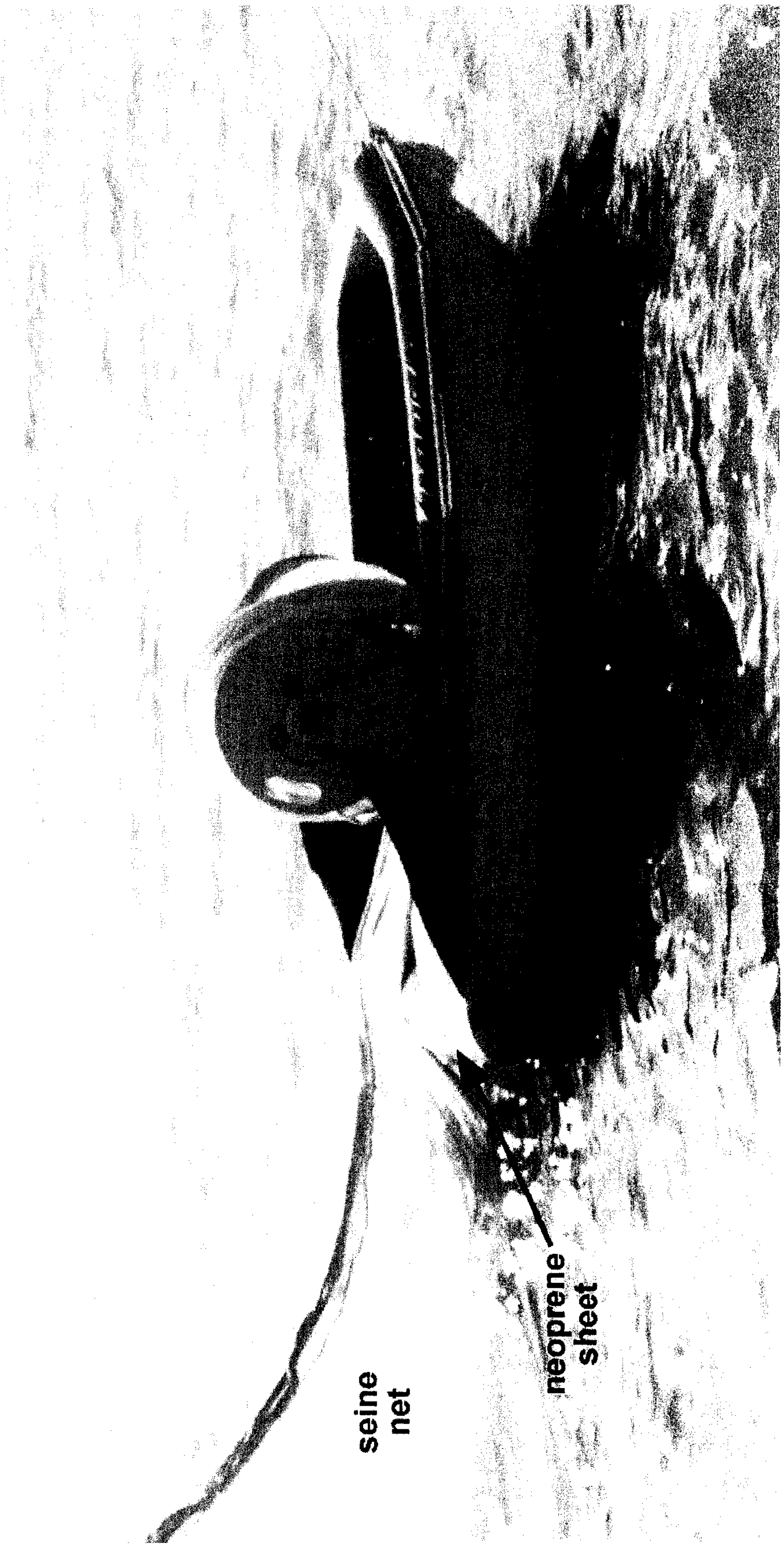

seine net
neoprene sheet

Figure 2: Diagram of enclosure seine cod end showing 5-sided mesh box about to be lowered into position. PVC connectors labeled A and B are shown in detail in Figure 3.

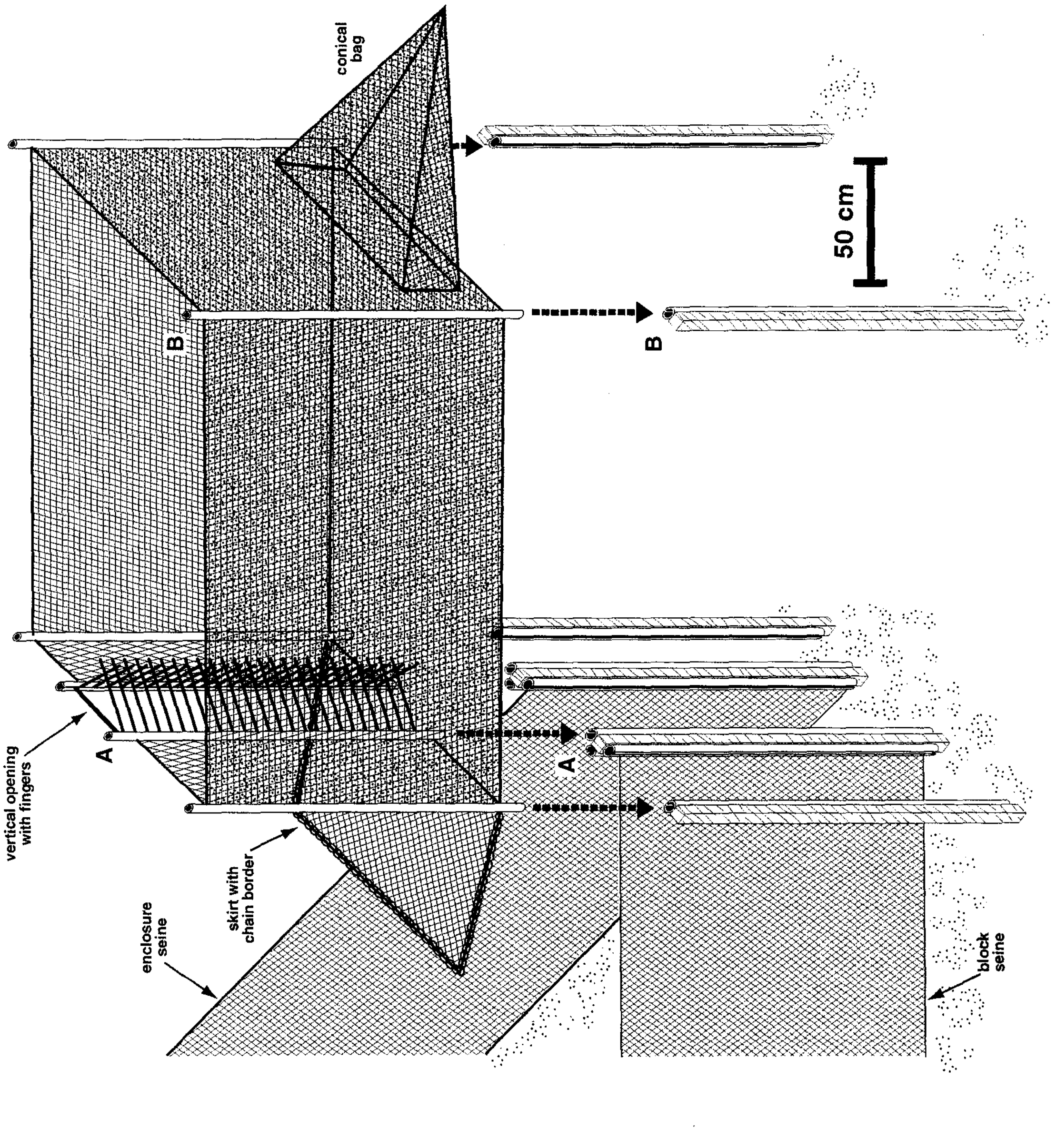

conical bag
50 cm
B
B
vertical opening with fingers
A
A
skirt with chain border
enclosure seine
block seine

Figure 3: Construction details of PVC net connectors and support posts used to achieve gapless connections between net elements.

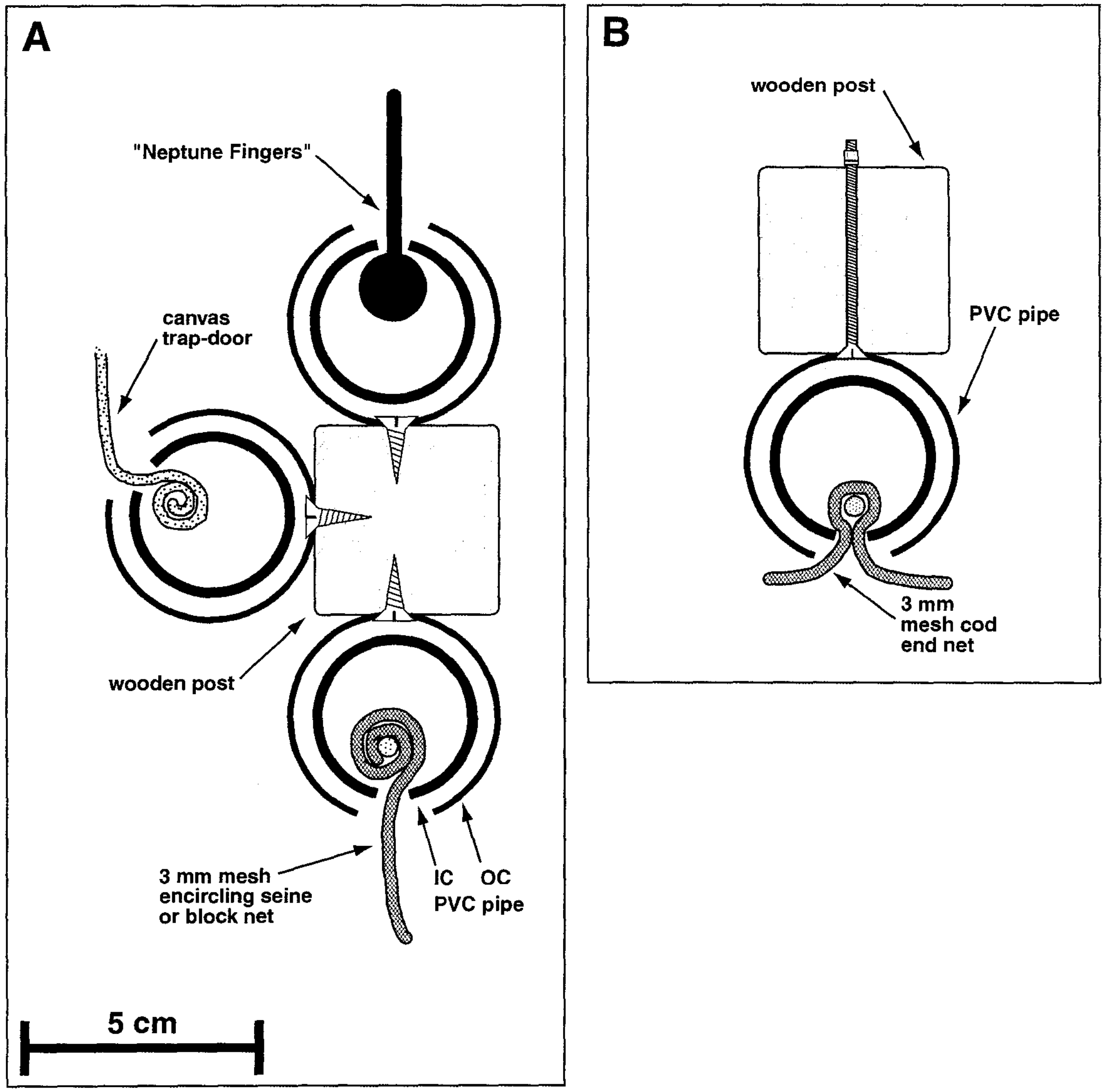

A
"Neptune Fingers"
canvas
trap-door
wooden post
3 mm mesh
encircling seine
or block net
IC
OC
PVC pipe
5 cm
B
wooden post
PVC pipe
3 mm
mesh cod
end net

Figure 4: Deployment of enclosure seine at an intertidal oyster reef habitat.

A. Set is begun when crest of reef is exposed above the tide level. A person positioned offshore of the reef begins to pull the small skiff (with net spool) away from shore and the net is unreeled from the stern to surround the sampling area. As the skiff approaches this person, the pull line is dropped and a second person positioned on the reef pulls the skiff in toward the reef.

B. The sampling area is enclosed and trapped nekton is forced toward the cod end. Starting at the end of the enclosure seine closest to the small skiff and moving down the reef toward the cod end, small sections of the net are sequentially pulled up onto the reef by hand and fish are corralled into the cod end.

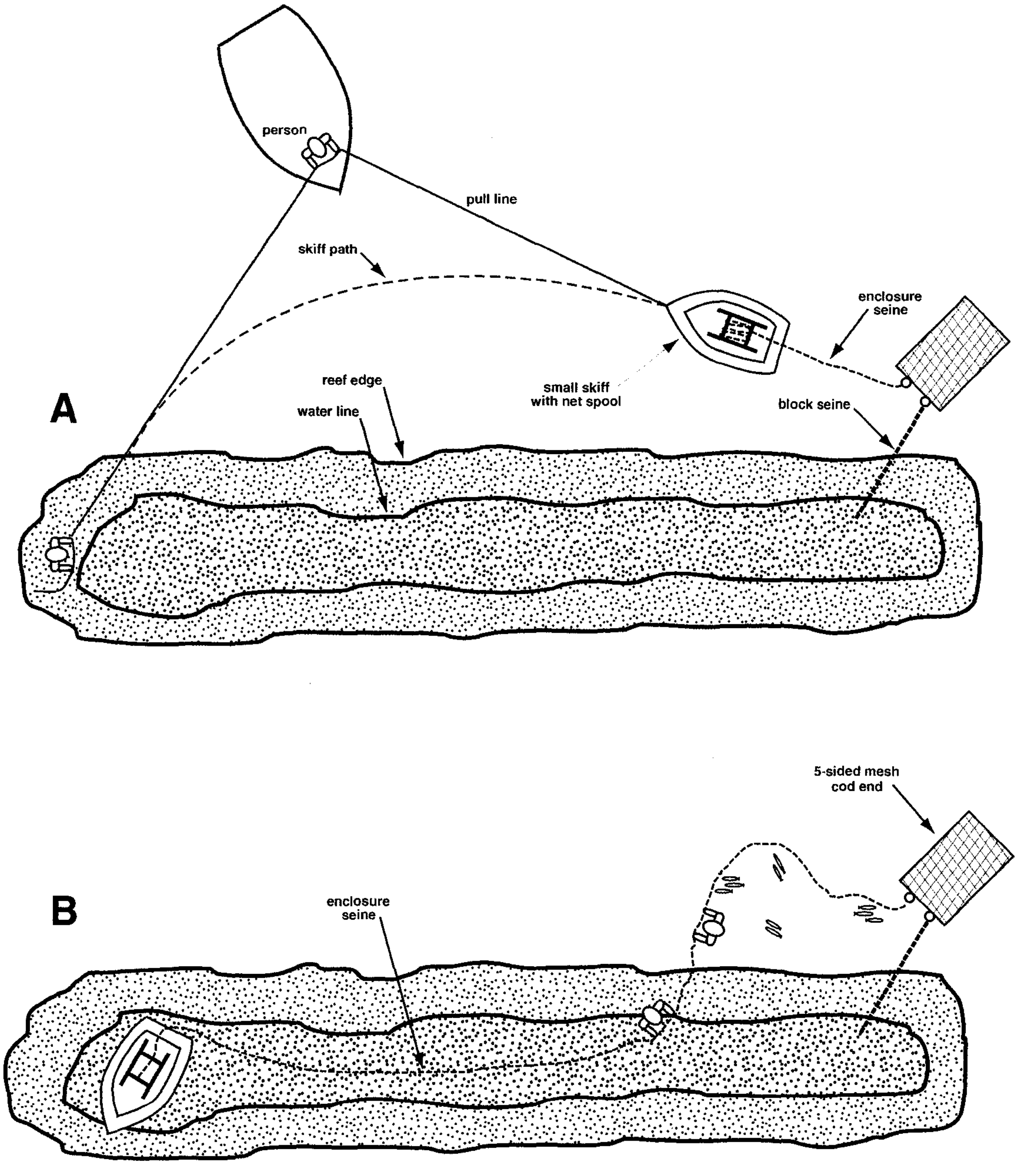
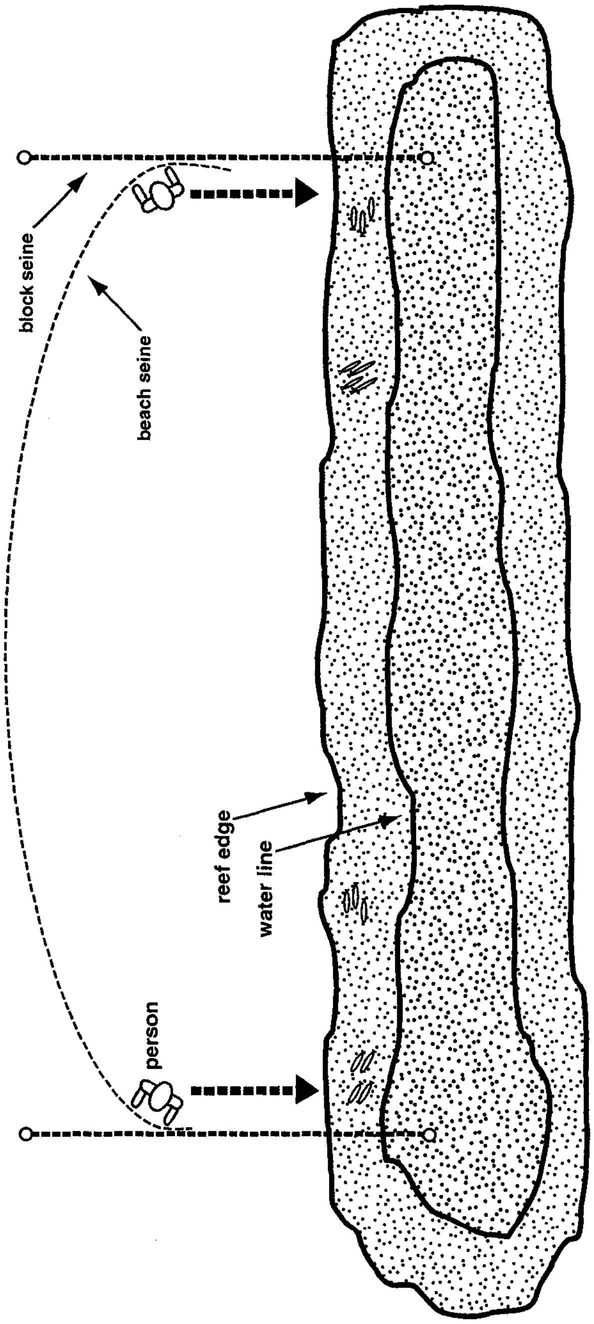

person
pull line
skiff path
enclosure seine
small skiff with net spool
reef edge
water line
block seine
A
5-sided mesh cod end
enclosure seine
B

Figure 5: Schematic of the haul seine arrangement used to compare gear removal efficiency of a haul seine with the enclosure seine.


block seine
beach seine
person
reef edge
water line

CHAPTER 3

BENTHIC COMMUNITY STRUCTURE OF INTERTIDAL CONSTRUCTED OYSTER REEF HABITATS AT FISHERMAN'S ISLAND, VIRGINIA

ABSTRACT

Invertebrate fauna associated with intertidal regions of oyster shell, clam shell, and pelletized coal ash reef habitats were sampled monthly over one year to identify faunal differences between the three reef types. Diversity, species richness, and secondary production were greatest on the oyster shell reef, with production driven by large individuals of the panopeid crab, *Panopeus herbstii*, found only on this substrate type. Species richness was lowest on the coal ash pellet reef due to fewer rare species; however, total community abundance was significantly greater than on the other two reef types, driven by numerical dominance of small crustaceans. Clam shell reefs showed intermediate abundance and diversity patterns but had the lowest values for secondary production. Differences in macrofaunal community metrics appear to reflect the quantity and quality of the interstitial space afforded by the substrate material (i.e., providing predation and foraging refuges) and are in part driven by the presence of living oysters which grew to form a living oyster crust on the oyster shell reef during the course of this study.

INTRODUCTION

Reefs created by the Eastern oyster, *Crassostrea virginica*, provide the predominate natural hard substrate in the characteristically soft sediment environment of estuaries of the middle Atlantic coastal plain. The three-dimensional structure of this habitat provides surface area for attachment and crevices for refuge for numerous small invertebrates and fishes (Wells 1961; Bahr 1974; Dame 1979; Zimmerman et al. 1989; Meyer and Townsend 2000). As oyster stocks in Chesapeake Bay diminished as a result of overfishing (Rothschild et al. 1994), disease (Paynter 1996), and degraded water quality, the complex habitat produced by the oyster disappeared with it.

While substantial state and federal funds have supported efforts to restore oyster stocks and reef habitat in Chesapeake Bay, the most common material used for oyster reef restoration, fresh and fossil oyster shell, is in short supply and has led to a search for alternative substrate materials. The reefs at Fisherman's Island (Figure 1) were built to investigate the feasibility of using surf clam (*Spisula solidissima*) shell and cement stabilized coal ash pellets as a reef base. Coal ash pellets were produced by mixing 88% coal combustion fly ash with 12% Portland cement (Andrews et al 1997, O'Beirn et al 2000) and have been shown to withstand the physical and biological forces of the marine environment without fracturing, leaching heavy metals, or significant bioaccumulation of metals in associated epibiota (Collins et al 1992, reviewed by Pickering 1996).

Constructed reef bases provide a steady, hard substrate elevated off the bottom and away from excessive sedimentation so that oysters and other epifauna may settle and grow (Lenihan et al 1996, Bartol et al 1999, Lenihan 1999). Over time, it is anticipated that a layer of live oysters forms a crust over the surface of the reef base so that the original substrate material is no longer visible from the surface (O'Beirn et al 2000). O'Beirn (2000) et al. report significant differences in the oyster population on each of these reef types with greatest densities occurring on the oyster shell substrate. While the physical structure and chemical composition of the substrate material likely influence the structure the macrobenthic community associated with it, it is important to keep in mind that the presence of oysters (and their biodeposits, interstices) may also enhance the surrounding reef macrobenthic community by providing habitat and food to associated fauna. Additionally, settlement and metamorphosis processes in many invertebrate larvae are triggered by specific chemical and/or physical cues associated with the adult habitat (Crisp 1974) such that the presence of adults triggers recruitment.

Large amounts of surface area are available to epifauna and reef-associated macrofauna on naturally formed intertidal oyster reefs. Bahr (1974) estimated that for every square meter of reef at least 50 m^2 of surface area is available to a highly diverse and dense faunal community of reef-associated macrofauna. Studies along the southeast coast report as many as 303 species associated with reef communities (Wells 1961) with abundances exceeding 125,000 individuals m^{-2} (Larsen 1974). Reef communities are typically dominated (in terms of number and biomass) by suspension feeders (i.e., oysters, mussels, polychaetes) that remove suspended particles from the water column and deposit this material to the bottom which is then further utilized by deposit feeding reef associates (Bahr and Lanier 1981). Reef macrofauna include sessile epibenthic and encrusting forms (e.g., barnacles, tunicates, bryozoans, serpulid polychaetes, sponges, tunicates) that live on the shells of live and dead oysters and infaunal species (e.g., amphipods, annelids, bivalves) that recruit to pockets of sediment in crevices of the reef matrix. Motile epifauna (e.g., crabs, shrimp, fishes) occupy convolutions between shells and move through the complex network of spaces below the reef surface. The multitude of fauna associated with oyster reef structure make up a complex community that contributes to the ecological functioning of reefs in estuarine systems.

The importance of temperate oyster reefs as habitats that support large numbers of resident consumers has long been recognized (Wells 1961; Bahr 1974; Larsen 1974; Dame 1979; Zimmerman et al. 1989), yet quantitative studies of the macrofaunal oyster reef assemblage are limited and, to the author's knowledge, none have examined secondary production at the habitat scale. Most benthic studies have attempted to describe oyster reef macrofaunal communities in terms of biomass or abundances. While these measurements are helpful in expressing the energy available at a moment in time, production gives a much better characterization of energy flow, yield, and growth, habitat resource value and the potential of oyster reef fauna for supporting resident and migratory consumer populations (Waters 1977, Fredette and Diaz 1986, Diaz and Schaffner 1990). Secondary production, analogous to "net production" in plants (Waters and Crawford 1973), is the rate of change in biomass of a population of organisms over a given period of time. It is the total of growth increments of all individuals existing at the start and end of the time period, the growth of newly born individuals, and the biomass of individuals that do not survive to be part of the population biomass at the end of that period (Diaz and Schaffner 1990).

Calculating secondary production estimates can be labor-intensive. Three of the four basic methods used to estimate secondary production, Growth Increment Summation, Mortality (or Removal) Summation, and Instantaneous Growth (or Allen Curve) (all reviewed by Waters and Crawford 1973), require cohort identification or knowing the age of a particular specimen to determine growth rates. A great disadvantage to these methods is that they are generally restricted to estimating production of single species rather than community production. Furthermore, most macrobenthic invertebrates are difficult to age and defining cohorts may be problematic because individuals of the same cohort may be spread out through several different size classes due to differing individual growth or prolonged spawning or recruitment periods. Sampling intervals must be sufficiently small, relative to the life span of the species present, to discern the age or cohort of individuals, and short-interval sampling may be necessary to avoid underestimating production in multivoltine species such as amphipods and isopods (Fredette at al. 1990). Community production is infrequently estimated because of the methodological and sampling difficulties in quantitatively estimating population size, following complex life histories of benthic species, and the substantial time and labor required to process the data (Diaz and Schaffner 1990).

The fourth production estimation method, the Hynes (1961) method (also known as the Size Frequency or Average Cohort method; reviewed by Waters and Crawford 1973), eliminates the need to identify individual cohorts because it treats individuals in terms of size classes that represent an average cohort and can be used on mixed-species populations to rough estimates of total community production. This approach estimates invertebrate production by estimating the total number of individuals that developed into each size class, and then calculates losses in numbers between size classes. Production is then estimated as the sum of biomass losses between successive size classes. Because this method does not require the recognition and tracking of individual cohorts, it is therefore suitable for populations with continuous reproduction. The Edgar sieve method for estimating community secondary production (Edgar 1990), a simplified modification of the Hynes method, requires relatively little sampling processing effort, is applicable to temperate marine and estuarine species, and is proven effective for estimating benthic community production in Chesapeake Bay (Hagy 2001). This method is based on the metabolic rate-body size relationship of individuals and the distribution of body sizes within a population. It estimates daily production rates by multiplying the abundance of animals in different size classes and mean individual daily production rates of animals retained on different sieve sizes.

The aim of this study is to highlight some aspects of secondary production estimates for macrobenthic invertebrates that could be used to assess ecological integrity in constructed oyster reef communities. Attention is paid to the relative production of the most representative and abundant taxa, also according to trophic groups, degree of mobility, and larval dispersal modes on different reef substrate types (oyster shell, surf clam shell, and pelletized coal ash). Patterns of macrobenthic community abundance, biomass, and diversity are compared among these constructed oyster reef substrate types to determine if reef structure affects community development and function.

METHODS

Site description

The study site is located at Fisherman's Island near the north side of the mouth of Chesapeake Bay and described previously by O'Beirn et al (2000) (Figure 1). Briefly, this polyhaline (20-32 psu) environment has a tidal amplitude of approximately 1.25 m and is surrounded by marsh islands and intertidal and subtidal mud/sand flats. In July 1996, 11 reef bases were constructed using three different substrates: oyster shell, surf clam shell, and pelletized coal ash. These reefs range in size from 80 to 900 m^2 and extend from the shallow subtidal into the intertidal zone. A natural channel separates the two rows of reefs, reaching a maximum depth of approximately 2 m at MLW.

Field collections

Permanent time-series stations were randomly established on reefs of each substrate type to minimize the impact of repeated destructive sampling on the limited surface area of the constructed reefs. Substrate basket traps (0.06 m^2, 0.1 m deep) were filled with defaunated reef substrate (cultch) material and embedded, flush with the reef surface at three tidal elevations on the reefs: approximately 0.25 m above (intertidal crest), at, and 0.25 m below mean low water. These baskets were constructed of the bottom 0.1 m of 5-gallon plastic buckets (0.27 m diameter) with 13 0.6 m diameter holes cut into the sides and bottom. The sides and bottom of the containers were lined with 6 mm plastic aquaculture mesh to permit exchange of interstitial pore water with the surrounding reef. Samples collected from the intertidal crests of the constructed reefs are the focus of this study. At monthly intervals between May 1997 and June 1998, substrate baskets were deployed, retrieved, and replaced on a falling tide when the water depth above reef surface was ≥ 0.15 m to promote capture of species that may migrate with a falling tide to leave the reef crest when it is aerially exposed. Upon recovery, baskets and cultch material were placed in cloth bags, stored on ice, transported to the lab, and stored in a freezer until further processing.

Samples were thawed and cultch material was elutriated over a 500μm sieve using filtered seawater to remove all organisms other than firmly attached species. The substrate material was inspected and attached fauna were removed using a scalpel blade and presence of encrusting species noted. All organisms were preserved in 10% buffered formalin. All macroalgae attached to the substrate were removed and identified. Macroalgae were dried for 48 h to a constant weight at 60° C and dry weight measured.

Production analyses

In the laboratory, macrobenthic organisms were separated from substrate material with the aid of a dissecting microscope and attached epifauna were removed from pieces of substrate using a scalpel blade. Specimens were sorted into size classes by rinsing the sample through a series of nested sieves, 8.0 - 5.6 – 4.0 – 2.8 – 2.0 – 1.4 – 1.0 – 0.71 – 0.5 mm (as per Edgar 1990). Each sieve was individually shaken in a bucket of water to allow animals smaller than the sieve mesh size to pass through and the contents of the bucket were then poured over the next smallest sieve. Individuals retained on each screen were identified to the lowest possible taxonomic level (usually species) and counted. Specimens retained on the 8.0 mm screen and all taxonomic groups (including echinoderms, cnidarians, and ascidians) not specified by the sieve production estimation method (see Edgar 1990: Table III) were dried for 48 h to a constant weight at 60° C and combusted at 550° C for 4 h to obtain their ash-free dry weight (AFDW). Abundance was converted to AFDW biomass using equations relating mean faunal AFDW biomass and screen mesh size (Edgar 1990) for those organisms retained on the smaller screens specified by the sieve production method.

Community production on each reef type was calculated using a relationship deduced in Edgar's (1990) empirical analysis of the effect of body mass on macrofaunal production:

$$P = 0.0049 \cdot B^{0.80} \cdot T^{0.89}$$

Where P = estimated daily macrofaunal production in μg m^{-2} day^{-1}, B = μg AFDW individual biomass, and T = water temperature in °C. This model, based on published production rates of 41 marine and estuarine invertebrate species ranging in size from $\sim 10^{-5}$ to 1 g and valid for temperatures from 5 – 30 °C. For each sample, production was determined separately for individuals in each size class using the equation above and then summed the nine size class production values into a total production value. Production values were converted to mg AFDW m^{-2} day^{-1} for this study.

Community Structure Analysis

Species richness, diversity, and evenness indices were calculated for each reef on each sampling date using the PRIMER (V 5.2.9, Plymouth Routines in Multivariate

Ecological Research, Plymouth Marine Laboratories, UK) software package (Clarke and Gorley 2001; Clarke and Warwick 2001). The observed species richness (*S*), or the total number of species collected in a sample, reflects the adequacy of resources within the habitat to support a variety of species (Connell 1978). This measure is highly dependent on sampling effort and eventually reaches an asymptote, which is rarely reached in most studies, that represents the true number of species in the community and beyond which no further increase in the cumulative number of species is expected by additional sampling. Species richness is predicted to be lower in disturbed or stressed habitats because fewer species possess the adaptive strategies necessary to overcome continual or periodic stress (Dauer 1993). Diversity is also expected to decrease with increasing environmental stress. The two estimates of diversity calculated were the Simpson index ($1\text{-}\lambda$) and the Shannon index (H', using $\log_2$). The Simpson index is the probability that any two individuals in a sample, chosen at random, are different species, with larger values corresponding to more diverse assemblages. The Simpson index is the preferred diversity measure to use for this study because it is relatively unbiased with respect to sample size (Lande 1996). H' is dependent on sampling effort, on the actual number of species in a community, and is insensitive to rare species (Lande 1996, Clarke and Warwick 2001). Despite its inherent bias, H' was calculated because of its widespread reporting in marine and estuarine studies. Pielou's evenness (J') index describes the distribution of abundance of individuals among species. Evenness compares the observed diversity (H') to a theoretical maximum diversity (H'_{max}). If all species have equal abundance, the distribution of abundances has a maximum evenness. It is common to find many rare species and few abundant ones in a multi-species collection (Larsen 1974).

As species counts are entirely dependent on sampling effort, true species richness of the macroinvertebrate community was estimated with species-effort curves. These curves were calculated for each reef type to estimate true community species richness using EstimateS (Colwell 1997; randomization iterations = 100). This program extrapolates species richness by plotting the curve of the mean cumulative number of species encountered in incrementally pooled samples over a large number (e.g. 100) of randomized permutations of the sample pool. These methods use the number of rare species to estimate the number of undiscovered species. Since the abundance and occurrence of rare species changes with increasing sampling effort, species-effort curves are an important way of noting how complete the sampling was and consequently, whether actual species counts could be higher than estimated (Walther and Morand 1998, Foggo et al. 2003).

Two-way analysis of variance (ANOVA) was used to investigate habitat and temporal differences in macrofaunal density and population biomass and macroalgal biomass using reef type and season as independent factors. Data were tested using the Shapiro-Wilk test of normality (Zar 1999) and Bartlett's test of homogeneity of variance (Underwood 1997) and transformed by log (X+1) or square root (X+0.5) where necessary to improve normality and homoscedasticity . Tukey Honestly Significant Difference tests (hereafter, Tukey test) were used for post-hoc comparisons when ANOVA detected significant differences (Zar 1999).

Similarity of species composition and abundance of macroinvertebrates among reef types was determined by hierarchical cluster analysis using COMPAH96 (http://www.es.umb.edu/edgwebp.htm) a version of the original program written and described by Boesch (1977). Abundance data were square-root transformed prior to analysis. The sample and species clusters were generated using flexible sorting with β of –0.25 and group-averaged Bray-Curtis similarity, calculated from simultaneous standardization of abundance (Boesch 1977):

$$Y = X / \sqrt{(\text{sample total}^* \text{ species total})}$$

where Y is the standardized value of abundance (X). Any species that was present in fewer than two samples was eliminated from the cluster analysis. This resulted in a total of 22 of 76 total taxa being dropped.

Results of the sample and species clusters were compared using nodal analysis of a two-way table of the original data matrix rearranged by sample and species clusters. Constancy and fidelity measures were calculated for each species group/sample group cluster. Constancy is a measure of how frequently a species cluster occurs within a given sample cluster (Boesch 1977):

$$C_{ij} = a_{ij} / (n_i * n_j)$$

where a_{ij} is the number of occurrences of members of species cluster *i* in sample cluster *j*, n_i is the total number of species in species cluster *i*, and n_j is the total number of samples in sample cluster *j*. A species cluster with a constancy value of 1.0 is present in every sample in a given sample cluster. A constancy value of 0 is obtained when none of the species in a species cluster occur in a sample cluster. Fidelity is a measure of how unique a species cluster is to a given sample cluster (Boesch 1977):

$$F_{ij} = (a_{ij}\,\Sigma\,n_j) / (n_j\,\Sigma\,a_{ij})$$

where a_{ij} and n_j are as described above. A species has a fidelity value of 1.0 when the constancy of the species cluster in the sample cluster is equal to the overall constancy of the species cluster to all samples collected. When fidelity is >1.0, the constancy of the species cluster in a particular sample cluster is greater than the total overall constancy. When fidelity is <1.0, the constancy of the species cluster in a sample cluster is less than the total overall constancy. Values of F >2.0 suggest a species cluster has a strong preference for a sample cluster. Values of F <0.7 suggest avoidance of the species from the sample cluster (Boesch 1977).

All taxa were categorized into one of four feeding types, one of four purchase (relationship to the substrate) types, and one of three dispersal types based on the system described by Larsen (1974) and on other published accounts (Appendix). The four assigned feeding types are: (1) carnivores, including carrion feeders; (2) omnivores, including general scavengers; (3) deposit feeders, including detritivores and herbivores; and (4) suspension feeders. The four purchase types are: (1) motile epifauna; (2) attached (sessile) epifauna; (3) free (motile) infauna; and (4) tube-dwelling (sedentary) infauna, including those with semi-permanent burrows. Larval dispersal types are: (1) nonpelagic; (2) short pelagic, i.e. two or three days; (3) pelagic. A list of all species and assigned feeding, purchase, and dispersal types is given in Appendix. Due to limited or conflicting information on the biology of many of these species, these designations cannot be considered rigid. Some species exhibit considerable plasticity in feeding or larval dispersal methods, however, each species was assigned to the category which is believed to be most characteristic of its behavior. When no information was available on a species, it was assigned the most appropriate category based on generic or familial characteristics (Larsen 1974).

RESULTS

Physical characteristics

Water temperature followed a sinusoidal pattern driven by season with a maximum of 27 C recorded on 9 August 1997 and a minimum of 11 C recorded on 26 January 1998 (Figure 2). Salinity followed no discernable pattern and ranged from 20 to 32 °/oo during the investigated period. The low salinity value recorded on 11 August was likely due to a high rainfall event associated with Tropical Storm Danny that crossed over eastern Virginia 24-25 July 1997 (Graumann et al. 1998).

Macroalgae

Seven macroalgal species were collected in the basket samples from the intertidal portion of the reefs at Fisherman's Island (Table 1). *Gracilaria foliifera*, a red algal species, occurred on all reef types and was the most abundant species collected during this study. *Enteromorpha* spp. and *Ulva curvata* were also collected from all three reef types. Macroalgal dry weight biomass was highly variable throughout the entire study period on all substrate types (Figure 3). Macroalgae was absent from the clam shell reef in the summer and macroalgal biomass on the other two reef types was generally lowest during the fall. Given the high variability of algal abundance and low replication, no statistically significant difference was detected in algal biomass by reef type or season (log transformed, two-way ANOVA: $p = 0.141$, $p = 0.233$, respectively). Clam shell reefs consistently yielded low overall dry weight biomass (< 0.4 g basket^{-1}). Neither macroalgal species diversity (Shannon index, H', using $\log_2$) nor evenness (J'), both calculated from dry weight biomass, varied significantly across reef type or season. Species richness (number of species, S) varied significantly across reef type ($p = 0.016$), with more species occurring on the ash pellet reef than on the clam shell reef. Macroalgal species richness on the oyster reef was intermediate but did not differ significantly from the other two reef types.

Patterns of total macrobenthic abundance and biomass among reef substrate types

A total of 76 macrobenthic taxa were collected across all three reef types during this study. Of these, 16 species were unique to samples collected from oyster shell, eight unique to clam shell, and five unique to coal ash. A subset of 21 species or genra accounted for >98% of the total abundance and >89% of the total biomass of the total fauna collected from all reef types (Table 2). Comprising this assemblage were six polychaete species (*Polydora websteri*, *Nereis succinea*, *Streblospio benedicti*, *Heteromastus filiformis*, *Podarke obscura*, *Hydroides dianthus*), five bivalve species (*Mytilus edulis*, *Crassostrea virginica*, *Mercenaria mercenaria*, *Spisula solidissima*, *Ensis directus*) and one bivalve species group (*Tellina* spp., grouped together because immature individuals are indistinguishable), three amphipod species (*Melita nitida*, *Corophium acherusicum*, *Gammurus mucronatus*), two Panopeid crab species (*Panopeus herbstii*, *Eurypanopeus depressus*), the gastropod *Mitrella lunata*, the barnacle *Balanus improvisus*, the caridean shrimp *Palaeomonetes vulgaris*, and an unidentified collembolan insect.

There was a significant effect of reef type on total macrofaunal abundance (Table 3). Total abundance ranged between 112 and 1891 individuals per 0.06 m^{-2} basket (1914 to 32322 individuals m^{-2}) and was significantly greater on the ash pellet reef than on the oyster shell reef (Table 3, Figure 4a). The clam shell reef was not significantly different from either the coal ash or oyster shell reefs (Table 3, Figure 4a). The larger abundance on the ash pellet reef was primarily attributed to high densities (>1400 individuals basket^{-1}) of the barnacle *Balanus improvisus*, the amphipod *Melita nitida*, and small panopeid crabs (carapace widths < 10 mm). Although total abundance differed significantly by reef type, reef type did not significantly influence total community biomass (Table 3, Figure 4b). The total biomass of the abundant small animals that dominated the ash and clam reefs was offset by the biomass of the few larger crabs and the shrimp collected on the oyster shell reef (Figures 7, 8, 9). Season did not have a significant effect on total overall abundance or biomass (Table 3). The large peak in biomass on the oyster shell reef in the fall is ascribed to the presence of large decapods (*P. vulgaris*, *P. herbstii* >10 mm carapace width, and the hermit crab *Clibanarius vittatus*) in samples collected during this period (Figure 8).

The classification of macrofauna taxa into one of four feeding types (Larsen 1974) further elucidated patterns in trophic structure of these reef habitats. Deposit feeding, detritivorous, and herbivorous taxa contributed little to the overall faunal abundance and biomass across all habitats throughout the study (Figures 10 and 11). The abundance of omnivores, exemplified by the gammaridean amphipods *Melitia nitida* and *Gammurus mucronatus*, was significantly greater on the ash and clam shell reef compared to the oyster shell reef (Table 7), yet there was no significant difference among reef types for omnivore biomass. While reef type did not have a significant effect on total overall abundance or biomass of the other feeding types, the abundance and biomass of carnivores and suspension feeders varied significantly by season (Table 7). Carnivores, of which the panopeid crabs *Panopeus herbstii* and *Eurypanopeus depressus* were most abundant, contributed very little to the overall abundance of the macrofaunal community through the year, with lowest counts occurring in the winter (0-2%) and highest in the summer and fall (1-10%) (Table 7, Figure 10). These carnivorous reef species were often large bodied and, although overall counts were relatively low compared to the rest of the community, comprised a greater proportion of the total community biomass (Table 2, Figure 11). Carnivore biomass was also lowest in the winter on all reef types and was consistently high on the oyster shell reef throughout the year with the lowest proportion occurring in the winter (39%) (Table 7, Figure 11).

Oyster reef habitats are characterized by high relative proportions of suspension feeders compared to other feeding types (Larsen 1974). Suspension feeders at Fisherman's Island varied seasonally and accounted for 51-86% of the total community abundance in the spring and as little as 2% in the summer; Neither summer or spring suspension feeder abundance differed significantly from that of the fall and winter (Table 7, Figure 10). The peak in abundance corresponds with the mass *Mytilus edulis* recruitment in the winter and spring. Spring and summer suspension feeder biomass, dominated by *M. edulis* and *Crassostrea virginica*, was significantly greater than that observed in the winter. Although small *M. edulis* winter recruits contributed 78% of the total suspension feeder biomass, suspension feeders made up only 5-6% of the total community biomass (Figure 11). Suspension feeders were more important in the spring and summer and comprised between 11-35% of the total community biomass (Table 7, Figure 11). One premise behind oyster reef restoration efforts is to bring back biological filtering capacity of estuarine habitats. Larsen (1974) reported suspension feeders comprised over 60% of the total community abundance on reefs in the polyhaline portion of the James River. The values reported in the present study are less than this figure and are likely an underestimate of the true suspension feeder community contribution because of the sampling gear bias associated with the monthly deployment of basket traps. Many suspension feeding species are attached epifaunal species and only those individuals recruiting to the surface of the substrate within the sampling basket are accounted for because defaunated substrate material was deployed in the baskets and retrieved monthly from each reef.

Defaunated substrate material was deployed in the baskets and retrieved monthly from each reef, so the presence of sessile and sedentary species (such as bivalves, barnacles, sedentary polychaetes, cnidarians, and tunicates) represents those individuals recruiting to the surface of the substrate within a month. It is plausible that older individuals could be washed into the basket on substrate material from the surface of the reef surrounding the basket opening (as per Cosby et al. 1991). These substrate baskets detect short-term (<1 month) recruitment pulses of sessile and sedentary epifaunal species but are best at quantitative sampling of motile species.

When only motile species (i.e. motile epifauna and free infauna) are considered, the overall abundance from all samples over the entire study period is reduced from >30,000 to >16,000 individuals while the total biomass is reduced by 8 g AFDW from 48.2 to 40.2 g AFDW (Tables 2 and 4). Analysis of total macrofaunal abundance and biomass calculated using data for motile species only reveals that clam shell and ash pellet reefs had significantly greater densities of motile species than the oyster shell reef (Table 5, Figure 5a). This relationship held true for abundance of the numerical dominant, the amphipod *Melita nitida* (Figure 7c). *Panopeus herbstii* and *Nereis succinea* abundance also differed between clam shell and oyster shell reefs but abundance on the ash pellet reef was not significantly different from either (Figure 7a,e). Season did not have a significant effect on the total abundance of motile species (Table 5), but was a significant factor affecting the abundance of two of the dominant species, *P. herbstii* and *N. succinea*. *Panopeus herbstii* was more abundant in summer, fall, and spring than in the winter months (Figure 7a). *Nereis succinea* was more abundant in the summer, primarily on the clam shell reef (Figure 7e).

There were no significant differences in total community biomass among reefs or seasons for the motile species group (Table 4b). Season was nearly significant ($P = 0.0534$) due to the high biomass of decapod crustaceans in oyster reef samples collected during the fall. The only individual species to exhibit a significant difference among reef types was the amphipod *Melita nitida* with greater biomass occurring on the clam shell and coal ash pellet reefs than on the oyster shell reef (Figure 8c). The biomass of *Panopeus herbstii*, the amphipods *Gammurus* spp. (including *G. mucronatus* and *G. palustris*), and *N. succinea* was each affected by season differently. *Panopeus herbstii* had the greater biomass in the fall, summer and spring than in the winter. *Gammurus* spp. had the greater biomass in winter than in the spring and fall (Figure 8d). As with abundance, *Nereis succinea* biomass was greatest in the summer and lowest in the winter (Figure 8e).

Analysis of total macrofaunal abundance and biomass calculated using data for sedentary and sessile species only (attached epifauna and tube-dwelling infauna; e.g., sedentary polychaetes, barnacles, tunicates, and anemones) reveals that this component of the total community did not vary significantly by reef type, nor did the dominant species, *Crassostrea virginica* and *Mytilus edulis* individually (Table 6, Figures 6, 7f, 7g, and 8f, 8g); however, there was a significant effect of season on biomass with greatest values in the spring and summer and lowest in the winter (Table 6, Figures 6 and 8f, 8g). The abundance of the numerical dominant sessile species, *M. edulis*, was greatest during recruitment periods in winter and spring, with only a few individuals collected in the summer and none during the fall (Figure 7f). The few individuals collected in the summer had a high AFDW per individual and are likely incidental captures and not reflective of natural recruitment during the sampling interval (Figures 8f and 12). Abundance patterns of *C. virginica* reflected recruitment events in the summer and fall. As with *M. edulis*, the high biomass of *C. virginica* on the clam shell reef during the summer was also driven by the few, large individual collected in these samples (Figures 8g and 13).

The percentage of taxa and proportional abundance and biomass in each of the three designated dispersal types is shown in Figure 14. The short pelagic dispersal type only occurred in 4 species from the oyster shell and 3 species from both the clam shell and ash reefs and contributed negligible amounts to the overall community abundance and biomass (Figure 14a). There was a slight trend of relatively greater percentage of pelagically dispersing individuals, including the panopeid crab *Panopeus herbstii* and the mussel *Mytilus edulis*, on the oyster shell reef and this was reflected in the community biomass patterns as well. The higher proportion of non-pelagically dispersed individuals on the other two reef types is accounted for by the numerical and biomass dominance of young-brooding gammaridean amphipods (Figure 14 b,c).

Species Richness and Diversity Indices

No significant differences were detected for any of the diversity indices calculated across the entire study. Species richness did not vary significantly by reef type (ANOVA, $P = 0.081$), but tended to be higher in the summer than during any of the other seasons (Figures 15 and 16). Although variable throughout the seasons and not statistically significant, the relative contributions of each feeding type (Larsen 1974) to species richness of the assemblages generally differed across reef type. The overall number and percentage of taxa in three of the four feeding types were greater on the oyster shell reef compared with the clam and ash reefs (Figure 16). Omnivores and scavengers dominated the oyster shell reef taxa while suspension feeders contributed the fewest number and percentage of taxa on this reef substrate. In contrast, suspension feeders made up the bulk of the taxa collected from the ash reef. Proportions of taxa in each feeding group on the clam shell reef appeared more reflective overall of the oyster shell reef community compared to that of the ash reef with a relatively high species richness of omnivorous taxa.

By examining within season, summer was the only season where diversity indices differed significantly across reef type. The Shannon diversity index, H', was significantly higher (ANOVA, $P = 0.003$) on the oyster shell reef than on the clam shell and coal ash pellet reefs (Figure 15). Similarly, the Simpson index was significantly higher (ANOVA, $P = 0.005$) on the oyster shell reef than the coal ash pellet reef, but not significantly different from that of the clam shell reef (Figure 15). Evenness was significantly higher (ANOVA, $P = 0.006$) on the oyster shell reef compared to the coal ash pellet and clam shell reefs.

Randomized species-effort curves, whereby cumulative number of species is plotted against cumulative number of samples show the extrapolated species richness values, were consistently higher on the oyster shell than on the clam shell and coal ash pellet reefs (Figure 17A). All three curves appear to approach an asymptote and thus further incremental sampling efforts beyond the twelve samples per reef type would likely yield few additional species. The patterns of species accumulation with increasing numbers of individuals sampled are varied by reef type (Figure 17B). Species accumulated more rapidly on the oyster shell reef than on the clam shell and coal ash reefs and attained a higher species richness even though fewer individuals were collected from that reef type during the duration of this study. As the oyster shell reef curve does not yet appear to approach an asymptote as the other reef type curves do, it can be extrapolated that the true species richness on the oyster shell substrate is greater.

Secondary Production

Total community secondary production estimates ranged between 1.4 and 282.3 mg AFDW m^{-2} day^{-1} for the 384 d study period with lowest production estimates occurring in the winter (ANOVA, $P < 0.001$, Figure 18, Table 9). Even though no significant differences were found, a slight trend in reef community secondary production rates, with oyster shell greatest, was evident from the proportional contribution of daily production from each reef type each season (Figure 18, Table 9).

As with biomass, large decapods and gammaridean amphipods were primarily responsible for driving the spatial and temporal patterns observed in estimated secondary production (Figures 19 and 20, Table 9). Production on the oyster shell reef was mainly by carnivores, mostly *Panopeus herbstii* (Figures 20C, 21C and 22, Table 10), which accounted for over half of the annual production estimate on the oyster shell habitat. Though of lesser magnitude, this species was also particularly productive on the clam shell and coal ash pellet reefs contributing 24 and 31% of the total annual production, respectively (Table 10). Production of this species, and carnivores in general, dropped off notably during the winter months across all habitat types (Figures 19, 20, 21, 22). Omnivores contributed a bulk of the production on the reef habitats and dominated production on the clam shell and ash pellet reefs (Figure 22, Table 10). The gammaridean amphipod *Melita nitida* was a major omnivorous producer on the clam shell and ash pellet reefs and contributed 27 and 32% of the total annual production yet only made up 5% of production on the oyster shell reef (Table 10). *Nereis succinea*'s contribution to total community production was greatest on the clam shell reef, driven by several large specimens collected during the summer months (Figure 19B, 20B, Table 10). Omnivores were the second-most important producers on the oyster shell reef, due in part to fall and winter productivity of *Palaeomonetes vulgaris*. This species was relatively unimportant elsewhere and only occurred in November samples from the coal ash and clam shell reefs (Figure 19).

Production estimates for sessile and sedentary species, many of which make up the deposit and suspension feeder feeding groups (Appendix), theoretically represent only those individuals recruiting to the surface of the substrate within a month because defaunated substrate material was deployed in the baskets and retrieved monthly from each reef. Therefore, production values reported for *Crassostrea virginica* and *Mytilus edulis* are likely to be gross underestimates because the sampling gear did not quantitatively sample all cohorts of this component of the community. Nonetheless, suspension feeder secondary production estimates for recent recruits of *C. virginica* and *M. edulis* accounted for much of the total community production. Fifteen percent of the macroinvertebrate production on the clam shell habitat was due to *C. virginica*, while *M. edulis* contributed 15% of the coal ash reef community production (Table 10, Figure 19). Suspension feeders contributed about 14% of the total community production on the oyster shell reef, the bulk of which were spring *M. edulis* recruits. Deposit feeders, mostly Tellinid clams present in spring collections, contributed little to the overall productivity estimates of the reef habitats at Fisherman's Island (Table 10).

Community analyses

Hierarchical cluster analysis, using abundance data, of the coal ash pellet, clam shell, and oyster shell reef macrofaunal data segregated the samples into eight dissimilar groups (Figure 23, Table 11) and species into fourteen dissimilar groups (Figure 24, Table 12). Constancy and fidelity are illustrated in Figures 25 and 26. The basic patterns in both species and sample cluster analyses appeared to be controlled by temporal effects.

The nine numerically dominant species that formed groups H and I displayed high constancy but low fidelity across all reef types, indicating their ubiquity and numerical importance. Group I was made up of the top two numerically dominant species, *Melita nitida* and *Mytilus edulis*. Members of Group H included the other numerically dominant bivalves *Crassostrea virginica*, *Mercenaria mercenaria*, *Spisula solidissima*, and *Tellina* spp, as well as the most numerically dominant crustaceans, *Panopeus herbstii* and *Balanus improvisus* and polychaete, *Nereis succinea*. Subdominant taxa within species groups F, G, and J were broadly distributed but usually in low numbers across all sample groups. Species groups F and G expressed moderate to high fidelity to summer sample groups. The taxa within the remaining species groups are considered rare and had low to very low constancy and fidelity for the majority of the sample groups, occasionally having a high constancy or fidelity for a particular sample group (Figures 25,26).

Sample groups 1 and 2 were closely associated (Figure 23) and represented collections from summer months (June and July) on all three reef types, with high occurrences of the dominant (species groups H and I) and subdominant (species groups F, G, and J) taxa. Sample group 1 also had high occurrences of individuals within species group M, which was comprised of taxa that were rare throughout the rest of the study. Sample group 2 had high constancy and fidelity of both of the rare species that made up species group L (Figures 25, 26). Neither group was comprised of individuals from species in groups A, B, or N.

Sample groups 3, 4, and 5 were closely associated and consisted of samples collected in the fall to early winter across all each reef types (Figure 23, Table 11). Sample group 3 represented all but one of the ash pellet samples and all of the clam shell reef samples collected during the last 5 months of 1997 (Table 11). Sample group 4 was made up of samples collected from the oyster shell reef in August and September. Rare taxa, except for those of species group N, were generally absent from this sample group (Figure 25). Sample group 5 was made up of oyster shell reef samples collected October through December and the November ash pellet reef collection. One factor separating these groups from others is the near absence of *Mytilus edulis* (of species group I) from the collections. The other species in species group I, *Melita nitida*, was prominent along with each of the other species in group H, all of which were dominant throughout the study period. Very few species from groups E, L, or M were found in the collections making up this sample group. It is noteworthy that the decapod *Palaeomonetes vulgaris* was most abundant in samples within group 5.

There was a high degree of similarity between sample groups 6, 7, and 8 (Figure 23), which were composed of samples collected from each reef type during the late winter and spring months (January through May; Table 11). The numerically dominant species of species of group I (*Melita nitida* and *Mytilus edulis*) had very high constancy (C = 1) to each of these sample clusters (Figure 25) and most species groups were collected (but often in low occurrences or abundances).

DISCUSSION

While the placement of any substrate in any structure-limited system will likely attract organisms, the physical and chemical nature of the structure and biological attributes of the system are important factors to consider in assessing whether that structure will have a significant impact on the ecological functioning of that system. In this study, a suite of physical and biological factors (i.e., structural differences in reef type, predation, recruitment/immigration, disturbance by currents and wave action, the presence of live oysters, metamorphosis cues secreted by adults in the habitat, etc.) could have likely influenced the observed patterns in the macrobenthic community on the Fisherman's Island reef.

Oyster shell reefs were the most productive habitat in the Fisherman's Island reef system, indicating that they are an important habitat for macrobethic invertebrates. However, oyster reefs cannot be considered in isolation, as closed boxes do not exist in nature. These reef habitats have vital ecological linkages with other ecosystems and high benthic secondary production on reefs likely contribute to neighboring habitats. While a fundamental goal of oyster reef restoration efforts is to establish viable, self-sustaining oyster populations, the formation of a productive community of reef-associated fauna including mud crabs, grass shrimp and other small crustaceans (i.e., amphipods, isopods) is important to restoring invertebrate prey for higher trophic level predators such as finfish and birds. All three reef substrate types demonstrated substantial production of these species, but the portion of the production consumed by higher trophic levels is unknown. Additional investigations (i.e. gut analysis) of the trophic role of each species collected in this study would provide a better understanding of the habitat's value to resident and transient predators.

Other investigators have noted high macroinvertebrate densities and biomass on oyster reefs (Wells 1961; Bahr 1974; Larsen 1974; Dame 1979; Zimmerman et al. 1989), however, little comparable community production data for macrobenthos, particularly on reef habitats, is available (Dame 1976). Dame (1976) estimated intertidal oyster production in South Carolina, omitting values for associated macrofauna in his estimate. He reports a production rate of 22312 g AFDW $m^{-2}y^{-1}$ for intertidal oysters (values converted from Kcal to ash-free dry mass using 1 g AFDW = 0.19 Kcal; Waters 1977), a value far exceeding the production rate of the entire reef community at Fisherman's Island. The estimated production values determined in the present study are more comparable to those reported for other estuarine communities. Sarda et al. (1998) calculated production of saltmarsh macroinfauna inhabiting sandy-organic sediments to be 69 g ADFW $m^{-2}y^{-1}$ (values converted from dry mass to ash-free dry mass using ash content = 10.4% dry mass; Benke and Wallace 1980). In Chesapeake Bay SAV habitats, Fredette et al. (1990) calculated community production values as high as 268 g ADFW $m^{-2}y^{-1}$ (values converted from dry mass to ash-free dry mass; Benke and Wallace 1980). Freshwater streams are on average much less productive with values typically less than 50 g ADFW $m^{-2}y^{-1}$ (Waters and Crawford 1973; Smock et al. 1985; Buffagni and Comin 2000).

Various errors were possible in estimating the secondary production rates for the communities of the constructed oyster reefs at Fisherman's Island. Because of the small size of these reef bases, destructive sampling was avoided and the alternative sampling approach employed (monthly replacement with clean substrate) was not quantitative for multiple cohorts of sessile or sedentary species. Therefore, production values reported for non-motile species such as *Crassostrea virginica* and *Mytilus edulis* are likely to be gross underestimates because the sampling gear targeted only individuals recruited within the each sample period. Another possible source of error was the use of sieve mesh size (500 μm) during sample processing that permitted the smallest individuals to escape. Because small bodied individuals have high production rates (reviewed by Diaz and Schaffner 1990), inclusion of the smallest size classes is important for accurate community production estimates. Benthic macrofauna juveniles (retained on 250 μm and 125 μm screens) contribute as much as 20% of the total community production during peak recruitment periods (Hinchey 2002), yet this component was not considered in the production estimates for the Fisherman's Island reefs. This factor may have been of greatest significance during the spring and summer when most temperate macrobenthic recruitment takes place (reviewed by Holland et al. 1988), resulting in a serious underestimate of smallest size classes of recruits during these seasons. Furthermore, categorizations into functional feeding groups, based on various sources, does not take into account plasticity exhibited by many in feeding modes, crossing the categories employed here. For example, tellinid clams are categorized in the present study as deposit feeders, but under certain flow regimes, they switch to suspension feeding (Holland et al. 1988). Additional investigations (i.e. gut analysis) of the trophic role of each species collected in this study should be carried out to allow a more truly representative assignment of functional feeding groups leading to more accurate interpretations of energy transfer patterns.

Seasonal cycles of phytoplankton abundance, productivity, and composition are strong in temperate estuaries due to changes in availability of light and nutrients and seasonal temperature variations (Tenore 1988). While water column food supplies drop to minimum levels in the winter months, competition among individuals for resources can regulate productivity and community structure and is reflected in reduced winter community productivity. The temporal differences in secondary production can be interpreted as a result of observed shifts in biomass because production is a function of population biomass and biomass turnover rate. Seasonal production on the constructed oyster shell reef habitat showed a moderate production in the summer, followed by peak in the fall and almost no production through winter, but production increased again in the spring. During the winter, *Panopeus herbstii* biomass decreased sharply suggesting mortality rates were above production rates at that time. Although overall production rates were lowest in the winter months, it is interesting to note that production of omnivorous and scavengers, particularly *Melita nitida* on the clam shell and ash pellet reefs, continued through the winter at levels that contributed to the annual production of this group.

Small-scale structural differences in the different reef substrates (oyster shell, clam shell, and coal ash pellet) could have contributed to the differences in community structure observed in this study. O'Beirn et al (2000) demonstrated that each reef type has significantly different interstitial volumes (oyster shell (0.70 L/L substrate) > clam shell (0.58 L/L substrate)> coal ash pellet (0.45 L/L substrate)). Substrates with greater interstitial space provide more volume and crevices for reef macrofauna to occupy (Figure 27). Oyster shell reefs, with large overall interstitial space volume and large individual interstitial spaces, likely provided good habitat for larger decapod crustaceans (Figure 27A), resulting in increased overall production relative to the clam shell and coal ash pellet reefs. The clam shell reef substrate, with intermediate interstitial space volume, high overall substrate surface area available for epibenthic settlement, yet small individual interstitial spaces, was more restrictive to larger bodied individuals and supported more individuals of smaller size classes than the oyster shell habitat (Figures 27B, 28). Coal ash pellets, with low overall interstitial volume and moderately sized individual interstitial spaces, supported macrofauna size classes reflective of those on the clam shell habitat (Figure 27C, 28).

Differential predation pressure may also explain some of the differences seen in macrofaunal community across reef type. Complex habitats affect predator foraging success and prey survival by limiting a predator's ability to move through a habitat to search, detect, and capture prey (reviewed by Heck and Crowder 1991, Bartholomew et al. 2000). Postsettlement predation is considered one of the potential key factors regulating population density and structure (Hines and Ruiz 1995) and smaller juveniles are also comparatively weak competitors for food and refuge, which should further reduce their probability of survival and growth (Hines 1986). However the varying sizes of the interstructural gaps between the pieces of oyster shell, clam shell and coal ash pellet reef substrate likely act to limit the body size of fauna that are able to occupy the space. These spaces may serve as predation refuges for smaller size classes relative to larger predators, increasing survivorship (Bartholomew et al. 2000) because the individual pieces of substrate may serve as physical barrier to faunal maneuverability through the substrate matrix. In this study, nearly half of the largest animals collected came from the oyster shell reef (Figure 28), which also had the largest interstitial volume (O'Beirn et al. 2000). Larger crabs (>21 mm carapace width) were not collected from the clam shell or coal ash pellet substrate, likely because these substrates lacked sufficient interstitial refuge space for these individuals to occupy.

Proportionately more individuals of smaller size class macrofauna were collected from the clam shell and ash pellet reefs compared to oyster shell reef. While clam and ash pellet reefs support higher abundances of small size class macrofauna, the interstices may not be large enough to support small resident reef fish or other intermediate level consumers (Figure 27). These trophic intermediate species between primary consumers and larger transitory fishes are important components of the oyster reef linking oyster reef secondary production with other open water habitats (Harding and Mann 1999). In essence, these reefs may be acting as trophic dead-ends with less production transferred to higher trophic levels via these intermediate consumers.

For example, the oyster shell reefs had proportionately lower abundances of the amphipod *Melita nitida* than the other two reef types. Although sufficient space was available to this species on the oyster shell reef, the spaces were large enough to permit access to the interior of the reef matrix by predatory fishes (Bartholomew et al 2000). Since cryptic oyster reef resident fishes rely on appropriately sized interstices within the oyster reef habitat for feeding and predator refugia (Breitburg 1999), it is likely that smaller bodied crustaceans fell prey to higher level predators occupying the reef habitat.

Investigations of gut contents of fishes collected from these reefs may further elucidate patterns of trophic transfer at Fisherman's Island.

Another factor that may influence faunal patterns observed on these reefs is recruitment and/or immigration of individuals to the different reef types. Geographic distribution of benthic invertebrate species is suggested to be related to larval mobility (Crisp 1978). The proportional majority of the taxa collected on all three reef types have planktonic larval development (Figure 14A) which facilitates dispersal and immigration (Newell and Newell 1977), yet the clam shell and coal ash pellet reefs had proportionally more individuals with non-pelagic development compared to the oyster shell reef (Figure 14B). The duration of the planktonic larval phase is positively correlated to the potential distance the larvae may be transported away form the point of release such that a species with a short, or no, planktonic stage is expected to have a small geographic range, while those with a long planktonic phase assume a wider distributional range. All of the sampled reefs at Fisherman's Island were within 0.5 km and presumably close enough such that the species pool for colonizing each reef type is equal for even species with short (1-2 day) larval duration. Johannesson (1988) however, suggests that passive transport of adult benthic invertebrates of low mobility, such as by rafting on floating and drift algae, in combination with a direct development may an effective means of dispersal means allowing direct developers to disperse and colonize new habitats. This transport may facilitate movements of individuals from a habitat with high predator densities (i.e., oyster shell reef) to those of lower predation pressure (i.e., clam shell or coal ash reefs) resulting in dense populations of species with non-planktonic larvae (i.e. gammaridean amphipods).

Although not directly measured, the stability of a substrate to resist physical disturbance could also have an effect on the macrofaunal community. Physical disturbance, in the form of currents or wave action (of sufficient force to turn over or move a piece of substrate) could cause localized extinction of the epifauna on a piece of substrate. While abundances of sessile and sedentary species did not vary significantly across reef types, trends in epifaunal species abundance were apparent. For example, lower abundances of newly settled *Mytilus edulis* on the clam shell reef than the oyster shell reef may be explained by the instability of the individual clam shell fragments to remain in place over time. A post-settlement juvenile *M. edulis* may settle a particle of clam shell, adding surface roughness to the individual clam shell fragment, and increase the susceptibility of the fragment to movement by predominate currents, dislodging the substrate fragment and organism from reef surface. As the oyster shell substrate became colonized with oysters, it became more stable and resistant to disturbance by wave action. Habitat stability has been shown to affect species abundance distributions of benthic invertebrate communities in freshwater streams and instability of a habitat can be viewed as resetting the successional stage of a community (Death 1996). Unstable and very stable stream communities were dominated by one or two taxa with a large number of rare species, while those of intermediate stability had relatively uniform species abundances with no species strongly dominant. Following this paradigm, habitats with maximum evenness (and therefore equal abundances of species), would indicate intermediate habitat stability. While no significant differences in evenness (*J*) were detected for the Fisherman's Island habitats across season or reef type, there was a general trend of the oyster shell habitat having greater evenness values (Figure 15).

Based on Death's characterization of evenness and its relation to habitat stability, it is not possible to discriminate as to whether generally lower evenness values on the clam shell and ash pellet reefs are due to those habitats being very stable or very unstable.

One last factor that may be influencing patterns in the macrofaunal community is the presence of live oysters. The timing of oyster recruitment to the reefs detected in the basket samples at Fisherman's Island is consistent with results reported for the same vicinity by Morales-Alamo and Mann (1998). They report oyster recruitment to shell-string collectors appeared 29 June through 19 October 1997. Oyster settlement was first recognized on substrate material retrieved from the oyster shell reef on 7 July 1997. Oysters from the clam shell reef collected 11 June and 7 July 1997 ranged in size from 12 to 27 mm shell height, larger than the 10 mm achieved by intertidal recruits one month after settlement (Roegner 1989; Crosby et al. 1991) and are presumably from a fall 1996 recruitment pulse. It is most likely that these oysters recruited to the reef at an earlier date and the pieces of shell that they were attached to washed into the substrate basket by tidal currents. Similarly, oysters were collected in samples retrieved from the clam shell reef on 26 January (6 – 8 mm shell height) and 26 May 1998 (21 mm shell height), months after recruitment was last detected in 1997 and before recruitment commenced in August 1998 at Fisherman's Island (Southworth et al. 1999) and it is likely that these oysters washed into the baskets and are individuals from the previous fall recruitment. Lateral transfer of oysters on shell fragments on the oyster shell reef did not occur, presumably because this substrate became stabilized with a matrix of live oysters over time (O'Beirn et at 2000).

Although recruitment to each of the reef types appeared equal, concurrent studies within the same reef system showed differential survival and growth of oysters on the different reefs. O'Beirn et al (2000) report significant differences in oyster abundance by reef type for the same time period covered by the present study. The oyster shell reefs showed significantly greater densities of live oysters compared to clam shell and coal ash pellet reefs. In fact, by the fall of 1998, a continuous crust of live oysters had formed on the oyster shell reef while the surface of the other two reefs retained their original appearance with little biofouling on the surface of the substrate material (O'Beirn et al 2000). The rank order of oyster density by reef type reported by O'Beirn et al (oyster > clam = ash) follows the same trend as demonstrated for total macrofaunal community secondary production and estimated species richness.

Live oysters, as habitat engineers, create a variety of structurally complex microhabitats and contribute to the overall biodiversity and secondary production of the reef community. The shells of oysters provide substrata for epifaunal attachment and the interstices offer refugia and collect sediment and biodeposits, creating carbon-rich habitat for deposit feeding and other infaunal and trophically intermediate species. In intertidal mussel beds of rocky intertidal communities, interstices provide refuge for species that would normally suffer intense predation (Whitman 1975) and physical refuge for infaunal and epifaunal species that would not normally survive the extreme physical stresses between periods of tidal inundation (Suchanek 1978). Oysters act in much the same manner (Bahr and Lanier 1981, Meyer 1994). The presence of live oysters, therefore, has important implications for evaluating the success of restored oyster reef habitats in terms of how they function ecologically as habitats for trophic exchange from primary and secondary consumers to higher predators (Coen et al 1999).

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Table 1: Macroalgae species sampled from the three reef types at Fisherman's Island throughout the course of this study.

SPECIES	ASH	CLAM	OYSTER
Rhodophyta			
Ceramium spp.	X	X	
Gracilaria foliifera	X	X	X
Phaeophyta			
Fucus vesiculous			X
Chlorophyta			
Bryopsis plumose	X		
Codium spp.			X
Enteromorpha spp.	X	X	X
Ulva curvata	X	X	X

Table 2: Dominant species from constructed reefs in this study (all reef substrate types combined). N is the number of individuals collected. Major taxa are: (A) Amphipoda; (B) Bivalvia; (C) Cirripedia; (D) Decapoda; (G) Gastropoda; (I) Insecta; (P) Polychaeta.

Taxa	N	% of total abundance	% of total biomass
Panopeus herbstii (D)	540	1.8	40.1
Melita nitida (A)	12880	41.9	18.7
Mytilus edulis (B)	9477	30.8	10.2
Palaeomonetes vulgaris (D)	107	0.3	5.7
Crassostrea virginica (B)	490	1.6	5.1
Nereis succinea (P)	865	2.8	5.0
Gammurus mucronatus (A)	362	1.2	2.0
Eurypanopeus depressus (D)	52	0.2	1.2
Mitrella lunata (G)	386	1.3	0.6
Balanus improvisus (C)	1769	5.6	0.5
Polydora websteri (P)	1083	3.5	0.1
Corophium acherusicum (A)	449	1.5	0.1
Mercenaria mercenaria (B)	407	1.3	0.1
Tellina spp. (B)	374	1.2	0.1
Spisula solidissima (B)	191	0.6	0.06
Ensis directus (B)	88	0.3	0.06
Heteromastus filiformis (P)	135	0.4	0.05
Podarke obscura (P)	67	0.2	0.05
Collembolidae (I)	345	1.1	0.04
Streblospio benedicti (P)	198	0.6	0.03
Hydroides dianthus (P)	61	0.2	0.03
	Cumulative percent	98.6	89.7
	Cumulative total abundance, biomass	30326 indiv.	43.3 g AFDW
	Overall total abundance, biomass	30767 indiv.	48.2 g AFDW

Table 3: Results of ANOVA and Tukey multiple comparisons tests for differences in total community abundance (no transformation necessary) and $\log_{10}$ (AFDW + 1) biomass among reef type (A – coal ash, C – clam shell, O – oyster shell) and seasons. *P* values < 0.05 are in bold. Reef types with underlines that overlap are not statistically different at *P* < 0.05.

Source (df)	SS	MS	F	*P*	Tukey's Test
Total abundance					
Season (3)	614462	204820	0.73	0.544	
Reef (2)	2801231	1400615	4.99	**0.015**	**A C O**
Season*Reef (6)	751108	125184	0.45	0.841	
Total biomass					
Season (3)	1.213	0.405	2.90	0.056	
Reef (2)	0.071	0.036	0.26	0.777	
Season*Reef (6)	1.236	0.206	1.48	0.228	

Table 4: Dominant motile species from constructed reefs in this study (all reef substrate types combined). N is the number of individuals collected. Major taxa are: (A) Amphipoda; (D) Decapoda; (G) Gastropoda; (I) Insecta; (P) Polychaeta (errantia)

Taxa	N	% of total abundance	% of total biomass
Panopeus herbstii (D)	540	3.3	48.1
Melita nitida (A)	12880	78.4	22.4
Palaeomonetes vulgaris (D)	107	0.7	6.8
Nereis succinea (P)	865	5.3	6.0
Gammurus mucronatus (A)	362	2.2	2.4
Paleanotus heteroseta (P)	47	0.3	1.8
Eurypanopeus depressus (D)	52	0.3	1.4
Mitrella lunata (G)	386	2.3	0.7
Corophium acherusicum (A)	449	2.7	0.1
Podarke obscura (P)	67	0.4	<0.01
Collembola sp. (I)	345	2.1	<0.01
Cumulative percent		98	90
Cumulative total abundance, biomass		16100 indiv.	36.1 g AFDW
Overall total abundance, biomass		16432 indiv.	40.2 g AFDW

Table 5: Results of ANOVA tests and Tukey multiple comparisons tests for differences in total motile species abundance ($\log_{10}$ (Abundance + 1)) and square-root transformed biomass (AFDW + 0.5) among reef type (A – coal ash, C – clam shell, O – oyster shell) and among seasons. *P* values < 0.05 are in bold. Reef types with underlines that overlap are not statistically different at *P* < 0.05.

Source (DF)	SS	MS	F	*P*	Tukey
Motile abundance					
Season (3)	0.27	0.09	1.02	0.40	
Reef (2)	3.57	1.78	19.77	**<0.001**	C A O
Season*Reef (6)	0.10	0.02	0.19	0.98	
Motile biomass					
Season (3)	1399.4	466.5	2.94	0.05	
Reef (2)	66.9	333.5	2.10	0.14	
Season*Reef (6)	1551.6	258.6	1.63	0.18	

Table 6: Results of ANOVA tests and Tukey multiple comparisons tests for differences in total sessile and sedentary species abundance ($\log_{10}$ (Abundance + 1)) and biomass ($\log_{10}$ (AFDW + 1)) among reef type and among seasons (Sp – Spring, Su – Summer, F – Fall, W – Winter). *P* values < 0.05 are in bold. Seasons with underlines that overlap are not statistically different at $P < 0.05$.

Source (DF)	SS	MS	F	*P*	Tukey
Sedentary and Sessile abundance					
Season (3)	2.62	0.87	2.27	0.106	
Reef (2)	1.30	0.65	1.70	0.204	
Season*Reef (6)	1.54	0.26	0.67	0.676	
Sedentary and Sessile biomass					
Season (3)	9.84	3.89	10.26	**0.002**	**Sp Su F W**
Reef (2)	0.30	0.15	0.47	0.630	
Season*Reef (6)	2.18	0.36	1.14	0.371	

Table 7: Results of ANOVA tests and Tukey multiple comparisons tests for differences in abundance ($\log_{10}$ (Abundance + 1)) and biomass ($\log_{10}$ (AFDW + 1)) of each feeding type among reef type (A – coal ash, C – clam shell, O – oyster shell) and among seasons (Sp – Spring, Su – Summer, F – Fall, W – Winter). *P* values < 0.05 are in bold. Reef types and seasons with underlines that overlap are not statistically different at *P* < 0.05.

Source (DF)	SS	MS	F	*P*	Tukey
Carnivore abundance					
Season (3)	2.58	0.86	4.44	**0.013**	**Su F Sp W**
Reef (2)	0.93	0.46	2.40	0.112	
Season*Reef (6)	0.34	0.06	0.29	0.935	
Carnivore biomass					
Season (3)	14.76	4.92	7.37	**0.001**	**Sp Su F** > **W**
Reef (2)	0.98	0.49	0.74	0.489	
Season*Reef (6)	2.08	0.35	0.52	0.787	
Omnivore abundance					
Season (3)	0.30	0.10	1.06	0.383	
Reef (2)	4.18	2.09	22.54	**<0.001**	**C A** > **O**
Season*Reef (6)	0.12	0.02	0.22	0.965	
Omnivore biomass					
Season (3)	0.69	0.23	1.16	0.347	
Reef (2)	0.46	0.23	1.16	0.329	
Season*Reef (6)	2.34	3.89	1.97	0.110	

Table 7 (continued)

Source (DF)	SS	MS	F	*P*	Tukey
Deposit feeder, detritivore, and herbivore abundance					
Season (3)	1.98	0.66	1.57	0.223	
Reef (2)	0.07	0.04	0.09	0.919	
Season*Reef (6)	1.74	0.29	0.69	0.661	
Deposit feeder, detritivore, and herbivore biomass					
Season (3)	0.92	0.31	0.63	0.604	
Reef (2)	0.41	0.20	0.42	0.664	
Season*Reef (6)	2.09	0.35	0.72	0.641	
Suspension feeder abundance					
Season (3)	4.23	1.41	3.41	**0.034**	**Su F W Sp**
Reef (2)	2.12	1.06	2.56	0.098	
Season*Reef (6)	1.55	0.26	0.62	0.710	
Suspension feeder biomass					
Season (3)	11.20	3.74	9.35	**<0.001**	**Sp Su F W**
Reef (2)	0.36	0.18	0.44	0.646	
Season*Reef (6)	2.21	0.37	0.92	0.497	

Table 8: Results of ANOVA tests and Tukey multiple comparisons tests for differences in abundance ($\log_{10}$ (Abundance + 1)) and biomass ($\log_{10}$ (AFDW + 1)) of each dispersal type among reef type (A – coal ash, C – clam shell, O – oyster shell) and among seasons (Sp – Spring, Su – Summer, F – Fall, W – Winter). *P* values < 0.05 are in bold. Reef types and seasons with underlines that overlap are not statistically different at *P* < 0.05.

Source (DF)	SS	MS	F	*P*	Tukey
Non-Pelagic abundance					
Season (3)	0.35	0.12	0.99	0.414	
Reef (2)	4.02	2.01	17.30	**<0.001**	**C A O**
Season*Reef (6)	0.20	0.03	0.29	0.935	
Non-Pelagic biomass					
Season (3)	1.13	0.38	1.98	0.143	
Reef (2)	3.33	1.67	8.78	**0.001**	**C A O**
Season*Reef (6)	0.50	0.08	0.44	0.844	
Short Pelagic abundance					
Season (3)	0.27	0.09	0.55	0.655	
Reef (2)	0.43	0.22	1.30	0.290	
Season*Reef (6)	0.14	0.02	0.14	0.990	
Short Pelagic biomass					
Season (3)	0.37	0.12	0.71	0.554	
Reef (2)	0.36	0.18	1.04	0.368	
Season*Reef (6)	0.30	0.05	0.29	0.936	
Pelagic abundance					
Season (3)	1.30	0.43	1.73	0.187	
Reef (2)	0.49	0.25	0.99	0.187	
Season*Reef (6)	1.34	0.22	0.90	0.513	
Pelagic biomass					
Season (3)	7.93	2.64	13.83	**<0.001**	**Sp Su F W**
Reef (2)	1.77	0.88	4.62	**0.020**	**O C A**
Season*Reef (6)	1.56	0.26	1.36	0.271	

Table 9: Estimated daily total community secondary production and production of numerical and biomass dominants from Coal Ash Pellet, Clam Shell, and Oyster Shell reefs at Fisherman Island, Virginia (as per Edgar 1990). Data are mg AFDW m^{-2} day^{-1} for each sampling interval.

			Panopeus herbsti			*Melita nitida*			*Mytilus edulis*			*Nereis succinea*		
Interval Ending	No. of days	water temperature	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER
11 June 97	33	24	8.856	9.626	40.740	5.243	8.781	2.685	5.371	1.476	13.392	1.511	57.253	2.637
7 July 97	25	25	4.457	48.435	51.771	0	20.981	3.436	0	0	5.818	6.393	50.040	2.970
12 August 97	36	27	50.225	27.368	53.185	51.016	24.169	2.735	0	0.143	0	8.267	18.592	0.435
11 September 97	30	25	46.687	31.887	57.949	51.967	32.944	7.305	0	0	0	1.273	16.128	0.958
16 October 97	35	23	33.296	6.361	213.944	27.541	14.537	4.379	0	0	0	0.168	0.716	0.610
12 November 97	27	14	18.939	34.175	3.227	4.324	9.378	3.695	0	0	0	0.831	0.422	0
11 December 97	29	9	0.188	8.078	1.540	14.344	10.460	2.659	0.016	0	0	0	0.152	0.092
26 January 98	46	7	0	0	0	15.790	8.491	0.222	0.602	0.339	0.353	0.122	0.061	0
27 February 98	32	8	0	0.956	0	12.599	19.804	0.478	3.092	1.878	4.546	0.238	0.034	0.616
27 March 98	28	11	9.311	1.536	0.196	11.513	9.038	3.508	9.935	9.163	14.180	2.271	0.182	1.152
27 April 98	31	16	23.022	15.736	30.812	18.061	35.217	19.101	37.752	20.399	24.072	5.146	1.141	3.719
29 May 98	32	21	27.865	1.788	78.410	18.973	15.490	0.398	52.481	0.876	63.936	6.565	3.049	4.671

			Crassostrea virginica			*Palaeomonetes vulgaris*			*Gammurus mucronatus*			Total Community		
Interval Ending	No. of days	water temperature	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER	ASH	CLAM	OYSTER
11 June 97	33	24	0	27.598	<0.001	0	0	0	0.043	0	1.026	44.800	115.678	76.579
7 July 97	25	25	0	61.608	2.405	0	0	7.678	1.036	0.199	0.182	34.702	186.171	88.995
12 August 97	36	27	8.875	1.392	14.608	0	0	0	0	0	0	124.596	74.893	92.861
11 September 97	30	25	8.707	8.611	1.986	0	0	0	0	0	0	110.793	94.425	207.948
16 October 97	35	23	6.104	6.985	1.073	0	0	59.520	0	0	0	70.123	39.476	282.335
12 November 97	27	14	0	0	0	9.240	7.829	28.710	0	0	0	36.457	54.997	36.072
11 December 97	29	9	0	0	0	<0.001	<0.001	7.348	0	0	0	14.748	19.300	12.036
26 January 98	46	7	0.148	1.510	<0.001	<0.001	<0.001	0	0.228	0.226	0	21.098	10.869	1.430
27 February 98	32	8	0.017	0	0	<0.001	<0.001	0	5.135	0.987	18.090	23.322	26.156	41.639
27 March 98	28	11	0	0	0	<0.001	<0.001	0	0	0	0	34.029	20.438	24.916
27 April 98	31	16	0	0	0.785	<0.001	<0.001	6.948	0	0	0	96.119	74.994	86.760
29 May 98	32	21	0	9.657	0	<0.001	<0.001	0	3.564	0	0.038	117.803	44.629	162.271

Table 10: Contribution of numerically and biomass dominant species and feeding groups to total average annual reef community production rates from constructed reef habitats at Fisherman's Island (g AFDW m^{-2} $year^{-1}$). Percentages of total reef production are given in parentheses.

	ASH	CLAM	OYSTER
By taxa			
Panopeus herbstii	6.78 (31)	5.66 (24)	16.17 (48)
Palaeomonetes vulgaris	0.28 (1)	0.24 (1)	3.35 (10)
Melita nitida	7.04 (32)	6.37 (27)	1.54 (5)
Gammurus mucronatus	0.30 (1)	0.04 (<1)	0.59 (2)
Crassostrea virginica	0.73 (3)	3.57 (15)	0.63 (2)
Mytilus edulis	3.32 (15)	1.04 (5)	3.84 (11)
Nereis succinea	1.00 (5)	4.49 (19)	0.54 (2)
Other	2.71 (12)	1.77 (8)	7.21 (21)
By feeding group			
Carnivores	7.08 (32)	6.52 (28)	17.60 (52)
Omnivores & scavengers	9.34 (42)	11.28 (49)	10.68 (32)
Deposit feeders / herbivores/ detritivores	0.51 (2)	0.31 (1)	0.92 (3)
Suspension feeders	5.23 (24)	5.07 (22)	4.68 (14)

Table 11: Sample clusters selected from numerical classification of macrobenthic organisms collected monthly from the intertidal region of reefs of each substrate type at Fisherman's Island.

Sample Cluster 1

Ash	June
Clam	June
Clam	July
Oyster	July

Sample Cluster 2

Ash	July
Oyster	June

Sample Cluster 3

Ash	August
Ash	September
Ash	October
Clam	August
Clam	September
Ash	December
Clam	November
Clam	December
Clam	October

Sample Cluster 4

Oyster	August
Oyster	September

Sample Cluster 5

Ash	November
Oyster	October
Oyster	November
Oyster	December

Sample Cluster 6

Ash	January
Clam	January
Ash	May
Clam	April
Clam	May
Oyster	April

Sample Cluster 7

Ash	February
Clam	February
Ash	March
Clam	March
Ash	April
Oyster	March
Oyster	February

Sample Cluster 8

Oyster	January
Oyster	May

Table 12: Species clusters selected from numerical classification of macrobenthic organisms collected monthly from the intertidal region of reefs of each substrate type at Fisherman's Island.

Species Cluster A
Alpheus heterochaelis
Dulichiella appendiculata

Species Cluster B
Ensis directus
Glycera americana
Uca spp.

Species Cluster C
Anadara transversa
Molgula manhattiensis
Erichthonius brasiliensis
Geukensia demissa

Species Cluster D
Caprella pentatus
Crepidula convexa
Palaeomonetes vulgaris
Retusa canaliculata

Species Cluster E
Corophium spp.
Diadumene leucolena
Ilyanassa obsoletus

Species Cluster F
Ampithoe valida
Gammurus palustris
Gammurus mucronatus
Mitrella lunata
Polydora websteri
Streblospio benedicti

Species Cluster G
Heteromastus filiformis
Podarke obscura

Species Cluster H
Balanus improvisus
Crassostrea virginica
Nereis succinea
Panopeus herbstii
Mercenaria mercenaria
Tellina spp.
Spisula solidissima

Species Cluster I
Melita nitida
Mytilus edulis

Species Cluster J
Collembola spp.
Corophium acherusicum
Eteone heteropoda
Skenopsis planorbis
Eurypanopeus depressus

Species Cluster K
Anachis obesa
Doridella obscura
Cymedusa compta

Species Cluster L
Dyspanopeus sayi
Sphaeroma quadradentatum

Species Cluster M
Bittium varium
Paracaprella tenuis
Nemertean sp.
Odostomia spp.
Stylochus ellipticus

Species Cluster N
Anadara ovalis
Callinectes sapidus
Hydroides dianthus
Anomia simplex
Stenothoe minuta
Lepidonotus sublevis
Odostomia impressa

Figure 1: Location of created oyster reef study area near Fisherman's Island at the mouth of Chesapeake Bay.

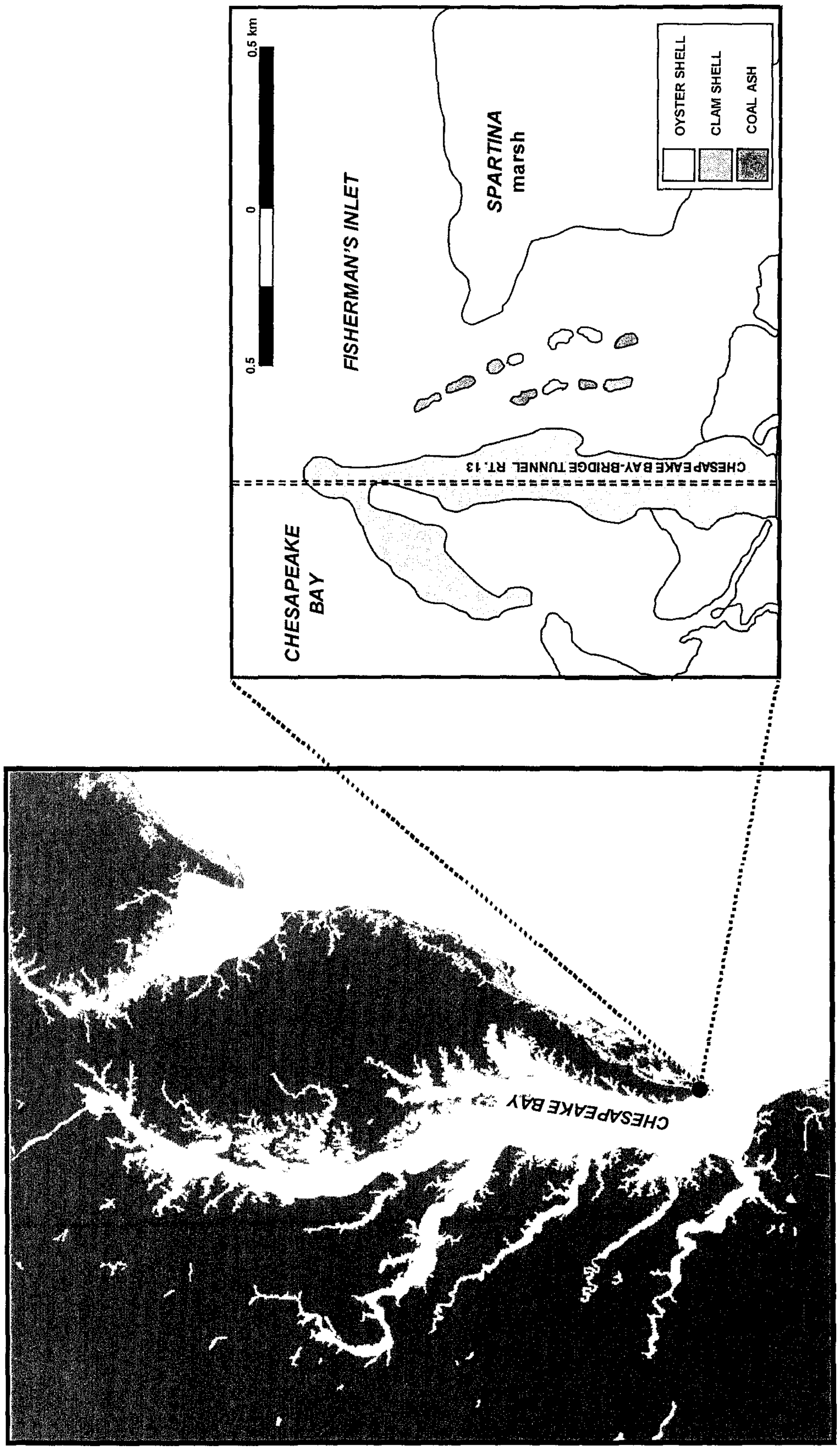

0.5
0
0.5 km
FISHERMAN'S INLET
SPARTINA marsh
OYSTER SHELL
CLAM SHELL
COAL ASH
CHESAPEAKE BAY
CHESAPEAKE BAY-BRIDGE TUNNEL RT. 13
CHESAPEAKE BAY

Figure 2: Water temperature (●) and salinity (□) measurements from Fisherman's Island constructed reef area from May 1997 to July 1998.

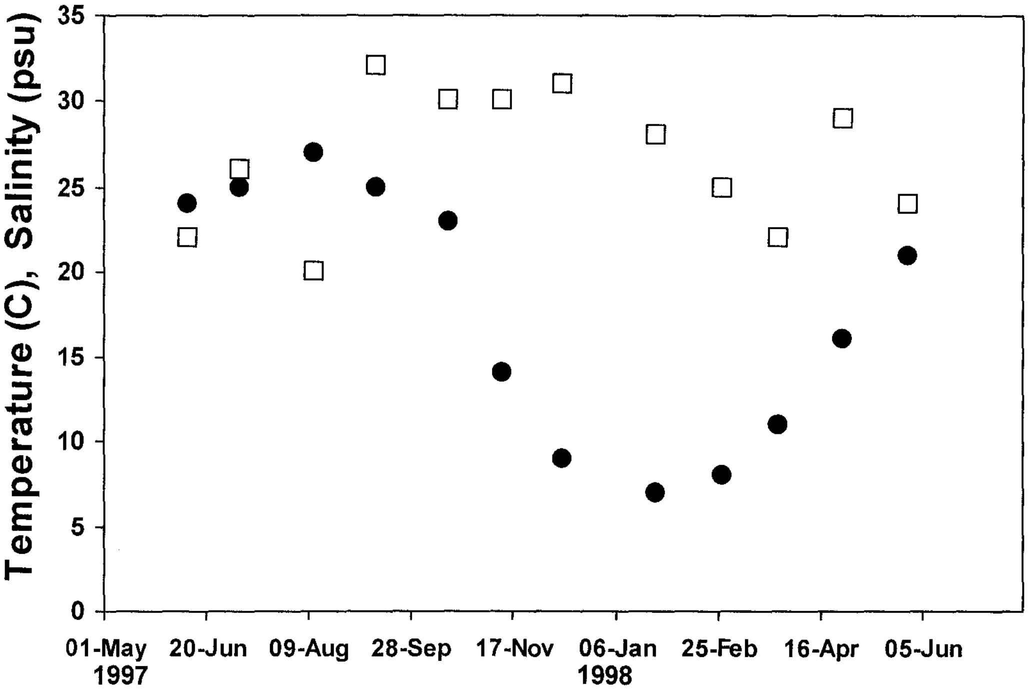

Temperature (C), Salinity (psu)
35
30
25
20
15
10
5
0
01-May 1997
20-Jun
09-Aug
28-Sep
17-Nov
06-Jan 1998
25-Feb
16-Apr
05-Jun

Figure 3: Mean dry weight (g 0.06 m^{-2} basket) of macroalgae collected from the intertidal region of each constructed reef type (pelletized coal ash, clam shell, and oyster shell) during Summer (June, July, and August 1997), Fall (September, October, and November 1997), Winter (December 1997, January and February 1998), and Spring (March, April, and May 1998). No algae was recovered from any of the clam shell samples collected during the summer, as indicated by the "0" in place of the bar on the figure.

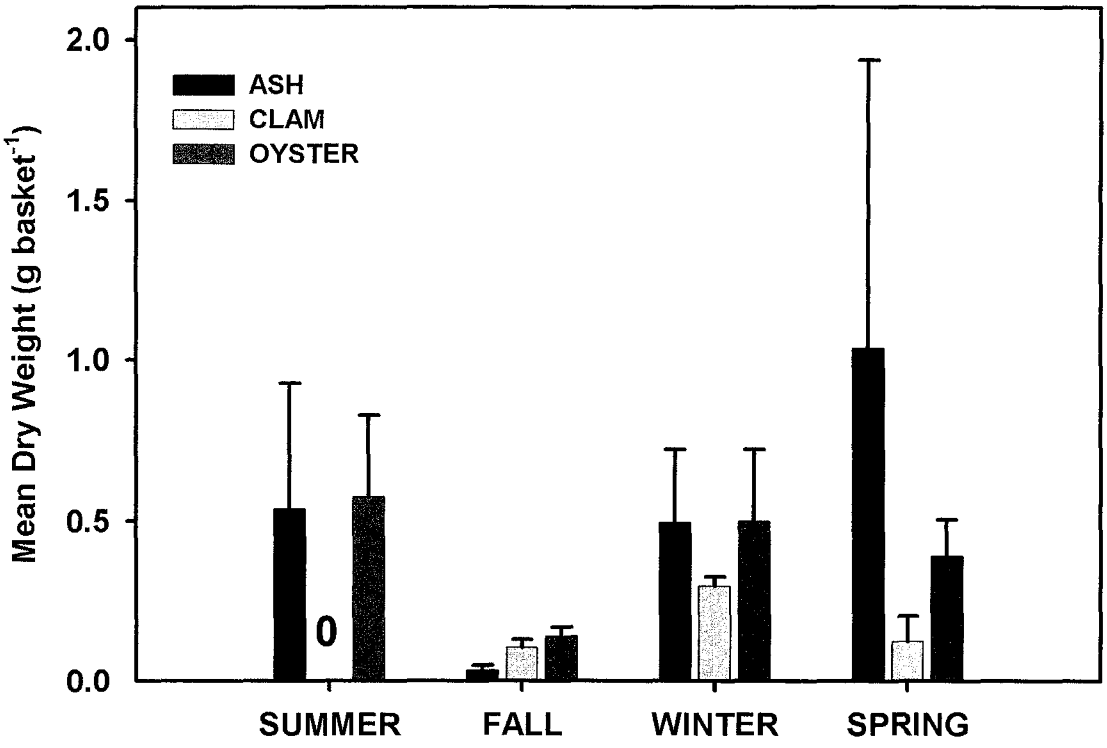

Mean Dry Weight (g basket^{-1})
2.0
1.5
1.0
0.5
0.0
ASH
CLAM
OYSTER
0
SUMMER
FALL
WINTER
SPRING

Figure 4 a, b: Mean macrobenthic community abundance (number per 0.06 m^{-2} substrate basket ± SE) and biomass (mg AFDW) for the intertidal region of the three reef types from June 1997 to May 1998 (n = 3).

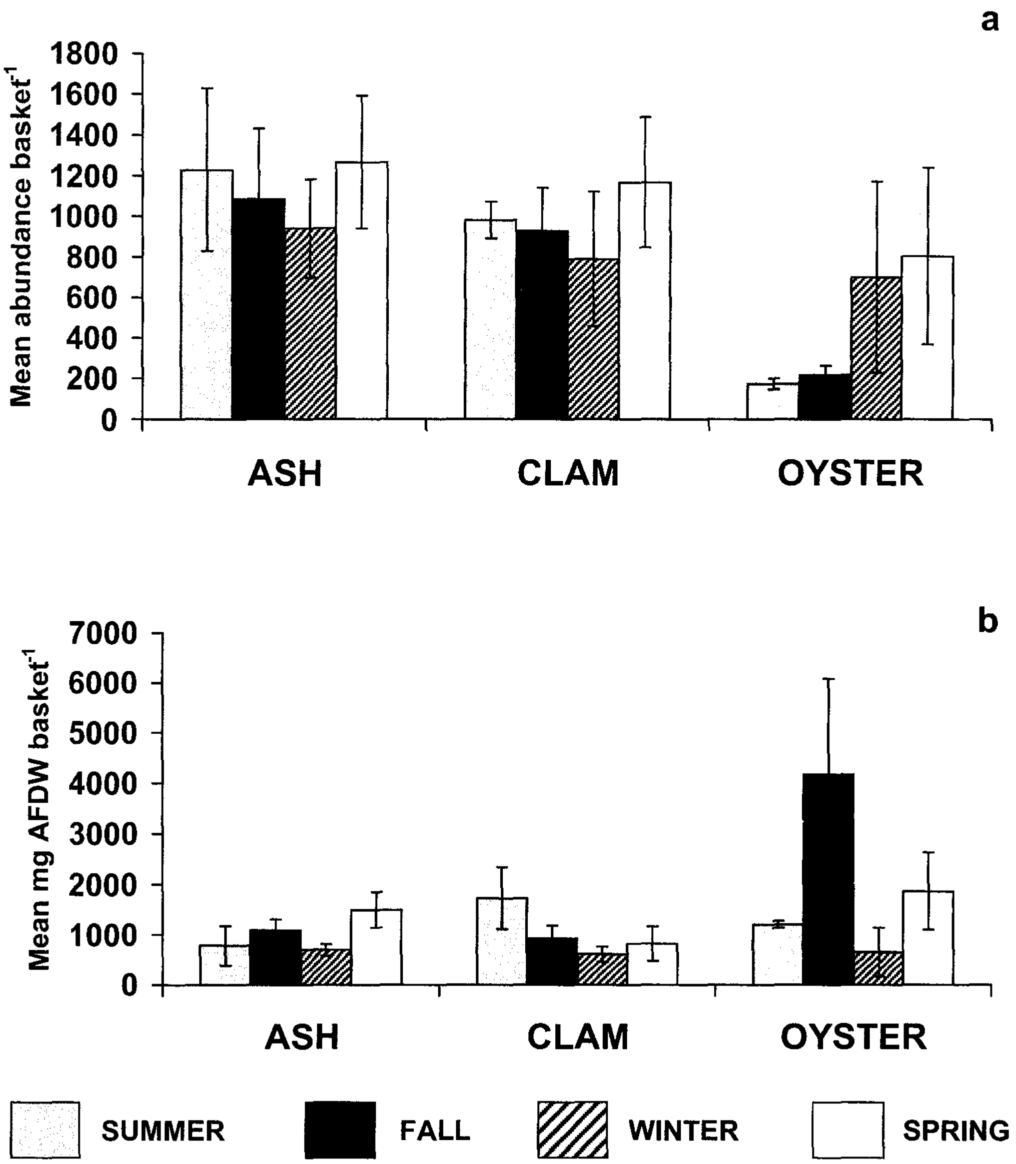

a
Mean abundance basket^{-1}
1800
1600
1400
1200
1000
800
600
400
200
0
ASH
CLAM
OYSTER
b
Mean mg AFDW basket^{-1}
7000
6000
5000
4000
3000
2000
1000
0
ASH
CLAM
OYSTER
SUMMER
FALL
WINTER
SPRING

Figure 5 a, b: Mean macrobenthic abundance (number per 0.06 m^{-2} substrate basket ± SE) and biomass (mg AFDW) for motile species only from the intertidal region of the three reef types from June 1997 to May 1998 (n = 3).

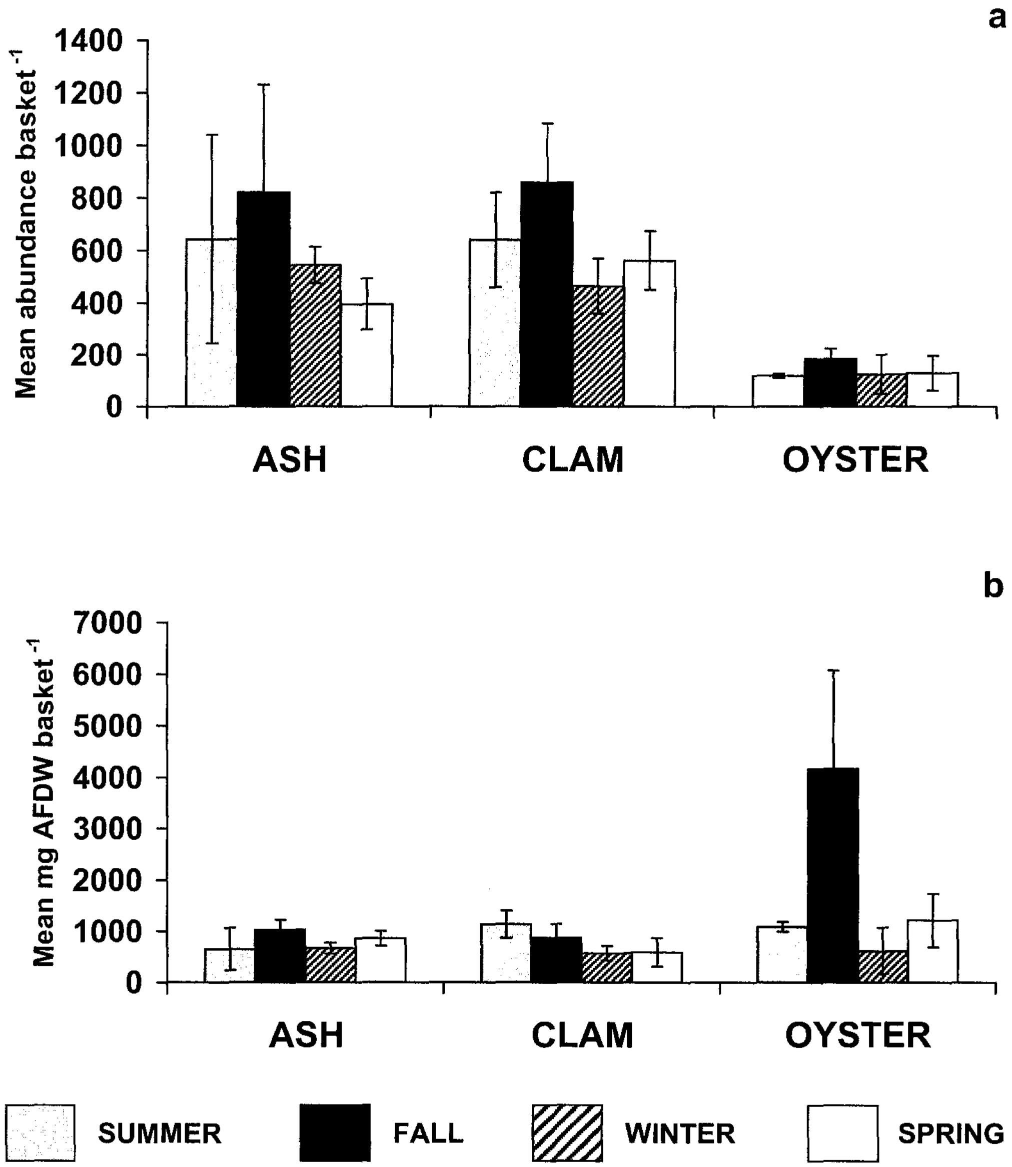

a
Mean abundance basket⁻¹
1400
1200
1000
800
600
400
200
0
ASH
CLAM
OYSTER
b
Mean mg AFDW basket⁻¹
7000
6000
5000
4000
3000
2000
1000
0
ASH
CLAM
OYSTER
SUMMER
FALL
WINTER
SPRING

Figure 6 a, b: Mean macrobenthic abundance (number per 0.06 m^{-2} substrate basket ± SE) and biomass (mg AFDW) for sessile and sedentary species only from the intertidal region of the three reef types from June 1997 to May 1998 ($n = 3$).

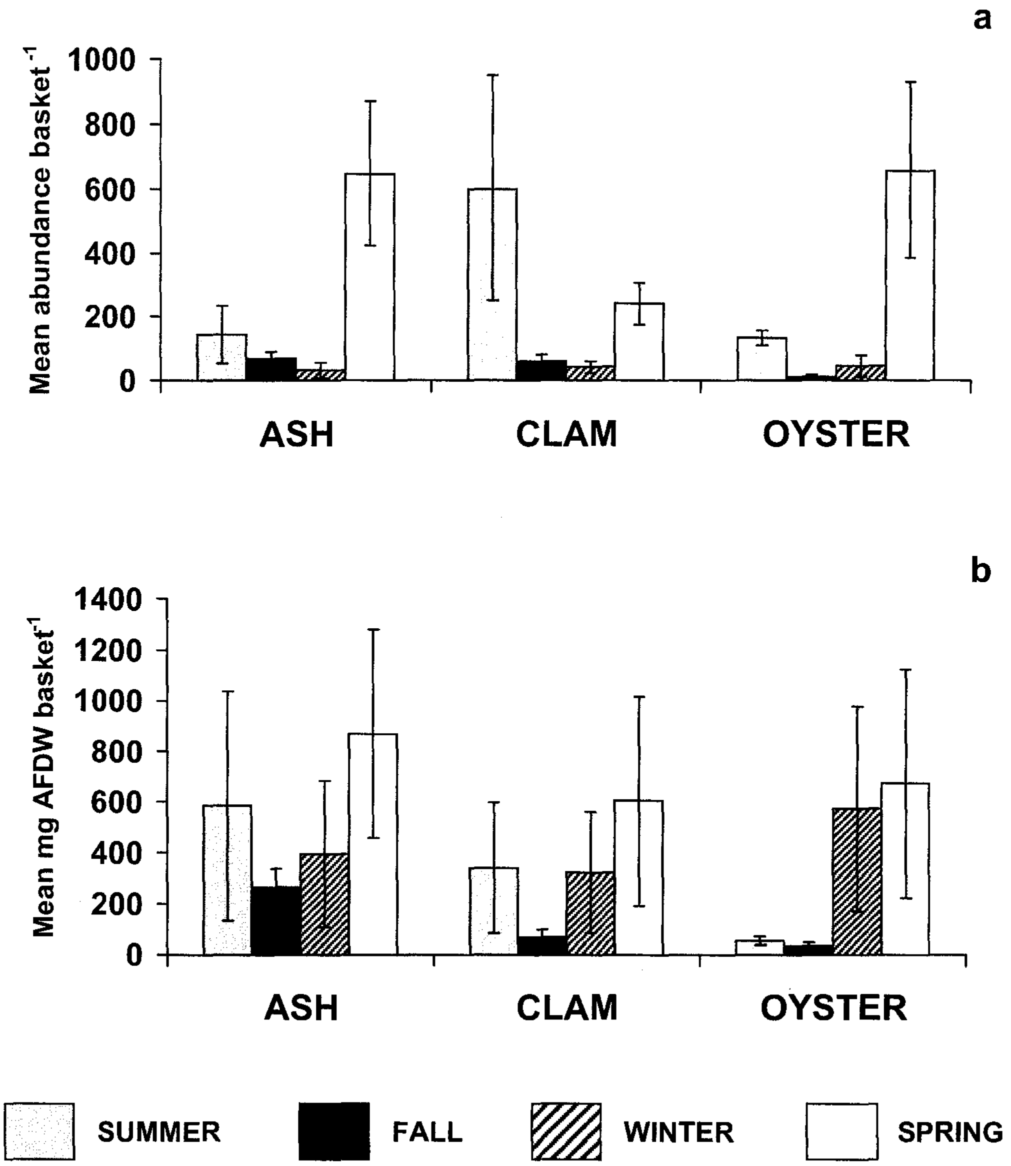

a
Mean abundance basket^{-1}
0
200
400
600
800
1000
ASH
CLAM
OYSTER
b
Mean mg AFDW basket^{-1}
0
200
400
600
800
1000
1200
1400
ASH
CLAM
OYSTER
SUMMER
FALL
WINTER
SPRING

Figure 7: Abundance (mean per 0.06 m^{-2} basket ± SE) of the numerical and biomass dominants from each reef substrate type from June 1997 to May 1998 ($n = 3$). When ANOVA revealed significant differences ($\log_{10}$ (Abundance + 1), $P < 0.05$), results of Tukey multiple comparisons for reef type (A – coal ash, C – clam shell, O – oyster shell) and season (Sp – Spring, Su – Summer, F – Fall, W – Winter) are illustrated for each species. Underlined factor levels and those with underlines that overlap are not statistically different.

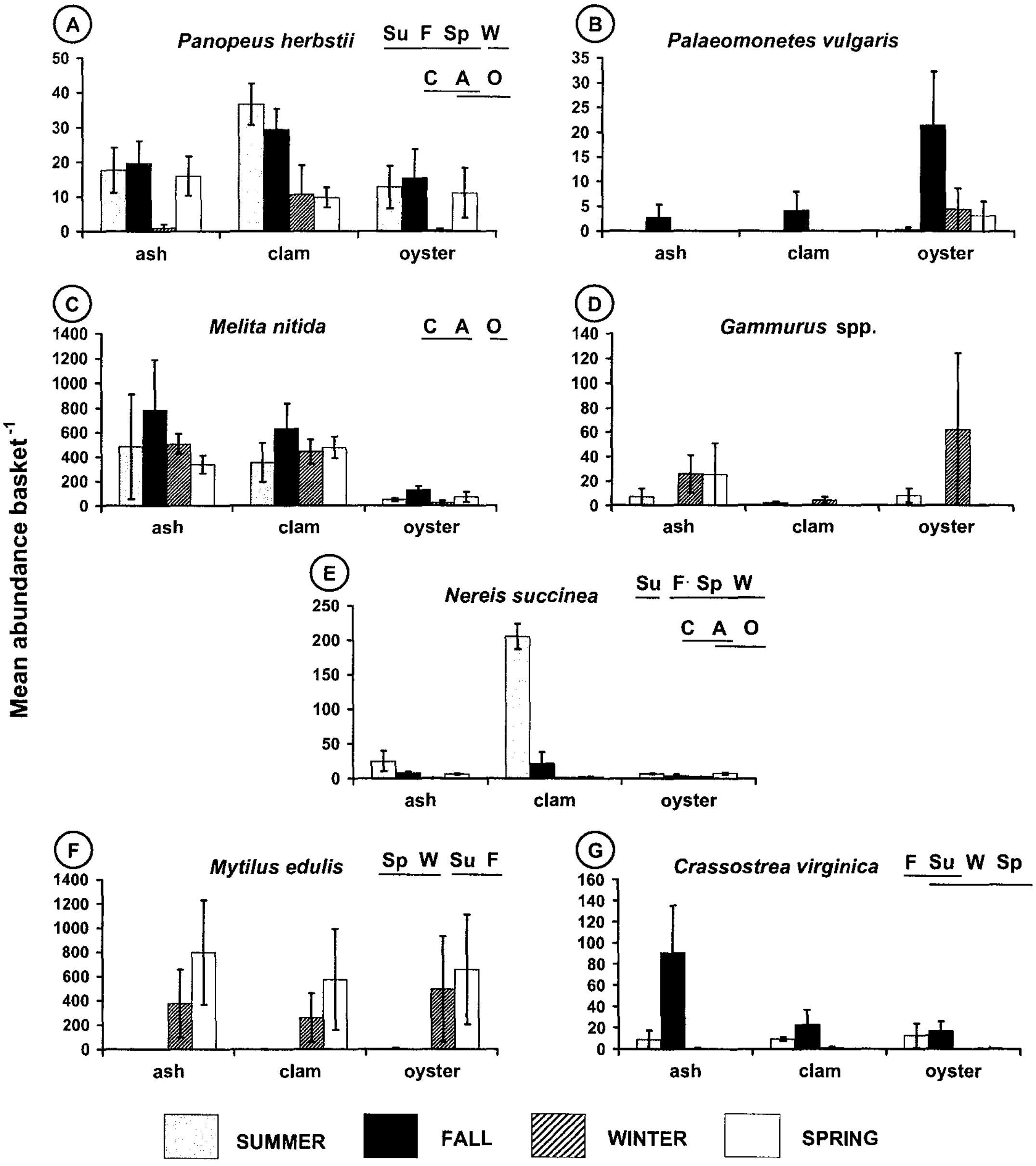

Mean abundance basket⁻¹
A
Panopeus herbstii
Su F Sp W
C A O
50
40
30
20
10
0
ash
clam
oyster
B
Palaeomonetes vulgaris
35
30
25
20
15
10
5
0
ash
clam
oyster
C
Melita nitida
C A O
1400
1200
1000
800
600
400
200
0
ash
clam
oyster
D
Gammurus spp.
140
120
100
80
60
40
20
0
ash
clam
oyster
E
Nereis succinea
Su F Sp W
C A O
250
200
150
100
50
0
ash
clam
oyster
F
Mytilus edulis
Sp W Su F
1400
1200
1000
800
600
400
200
0
ash
clam
oyster
G
Crassostrea virginica
F Su W Sp
160
140
120
100
80
60
40
20
0
ash
clam
oyster
SUMMER
FALL
WINTER
SPRING

Figure 8: Biomass (mean mg AFDW per 0.06 m^{-2} basket ± SE) of the numerical and biomass dominants from each reef substrate type from June 1997 to May 1998 ($n = 3$). When ANOVA revealed significant differences ($\log_{10}$ (Biomass + 1), $P < 0.05$), results of Tukey multiple comparisons for reef type (A – coal ash, C – clam shell, O – oyster shell) and season (Sp – Spring, Su – Summer, F – Fall, W – Winter) are illustrated for each species. Underlined factor levels and those with underlines that overlap are not statistically different.

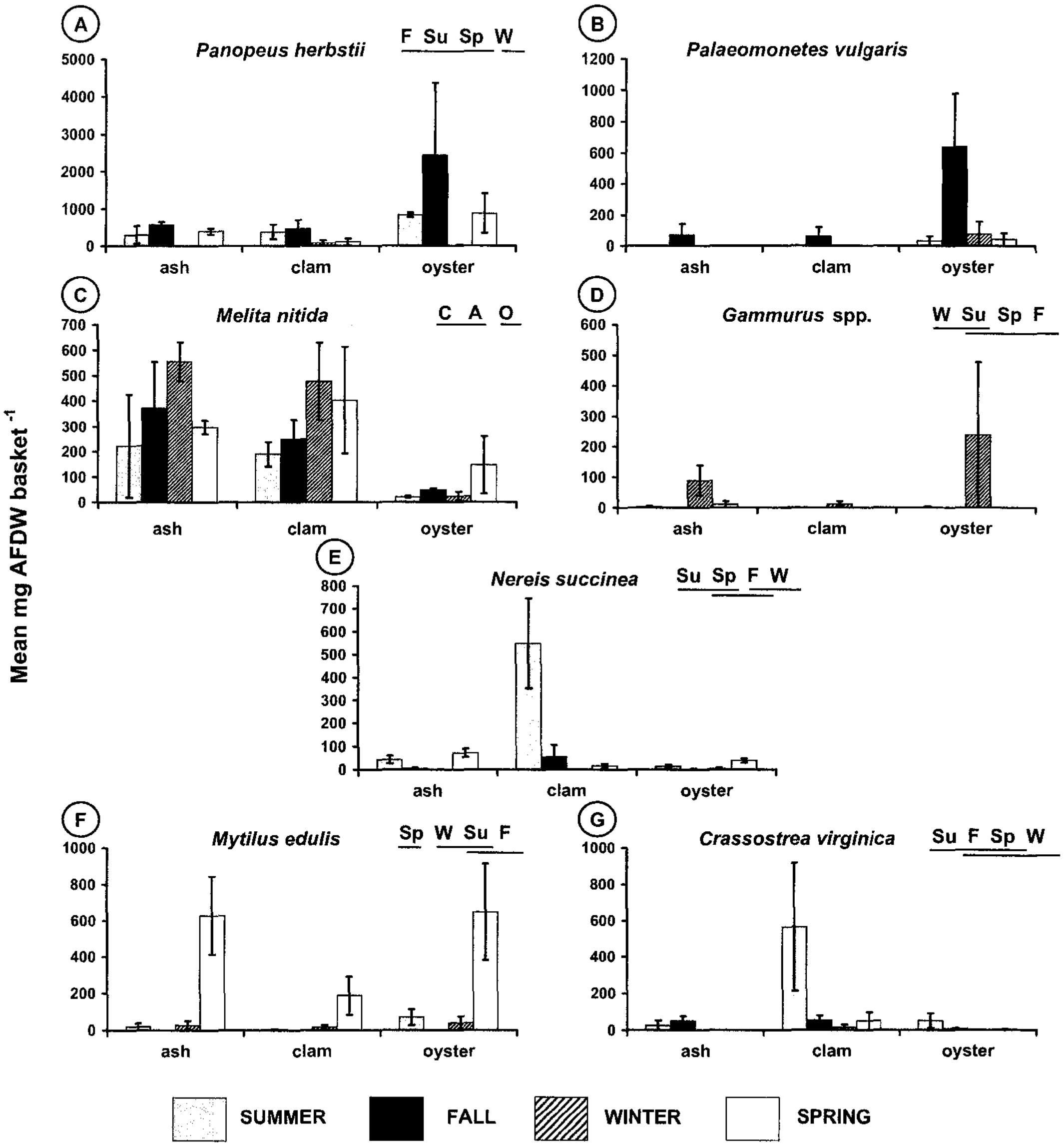

A
Panopeus herbstii
F Su Sp W
5000
4000
3000
2000
1000
0
ash
clam
oyster
B
Palaeomonetes vulgaris
1200
1000
800
600
400
200
0
ash
clam
oyster
C
Melita nitida
C A O
700
600
500
400
300
200
100
0
ash
clam
oyster
D
Gammurus spp.
W Su Sp F
600
500
400
300
200
100
0
ash
clam
oyster
Mean mg AFDW basket -1
E
Nereis succinea
Su Sp F W
800
700
600
500
400
300
200
100
0
ash
clam
oyster
F
Mytilus edulis
Sp W Su F
1000
800
600
400
200
0
ash
clam
oyster
G
Crassostrea virginica
Su F Sp W
1000
800
600
400
200
0
ash
clam
oyster
SUMMER
FALL
WINTER
SPRING

Figure 9: Size frequency distribution of all panopeid crabs (*Panopeus herbstii*: n = 540, mean carapace width = 6.8 mm; *Eurypanopeus depressus* n = 52, mean carapace width = 6.6 mm; and *Dyspanopeus sayi* n = 4, mean carapace width = 8.2 mm) collected from the three reef types at Fisherman's Island, June 1997 – May 1998.

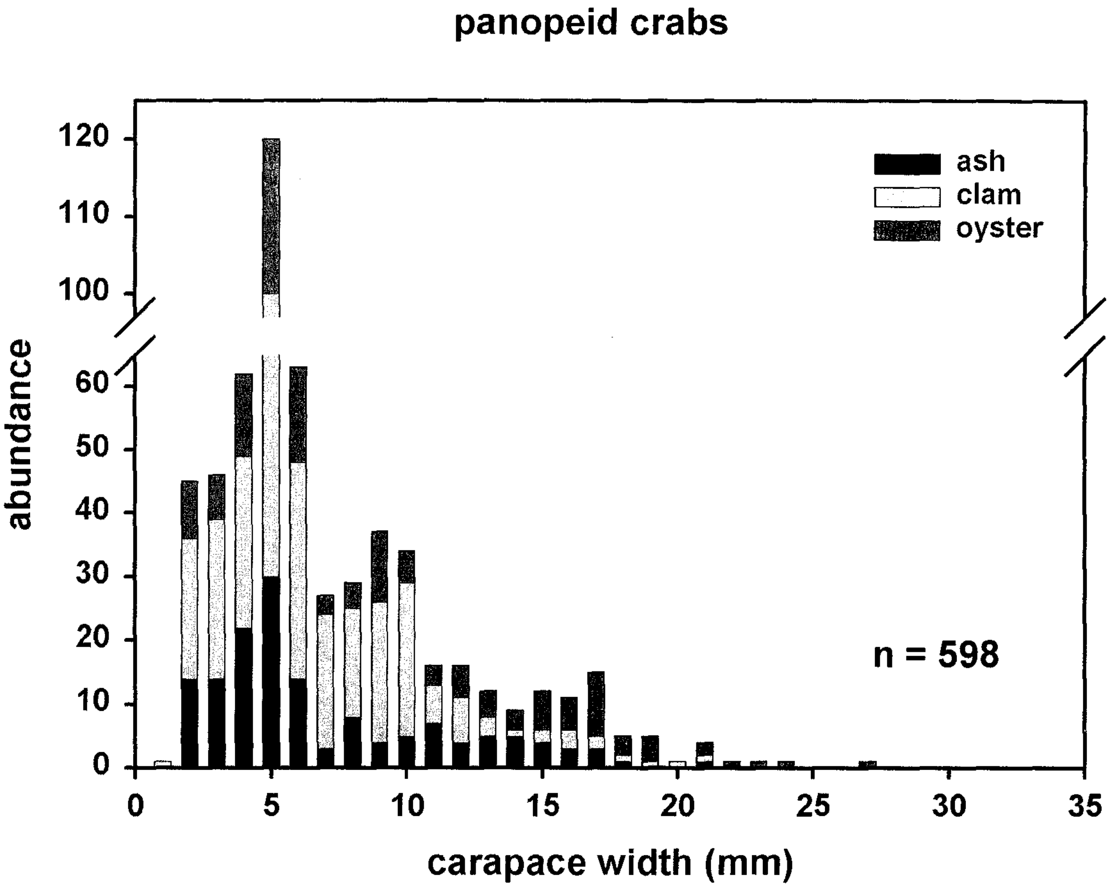

panopeid crabs
abundance
120
110
100
60
50
40
30
20
10
0
ash
clam
oyster
n = 598
0
5
10
15
20
25
30
35
carapace width (mm)

Figure 10: Distribution of macrofaunal feeding types across season and reef type. Bars represent the percentage of individuals within each feeding type category.

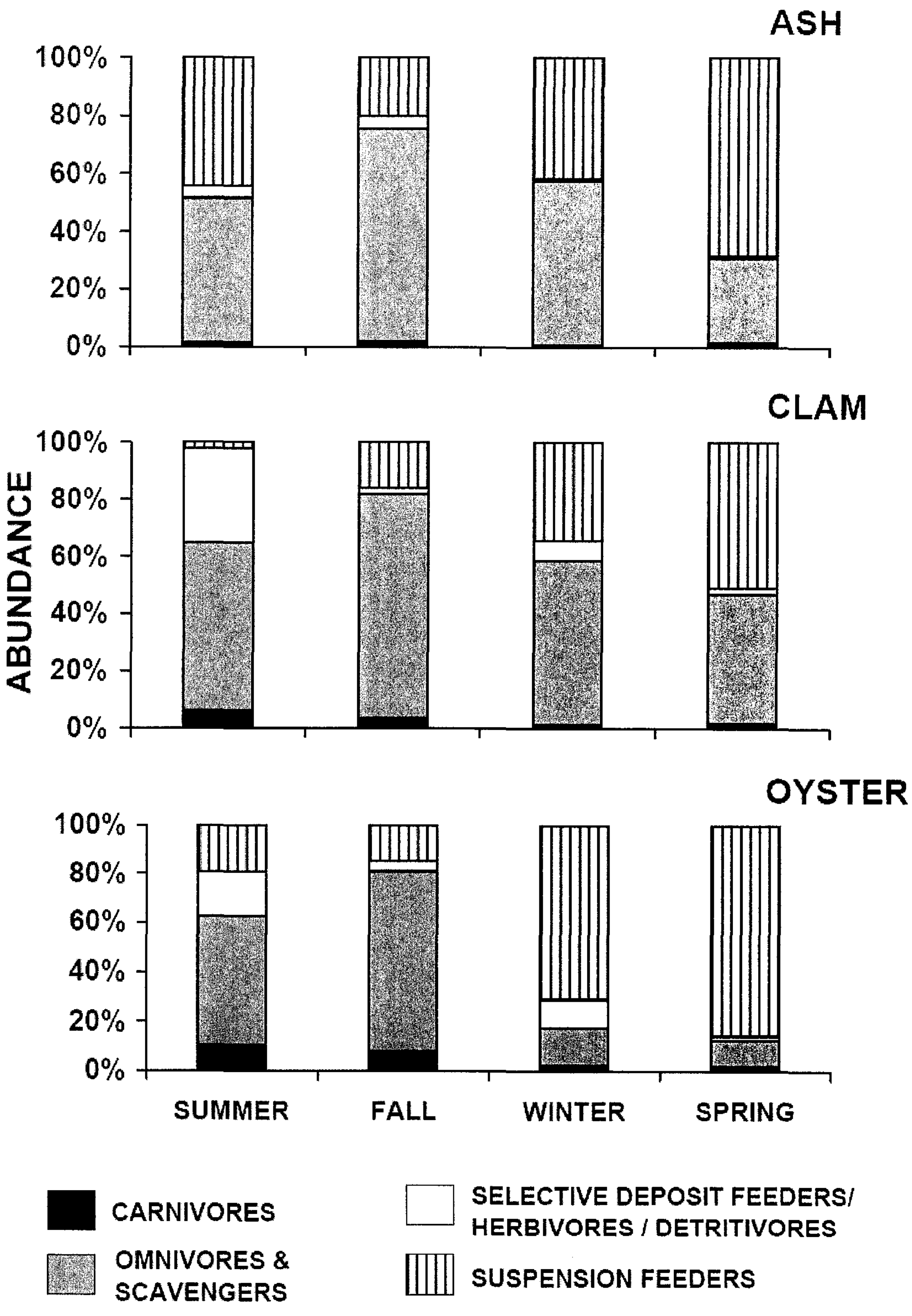

ASH
CLAM
OYSTER
ABUNDANCE
100%
80%
60%
40%
20%
0%
SUMMER
FALL
WINTER
SPRING
CARNIVORES
OMNIVORES & SCAVENGERS
SELECTIVE DEPOSIT FEEDERS/ HERBIVORES / DETRITIVORES
SUSPENSION FEEDERS

Figure 11: Distribution of macrofaunal feeding types across season and reef type. Bars represent the percentage of total biomass within each feeding type category.

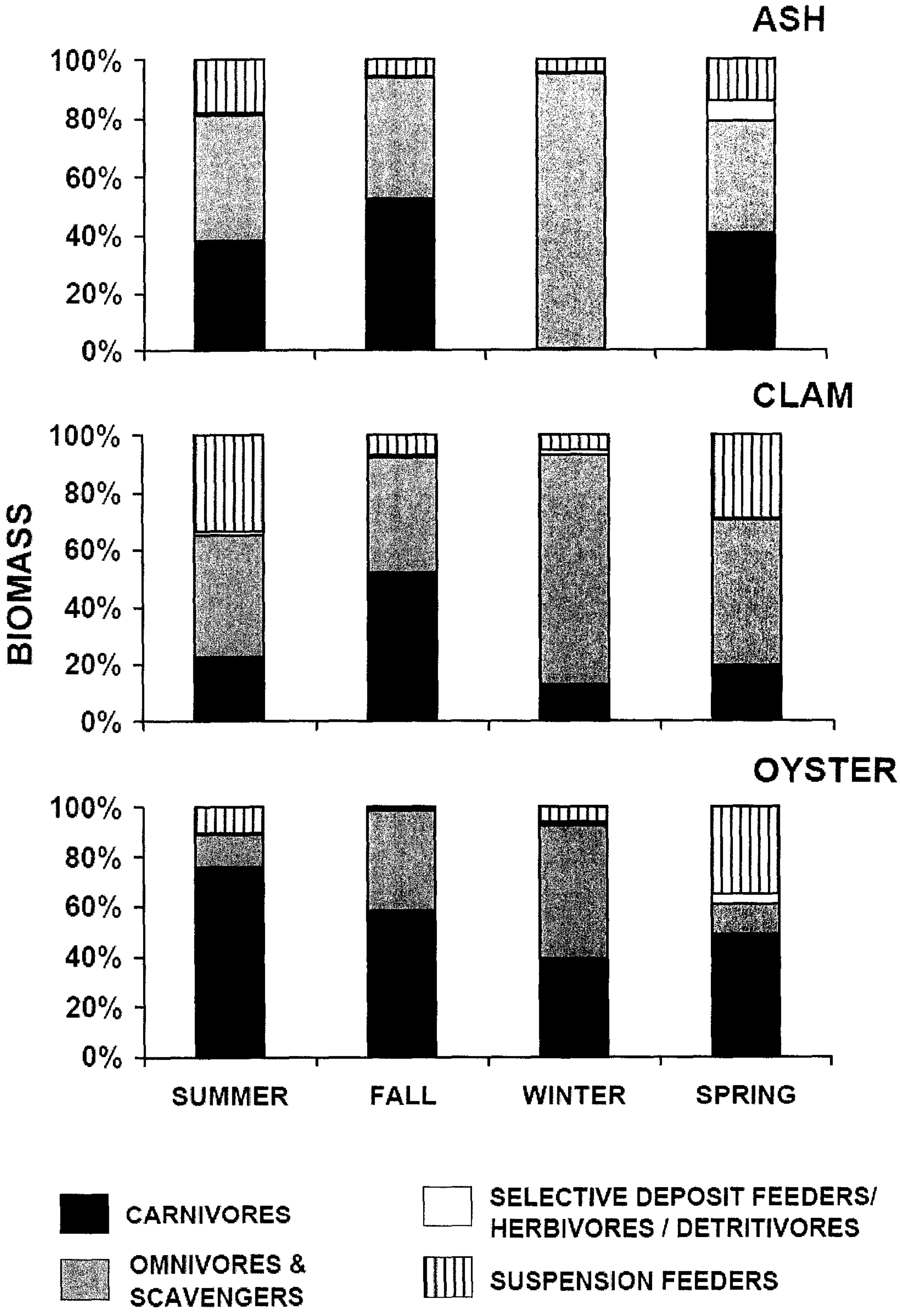

ASH
CLAM
OYSTER
BIOMASS
100%
80%
60%
40%
20%
0%
SUMMER
FALL
WINTER
SPRING
CARNIVORES
OMNIVORES & SCAVENGERS
SELECTIVE DEPOSIT FEEDERS/ HERBIVORES / DETRITIVORES
SUSPENSION FEEDERS

Figure 12: Size frequency distribution of all *Mytilus edulis* collected from each reef type at Fisherman's Island, June 1997 – May 1998.

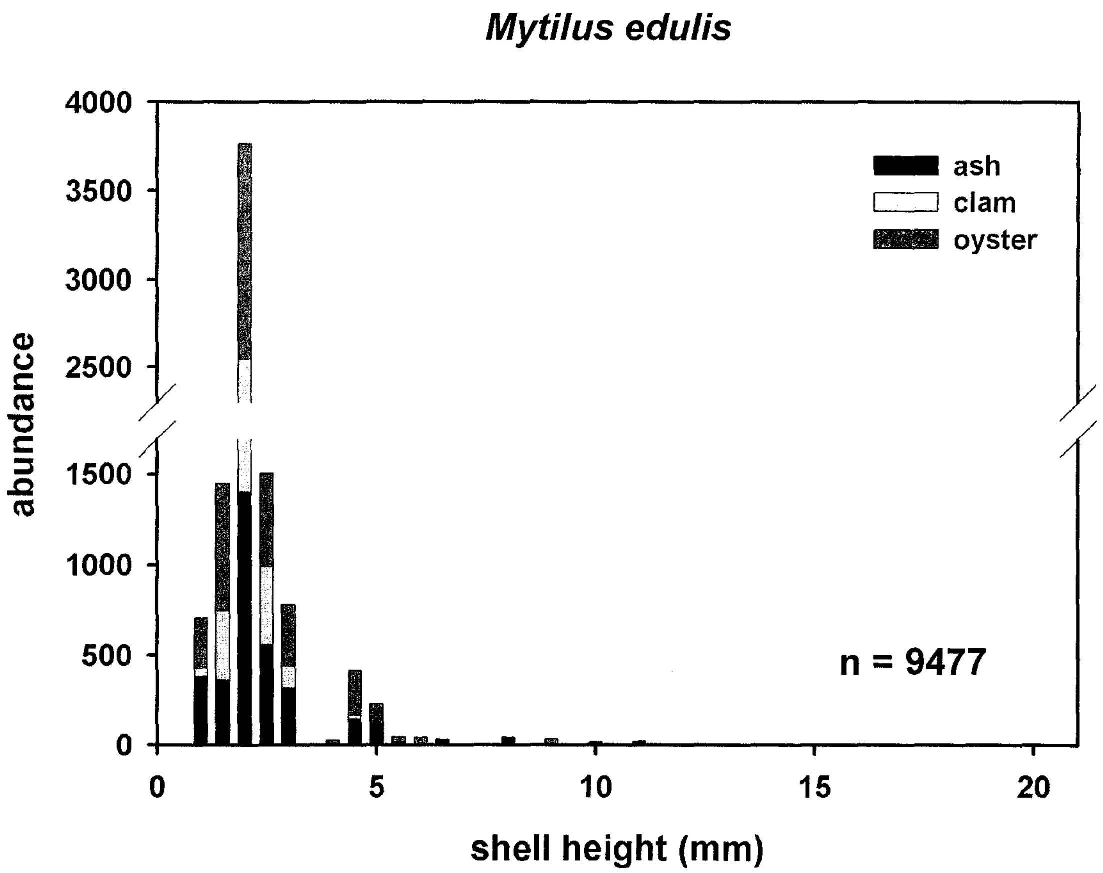

Mytilus edulis
abundance
4000
3500
3000
2500
1500
1000
500
0
0
5
10
15
20
shell height (mm)
ash
clam
oyster
n = 9477

Figure 13: Size frequency distribution of all oysters (*Crassostrea virginica*) collected from each reef type at Fisherman's Island, June 1997 – May 1998.

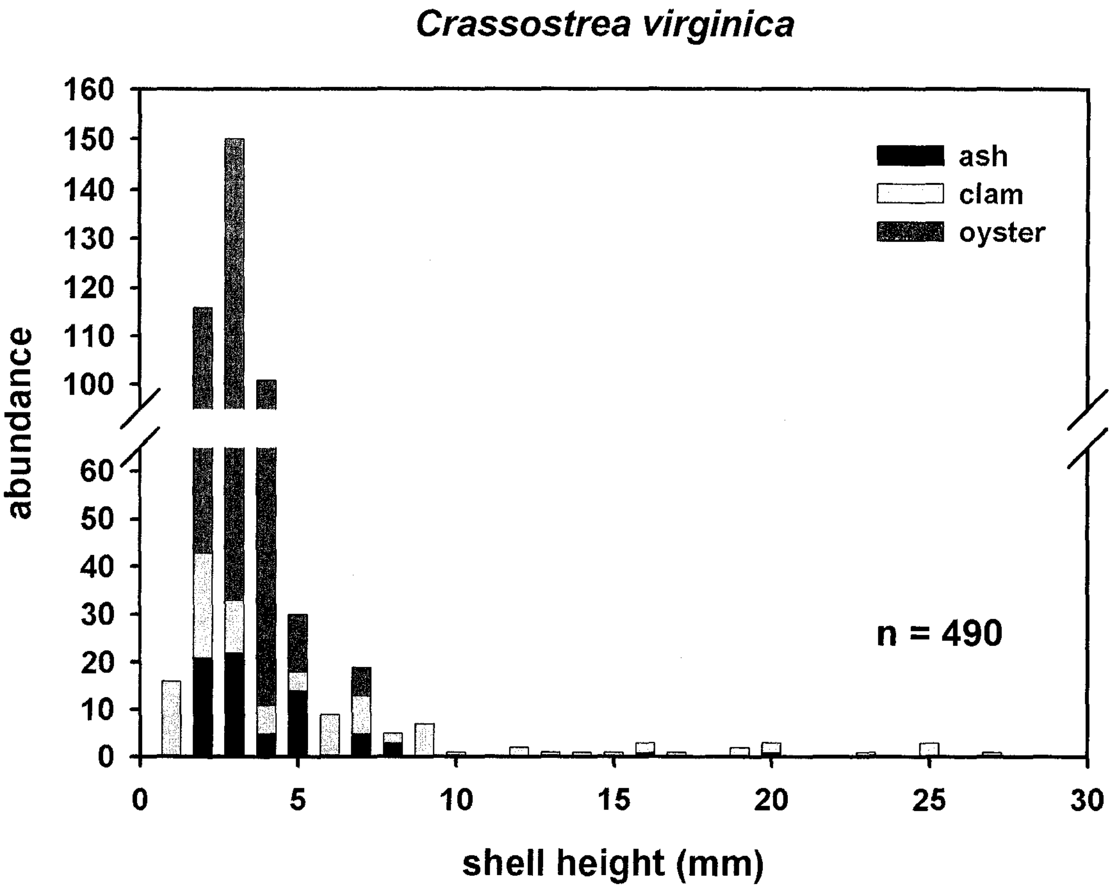

Crassostrea virginica
abundance
160
150
140
130
120
110
100
60
50
40
30
20
10
0
0
5
10
15
20
25
30
shell height (mm)
ash
clam
oyster
n = 490

Figure 14: Distribution of macrofaunal dispersal types across reef type. Bars represent (A) the percent of taxa (the number to the right of the bar is the total number of taxa of the category collected), (B) total abundance of individuals, and (C) total biomass for each dispersal type category.

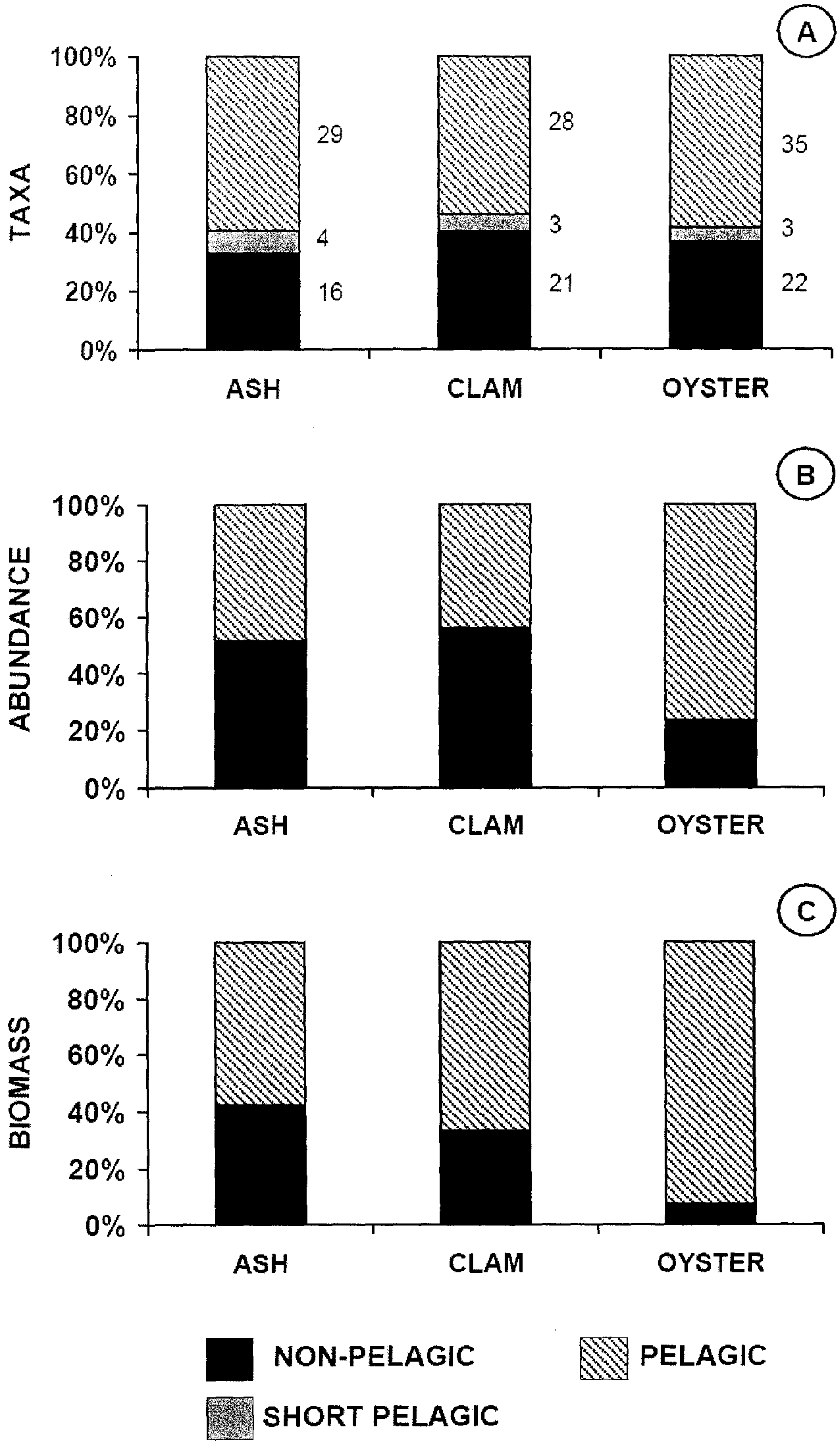

A
TAXA
100%
80%
60%
40%
20%
0%
29
4
16
28
3
21
35
3
22
ASH
CLAM
OYSTER
B
ABUNDANCE
100%
80%
60%
40%
20%
0%
ASH
CLAM
OYSTER
C
BIOMASS
100%
80%
60%
40%
20%
0%
ASH
CLAM
OYSTER
NON-PELAGIC
PELAGIC
SHORT PELAGIC

Figure 15: A: Species richness (number of species, *S*), B: Shannon's diversity (*H'*), C: Simpson's Index (*1-λ*), and D: Pielou's evenness (*J'*) for each reef type.

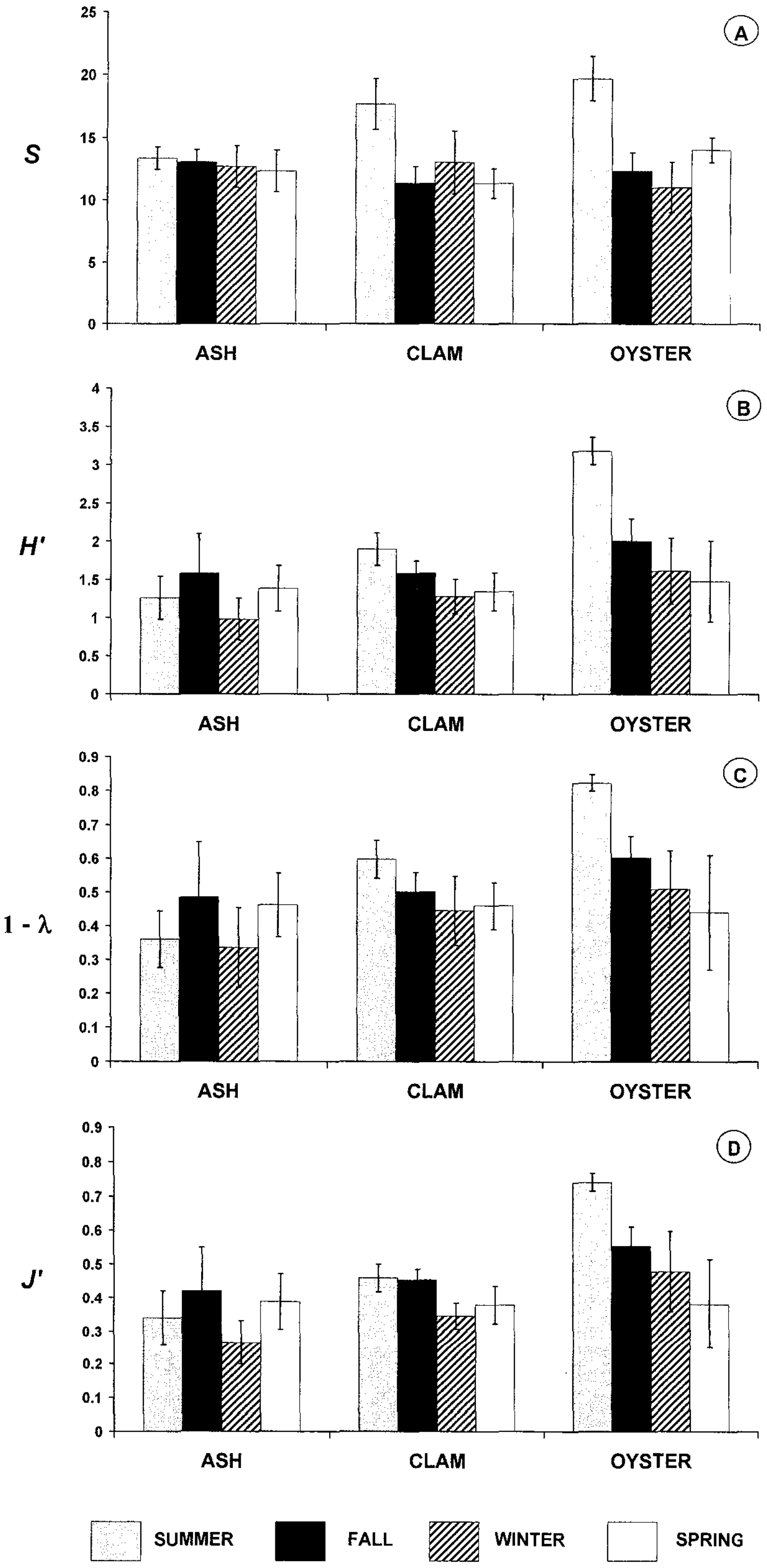

S
25
20
15
10
5
0
A
ASH
CLAM
OYSTER
H'
4
3.5
3
2.5
2
1.5
1
0.5
0
B
ASH
CLAM
OYSTER
1 - λ
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
C
ASH
CLAM
OYSTER
J'
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
D
ASH
CLAM
OYSTER
SUMMER
FALL
WINTER
SPRING

Figure 16: Distribution of macrofaunal feeding types across season and reef type. Bars represent the percentage of taxa within each feeding type category and the number to the right of the bar is the total number of taxa of the category collected.

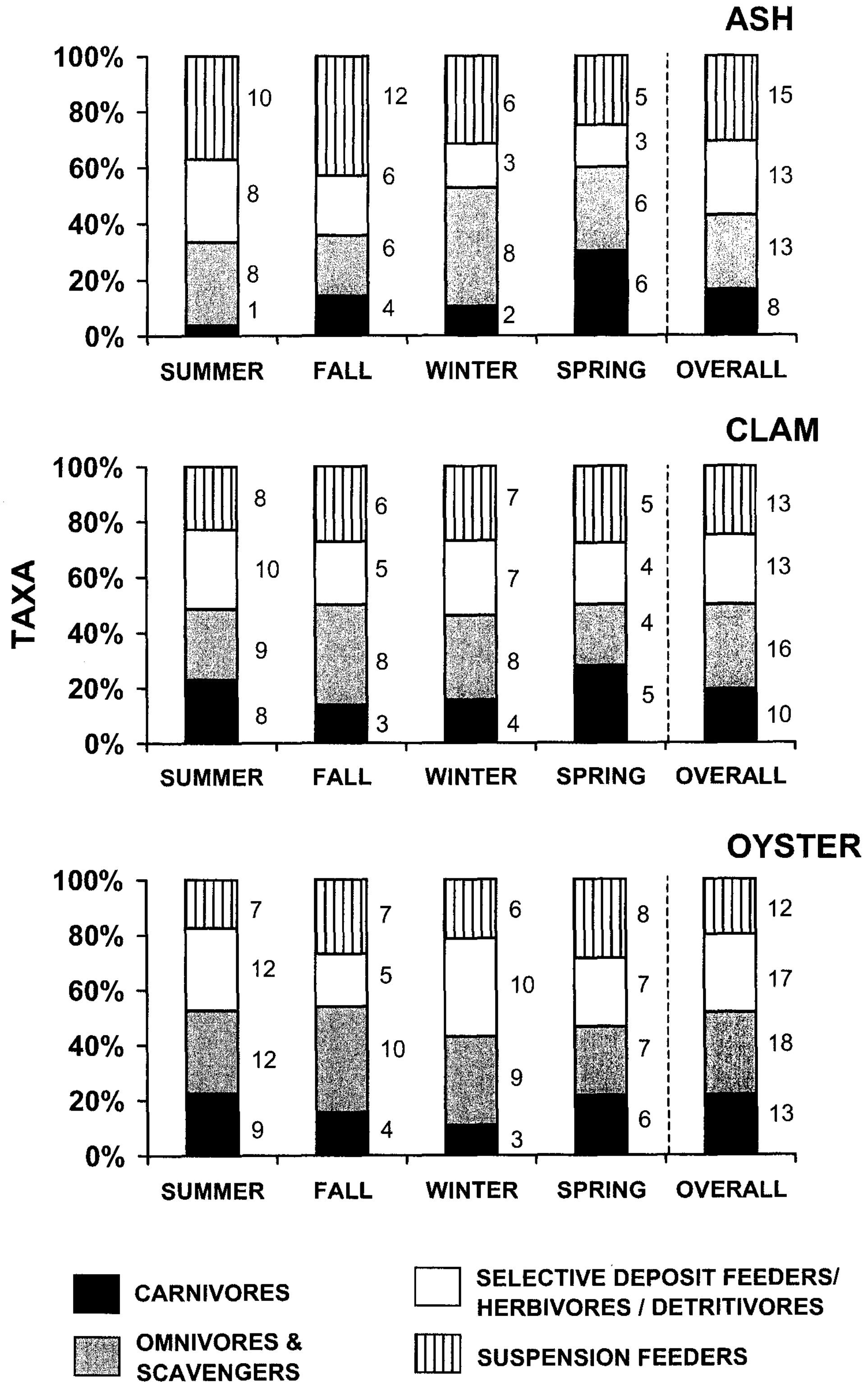

ASH
100%
80%
60%
40%
20%
0%
SUMMER 10 8 8 1
FALL 12 6 6 4
WINTER 6 3 8 2
SPRING 5 3 6 6
OVERALL 15 13 13 8
CLAM
TAXA
SUMMER 8 10 9 8
FALL 6 5 8 3
WINTER 7 7 8 4
SPRING 5 4 4 5
OVERALL 13 13 16 10
OYSTER
SUMMER 7 12 12 9
FALL 7 5 10 4
WINTER 6 10 9 3
SPRING 8 7 7 6
OVERALL 12 17 18 13
CARNIVORES
OMNIVORES & SCAVENGERS
SELECTIVE DEPOSIT FEEDERS/ HERBIVORES / DETRITIVORES
SUSPENSION FEEDERS

Figure 17: Species-effort curves. (A) Observed species accumulation (± SD) vs. cumulative number of 0.06 m^{-2} substrate basket samples from each reef substrate type at Fisherman Island. (B) Observed species accumulation (± SD) vs. cumulative number of individuals.

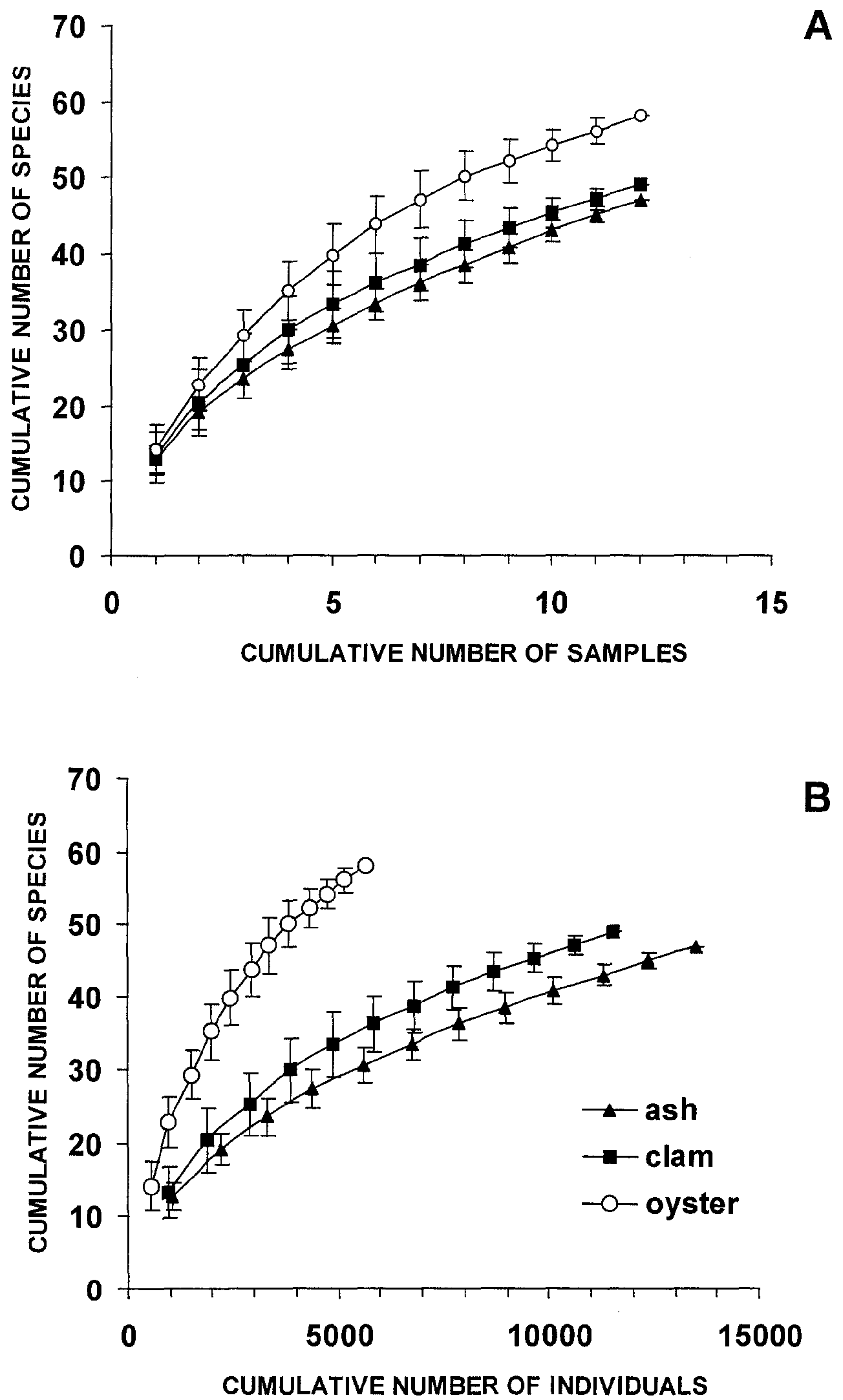

A
CUMULATIVE NUMBER OF SPECIES
70
60
50
40
30
20
10
0
0
5
10
15
CUMULATIVE NUMBER OF SAMPLES
B
CUMULATIVE NUMBER OF SPECIES
70
60
50
40
30
20
10
0
0
5000
10000
15000
CUMULATIVE NUMBER OF INDIVIDUALS
ash
clam
oyster

Figure 18: Mean total community secondary production estimates (+ SE) for each season. Shading of each bar and number in parentheses to the right of the bar are representative of the relative percentage of production from each reef type to the mean total for the season.

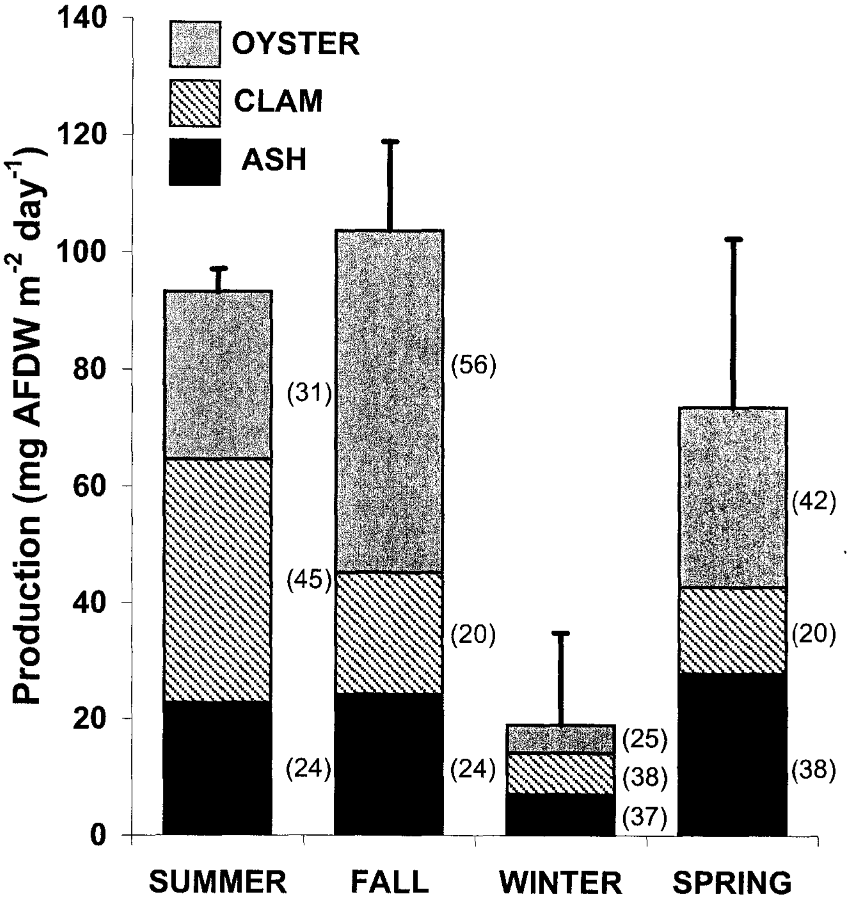

140
120
100
80
60
40
20
0
Production (mg AFDW m^{-2} day^{-1})
OYSTER
CLAM
ASH
(31)
(45)
(24)
(56)
(20)
(24)
(25)
(38)
(37)
(42)
(20)
(38)
SUMMER
FALL
WINTER
SPRING

Figure 19: Proportion of monthly total community secondary production estimates attributed to numerical and biomass dominants from Coal Ash Pellet, Clam Shell, and Oyster Shell Reefs between June 1997 and May 1998. Legend abbreviations for dominant species are for decapods *Panopeus herbstii* (Pan_her) and *Palaeomonetes vulgaris* (Pal_vul), gammaridean amphipods *Melita nitida* (Mel_nit) and *Gammurus mucronatus* (Gam_muc), bivalves *Crassostrea virginica* (Cra_vir) and *Mytilus edulis* (Myt_edu), and polychaete *Nereis succinea* (Ner_suc). "Other" represents the remaining grouped taxa of the community not listed above.

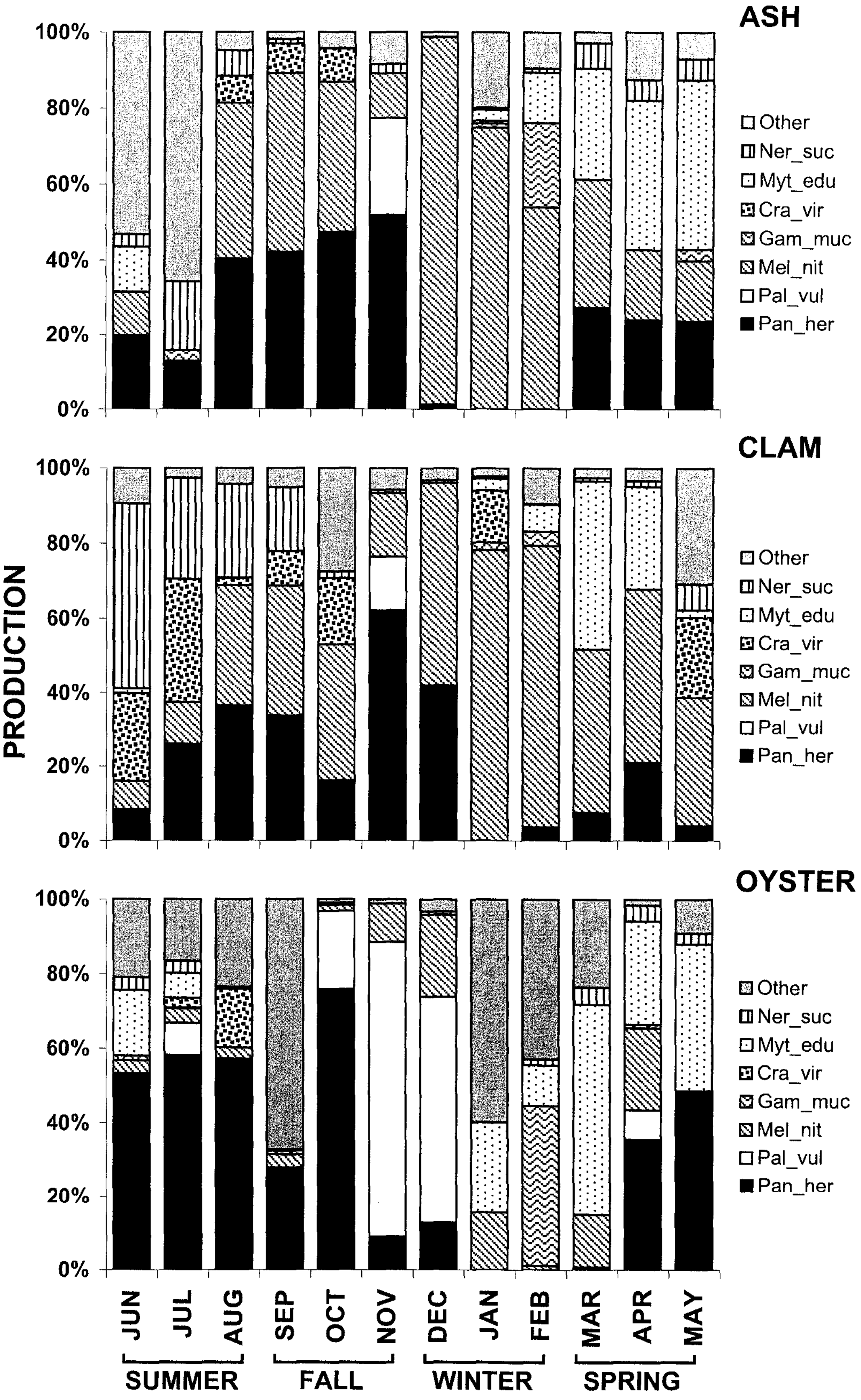

ASH
CLAM
OYSTER
PRODUCTION
100%
80%
60%
40%
20%
0%
Other
Ner_suc
Myt_edu
Cra_vir
Gam_muc
Mel_nit
Pal_vul
Pan_her
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
SUMMER
FALL
WINTER
SPRING

Figure 20: Mean total community production (+SE) for each season on (A) Coal Ash Pellet, (B) Clam Shell, and (C) Oyster Shell reefs. Shading in each bar represents the proportion of production contributed by each of the numerical and biomass dominant species listed in Table 9. Legend abbreviations for dominant species are for decapods *Panopeus herbstii* (Pan_her) and *Palaeomonetes vulgaris* (Pal_vul), gammaridean amphipods *Melita nitida* (Mel_nit) and *Gammurus mucronatus* (Gam_muc), bivalves *Crassostrea virginica* (Cra_vir) and *Mytilus edulis* (Myt_edu), and polychaete *Nereis succinea* (Ner_suc). "Other" represents the remaining grouped taxa of the community not listed above. Note differences in scale on each vertical axis.

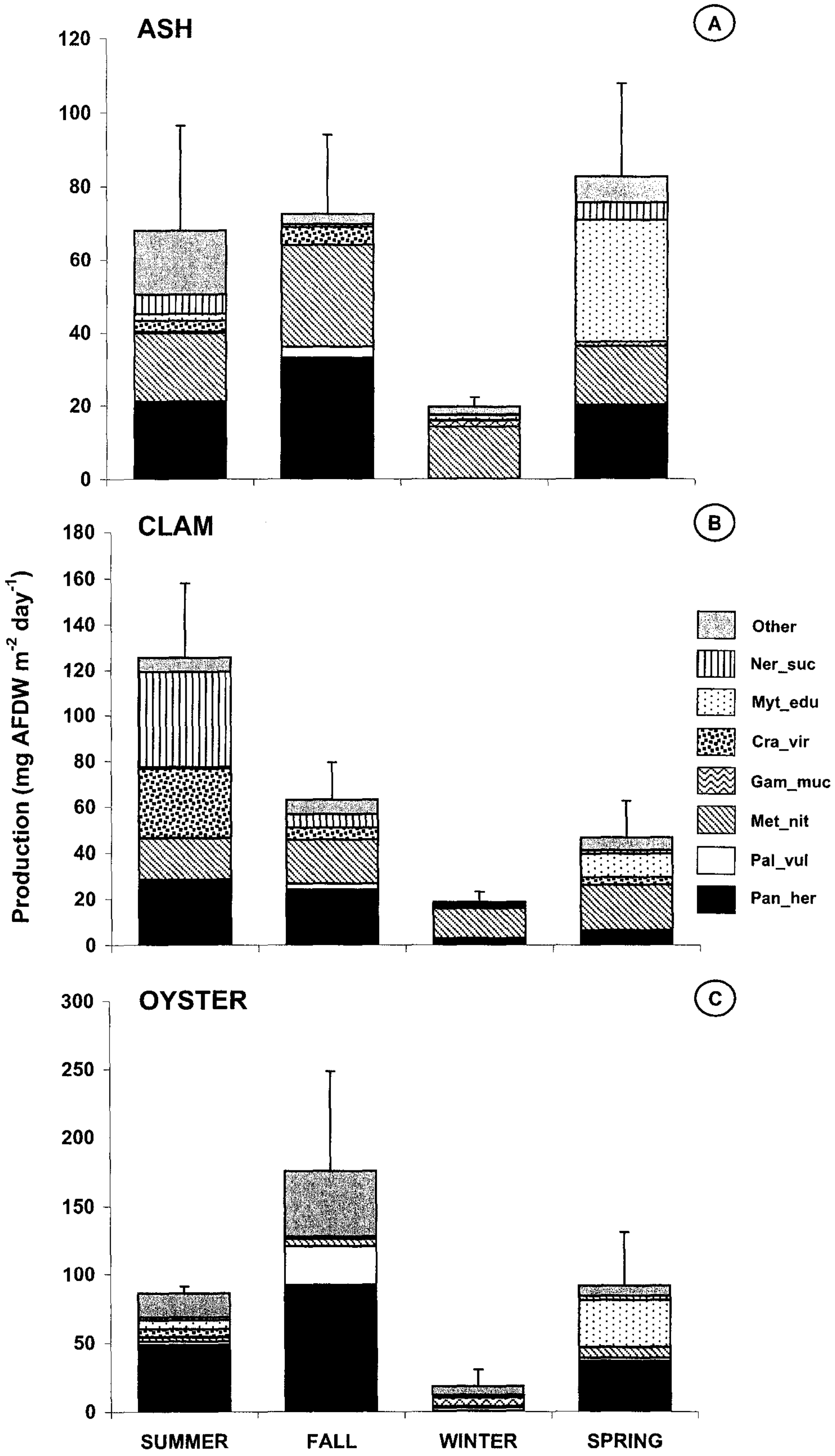

ASH
A
CLAM
B
OYSTER
C
Production (mg AFDW m-2 day-1)
120
100
80
60
40
20
0
180
160
140
120
100
80
60
40
20
0
300
250
200
150
100
50
0
Other
Ner_suc
Myt_edu
Cra_vir
Gam_muc
Met_nit
Pal_vul
Pan_her
SUMMER
FALL
WINTER
SPRING

Figure 21: Mean total community production estimates (+SE) for each season on (A) Coal Ash Pellet, (B) Clam Shell, and (C) Oyster Shell reefs. Shading in each bar represents the proportion of production contributed by each feeding typre each season. Note differences in scale on each vertical axis.

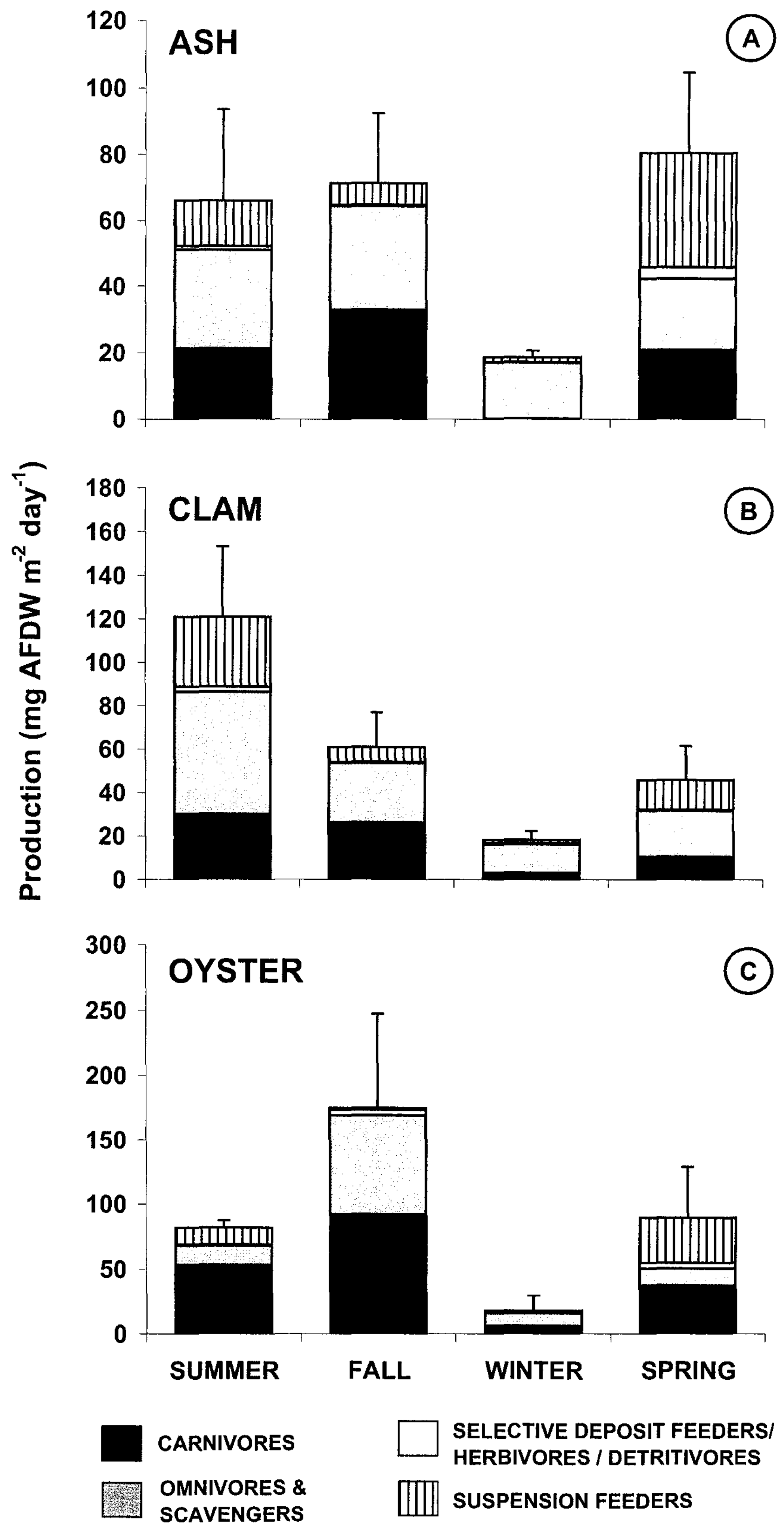
Production (mg AFDW m^{-2} day^{-1})
120
100
80
60
40
20
0
ASH
A
180
160
140
120
100
80
60
40
20
0
CLAM
B
300
250
200
150
100
50
0
OYSTER
C
SUMMER
FALL
WINTER
SPRING
CARNIVORES
OMNIVORES & SCAVENGERS
SELECTIVE DEPOSIT FEEDERS/ HERBIVORES / DETRITIVORES
SUSPENSION FEEDERS

Figure 22: Proportion of monthly total community secondary production estimates attributed to each macroinvertebrate feeding type on Coal Ash Pellet, Clam Shell, and Oyster Shell Reefs between June 1997 and May 1998.

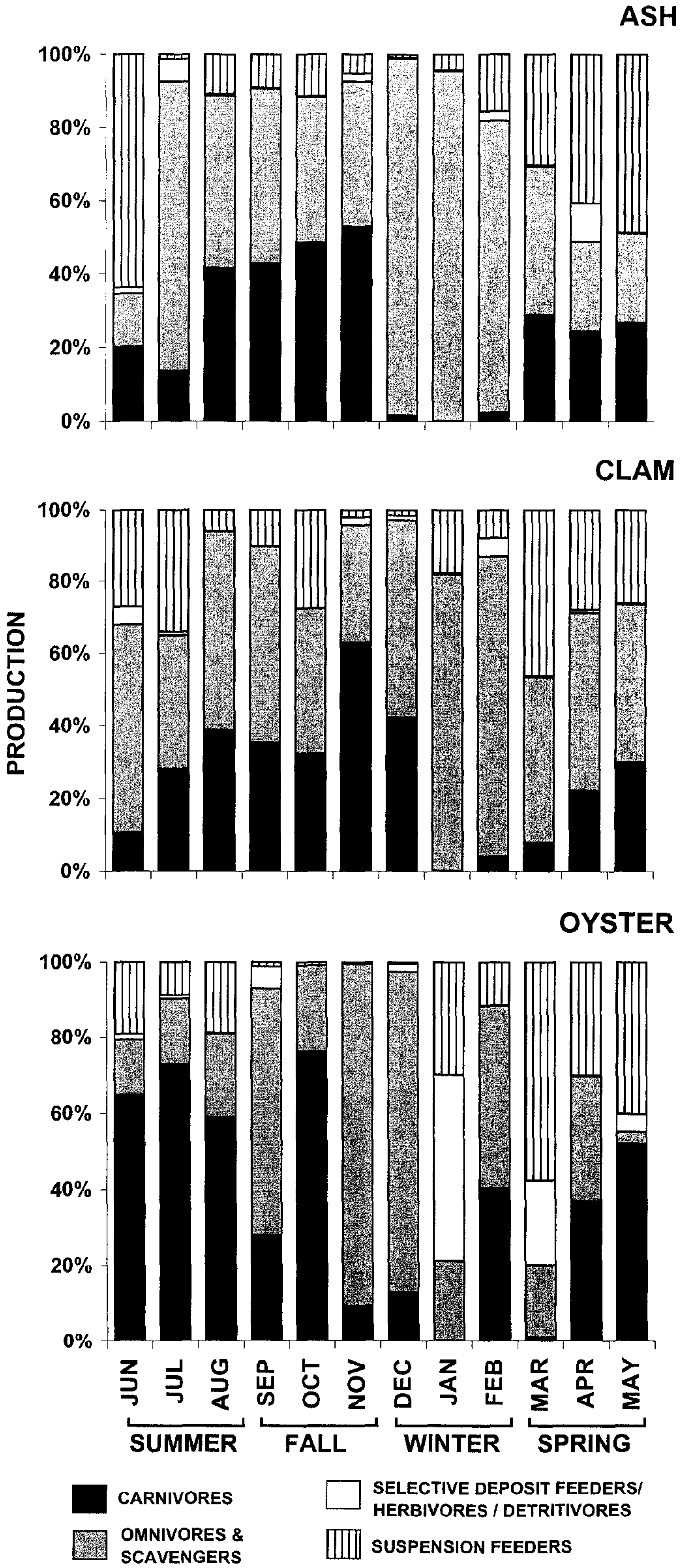

ASH
CLAM
OYSTER
PRODUCTION
100%
80%
60%
40%
20%
0%
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
SUMMER
FALL
WINTER
SPRING
CARNIVORES
OMNIVORES & SCAVENGERS
SELECTIVE DEPOSIT FEEDERS/ HERBIVORES / DETRITIVORES
SUSPENSION FEEDERS

Figure 23: Hierarchies resulting from clustering of using Bray-Curtis similarity values for all collections of macrofauna made monthly from each reef substrate type at Fisherman Island.

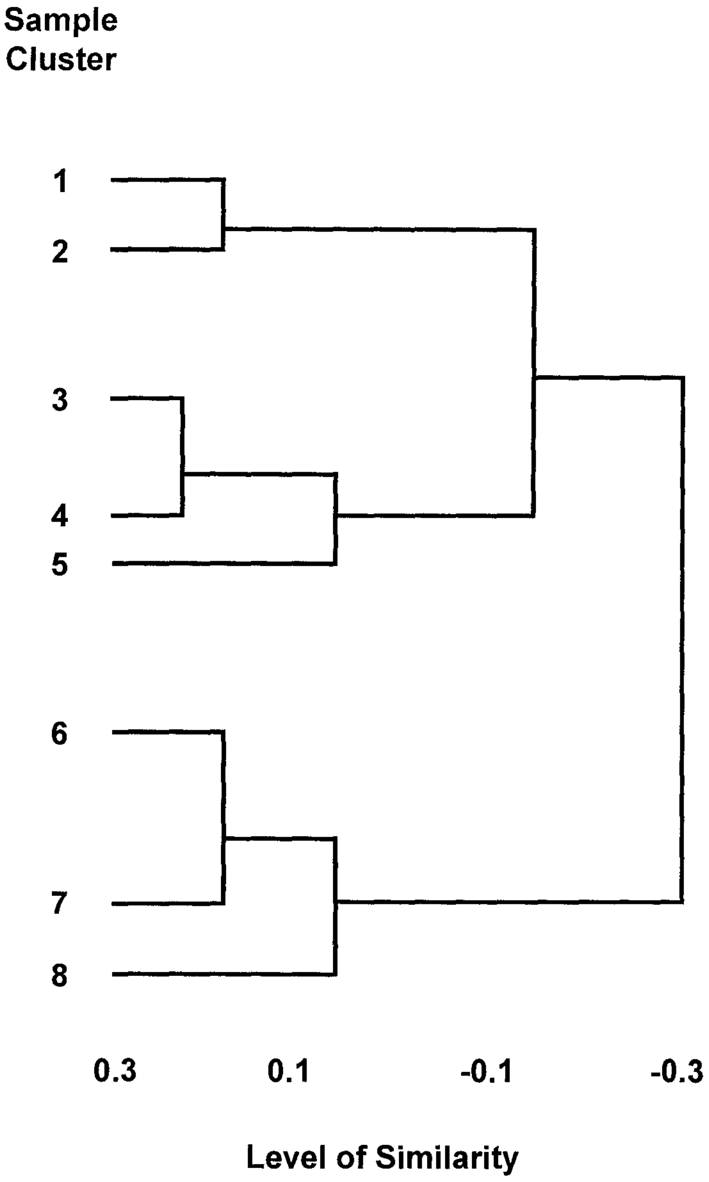

Sample
Cluster
1
2
3
4
5
6
7
8
0.3
0.1
-0.1
-0.3
Level of Similarity

Figure 24: Hierarchies resulting from clustering of using Bray-Curtis similarity values for all macrofaunal species collected monthly from each reef substrate type at Fisherman Island.

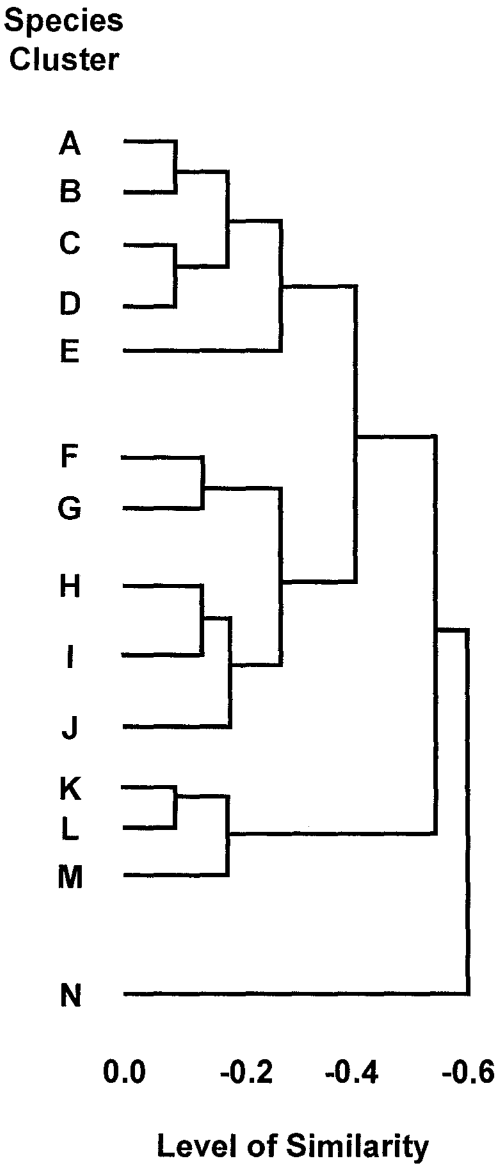

Species
Cluster
A
B
C
D
E
F
G
H
I
J
K
L
M
N
0.0
-0.2
-0.4
-0.6
Level of Similarity

Figure 25: Nodal constancy in a two-way table of species groups and sample groups from an analysis of abundance patterns of macrobenthos from intertidal oyster reefs of different substrate types.

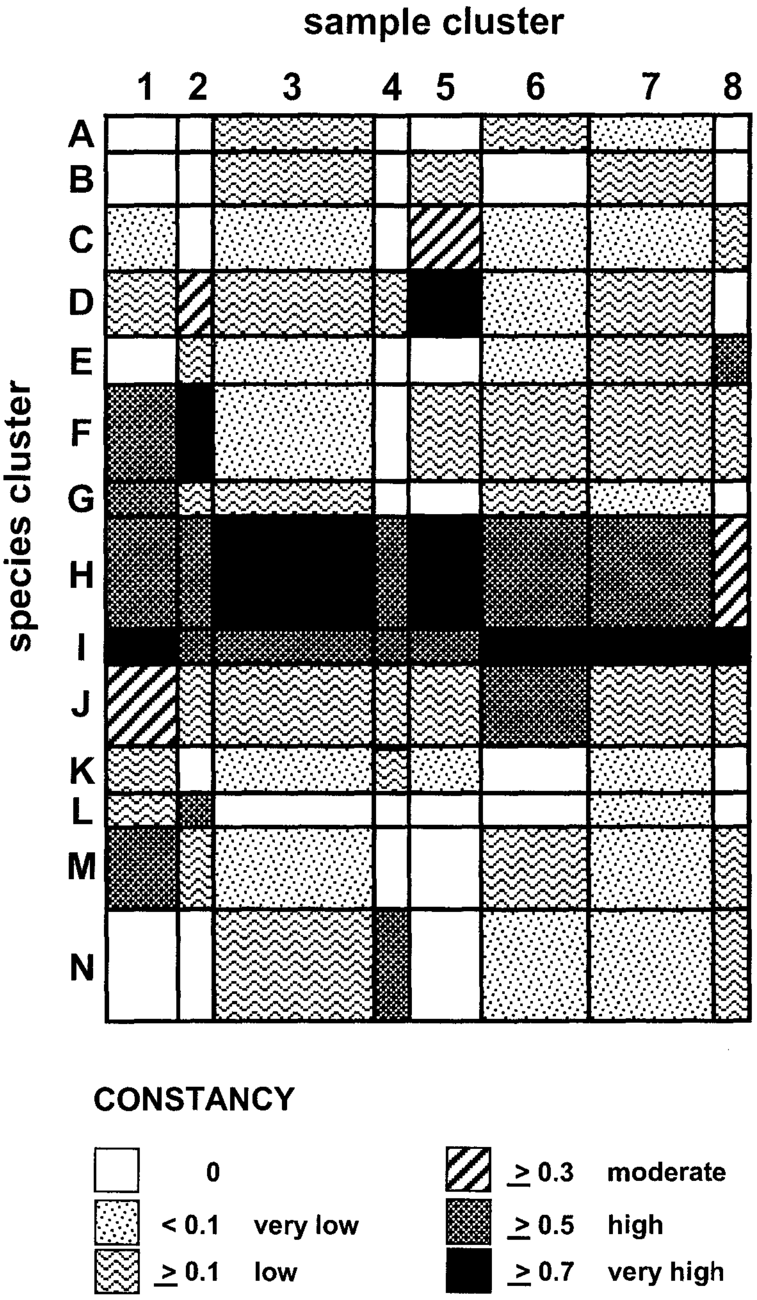

sample cluster
1
2
3
4
5
6
7
8
species cluster
A
B
C
D
E
F
G
H
I
J
K
L
M
N
CONSTANCY
0
< 0.1 very low
≥ 0.1 low
≥ 0.3 moderate
≥ 0.5 high
≥ 0.7 very high

Figure 26: Nodal fidelity in the same two-way table as in Figure 25.

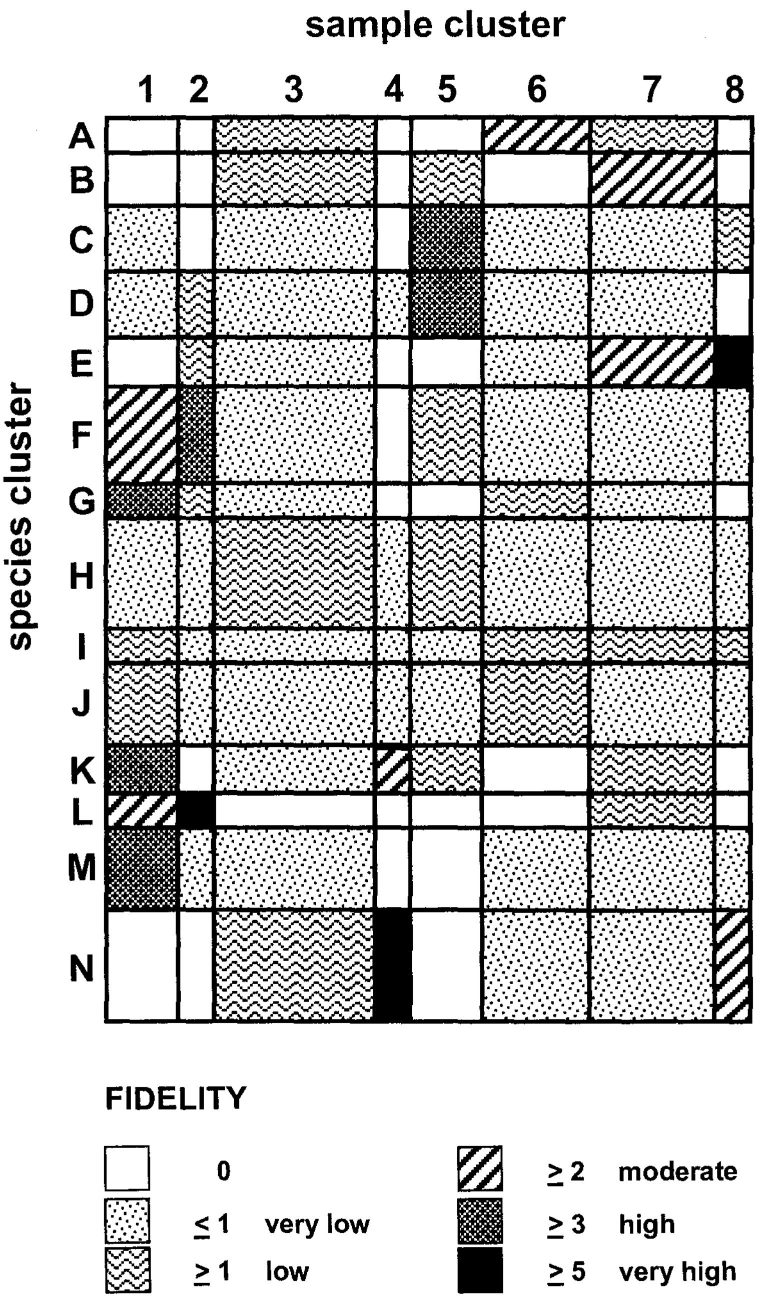

sample cluster
1
2
3
4
5
6
7
8
species cluster
A
B
C
D
E
F
G
H
I
J
K
L
M
N
FIDELITY
0
≤ 1 very low
≥ 1 low
≥ 2 moderate
≥ 3 high
≥ 5 very high

Figure 27: Examples of profiles of reef substrate material imbedded in Portland cement and cross-sectioned to show differences in substrate surface area available for epifaunal colonization and volume of interstitial spaces between substrate pieces (Nestlerode, unpublished data). Light features represent cross-sections of individual substrate elements and black is the void interstitial spaces between these elements (reef material profiling adapted from mussel bed cast procedure described in Commito and Rusignuolo 2000). (A) Oyster shell, (B) Clam shell, (C) Coal ash pellet. Scale bar in top right of each panel is 5 cm.

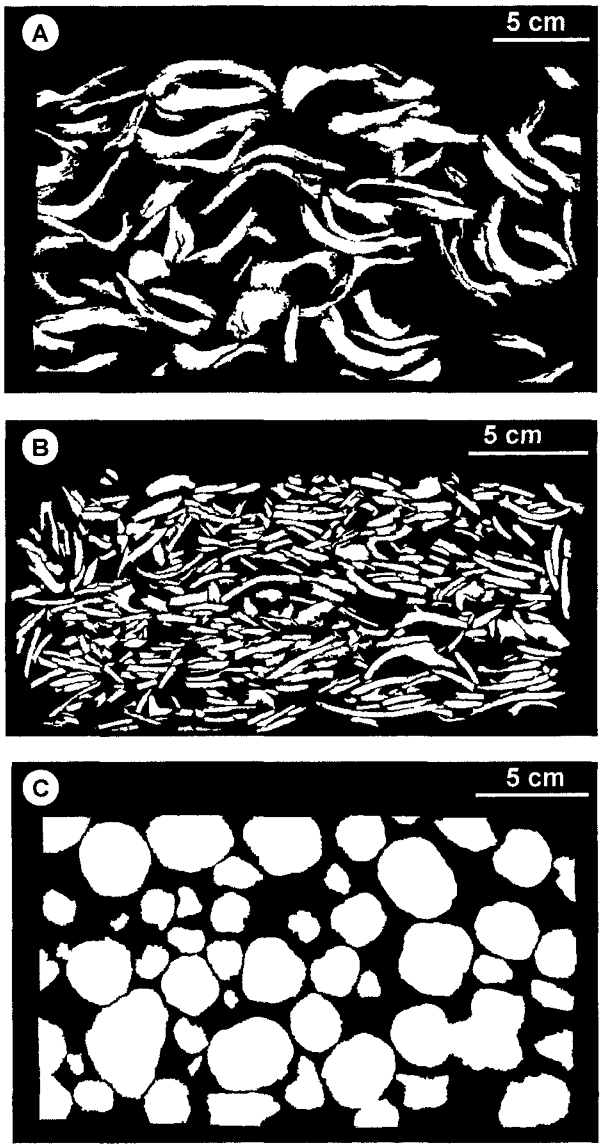
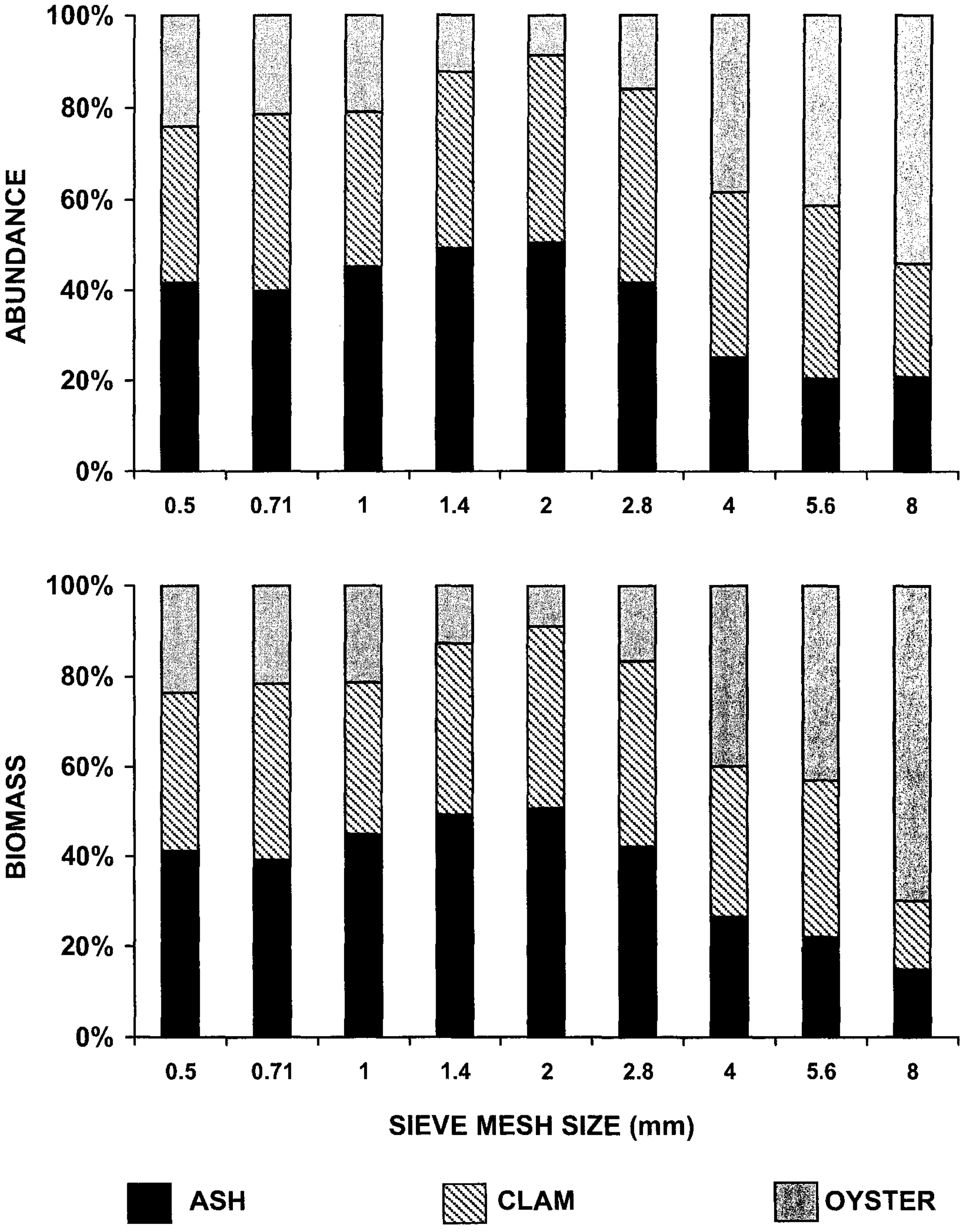

A
5 cm
B
5 cm
C
5 cm

Figure 28: Distribution of macrofauna by body size across each reef type. Bars represent the percentage of individuals (top panel) and biomass (bottom panel) retained on each nested sieve of varying mesh size (as per Edgar 1990).


100%
80%
60%
40%
20%
0%
ABUNDANCE
0.5
0.71
1
1.4
2
2.8
4
5.6
8
100%
80%
60%
40%
20%
0%
BIOMASS
0.5
0.71
1
1.4
2
2.8
4
5.6
8
SIEVE MESH SIZE (mm)
ASH
CLAM
OYSTER

CHAPTER 4

NEKTON USE OF CREATED INTERTIDAL OYSTER REEF HABITATS OF CHESAPEAKE BAY

ABSTRACT

Efforts to restore the Eastern oyster, *Crassostrea virginica*, reef habitats have resulted in the placement of constructed oyster reef bases in several locations within Chesapeake Bay. A shortage of oyster shell for creating these large-scale reefs has led to widespread use of other materials. Reefs constructed of oyster shell, clam shell and pelletized coal ash were built in 1996 at Fisherman's Island, Virginia. This study examined differences in the abundance, diversity, and community structure of nekton species collected using a remotely deployed enclosure trap between these reef substrate types, as well as an adjacent bare-sand beach that served as a proxy pre-reef-construction control to assess the importance of these oyster reefs as fish habitat. Using multivariate non-metric statistics, the data show distinct differences in nekton community structure across habitat types. Species richness was greatest on the oyster shell and coal ash pellet habitats. It was found that there were significant differences in the presence and abundance of nekton species between oyster shell and clam shell reefs and that clam shell reefs were similar in species composition and abundance to the bare-sand beach habitat. These reef habitat have refuge value, as demonstrated by the transient nekton species that numerically dominated all of these habitats. Additionally, the oyster shell and coal ash pellet reef served as habitat to many ecologically, commercially, and recreationally important species that use the reef habitat for food and shelter during juvenile life stages, suggesting the reef habitats may be of great importance as habitat to finfish communities.

INTRODUCTION

Oyster reef habitats support characteristically high animal diversities and abundances and increased recognition of the interconnection of oyster reef habitats and fish assemblages has further incited efforts to restore oyster reefs as functional estuarine habitats to Chesapeake Bay. Oyster reefs serve as feeding and nursery grounds to several decapod and finfish species (Eggleston 1990, Breitburg 1999, Harding and Mann 1999) and restoration efforts have the potential to influence populations of many estuarine fishes (Breitburg 1999) and other investigators have highlighted the prominence of transient predatory species on and around oyster reefs along the east coast of the United States (Powell 1994, Wenner and Coen 1996, Breitburg 1999, Harding and Mann 1999).

It has been hypothesized that the three-dimensional structure of oyster reefs functions similar to aquatic vegetated habitats in providing refuge and foraging habitat for many estuarine species (Posey 1999). Unlike seagrass beds, which are primarily subtidal, nekton use in marshes and intertidal oyster reefs is intermittent and tidally-dependent because most nekton can only gain access when these habitats are submerged. If these nekton are also foraging predators, these habitats provide a wealth of benthic biomass and food webs are primarily characterized by omnivorous feeding (see Chapter 3 of this dissertation). Posey et al.'s study (1999) demonstrates preferential use of oyster habitats by several fish and decapod species compared with adjacent sandflats. These transient species appeared to use the reef during higher tidal stages and move to subtidal areas at low tide. Small transient fish and crustaceans, which are known to be important food items for many larger fish predators (Murdy et al. 1997), may also feed at the reef while they are using it as a refuge from predation. If so, then they are potentially important as trophically intermediate "vector" species that mediate energy flow through the reef and surrounding shallow water system (Posey et al. 1999). Similar food webs have been documented in salt marsh ecosystems (Cicchetti 1998a) and many of these species are believed to be important vectors of energy from the marsh to adjacent shallow water habitats.

Larger estuarine fish species are difficult to sample quantitatively because they are often less abundant, more motile, and more sparsely distributed than smaller sized species (Kjelson 1977). Oyster reef habitats are exceedingly difficult areas in which to quantitatively assess fish and macroinvertebrate populations because the nature of the reef structure hampers techniques normally employed for sampling aquatic organisms. Quantitative estimates of larger estuarine fish species associated with oyster reef habitats is fundamental to understanding ecological interconnections between these species and oyster reefs as fish habitat. In this study, a remotely deployed enclosure trap was used (see Chapter 2 of this dissertation for a full description) to quantitatively sample nekton associated with intertidal reef habitats.

Oyster reef restoration activities in the Virginia portion of Chesapeake Bay typically involve the placement of hard substrata on the seabed to form three-dimensional mounds to serve as a base for oyster recruitment and growth. A shortage of oyster shell for creating large-scale reefs has led to widespread use of other materials, such as surf clam (*Spisula solidissima*) shell, as a substitute for oyster shell. The goal of this study was to compare nekton use and community composition of intertidal constructed oyster reef habitats of different substrate construction materials while using a nearby bare-sand beach habitat as a proxy pre-reef-construction control to assess the importance of these oyster reefs as fish habitat.

METHODS

Study site

This study was conducted at Fisherman's Island near the north side of the mouth of Chesapeake Bay, previously described in detail by O'Beirn et al (2000) (Figure 1). Briefly, this polyhaline environment has a tidal amplitude of approximately 1.25 m and is surrounded by marsh islands and intertidal and subtidal mud/sand flats. In July 1996, 11 reef bases were constructed using three different substrates: oyster shell, surf clam shell, and pelletized coal ash. These reefs range in size from 80 to 900 m^2 and extend from the shallow subtidal into the intertidal zone. A natural channel separates the two rows of reefs, reaching a maximum depth of approximately 2 m at MLW.

Sampling for transient fishes and mobile macroinvertebrates

Nekton was collected from constructed oyster shell, clam shell, and coal ash pellet reefs and a nearby bare-sand beach habitat at Fisherman's Island (Figure 1). Sampling was conducted monthly from April to October 1999 over three consecutive days at neap tide preceding a full moon using the encircling seine gear depicted in Figure 4, Chapter 2. A full description of the encircling seine gear, techniques, and sampling design is provided in Chapter 2 of this dissertation. All samples were collected during the ebb tide stage and sampling was initiated only after the crest of the reef became exposed by the falling tide. Samples were collected by surrounding one side of an intertidal reef habitat (or a section of bare-sand beach habitat) with the enclosure seine while using the emergent portion of the reef or beach as a barrier to fish escapement. All collected animals were identified, counted, and measured to the nearest mm for total length (carapace width for crabs, carapace length for shrimp). Length of reef (or beach habitat, in m) enclosed by the seine, temperature (°C) and salinity (psu) were recorded with each sample. Poor weather or gear failure occasionally prevented full replication on three consecutive days per monthly sampling period; therefore, the data presented here are only from the first two replicates from each reef habitat each sampling period. Sampling of the beach habitat was added in July 1999 as a proxy pre-reef-construction control and continued on through the end of the study. The effects of Hurricane Floyd prohibited sampling in September 1999.

Data analysis

Nekton species abundance values in each enclosure trap sample were converted to density per linear meter of reef edge (or bare-sand beach habitat) to account for differences in length of habitat sampled by each replicate sample. This measure is appropriate because results of a separate video study showed most fishes (>94%) use the reef edge compared to the off-reef subtidal habitat also included by the enclosure trap gear (Nestlerode, unpublished).

Two-way analysis of variance (ANOVA) was used to investigate habitat and temporal differences in nekton density using habitat type and season as independent factors. Data were tested using the Shapiro-Wilk test of normality (Zar 1999) and Bartlett's test of homogeneity of variance (Underwood 1997) and transformed by log

(X+1) to improve normality and homoscedasticity. Tukey Honestly Significant Difference tests (hereafter, Tukey test) were used for post-hoc comparisons when ANOVA detected significant differences (Zar 1999). Because of the unbalanced sample design with the bare-sand beach habitat samples restricted to the latter half of the study, separate analyses were conducted to compare differences in nekton density for April – October 1999 samples from oyster shell, clam shell, and coal ash pellet reefs and for July – October 1999 samples from oyster shell, clam shell, and coal ash pellet reefs and the bare-sand beach habitat.

The PRIMER software package (V 5.2.9, Plymouth Routines in Multivariate Ecological Research, Plymouth Marine Laboratories, UK; Clarke and Gorley 2001; Clarke and Warwick 2001) was used to test differences in nekton communities between habitat types. Square-root transformed nekton densities from each habitat and sampling month were used to create a triangular similarity matrix based on the Bray-Curtis similarity coefficient (Bray and Curtis 1957). The Bray-Curtis coefficient was also computed for presence-absence data using a matrix of 1's (presence) and 0's (absence) (Clarke and Warwick 2001). This approach was employed because simplification of density data to presence/absence down-weighs the effects of common species such that rare species contribute the same as common species and reduces possible gear bias (such as possible unequal collection of each species based on behavior, gear avoidance, etc.) on community composition represented in the samples. While this analysis does not account for relative abundances of species within samples, it provides a general categorization of community composition.

Samples were classified by hierarchical agglomerative cluster analysis using group-average linking method and ordinated using non-metric, multidimensional scaling (MDS) techniques. On the two-dimensional plots generated from the MDS analysis, points that appear closer together represent samples that are highly similar in species composition and have high rank similarities. Points that are farther apart correspond to very different communities with lower rank similarities. "Stress" is a measure that indicates how faithfully the high-dimensional relationships among the samples are represented in the two-dimensional orientation plot. Stress values of <0.1 correspond to good ordination with little chance of a misleading interpretation of the MDS analysis; Stress <0.2 gives a potentially useful two-dimensional representation of the data but conclusions should be further evaluated by superimposing cluster groups on the MDS ordination to verify grouping of samples. Stress >0.3 indicates points are close to being placed arbitrarily on the two-dimensional orientation plot and positions should be treated with skepticism (Clarke and Warwick 2001).

Nekton assemblages were compared with a two-way analysis of similarities (ANOSIM) with reef type and month as the main effects. ANOSIM is roughly analogous to ANOVA and tests *a priori* defined groups against random groups in ordinate space (Clarke and Warwick 2001). ANOSIM generates R_{ANOSIM} statistic values, which are a relative measure of separation of the *a priori* defined groups. The test statistic was computed over 5000 permutations. Although R_{ANOSIM} can vary between 1 and −1, values usually fall between 0 and 1. Values less than one indicate the generally unusual situation of lower levels of similarity within treatments or groups than between them (Clarke and Warwick 2001). A R_{ANOSIM} value of zero (0) indicates that the null hypothesis is true and that there are no differences between the assessed factors, while a R_{ANOSIM} value of one (1) indicates that all replicates within a treatment/group are more similar to each other than to any others from different treatments/groups. A R_{ANOSIM} value of –1 indicates that all replicates within a treatment/group are more similar to those from different treatments/groups (Clarke and Gorley 2001). As a general rule, R_{ANOSIM} values can be categorized into 3 broad categories (Clarke and Gorley 2001):

i. $R_{ANOSIM} > 0.75$ indicates that there are large differences and the treatments/groups are well separated

ii. $R_{ANOSIM} > 0.5$ indicates clear differences, but the treatments/groups are overlapping

iii. $R_{ANOSIM} < 0.25$ indicates little/no difference and the treatments/groups are barely separable.

Significant ANOSIM results were followed with the similarity percentages (SIMPER) routine to identify the species responsible for contrasts in the community analysis. The SIMPER analysis results were calculated from the data matrix with a square-root transformation and were limited to species contributing to the top 50% of similarity between habitat types.

Various univariate indices, the observed species richness (S), Shannon diversity index (H', using $\log_2$), and Pielou's evenness (J') index, were calculated from untransformed data for each sample collected each month from each habitat type using PRIMER (Clarke and Warwick 2001).

RESULTS

Environmental conditions

Salinity measurements at the study area fluctuated within the polyhaline range and varied between 25 psu (20-22 October 1999) and 31 psu (26-28 April 1999). Water temperature measurements during the study period were lowest in April (14 °C) and October (16 °C) and reached a seasonal maximum of 34 °C recorded 26-28 July 1997 (Figure 2).

General community patterns

A total of 20540 individuals representing 40 species (Figure 3) were collected during this study. The most abundant species were the grass shrimp, *Palaemonetes vulgaris* (contributing to 40% of the total overall abundance across all habitats), followed by the rough silverside, *Membras martinica* (38%), killifish *Fundulus heteroclitus* (12%), *F. majalis* (5%), and *Lucania parva* (2%), and the blue crab, *Callinectes sapidus* (1.6%) (Table 1; Appendix II). *P. vulgaris* and *M. martinica* made up 98% of all individuals collected from the oyster shell reef, 90% from the clam shell reef, 53% from the coal ash pellet reef, and 40% from the bare-sand beach habitat.

Many of the remaining species were unique to specific habitat types and occurred in only one or two samples from a particular habitat. Eight species were unique to the oyster shell habitat, four were unique to the ash pellet reef, and two were unique to the clam shell reef. All species collected at the bear-sand beach were also collected on at least one of the other reef habitat types. It is noteworthy that two of the unique species, *Opsaus tau* from the oyster shell and *Chaetodon ocellatus* from the coal ash pellet, were also found on the coal ash pellet and oyster shell reef, respectively, but these individuals are not included in abundance and diversity calculations here because they occurred in a third replicate enclosure trap sample that was not included in this analysis

Nekton species were assigned to habitat use categories based on biological data in Murdy et al. (1997), Baltz et al. (1993), Breitburg (1999), and personal observations. Species were classified into one of four categories (Tables 1 and 2): resident oyster reef species; facultative reef residents; demersal transients; and nektonic transients. Reef residents are those species that spend the majority of their life history associated with the reef structure and are dependent on the reef for feeding, shelter, and reproduction. These species, such as gobies, blennies, and oyster toadfish, feed primarily on benthic invertebrates and find shelter and nest sites among shells of live and dead oysters. Facultative reef residents are those species that use the reef habitat for food and shelter during juvenile life stages. This group includes tautog, sheepshead, pigfish, and pinfish. They feed on small crustaceans, worms, and mollusks and seek shelter among the oyster shells until they outgrow the complex matrix of spaces between the oyster shells on the surface of the reef. As adults, these species may continue to intermittently visit the reef habitat in search of food and are found associated with a variety of other habitats. It is likely that some facultative reef residents may also be considered transient, depending on their life stage. Transient species, those species that may be abundant on oyster reefs but are also found in a wide range of estuarine habitats, are divided into two categories based on their behavior and favored position in the water column: demersal transients and nektonic transients. Demersal transients, such as silver perch, spot, killifish, blue crab *Callinectes sapidus*, and grass shrimp, are highly mobile and feed from the benthos. Nektonic transients, such as silversides, mullet, and anchovies, are primarily associated with the water column. This group includes highly aggregated planktivorous species that are active swimmers and prefer surface waters.

Of the thirteen species collected from the beach habitat, all were "transients" in terms of oyster reef habitat use. Eleven of these species were demersal tranisients and two were nektonic transients (Table 2). The ash pellet reef had the greatest overall number of species collected over the study period, however, the oyster shell habitat had the greatest number of reef resident and facultative resident species compared with the other habitat types (Table 2). The clam shell reef had the lowest overall observed species richness with fewer numbers of species within each category compared to the other two reef types (Table 2; Figure 4A). Shannon diversity and Pielou's evenness were lowest for all habitats sampled in April 1999, but no other temporal or habitat patterns in Shannon diversity were observed (Figure 4B, 4C). Evenness values tended to be lowest on the oyster shell reef habitat each month compared to the other two reef types indicating these samples had many rare species and were dominated by a few taxa (Figure 4C).

Total nekton abundance varied significantly by reef type and month between April and October 1999 (Table 3). There was a significant effect of reef type on total nekton abundance (Table 3). Total abundance across all samples ranged between 0.4 and 216 individuals per m^{-1} of reef edge and was significantly greater on the oyster shell (2 –

216 individuals per m^{-1}) reef than on the clam shell reef (2 – 25 individuals per m^{-1}) (Table 3, Appendix II). The coal ash pellet reef was not significantly different from either the clam shell or oyster shell reefs (Table 3, Figure 5A). The larger abundance on the oyster shell reef was primarily attributed to above average high densities of *Palaemonetes vulgaris* and *Membras martinica* (Figure 5A, 5C). Temporal differences in nekton abundance also significantly influenced the patterns observed. Overall nekton abundance was greatest in June collections compared to that observed in May (Table 3, Figure 5A).

Total nekton abundance also varied significantly by habitat type and month between July and October 1999 (Table 3). There was a significant effect of habitat type on total nekton abundance (Table 3). Total abundance across all samples ranged between 1.4 and 103 individuals per m^{-1} of reef edge and was again significantly greater on the oyster shell (16 – 103 individuals per m^{-1}) reef than on the clam shell reef (1.4 – 23 individuals per m^{-1}) (Table 3, Figure 5). Nekton abundance on the bare-sand beach habitat did not differ significantly from any of the other habitats and coal ash pellet reef nekton was not significantly different from that of the oyster shell reef (Table 3, Figure 5) and. Again, the larger abundance on the oyster shell reef was primarily attributed to above average high densities of *Palaemonetes vulgaris* and *Membras martinica.* Temporal differences in nekton abundance also significantly influenced the patterns observed with overall nekton abundance was greatest in July and August collections compared to that observed in October (Table 3, Figure 5C). There was also a significant interaction between month and habitat (Table 3; Figure 6) and this interaction is accounted for by differences in temporal patterns on different habitat types. Nekton abundance on the coal ash pellet and bare-sand each habitats decreased over time, where nekton abundance on the clam shell and oyster shell reefs reached a maximum during the August sampling period. High nekton abundances during the July sampling period (Figure 5C) on the coal ash pellet and beach habitats were driven by high killifish (*Fundulus heteroclitus*, *F. majalis,* and *Lucania parva*) abundances (mean total killifish abundance on the coal ash pellet reef and bare-sand beach habitat were 86 and 31 individuals m^{-1}, respectively). Killifish abundances did not exceed 2 individuals m^{-1} on the oyster shell or clam shell reefs during this sampling period (Figure 6; Appendix II).

In examining the constructed oyster reef habitats between April and October 1999, nekton assemblages were again found to be significantly different between clam shell and oyster shell reefs (ANOSIM test with $R_{ANOSIM} = 0.542$, $p = 0.01$). Nekton species richness and total overall abundance differed between these habitat types (Tables 1 and 2). The MDS ordination (Figure 7) shows a general separation of clam shell reef on the right and oyster reef samples on the left. Using SIMPER, the species most responsible for the different assemblages on these two habitat types were *M. martinica* (32%) and *P. vulgaris* (31%).

Evaluation of nekton communities across the four habitat types (oyster shell, clam shell, and coal ash pellet reefs and the bare-sand beach habitat) between July and October 1999 using ANOSIM revealed slightly different patterns than described by ANOVA (Table 3). Pairwise tests revealed significant differences between coal ash and beach habitats (ANOSIM test with $R_{ANOSIM} = 1.00$, $p = 0.03$), clam shell and oyster shell habitats (ANOSIM test with $R_{ANOSIM} = 0.67$, $p = 0.03$), and oyster shell and beach habitats (ANOSIM test with $R_{ANOSIM} = 0.83$, $p = 0.03$). Additionally, pairwise tests between sampling periods revealed a significant difference between July and August samples (ANOSIM test with $R_{ANOSIM} = 0.81, p = 0.01$). Nekton species richness differed between these habitat types with the oyster shell and coal ash reefs having greater values than those of the other two habitats (Table 2). Total overall abundance followed similar relative patterns to species richness with oyster and coal ash reefs having highest abundances compared to the clam shell reef and bare-sand beach habitat (Table 1). The MDS ordination (Figure 9) shows a general separation of clam shell reef and beach habitats from coal ash and oyster shell reefs. Using SIMPER, the species most responsible for the different assemblages on the coal ash and beach habitats were *M. martinica* (21%), *F. heteroclitus* (20%), *F. majalis* (14%), and *P. vulgaris* (14%). The species most responsible for the differences in assemblages on the clam and oyster shell reefs were *M. martinica* (30%) and *P. vulgaris* (27%). The species most responsible for the assemblage differences on the oyster shell and beach habitats were the same as those driving dissimilarities in the coal ash and beach comparison: *P. vulgaris* (24%), *M. martinica* (20%), *F. majalis* (12%), and *F. heteroclitus* (11%). Further simplification of these data with a presence/absence transformation reveal an even clearer MDS ordination pattern of oyster shell reef samples grouped with coal ash pellet reef samples and clam shell and beach samples sharing higher similarity groupings (Figure 11).

DISCUSSION

Nekton assemblages were highly variable across all habitats sampled. The physical characteristics of a habitat can influence fish assemblages associated with this it. Structurally complex reef substrate configurations (see Chapter 3, Figure 27), such as those of oyster shell and coal ash pellet reefs, generally supported higher densities and diversities of nektonic species.

The clam shell reef habitat was comparable to the bare-sand beach in terms of general species composition, abundance, and diversity. Transient species dominated the nekton communities of these habitats and were responsible for separating these assemblages from those of the other to reef substrate types. The beach habitat community, which was entirely comprised of transient species, was numerically dominated by the rough silverside, *Membras martinica*, and killifish *Fundulus heteroclitus* and *F. majalis*. The clam shell reef, with low surface roughness from the compaction of fractured shell fragments over time (see Chapter 3 of this dissertation), was also numerically dominated by the rough silverside, *Membras martinica*, and grass shrimp, *Palaemonetes vulgaris*.

Facultative resident species, such as pigfish, pinfish, sheephead, and tautog, were present as juveniles on the oyster shell habitat (Appendix II). Though also present in on the ash pellet reef, these species were more frequently encountered in samples collected form the oyster shell habitat. The living veneer of oysters that formed on the oyster shell habitat by the time of this investigation and higher benthic secondary productivity (see chapter 3, of this dissertation) may have had some influence on the development of these abundant and diverse nekton assemblages associated with this habitat.

This study demonstrates the profound use by nekton of constructed oyster reef habitats. High densities of nekton on structurally complex habitat types suggest these habitats should be designed to provide adequate refuge, not only for the oysters they are intended to support, but for also the multitude of reef macroinvertebrates and nekton that utilize the reef matrix as for foraging on the high benthic secondary productivity and as shelter from transient predatory species.

Table 1: Summary of the nekton catches from each habitat at Fisherman's Island during this study. Data presented are raw numbers per enclosure net sample and are not adjusted to take into account different lengths of habitat sampled by the gear with each replicate. Values for the Ash, Clam Shell, and Oyster Shell habitats are totaled across 2 replicates collected monthly over 6 months. Values for the bare-sand beach habitat are totaled across two replicates collected monthly over 3 months. Habitat use categories are denoted in parentheses after each species name adapted from Breitburg (1999) and Baltz (1993): R = resident oyster reef species, F = facultative oyster reef species, DT = demersal transient species; NT = nektonic transient species. See text for further descriptions.

Species Name	Common Name	Habitat Use	ASH	CLAM	OYSTER	BEACH	Total	overall species rank
Anchoa hepsetus	striped anchovy	NT	0	0	42	0	42	10
Archosargus probatocephalus	sheepshead	F	2	0	10	0	12	17
Bairdiella chrysoura	silver perch	DT	1	0	22	0	23	15
Callinectes sapidus	blue crab	DT	67	43	14	20	144	6
Centropristis striata	black sea bass	F	4	1	3	0	8	20
Chasmodes bosquianus	striped blenny	R	6	0	2	0	8	20
Chaetodon ocellatus	spotfin butterflyfish	F	2	0	0	0	2	24
Cyprinodon variegatus	sheepshead minnow	DT	8	0	0	4	12	17
Epinephelus sp.	grouper	F	1	0	0	0	1	25
Eucinostomus argenteus	spotfin mojarra	DT	2	0	1	0	3	23
Eucinostomus gula	silver jenny	DT	2	1	2	6	11	18
Fundulus heteroclitus	mummichog	DT	1884	22	30	603	2539	3
Fundulus majalis	striped killifish	DT	607	3	0	357	967	4
Gobiosoma bosc	naked goby	R	16	5	18	0	39	11
Gobiosoma ginsburgi	seaboard goby	R	10	9	6	0	25	14
Hypsoblennius hentz	feather blenny	R	4	0	19	0	23	15
Lagodon rhomboides	pinfish	F	3	4	36	0	43	9
Leiostomus xanthurus	spot	DT	13	6	15	5	39	11
Lucania parva	rainwater killifish	DT	300	1	26	7	334	5
Lutjanus griseus	gray snapper	F	0	0	4	0	4	22
Membras martinica	rough silverside	NT	1638	895	5011	656	8200	1
Morone saxatilis	striped bass	NT	10	0	0	0	10	19
Mugil curema	white mullet	NT	9	8	0	2	19	16
Mycteroperca microlepis	gag	F	0	0	1	0	1	25
Opsanus tau	oyster toadfish	R	0	0	7	0	7	21
Orthopristus chrysoptera	pigfish	F	1	0	31	0	32	12
Palaemonetes vulgaris	grass shrimp	DT	1724	490	5607	7	7828	2
Paralichthys dentatus	summer flounder	DT	6	33	5	1	45	8
Penaeus aztecus	brown shrimp	DT	21	5	1	2	29	13
Peprilus triacanthus	butterfish	DT	1	0	0	0	1	25
Prionotus carolinus	northern searobin	DT	0	1	0	0	1	25
Scorpaena plumeiri	scorpionfish	DT	0	1	0	0	1	25
Sphyreana borealis	northern sennet	NT	0	0	4	0	4	22
Sphoeroides maculatus	northern puffer	DT	0	0	1	0	1	25
Strongylura marina	Atlantic needlefish	NT	3	0	0	0	3	23
Syngnathus floridae	dusky pipefish	F	0	0	1	0	1	25
Syngnathus fuscus	northern pipefish	F	25	14	26	0	65	7
Symphurus plagiusa	blackcheek tonguefish	DT	2	0	0	2	4	22
Synodus foetens	inshore lizardfish	DT	0	0	1	0	1	25
Tautog onitis	tautog	F	1	1	6	0	8	20
	Grand Total		**6373**	**1543**	**10952**	**1672**	**20540**	

Table 2: Number of species within each habitat use category (adapted from Breitburg (1999) and Baltz (1993)) collected from each habitat type at Fisherman's Island between April and October 1999.

Habitat Use	ASH	CLAM	OYSTER	BEACH
Resident	4	2	5	0
Facultative Resident	8	4	9	0
Demersal Transient	14	11	12	11
Nektonic Transient	4	2	3	2
Totals	30	19	29	13

Table 3: Results of ANOVA tests and Tukey multiple comparisons tests for differences in total nekton abundance ($\log_{10}$ (Abundance + 1)) among reef type (A – coal ash, C – clam shell, O – oyster shell) for all months sampled in 1999 (Ap – April, M – May, Jn – June, Jy – July, Ag – August, O – October) and among habitat type (A - . coal ash, C – clam shell, O – oyster shell, B – bare-sand beach) for July through October 1999. *P* values < 0.05 are in bold. Reef types with underlines that overlap are not statistically different at $P < 0.05$.

Source (DF)	**SS**	**MS**	**F**	***P***	**Tukey**
Reefs only					
Month (5)	3.11	0.62	2.72	**0.05**	**M O Jy Ap Ag Jn**
Reef (2)	3.34	1.67	7.29	**0.005**	**C A O**
Month*Reef (10)	2.53	0.25	1.11	0.41	
Reefs and Beach					
Month (2)	0.66	0.33	4.74	**0.03**	**O Jy Ag**
Habitat (3)	2.28	0.76	10.87	**0.001**	**C B A O**
Month*Habitat (6)	1.49	258.6	3.54	**0.03**	

Figure 1: Schematic of Fisherman's Island study area showing orientation of the constructed oyster reef habitats. Stars indicate the location of enclosure trap sampling stations adjacent to reefs and a bare-sand beach habitat.

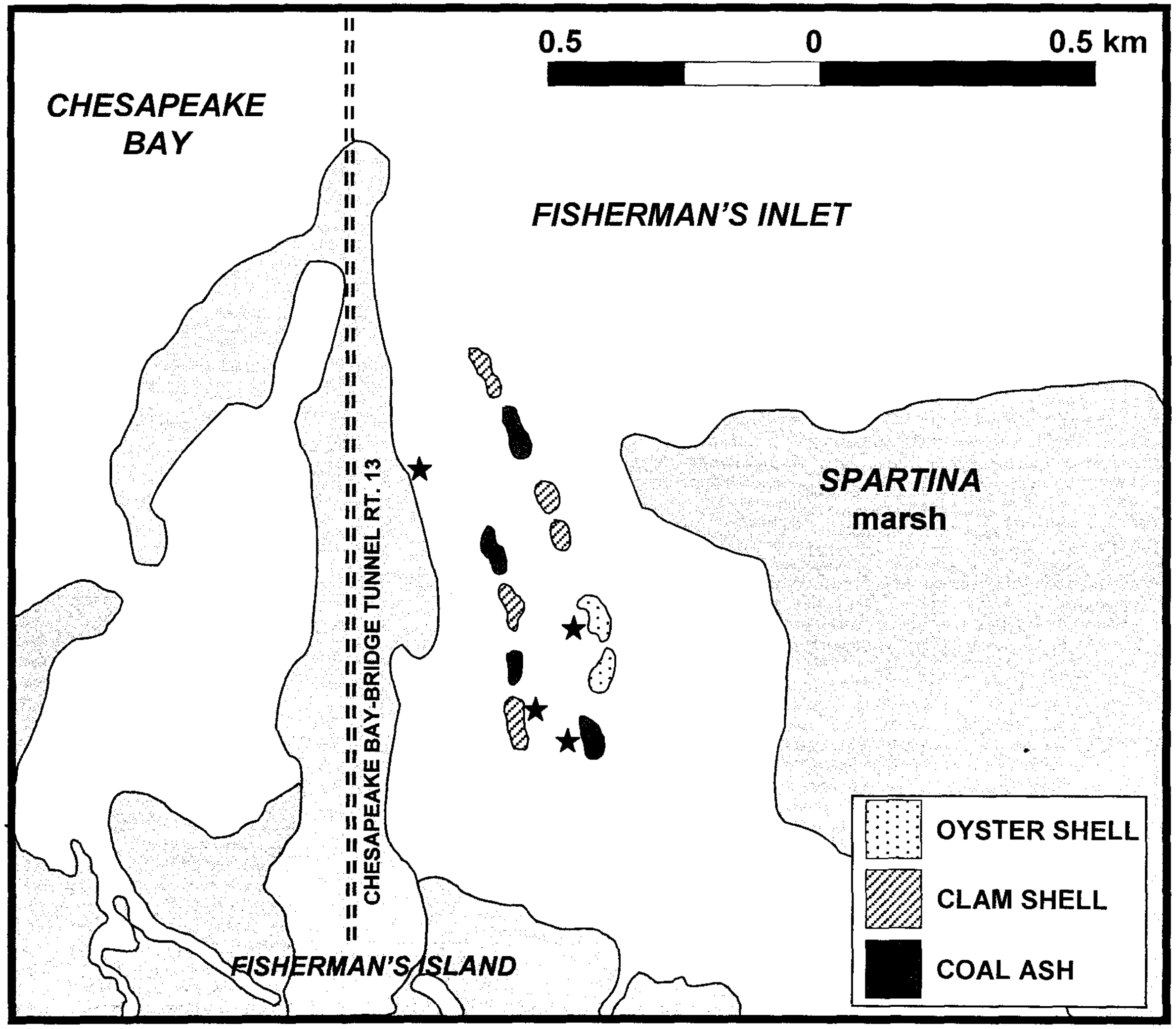

CHESAPEAKE BAY
0.5
0
0.5 km
FISHERMAN'S INLET
SPARTINA marsh
CHESAPEAKE BAY-BRIDGE TUNNEL RT. 13
FISHERMAN'S ISLAND
OYSTER SHELL
CLAM SHELL
COAL ASH

Figure 2: Mean water temperature and salinity (+SE) recorded at the Fisherman's Island study area over each monthly three-consecutive day sampling period from April to October 1999.

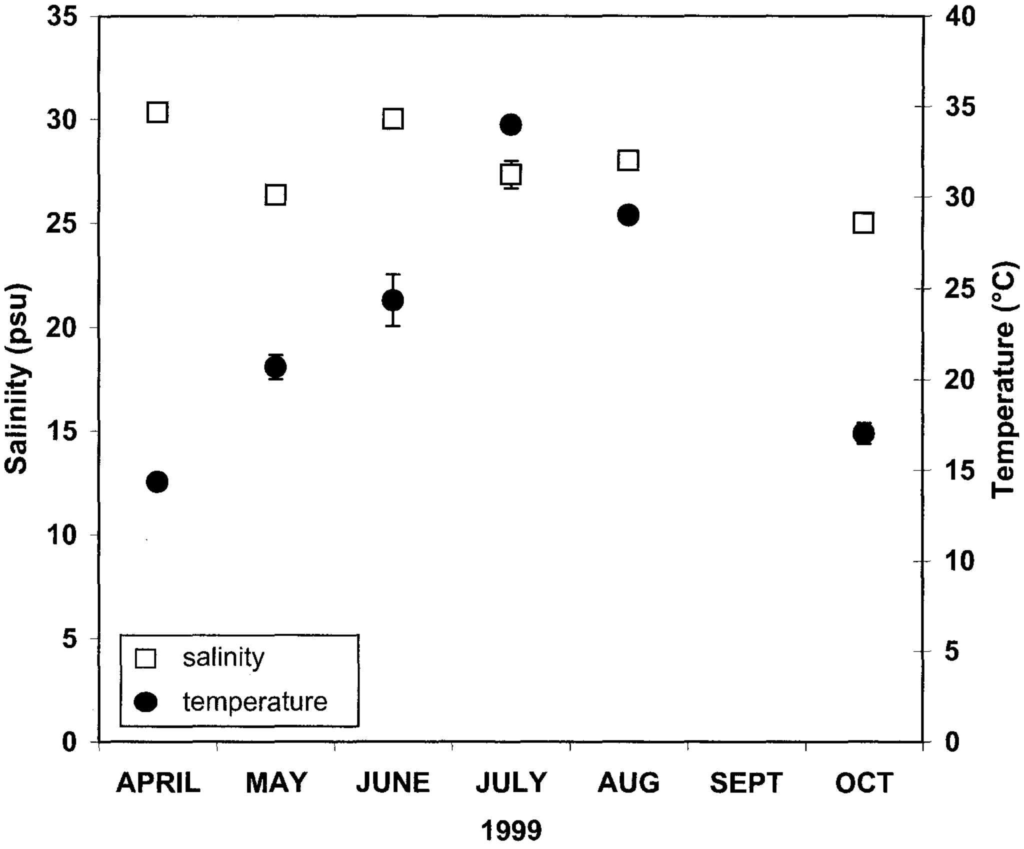

35
30
25
20
15
10
5
0
Salinity (psu)
40
35
30
25
20
15
10
5
0
Temperature (°C)
☐ salinity
● temperature
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT
1999

Figure 3: Fish species caught during 1999 using enclosure trap gear at the Fisherman's Island reef area. Shaded lines span the time interval during which a species was collected. Shading within these lines corresponds with the habitat type.

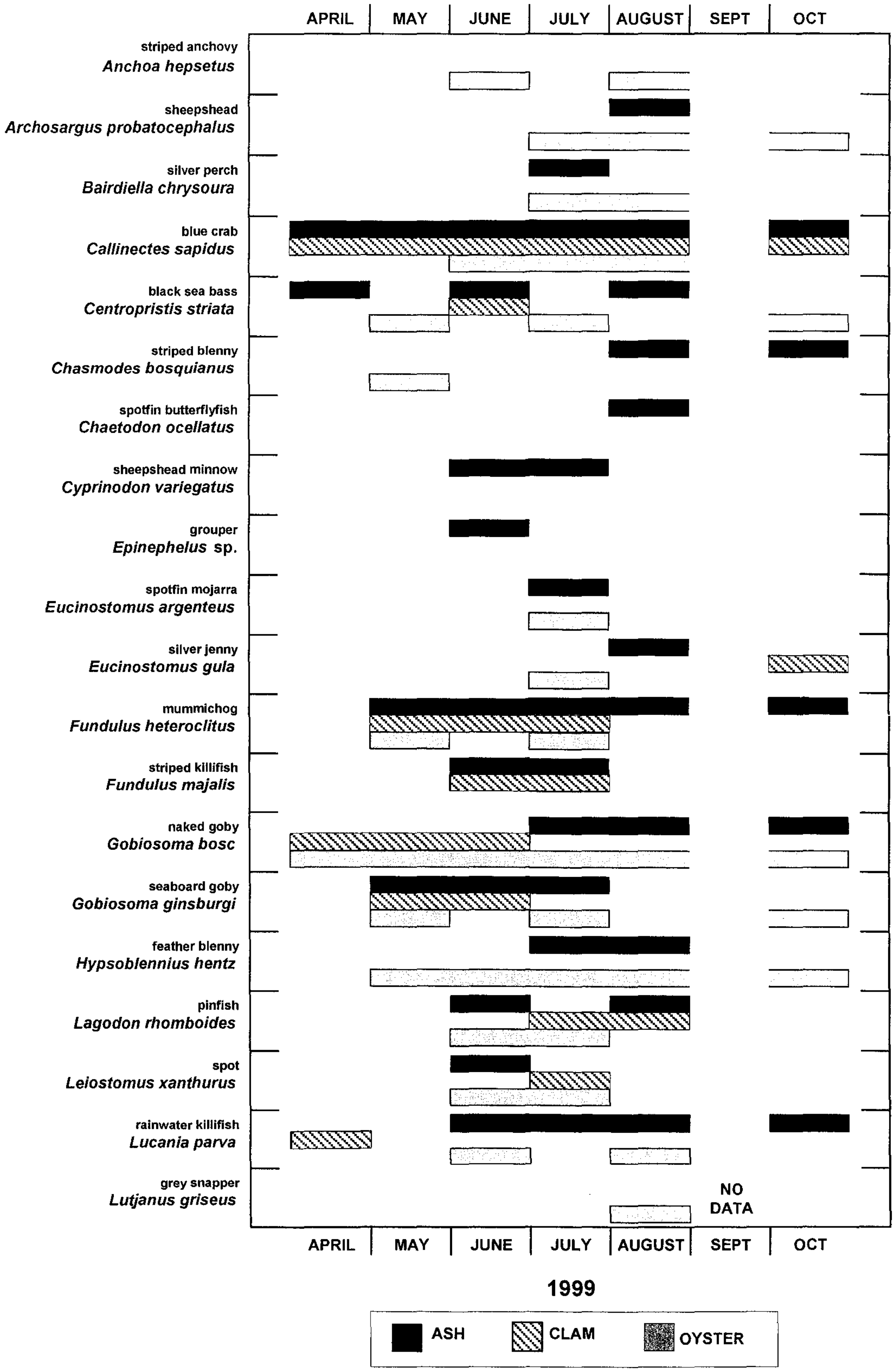

APRIL
MAY
JUNE
JULY
AUGUST
SEPT
OCT
striped anchovy
Anchoa hepsetus
sheepshead
Archosargus probatocephalus
silver perch
Bairdiella chrysoura
blue crab
Callinectes sapidus
black sea bass
Centropristis striata
striped blenny
Chasmodes bosquianus
spotfin butterflyfish
Chaetodon ocellatus
sheepshead minnow
Cyprinodon variegatus
grouper
Epinephelus sp.
spotfin mojarra
Eucinostomus argenteus
silver jenny
Eucinostomus gula
mummichog
Fundulus heteroclitus
striped killifish
Fundulus majalis
naked goby
Gobiosoma bosc
seaboard goby
Gobiosoma ginsburgi
feather blenny
Hypsoblennius hentz
pinfish
Lagodon rhomboides
spot
Leiostomus xanthurus
rainwater killifish
Lucania parva
grey snapper
Lutjanus griseus
NO DATA
APRIL
MAY
JUNE
JULY
AUGUST
SEPT
OCT
1999
ASH
CLAM
OYSTER

FIGURE 3 CONTINUED

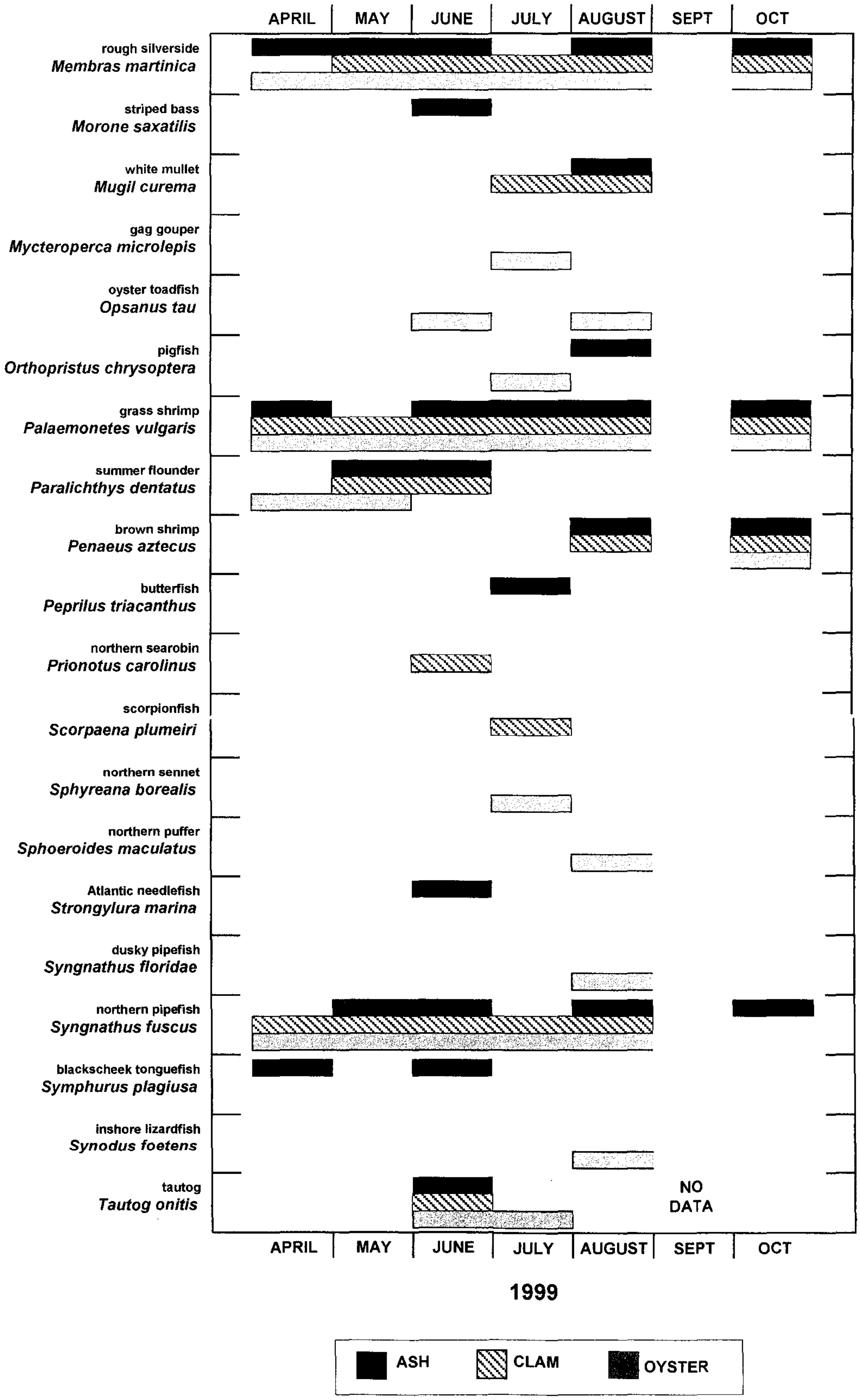


Figure 4: Univariate community indices calculated from species density measurements from each sample using Primer. Asterisks (*) indicate no data were collected April through June from the beach habitat. No data were collected from any habitat in September 1999 due to Hurricane Floyd.

A) Observed species richness, *S*

B) Shannon diversity index (*H'*) using $\log_2$

C) Pielou's evenness (*J'*)

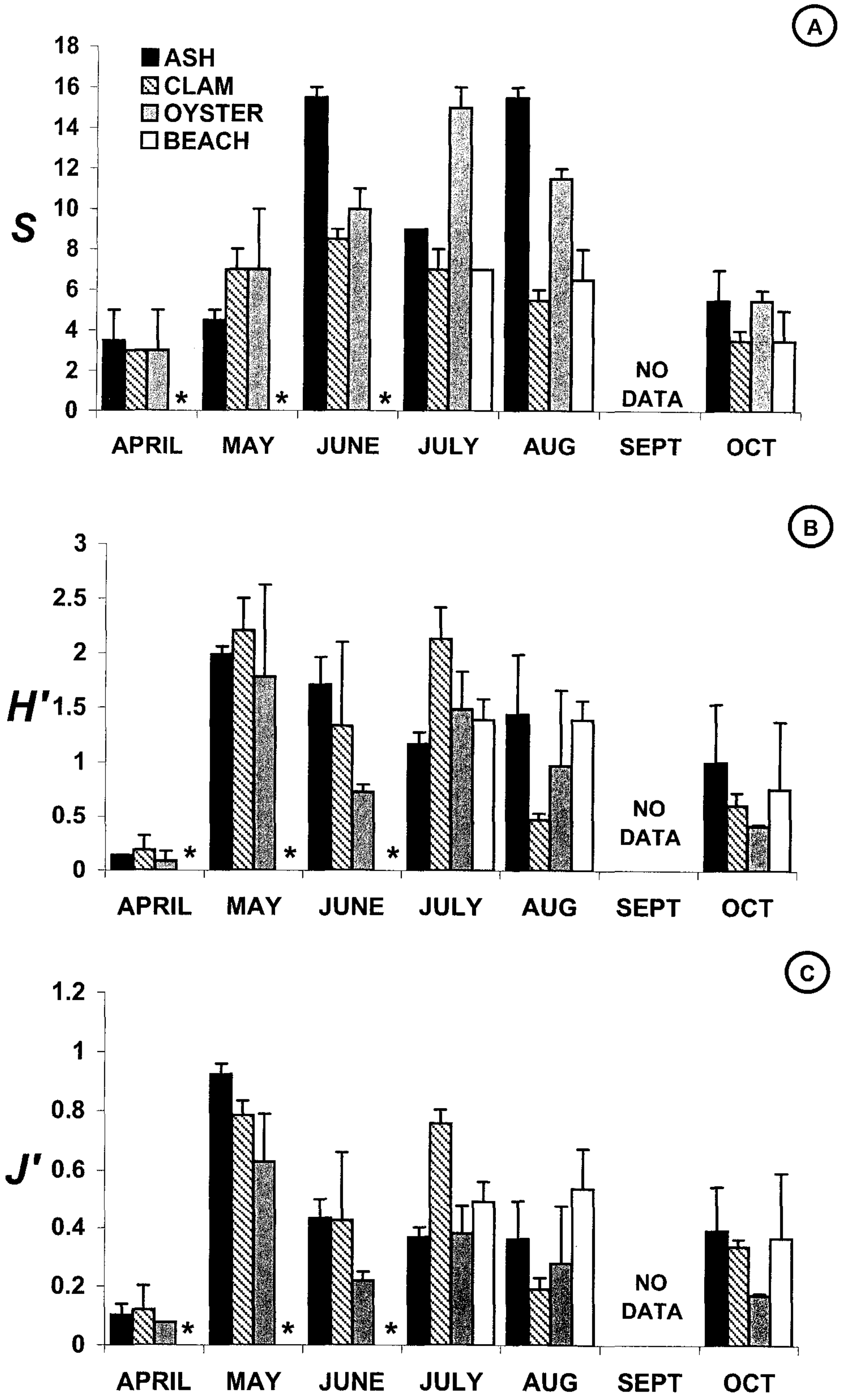

A
S
18
16
14
12
10
8
6
4
2
0
■ ASH
▨ CLAM
▩ OYSTER
☐ BEACH
*
*
*
NO DATA
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT
B
H'
3
2.5
2
1.5
1
0.5
0
*
*
*
NO DATA
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT
C
J'
1.2
1
0.8
0.6
0.4
0.2
0
*
*
*
NO DATA
APRIL
MAY
JUNE
JULY
AUG
SEPT
OCT

Figure 5: Mean total abundance (+SE) of nekton per linear meter of reef edge (or bare-sand beach habitat) for each sampling period calculated from two replicate sampled collected over two consecutive days. Asterisks (*) indicate no data were collected April through June from the beach habitat. No data were collected from any habitat in September 1999 due to concurrence of Hurricane Floyd with the planned sampling period.

A) Mean total abundance of all species across each habitat type and sampling period.
B) Mean total abundance omitting the numerical dominant *Membras martinica* to elucidate patterns of intermediate abundant species.
C) Mean total abundance omitting *Membras martinica* and *Palaemonetes vulgaris* to further elucidate patterns of intermediate abundant species.

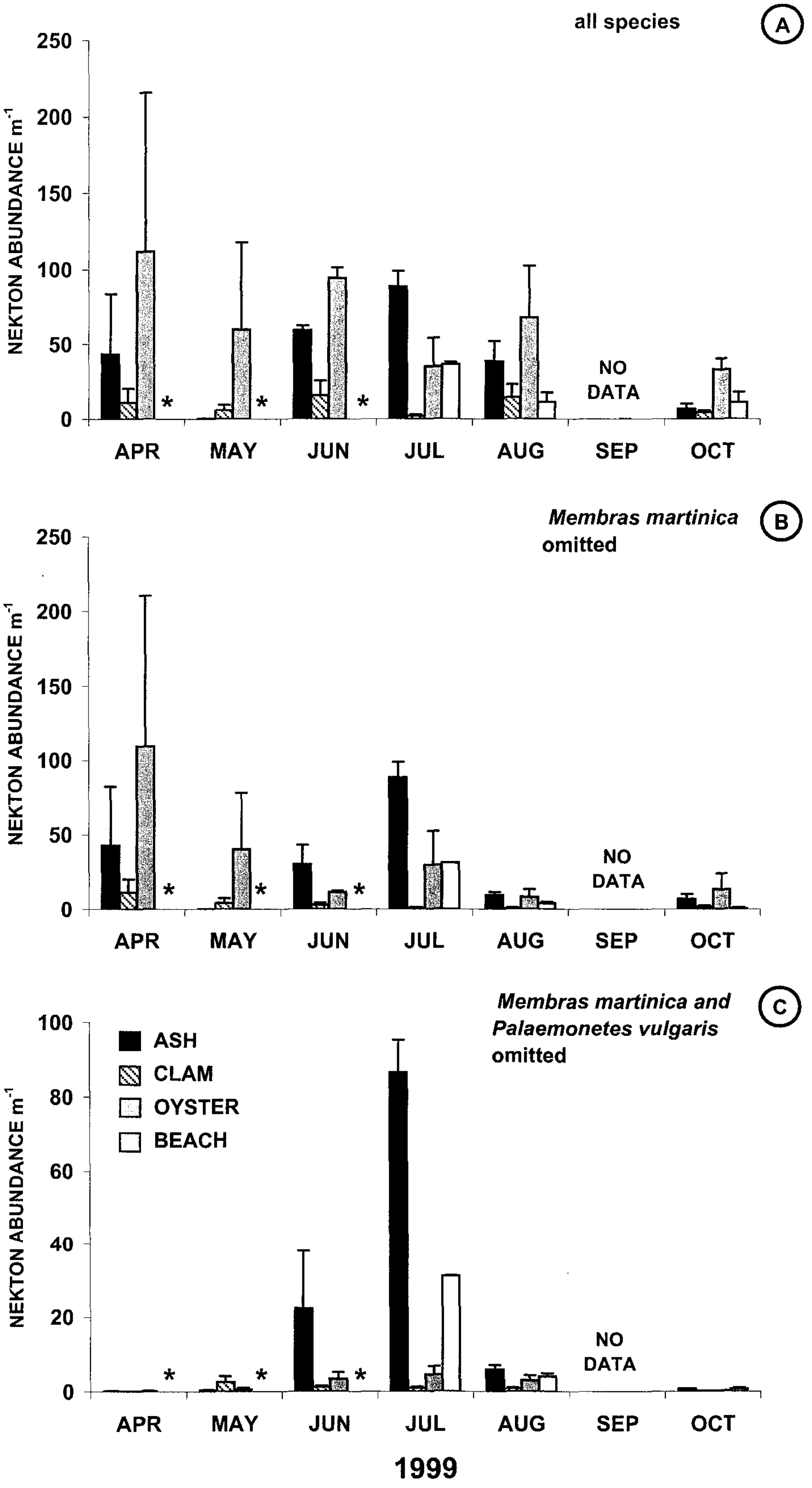

all species
A
NEKTON ABUNDANCE m^{-1}
250
200
150
100
50
0
*
*
*
NO DATA
APR
MAY
JUN
JUL
AUG
SEP
OCT
Membras martinica
omitted
B
NEKTON ABUNDANCE m^{-1}
250
200
150
100
50
0
*
*
*
NO DATA
APR
MAY
JUN
JUL
AUG
SEP
OCT
Membras martinica and
Palaemonetes vulgaris
omitted
C
■ ASH
▨ CLAM
☐ OYSTER
☐ BEACH
NEKTON ABUNDANCE m^{-1}
100
80
60
40
20
0
*
*
*
NO DATA
APR
MAY
JUN
JUL
AUG
SEP
OCT
1999

Figure 6: Mean nekton abundance per linear meter of habitat sampled with the enclosure trap gear (with SE) for July, August, and October 1999. The coal ash pellet reef and bare-sand beach habitat exhibited slopes for temporal abundance patterns different than those of the clam shell and oyster shell reefs, explaining the significant interaction observed between habitat type and sampling period (ANOVA, $p = 0.03$).

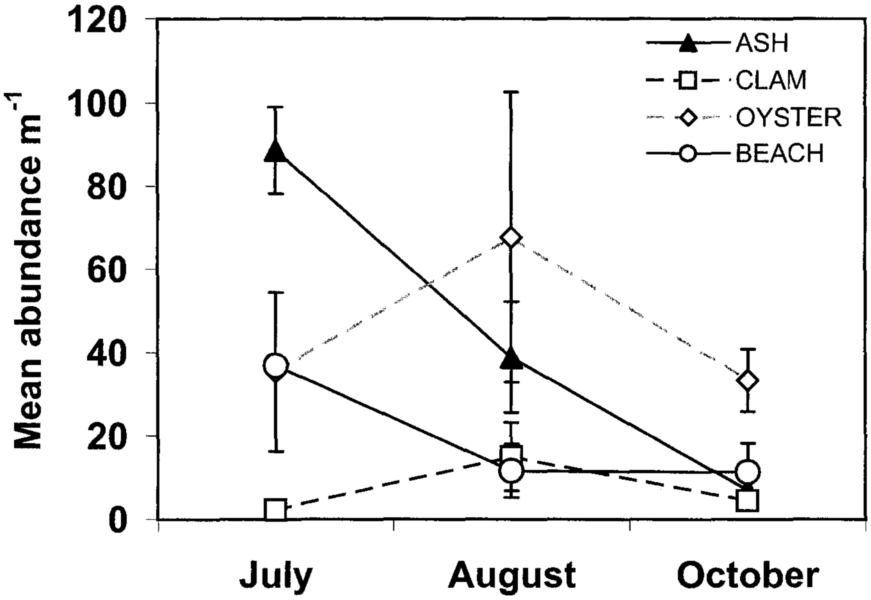

120
100
80
60
40
20
0
Mean abundance m^{-1}
ASH
CLAM
OYSTER
BEACH
July
August
October

Figure 7: Multi-dimensional scaling (MDS) ordination of the 36 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs at Fisherman's Island between April and October 1999. MDS ordination is based on square-root transformed abundances on Bray-Curtis similarities (stress = 0.19) with superimposed clusters from Figure 8 at similarity levels of 30% (solid ovals) and 45% (dashed ovals). The small number next to each symbol corresponds with the sample label designated in the dendrogram in Figure 8. Larger grey shaded numbers within the ovals correspond to the assigned groups separated at the 45% threshold in Figure 8.

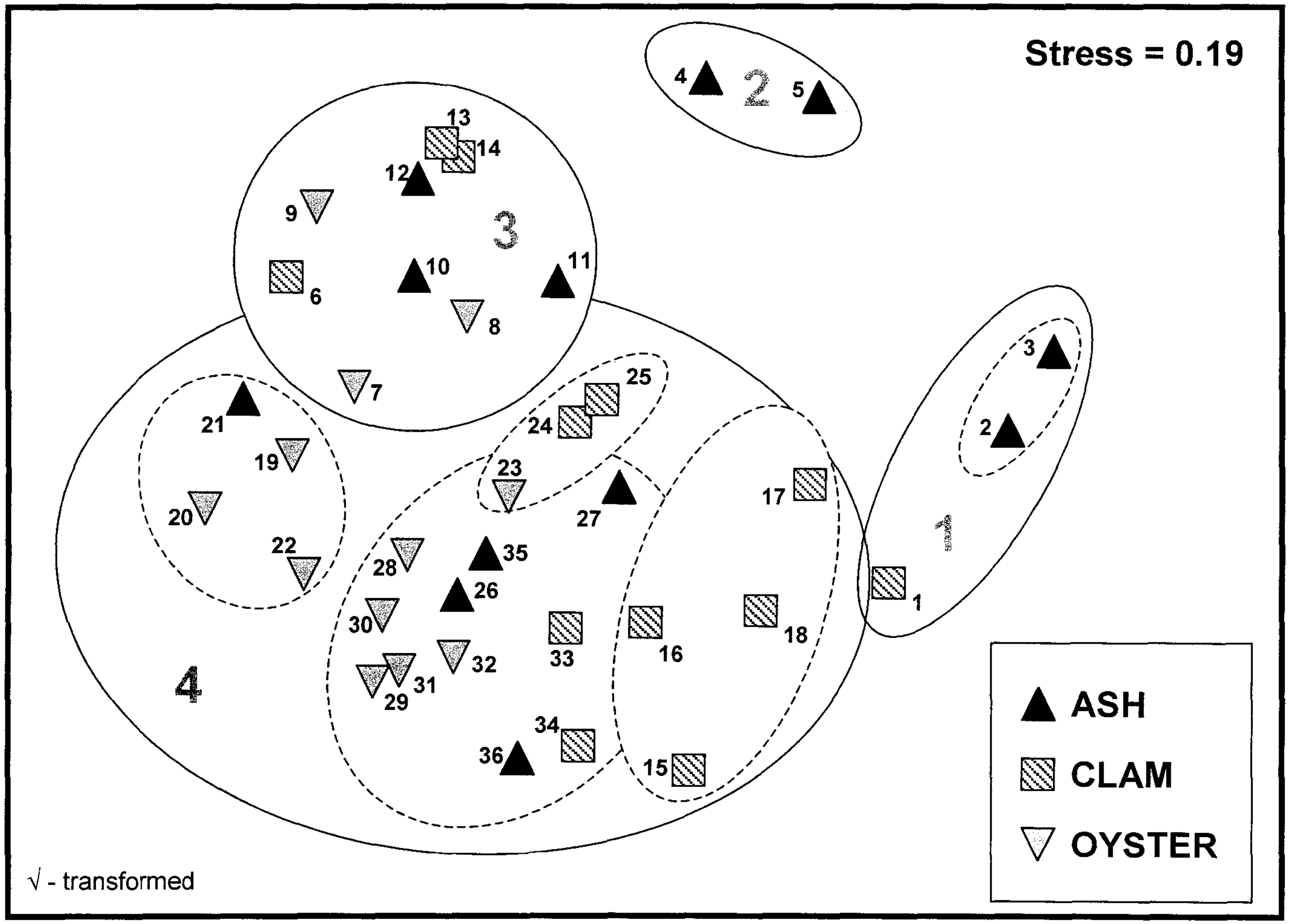

Stress = 0.19
1
2
3
4
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
ASH
CLAM
OYSTER
√ - transformed

Figure 8: Dendrogram of the 36 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs at Fisherman's Island between April and October 1999. Dendrogram is based on group-average clustering from Bray-Curtis similarities on square-root transformed abundances. The number (1-36) preceding the sample label along the horizontal axis corresponds with the MDS ordination plot in Figure 7. The four groups of samples separated at a 40% threshold (solid line) are indicated by circled numbers 1, 2, 3, and 4 . These numbers correspond to the larger grey shaded numbers within the ovals in Figure 7.

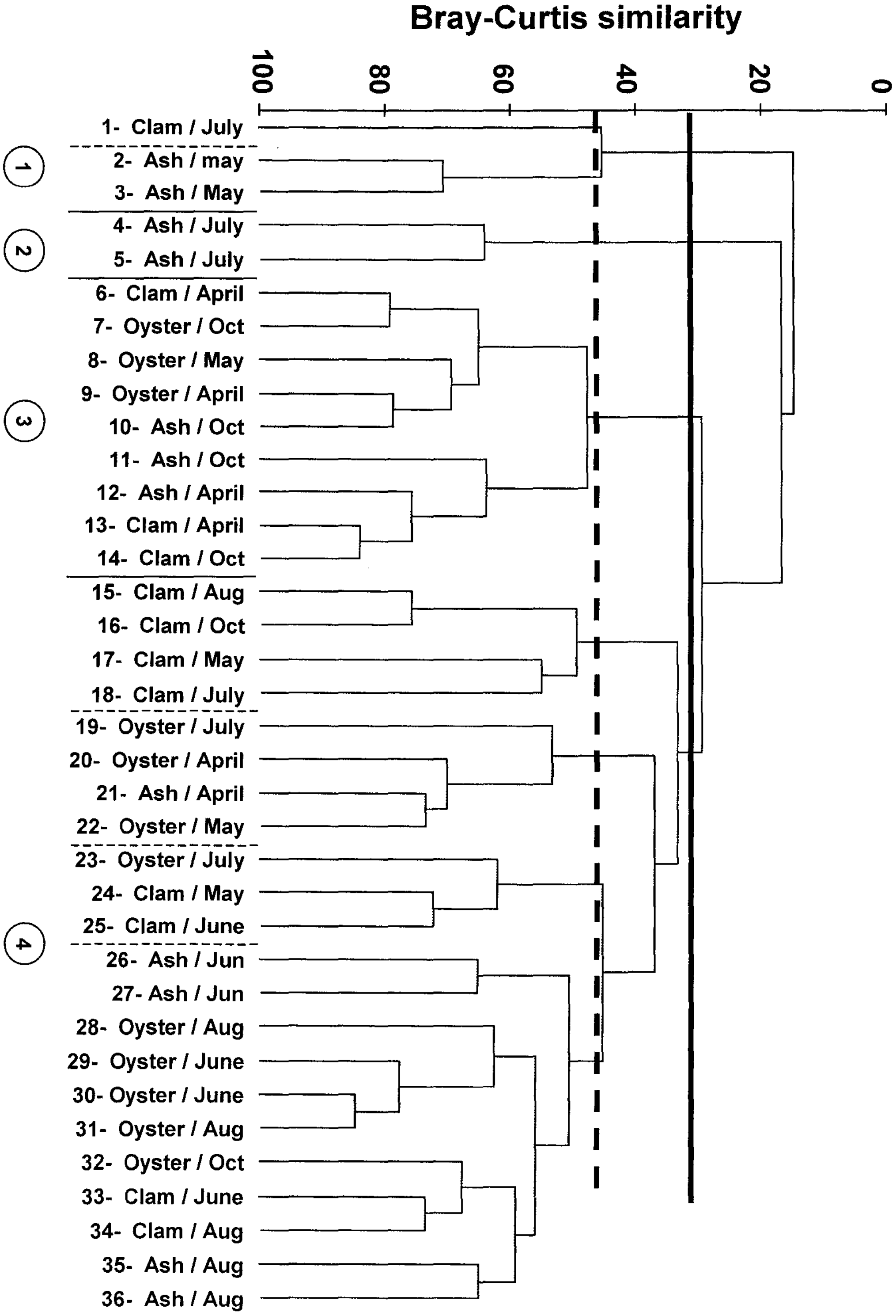
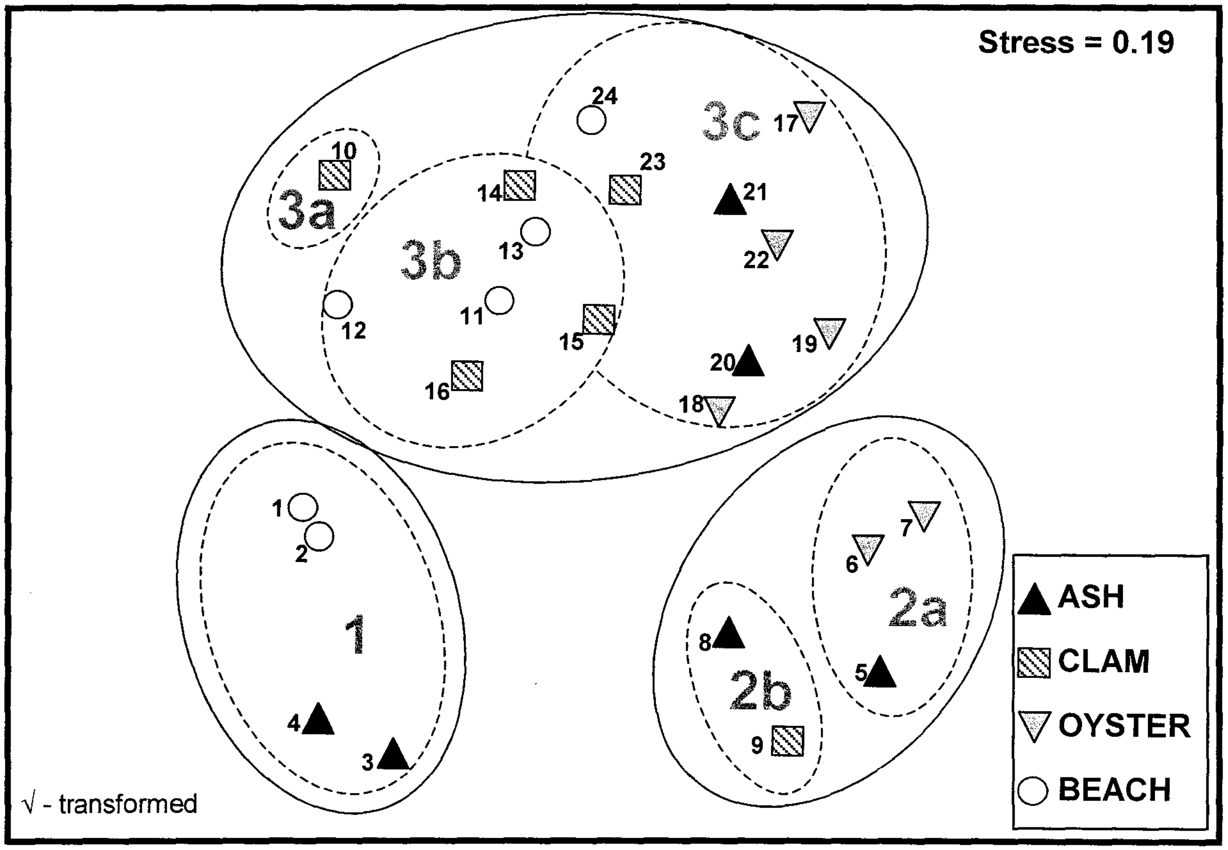

Bray-Curtis similarity
100
80
60
40
20
0
1- Clam / July
2- Ash / may
3- Ash / May
4- Ash / July
5- Ash / July
6- Clam / April
7- Oyster / Oct
8- Oyster / May
9- Oyster / April
10- Ash / Oct
11- Ash / Oct
12- Ash / April
13- Clam / April
14- Clam / Oct
15- Clam / Aug
16- Clam / Oct
17- Clam / May
18- Clam / July
19- Oyster / July
20- Oyster / April
21- Ash / April
22- Oyster / May
23- Oyster / July
24- Clam / May
25- Clam / June
26- Ash / Jun
27- Ash / Jun
28- Oyster / Aug
29- Oyster / June
30- Oyster / June
31- Oyster / Aug
32- Oyster / Oct
33- Clam / June
34- Clam / Aug
35- Ash / Aug
36- Ash / Aug
①
②
③
④

Figure 9: Multi-dimensional scaling (MDS) ordination of the 24 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs and a bare-sand beach habitat between July and October 1999. The two-dimensional MDS ordination is based on square-root transformed abundances on Bray-Curtis similarities (stress = 0.19) with superimposed clusters from Figure 10 at similarity levels of 30% (solid ovals) and 40% (dashed ovals). The small number next to each symbol corresponds with the sample label designated in the dendrogram in Figure 10. Larger grey shaded numbers within the ovals correspond to the assigned groups separated at the 40% threshold in Figure 10.



Stress = 0.19
3a
3b
3c
1
2a
2b
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
▲ ASH
▨ CLAM
▽ OYSTER
○ BEACH
√ - transformed

Figure 10: Dendrogram of the 24 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs and a bare-sand beach habitat between July and October 1999. Dendrogram is based on group-average clustering from Bray-Curtis similarities on square-root transformed abundances. The number (1-24) preceding the sample label along the horizontal axis corresponds with the MDS ordination plot in Figure 9. The three groups of samples separated at a 40% threshold (solid line) and six subgroups are indicated by circled numbers 1, 2a, 2b, 3a, 3b, and 3c. These numbers also correspond to the larger grey shaded numbers within the ovals in Figure 9.

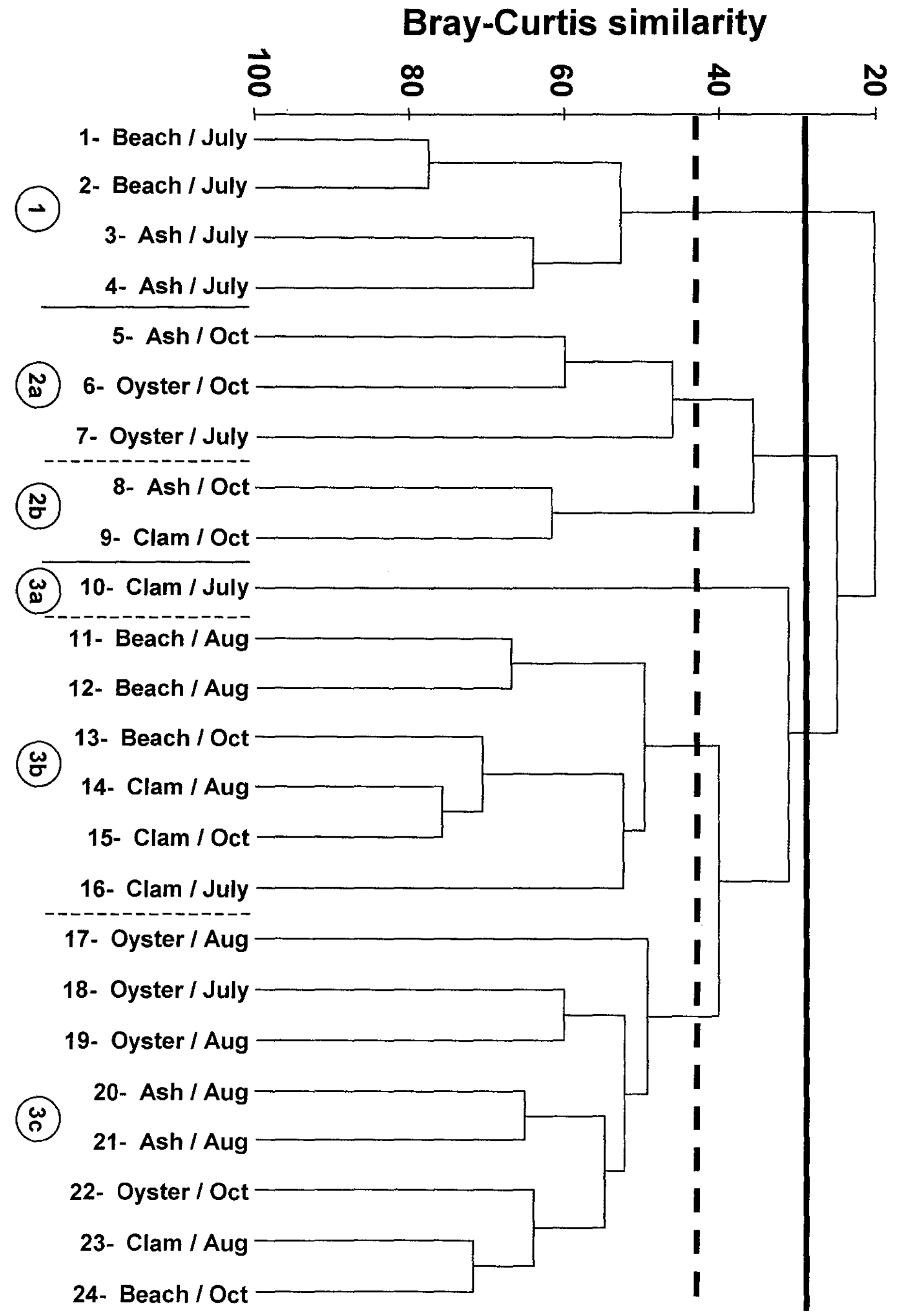

Bray-Curtis similarity
100
80
60
40
20
1- Beach / July
2- Beach / July
3- Ash / July
4- Ash / July
5- Ash / Oct
6- Oyster / Oct
7- Oyster / July
8- Ash / Oct
9- Clam / Oct
10- Clam / July
11- Beach / Aug
12- Beach / Aug
13- Beach / Oct
14- Clam / Aug
15- Clam / Oct
16- Clam / July
17- Oyster / Aug
18- Oyster / July
19- Oyster / Aug
20- Ash / Aug
21- Ash / Aug
22- Oyster / Oct
23- Clam / Aug
24- Beach / Oct
1
2a
2b
3a
3b
3c

Figure 11: Multi-dimensional scaling (MDS) ordination of the 24 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs and a bare-sand beach habitat between July and October 1999. The two-dimensional MDS ordination is based on presence-absence transformed abundances on Bray-Curtis similarities (stress = 0.19) with superimposed clusters from Figure 12 at similarity levels of 30% (solid ovals) and 45% (dashed ovals). The small number next to each symbol corresponds with the sample label designated in the dendrogram in Figure 12. Larger grey shaded numbers within the ovals correspond to the assigned groups separated at the 45% threshold in Figure 12.

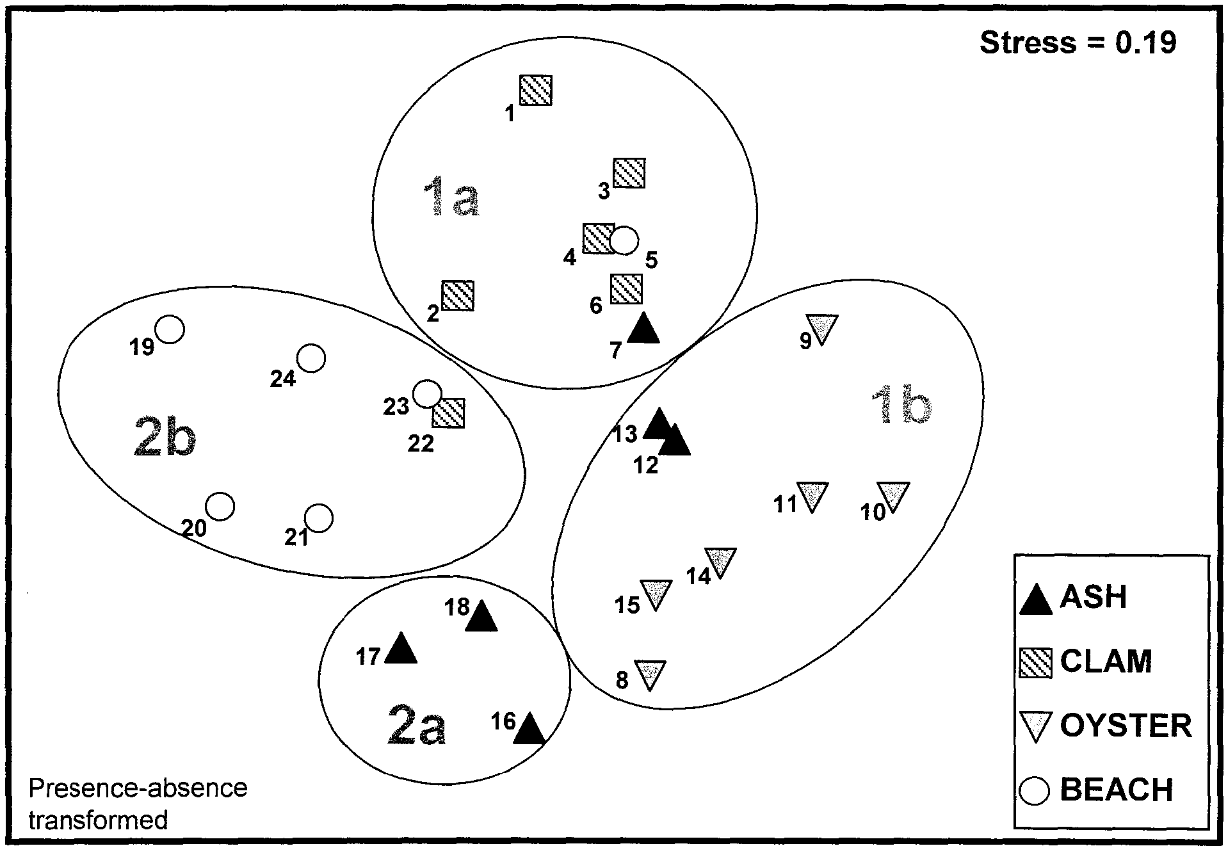
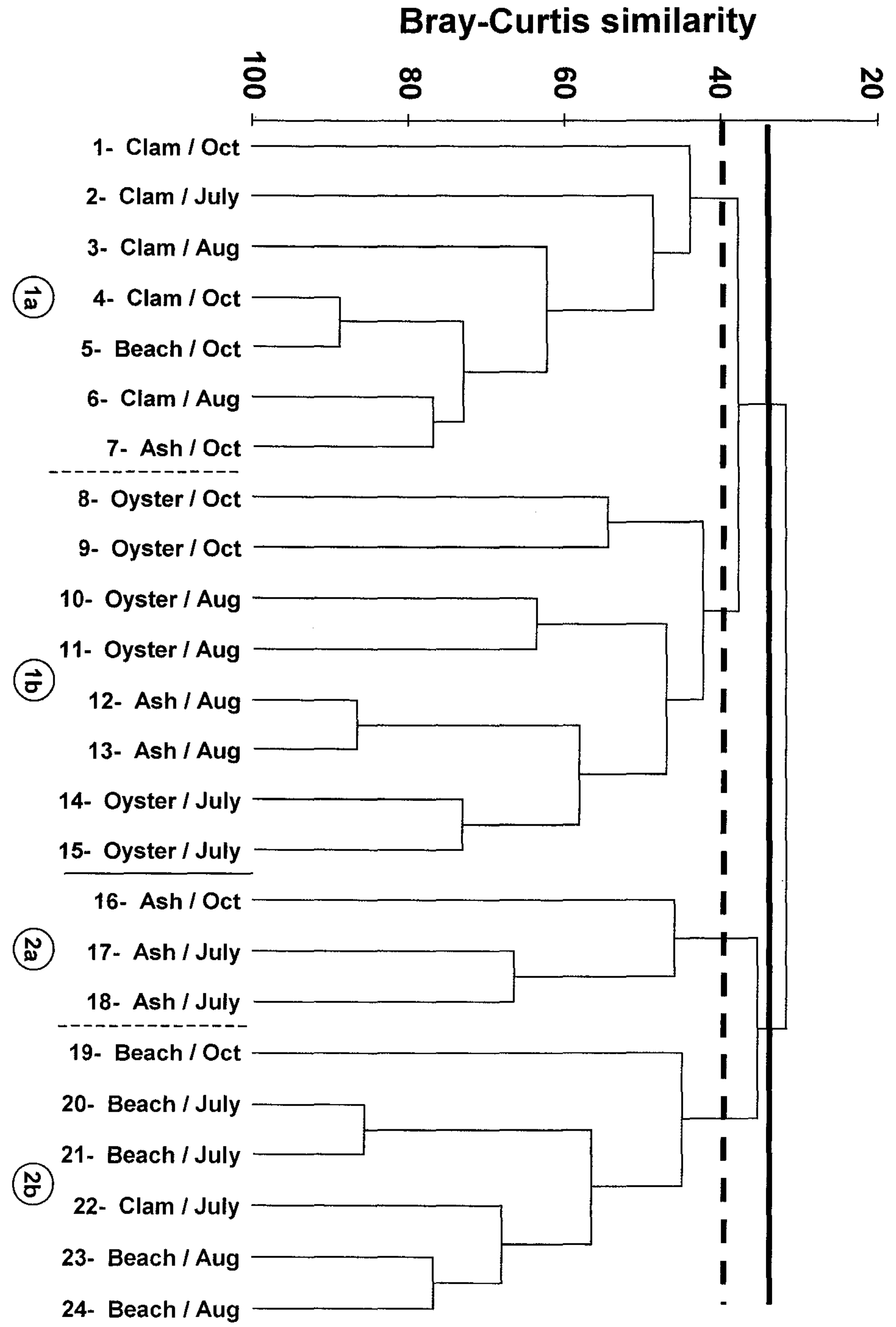

Stress = 0.19
1
1a
3
4
5
2
6
7
9
1b
19
24
23
22
2b
13
12
11
10
20
21
14
15
18
17
8
2a
16
ASH
CLAM
OYSTER
BEACH
Presence-absence transformed

Figure 12: Dendrogram of the 24 enclosure trap samples collected from oyster shell, clam shell, and coal ash pellet reefs and a bare-sand beach habitat between July and October 1999. Dendrogram is based on group-average clustering from Bray-Curtis similarities on presence-absence transformed abundances. The 35% similarity threshold (solid line) separates the samples into two groups. These groups are further subdivided into four groups by the 45% similarity threshold (dotted line). These groups, 1a, 1b, 2a, and 2b, correspond to the larger grey shaded numbers within the ovals in Figure 11. The number (1-24) preceding the sample label along the horizontal axis corresponds with the MDS ordination plot in Figure 11.


Bray-Curtis similarity
100
80
60
40
20
1- Clam / Oct
2- Clam / July
3- Clam / Aug
4- Clam / Oct
5- Beach / Oct
6- Clam / Aug
7- Ash / Oct
8- Oyster / Oct
9- Oyster / Oct
10- Oyster / Aug
11- Oyster / Aug
12- Ash / Aug
13- Ash / Aug
14- Oyster / July
15- Oyster / July
16- Ash / Oct
17- Ash / July
18- Ash / July
19- Beach / Oct
20- Beach / July
21- Beach / July
22- Clam / July
23- Beach / Aug
24- Beach / Aug
1a
1b
2a
2b

Appendix I: Life Form code for noncolonial macrofaunal species (based on Larsen 1974). First digit represents feeding type [(1) carnivores, including carrion feeders; (2) omnivores, including general scavengers; (3) deposit feeders, including detritivores and herbivores; and (4) suspension feeders], second digit represents purchase type [(1) motile epifauna; (2) attached epifauna; (3) free infauna; and (4) tube-dwelling infauna, including those with semi-permanent burrows], and third digit represents dispersal type [(1) nonpelagic; (2) short pelagic, i.e. two or three days; (3) pelagic].

Taxa	Life Form Code	References
Cnidaria		
Hydrozoa		
Sertularia argentea	423	Barnes 1980
Anthozoa		
Diadumene leucolena	122	Larsen 1974, Holland et al. 1988
Haliplanella luciae	423	Barnes 1980
Platyhelminthes		
Turbellaria		
Stylochus ellipticus	113	Larsen 1974, Holland et al. 1988
Rhynchocoela		
Cerebratulus lacteus	131	Larsen 1974
Tubulanus pellucidus	131	Larsen 1974
Nemertean a	131	Larsen 1974
Annelida		
Polychaeta		
Asychis elongata	343	Larsen 1974; Ulanowicz et al. 1998
Capitellidae spp	343	Gaston et al. 1998; Ulanowicz et al. 1998
Cirriforma grandis	343	George 1980; Ulanowicz et al. 1998
Clymenella torquata	343	Larsen 1974; Ulanowicz et al. 1998

Appendix I: Life Form code for noncolonial macrofaunal species (based on Larsen 1974). First digit represents feeding type [(1) carnivores, including carrion feeders; (2) omnivores, including general scavengers; (3) deposit feeders, including detritivores and herbivores; and (4) suspension feeders], second digit represents purchase type [(1) motile epifauna; (2) attached epifauna; (3) free infauna; and (4) tube-dwelling infauna, including those with semi-permanent burrows], and third digit represents dispersal type [(1) nonpelagic; (2) short pelagic, i.e. two or three days; (3) pelagic].

Taxa	Life Form Code	References
Cnidaria		
Hydrozoa		
Sertularia argentea	423	Barnes 1980
Anthozoa		
Diadumene leucolena	122	Larsen 1974, Holland et al. 1988
Haliplanella luciae	423	Barnes 1980
Platyhelminthes		
Turbellaria		
Stylochus ellipticus	113	Larsen 1974, Holland et al. 1988
Rhynchocoela		
Cerebratulus lacteus	131	Larsen 1974
Tubulanus pellucidus	131	Larsen 1974
Nemertean a	131	Larsen 1974
Annelida		
Polychaeta		
Asychis elongata	343	Larsen 1974; Ulanowicz et al. 1998
Capitellidae spp	343	Gaston et al. 1998; Ulanowicz et al. 1998
Cirriforma grandis	343	George 1980; Ulanowicz et al. 1998
Clymenella torquata	343	Larsen 1974; Ulanowicz et al. 1998

Appendix I. continued

Taxa	**Life Form Code**	**References**
Polychaeta (continued)		
Drilonereis longa	133	Larsen 1974
Drilonereis magna	133	Larsen 1974
Eteone heteropoda	113	Larsen 1974
Eusyllis lamelligera	113	Larsen 1974
Glycera americana	243	Larsen 1974
Glycera dibranchiata	243	Larsen 1974
Glycinde solitaria	133	Larsen 1974; Holland et al. 1988
Heteromastus filiformis	343	Larsen 1974; Ulanowicz et al. 1998
Hydroides dianthus	422	Larsen 1974
Laeonereis culveri	343	Pettibone 1963; Holland et al. 1988
Leitoscoloplos spp	332	Pettibone 1963
Lepidonotus sublevis	113	Pettibone 1963; Holland et al. 1988
Nereis succinea	233	Larsen 1974; Holland et al. 1988
Paleanotus heteroseta	113	Larsen 1974
Paraprionospio pinnata	343	Larsen 1974
Pectinaria gouldii	343	Larsen 1974; Holland et al. 1988
Piromis eruca	333	Blake 2000
Pista palmata	343	Pettibone 1963; Ulanowicz et al. 1998
Podarke obscura	133	Pettibone 1963
Polydora websteri	323	Larsen 1974; Holland et al. 1988
Sabellaria vulgaris	423	Larsen 1974; Holland et al. 1988
Scoletoma fragilis	131	Larsen 1974; Ulanowicz et al. 1998
Scoletoma tenuis	343	Ulanowicz et al. 1998
Scoloplos rubra	332	Pettibone 1963
Streblospio benedicti	343	Larsen 1974; Holland et al. 1988
Websterinereis tridentata	243	Pettibone 1963
Oligochaeta		
Tubificidae spp	331	Gaston et al. 1998

Appendix I. continued

Taxa	Life Form Code	References
Mollusca		
Pelecypoda		
Bivalve a	333	
Anadara ovalis	423	Larsen 1974; Holland et al. 1988
Anadara transversa	423	Larsen 1974; Holland et al. 1988
Anomia simplex	423	Larsen 1974
Crassostrea virginica	423	Larsen 1974
Ensis directus	433	Miller et al. 1992
Gemma gemma	433	Larsen 1974; Holland et al. 1988
Geukensia demissa	423	Larsen 1974
Macoma tenta	333	Larsen 1974; Holland et al. 1988
Macoma balthica	333	Larsen 1974; Holland et al. 1988
Mercenaria mercenaria	433	Larsen 1974
Mya arenaria	433	Larsen 1974
Mytilus edulis	423	Gosling 1992
Noetia ponderosa	423	Larsen 1974
Periploma spp	433	Carter 2004
Petricola pholadiformis	433	Gaston et al. 1998
Spisula solidissima	433	Larsen 1974
Tellina agilis	333	Larsen 1974; Holland et al. 1988
Tellina spp	333	Larsen 1974; Holland et al. 1988
Gastropoda		
Gastropod a	211	
Doridella obscura	113	Larsen 1974
Anachis obesa	211	Larsen 1974
Busycon canaliculatum	213	Edwards and Harasewych 1988
Busycon carica	213	Edwards and Harasewych 1988
Crepidula fornicata	313	Larsen 1974; Ulanowicz et al. 1998
Crepidula convexa	313	Larsen 1974; Ulanowicz et al. 1998

Appendix I. continued

Taxa	**Life Form Code**	**References**
Gastropoda (continued)		
Crepidula plana	313	Larsen 1974; Ulanowicz et al. 1998
Diastoma varium	313	Ulanowicz et al. 1998
Diodora cayenensis	311	Abbott 1974
Eupleura caudata	111	Larsen 1974
Ilyanassa obsoleta	311	Miller et al. 1992; Ulanowicz et al. 1998
Mitrella lunata	211	Larsen 1974
Muricidae sp	111	Larsen 1974
Odostomia sp	111	Larsen 1974
Odostomia impressa	111	Larsen 1974
Polineces duplicatus	113	Abbott 1974
Pyrgocythara plicosa	213	Abbott 1974
Retusa canaliculata	113	Berry 1988; Gaston et al.1998
Skenopsis planorbis	211	Larsen 1974
Triphora nigrocinta	213	Larsen 1974
Urosalpinx cinera	111	Larsen 1974
Arthropoda		
Copepod		
Harpacticoid sp	231	Barnes 1980
Cirripedia		
Balanus improvisus	423	Larsen 1974
Mysidacea		
Mysidopsis sp	211	Barnes 1980; Holland et al. 1988
Tardigrada		
Stygarctus sp	331	Gaugler 2002
Pycnogonidae		
Pycnogonid sp	213	Arnaud and Bamber 1987
Isopoda		
Cyanthura burbanki	241	Larsen 1974

Appendix I. continued

Taxa	Life Form Code	References
Isopoda (continued)		
Edotea triloba	411	Larsen 1974
Erichsonella filiformis	411	Kensley and Schotte 1989
Ligia baudiniana	411	Kensley and Schotte 1989
Probopyrus pandalicola	411	Kensley and Schotte 1989
Sphaeroma quadridentatum	211	Barnes 1980
Amphipoda		
Ampelisca macrocephala	441	Larsen 1974
Ampithoe valida	421	Larsen 1974; Duffy and Hay 1991
Ampithoe longimana	421	Duffy and Hay 1991
Batea catharinensis	211	Bousfield 1973
Caprella pentatus	411	Luczkovich et al. 2002
Caprella equilibra	411	Luczkovich et al. 2002
Corophium spp	321	Larsen 1974; Holland et al. 1988
Corophium bonelli	321	Larsen 1974; Holland et al. 1988
Corophium acherusicum	321	Larsen 1974; Holland et al. 1988
Cymedusa compta	421	Larsen 1974
Dulichiella appendiculata	211	Bousfield 1973
Erichthonius brasiliensis	221	Bousfield 1973
Gammurus mucronatus	211	Duffy and Hay 1994
Gammurus palustris	211	Larsen 1974
Leptochirus plumulosus	431	Larsen 1974
Melita nitida	211	Larsen 1974; Holland et al. 1988
Orchestia grillus	211	Bousfield 1973
Paracaprella tenuis	411	Luczkovich et al. 2002
Stenothoe minuta	411	Larsen 1974
Decapoda		
Alpheus heterochaelis	212	Williams 1984
Alpheus normanni	212	Williams 1984

Appendix I. continued

Taxa	**Life Form Code**	**References**
Decapoda (continued)		
Brachyuran zoea	213	Williams 1984
Brachyuran megalopa	213	Williams 1984
Callianassa atlantica	243	Williams 1984
Callinectes sapidus	113	Larsen 1974
Caridean larva	213	Williams 1984
Clibanarius vittatus	213	Williams 1984
Crangon septemspinosa	113	Larsen 1974
Dyspanopeus sayi	113	Larsen 1974
Eurypanopeus depressus	113	Larsen 1974
Hemigrapsus sanguineus	213	McDermott 1998 a, b
Hippolyte pleuracantha	213	Williams 1984
Pagurus longicarpus	213	Williams 1984; Miller et al. 1992
Pagurus arcuatus	213	Williams 1984
Pagurus pollicaris	213	Williams 1984
Palaemonetes pugio	213	Larsen 1974
Palaemonetes vulgaris	213	Larsen 1974
Panopeidae spp	113	Larsen 1974
Panopeus herbsti	113	Larsen 1974
Pinnixa sayana	213	Williams 1984; Holland et al. 1988
Uca sp	413	Williams 1984
Upogebia affinis	443	Larsen 1974
Insecta		
Collembola sp	211	Barnes 1980
Diptera spp	111	
Chordata		
Urochordata		
Molgula manhattiensis	422	Larsen 1974

Appendix II: Raw nekton abundance data for two replicate samples collected on two consecutive days using the enclosure trap gear, April - October 1999 from the constructed reef and beach habitats at Fisherman's Island, Virginia. Numbers in parentheses are mean total length and standard error, respectively, in mm, for fishes; carapace width in mm for crabs, and carapace length in mm for shrimp. No samples were collected in September due to Hurricane Floyd occurring during target tidal sampling period. Habitat use categories are denoted in parentheses after each species name adapted from Breitburg (1999) and Baltz (1993): R = resident oyster reef species, F = facultative oyster reef species, DT = demersal transient species; NT = nektonic transient species.

OYSTER SHELL REEF

	APRIL		MAY		JUNE		JULY		AUGUST		OCTOBER	
replicate	1	2	1	2	1	2	1	2	1	2	1	2
length of reef edge sampled (m)	14.0	14.0	14.0	14.0	13.5	10.0	14.0	14.0	14.0	14.0	14.0	17.0
Anchoa hepsetus (NT)	0	0	0	0	0	3 (125.3, 3.4)	0	0	4 (50.0, 2.0)	35 (56.7, 1.4)	0	0
Archosargus probatocephalus (F)	0	0	0	0	0	0	2 (53.0, 0)	0	4 (55.3, 9.4)	3 (49.0, 2.5)	0	1 (51.0)
Bairdiella chrysoura (DT)	0	0	0	0	0	0	15 (51.1, 1.0)	6 (46.2, 6.4)	1 (49.3)	0	0	0
Callinectes sapidus (DT)	0	0	0	0	0	1 (21.0)	4 (82.8, 17.5)	3 (97.3, 21.1)	3 (113.3, 25.2)	3 (66.0, 45.0)	0	0
Centropristis striata (F)	0	0	0	1 (49.0)	0	0	0	1 (108.0)	0	0	0	1 (72.0)
Chasmodes bosquianus (R)	0	0	0	2 (68.5, 1.5)	0	0	0	0	0	0	0	0
Chaetodon ocellatus (F)	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinodon variegatus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Epinephelus sp. (F)	0	0	0	0	0	0	0	0	0	0	0	0
Eucinostomus argenteus (DT)	0	0	0	0	0	0	0	1 (46.0)	0	0	0	0
Eucinostomus gula (DT)	0	0	0	0	0	0	2 (47.0, 2.0)	0	0	0	0	0
Fundulus heteroclitus (DT)	0	0	0	1 (40.0)	0	0	20 (44.9, 1.1)	9 (46.2, 2.5)	0	0	0	0
Fundulus majalis (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Gobiosoma bosc (R)	0	2 (34.0, 3.0)	1 (41.0)	2 (39.0, 1.0)	3 (47.3, 4.1)	4 (51.5, 3.9)	0	1 (34.0)	0	3 (30.3, 8.9)	2 (45.0, 3.0)	0
Gobiosoma ginsburgi (R)	0	0	0	1 (34.0)	0	0	2 (25.5, 0.5)	2 (26.5, 3.5)	0	0	1 (26.0)	0
Hypsoblennius hentz (R)	0	0	0	1 (57.0)	1 (74.0)	2 (72.5, 2.5)	5 (76.4, 2.8)	2 (85.0, 0)	1 (72.0)	5 (65.2, 7.1)	1 (64.0)	1 (52.0)
Lagodon rhomboides (F)	0	0	0	0	31 (51.1, 1.2)	0	4 (79.3, 3.6)	1 (60.0)	0	0	0	0
Leiostomus xanthurus (DT)	0	0	0	0	12 (35.2, 0.8)	0	3 (58.0, 2.0)	0	0	0	0	0
Lucania parva (DT)	0	0	0	0	20 (34.6, 0.8)	1 (42.0)	0	0	5 (24.0, 0.6)	0	0	0
Lutjanus griseus (F)	0	0	0	0	0	0	0	0	0	4 (65.8, 0.8)	0	0
Membras martinica (NT)	0	71 (86.6, 1.1)	550 (21.5, 0.7)	1 (115.0)	1029 (38.4, 1.6)	890 (32.2, 0.8)	27 (49.0, 1.0)	125 (46.2, 0.7)	1390 (55.1, 1.0)	268 (58.0, 0.8)	20 (61.1, 1.2)	640 (56.9, 0.2)
Morone saxatilis (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Mugil curema (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Mycteroperca microlepis (F)	0	0	0	0	0	0	1 (71.0)	0	0	0	0	0
Opsanus tau (R)	0	0	0	0	2 (85.5, 9.5)	1 (98.0)	0	0	1 (52.0)	3 (50.0, 3.6)	0	0
Orthopristus chrysoptera (R)	0	0	0	0	0	0	30 (46.1, 0.6)	1 (47.0)	0	0	0	0
Palaemonetes vulgaris (DT)	123	2945	1094	13	78	110	638	72	20	129	336	49
Paralichthys dentatus (DT)	0	1 (21.0)	0	3 (35.0, 5.2)	0	1 (62.0)	0	0	0	0	0	0
Penaeus aztecus (DT)	0	0	0	0	0	0	0	0	0	0	0	1 (24.0)
Peprilus triacanthus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Prionotus carolinus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Scorpaena plumeiri (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Sphyreana borealis (NT)	0	0	0	0	0	0	4 (64.5, 1.7)	0	0	0	0	0
Sphoeroides maculatus (DT)	0	0	0	0	0	0	0	0	1 (114.0)	0	0	0
Strongylura marina (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus floridae (F)	0	0	0	0	0	0	0	0	0	1 (122.0)	0	0
Syngnathus fuscus (F)	0	2 (105.0, 6.0)	2 (163.5, 31.5)	5 (138.0, 8.0)	2 (110.5, 5.5)	1 (145.0)	1 (100.0)	4 (121.3, 7.9)	4 (106.5, 7.2)	5 (102.6, 4.3)	0	0
Symphurus plagiusa (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Synodus foetens (DT)	0	0	0	0	0	0	0	0	1 (87.0)	0	0	0
Tautog onitis (F)	0	0	0	0	0	2 (20.5, 1.5)	3 (55.0, 5.0)	1 (53.0)	0	0	0	0
total	123	3021	1647	30	1178	1016	761	229	1435	459	360	693

Appendix II: Continued.

CLAM SHELL REEF

	APRIL		MAY		JUNE		JULY		AUGUST		OCTOBER	
replicate	1	2	1	2	1	2	1	2	1	2	1	2
length of reef edge sampled (m)	15.0	16.0	16.0	8.0	16.0	16.0	16.0	16.0	12.3	16.0	8.6	8.4
Anchoa hepsetus (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Archosargus probatocephalus (F)	0	0	0	0	0	0	0	0	0	0	0	0
Bairdiella chrysoura (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Callinectes sapidus (DT)	1 (10.0)	0	3 (56.8, 31.1)	5 (20.3, 3.1)	2 (19.0, 1.0)	6 (37.5, 7.4)	7 (87.7, 11.8)	1 (30.0)	10 (22.5, 7.1)	6 (22.5, 6.3)	1 (22.0)	1 (19.0)
Centropristis striata (F)	0	0	0	0	1 (72.0)	0	0	0	0	0	0	0
Chasmodes bosquianus (R)	0	0	0	0	0	0	0	0	0	0	0	0
Chaetodon ocellatus (F)	0	0	0	0	0	0	0	0	0	0	0	0
Cyprinodon variegatus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Epinephelus sp. (F)	0	0	0	0	0	0	0	0	0	0	0	0
Eucinostomus argenteus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Eucinostomus gula (DT)	0	0	0	0	0	0	0	0	0	0	0	1 (59.0)
Fundulus heteroclitus (DT)	0	0	1 (50.0)	1 (46.0)	12 (32.7, 1.1)	2 (21.5, 7.5)	1 (37.0)	5 (39.4, 2.3)	0	0	0	0
Fundulus majalis (DT)	0	0	0	0	0	2 (60.0, 22.0)	1 (60.0)	0	0	0	0	0
Gobiosoma bosc (R)	0	1 (32.0)	0	3 (41.0, 1.5)	0	1 (45.0)	0	0	0	0	0	0
Gobiosoma ginsburgi (R)	0	0	1 (39.0)	7 (35.4, 1.3)	1 (40.0)	0	0	0	0	0	0	0
Hypsoblennius hentz (R)	0	0	0	0	0	0	0	0	0	0	0	0
Lagodon rhomboides (F)	0	0	0	0	0	0	3 (84.3, 1.8)	0	0	1 (122.0)	0	0
Leiostomus xanthurus (DT)	0	0	0	0	0	0	6 (81.5, 0.8)	0	0	0	0	0
Lucania parva (DT)	1 (26.0)	0	0	0	0	0	0	0	0	0	0	0
Lutjanus griseus (F)	0	0	0	0	0	0	0	0	0	0	0	0
Membras martinica (NT)	0	0	17 (90.5, 2.2)	19 (93.0, 2.2)	33 (40.1, 2.2)	378 (33.2, 2.9)	22 (52.2, 1.7)	13 (56.6, 2.6)	269 (60.6, 0.9)	99 (60.3, 0.8)	45 (62.0, 1.0)	0
Morone saxatilis (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Mugil curema (NT)	0	0	0	0	0	0	5 (147.2, 14.5)	1 (111.0)	1 (136.0)	1 (142.0)	0	0
Mycteroperca microlepis (F)	0	0	0	0	0	0	0	0	0	0	0	0
Opsanus tau (R)	0	0	0	0	0	0	0	0	0	0	0	0
Orthopristus chrysoptera (R)	0	0	0	0	0	0	0	0	0	0	0	0
Palaemonetes vulgaris (DT)	40	326	3	26	45	17	5	0	1	0	5	22
Paralichthys dentatus (DT)	0	0	13 (44.2, 2.0)	13 (42.5, 2.7)	3 (44.7, 7.3)	4 (47.3, 5.6)	0	0	0	0	0	0
Penaeus aztecus (DT)	0	0	0	0	0	0	0	0	3 (45.0, 0)	1 (57.0)	1 (26.0)	0
Peprilus triacanthus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Prionotus carolinus (DT)	0	0	0	0	1 (52.0)	0	0	0	0	0	0	0
Scorpaena plumeiri (DT)	0	0	0	0	0	0	0	1 (35.0)	0	0	0	0
Sphyreana borealis (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Sphoeroides maculatus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Strongylura marina (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus floridae (F)	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus fuscus (F)	0	1 (118.0)	0	4 (145.8, 10.4)	6 (115.0, 6.5)	0	0	2 (87.5, 15.5)	1 (142.0)	0	0	0
Symphurus plagiusa (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Synodus foetens (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Tautog onitis (F)	0	0	0	0	0	1 (20.0)	0	0	0	0	0	0
total	42	328	38	78	104	411	50	23	285	108	52	24

Appendix II: Continued.

ASH PELLET REEF

	APRIL		MAY		JUNE		JULY		AUGUST		OCTOBER	
replicate	1	2	1	2	1	2	1	2	1	2	1	2
length of reef edge sampled (m)	15.0	15.0	16.0	14.0	12.6	12.7	12.8	13.0	15.3	15.0	4.2	15.0
Anchoa hepsetus (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Archosargus probatocephalus (F)	0	0	0	0	0	0	0	0	1 (50.0)	1 (26.0)	0	0
Bairdiella chrysoura (DT)	0	0	0	0	0	0	1 (113.0)	0	0	0	0	0
Callinectes sapidus (DT)	0	3 (12.0, 1.5)	1 (12.0)	0	10 (31.7, 4.0)	6 (57.2, 18.5)	3 (48.3, 17.1)	2 (59.5, 43.5)	23 (12.4, 0.7)	17 (24.4, 7.4)	0	2 (24.0, 10.0)
Centropristis striata (F)	0	1 (48.0)	0	0	1 (78.0)	1 (103.0)	0	0	0	1 (36.0)	0	0
Chasmodes bosquianus (R)	0	0	0	0	0	0	0	0	4 (45.8, 8.2)	1 (51.0)	0	1 (48.1)
Chaetodon ocellatus (F)	0	0	0	0	0	0	0	0	2 (35.0, 1.0)	0	0	0
Cyprinodon variegatus (DT)	0	0	0	0	0	7 (27.0, 0.7)	1 (30.0)	0	0	0	0	0
Epinephelus sp. (F)	0	0	0	0	1 (24.0)	0	0	0	0	0	0	0
Eucinostomus argenteus (DT)	0	0	0	0	0	0	0	2 (21.0, 2.0)	0	0	0	0
Eucinostomus gula (DT)	0	0	0	0	0	0	0	0	1 (79.0)	1 (69.0)	0	0
Fundulus heteroclitus (DT)	0	0	4 (42.0, 0.41)	2 (65.0, 3.0)	11 (30.2, 0.8)	395 (35.2, 1.2)	698 (39.3, 1.3)	766 (44.9, 1.0)	1 (54.0)	6 (44.0, 3.7)	1 (44.0)	0
Fundulus majalis (DT)	0	0	0	0	15 (34.2, 0.9)	45 (36.1, 1.6)	508 (41.5, 2.2)	38 (47.6, 1.8)	0	1 (61.0)	0	0
Gobiosoma bosc (R)	0	0	0	0	0	0	3 (36.7, 3.2)	2 (30.5, 0.5)	4 (29.3, 1.4)	6 (35.0, 3.8)	1 (50.0)	0
Gobiosoma ginsburgi (R)	0	0	0	1 (39.0)	2 (40.5, 1.5)	2 (38.5, 0.5)	4 (29.0, 0.8)	1 (26.0)	0	0	0	0
Hypsoblennius hentz (R)	0	0	0	0	0	0	0	1 (25.0)	1 (48.0)	2 (58.5, 6.5)	0	0
Lagodon rhomboides (F)	0	0	0	0	1 (34.0)	0	0	0	2 (128.5, 5.5)	0	0	0
Leiostomus xanthurus (DT)	0	0	0	0	5 (39.8, 6.7)	8 (37.1, 4.8)	0	0	0	0	0	0
Lucania parva (DT)	0	0	0	0	16 (36.3, 1.2)	6 (35.5, 2.0)	0	200 (28.2, 0.4)	10	61 (24.2, 0.3)	0	7 (21.7, 1.0)
Lutjanus griseus (F)	0	0	0	0	0	0	0	0	0	0	0	0
Membras martinica (NT)	1 (83)	17 (82.8, 0.6)	1	0	567 (31.6, 1.1)	166 (35.9, 1.1)	0	0	211 (61.5, 0.8)	673 (64.0, 0.9)	0	2 (47.5, 6.5)
Morone saxatilis (NT)	0	0	0	0	9 (39.2, 1.6)	1 (39.0)	0	0	0	0	0	0
Mugil curema (NT)	0	0	0	0	0	0	0	0	6 (140.3, 0.9)	3 (143.0, 0.6)	0	0
Mycteroperca microlepis (F)	0	0	0	0	0	0	0	0	0	0	0	0
Opsanus tau (R)	0	0	0	0	0	0	0	0	0	0	0	0
Orthopristus chrysoptera (R)	0	0	0	0	0	0	0	0	1 (50.0)	0	0	0
Palaemonetes vulgaris (DT)	49	1235	0	0	136	64	49	5	107	1	40	38
Paralichthys dentatus (DT)	0	0	1 (27.0)	1 (41.0)	2 (56.5, 8.5)	2 (121.0, 11.0)	0	0	0	0	0	0
Penaeus aztecus (DT)	0	0	0	0	0	0	0	0	15 (53.4, 3.4)	5 (38.0, 4.5)	0	1 (25.0)
Peprilus triacanthus (DT)	0	0	0	0	0	0	1 (40.0)	0	0	0	0	0
Prionotus carolinus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Scorpaena plumeiri (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Sphyreana borealis (NT)	0	0	0	0	0	0	0	0	0	0	0	0
Sphoeroides maculatus (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Strongylura marina (NT)	0	0	0	0	1 (102.0)	2 (84.5, 11.5)	0	0	0	0	0	0
Syngnathus floridae (F)	0	0	0	0	0	0	0	0	0	0	0	0
Syngnathus fuscus (F)	0	0	2 (140.6, 14.1)	1 (132.0)	7 (129.6, 9.9)	8 (99.8, 10.2)	0	0	1 (92.0)	2 (86.0, 12.0)	1 (111.0)	3 (113.0, 16.9)
Symphurus plagiusa (DT)	0	1 (26.0)	0	0	0	1 (65.0)	0	0	0	0	0	0
Synodus foetens (DT)	0	0	0	0	0	0	0	0	0	0	0	0
Tautog onitis (F)	0	0	0	0	1 (20.0)	0	0	0	0	0	0	0
total	50	1257	9	5	785	714	1268	1017	390	781	43	54

Appendix II: Continued.

BEACH

	APRIL		MAY		JUNE		JULY		AUGUST		OCTOBER	
replicate	1	2	1	2	1	2	1	2	1	2	1	2
length of habitat sampled (m)	-	-	-	-	-	-	14.0	14.0	14.0	14.0	14.0	14.0
Anchoa hepsetus (NT)	-	-	-	-	-	-	0	0	0	0	0	0
Archosargus probatocephalus (F)	-	-	-	-	-	-	0	0	0	0	0	0
Bairdiella chrysoura (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Callinectes sapidus (DT)	-	-	-	-	-	-	0	0	7 (27.9, 14.6)	5 (12.8, 1.1)	0	8 (18.6, 1.5)
Centropristis striata (F)	-	-	-	-	-	-	0	0	0	0	0	0
Chasmodes bosquianus (R)	-	-	-	-	-	-	0	0	0	0	0	0
Chaetodon ocellatus (F)	-	-	-	-	-	-	0	0	0	0	0	0
Cyprinodon variegatus (DT)	-	-	-	-	-	-	1 (33.0)	3 (35.0, 1.2)	0	0	0	0
Epinephelus sp. (F)	-	-	-	-	-	-	0	0	0	0	0	0
Eucinostomus argenteus (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Eucinostomus gula (DT)	-	-	-	-	-	-	0	0	0	0	0	6 (69.6, 4.8)
Fundulus heteroclitus (DT)	-	-	-	-	-	-	383 (50.7, 1.2)	216 (48.0, 0.7)	1 (80.0)	3 (58.0, 5.6)	0	0
Fundulus majalis (DT)	-	-	-	-	-	-	51 (45.9, 1.6)	209 (37.5, 1.2)	55 (58.8, 2.3)	37 (51.1, 2.1)	5 (51.0, 5.3)	0
Gobiosoma bosc (R)	-	-	-	-	-	-	0	0	0	0	0	0
Gobiosoma ginsburgi (R)	-	-	-	-	-	-	0	0	0	0	0	0
Hypsoblennius hentz (R)	-	-	-	-	-	-	0	0	0	0	0	0
Lagodon rhomboides (F)	-	-	-	-	-	-	0	0	0	0	0	0
Leiostomus xanthurus (DT)	-	-	-	-	-	-	1 (87.0)	4 (83.3, 5.7)	0	0	0	0
Lucania parva (DT)	-	-	-	-	-	-	2 (42.5, 3.5)	3 (28.0, 2.3)	2 (26.0, 0)	0	0	0
Lutjanus griseus (F)	-	-	-	-	-	-	0	0	0	0	0	0
Membras martinica (NT)	-	-	-	-	-	-	98 (51.2, 1.8)	56 (47.0, 0.9)	181 (61.5, 2.2)	27 (60.0, 2.0)	250 (57.7, 0.5)	44 (53.7, 0.6)
Morone saxatilis (NT)	-	-	-	-	-	-	0	0	0	0	0	0
Mugil curema (NT)	-	-	-	-	-	-	0	0	2 (135.0, 5.0)	0	0	0
Mycteroperca microlepis (F)	-	-	-	-	-	-	0	0	0	0	0	0
Opsanus tau (R)	-	-	-	-	-	-	0	0	0	0	0	0
Orthopristus chrysoptera (R)	-	-	-	-	-	-	0	0	0	0	0	0
Palaemonetes vulgaris (DT)	-	-	-	-	-	-	0	2	3	0	0	2
Paralichthys dentatus (DT)	-	-	-	-	-	-	1 (51.0)	0	0	0	0	0
Penaeus aztecus (DT)	-	-	-	-	-	-	0	0	0	0	0	2 (21.0, 0)
Peprilus triacanthus (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Prionotus carolinus (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Scorpaena plumeiri (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Sphyreana borealis (NT)	-	-	-	-	-	-	0	0	0	0	0	0
Sphoeroides maculatus (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Strongylura marina (NT)	-	-	-	-	-	-	0	0	0	0	0	0
Syngnathus floridae (F)	-	-	-	-	-	-	0	0	0	0	0	0
Syngnathus fuscus (F)	-	-	-	-	-	-	0	0	0	0	0	0
Symphurus plagiusa (DT)	-	-	-	-	-	-	0	0	1 (30.0)	1 (23.0)	0	0
Synodus foetens (DT)	-	-	-	-	-	-	0	0	0	0	0	0
Tautog onitis (F)	-	-	-	-	-	-	0	0	0	0	0	0
total	0	0	0	0	0	0	537	493	252	73	255	62

LITERATURE CITED

Abbe G. R. (1986) A review of some factors that limit oyster recruitment in Chesapeake Bay. Amer. Malac. Bull. 3: 59-70.

Abbott R.T. (1974) American Seashells: The marine Mollusca of the Atlantic and Pacific Coasts of North America. Van Nostrand Reinhold Company, 663 pp.

Allen D.M., S.K. Service, and M.V. Ogburn-Matthews (1992) Factors influencing the collection efficiency of estuarine fishes. Transactions of the American Fisheries Society 121: 234-244.

Andrews J. D. (1951) Seasonal patterns of oyster settling in the James River and Chesapeake Bay. Ecology 32: 752-758.

Andrews J. D. 1979. Pelecypoda: Ostreidae. Pages 293-341 in A. C. Giese and J. S. Pearse (eds.). Reproduction in Marine Invertebrates, Volume V. Molluscs: Pelecypods and Lesser Classes. Academic Press, New York.

Andrews R.S., R.W. Alden III, M.W. Luckenbach, J.A. Wesson (1997) The use of coal combustion substrate for oyster reef development. Pp 363-375 In: B.A. Sakkestad (ed) Proceedings of the 22nd International Technical Conference on Coal Utilization and Fuel Systems. Coal and Slurry Technology Association of America, Washington, DC.

Arnaud F. and R.N. Bamber (1987) The Biology of the Pycnogonida, pp. 1-96 in Blaxter, J.H.S. and Southward, A.J. (eds), Advances in Marine Biology, vol. 24. New York: Academic Press.

Bahr L.M. (1974) Aspects of the structure and function of the intertidal oyster reef community in Georgia. PhD dissertation, University of Georgia. 149 pp.

Bahr L.M., W.P. Lanier (1981) The Ecology of intertidal oyster reefs of the South Atlantic Coast: a community profile. U.S. Fish Wildl. Serv. Program FWS/OBS/-81/15, 105 pp.

Baltz D.M., C. Rakocinski, and J.W. Fleeger (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36: 109-126.

Barnes R.D. (1980) Invertebrate Zoology, Saunders College and Holt, Rinehart and Winston.

Bartholomew A., R.J. Diaz, G. Cicchetti (2000) New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. Marine Ecology Progress Series 206: 45-58.

Bartol I.K., R. Mann (1999) Small-scale patterns of recruitment on a constructed intertidal reef: The role of spatial refugia. pp. 159-170 *In* M. W. Luckenbach, R. Mann, & J. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.

Bartol I.K., R. Mann, M.W. Luckenbach (1999) Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. Journal of Experimental Marine Biology and Ecology. 237: 157-184

Benke A.C., J.B. Wallace (1980) Trophic basis of production among net-spinning caddiflies in a southern Appalachian stream. Ecology 61: 108-118.

Berry A.J. (1988) Annual cycle in *Retusa obtusa* (Montagu) (Gastropoda, Ophisthobranchia) of reproduction, growth and predation upon *Hydrobia ulvae* (Pennant). Journal of Experimental Marine Biology and Ecology, 117:197-209.

Bisker R., M. Castagna (1987) Predation on single spat oysters, Crassostrea virginica Gmelin by blue crabs, *Callinectes sapidus* Rathburn and mud crabs, *Panopeus herbstii* Milne-Edwards. J. Shellfish. Res. 6: 37-40.

Blake J. (2000) Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel; vol. 7, Annelida Part 4. Santa Barbara Museum of Natural History. 377 pp.

Boesch D.F. (1977) Application of numerical classification in ecological investigations of water pollution. Report prepared for US EPA Ecological Research Series (EPA-600/3-77-033).

Bousfield E.L. (1973) Shallow-water Gammaridean amphiopda of New England. Cornell University Press.

Bray J.R., J.T. Curtis (1957) An ordination of the upland forest communities of Southern Wisconson. Ecological Monographs 27: 325-349.

Breitburg D.L. (1999) Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? Pp 239-250, in M.W. Luckenbach, R. Mann and J.A. Wesson (eds) Oyster reef habitat restoration: a synopsis and synthesis of approaches. VIMS Press, Gloucester Point, VA.

Buffagni A., E. Comin (2000) Secondary production of benthic communities at the habitat scale as a tool to assess ecological integrity in mountain streams. Hydrobiologia 422/423: 183-185.

Burreson E.M., E. Robinson, A. Villaba (1988) A comparison of paraffin histology and hemolymph analysis for the diagnosis of *Haplosporidium nelsoni* (MSX) in Crassostrea virginica (Gmelin). J. Shellfish Res. 7: 19-23.

Cairns J. Jr. (1993) Ecological restoration: replenishing our national and global ecological capital. Pp 193-208 *In:* Saunders D.A., R.J. Hobbs, P.R. Ehrlich (eds) Nature Conservation 3: Reconstruction of Fragmented Ecosystems, Surrey Beatty & Sons.

Carter M.C. (2004) *Spisula solidissima.* Atlantic surf clam. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Plymouth: Marine Biological Association of the United Kingdom.

Chick J.H., J.P. Smith, and C.C. McIvor (1992) A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. Journal of Freshwater Ecology 7: 353-361.

Cicchetti G. (1998a) Habitat use, secondary production, and trophic export by salt marsh nekton in shallow waters. PhD dissertation, College of William and Mary, 276 pp.

Cicchetti G. (1998b) Use of salt marsh edge by economically valuable fishes and crustaceans. Final Report submitted to the NOAA Office of Ocean and Coastal Research Management, NOAA/SRD Award #97-066-CBV.

Cicchetti G., and R.J. Diaz (2000) A dynamic budget model of energy flow from infauna to nekton in a polyhaline Virginia salt marsh. In *Concepts and controversies in tidal marsh ecology.* Pp 515-541, in M. Weinstein & D.A. Kreeger. Dordrecht: Kluwer.

Clarke K.R., R.N. Gorley (2001) 'Primer v5: User Manual/Tutorial.' (Primer-E Ltd: Plymouth, UK).

Clarke K.R., R.M. Warwick (2001) Change in marine communities: as approach to statistical analysis and interpretation. 2nd edition. PRIMER-E. Plymouth.

Coen L.D., MW Luckenbach, D.L. Breitburg (1999) The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. American Fisheries Society Symposium. 22: 438-454.

Colwell R.K. (1997) EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

Commito J.A., B.R. Rusignuolo (2000) Structural complexity in mussel beds: the fractal geometry of surface topography. Journal of Experimental Marine Biology and Ecology 255: 133-152.

Connell J.H. (1978) Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Connolly R.M. (1994) Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. Marine Ecology Progress Series 109: 305-309.

Connor W.G., J.L. Simon (1979) The effects of oyster shell dredging on an estuarine benthic community. Estuarine and Coastal Marine Science 9: 749-758.

Cox C., R. Mann (1992) Temporal and spatial changes in fecundity of Eastern oysters, *Crassostrea virginica* (Gmelin, 1791) in the James River, Virginia.). J. Shellfish Res. 11: 49-54.

Crisp D. J. (1967) Chemical factors inducing settlement in *Crassostrea virginica* (Gmelin), Journal of Animal Ecology 36: 329-335.

Crisp D.J. (1974) Factors influencing the settlement of marine invertebrate larvae. Pp. 177-265 *in*: PT Grant & AM Mackie (eds) Chemoreception in marine organisms. Academic Press, London, United Kingdom.

Crisp D.J. (1978) Genetic consequences of different reproductive strategies in marine invertebrates. Pp. 257–273 *in* B. Battaglia and J.A. Beardmore (eds) Marine organisms: genetics, ecology, and evolution. Plenum Press, New York.

Crosby M.P., C.F. Roberts, P.D. Kenny (1991) Effects of immersion time and tidal position on *in situ* growth rates of naturally settled eastern oysters, *Crassostrea virginica* (Gmelin, 1791). Journal of Shellfish Research 10: 95-103.

Dame R.F. (1976) Energy flow in an intertidal oyster population. Estuarine and Coastal Marine Science 4: 243-253.

Dame R.F. (1979) The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Proceedings of the National Shellfisheries Association 68:6-10.

Davis H. C., P. E. Chanley (1956) Spawning and egg production of oysters and clams. Proc. Nat. Shellfish. Assoc. 46: 40-51.

Death R.G. (1996) The effect of habitat stability on benthic invertebrate communities: the utility of species abundance distributions. Hydrobiologia 317: 97-107.

Diaz R.J., L.C. Schaffner (1990) The functional role of estuarine benthos. Pp. 25-56 In: M. Haire and E.C. Krome (eds) Perspectives on the Chesapeake Bay, 1990, Advances in Estuarine Sciences, Chesapeake Research Consortium, Gloucester Point, VA.

Dauer D.M. (1993) Biological criteria, environmental health and estuarine macrobenthic community structure. Marine Pollution Bulletin 26:249-257.

Duffy J.E. , M.E. Hay (1991) Host plants as food and shelter: determinants of food choice in an herbivorous marine amphipod. Ecology 72: 1286-1298.

Duffy J.E., M.E. Hay (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. Ecology 75:1304-1319.

Edwards A.L., M.G. Harasewych (1988) Biology of the recent species of the subfamily Busyconinae. Journal of Shellfish Research 7: 467-472

Edgar G.J. (1990) The use of size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. Journal of Experimental Marine Biology and Ecology 137:195-214.

Eggleston D. B. (1990) Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: Effects of prey density and size. Bulletin of Marine Science 46: 62-82.

Foggo A., M.J. Atrill, M.T. Frost, A.A. Rowden (2003) Estimating marine species richness: an evaluation of six extrapolative techniques. Marine Ecology Progress Series 248: 15-26.

Fredette T.J., R.J. Diaz (1986) Secondary production of *Gammurus mucronatus* Say (Amphipoda: Gammaridae) in warm, temperate estuarine habitats, York River, Virginia. Journal of Crustacean Biology 6: 729-741.

Fredette T.J., R.J. Diaz, J. van Montfrans, R.J. Orth (1990) Secondary production within a seagrass bed (*Zostera maritima*) in lower Chesapeake Bay. Estuaries 13: 431-440.

Galtsoff P. S. (1964) The American oyster *Crassostrea virginica* Gmelin. Fishery Bulletin 64: 1-480.

Gaugler M.S. (2002) Marine interstitial tardigrades and other meiofauna of Huntington Beach, South Carolina. MS Thesis, East Tennessee State University. 148 pp.

George J.D. (1980) The life history of the cirratulid worm, *Cirriforma tentaculata*, in an intertidal mudflat. Journal of the Marine Biological Association of the UK. 44:47-65.

Gosling E.M. (ed.), (1992) The mussel *Mytilus*: ecology, physiology, genetics and culture. Amsterdam: Elsevier Science Publ.. Developments in Aquaculture and Fisheries Science, no. 25.

Graumann A., D. Ross, M. Sittel-Orkand (1998) 1997 Atlantic tropical storms: Views from the NOAA satellites. National Climatic Data Center Technical Report 98-01.

Gunter G. (1979) The grit principle and the morphology of oyster reefs. Proc. Natl. Shellfish. Assoc. 69: 1-5.

Gutiérrez J.L., C.G. Jones, D.L. Strayer, O.O. Iribarne (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101: 79-90.

Hagy J. (2001) Patterns of macrobenthic biomass and community bioenergetics in Chesapeake Bay during summer in relation to habitat quality and organic carbon supply. Chapter 4 of Ph.D. Dissertation. University of Maryland, Center for Environmental Studies.

Harding J.M., R. Mann (1999) Fish species richness in relation to restored oyster reefs, Painkatank River, Virginia. Bulletin of Marine Science 65: 289-300.

Hargis W.J. (1999) The evolution of the Chesapeake oyster reef system during the Holocene Epoch. pp 5-23 *In* M.W. Luckenbach, R. Mann, J. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.

Hargis W.J., D.S. Haven (1999) Chesapeake oyster reefs: their importance, destruction, and guidelines for restoring them. pp 329-358 *In* M.W. Luckenbach, R. Mann, J. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.

Heck K.L. Jr., L.B. Crowder (1991) Habitat structure and predator-prey interactions in vegetated aquatic systems. pp 281-299 *In*: S.S. Bell, E.D. McCoy, H.R. Mushinsky (eds) Habitat structure, the physical arrangement of objects in space. Chapman and Hall, New York.

Hettler W.F. Jr. (1989) Nekton use of a regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. Marine Ecology Progress Series 56: 111-118.

Hinchey E.K. (2002) Organism-sediment interactions: the role of seabed dynamics in structuring the mesohaline York River macrobenthic community. Ph. D. dissertation. The College of William and Mary. 245 pp.

Hines A.H. (1986) Larval patterns in the life histories of brachyuran crabs. Bulletin of Marine Science 39: 444-446.

Hines A.H., G.M. Ruiz (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. Bulletin of Marine Science 57: 884-901.

Holland A.F ., A.T. Shaughnessy, L.C. Scott, V.A. Dickens, J.A. Ranasinghe, J.K. Summers (1988) Long-term benthic monitoring and assessment progam for the Maryland portion of Chesapeake Bay (July 1986-October 1987). Progress Report, Volume 1 prepared for Power Point Research Program, Maryland Department of Natural Resources and Maryland Department of the Environment. Versar, Inc.

Hynes H.B.N. (1961) The invertebrate fauna of a Welsh mountain stream. Archiv fuer Hydrobiologie 57: 344-388.

Johannesson K. (1988) The paradox of Rockall - why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). Marine Biology 99: 507-513.

Kennedy, V.S., L.P. Sanford (1999) Characteristics of relatively unexploited beds of the Eastern Oyster, Crassostrea virginica, and early restoration programs. pp 25-46 *In* M. W. Luckenbach, R. Mann, & J. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.

Kensley B., M. Schotte (1989) Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington, D.C.

Kjelson M.A. (1977) Estimating the size of juvenile fish populations in southeastern coastal-plain estuaries, p. 71-90. *In:* W Van Winkle (ed) Proceedings of the Conference on Assessing the Effects of Power-Plant-Induced Mortality on Fish Populations. Pergamon Press, New York.

Kjelson M.A. and G.N. Johnson (1974) Description and evaluation of a long-haul seine for sampling fish populations in offshore estuarine habitats. Proceedings of the 28th Annual Conference of the Southeastern Association of Game and Fish Commissioners. 28(1974): 171-179.

Kjelson M.A., G.N. Johnson (1978) Catch efficiency of a 6.1 m trawl for estuarine fish populations. Transactions of the American Fisheries Society 107: 246-254.

Kneib R. T. (1991) Flume weir for quantitative collection of nekton from vegetated intertidal habitats. Marine Ecology Progress Series 75: 29-38.

Krantz, G.E., J.V. Chamberlin (1978) Blue crab predation on cultchless oyster spat. Proc. Natl. Shellfish. Assoc. 68: 38-41.

Lande R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5-13.

Larsen P.F. (1974) Quantitative studies of the macrofauna associated with the mesohaline oyster reefs of the James River, Virginia. Ph. D. dissertation. The College of William and Mary. 182 pp.

Lenihan H.S. (1999) Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Lenihan H.S., C.H. Peterson, J.M. Allen (1996) Does flow speed also have a direct effect on growth of active suspension feeders: an experimental test on oysters, *Crassostrea virginica* (Gmelin). Limnology and Oceanography 41:1359-1366.

Loesch J., H. Bishop, A. Crowe, R. Kuckyr, P. Wagner (1976) Technique for estimating trawl efficiency in catching brown shrimp (*Penaeus aztecus*), Atlantic croaker (*Micropogon undulatus*) and spot (*Leiostomus xanthurus*). Gulf Research Reports 5: 29-33.

Lotrich V.A., W.H. Meredith (1974) A technique and the effectiveness of various acrylic colors for subcutaneous marking of fish. Transactions of the American Fisheries Society 103: 140-142.

Luczkovich, J.J., G.P. Ward, J.C. Johnson, R.R. Christian, D. Baird, H. Neckles, W.M. Rizzo (2002) Determining the trophic guilds of fishes and macroinvertebrates in a seagrass food web. Estuaries 25 (6A): 1143-1163.

MacKenzie, C.L. (1977) Development of an aquacultural program for rehabilitation of damaged oyster reefs in Missippi. Marine Fisheries Review 39: 1-13.

MacKenzie C.L. (1996) History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. Marine Fisheries Review 58: 1-78

Mann, R. (2000) Restoring the oyster reef communities in the Chesapeake Bay: A commentary. J. Shellfish Res. 19: 335-339.

McDermott, J. J. (1960) The predation of oysters and barnacles by crabs of the family Xanthidae. Proceedings of the Pennsylvania Academy of Science 34: 199-211.

McDermott, J..J. (1998a) The western Pacific brachyuran (*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology. ICES Journal of Marine Science 55: 289-298.

McDermott, J..J. (1998b) The western Pacific brachyuran *Hemigrapsus sanguineus*: (Grapsidae), in its new habitat along the Atlantic coast of the United States: reproduction. Journal of Crustacean Biology 18: 308-316.

McDermott, J. J., F. B. Flower (1952) Preliminary studies of the common mud crabs on oyster beds of Delaware Bay. Conv. Addr. National Shellfisheries Association 47-50.

McIvor C.C., W.E. Odum (1986) The flume net: A quantitative method for sampling fishes and macrocrustaceans on tidal marsh surfaces. Estuaries 9: 219-224.

Meisner, B. (1995) Goodwin Island reserve is site of new oyster reef. A Fair Bay, Newsletter for Friends of the Chesapeake Bay National Estuarine Research Reserve in Virginia, 4(3,4): 1-2.

Meyer D.L. (1994) Habitat partitioning between the Xanthid crabs *Panopeus herbstii* and *Eurypanopeus depressus* on intertidal oyster reefs (*Crassostrea virginica*) in southeastern North Carolina. Estuaries 17: 674-679.

Meyer D.L., E.C. Townsend (2000) Faunal utilization of created intertidal eastern oyster (*Crassostrea virginica*) reefs in the southeastern United States. Estuaries 23:33-45.

Miller A.G., M.J. Bock, E.T. Turner (1992) Deposit and suspension feeding in oscillatory flows and sediment fluxes. Journal of Marine Research 50: 489-520.

Morales-Alamo R., R. Mann (1996) The status of Virginia's public oyster fishery 1995. Marine Resource Special Report. Virginia Institute of Marine Science, Gloucester Point, Virginia. 42 p.

Morales-Alamo R., R. Mann (1997) The status of Virginia's public oyster resource 1996. Virginia Marine Resource Report 97-5. Virginia Institute of Marine Science, Gloucester Point, Virginia. 46 p.

Morales-Alamo R., R. Mann (1998) The status of Virginia's Public Oyster Resource 1997. Virginia Marine Resource Report 98-2. 49 pp.

Morton R.M. (1990) Community structure, density, and standing crop of fishes in a subtropical Australian mangrove area. Marine Biology 105: 385-394.

Murdy E.O., R.S. Birdsong, J.A. Musick (1997) Fishes of Chesapeake Bay. Smithsonian Institution Press, Washington, D. C., 324 pp.

Newell R.I.E., C.J. Langdon (1996) Mechanisms and physiology of larval and adult feeding. pp 185-229 *In* V.S. Kennedy, R.I.E. Newell, A.F. Eble (eds) The Eastern Oyster *Crassostrea virginica.* Maryland Sea Grant College, University of Maryland System, College Park.

Newell G.E., R.C. Newell (1977) Marine plankton: a practical guide. Hutchinson, London. 244 pp.

O'Beirn F.X., M.W. Luckenbach, R. Mann, J. Harding, J. Nestlerode (1999) Ecological functions of constructed oyster reefs along a salinity gradient in Cheaspeake Bay. Final report, Year 3 submitted to the Aquatic Reef Habitat Program, Chesapeake Bay Program, US EPA. 69 pp.

O'Beirn F.X., M.W. Luckenbach, J.A. Nestlerode, G.M. Coates (2000) Toward design criteria in constructed oyster reefs: oyster recruitment as a function of substrate type and tidal height. Journal of Shellfish Research 19:387-395.

Orth R.J., J. van Montfrans (1987) Utilization of a seagrass meadow and tidal marsh creek by blue crabs, Callinectes sapidus. I. Seasonal and annual variation in abundance with emphasis on post-settlement juveniles. Marine Ecology Progress Series 41: 283-294.

Parsley M.J., D.E. Palmer, R.W. Burkhardt (1989) Variation in capture efficiency of a beach seine for small fishes. North American Journal of Fisheries Management 9: 239-244.

Paynter K. (1996) The effects of *Perkinsus marinus* infection of physiological processes in the eastern oyster, *Crassostrea virginica.* Journal of Shellfish Research 15:119-125.

Pettibone M.H. (1963) Marine polychaete worms of the New England region: 1. Aphroditidae through Trochochaetidae. United States National Museum Bulletin 227.

Pickering H. (1996) Artificial reefs of bulk waste materials: a scientific and legal review of the suitability of using the cement stabilised by-products of coal-fired power stations. Marine Policy 20: 483-497.

Posey M.H., T.D. Alphin, C.M. Powell, E. Townsend (1999) Use of oyster reefs as habitat for epibenthic fish and decapods. Pp 229-237 *In:* M.W. Luckenbach, R. Mann, J.A. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. VIMS Press.

Powell C.M. (1994) Trophic linkages between intertidal reefs and their adjacent sandflat communities. M.S. Thesis, University of North Carolina at Wilmington, 43 pp.

Ragone Calvo, L. M., E. M. Burreson (1999) Status of the major oyster diseases in Virginia 1998: A summary of the annual monitoring program. Virginia Institute of Marine Science Marine Resource Report 99-3.

Ragone Calvo, L. M., E. M. Burreson (2000) Status of the major oyster diseases in Virginia 1999: A summary of the annual monitoring program. Virginia Institute of Marine Science Marine Resource Report 00-2.

Ragone Calvo, L. M., E. M. Burreson (2001) Status of the major oyster diseases in Virginia 2000: A summary of the annual monitoring program. Virginia Institute of Marine Science Marine Resource Report 01-8.

Roegner G.C. (1989) Recruitment and growth of juvenile *Crassostrea virginica* (Gmelin) in relation to tidal zonation. M.A. thesis. The College of William and Mary. 145 pp.

Rothschild B.J., J.S. Ault, P. Goulletquer, M. Héral (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Marine Ecology Progress Series 111,29-39.

Rozas L.P. (1992) Bottomless lift net for quantitatively sampling nekton on intertidal marshes. Marine Ecology Progress Series 89: 287-292.

Rozas L.P., T.J. Minello (1997) Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with a focus on gear selection. Estuaries 20: 199-213.

Sarda R., K. Foreman, C.E. Werme, I. Valiela (1998) The impact of epifaunal predation on the structure of macroinfaunal invertebrate communities of tidal saltmarsh creeks. Estuarine, Coastal, and Shelf Science 46: 657-669.

Seed, R. (1980) Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. Estuarine and Coastal Marine Science 11: 445-458.

Smock L.A., E. Gilinsky, D.L. Stoneburner (1985) Macroinvertebrate production in a southeastern United States blackwater stream. Ecology 66: 1491-1503.

Sokal R.R., F.J. Rohlf (1981) Biometry. W. H. Freeman and Co., San Francisco. 859 pp.

Southworth M., J.M. Harding, R. Mann (1999) The status of Virginia's public oyster resource 1998. Virginia Marine Resource Report 99-6. Virginia Institute of Marine Science, Gloucester Point, Virginia. 37 p.

Southworth M., J.M. Harding, R. Mann (2000) The status of Virginia's public oyster resource 1999. Virginia Marine Resource Report 2000-03. Virginia Institute of Marine Science, Gloucester Point, Virginia. 38 p.

Southworth M., J.M. Harding, R. Mann (2001) The status of Virginia's public oyster resource 2000. Virginia Institute of Marine Science, Gloucester Point, Virginia. 56 p.

Suchanek T.H. (1978) The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31: 105-120.

Tenore K.R. (1988) Nitrogen in benthic food chains. *In:* Nitrogen Cycling in Coastal Marine Environments. T.H. Blackburn and J. Sorensen (eds.), Wiley, Chichester.

Ulanowicz R.E., C. Bondavalli, M.S. Egnotovich (1998) Network analysis of trophic dynamics in south Florida ecosystem, FY 97: The Florida Bay ecosystem. Annual report to the United States Geological Service, Biological Resources Division.

Underwood A.J. (1997) Experiments in ecology: Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK, 504 pp.

Veitch, F.P., H. Hidu (1971) Gregarious settling in the American oyster *Crassostrea virginica* Gmelin. I. Properties of a partially purified “setting factor”. Chesapeake Science 12: 173-178.

Volety, A.K., F.O. Perkins, R. Mann, P.R. Hershberg (2000) Progression of diseases caused by the oyster parasites, *Perkinsus marinus* and *Haplosporidium nelsoni*, in Crassostrea virginica on constructed intertidal reefs. J. Shellfish Res. 17: 341-347.

Walther B.A., S. Morand (1998) Comparative performance of species richness estimation methods. Parasitology 116: 395-405.

Waters T.F. (1977) Secondary production in inland waters. Advances in Ecological Research. 14: 91-164.

Waters T.F., G.W. Crawford (1973) Annual production of a stream mayfly population: A comparison of methods. Limnology and Oceanography 18: 286-296.

Wells H.W. (1961) The fauna of oyster beds, with special reference to the salinity factor. Ecological Monographs 31:239-266.

Wenner E., H.R. Beatty, L. Coen (1996) A method for quantitatively sampling nekton on intertidal oyster reefs. Journal of Shellfish Research 15: 769-775.

Wesson, J. R. Mann, M.W. Luckenbach (1999) Oyster restoration efforts in Virginia. . pp 117-129 *In* M.W. Luckenbach, R. Mann, and J. Wesson (eds.). Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science, Gloucester Point, Virginia.

White, M.E., E.A. Wilson (1996) Predators, pests, and competitors. Pp. 559-579 In V.S. Kennedy, R.I.E. Newell & A.F. Eble (eds.) The Eastern Oyster *Crassostrea virginica*. Maryland Sea Grant College.

Whitman J.D. (1985) Refuges, biological disturbance and rocky subtidal community structure in New England. Ecological Monographs. 55: 167-187.

Williams A.B. (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press.

Zar J.H. (1999) Biostatistical Analysis. 4th edn. Prentice Hall, Upper Saddle River, New Jersey.

Zimmerman R.J., T.J. Minello, G. Zamora (1984) Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. Fishery Bulletin 82: 325-336.

Zimmerman R., T.J. Minello, T. Baumer, M. Castiglione (1989) Oyster reef as a habitat for estuarine macrofauna. NOAA Technical Memorandum NMFS-SEFC-249

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