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EFFECTS OF HABITAT QUALITY ON SECONDARY PRODUCTION IN SHALLOW ESTUARINE WATERS AND THE CONSEQUENCES FOR THE BENTHIC-PELAGIC FOOD WEB

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

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

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by
David James Gillett
2010

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

David J. Gillett

Approved, by the Committee, January, 2010

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DEDICATION

This work is dedicated in part to my family, who have always trusted that I knew what I was doing (even if they did not) and in part to Dr. A. Fred Holland, who was the first real mentor I ever had and who taught me how to do ecology.

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Field-based, ecosystem-scale benthic ecology is a relatively difficult and time-consuming process that requires the work of many hands. This is further exacerbated when incorporating multiple trophic levels and biogeochemical processes into the structure and functioning of the macrobenthic community. As such, I must first and foremost acknowledge the hard work and support of all the members of the Benthic Processes and Anderson labs for their help with the collection and processing of samples this dissertation is based upon. Alice Brylawski, Leandra Lockwood, Jennifer Buehrle, Shanay Butler, Elizabeth Wells, Payal Dharia, Bill Metcalfe, and Treda Grayson all deserve special recognition for countless hours they spent in the field and the lab with me, putting up with my odd sense of humor and the physical/mental rigors of long days spent slogging through the shallow estuarine waters of Chesapeake Bay.

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ABSTRACT

Anthropogenic degradation of coastal and estuarine habitats is an ongoing problem facing scientists, natural resource mangers, and the general public. Decreases in habitat quality produce relatively predictable changes in the structure and composition of macrobenthic communities and it has traditionally been assumed that the ecosystem functions of the community change as well. In Chesapeake Bay, the most pervasive cause for the degradation of benthic habitats is the excessive inputs of nutrients that lead to eutrophication and the accumulation of organic matter in the system. Working within this framework, a study was conducted investigating changes in macrobenthic (i.e., secondary) production along a gradient of eutrophication-driven changes in habitat quality in shallow subtidal Chesapeake Bay. To determine if changes in macrobenthic community structure and function alter the food web of these systems, the effects of habitat quality on the utility of the macrobenthos as a food source to nekton via a predator exclusion experiment and a stable isotopic (^{15}N and ^{13}C) study on the diet of the macrobenthos and nekton were examined along a portion of the aforementioned gradient in habitat quality.

There was strong evidence indicating that in depositional habitats of the saline estuary, macrobenthic 2° production decreased with decreasing habitat quality. There was also some indication that in non-depositional habitats, water column eutrophication did not act as a stressor to the benthos; instead providing food subsidies to the macrobenthos and leading to an increase in community 2° production (primarily filter-feeders). The predator exclusion experiment illustrated that changes in macrobenthic community structure and production had an impact on the suitability of the habitat as forage areas for benthivoric nekton. The degree of predation pressure was not, however, related to habitat quality. Instead it appears to have been related to the presence/absence of large amounts of bivalve production. Additionally, results indicate that bioturbation of sediments by nekton searching for prey items also had negative effects on the production of deep deposit-feeding and small interface-feeding fauna. Based upon the patterns in stable isotopes of the fauna and the organic matter pools, there was little impact of habitat degradation on consumption by most of the macrobenthic feeding guilds. There was some indication of prey/organic matter switching among the omnivores and shallow-deposit feeding fauna at different sites, but not in relation to habitat quality. Results also showed that most of the macrobenthos collected from shallow subtidal habitats were not dependent upon microphytobenthos as a primary food source. Isotopic values indicate that most of the macrobenthos were feeding upon a mix of microphytobenthos, phytoplankton, sediment, and detritus, all of which was likely processed, to some degree, by sediment bacteria.

Considered together, these results illustrate how eutrophic-driven habitat degradation negatively impacts the functioning of shallow water estuarine food webs and that the impacts are realized through the macrobenthos. This dissertation provides evidence supporting the assumptions that ecosystem function can be linked to macrobenthic community structure and provides an avenue to incorporate changes of environmental quality into predictions about the productivity, and consequently, the management of natural resources.

EFFECTS OF HABITAT QUALITY ON SECONDARY PRODUCTION IN SHALLOW ESTUARINE WATERS AND THE CONSEQUENCES FOR THE BENTHIC-PELAGIC FOOD WEB

Chapter I

Assessment of Habitat Degradation in the Coastal Zone and the Consequences for Resident Biota

An Introduction and Research Motivations

INTRODUCTION

Since the industrial revolution, much of the coastal waters and sediments within the United States have become increasingly polluted with a variety of nutrients, heavy metals, organic compounds, pesticides, biological agents, and other substances to the point that more than 34% of US coastal habitat is significantly impaired (Pew Oceans Commission 2003; U.S. Commission on Ocean Policy 2004; USEPA 2008). However, as the value and the susceptibility of the coastal ocean and estuaries to degradation has become more apparent to the public, there has been a concomitant increase in the desire to quantify the degree of pollution and the degree to which ecosystem services are impaired.

In measuring the degree of pollution in estuarine and coastal waters there are two general approaches, which can be framed in the concept of a stressor-response model: 1.) the direct measurement of the stressor(s), i.e., the pollutant; or 2.) a measurement of the response(s), i.e. the impacted environmental resource (USEPA 2003). Over the years a multiplicity of techniques have evolved to measure the degree and effects of pollution following both approaches. Little consensus exists, however, on what is the best method and approach, due in large part to the environmental complexity of estuaries, as well as the diverse network of stakeholders that utilize and study estuaries (Bortone 2005). In the United States, maintaining the health of estuaries is legally mandated by the Clean Water Act and is the domain of the United States Environmental Protection Agency (USEPA) and its regional partners. As such, in this short review of approaches to measuring pollution and subsequent effects in estuarine and coastal waters, different methods will be discussed and evaluated loosely within the guidelines of the USEPA (Table 1) (Jackson et al. 2000).

What makes a good environmental indicator of pollution? – A given indicator should provide a measure of variables that are of interest to both local and regional management agencies, e.g., mussels in New England (O'Conner 2000) or grouper in southern Florida (Eklund, 2005), as well as an important role in the ecosystem of interest, e.g., macrobenthos in Chesapeake Bay (Weisberg et al. 1997). In the creation

of an environmental indicator, the scale (both spatial and temporal) and the response time of the indicator to the insult must be considered. Indicators can range from extremely localized and near instantaneous response of sub-lethal, cellular-level indicators in a single animal or plant (e.g., heat-stress protein expression or membrane failure), to long-term, integrative stresses (both direct and indirect) expressed in community composition changes (Fig. 1) (Diaz 1992; Ringwood et al. 1999; Adams 2005). The appropriate choice of a measurement approach from biomarkers, bioindicators, or direct pollutant measurement will depend in large part upon the nature of the pollution (if that is known), the goals of the investigators, and the funding and resources available (Jackson et al. 2000; Adams 2005).

Nutrient & Contaminant Measurements – The most conceptually simple indicator of a pollutant in the environment is a direct measurement. From at least the early 1970's (Carpenter and Huggett 1984; Long and Chapman 1985; Boynton et al. 1994; Howarth et al. 2002), investigators have been measuring the concentrations of organic compounds (PAHs, PCBs, etc), heavy metals (Cu, Cd, Hg, etc), various pesticides and herbicides (DDT, atrazene, etc.), as well as nutrients (NH_3, NO_x PO_4) in the sediments and waters of the coastal ocean. More recently, measurements of pharmaceuticals and other modern chemicals, such as fire retardants, are being made in marine systems around the globe (Hoenicke et al. 2007; Caliman and Gavrilescu 2009). Measuring the amounts of various chemical pollutants in the sediment and water column provides investigators a direct quantification and identification of the chemical stressor(s) in the system, from a single compound, a mix of multiple chemicals, or their degradation products. A profile of the pollutants in a system can also provide insight into source(s) of the pollution, as many compounds, or ratios of compounds, are indicative of their source (Sanger et al. 1999; Walker and Dickhut 2001).

The primary limitation of this approach is that contaminant levels by themselves do not provide any insight into the effects of the pollutant, how it affects the functioning of the ecosystem, and the bioavailability of the compounds, which will in part determine the impact of the pollution on the ecosystem (Long and Chapman 1985; Long et al. 1995; Lee and Lee 2005). While sample collection for contaminant measurement is simple and can be done with broad spatial and temporal coverage (e.g., Long and Chapman 1985; Hyland et al. 1999; Holland et al. 2004), processing of large numbers of samples requires very specialized equipment (atomic adsorption spectrophotometry, gas chromatograph or high pressure liquid chromatograph mass spectrometry, etc) and considerable expense to analyze the typical suite of organics,

metals, and pesticides, let alone the newer compounds of interest for which analysis protocols are being developed (D. Sanger, pers. comm.).

Biotic Measurements – If bulk measurements of a pollutant in an ecosystem can be viewed as quantification of the stressor, then the measurements of the biota are a quantification of the response to the stressor. As noted earlier (Fig. 1), biotic measurements can vary from biomarkers that are highly sensitive to stressors, often with compound specific responses, that quantify exposure to pollutants to bioindicators that illustrate the ecological effects of pollutants and integrate to varying degrees over space and time. Measurements of the biotic response to pollution are some of the most commonly used approaches to the assessment of environmental pollution in estuaries and coastal systems for reasons discussed below. Biotic measurements typically used to assess habitat quality, in order of both increasing complexity and ecological relevance, include: 1.) sediment or water toxicity bioassays - exposing organisms with known response profiles to potentially contaminated material (e.g., Long and Chapman 1985; Rand et al. 1995; Ringwood and Keppler 1998); 2.) biomonitoring – measuring the pollutant load in tissues of organisms placed, or naturally occurring in the environment (e.g., O'Conner 2002; Chiuchiolo et al. 2004; Downing et al. 2004; Tuerk et al. 2005); and 3.) community monitoring – comparing differences in the community structure between "reference conditions" and those in habitats of interest (e.g., Weisberg et al. 1997; Van Dolah et al. 1999; Borja et al. 2000; Llansó et al. 2002).

Most of the widely used biotic measurements of environmental pollution are based upon the 3rd approach: the assessment of estuarine and coastal communities (Diaz 1992; Cairns 2003; Adams 2005). This is in large part because changes in community structure are the most ecologically relevant measurement of a response to the stressor that pollutants create (Fig. 1) and can be done at a moderate expense. Community composition at all trophic levels represents an integrative endpoint of single or multiple environmental stressors, both natural and anthropogenic, that can be placed into a functional context of food web dynamics, nutrient cycling, or fisheries production (Mc Intyre 1985; Diaz 1992; Weisberg et al. 1997; Raposa et al. 2003; Jordan and Smith 2005; Paerl et al. 2005). Three of the major problems with using community structure to assess the effects of pollution on an ecosystem are determining appropriate, habitat specific reference conditions for comparisons (Alden et al. 2002; Diaz et al. 2004), making sense of the complex changes that occur in communities under stress, and presenting these changes

in a simple, straightforward manner (Mc Intyre 1985; Warwick 1986; Diaz 1992). Despite the variety of organisms inhabiting the coastal ocean, most monitoring and assessment programs (e.g., USEPA Environmental Monitoring and Assessment Program [EMAP] and National Coastal Assessment [NCA], The Chesapeake Bay Program, European Union [EU] Water Framework Directive) use macrobenthic communities as their target because of their relatively sessile nature, length of lifespan, and thei varied, important ecological functions they provide (Bilyard 1987; Dauer 1993; Weisberg et al. 1997; Casazza et al. 2002).

Even though there are a variety of ways to quantify habitat quality, what constitutes good or poor quality is inherently a judgment without universal benchmarks (Elliott and Quintino 2007; Weisberg et al. 2007; Tillin et al. 2008). Consequently, for the purposes of my dissertation I chose to use a weight of evidence approach to quantify habitat quality (e.g., Long and Chapman 1985; Weisberg et al. 1997; Hyland et al. 2000; Alden et al. 2002), with the assumption that if patterns in biotic responses to different measures of habitat quality are concordant, then the observed trends will be reflective of real relationships in the ecosystem. The habitat quality measures I used included both biotic measurements and a sediment quality indicator of eutrophication, all of which were related to the direct measurement of the stressor in the environment (e.g., historical nutrient inputs) (Schaffner, unpublished). Habitat quality was measured with multi-metric indices that quantify changes in benthic community structure (Chesapeake Bay B-IBI [Weisberg et al. 1997; Alden et al. 2002] and US EPA MAIA [Llansó et al. 2002] benthic indices), univariate measures of macrobenthic community structure (species richness [S] and Shannon-Weiner diversity [H']), and a measure of accumulated organic matter in the sediment (total nitrogen).

Macrobenthos and degraded habitats – The utility of both the multi-metric and univariate biotic measurements rely upon one of the central paradigms of benthic ecology: that with perturbation, especially organic matter accumulation or physical disturbance, the structure and composition of the resident macrobenthic community will change in a relatively predictable fashion (e.g., Pearson and Rosenberg 1978; Rhoads and Young 1978; Warwick 1988; Peterson et al. 1996; Gray et al. 2002). This relationship is due in large part to the association of the animals with the sediment, where most pollution effects are concentrated; their sessile nature, which prevents them from avoiding pollution; their relatively long

lifespan, which integrates environmental insults over time, and the diversity of the community, which can lead to many different community states (Weisberg et al. 1997; Van Dolah et al. 1999; Llansó et al. 2002).

The degradation of benthic habitat in estuaries is typically linked to eutrophication/hypoxia, chemical contamination, or a combination of the two (Peterson et al. 1996; Dauer et al. 2000; Lerberg et al. 2000; Christman and Dauer 2003; Holland et al. 2004). In general, the benthic communities of soft sediments shift from spatially and trophically complex suites of large and small bivalves, polychaetes, and crustaceans, which are easily processed by nektonic predators, to simplified groups of relatively small polychaetes and oligochaetes, which are less usable to higher nekton because of their small size (Pearson and Rosenberg 1978; Weisberg et al. 1997; Peterson et al. 2000). Increased organic matter input to the benthos and subsequent increases in sulfides and ammonia have been linked with reduced species and trophic guild diversity, abundance, biomass, and the depth at which macrofauna are found (Pearson and Rosenberg 1978; Jørgensen 1996l; Gray et al. 2002). However, because the organic matter can be used as a food source, the community biomass may increase (Sardá et al. 1996; Nixon and Buckley 2002). Chemical contaminants, e.g., heavy metals, hydrocarbons, organo-chlorides, can have similar effects on the benthos at the community level, reduction in sensitive taxa, lower biomass, etc, but typically without the added food benefits that eutrophication typically provides (reviewed in Peterson et al. 1996; Gaston et al. 1998). Additionally, many contaminants have taxa specific effects (e.g., organotins and gastropods; pesticides and crustaceans), which disproportionately affect select parts of the macrobenthic community, altering trophic relationships (Rand et al. 1995; Valiela 1995).

All of the aforementioned studies deal almost exclusively with linking structure of macrobenthic communities (i.e., abundance, biomass, taxonomic composition, etc.) to different levels and types of perturbation; creating characteristic disturbed/degraded macrobenthic communities. Implicit in this concept of a degraded benthic habitat is that the change in community structure results in changes in the ecological function of the community, which are in turn, realized throughout the ecosystem via changes in trophic relationships, nutrient cycling, and other key processes. One of the most ecologically important, and far-reaching aspects of these changes are the alterations to the estuarine food web, which has ramifications for microbes, nekton, and humans alike.

Benthic organisms directly consume organic matter from a variety of sources, which are typically not directly available to other trophic levels (e.g., Fauchald and Jumars 1979; Commito and Ambrose 1985; Diaz and Schaffner 1990; Gaudênci and Cabral 2007) due to size or digestion limitations (e.g., bacteria or detritus to fish). Nektonic predators are able, however, to indirectly utilize the wide array of organic matter in estuaries by preying upon the benthic consumers (e.g., Virnstein 1979; Holland et al. 1980; Edgar and Shaw 1995). Point-in-time measurements of macrobenthic abundance and biomass alone do not provide enough information about these processes (Diaz and Schaffner 1990; Tumbiolo and Downing 1994; Wilber and Clarke 1998). The estimation of organic matter production (primary, secondary, etc.) does, however, provide an ecological currency that can be measured at one or more trophic levels and can be used to quantify the energy and material flows within the food web (e.g., Crisp 1984; Diaz and Schaffner 1990; Gerritsen et al 1994)

A small number of published studies demonstrate how changes in the structure of the macrobenthic community induced by chemical contaminants or nutrient over-enrichment alter production and affect other trophic levels. Shieh et al. (2002) and Carlisle and Clemens (2003) observed reduced macrobenthic 2° production and altered community structure in freshwater streams exposed to heavy metals and pesticides. In both studies, structural changes in the communities from chemical contamination led to altered production and flow of material in the stream ecosystems that impacted both primary producers and secondary consumers. Increases in nutrient and organic matter input, in contrast, have been shown to increase macrobenthic production beyond background/non-enriched levels despite changes in community composition (Sardá et al. 1996; Nixon and Buckley 2002). At high levels of organic matter input, persistent hypoxia in the water column can become a problem, killing the macrobenthos and reducing annual production (Diaz and Rosenberg 1995; Rakocinski 2009; Seitz et al. 2009). Even in shallow, well-mixed environments high nutrient input and periodic hypoxia (typically at night when respiration exceeds oxygen production) impact the macrobenthic community structure and function, reducing diversity and selecting for more hypoxia-tolerant and opportunistic fauna (Lerberg et al. 2000; Holland et al. 2004; Gillett et al. 2007).

Estuarine Shallows – Estuaries are among the most biologically productive areas of the world's coastal oceans, supporting a vast array of benthic and nektonic organisms (Day et al. 1989; Heip et al.

1995; Underwood and Kromkamp 1999). They also represent a confluence of the land and the ocean with significant human activity. In many respects, the most ecologically important parts of estuaries are the shallow, marsh-lined fringes. The benthic communities of shallow estuarine habitats are composed of abundant, fast-growing (Seitz & Schaffner 1995; Sardá et al. 1996 Herman et al. 1999; Gillett et al. 2005), energetically rich organisms (Cummins and Wuycheck 1971) that are supported by high levels of benthic and planktonic primary production (Tenore 1988; Cloern et al. 1996; MacIntyre et al. 1996; Miller et al. 1996), as well as upland and salt marsh production (Goñi et al. 1997; Mitsch and Gosselink 2000; Seitzinger et al. 2002). In turn, these areas support a wide variety of transient and resident finfish and crustaceans that have important ecological, economical, and social value (Hines et al. 1990; Ruiz et al. 1993; Cicchetti 1998; Peterson, et al. 2000; Ross 2003).

In addition to their ecological value, estuaries are also very desirable, and therefore valuable, places for human development. The coastal zone of the United States comprises approximately 17% of the total land area of the country, yet more than half of the population lives there. Many of the largest, fastest growing cities in the United States are located within an estuarine watershed. Over the next 15 years, the population of these areas is predicted to grow by approximately 27 million inhabitants; greater than 50% of the entire nation's population growth (Beach 2002). In the coastal zone of the United States, urban growth (i.e., the roads, homes, buildings, etc.) is increasing at a rate approximately 2.5 times that of population growth; this pattern of growth is often termed sprawl and has deleterious effects on sensitive ecosystems (Beach 2002).

The shallow parts of estuaries are where the impacts are first, and often hardest felt, due in part to their proximity to the uplands and the complex nature of their trophic structure (Dauer et al. 2000; Lerberg et al. 2000; Holland et al. 2004). As an example, benthic monitoring data collected by the Chesapeake Bay Program indicate that more than 50% of the unvegetated, shallow-water ($\leq$3 m) benthic habitat area of Chesapeake Bay is classified as degraded using the Benthic Index of Biotic Integrity (unpublished B-IBI data for random stations 1996-2002, Chesapeake Bay Program). Furthermore, analysis of trends in benthic habitat condition at all depths around Chesapeake Bay ecosystem for the last 18 years indicates that the extent of degraded areas will remain the same or get worse if current management strategies remain the status quo (Llansó et al., 2003).

Macrobenthos and nekton – The links between the integrity of benthic habitat and the continued productivity of our fisheries is being increasingly emphasized in the scientific and political communities (Dalton 1999). The Pew Oceans Commission, the U.S. Commission on Ocean Policy, and many leading scientists have warned that continuing decreases in productivity and shifts in the composition of prey communities from desirable to undesirable or noxious species will lead to greatly reduced fisheries yields (Pauly & Christensen 1995; Pauly 2000; Peterson et al. 2000; Pew Oceans Commission 2003; U.S. Commission on Ocean Policy 2004). The continued degradation of shallow water benthic habitats in Chesapeake Bay and other estuarine ecosystems will likely result in reductions in the suitability of these areas as essential fish habitat, contributing to further declines in fisheries yield. At present though, this problem is difficult to address because the relationships between benthic habitat quality and nekton production remains poorly resolved for shallow water habitats (Diaz and Schaffner 1990; McGee 2004).

Most research in this area has focused on basic measures of nekton abundance, diversity, and/or growth rate associated with a given habitat type (e.g., Currin et al. 1984; Ruiz et al. 1993; Cicchetti 1998; Ross 2003). Results demonstrate that shallow, unvegetated estuarine habitats are important for the growth of commercially important nekton. Additionally, the authors implicitly suggest that loss or degradation of these habitats would have negative affects on the nekton that use them as a source of food. Fewer studies directly relate changes in nektonic production and growth to habitat degradation and changes in macrobenthic community structure. The consensus from these studies is that most of the species of nekton that normally inhabit a particular area will continue to associate with the same, moderately degraded habitat, but at lower densities (Burke et al. 1993; Peterson et al. 2000; Holland et al. 2004). Additionally, there is evidence that the nekton experience reduced growth and production at both the species and community level as a result of alterations to the benthic community that the nekton feed upon (McIvor and Odum 1984; Kesminas et al. 1994; Wilber and Clarke 1998; Peterson et al. 2000). As an illustration, Sherwood et al. (2002) observed a reduction in growth of yellow perch (*Perca flavescens*) in lakes that had simplified benthic communities (due to heavy metal contamination of the sediments) compared to those from lakes with healthy, diverse benthic communities. The benthos in the contaminated lakes did not provide as much energy for the fish as those taxa in the non-contaminated lake, thereby limiting the maximum potential size of the perch and altering their population and trophic dynamics.

In highly contaminated systems, sediment contaminants can have toxic effects directly on the nekton, impairing their physiology and growth (Weeks and Warinner 1984; Kesminas 1994; Hinkle-Conn et al. 1998); however, sites with that degree of contamination are limited in Chesapeake Bay (e.g., Elizabeth River, Baltimore Harbor, etc). Eutrophication can also adversely affect nekton by creating hypoxic conditions in the water column (Kesminas et al 1994; Diaz and Rosenberg 1995; Eby et al. 2005), but typically not in shallow water where there is sufficient wind-induced mixing and hypoxic episodes there are relatively short in duration (e.g., Pihl et al 1992).

The studies discussed above suggest that a stronger link between habitat integrity and nektonic production can be made through studying the estuarine food web where the macrobenthos serve as a conduit between varied, highly productive organic matter sources of the shallows and ecologically and economically important nekton that spend at least some portion of their lifecycle in this habitat. As the composition and production of the macrobenthic community is altered, changes should cascade through to other trophic levels. Reductions in benthic 2° production associated with inputs of chemicals and excess nutrients to an area should result in a concomitant reduction in the potential nektonic production of an area. Furthermore, degradation-driven changes in the prey community structure towards smaller, less motile fauna (e.g., Pearson and Rosenberg 1978; González-Oreja and Saiz-Salinas 1999; Gray et al. 2002) may limit the utility of the 2° production that is available as a food source to benthivoric nekton.

MOTIVATIONS AND INVESTIGATIVE APPROACH

At present, there is a paucity of information available detailing the links between macrobenthic community structure and ecosystem function, especially in relation to changes in habitat quality. The macrobenthic function that is of particular interest here is how the macrobenthos serve as a conduit for the energy and materials that are produced or accumulate in the estuary to subsequent, often economically important, trophic levels. Given their structural and potentially functional responses to habitat quality, this role of the macrobenthos has the capability to serve as a mechanism for the translation of habitat degradation to multiple trophic levels throughout the estuary. The primary goal of this research was to determine how eutrophication-driven degradation of estuarine habitats affected macrobenthic 2° production, the availability of this production to higher trophic levels, and if there were changes in what types of organic matter supported the benthic-pelagic food web. Formally, the three major research questions were:

1.) Is macrobenthic 2° production in shallow water estuarine systems related to the degree of habitat degradation? **Chapter 2**

2.) Do changes in macrobenthic community structure and production related to habitat degradation alter the utility of the benthos as a food source to benthivoric nekton? **Chapter 3**

3.) What organic matter pools support macrobenthic 2° production in shallow estuarine waters and do those relationships change with habitat degradation? **Chapter 4**

Estimates of 2° production were a central part of this work. Production measurements provide rates of energy and material movement in an ecosystem. They represent an integration of the biomass inputs (food intake, births, immigration) and outputs (reproduction, emigration, or death) of an ecosystem more so

than traditional standing-stock measurements. Due to the expense and time involved with directly measuring production for complex benthic communities at multiple sites, I chose to estimate macrobenthic production using published relationships between biomass and environmental variables with 2° production (e.g., Edgar 1990; Wilber and Clarke 1998; Hagy 2002), which provides reasonable estimates of production with less frequent sampling than that needed for more traditional methods (e.g., Hynes and Coleman 1968; Crisp 1984; Downing and Rigler 1984).

To assess the effects of habitat quality on the productivity of the macrobenthic communities of shallow estuarine systems, empirical estimates of 2° production were calculated at a series of sites that comprised a gradient in eutrophication in mesohaline, oligohaline, and tidal freshwater portions of Chesapeake Bay, USA. The designation of the eutrophication gradient was based upon ten years (1993 – 2003) of historical water quality data collected by the Chesapeake Bay Program and the Virginia Department of Environmental Quality, as detailed in Schaffner et al. (2008). The patterns in 2° production estimates were then compared to patterns in five habitat quality metrics: the Chesapeake Bay Benthic Index of Biotic Integrity (B-IBI), the Mid-Atlantic Integrated Assessment (MAIA) benthic index, species richness (S), Shannon-Wiener species diversity (H'), and sediment nitrogen concentrations. To determine if alterations in the structure of the macrobenthic community affected the utilization of a particular habitat as a food source by nekton, I compared macrobenthic 2° production between areas where nektonic predators were excluded and areas exposed to the natural level of predation at a sub-set of the sites along the eutrophication gradient. Lastly, natural abundance ^{15}N and ^{13}C stable isotopes were used to characterize a variety of organic matter pools from estuarine shallows (microphytobenthos, seston, and bulk sediment) and their contributions to the diet of the macrobenthos and eventually their nektonic predators. These characterizations were conducted at a similar sub-set of sites along the eutrophication gradient to determine if habitat quality, particularly the resultant changes in macrobenthic community structure, alter those diet relationships.

In the following chapters, I present a line of evidence that shows a response in an important ecosystem function of macrobenthic communities (i.e., as a conduit of organic matter through the food web) in shallow estuarine waters that is related to changes in community structure. The changes in

community structure, in turn, are reflective of exposure to varying degrees of eutrophic stressors, but surprisingly the responses were not uniform across the estuarine landscape. The environmental setting and population/predator-prey dynamics appear to influence the magnitude and direction of the relationship between the stressor and the structural and functional responses.

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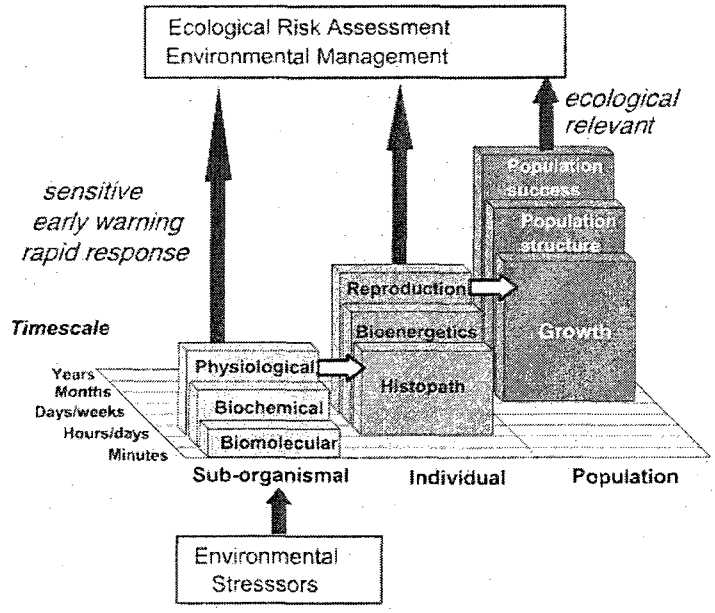
Table 1. A summary of the US Ecological Protection Agency's Environmental Monitoring and Assessment Program (EMAP) guidelines for the creation and evaluation of environmental pollution indicators. Summarized from Jackson et al. 2000.

Evaluation Points	Brief Description
Relevance to the Assessment	A potential indicator should be responsive to the management objective and complement other indicators where possible.
Relevance to Ecological Function	An indicator should directly measure, or be conceptually linked to ecosystem function and be conceptually linked to the stressor(s) of concern
Data Collection Methods	Methods should for collection of indicator data should be standardized such that data will be comparable between sites and not significantly disturb the site during repeated visits. Analysis and expected sources of error should also be described *a priori*
Logistics	Logistics of data collection and processing should be kept within the support and potential funding of the management program
Information Management	Methods for data processing, analysis, storage, retrieval, and meta data documentation must be considered.
Quality Assurance	An indicator should have a quality assurance quality control program for all measures.
Temporal Variability	Potential indicators should collect data that are comparable between sites within the designated field season of the indicator. Data should also be comparable between years.
Discriminatory Ability	A potential indicator should be able to discriminate between different sites along a known degradation gradient.

Figure 1. Conceptual diagram illustrating the ecological and temporal scale of different approaches to monitoring environmental pollution in estuaries and coastal oceans from the sub-cellular to the population level and the links that can be made between the different levels. Reproduced from Adams (2005).


Ecological Risk Assessment
Environmental Management
ecological
relevant
sensitive
early warning
rapid response
Population
success
Population
structure
Reproduction
Bioenergetics
Growth
Timescale
Physiological
Histopath
Biochemical
Biomolecular
Years
Months
Days/weeks
Hours/days
Minutes
Sub-organismal
Individual
Population
Environmental
Stresssors

Chapter II:

The Influence of Habitat Quality on Secondary Production in Shallow Estuarine Waters

For potential submission to Ecological Applications

ABSTRACT

Eutrophication is one of the most widespread agents of benthic habitat degradation and change in benthic community structure in estuaries and coastal oceans around the world. To evaluate the effects of eutrophication on benthic function, secondary production of the macrobenthic community was measured at a series of sites along a eutrophication/habitat quality gradient in Chesapeake Bay, USA, encompassing both the saline and tidal freshwater regions of the estuary. Habitat degradation was measured using a variety of approaches including multi-metric biotic indices, biodiversity, and sediment organic matter content. Eutrophication-driven degradation of macrobenthic secondary production within the estuary varied for two major habitat types and results were consistent among most metrics. In sandy non-depositional habitats, there were positive relationships between eutrophication and production of filter-feeding taxa. Conversely, in muddy depositional habitats, where sediments had relatively high concentrations of organic matter, there was a decline in secondary production with increasing eutrophication and degradation of habitat quality. In tidal freshwater habitats, there was a less uniform response, with some metrics indicating increasing production with increasing habitat degradation and others indicating an inverse relationship. These results, especially from the saline estuary, represent a quantification of ecosystem productivity in relation to changing habitat quality. This approach could be incorporated into ecosystem-scale management of fisheries and other natural resources, expanding their scope beyond biotic interactions to include the influence of environmental conditions.

INTRODUCTION

Both terrestrial and aquatic ecologists are interested in relationships between ecosystem structure and function. Much work has been focused on how species richness and species identity influence key functional processes of food webs (e.g., Covich et al. 2004; Cardinale et al. 2006; Stachowicz et al. 2007). The consensus from this work is that biodiversity and species composition at a given trophic level influences the composition and production of either preceding or subsequent levels (Covich 2004; Duffy et al. 2007). These linkages are particularly important for habitat conservation and restoration because restored structural aspects do not always ensure the restoration of food webs and productivity. The soft-sediment macrobenthic communities of estuaries provide an opportunity to investigate how relatively predictable changes in community structure influence ecosystem processes such as organic matter production, trophic relationships, or nutrient cycling.

Changes in habitat quality for soft-sediment macrobenthic communities of temperate estuaries have been shown to produce predictable changes in abundance, biomass, and community composition (e.g., Bilyard 1987; Warwick 1988; Peterson et al. 1996). The degradation of benthic habitats in estuaries is typically linked to eutrophication and hypoxia, chemical contamination, or a combination of the two (Dauer et al. 2000; Lerberg et al. 2000; Christman and Dauer 2003; Holland et al. 2004). When organic matter inputs are excessive, many benthic communities shift from spatially and trophically complex suites of large and small bivalves, polychaetes, and crustaceans, which are easily processed by nektonic predators, to a simplified group of relatively small polychaetes and oligochaetes, which are less available to nekton due to their small size (Pearson and Rosenberg 1978; Weisberg et al. 1997; Peterson, et al. 2000; Gray et al. 2002). Chemical contaminants (e.g., heavy metals, hydrocarbons, organo-chlorides) may also have similar effects on the benthos at the community level, resulting in a reduction in sensitive taxa and lower biomass (Peterson et al. 1996; Gaston et al. 1998).

From a holistic, ecosystem view, one of the most important functions or services of the macrobenthos is the production of organic matter. Broadly referred to as 2° production, macrofaunal heterotrophic production is ultimately derived from autotrophic 1° production. Secondary production typically is a measure of somatic growth without explicit consideration of respiration, excretion, or dispersed reproductive effort (Hynes 1968; Crisp 1984; Downing 1984). Secondary production provides an estimate of resource utilization by the macrobenthos (e.g., Thompson and Schaffner 2001; Gerritsen et al. 1994; Buzzelli et al. 2007), as well as an estimate of the amount of material available to subsequent trophic levels (e.g., Diaz and Schaffner 1990; Sardá et al. 1996; Wilbur and Clarke 1998; Hagy 2002).

A multitude of feeding guilds and trophic levels characterize benthic food webs in most estuaries. Macrobenthos may consume phytoplankton, microphytobenthos, macroalgae, meiofauna, and allochthonous or autochthonous plant detritus (Fauchald and Jumars 1979; Goedkoop et al. 1998; Fry et al. 1999), which might otherwise be unavailable for higher trophic levels (e.g., detritus or microphytobenthos to fish or swimming crabs). As a result, the benthos serve as important conduits and transformers of energy and nutrients in the food web. Understanding the nature of these linkages is key for understanding the factors that determine overall productivity.

The production of macrobenthos, and their role as a food source, is of particular economic and ecological concern in Chesapeake Bay. It has been estimated that 11 – 50% of total nektonic production in the estuary is derived from the benthos (Baird and Ulanowicz 1989; Diaz and Schaffner 1990; Hagy 2002) and that 40% of the 2006 and 2007 fisheries landings from Chesapeake Bay in dollars (8% by mass) were benthivores (NMFS 2008 Pers. Comm.). This pattern is similar for many other estuaries around the world and consequently the use of 2° production estimates to assess habitat quality has increased recently (González-Oreja and Saiz-Salinas 1999; Gillett et al. 2005; Ferguson and Rakocinski 2008). Unlike static measurements limited to one trophic level or environmental niche, measures of key rates represent connections between different biota (e.g., production, consumption) or parts of the environment (e.g., nutrient flux, sediment stabilization) that are functionally important. A focus on rate measures in addition to static standing stocks will provide an improved understanding of ecosystem health and function.

This study was designed to address how macrobenthic community structure and function are influenced by habitat quality. Specifically: Does macrobenthic production change with changes in habitat

quality? If so, is the relationship between 2° production and habitat quality positive or negative? While, there have been no studies explicitly addressing these issues, the ecological literature does provide some starting points. Nixon and Buckley (2002) reviewed a series of studies linking increased production of nekton in Scottish lochs and nekton and macrobenthos from the North and Baltic seas to increasing eutrophication. They emphasized a fertilization effect, where the negative aspects of eutrophication-driven habitat degradation (hypoxia and toxic reduced compounds in the sediment) were offset by the benefits of increased amounts of food. Rakocinski and Zapf (2005) put forth a conceptual model of macrobenthic function related to eutrophication in marine ecosystems, based largely upon the paradigm of Pearson and Rosenberg (1978). Their model suggests an initial increase in function with increasing eutrophication, followed by a plateau, and then a decline; giving the relationship between production and habitat quality a unimodal, concave-down pattern (Fig 1). The analyses of production and habitat quality data collected in the present study were designed to test for the presence of a relationship, the direction, either positive or negative, and the shape of the pattern: either polynomial or simple linear.

MATERIALS AND METHODS

Site Selection - Twelve sampling sites were selected throughout Chesapeake Bay, USA to comprise a gradient of habitat quality in each of the major salinity zones of the Bay. The habitat gradients were established *a priori* based upon historical water quality collected from the Chesapeake Bay Program (CBP) and the Commonwealth of Virginia Department of Environmental Quality (VADEQ) monitoring databases, and regional Benthic Index of Biotic Integrity (B-IBI) scores from the CBP's benthic monitoring program, when available (Schaffner et al. 2008; Chesapeake Bay Program, 2005; VA Department of Environmental Quality 2005). The selected sites included portions of the Virginia and Maryland National Estuarine Research Reserve System (NERRS) sites (Sweet Hall Marsh, VA and Monie Bay, MD), two Regions of Concern designated by the CBP (Atlantic Woods Creek, VA and Anacostia River, DC) and eight other sites with similar environmental settings within distinct salinity regimes (Fig. 2). At each site, a relatively quiescent, sheltered, depositional environment (referred to as the near-field stratum) and a more exposed, well-flushed, non-depositional environment (referred to as the far-field stratum) were selected for sample collection. Within each stratum, sampling locations were constrained to areas with relatively similar sediment composition, water depth, and hydrodynamics to minimize the influence of other environmental variables, beyond the eutrophication-driven habitat quality, on the macrobenthic communities (Schaffner et al. 2008). The Patuxent River near-field site was located in a semi-enclosed lagoon and after the data were collected and analyzed it was determined that it had distinctly different biogeochemical and biological patterns than the other near-field sites (Schaffner et al. 2008). As a consequence, it was excluded from the subsequent analyses, but the far-field data were retained.

The primary stressor along the gradient of sites was excess (i.e., greater than in the least disturbed parts of the estuary) nutrient loading that led to the accumulation of organic matter in the sediment (Schaffner and Gillett, *in prep*). Given the relatively shallow depth (<0.75 m) at which the study sites were located, the accumulation of toxic, reduced compounds in the sediments (e.g., sulfides or ammonia) was hypothesized to be primary stressor to the macrobenthos (e.g., Fenchel and Riedl 1970; Pearson and Rosenberg 1978; Jørgensen 1996; Gray et al. 2002); as opposed to persistent hypoxia associated with deeper, vertically stratified portions of Chesapeake Bay and its tributaries (e.g., Diaz and Rosenberg 1995;

Hagy et al. 2004). As an example, increasing sediment/porewater concentrations were measured with increasing eutrophication in both near- and far-field strata at all of the sites where macrobenthic samples were collected (Schaffner et al. 2008). It should be noted that the Sarah Creek near-field site may have experienced periodic diurnal hypoxia during summer nights (Gillett pers. obs.), where as hypoxia sensitive benthic taxa (i.e., amphipods and isopods) were observed at nearly all the other sites (Schaffner et al. 2008), suggesting that hypoxia was not a significant problem at all the other sampling sites. Additionally, the Atlantic Woods near-field site is known to have significant polycyclic aromatic hydrocarbon (PAH) sediment contamination (Dauer 2001; Walker et al. 2004) that likely influenced the macrobenthic community structure.

Data Collection – Within each stratum of each site, nine 13.3-cm diameter cores were taken to a depth of 25 cm at a series of pre-determined random points along a constant depth contour of 0.5 – 0.75 m below mean low water. Sediment cores were sectioned into 0-5-cm and >5-cm sections and sieved on a 500-μm screen, with the retained material fixed in 10% buffered formalin with rose bengal dye. An additional 5.7-cm diameter core was taken to a depth of 25 cm adjacent to each of the larger macrobenthic cores for analysis of sediment total organic carbon (TOC) and total nitrogen (TN).

Macrobenthic organisms were picked from the fixed samples, identified to the lowest possible taxonomic level, typically species, and stored in 2% buffered formalin. A random 10% of every 10 macrobenthic samples were re-sorted, identified, and enumerated by another benthic taxonomist. If samples were less than 95% accurate, then all 10 samples were reprocessed. Ash free dry mass (AFDM) was determined for each taxon by drying organisms at 65° C for ~48 hours and then subsequently combusting at 550°C for 4.5 hours. If a given taxon's AFDM in a sample was less than the detection limit of the balance (0.1 mg), then it was set to 0.1 mg (e.g., Llansó 2002). Sediment TOC and TN from 0-5 cm were analyzed from dried and acidified sediments with a Carlo Erba NA1500 elemental analyzer (Hedges and Stern 1984).

Within the mesohaline (18-5 PSU) and oligohaline (5-0.5 PSU) regions (referred to as the saline estuary), macrobenthic production was empirically estimated as daily production using the equations of Edgar (1990), which calculate production **P** (μg AFDM m^{-2} d^{-1}) from total taxon-specific biomass **B** (mg

AFDM m^{-2}) and mean monthly water temperature **T** (°C) (Eq. 1, 2, and 3). These equations were based upon a survey of the directly measured 2° production rates for different species of macrobenthos from a wide variety of temperate (5 – 30 °C) marine and estuarine habitats. Production for each taxon within each core was summed for an estimate of total macrobenthic community production. The macrobenthic communities of the tidal freshwater (< 0.5 PSU) sites were distinctly different than those of the saline sites, being dominated by oligochaetes and chironomid larvae (Schaffner et al. 2008). To better reflect the ephemeral nature of much of the macrobenthos of these sites (i.e., the chironomid and other insect larvae), the production equation of Morin and Bourassa (1992), which was developed for use in temperate lotic systems, was used to empirically estimate production. In this equation (Eq. 4), annual dry mass (DM) production **P** (g DM m^{-2} y^{-1}) is a function of annual taxon-specific biomass **B** (g DM m^{-2}), mean individual biomass **W** (mg DM), and temperature **T** (°C). To convert these estimates of annual DM production to annual AFDM, regressions of DM to AFDM were created from the biomass data of the non-bivalves (Eq. 5) and bivalves (Eq. 6) collected in this study (e.g., Ricciardi and Bourget 1998).

$$\mathrm{Log}_{10}P = -2.31 + (0.8*\mathrm{Log}_{10}B) + (0.89*\mathrm{Log}_{10}T) \quad \textbf{Eq 1}$$

(general invertebrates - Edgar 1990)

$$\mathrm{Log}_{10}P = -2.86 + (0.81*\mathrm{Log}_{10}B) + (1.32*\mathrm{Log}_{10}T) \quad \textbf{Eq 2}$$

(crustaceans - Edgar 1990)

$$\mathrm{Log}_{10}P = -2.18 + (0.87*\mathrm{Log}_{10}B) + (0.46*\mathrm{Log}_{10}T) \quad \textbf{Eq 3}$$

(molluscs - Edgar 1990)

$$\mathrm{Log}_{10}P = -.075 + (1.01*\mathrm{Log}_{10}B) - (0.34*\mathrm{Log}_{10}W) + (0.037*\mathrm{Log}_{10}T) \quad \textbf{Eq 4}$$

(Morin and Bourassa 1992)

$$AFDM = -0.00005 + 0.8198*DM \quad \textbf{Eq 5}$$

$$(n=972;\ r^2=0.992;\ p < 0.0001)$$

$$AFDM = 0.00130 + 0.05137*DM \quad \textbf{Eq 6}$$

$$(n=88;\ r^2=0.999;\ p < 0.0001)$$

Habitat quality or the degree of habitat degradation are ever-changing, multifaceted concepts related to management goals and, therefore, numerous cultural and political forcing factors (Elliott and Quintino 2007; Weisberg et al. 2007; Tillin et al. 2008). Habitat quality was measured with a variety of metrics, using a weight of evidence approach to determine the validity of any relationships between quality and production (e.g., Long and Chapman 1985; Weisberg et al. 1997; Hyland et al. 2000; Alden et al. 2002). The greater the number of relationships between different habitat quality metrics and 2° production that were concordant, the greater the likelihood that those relationships were not spurious. Initially, habitat quality was characterized with each core from each site/stratum using biologically-based metrics: the Chesapeake Bay Benthic Index of Biotic Integrity (B-IBI) (Weisberg et al. 1997); the Mid Atlantic Integrated Assessment (MAIA) benthic index (Llansó et al 2002); species richness (S); and Shannon-Weiner Diversity (H′); as well as a nutrient-based metric: sediment nitrogen content (% by mass). Subsequent analysis of these measures in relation to eutrophication and habitat quality (Schaffner and Gillett, *in prep*) however, suggested that within the far-field strata the water column eutrophication did not act as a stressor to the macrobenthos but as an organic matter subsidy (e.g., Nixon and Buckley 2002). In these shallow water systems that likely did not experience hypoxia, the subsidy obscured any relationship between B-IBI score, MAIA benthic index, species richness, and species diversity with the eutrophication gradient, rendering them useless in tracking habitat degradation. Sediment nitrogen content was the only measure of habitat degradation that was statistically related to the observed eutrophication gradient (Schaffner and Gillett, *in prep*). Consequently, 2° production in the far-field sites was analyzed with sediment nitrogen content as the sole measure of habitat quality, while all of the aforementioned measures were used with the near-field data.

The Chesapeake Bay B-IBI and the MAIA benthic index are two examples of multi-metric indices of benthic habitat condition used by the states of Maryland and Virginia (B-IBI) and the United States Ecological Protection Agency (MAIA) in the monitoring of the Chesapeake Bay and other Mid-Atlantic estuarine and coastal waters. Both indices are based upon the biological monitoring concepts of Karr (1991) and assess benthic habitat condition based upon various measures of macrobenthic community composition (e.g., abundance, dominance, species diversity, pollution indicative species, etc.) (Weisberg et al. 1997; Llansó et al. 2002). Both indices were designed to be used across the range of salinity and sediment composition of estuaries, while still allowing for comparisons of relative condition scores among samples from different locations and years. The comparisons are possible because for each distinct salinity-sediment combination, a series of different biotic measures with habitat specific thresholds are scored and then averaged so that environments fall along a gradient of 5 (best) to 1 (worst) (Weisberg et al. 1997; Alden et al. 2002; Llansó et al. 2002). Used in stratified-random sampling design, the Chesapeake B-IBI has provided a statistically rigorous method for the assessment of the benthic resources and habitat quality of the Chesapeake Bay and its tributaries for over a decade (Dauer 2000; Dauer et al. 2000; Llansó et al. 2003; Llansó et al. 2007).

Analysis - Relationships between macrobenthic production and habitat quality in the near-field sites, with the exception of sediment nitrogen, were assessed using mixed-model maximum likelihood regression in SAS v9.1 (α =0.05) (Littell et al. 2006). Each habitat quality metric was set as a fixed effect and the site was set as a random effect. Mixed model regression was used instead of fixed, least squares regression so that all 9 replicate cores could be used, but any covariance between cores from the same site would be accounted for in the calculation of sample variance and model parameter estimates. As noted above, sediment nitrogen was measured near each benthic core, but not in the actual core. Thus, it was more appropriate to compare site means of production and sediment nitrogen rather than the individual paired production and nitrogen replicates. The relationship of the means was assessed using fixed least squares regression in SAS v9.1 (α =0.05) (Freund and Littell 2000). Sediment nitrogen content was the only measure of habitat quality that was observed to represent the eutrophication gradient across the variety of sediment types in the estuarine environment, so these data were analyzed separately to allow us to comment

on the estuary as a whole; not just the muddy parts or the sandy parts. The nitrogen and 2° production relationships were fit with both simple linear and 2nd degree polynomial models to address the *a priori* hypotheses about the shape and direction of the relationships between habitat quality and macrobenthic production. Akaike's Information Criteria corrected (AICc) (Burnham and Anderson 2002) was calculated for both model configurations to assist with determining the most appropriate model for the data.

There are well documented differences in the production dynamics of relatively large, long-lived, benthic organisms with lower annual Production:Biomass ratios (P:B) compared to smaller, shorter-lived organisms with higher P:B (Nichols 1975; Banse and Mosher 1980; Diaz and Schaffner 1990; Seitz and Schaffner 1995). The bivalves found in the saline study sites (*Macoma balthica*, *M. tenta*, or *Mulinia lateralis*.) were relatively large, univoltine, typically with multi-year lifespans, and a uniformly muted response to low levels of reduced sediment compounds (Dame 1996; Gray et al 2002). The non-bivalve portion of the community was composed primarily of smaller, shorter-lived annelids and crustaceans capable of reproduction multiple times a year and with wide-ranging sensitivities to sediment stressors (Diaz and Schaffner 1990; Gray et al. 2002).

In recognition of the differences in life history, stress-tolerance, and organic matter utilization characteristics, the macrobenthic production data of the saline sites separated into bivalves and non-bivalves for analysis. By separating the macrobenthic community into two components any potential differential responses of growth to habitat quality could be elucidated and provide some context to the patterns seen in the community as a whole. The macrobenthic community of the tidal freshwater sites was comprised almost entirely of chironomid larvae and oligochaetes, which have similarly short-lived, mulitvoltine lifestyles. As such, no trophic distinctions were made in the analysis of those data.

RESULTS

A number of significant relationships were apparent in the mixed-model regressions between daily macrobenthic community production and habitat quality metrics in the saline portions of the Chesapeake Bay (Table 1). In the near-field stations, there were significant positive relationships with habitat quality (increasing habitat quality associated with increased production) expressed as Chesapeake Bay B-IBI score, species richness, and Shannon-Wiener diversity (Fig 3a–c), but no relationship was observed with the MAIA benthic index (Fig 3d). At the near-field of the tidal freshwater sites there were positive relationships between annual community production and habitat quality expressed as Chesapeake Bay B-IBI score, the % abundance of pollution indicative taxa, and species richness (Table 1). The species richness relationship with production represented positive relationship with habitat quality, like those observed in the saline sites, but the patterns of B-IBI score and pollution indicative taxa represented inverse relationships between habitat quality and production (Fig 4 a-c). There was no relationship between mean community production and mean sediment nitrogen at the near-field sites of the saline estuary, but there was a positive simple linear relationship (increasing production with increasing sediment nitrogen) in far-field stratum (Table 2). When the data from the two strata were combined, there was a significant concave-down relationship (modeled as a polynomial function) (Table 2), with initial increase in production with increasing sediment nitrogen but eventually decline as % nitrogen increases in the sediment (Fig 5 a-c). Unlike the saline estuary, there were no significant relationships (related in part to small sample size) between mean production and mean sediment nitrogen content in the near- or far-field strata in the tidal freshwater (Table 2), but the trends in the data have the same pattern as seen in the saline sites (Fig 5 j-l).

Production of the bivalve portion of the macrobenthic community in the near-field was less strongly related to habitat quality compared to the total community (Table 1), but there were significant positive relationships between daily production and habitat quality expressed as B-IBI score and community species richness (Fig 6 a&b). There was no significant relationship between mean bivalve production and sediment nitrogen content in the near-field, but there was a positive relationship in the far-field sites (Table 2, Fig 5 d&e). When the data from both strata were combined, the pattern was a similar shaped, though non-

significant, concave-down pattern between 2° production and increasing sediment nitrogen (Fig. 5f), like that seen with the total macrobenthic community.

The non-bivalve portion of macrobenthic community production was significantly related to habitat quality expressed as B-IBI score, species richness, and Shannon-Wiener diversity (Table I), though there was no relationship to the MAIA benthic index score. All of the significant relationships illustrate increased production with increasing habitat quality (Fig 7 a–c). The production of the non-bivalve portion of the community was the only aspect of macrobenthic production in the near-field that was significantly related to mean sediment nitrogen content (Table 2). As with the other measures of habitat quality, the pattern was positive; as habitat quality decreased (i.e., sediment nitrogen content increased) so did 2° production (Fig 5g). There was no relationship between non-bivalve production and sediment nitrogen content in the far-field sites, but there was a significant relationship when the data from both strata were analyzed together (Table 2). Both the simple linear and polynomial models were significant and both provided equivalent fits to the data (a difference in AICc scores of 0.002) (Table 2). As a consequence, the data were modeled as the polynomial, concave-down pattern (Fig 5i) because the pattern was was similar to that of the entire community and for ecological/conceptual reasons presented in the discussion.

DISCUSSION

Secondary production is an important aspect of ecosystem functioning, particularly in shallow water estuarine habitats, which are known to serve as nursery areas for a variety of nekton (Kneib 1997; Cicchetti 1998; Meise and Stehlik 2003). With the exceptions of Sardá et al. (1996), Rakocinski et al. (1997), Hagy (2002), or Rakocinski and Zapfe (2005), relatively little work has been done in estuarine and aquatic ecosystems to address the potential impacts of environmental degradation on this important ecosystem service. In muddy, depositional environments, there was a consistent pattern of decreasing macrobenthic production with eutrophication-driven decreases in habitat quality in the saline estuary, which represents a breakdown of ecosystem function in the shallow waters of Chesapeake Bay and its tributaries. In contrast, at sandy, non-depositional environments some evidence was observed for regional eutrophication to potentially stimulate 2° production, but only if the setting is right: low potential for hypoxia, sandy sediments with relatively low organic matter content, and a macrobenthic community dominated by filter-feeders, as alluded to in Nixon and Buckley (2002). While nektonic production was not measured in this study, the reduction of macrobenthic production (i.e., the food available to benthivoric nekton) should lead to a reduction of benthivoric nektonic production (e.g., Wilber and Clarke 1998; Powers et al. 2005). This study provides much needed support for the assumptions of many benthic ecologists that the changes in macrobenthic community structure caused by eutrophication-related habitat degradation represent a loss of community function; a paradigm built upon the framework of Pearson and Rosenberg (1978).

In shallow water estuarine systems, where hypoxia tends to occur only in the most severe cases of eutrophication and hydrodynamic constriction, excess nutrients and 1° production in the water column may degrade benthic habitat via the accumulation of organic matter and their subsequent breakdown products in the sediment (Schaffner and Gillett, *in prep*). The response pattern should be setting-specific though, as within these shallow water systems there is a gradient of habitats from sandy, organic matter deplete sediments to muddy, organic-rich sediments and the influence of eutrophication on secondary production will vary as well. The data from the present study illustrate this differential pattern, where increases in 2° production were observed in environments with low levels of sediment nitrogen, but eventually there was

an inhibition of production with greater amounts of organic matter in the sediment and changes in community structure. This pattern supports the conceptual models of Pearson and Rosenberg (1978) and Rakocinski and Zapfe (2005).

"Habitat quality", or "habitat integrity", are inherently value judgments without a singular, widely accepted set of benchmarks (Weisberg et al. 2007; Tillin et al. 2008). As such, a weight of evidence approach was chosen, comparing secondary production to a variety of assessments of quality and integrity. These assessments were based upon the structure of the macrobenthic community and sediment organic matter content at a series of sites that included highly modified and degraded urban areas, as well as conservation reserves that are protected because of their natural integrity. The results demonstrate a distinct, positive relationship between the quality or integrity of a system and the production of the resident macrobenthic community. A majority of the relationships were statistically significant and concordant across multiple metrics of habitat quality in the saline estuary. The repeated detection of these patterns supports the interpretation as a valid, underlying relationship between macrobenthic community structure and function. The results from this study indicate that as a system is degraded, typically due to excess nutrient inputs from anthropogenic alterations of upland watersheds and atmospheric deposition (Nixon 1995; Dauer et al. 2001; Holland et al. 2004), there is a concurrent decrease in the amount of food available to benthivoric nekton, which are important ecological and economical components of many estuarine ecosystems.

There were notable differences in the ecology of the shallow water macrobenthic communities of the saline and tidal freshwater regions of Chesapeake Bay (Schaffner et al. 2008) and this is reflected in the relationship observed between the production dynamics and habitat quality. In the saline sites, the effects of habitat quality created local variation in the community structure and subsequently productivity as roughly predicted by the conceptual models of Pearson and Rosenberg (1978) and Rakocinski and Zapf (2005). In contrast, the macrobenthic communities of the shallow tidal freshwater sites did not display a uniform response between production and the different measures of habitat quality, in part because this salinity zone represents an ecotone that is naturally highly disturbed by salinity fluctuations and heavy sedimentation (Diaz 1994; Draheim 1998; Attrill and Rundle 2002).

These results support patterns reported throughout the literature, in which saline and freshwater estuarine communities respond in diametrically opposite directions to eutrophication and the accumulation of excess organic matter in the sediment. In the saline estuary, degradation-driven changes in community composition create a community that is, typically, smaller-sized, shorter-lived, and less productive than that of a non-disturbed community (Pearson and Rosenberg 1978; Schwinghamer 1988; Gray et al. 2002). The pattern in the data was most evident in the non-bivalve portion of the macrobenthic community in the near-field strata, which displayed a smooth, gradient-like transition towards lower abundance and diversity and communities dominated by high-turnover, opportunistic fauna. The transition for the bivalves was not as smooth because there was considerable variation in the abundance and productivity of the bivalves in moderately and non-disturbed habitats (likely due to recruitment dynamics, predation, and a multi-year life history), with total absence in the disturbed habitats (Schaffner et al. 2008). In contrast, the communities of organically enriched freshwater habitats are dominated by taxa that can tolerate reduced organic compounds in the sediment, are more productive, and generally are longer-lived (e.g., tubificid and naidid oligochaetes) than those of the non-disturbed communities (dipterid and trichopterid larvae, sphaeriid and unionid bivalves) (McCullough and Jackson 1985; Martinet et al. 1993; Alden et al. 2002). A similar pattern was observed in the tidal freshwater data, where the biomass dominants were oligochaetes and, at one site, the invasive bivalves *Corbicula fluminea* and *Rangia cuneata* (Schaffner et al. 2008); taxa that are not strongly affected by disturbed, depositional environments with high organic matter content sediments (Diaz 1994; Miller and Payne 1998). Given the compositional differences in the macrobenthic communities between the saline and freshwater estuary, the dissimilar patterns in 2° production-habitat quality relationships are not surprising.

Interpreting the Saline Estuary - Rakocinski and Zapf's (2005) model relating macrobenthic community function (production in this study) and eutrophication was a unimodal, concave-down curve, with an initial increase in function with low-levels of eutrophication followed by a precipitous decline as eutrophication increases (Fig 1). This conceptual model was based largely on the ecology of relatively open, well-flushed marine and estuarine ecosystems and builds upon the concepts of intermediate disturbance and macrobenthic fertilization models (e.g., Connell 1978; Pearson and Rosenberg 1978; Xu et al. 1999; Gray et al. 2002). In the model, the initial increase in function with eutrophication is attributed to

a release from food limitation (i.e. a fertilization effect) leading to an overall increase in abundance and the appearance of stress-tolerant, opportunistic macrofauna (e.g., spionid or capitellid polychaetes) in addition to the species that dominated prior to enrichment. The decline in community function is due to the toxic effects of sulfides and ammonia in the sediment, as well as the onset of hypoxia, which cause the mortality of less tolerant taxa and then the inhibition of production as conditions continue to degrade (Pearson and Rosenberg 1978; Gray et al. 2002; Quiroga et al. 2005). In considering the present data in the context of these models, splitting the near-field and far-field data into different portions of the model, termed the fertilization side (left hand side of Fig. 1) for the far-field data and the degradation side of the model (right-hand side of Fig. 1) for the near-field, seemed appropriate.

The sediments of sandy, well-flushed systems do not seem to be as tightly biogeochemically coupled to the water column and eutrophic conditions appear not to act as a stressor to the macrobenthos. What connection there is between the water column and the benthic system, is biologically mediated by the feeding of filter-/interface-feeders in the sediments (Schaffner and Gillett, *in prep*) and therefore the community experiences a fertilization effect from eutrophication (e.g., Beukema and Cadée 1991; Nixon and Buckley 2002; Kirby and Miller 2005). However, without the appropriate fauna that can access the water column 1° production, eutrophication may have little positive or negative effect on functioning of the system. This is illustrated by the increased production of bivalves (filter- and interface-feeders) with increasing eutrophication in the far-field sites, while the non-bivalve portion of the community (grazers, deposit-feeders, or predators) showed no change in production along the gradient

In contrast, depositional ecosystems have a tight association with the upland watershed and water column processes (Schaffner and Gillett, *in prep*). While these characteristics make them productive, they are also easily disturbed and are often the first portions of the estuary to show signs of anthropogenic degradation (e.g., Lerberg et al. 2000; Holland et al. 2004). These areas have sediments that are naturally rich in organic matter from allochthonous and autochthonous detrital material, as well as planktonic and benthic 1° production (Schaffner et al. 2008). As such, resident organisms do not experience seasonal food limitation observed in deeper marine and estuarine systems (e.g., Marsh and Tenore 1990; Schaffner 1990; Reiss and Kröncke 2005) or shallow sandy areas and therefore the positive, fertilization aspect of eutrophication is not realized. Consequently, moving along the eutrophication/habitat quality gradient,

only decreases were observed in 2° production of the bivalves, the non-bivalves, and the community as whole, regardless of how habitat quality was measured. Interestingly, the results of Sardá et al. (1996) and Buzzelli et al. (2007) both demonstrated fertilization effects in muddy, depositional habitat. The communities they studied were dominated by oligochaetes though, which have unique production dynamics and show an unusually positive response to organic matter enrichment, relative to most other estuarine macrobenthos (Gray et al. 2002; Gillett et al. 2005).

Using sediment nitrogen content to represent the eutrophication gradient provided a measure of degradation that spanned most of the range of environmental settings observed in the shallow waters of estuaries and made it possible to combine the near- and far-field data. When the larger spectrum of potential estuarine habitats is considered (i.e., both depositional and non-depositional settings), both the positives and the negatives of eutrophication on the macrobenthic community can be seen, as predicted by Pearson and Rosenberg (1978) and others (Gray et al. 2002; Rakocinski and Zapfe 2005) (Fig 1 versus Fig 5 c,f, & i). With some generalizations, the spatial patterns that were observed along the eutrophication gradient can be used to predict the dynamics of a benthic community in a system experiencing an increasing degree of eutrophication through time (e.g., Underwood 1994). Following suit, there is an initial increase in 2° production (primarily filter- and interface-feeding bivalves) as the production of organic matter increases. But as organic matter loadings continue to increase and there is retention of that matter in the sediment, there is a decline in 2° production that can likely be attributed to the negative aspects of eutrophication (e.g., accumulation of sulfides and ammonia, reduction of oxygen in the sediment). These eutrophic by-products first inhibit the production of the less resistant non-bivalves and then the bivalves, until only the resistant, opportunistic taxa remain.

As the shapes of the different polynomial curves in Figure 5 illustrate, the production of the non-bivalves (which were predominantly grazers, deposit feeders, and predators) is approximately asymptotic in shape, suggesting that they did not reap the benefits of increasing organic matter, only the negatives. The bivalve response is strongly concave, with production responding to the fertilization effect and then eventually negatively responding to the degradation of the habitat (more clearly illustrated in Fig 6). The curve for the entire community is obviously a mix of the two other curves, but overall still illustrates the

principle of initial fertilization of production, until a tipping point is reached and the physiological stresses of the reduced compounds in the sediment presumably outweigh the benefits of increased amounts of food.

Interpreting the Tidal Freshwater – There are no widely accepted and published conceptual models for tidal freshwater habitats and ecosystem services similar to those discussed above for saline estuary. The near-field sites of the tidal freshwater showed a limited number of significant relationships between habitat quality and macrobenthic community production. Interestingly, those significant patterns were not concordant in describing the changes in 2° production and habitat degradation. Though not explicitly stated in the freshwater literature, the larger, longer-lived fauna (which tend to be the most productive) of tidal freshwater ecosystems seem better adapted for dealing with excessive organic matter and other disturbances, while the stress-intolerant fauna are relatively less productive (McCullough and Jackson 1985; Martinet et al. 1993; Draheim 1998; Carlisle and Clements 2003). This pattern held true when habitat quality was expressed as B-IBI score or % abundance of pollution indicative taxa, but not when expressed as species richness. The positive relationship between 2°production and species richness in these tidal freshwater habitats provides an interesting contrast to the other two measures of habitat quality. Among the tidal freshwater sites studied, there was greater species richness at the most degraded site than the least degraded site (Sweet Hall Marsh [Schaffner et al. 2008]). The Sweet Hall Marsh site has a record of periodic intrusions of saline waters during low rainfall periods or strong spring tides; whereas the other tidal freshwater sites did not (Reay and Moore 2009; Schaffner et al. 2008). These periodic salinity intrusions likely have a detrimental effect on to the freshwater fauna of the Sweet Hall Marsh site, creating an osmotically unstable environment and suppressing species richness, even in the absence of eutrophication-related habitat degradation (e.g., Diaz, 1989; Draheim, 1998; Attrill 2002; Attrill and Rundle 2002).

The limited number of significant relationships, especially with sediment nitrogen, and the contrasting patterns of production with habitat quality may also be due to the limited number of tidal freshwater sampling sites sampled for this study and that all of the tidal freshwater portions of Chesapeake Bay have high nutrient and sediment loads (e.g., Alden et al. 2002). These combined factors prevented the establishment of a sharp stressor gradient along which to measure macrobenthic production and therefore

limiting the confident extrapolation of the patterns that were observed to other systems. The ecology of tidal freshwater habitats is relatively understudied compared to those of the saline estuary or non-tidal freshwater systems, so it remains difficult to place these results into the context of those of other researchers. More research on changes in community structure and composition with pollution and habitat disturbance needs to be done to create a better understanding of macrobenthic production dynamics in tidal freshwater habitats; a valuable, but often overlooked component of estuaries (Draheim 1998).

Some Comments on Biodiversity and Productivity – As noted earlier, there have been a number of studies where researchers have experimentally manipulated community diversity or species richness and shown effects on community biomass (from which production is inferred) (reviewed in Covich et al. 2004 and Stachowicz et al. 2007). The proposed mechanisms behind these phenomena have primarily been grouped into niche complimentarity, facilitation, or sampling/species identity effects, which have been defined and reviewed in detail by Tilman et al. (2001) and Stachowicz et al. (2007). Though not the strict experimental manipulations of community composition as are seen in most studies, the degradation gradient of the near-field sites sampled in this study represent a gradient in macrobenthic community composition and diversity. In shallow saline estuarine habitats, there is a positive relationship between macrofaunal community production and both the number and the diversity of component species. Among the study sites analyzed here, many of the highly productive communities, which also had the highest diversity, tended to contain long-lived, high biomass bivalves (Schaffner et al. 2008), suggesting a sampling effect; i.e., samples with larger numbers of species have a greater probability to include highly productive taxa (bivalves in the present example). However, the patterns of high productivity with high species richness and diversity persisted when the production of bivalves was removed from the analysis, implying that niche complimentarity, not a sampling effect, may be the mechanism behind the observed relationships. The niche complimentarity concept proposes that as species diversity increases feeding guild diversity increases, as does specialization, both of which provide for a more complete utilization of the available 1° production and subsequently increased 2° production (Stachowicz et al. 2007). Indeed, in the macrobenthic communities examined in this study, there is a greater trophic diversity and spatial distribution of fauna through the sediment column in the least disturbed sites. This should facilitate a

greater, more efficient utilization of the variety of organic matter present in shallow estuarine habitats (Schaffner et al. 2008; Chapter 4).

Some of the common criticisms of many biodiversity – production experiments done in marine and aquatic systems have been that the experimental communities used were artificially constructed (e.g., random species removal), overly simplified, and were comprised of single trophic levels, all of which limit the applicability of the experimental data to real-world ecosystems (Covich et al. 2004). Because the current study contrasted similar habitats with environmentally altered community diversities, these data support the more experimental work of others (Balvanera et al. 2006; Cardinale et al. 2006; Stachowicz et al. 2007) while still being directly applicable to "real world" ecosystems and those tasked with managing them. Furthermore, by focusing on shallow water estuarine macrobenthic communities, the present study, more so than most experimental manipulations, encompasses the diversity and function of multiple trophic levels and feeding guilds that utilize an array of food sources (microphytobenthos, detritus, phytoplankton, or smaller fauna). Supporting what has been observed in simpler, experimental systems, the positive relationships between 2° production and macrobenthic species richness and diversity that were detectable in this field study with multiple interactions and feedbacks provide strong evidence for the positive influence of biodiversity on ecosystem functioning and that this influence is not specific to one trophic level or trophic interaction (e.g., Cardinale et al. 2006; Duffy et al. 2007).

CONCLUSIONS

In estuarine sites with salinity greater than 0.5 psu, there was strong evidence for negative impacts of habitat degradation on 2° production of the macrobenthos, a vital part the estuarine ecosystem that serves to effectively couple subsequent trophic levels to the large amounts of organic matter that is produced or accumulates there. However, when eutrophic water column conditions do not act as a stressor the macrobenthic community, there is the potential for stimulation of 2° production, but only when filter- and interface-feeding taxa capable of utilizing water column 1° production are present. Much as there is a sharp break in the estuarine continuum of community composition between the saline and the tidal freshwater regions, there appears to be contrasting responses of macrobenthic community production to changes in habitat quality. The patterns of 2° production with habitat quality were inconsistent in the tidal freshwater estuary, but the trends suggested that there is an increase in production with eutrophication-driven habitat degradation. Finally, the observed relationships across the entire estuary should be of value to those scientists and managers interested in ecosystem energetics and the modeling of changing estuarine landscapes on the productivity of valuable resources.

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Table 1. Summary of the simple linear restricted maximum likelihood mixed-model regressions between macrobenthic production and metrics of habitat quality in saline and freshwater sites in Chesapeake Bay: **B-IBI** - Chesapeake Bay benthic index of biotic integrity; **MAIA** - Mid-Atlantic Integrated Assessment benthic index; **S** - species richness; **H** - Shannon Wiener Diversity; and **% Pollution Indicative** - percent abundance of pollution indicative taxa. In all models, sampling site was set as a random variable and individual habitat quality as a fixed variable. An α of 0.05 was used in the interpretation of all analyses.

Salinity Zone	Dependent Variable	Stratum	Independent Variable	N	Intercept	Ind. Var. Estimate	Independent *p*
Saline	Log_{10} Community Production (mg AFDM m^{-2} d^{-1})	Near Field	B-IBI	70	0.6779	0.2696	<0.0001
		Near-Field	MAIA	70	1.2463	0.0348	0.4991
		Near-Field	S	70	0.9706	0.0315	0.0006
		Near-Field	H	70	0.9425	0.2008	0.0019
		Far-Field	BIBI	80	1.1570	0.1470	0.0320
		Far-Field	MAIA	80	0.8227	0.1889	0.0018
		Far-Field	S	80	1.0217	0.0404	<0.0001
		Far-Field	H	80	0.9404	0.2286	0.0052
	Log_{10} Bivalve Production (mg AFDM m^{-2} d^{-1})	Near-Field	B-IBI	70	-56.0500	0.4783	<0.0001
		Near-Field	MAIA	70	0.4951	0.0457	0.6049
		Near-Field	S	70	0.1708	0.0382	0.0190
		Near-Field	H	70	0.3081	0.1591	0.1680
		Far-Field	BIBI	80	-0.0352	0.2616	0.0503
		Far-Field	MAIA	80	-0.6648	0.3448	0.0043
		Far-Field	S	80	0.0993	0.0442	0.0282
		Far-Field	H	80	-0.6852	0.5029	0.0019
	Log_{10} Non-bivalve Production (mg AFDM m^{-2} d^{-1})	Near-Field	B-IBI	70	0.7721	0.1600	0.0002
		Near-Field	MAIA	70	1.0803	0.0306	0.4167
		Near-Field	S	70	0.8223	0.0290	<0.0001
		Near-Field	H	70	0.7283	0.2184	<0.0001
		Far-Field	BIBI	80	1.0394	0.1251	0.0090
		Far-Field	MAIA	80	1.0782	0.0790	0.0612
		Far-Field	S	80	0.9426	0.0330	<0.0001
		Far-Field	H	80	1.1276	0.0955	0.0897
Tidal Freshwater	Log_{10} Community Production (g AFDM m^{-2} y^{-1})	Near-Field	B-IBI	26	1.5347	-0.2266	0.0470
		Near-Field	MAIA	26	0.8223	0.08702	0.3696
		Near-Field	S	26	0.2949	0.07957	0.0062
		Near-Field	H	26	1.1134	-0.04981	0.7824
		Near-Field	% Pollution Indicitive	26	0.5343	0.00988	0.0069
		Far-Field	B-IBI	27	2.5441	-0.4479	<0.0001
		Far-Field	MAIA	27	1.8531	-0.2170	0.0009
		Far-Field	S	27	0.9442	0.0234	0.4077
		Far-Field	H	27	1.0578	0.0579	0.6467
		Far-Field	% Pollution Indicitive	27	1.2565	-0.0017	0.5879

Table 2. A summary of the simple and polynomial least squares regressions of mean sediment nitrogen (% by mass) and mean secondary production of the macrobenthic community in saline and freshwater sites in Chesapeake Bay. **Independent Variable 1** is always the 1st order term and **Independent Variable 2** is the 2nd order term in the polynomial models. The fit of the simple and polynomial linear models to the combined near-field and far-field data was assessed using Akaike's Information Criterion corrected (AICc), where the smaller the number the better the fit. An α of 0.05 was used in the interpretation of all analyses.

Salinity Zone	Dependent Variable	Stratum	Independent Variable 1	Independent Variable 2	N	r^2	Intercept Estimate	Ind. Var. 1 Estimate	Ind. Var. 2 Estimate	Model *p*	AICc
Saline	Mean Log_{10} Community Production (mg AFDM m^{-2} d^{-1})	Near-Field	Mean Sediment N		8	0.436	1.87453	-1.76372		0.0746	
		Far-Field	Mean Sediment N		9	0.4608	1.1309	24.0451		0.0444	
		Both	Log_{10} Mean Sediment N		17	0.1828	1.2823	-0.2069		0.0869	-40.682
		Both	Log_{10} Mean Sediment N	(Log_{10} Mean Sediment N)^2	17	0.4713	0.4921	-2.2165	-0.9035	0.0115	-45.097
	Mean Log_{10} Bivalve Production (mg AFDM m^{-2} d^{-1})	Near-Field	Mean Sediment N		8	0.078	1.03865	-1.3805		0.5027	
		Far-Field	Mean Sediment N		9	0.5488	-0.3210	61.8721		0.0224	
		Both	Log_{10} Mean Sediment N		17	0.0126	0.7548	-0.1103		0.6676	-13.420
		Both	Log_{10} Mean Sediment N	(Log_{10} Mean SedimentN)^2	17	0.1945	-0.5179	-3.3471	-1.4551	0.2199	-13.893
	Mean Log_{10} Non-Bivalve Production (mg AFDM m^{-2} d^{-1})	Near-Field	Mean Sediment N		8	0.799	1.82775	-2.19823		0.0028	
		Far-Field	Mean Sediment N		9	0.0190	1.5121	-4.5025		0.7235	
		Both	Log_{10} Mean Sediment N		17	0.3229	1.0147	-0.2541		0.0173	-46.557
		Both	Log_{10} Mean Sediment N	(Log_{10} Mean Sediment N)^2	17	0.4322	0.5653	-1.3970	-0.5138	0.0190	-46.559
Tidal Freshwater	Mean Log_{10} Community Production (g AFDM m^{-2} y^{-1})	Near-Field	Mean Sediment N		3	0.667	90.01214	-160.67464		0.3914	
		Far-Field	Mean Sediment N		3	0.7486	0.4605	17.4312		0.3343	
		Both	Log_{10} Mean Sediment N		6	0.0191	1.0566	-0.1422		0.7941	0.040
		Both	Log_{10} Mean Sediment N	(Log_{10} Mean Sediment N)^2	6	0.3562	-0.0026	-3.3919	-1.7519	0.5166	7.514

Figure 1. The hypothetical response of macrobenthic function to increasing eutrophication, after Rakocinski and Zapf (2005). Secondary production was used as a specific function performed by the macrobenthos and divided the model into a eutrophication-driven fertilization period and a eutrophication-driven degradation period.

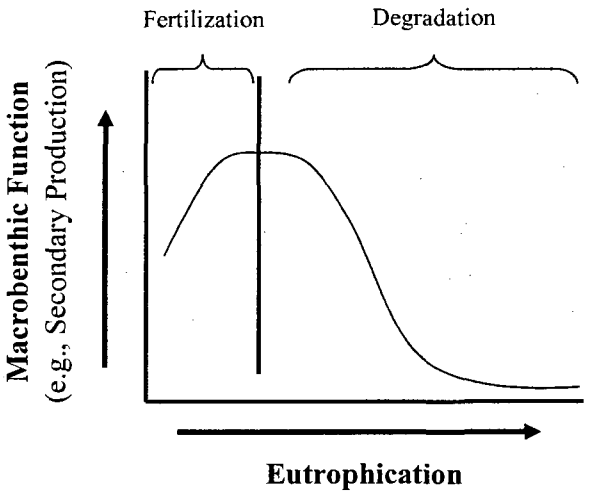

Fertilization
Degradation
Macrobenthic Function
(e.g., Secondary Production)
Eutrophication

Figure 2. Locations of the eleven sampling stations in Chesapeake Bay, USA, with the inset showing the location of the estuary on the Northwest Atlantic coast. ● = High mesohaline sites, ■ = Low mesohaline sites, ▲ = Oligohaline sites, and ♦ = Tidal freshwater sites.

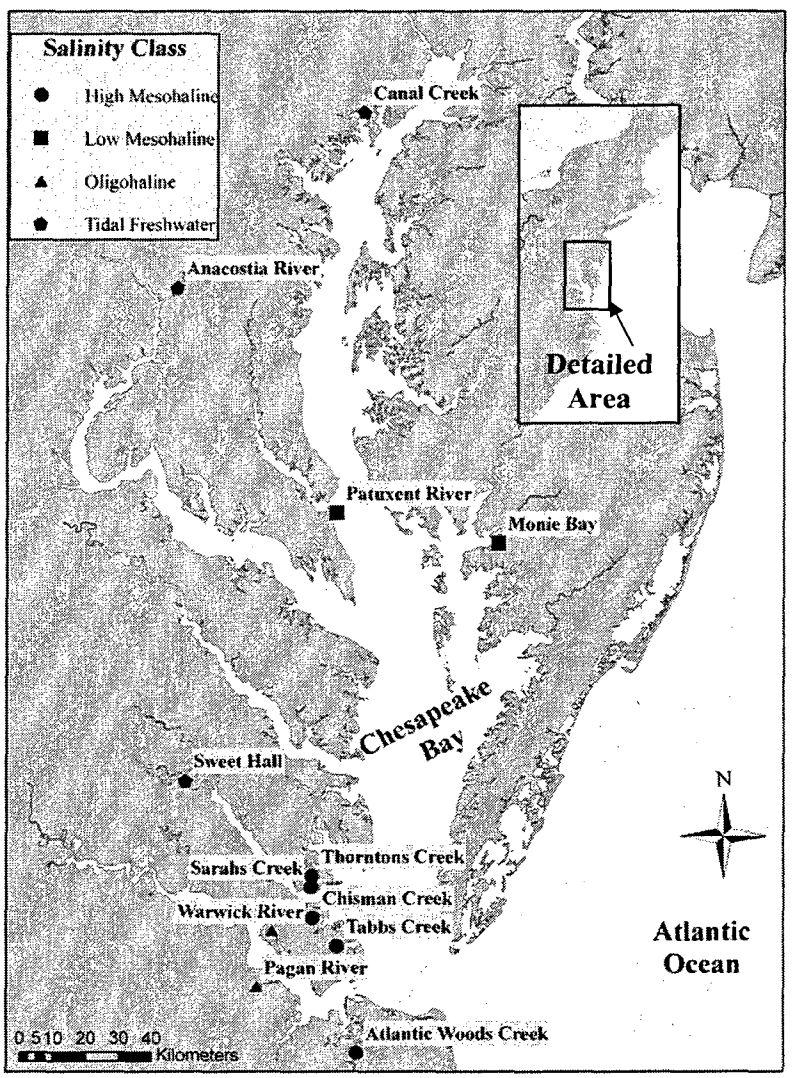

Salinity Class
High Mesohaline
Low Mesohaline
Oligohaline
Tidal Freshwater
Canal Creek
Anacostia River
Detailed Area
Patuxent River
Monie Bay
Chesapeake Bay
Sweet Hall
N
Sarahs Creek
Thorntons Creek
Chisman Creek
Warwick River
Tabbs Creek
Pagan River
Atlantic Ocean
Atlantic Woods Creek
0 5 10 20 30 40
Kilometers

Figure 3. Daily macrobenthic production and four measures of habitat quality from the near-field stratum of the saline sampling sites: **a** Chesapeake Bay Benthic Index of Biotic Integrity; **b** Species richness; **c** Shannon Weiner Diversity; and **d** Mid-Atlantic Integrated Assessment benthic index. The heavy line represents the mixed-model, restricted maximum likelihood regression model with the probability of the degradation metric in modeling the production value presented on each figure ($\alpha = 0.05$). With all plots, higher quality habitats are to the right side of the figure and lower quality habitats towards the left.

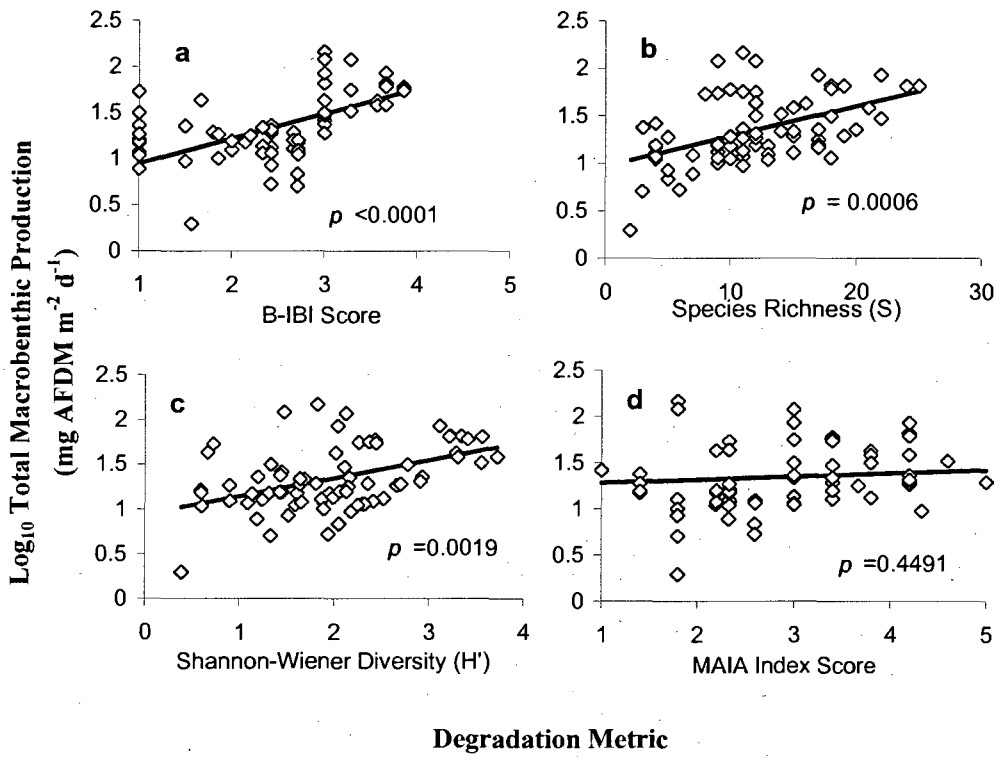

a
b
c
d
p <0.0001
p = 0.0006
p =0.0019
p =0.4491
B-IBI Score
Species Richness (S)
Shannon-Wiener Diversity (H')
MAIA Index Score
Log10 Total Macrobenthic Production
(mg AFDM m-2 d-1)
Degradation Metric

Figure 4. Annual macrobenthic production and four measures of habitat quality from the near-field stratum of the tidal freshwater sampling sites: **a** Chesapeake Bay Benthic Index of Biotic Integrity; **b** Species richness; **c** Percent abundance of pollution indicative species; and **d** Mid-Atlantic Integrated Assessment benthic index. The heavy line represents the mixed-model, restricted maximum likelihood regression model, with the probability of the degradation metric in modeling the production value presented on each figure ($\alpha = 0.05$). With plots **a**, **b**, and **d**, higher quality habitats are to the right side of the figure and lower quality habitats towards the left, but in plot **c** higher quality habitats are to the left side of the figure and the lower quality ones towards the right.

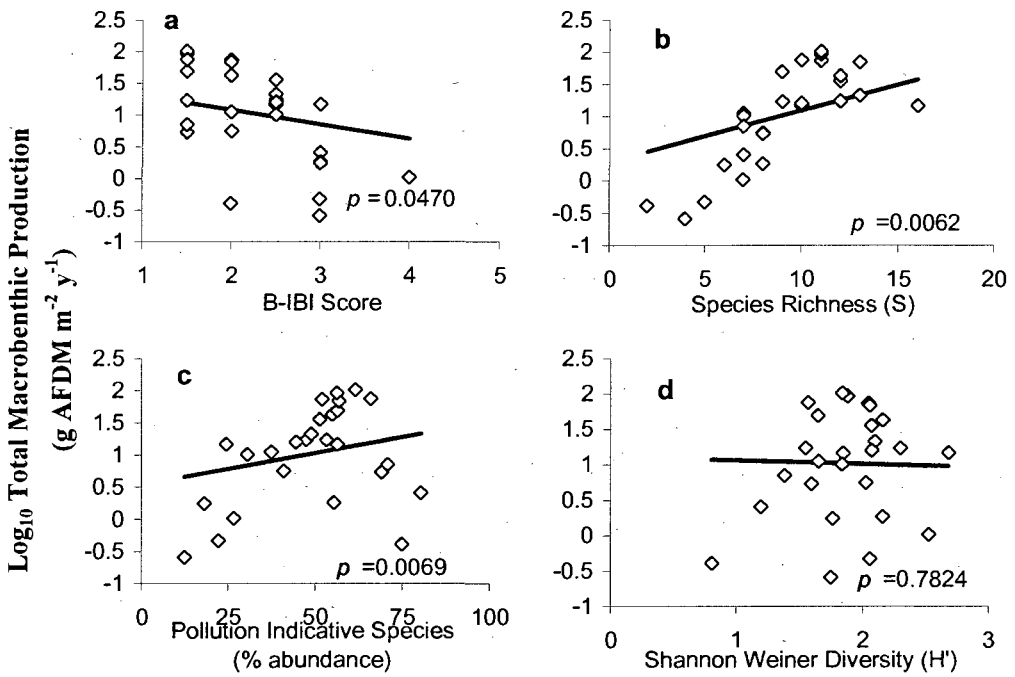

a
b
c
d
p =0.0470
p =0.0062
p =0.0069
p =0.7824
B-IBI Score
Species Richness (S)
Pollution Indicative Species
(% abundance)
Shannon Weiner Diversity (H')
Log10 Total Macrobenthic Production
(g AFDM m-2 y-1)
Degradation Metric

Figure 5. Mean daily 2° production from the saline sites (**a** – **i**) and mean annual 2° production from the tidal freshwater sites(**j** - **l**) for the entire macrobenthic community, the bivalve portion of the community, and the non-bivalve portion and mean sediment nitrogen content. Plots **a**, **d**, **g**, and **f** are only near-field data; **b**, **e**, **h**, and **k** are only far-field data; and **c**, **f**, **i**, and **l** are a combination of both the near- and far-field data. The heavy line represents the least-squared means regression model, with the probably of the model significance presented in each panel ($\alpha = 0.05$).

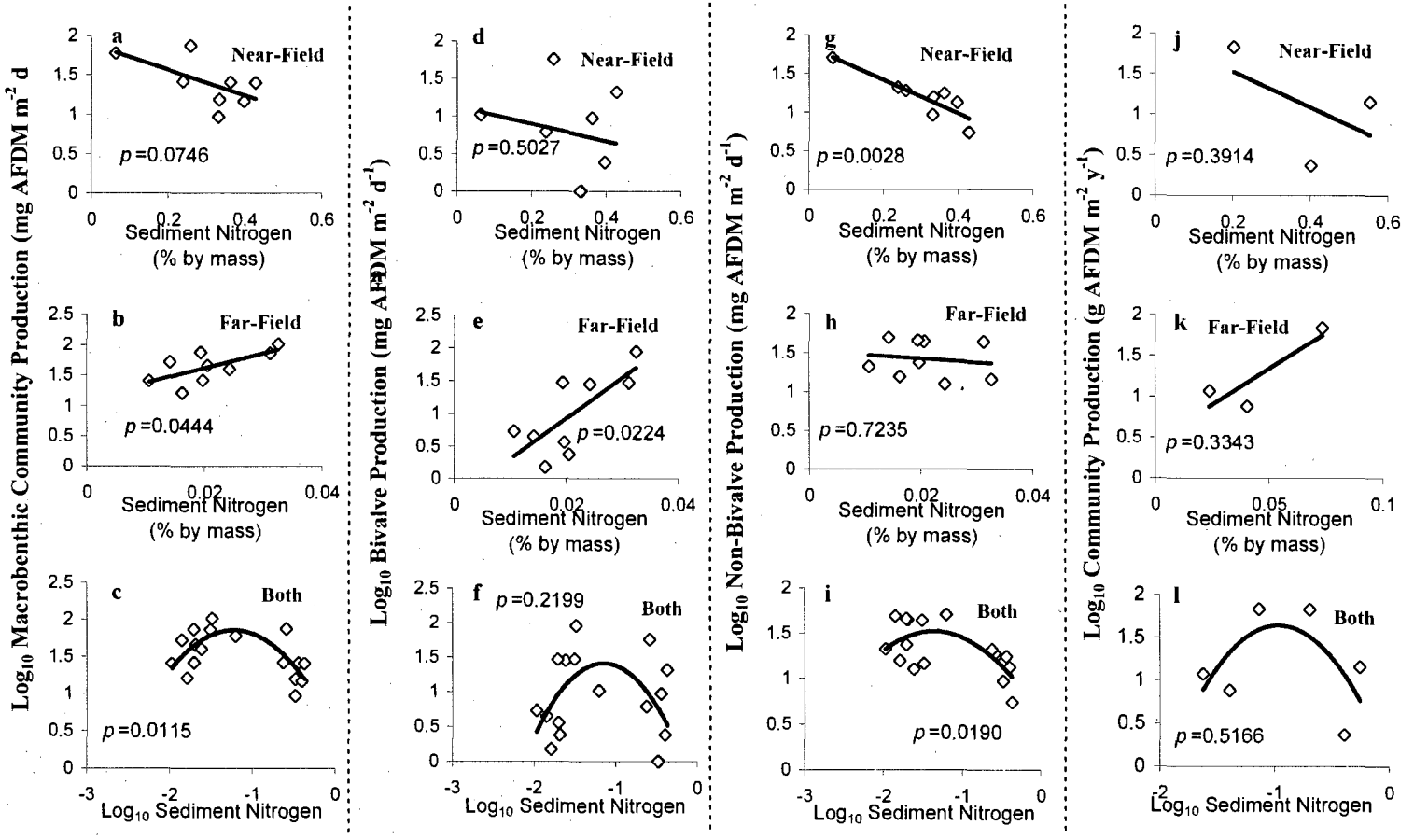

Log10 Macrobenthic Community Production (mg AFDM m-2 d
Log10 Bivalve Production (mg AFDM m-2 d-1)
Log10 Non-Bivalve Production (mg AFDM m-2 d-1)
Log10 Community Production (g AFDM m-2 y-1)
a
Near-Field
p =0.0746
b
Far-Field
p =0.0444
c
Both
p =0.0115
d
Near-Field
p =0.5027
e
Far-Field
p =0.0224
f
p =0.2199
Both
g
Near-Field
p =0.0028
h
Far-Field
p =0.7235
i
Both
p =0.0190
j
Near-Field
p =0.3914
k
Far-Field
p =0.3343
l
Both
p =0.5166
Sediment Nitrogen
(% by mass)
Log10 Sediment Nitrogen

Figure 6. Daily production of the bivalves and four measures of habitat quality from the near-field stratum of the saline sampling sites: **a** Chesapeake Bay Benthic Index of Biotic Integrity; **b** Species richness; **c** Shannon Weiner Diversity; and **d** Mid-Atlantic Integrated Assessment benthic index. The heavy line represents the mixed-model, restricted maximum likelihood regression model, with the probability of the degradation metric in modeling the production value presented on each figure ($\alpha = 0.05$). With all plots, higher quality habitats are to the right side of the figure and lower quality habitats towards the left.

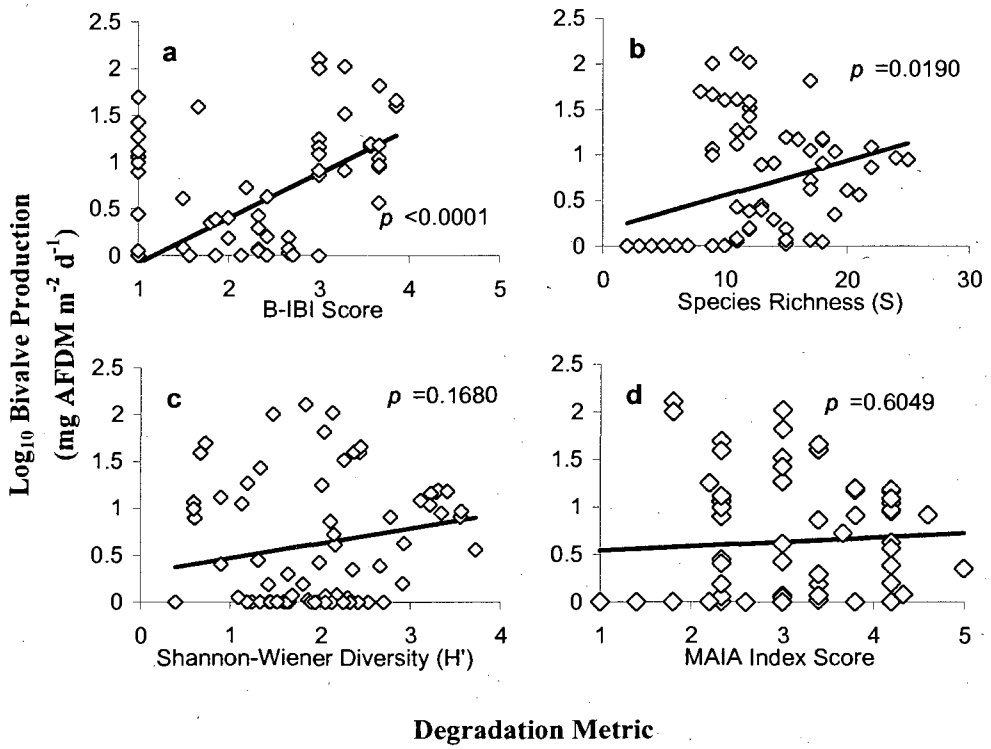
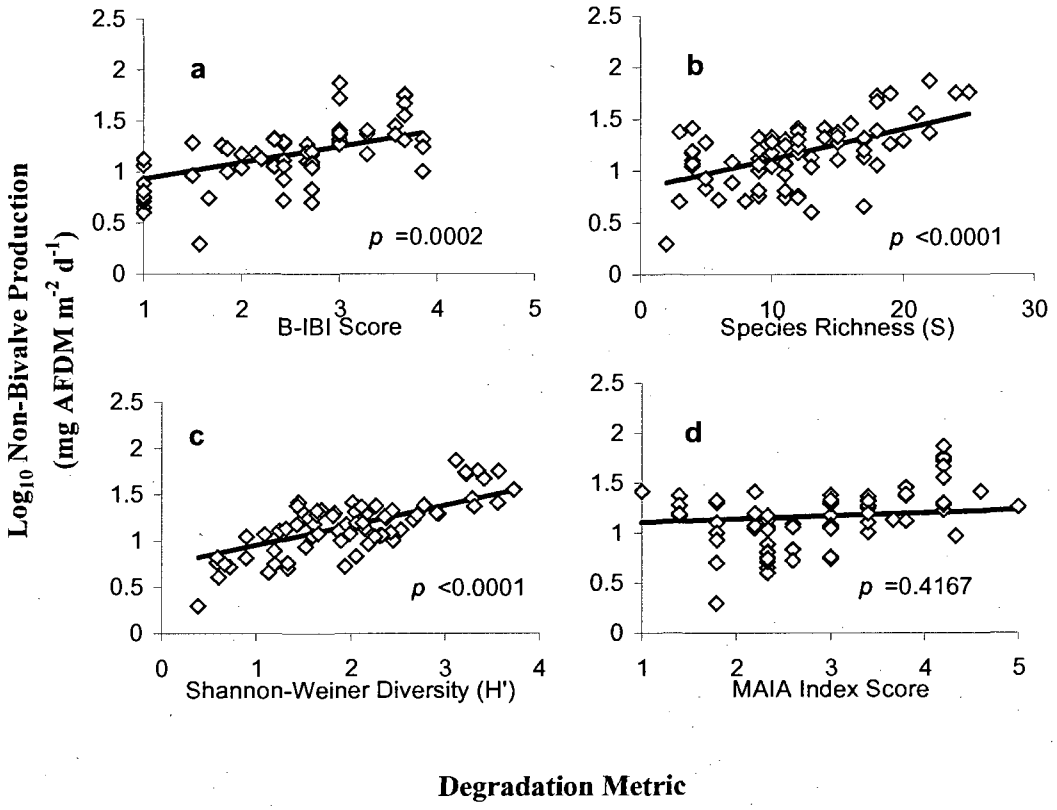

a
p <0.0001
B-IBI Score
b
p =0.0190
Species Richness (S)
c
p =0.1680
Shannon-Wiener Diversity (H')
d
p =0.6049
MAIA Index Score
Log10 Bivalve Production
(mg AFDM m-2 d-1)
Degradation Metric

Figure 7. Daily production of the non-bivalves and four measures of habitat quality from the near-field stratum of the saline sampling sites: **a** Chesapeake Bay Benthic Index of Biotic Integrity; **b** Species richness; **c** Shannon Weiner Diversity; and **d** Mid-Atlantic Integrated Assessment benthic index. The heavy line represents the mixed-model, restricted maximum likelihood regression model, with the probability of the degradation metric in modeling the production value presented on each figure ($\alpha = 0.05$). With all plots, higher quality habitats are to the right side of the figure and lower quality habitats towards the left.


Log10 Non-Bivalve Production
(mg AFDM m-2 d-1)
a
p =0.0002
B-IBI Score
b
p <0.0001
Species Richness (S)
c
p <0.0001
Shannon-Weiner Diversity (H')
d
p =0.4167
MAIA Index Score
Degradation Metric

Chapter III:

The Influence of Habitat Quality and Macrobenthic Community Composition on Nekton Utilization of Secondary Production as a Food Source

For potential submission to Journal of Experimental Marine Biology and Ecology

ABSTRACT.

The macrobenthos play an important role in transforming the variety of organic matter sources found in estuaries to forms that are usable by higher trophic levels in the food web. This process is expected to be contingent, in part, upon a macrobenthic community composed of different feeding guilds, which will ensure effective utilization of diverse food sources. Previous studies have also shown that community structure is sensitive to habitat degradation, especially as a result of eutrophication. For the present study, the influence of habitat quality-driven changes in macrobenthic community structure on the utility of the macrobenthos as a food source to benthivoric nekton was determined by comparing macrobenthic production in and out of predator exclusion cages along a gradient of eutrophication in Chesapeake Bay, USA. Predation patterns were analyzed at the scale of total macrobenthic community, living position in the sediment, feeding guild, and species. Patterns in nektonic predation did not correspond to habitat quality, but instead depended on the presence of infaunal bivalves. Bivalves were the most productive and most preyed upon taxon at all sites, especially those of the genus *Macoma*. Furthermore, the community with the most bivalve production experienced the greatest amount of predation on all fauna in the community. It appears that bivalves served as a cue to benthivoric nekton regarding the utility of particular habitats as good forage areas. There is also evidence for indirect, negative non-predatory effects of nekton on normally inaccessible deep deposit-feeding and small interface-feeding polychaetes, possibly via the bioturbation of sediments by nekton searching for prey items. That the patterns of predation contrasted with our perceived gradient of habitat quality, illustrates the potential disconnect between how habitat quality in the coastal zone is perceived by ecosystem managers weighing the concerns of multiple stakeholders and how it is perceived by nekton searching for desired prey items. Rectifying these two scales of valuation will be an important task for the incorporation of environmental quality into ecosystem-based management plans.

INTRODUCTION

Estuaries, in particular their shallow flanks and tributaries, serve as essential habitats that provide a variety of benefits for ecologically and economically important fishes and crustaceans (Day et al. 1986; Peterson et al. 2000; Ross 2003). Both structurally complex habitats, like seagrass meadows, salt marshes, or bivalve reefs (Cicchetti 1998; Coen et al. 1999; Heck et al. 2003; Kneib 1997) and unvegetated mud flats and shoals (Ross 2003; Ruiz et al. 1993) of estuarine shallows are thought to provide a refuge for smaller nekton from predation. Furthermore, these shallow water habitats supply a rich source of food for nekton because of the high primary (Cahoon 1999; MacIntyre et al. 1986) and secondary production (Cusson and Bourget 2005; Gillett et al. 2005; Sardá et 1995), as well as the large amounts of allochthonous matter that accumulate there (Kennish 1986; Valiela 1995). The available production provides energy that transitory nekton need to grow and survive during their time in the estuary or for residents to complete their lifecycle.

The high productivity of shallow estuarine areas is related to their position at the interface between the upland and tidal waters, as well as their position within the photic zone (Holland et al. 2004; Rizzo and Wetzel 1985; Schaffner et al. 2008). Close proximity to the uplands results in the delivery of large amounts of detritus from salt marshes and other upland plants, which support benthic bacteria and deposit feeding organisms (Heip et al. 1995; Lopez and Levinton 1987), as well as a large amount of nutrients and dissolved organic matter. In addition, light allows for the growth of microphytobenthos (Cahoon 1999; MacIntyre et al. 1986), as well as phytoplankton (e.g., Cloern 1996; Underwood and Kromkamp 1999). Most of this production however, is not directly accessible to the nekton that reside in shallow estuarine waters, with the exceptions of species like menhaden *Brevoortia tyrannus* that directly feed upon phytoplankton.

Macrobenthos serve as a critical link between the multitude of primary/bacterial producers and the commercially and ecologically important, mobile nekton. A healthy, well-developed macrobenthic community consists of a diverse array of trophic levels and feeding guilds that utilize the variety of organic matter produced or deposited in the shallow waters of estuaries (e.g., Diaz and Schaffner 1990; Fauchald and Jumars 1979; Gaudênci and Cabral 2007). As an example, in Chesapeake Bay it has been estimated that between 11 and 50% of total nektonic production in the estuary is derived from benthic fauna (Baird and Ulanowicz 1989; Diaz and Schaffner 1990; Hagy 2002) and 40% of 2006 and 2007 Chesapeake Bay fisheries landings (in US Dollars) were benthivores (NMFS 2008, pers. comm.). The guild of benthivoric nekton in Chesapeake Bay is composed of both fishes (e.g., Spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; and Hogchoker *Trinectes maculatus*) and crabs (e.g., Blue Crab *Callinectes sapidus*) that feed on infaunal and epifaunal benthos (Chao and Musick 1977; Hines et al. 1990).

Some of the factors that contribute to high productivity in the shallow waters of estuaries also make them very susceptible to degradation from anthropogenic disturbances (Holland et al. 2004). The principle stressors in estuarine ecosystems are excess nutrient inputs that can lead to eutrophication and input of toxic heavy metals and organic chemicals (e.g., PAHs, PCBs, etc) (Christman and Dauer 2002; Lerberg et al. 2000; USEPA 2007). Habitat degradation, especially the accumulation of excess organic matter in sediments, leads to predictable changes in macrobenthic community structure: shifting from a diverse array large and small bivalves, crustaceans and annelids to a low diversity community composed primarily of small, opportunistic polychaete and oligochaete annelids (Gray et al. 2002; Pearson and Rosenberg 1978; Schwinghamer 1988). Importantly, for the nekton that feed upon the macrobenthos, changes in macrobenthic community structure caused by the accumulation of organic matter in the sediment lead to a reduction in secondary production available to be preyed upon (Chapter 2), particularly in muddy, depositional environments.

Given their relatively advanced sensory organs and mobility, the effects of habitat degradation on nekton are typically indirect and mediated through trophic pathways (e.g. Partyka and Peterson 2008; Peterson et al. 2000; Pihl et al. 1992; Wannamaker and Rice 2000). It should be noted though, that toxic compounds in the sediment can be directly transferred to the nekton by direct contact or incidental consumption of the sediment during predation (Hinkle-Conn et al. 1998; Kesminas et al. 1994; Weeks and

Warinner 1984). Similarly, eutrophication can lead to the formation of toxic harmful algal blooms (HABs) that can directly harm nekton (e.g., Anderson et al. 2002; Lewitus et al. 2008) or if an impacted area is very large, below the photic zone, or semi-enclosed, eutrophication driven hypoxia and anoxia can kill large numbers of nekton before they can escape (Luther et al. 2004; May 1973).

The more common impact of eutrophication on nekton though, is through the food web. Degraded benthic communities in freshwater lakes have been shown to limit the growth of nekton. Anthropogenic contaminants and eutrophic conditions change the benthic community to a low diversity suite of small-sized fauna that do not provide enough energy to predators, creating an energetic bottleneck limiting the maximum growth of the nekton (Hayward and Margraf 1987; Kövecses et al. 2005; Sherwood et al. 2002). Similarly, in estuarine systems receiving excessive organic matter deposition (i.e., levels beyond natural rates for similar, non-disturbed environments) macrobenthic production is reduced (Chapter 2), community structure is altered, and there is a shift in the community toward smaller, shorter-lived species (González-Oreja and Saiz-Salinas 1999; Quiroga et al. 2004).

Benthic prey items from degraded habitats may not have a high value as a food source to the benthivoric nekton, not only because of the lower productivity of the community, but also because of the size of the organisms and availability to the nekton. The benthivoric nekton of temperate estuaries like Chesapeake Bay detect and acquire their food by tactile/chemosensory searching or sediment gulping (Chao and Musick 1977; Hughes and Seed 1995; Wootton 1998). This feeding-mode makes the likelihood of encountering small macrobenthic fauna less likely. While there are admitted biases in gut content studies (e.g., biases towards larger fauna and those with hard parts) most studies show that tellinid bivalves, glycerid polychaetes, gammarid amphipods are some of the preferred prey items for benthivoric nekton (Chao and Musick 1977; Hines et al. 1990; Horvath 1997). These fauna, however, are also typically the first taxa to disappear from the benthic community as conditions degrade.

The objective of this study was to determine if there were differences in the consumption of macrobenthic production from communities in habitats with varying degrees of degradation and, therefore, different macrobenthic community composition. It is hypothesized that benthivoric nekton would consume a larger amount of 2° production from diverse macrobenthic communities in non-degraded habitats that were composed of larger, more productive species, which are more easily detectable and preferred by the

nekton. Conversely, little nektonic predation would be experienced in the simplified communities of degraded habitats. This hypothesis was tested by conducting a predator exclusion experiment at a series of shallow water sites in the high mesohaline portion of Chesapeake Bay, USA that previous work (Schaffner et al. 2008; Schaffner and Gillett, *in prep*) has shown to comprise a gradient of habitat quality related to nutrient loading, eutrophication and, most likely, the accumulation of excess organic matter in the sediment system. At the less-degraded sites, the expected result would be significantly greater 2° production in the sediments protected from benthivoric nekton compared to those exposed to the nekton; illustrating a high demand for the species in that community as a food source. At the degraded sites, there should be little difference in production between the caged and ambient sediments, as the fauna there are predicted to be less desirable and available to nektonic predators.

MATERIALS AND METHODS

Site Selection - Four sampling sites were selected from within the high-mesohaline portion of Chesapeake Bay, USA. As described in previous work (Chapter 2; Schaffner and Gillett, *in prep*), the sites have been exposed to different degrees of habitat degradation and are representative of much of the shallow water habitat in the mesohaline portions of the estuary. The selected sites included portions of the Virginia National Estuarine Research Reserve System (NERRS) site (Catlett Islands, VA) and three other sites with similar environmental settings (Fig. 1). At each site, a relatively quiescent, sheltered, depositional habitat was selected for sample collection to minimize the influence of waves and other physical disturbances, while maximizing the impact of anthropogenic stressors (near field sites described in Schaffner et al. 2008; Schaffner and Gillett, *in prep*).

The primary stressor at the study sites, and most estuaries in general, was excess water column nutrients, which can create eutrophication and lead to the accumulation of organic matter in the sediment (Schaffner and Gillett, *in prep*). Given the relatively shallow depth (<0.75 m) at which the study sites are located, the accumulation of toxic, reduced compounds in the sediments (e.g., sulfides or ammonia) is thought to be the aspect of eutrophication that was affecting the macrobenthos (e.g., Fenchel and Riedl 1970; Gray et al. 2002; Jørgensen 1996; Pearson and Rosenberg 1978); as opposed to persistent, stratification-driven hypoxia, which is typically observed in deeper parts of Chesapeake Bay and its tributaries (e.g., Diaz and Rosenberg 1995; Hagy et al. 2004). It should be noted, however, that one site (Sarah Creek) may have experienced periodic diurnal hypoxia during Summer nights (Gillett, pers. obs).

Data Collection –Nekton were excluded from the sediment surface by placing cylindrical cages over the sediment. The full cages (complete sides and top) were constructed of uv-resistant Vexar® with a 7-mm mesh that measured 29-cm tall above the sediment surface, 26-cm in diameter, and with a 9-cm X 9-cm access door in the top panel; all seams were sewn shut with uv-resistant polyethylene cable ties. The cages also had a solid polyethylene plastic ring that extended 12.5 cm in to the sediment to inhibit crabs from burrowing under the cage (e.g., Seitz 1996) (Fig. 2). Partial cages allowed nekton free access to the sediment surface and consisted of a top panel and in-sediment plastic rings. These were used to assess the effects of structure on environmental variables that may also affect macrobenthic community structure and

production (e.g., sediment erosion/deposition and shading of microphytobenthos). Partial cages consisted of plastic rings that extended 12.5 cm into the sediment, three 19-mm diameter polyvinyl-chloride poles that extended 27-cm above the sediment surface, and a 29-cm diameter top panel of 7-mm mesh Vexar® attached to the poles (Fig. 2). In the late Spring of 2006 (May – early June) 12 partial cages and 12 full cages (3 replicates for 3 months, plus 3 potential alternates) were placed in each site at a series of pre-determined, random points along a constant depth contour of 0.5 – 0.75 m below mean low water. The outsides of partial and full cages were scrubbed every 3-4 weeks to prevent the build up of excess fouling flora and fauna.

Ambient (i.e., non-caged) sediments along the same depth contour were sampled from each site in late spring when the cages were placed and then subsequently along with, partially caged, and fully caged sediments, which were sampled in a non-repeated fashion in July, August, and September of 2006. During each sampling event, cores for macrobenthos (8.9-cm i.d. X 25-cm deep), microphytobenthos (12-mm i.d. X 3-cm deep), and sediment bulk properties, including grain size, total organic carbon (TOC), and total nitrogen content (TN) (25-mm i.d. X 5-cm deep) were collected from within 3 randomly selected full cages, 3 partial cages, and 3 ambient locations. Samples were collected from the center of the caging structures to minimize edge-effects and after sampling the cage was removed. If a cage was damaged or a full cage contained any nekton, it was considered invalid and an alternate cage was randomly selected for sampling. Macrobenthic cores were sectioned into 0-5-cm and >5-cm sections and sieved on a 500-μm screen on site, with the retained material returned to the laboratory and fixed in 10% buffered formalin with rose bengal stain. Microphytobenthos and sediment composition samples were kept on ice and subsequently frozen (-20°C) upon return to the laboratory.

Macrobenthic organisms were picked from the fixed samples, identified to the lowest possible taxonomic level, typically species, and stored in 2% buffered formalin. A random 10% of every 10 macrobenthic samples were re-sorted, identified, and enumerated by another benthic taxonomist. If samples were less than 95% accurate, then all 10 samples were reprocessed. Ash free dry mass (AFDM) was determined for each taxon by drying organisms at 65° C for ~48 hours and then subsequently combusting at 550°C for 4.5 hours. If a given taxon's AFDM in a sample was less than the detection limit

of the balance (0.1 mg), then it was set to 0.1 mg (e.g., Llansó 2002). Macrobenthic production was empirically estimated as daily production using the equations of Edgar (1990), which calculate production **P** (μg AFDM m^{-2} d^{-1}) from total taxon-specific biomass **B** (mg AFDM m^{-2}) and water temperature **T** (°C) (Eq. 1, 2, and 3).

$$Log_{10}P = -2.31 + (0.8*Log_{10}B) + (0.89*Log_{10}T) \quad \textbf{Eq 1}$$

(general invertebrates - Edgar 1990)

$$Log_{10}P = -2.86 + (0.81*Log_{10}B) + (1.32*Log_{10}T) \quad \textbf{Eq 2}$$

(crustaceans - Edgar 1990)

$$Log_{10}P = -2.18 + (0.87*Log_{10}B) + (0.46*Log_{10}T) \quad \textbf{Eq 3}$$

(molluscs - Edgar 1990)

Within 2 months of collection, samples for microphytobenthos, as benthic chl *a* content, were analyzed using a modification of the Lorenzen (1967) method (Neubauer et al. 2000). Samples were thawed, extracted in an acetone-methanol mixture, centrifuged, and the supernatant was then analyzed in a UV-Vis spectrophotometer. Benthic chl *a* is indicative of primary producer biomass and therefore represents a potential food source to the macrobenthos. Sediment grain size composition, which can affect macrobenthic community composition (e.g., Sanders 1958; Snelgrove and Butman 1994), was determined with the wet sieving and pipette method (Plumb 1981). Sediment TOC and TN from 0-5 cm, which also provides an estimate of food availability to some macrobenthic species, were measured from dried and acidified sediments with a Carlo Erba NA1500 elemental analyzer (Hedges and Stern 1984).

Given that habitat quality or the degree of habitat degradation are somewhat qualitative concepts (Tillin et al. 2008; Weisberg et al. 2007), habitat quality was measured using a variety of metrics. Chesapeake Bay Benthic Index of Biotic Integrity (B-IBI) scores (Weisberg et al. 1997), Mid Atlantic Integrated Assessment (MAIA) benthic index scores (Llansó et al 2002), species richness (S), Shannon-Weiner Diversity (H′), and sediment nitrogen content (% by mass) were calculated/measured for ambient

samples collected in July, August, and September. The Chesapeake Bay B-IBI and the MAIA benthic index are multi-metric indices of benthic habitat condition used by the states of Maryland and Virginia (B-IBI) and the United States Ecological Protection Agency (MAIA), respectively, in the monitoring of the Chesapeake Bay and other Mid-Atlantic estuarine and coastal waters. For these indices, a variety of macrobenthic community metrics are scored in reference to relatively non-degraded conditions, such that a higher index score is indicative of a higher quality habitat.

Analysis –To test the influence of the caging structure on the environmental setting at each site through time, 3-way analyses of variance (ANOVA) were conducted with site (Chisman Creek, Catlett Islands, Sarah Creek, and Thorntons Creek), cage-type (ambient, partial, and full cage), and month (July, August, and September) as treatment variables and a series of environmental response variables: sediment composition (% sand, % silt, and % clay content); benthic chlorophyll *a*; sediment total organic carbon (TOC) and total nitrogen (TN); and benthic community structure (Shannon-Weiner diversity [H'], species richness [S], and Pielou's evenness [J']). All of the response variables were transformed as necessary to maintain normality and homoskedasticity of the model residuals. To directly test the cage effect, a post-hoc test of least square means with the Dunnett's adjustment for multiple comparisons (α =0.05) was made with the ambient samples as a control (Little et al. 2002). A significant difference between the partial cage and the ambient samples was considered an indication of a caging artifact. Any differences between the ambient and the full caged samples, however, could not definitively be considered indicative of a caging artifact, as the difference could also be attributed to predator exclusion. These differences though, if present, were noted and taken into consideration for interpretation of the results. The rest of the post hoc comparisons in the ANOVAs (site, month, and the interaction terms) were unprotected comparisons of the least square means. These multiple comparisons obviously lead to a potential increase in Type I error (Day and Quinn 1989; Neter et al. 1990), but there was greater concern with minimizing the Type II error in the analyses and the potential of obscuring any caging artifacts in the interaction terms. These, and all the other univariate analyses, were conducted with SAS 9.1.

A series of multivariate analyses were done to illustrate the differences between the habitat quality and, consequently, the macrobenthic community structure at the four sampling sites. Principal components analysis (PCA) of normalized H', species richness, TN, Chesapeake Bay B-IBI score, and MAIA benthic

index score for each ambient sample from July, August, and September was done. Differences in macrobenthic community composition in the ambient sediments were examined with multi-dimensional scaling (MDS) of Bray-Curtis similarities for each sample from Spring, July, August, and September and then a subsequent analysis of similarity (ANOSIM) (Clarke and Warwick 2001). All of the multivariate analyses were done using Primer-e v5.

To test the influence of benthic habitat quality on the utilization of 2°production by benthivoric nekton, the interaction of cage-type and site were analyzed with a 2-way ANOVA (initial analyses revealed that month was not a significant term in the ANOVA model, so it was removed), where each site was used to represent a different degree of habitat degradation. All production data were $\log_{10}$ transformed to maintain the normality and homoskedasticity of the ANOVA model residuals. Post hoc analyses (α =0.05) were done as contrasts and estimates of the interaction term between 2° production inside the full cages and the ambient sediments at the different sites, testing that the differences between the treatments were $\neq 0$. The *apriori* hypotheses on the utilization of 2° production by nekton should be sensitive to the macrobenthic community structure and the autecology of the different component species (e.g., living position, feeding style, mobility, etc.). As such, 2° production of the macrofauna was analyzed as that of the total community, that in the top 0-5 cm of the sediment, below 5 cm, amphipods, bivalves, nemerteans, oligochaetes, polychaetes, the dominant species across all 4 sites (*Macoma* spp., *Heteromastus filiformis, Leptocheirus plumulosus, Neanthes succinea, Streblospio benedicti*) and feeding guild (filter-feeders, grazers, bivalve interface-feeders, non-bivalve interface-feeders, shallow deposit-feeders, deep deposit-feeders, carnivores, and omnivores).

Separation of the macrobenthic community into different feeding guilds provides the opportunity to investigate how differences in living position, motility, body size, and life history of the different macrobenthic species combine to influence their utility to nekton as a prey item. Individual taxa were assigned to 1 of 8 different feeding guilds recognized by most benthic ecologists (Table 1) (Fauchald and Jumars 1979; Gaston 1987; Gillett and Schaffner 2009; Sanchez-Mata et al. 1993; Weisberg et al. 1997): *Filter-feeders* – those organisms that actively or passively remove food particles from the water column, which may or may not expose feeding appendages, such as palps, siphons, or tentacles above the sediment

surface in the process of feeding; *Grazers* – typically motile organisms, which consume microphytobenthos or settled phytoplankton from the sediment surface, and which are relatively exposed to epibenthic predators; *Interface-feeders* – those relatively non-mobile organisms that are capable of feeding upon organic matter collected from the water column or on the sediment surface, many of which are capable of switching between the two depending upon hydrodynamics and food availability (Pohlo 1982; Taghon et al. 1980). This latter group was subdivided into a bivalve component that are relatively large and can live deep in the sediment with siphons extending to the surface (e.g., Hines and Comtois 1985; Seitz et al. 2001) and a non-bivalve component that is typically smaller and living close to the sediment-water interface; *Deposit-feeders* – mobile or sessile fauna that feed upon microorganisms and organic matter in the sediment. This group was subdivided into shallow deposit-feeders that typically live in the top few centimeters of the sediment, which makes them more susceptible to predation and deep deposit-feeders that live deeper in the sediment and are less susceptible to predators; *Carnivores* – relatively large, mobile organisms that feed solely upon meiofauna and other macrofauna; and *Omnivores* – relatively large, mobile fauna that feed upon other organisms, microphytobenthos, and sediment organic matter.

RESULTS

Site Characterization – The PCA of the degradation metrics measured in the ambient sediments of the 4 sites in Spring, July, August, and September (Fig. 3) showed a separation of sites, primarily along the axis of PC1 (70.7% of variance). The Thorntons Creek samples clustered towards values of high habitat quality (higher species richness, species diversity, and MAIA score), Sarah Creek samples clustered together along the low quality end of the plot (high sediment nitrogen and low species richness, species diversity, and MAIA score), and Chisman Creek and Catlett Islands samples were intermediate between the two end-members. The separation of the benthic communities in the 2-d MDS plot of Bray-Curtis similarities was less distinct, but the samples from the 4 sites still tended to cluster together (Fig. 4). The ANOSIM of the Bray-Curtis similarities showed significant differences in community structure among the sites ($R=0.661$, $p=0.001$). The overall difference in community structure between all of the samples was driven primarily by the uniqueness of the Sarah Creek and Thorntons Creek samples from the Catlett Islands and Chisman Creek samples, which were relatively similar to each other (Table 2). Taken together, the multivariate analyses show a similar pattern: Thorntons Creek had the overall highest habitat quality leading to a distinct benthic community associated with it throughout the late Spring and Summer; Sarah Creek had the lowest habitat quality and also had a relatively unique benthic community. Chisman Creek and Catlett Islands had relatively similar, good habitat quality and similar benthic communities, which were intermediate to the other 2 sites.

Caging Artifacts and Environmental Parameters – The summary of the 3-way ANOVAs (cage type, month, and site as treatments) on environmental and community structure measurements that could potentially be affected by the presence of the predator exclusion cages are presented in Table 3. There were significant differences in sediment clay content, benthic chl *a*, TN, species richness and species evenness (J') among the different cage treatments (Figs 5-7). There were, however, no significant differences between ambient and partial cage samples in sediment composition measured as % sand, silt, and clay (Fig. 5), benthic chlorophyll *a*, sediment TOC, sediment TN (Fig. 6), or community structure, measured as Shannon-Weiner diversity (H'), species richness (S), and Pielou's evenness (J') (Fig. 7). Benthic chl *a* content ($p=0.001$) and species richness ($p = 0.0215$) were significantly greater in full-caged

samples than those from ambient sediments (Figs. 6 & 7) and cage-type accounted for 23.6 and 3.1% of the model variance in their respective ANOVAs. Since those differences cannot be exclusively attributed to the presence of the structure (i.e., exclusion of fish and crabs could influence both parameters), the data from the 3-way ANOVAs were interpreted to mean that there were no detectable artifacts of the cages on the local physical environment at each site that could in turn effect 2° production.

In consideration of the other treatment effects (month and site) in the 3-way ANOVAs, there was no significant effect of month on any of the environmental and community structure measurements (Table 3a). There were significant site effects for all of environmental and community structure metrics, which was anticipated because many of those parameters are site-specific and influenced by the eutrophication-driven changes in habitat quality (Schaffner and Gillett, *in prep*). The site term typically accounted for greater than 75% of the variance in the ANOVA models, with the exceptions of species richness (45% of model variance) and species evenness (13.6% of model variance) where the interaction terms accounted for similar amounts of variance. In general, Catlett Islands and Sarah Creek were the muddiest sites, with Catlett Island sediments having a greater amount of silt and Sarah Creek having a greater amount of clay. Sediments from Chisman Creek were muddier than those from Thorntons, but less so than the other sites and the same held true for silt and clay content. Benthic chl *a* content was highest in Thorntons Creek, similar in Sarah Creek and Catlett Islands, and lowest in Chisman Creek. TOC and TN were highest in sediments from Sarah Creek, then Chisman Creek, Catlett Islands, with lowest amounts in Thorntons Creek sediments (Chisman Creek and Catlett Islands had similar TN content). Species richness and H' were greatest in Thorntons Creek, followed by Chisman Creek, Catlett Islands (both sites had equivalent H'), and then Sarah Creek. There was greater species evenness in samples from Catlett Islands and Sarah Creek relative to those from Chisman Creek, while Thorntons Creek values were similar to all other sites (Table 3a).

As should be expected from 3-way analyses of biological metrics influenced by a number of processes (recruitment, competition, etc), patterns of species diversity, richness, and evenness were not uniform across all sites or cage types throughout the duration of the study. There were 2 significant interaction terms in the species diversity model: site*month and site*cage-type (Table 3b). The interaction terms were significant because the month-to-month patterns in H' were not consistent among the sites, as

well as among the different cage types at the 4 sites (Fig 7a). The 2 significant interaction terms for the species richness model were site*cage-type and month*cage-type (Table 3). The interaction represented the inconsistent relationship of species richness among the cage types across the 4 sites and also across the 3 months (Fig 7b). The evenness model also had two significant interaction terms site*month and site*cage-type (Table 3). Much like the patterns for H', J' was not consistently the same across the 4 sites between cage types or months (Figs. 7c).

Production – The impact of predation was evaluated at each site by comparing the 2° production in sediments exposed to nekton and those protected from them. For ease of illustration, the mean production value in the ambient sediments subtracted from mean value in the caged sediments have been plotted in combination with mean production values from the ambient samples (Figs 8 – 12). The mean rates of 2° production of each group of organisms in each cage and site combination are presented in Appendices 1-4. In many of the analyses, the difference in 2° production of the macrobenthos between the ambient and caged treatments was not statistically significantly different than zero. This can arise from there being equivalent amounts of production measured in each treatment, which may imply no predation effect, from there being little or no production measured in either treatment, implying a site effect independent of predation, or it could be the combination of patchy faunal distributions and the size of the cores used, which lead to high sample variance. If low abundance/absence or patchiness is the likely reason for non-significant results it will be noted below in the descriptions of the production patterns.

There were varying rates of production in the ambient sediments at all of the sites, but there was a consistent pattern of greater total community 2° production in caged than ambient sediments (Fig. 8). At the least degraded site, Thorntons Creek, there was no significant difference in total community production between the 2 treatments due to large variance (Appendix 1). In a pattern that will be echoed by many of the subsequent analyses, there was significantly greater production measured in caged sediments of Chisman Creek, while at Catlett Islands there was no significant difference in total community production between the ambient and caged sediments. At Sarah Creek, the most degraded site, production was the lowest, but there was significantly greater production in the caged than ambient sediments.

To investigate taxonomic differences in 2° production that was utilized by predatory nekton, production of the dominant, cosmopolitan taxa from all 4 sites was compared between the ambient and nekton-excluded sediments. The difference in the mean production values between the treatments for amphipods, bivalves, nemerteans, oligochaetes, and polychaetes at all of the sites are presented in Fig 9. The production of bivalves, when they were present, was typically the largest component of community production; especially at the highly productive Chisman and Thorntons creek sites. When bivalves were present, the trend at all sites was towards greater production in cages, relative to the ambient sediments (Fig. 9b). There was significantly greater production of bivalves in the caged than ambient sediments at Thorntons Creek (primarily *Macoma* spp. and *Tagelus plebius*) and at Chisman Creek (*Macoma* spp. and *Mulinia lateralis*) (Fig. 9b). There was no significant difference in bivalve production between the two treatments at Catlett Islands, even though there was a moderately high amount of production in the ambient sediments (Appendix 2). In Sarah Creek bivalves were present only in July and there was no significant difference in production of bivalves in the caged versus the ambient sediments across the entire sampling period.

With the exception of Sarah Creek, the differences in mean production of nemerteans in caged and ambient sediments are plotted in Fig. 9c, but none of the values were significantly different from zero. At Thorntons Creek the non-significant trend was towards greater production in ambient sediment, though there was considerable variance in both treatments (Appendix 2). The trend in nemertean production was towards greater values in the caged sediments at Chisman Creek, but the values were relatively small between both treatments. There was no difference in production between the 2 treatments at Catlett Islands because there were very few individuals collected. Similarly, few nemerteans were collected from Sarah Creek, but there was a non-significant trend towards greater production in the ambient sediments.

There was relatively little difference in the production of oligochaetes between caged and ambient sediments (Fig 9d) because there were equivalent, though patchy, amounts of production in each treatment in most instances (Appendix 2). There were no significant differences observed at Thorntons Creek, Chisman Creek, or Catlett Islands, though the trend was towards greater production (primarily *Tubificoides brownae* and *T. heterochaetus*) in the ambient than the caged sediments. At Sarah Creek, there was significantly more production (*Limnodriloides anxius*) in caged sediments compared to the ambient sediments.

The differences in mean production of polychaetes between caged and ambient sediments at all of the sites were all relatively large, but there was a large amount of variance as well (Appendix 2). The trend was always towards greater production in the caged sediments, but the differences were not always statistically different from zero. At Thorntons Creek, there was a large amount of polychaete production, but due to the variance there were no statistical difference. There was significantly more production of polychaetes in caged sediments from Chisman Creek and the magnitude of the difference was typically greater than the other sites (Fig. 9e). At Catlett Islands, there was a difference in polychaete production between the two treatments. There was significantly greater production of polychaetes in the caged sediments at Sarah Creek, though the magnitude of the difference was less than at Chisman or Thorntons creeks.

The pattern of amphipod production was the most dissimilar from all of the other taxa analyzed because, when they were present, their production was almost always greater in ambient sediments than those protected from nekton (Fig 9a). There was a significant difference in the production of amphipods (primarily *Leptocheirus plumulosus* and *Listriella clymenellae*) at Thorntons Creek, with greater amounts of production in the ambient sediments. There was no significant difference in amphipod production between the 2 treatments in Chisman Creek because amphipods were relatively rare at the site. At Catlett Islands, there was significantly more production of amphipods (primarily *L. plumulosus*) in the ambient sediments than the caged sediments. There was no significant difference in amphipod production between the 2 treatments in Sarah Creek across the Summer, as there were few, if any, amphipods present in the samples.

Patterns of 2° production for certain key species were also analyzed (Fig. 11). When present in the macrobenthic community, the tellinid bivalves *Macoma balthica*, *M. tenta*, and *M. mitchelli* were typically the biomass-dominants and were grouped together as *Macoma* spp. for analysis. These sessile interface feeders live relatively deep in the sediment, but have siphons that extend to the sediment-water interface (Hines and Comtois 1985; Schaffner et al. 1987). When present, the 2° production of *Macoma* spp. was always greater in caged sediments than in the ambient sediments. The difference in production between the two treatments was comparatively small and not significantly different from zero at Thorntons Creek. The

predation of *Macoma* spp. production was greatest and was significantly greater than zero at Chisman Creek (Fig 10a). The difference in production of *Macoma* spp. between the 2 treatments was relatively small and was not significantly different than zero at Catlett Islands, despite relatively large amounts of 2° production available to predators in the ambient sediments. No *Macoma* spp. individuals were found at Sarah Creek in any of the 3 months.

Heteromastus filiformis is a large, head-down, deposit feeding, capitellid polychaete that typically lives relatively deep below the sediment-water interface (e.g., Fauchald and Jumars 1979; Hines and Comtois 1985). There were no significant differences between production of *H. filiformis* in ambient and caged sediments at any of the sites over the Summer, due to relatively large variance in the caged samples. Most of the trends were towards greater production in the caged sediments (Fig 10b). The difference in *H. filiformis* production between the 2 treatments at Thorntons Creek trended towards greater production in the caged sediment, with relatively little production in the ambient sediments. The trend was similar at Chisman Creek, though there was more production of *H. filiformis* in both treatments than at Thorntons Creek. The trend in *H. filiformis* production at Catlett Islands was towards greater rates of production in the caged sediments, though as seen with many other taxa, there was relatively high production in both the ambient and caged-sediment treatments. There were no *H. filiformis* collected in most samples from Sarah Creek and, therefore, no difference between the 2 treatments.

The aorid amphipod *Leptocheirus plumulosus* is a mobile, filter-feeder that builds shallow U-shaped burrows near the sediment surface, but often moves around on the sediment surface and in the benthic boundary layer. The patterns of nekton consumption of *L. plumulosus* production showed the most variability among the sampling sites compared to other taxa. At Thorntons Creek, there was significantly more production of *L. plumulosus* in the ambient sediments than those exposed to nekton predation (Fig. 10c). The trend in *L. plumulosus* production at Chisman Creek was towards greater rates in the caged sediments, but due to the large variance in the caged samples (Appendix 3), the difference was not statistically significant. Catlett Islands had the greatest amounts of *L. plumulosus* production in the ambient sediments, which were significantly greater than in the caged sediments. No *L. plumulosus* were collected in any of the samples from Sarah Creek.

The next species of interest was the nereid polychaete *Neanthes succinea* (Fig. 10d). *Neanthes succinea* is a relatively large, mobile, omnivorous polychaete that lives close to and on the surface of the sediment (Fauchald and Jumars 1979; Hines and Comtois 1985). At Thorntons Creek there was no significant difference in the production of *N. succinea* in ambient or caged sediments due to the large variance in the caged samples, though the trend was towards greater production in the caged sediments. At Chisman Creek, there was significantly greater production in the caged sediments. There was no significant consumption of *N. succinea* production at Catlett Islands, despite relatively large amounts of production in both the ambient and caged sediments. There was no significant difference in production between treatments at Sarah Creek because of patchy distribution and high variance, though the trend was towards greater production in caged sediments.

The small, infaunal spionid polychaete *Streblospio benedicti* feeds and lives near the sediment surface. Production of *S. benedicti* at Thorntons and Chisman creeks was significantly greater in the caged sediments (Fig. 10e). There was no significant difference in *S. benedicti* production between caged and ambient sediments at Catlett Islands because of the patchiness and variance associated with the samples, but the trend was towards greater production in the caged sediments. At Sarah Creek, the difference in *S. benedicti* production between the 2 treatments was not significantly different than zero.

Because the depth at which organisms live in the sediment can influence how susceptible they are to predation by nekton (Hines et al. 1990; Seitz et al. 2001), the influence of predation on the production of fauna located in the first 5 cm below the sediment-water interface (shallow) and those located below 5 cm (deep) was investigated (Fig. 11). At Thorntons Creek, there was no significant difference in the production of shallow fauna. In contrast, there was significantly greater production of shallow fauna in the caged sediments of Chisman Creek than those exposed to predation. At Catlett Islands there was no significant difference in production between the treatments, but the trend was towards greater production in the ambient sediments. At Sarah Creek, the difference in 2° production of shallow fauna between the 2 treatments was not significant, but the trend was towards greater production in the caged sediments. The trend for the deep-dwelling fauna at all of the sites was towards greater 2° production in the caged sediments compared to the ambient sediments, but the differences were not statistically significant at Thorntons Creek, Catlett Islands, and Sarah Creek because of the variance at each of the sites (Fig. 11b).

There was, however, significantly greater production of deep dwelling fauna in caged sediments at Chisman Creek.

The last iteration of production analyses were based upon the 2° production of the different feeding guilds found in the macrobenthic community. Filter-feeders at Thorntons Creek showed no significant difference between production in ambient versus caged sediments due to large sample variance, with the trend towards greater production in the cages (Fig. 12a). At Chisman Creek the production of filter-feeding macrobenthos was significantly greater in the caged sediments. Conversely, filter-feeder production was significantly greater in the ambient sediments from Catlett Islands compared to the caged sediments. Very few filter-feeding fauna were collected from Sarah Creek and therefore there was no difference in production between the 2 treatments.

At most of the sites sampled there was little grazer biomass and therefore, little production. As a result, all of the differences were not significantly different than zero (Fig. 12b). There was a trend towards greater production of grazing fauna in caged sediments of Thortons Creek, but there was considerable patchiness and variance in the caged samples. At the remaining other three sites, there was no appreciable amount of grazer biomass consistently collected.

Though there was relatively little biomass of shallow deposit-feeders compared to some of the other guilds, there were still significant impacts of predation on the patterns of production (Fig. 12c). At Thorntons Creek, there was greater production of shallow deposit-feeding taxa (primarily *Mediomastus ambiseta* and *Tubificoides brownae*) in the ambient sediments than in the caged sediments. There were no significant differences between the 2 treatments at Chisman Creek or Catlett Islands. In contrast to Thortons Creek, there was significantly more production in the caged sediments at Sarah Creek, where the shallow deposit feeding fauna were different species of capitellid polychaetes (*Capitella capitata*) and the oligochaetes (*Limnodriloides anxius*) than at the higher quality site.

There were no significant differences in the production of deep-dwelling deposit-feeding macrofauna (Fig. 12d) at any of the sites, in large part due to the variance in the measurements (Appendix 4). The trend though, was consistently towards greater production in the caged sediments. It should be noted that there were large amounts of production of deep-deposit feeders in the ambient sediments at

Thorntons Creek and, to a lesser magnitude, at Chisman Creek and Catlett Islands, and it appears to have not been consumed. At Sarah Creek, very few deep-deposit feeding fauna were collected.

The trend in the production of omnivores at Thorntons Creek was towards greater production in the caged sediments than the ambient sediments because of the high variance in the samples. At Chisman Creek, there was significantly greater production in the caged sediments (Fig. 12e). There was no significant difference in omnivore production at Catlett Islands, but there were relatively large amounts of production in both treatments. Omnivore production at Sarah Creek was significantly greater in the caged sediments compared to the ambient sediments.

At Thorntons Creek there was no difference in production of carnivorous macrofauna between the 2 treatments, due to the high variance (Fig 12f). There was significantly greater production of carnivores in the caged sediments compared to the ambient sediments at Chisman Creek. The differences in production of carnivores between the caged and ambient sediments were not significantly different than zero at Catlett Islands and Sarah Creek, primarily because very few individuals were collected (Appendix 4).

Though productive when present, there was a large amount of sample variance in the samples of non-bivalve interface-feeders at Thorntons Creek and therefore the difference between the treatments was not statistically different than zero (Fig. 12g). At Chisman Creek, there was significantly greater production of non-bivalve interface feeders in the caged sediments. The trend in production at Catlett Islands was towards greater production in the ambient sediments, but the difference was not statistically significant. There was no significant difference in production between the caged and ambient sediments at Sarah Creek, as very little biomass was collected.

At the sampling sites, the bivalve interface-feeding guild was comprised solely of the tellinids *Macoma balthica*, *M. tenta*, and *M. mitchelli*, which are covered above in the *Macoma* spp. section (Fig 10a). To recount though, there was significantly greater production in caged than ambient sediments at Chisman Creek. At Thorntons Creek and Catlett Islands there was relatively equivalent amounts of production in the 2 treatments and there were no significant differences between them (Appendix 4). Similarly, there was no significant difference at Sarah Creek, but in this instance it was because there were almost no individuals collected.

DISCUSSION

Most predator exclusion studies are conducted to investigate the role of predation in structuring prey communities from relatively non-degraded, "normal" systems (e.g., Holland et al. 1980; Sardá et al 1998; Virnstein 1979; Wilson 1991). Often these experiments are framed to contrast predation with recruitment processes (reviewed in Ólafsson et al. 1994; Seitz 1998) or paired with nutrient enrichment to examine the "top-down/bottom-up" relationships in macrobenthic communities (Douglas 2008; Fleeger et al. 2008; Johnson and Fleeger 2009; Posey et al. 2002). Across all of these studies there does not seem to be an agreement on the primacy of any one process in influencing macrobenthic community structure, especially in soft-bottomed communities. Processes such as predation pressure, recruitment, and food availability are going to interact in time and space, particularly in spatially complex and physically dynamic ecosystems like estuaries.

In the current study however, the predation of macrobenthos was examined at 4 sites with similar environmental settings but macrobenthic communities that differed in composition, largely due to anthropogenic, eutrophication-driven stressors. Furthermore, the 2° production of the macrobenthic communities was estimated instead of simply measuring abundance and biomass. Secondary production, even empirically estimated production like that used here, is a better estimate of the macrobenthos in the context of the ecosystem than abundance or biomass because it tracks changes in growth and loss in the community (Cusson and Bourget 2005; Gillett et al. 2005; Wilbur and Clarke 1998). Because almost no significant caging effects on environmental characteristics that would have increased 2° production rates (i.e., TOC, TN, benthic chl *a*) were observed, the differences between production in sediments protected from predatory nekton and those exposed to them can be interpreted as an indication of those macrofauna's usefulness or desirability to the nekton as a food source.

One of the underlying assumptions in this approach is that the macrobenthos of impacted or degraded communities will be less useful as a food source due to their low production, small size, and high turnover rate. Most benthivoric nekton commonly found in Chesapeake Bay (e.g., *Callinectes. sapidus*, *Leiostomus xanthurus*, and *Micropogonias undulatus*) search for prey items through a combination of

tactile and chemosensory mechanisms. This should make them sensitive to the changes in macrobenthic community composition that accompany the degradation of estuarine ecosystems. Experimentally, this has been observed in freshwater systems where macrobenthic communities of degraded lakes are energetically limiting to benthivoric nekton (Haywood and Margraf 1987; Kövecses et al. 2005; Sherwood et al. 2002) and in New England tidal creek systems where there was predatory selection for larger, longer-lived macrofauna among fertilized and non-fertilized creeks (Sardá et al. 1998). Additionally, the interpretation of the pair-wise comparisons between treatments assumes a lack of competition for space at these temperate, soft sediment communities (e.g., Ólafsson et al. 1994; Seitz 1996) where removal of individuals from the community via predation would open space for new recruits replacing them, as might be expected in hard bottom communities (Connell 1961; Paine 1966).

Predation Patterns Among Sites – The utilization of macrobenthos as a food source by nekton should be a function of the macrobenthos available and the presence of the nekton to feed upon them. Unlike most macrobenthic species, which are largely sedentary, nekton are highly mobile and can move from place to place, searching for prey (e.g., Lipcius and Hines 1986; Seitz et al. 2001; Weinstein and O'Neil 1986) or to avoid environmental perturbations (e.g., Eby et al. 2005; Peterson et al. 2000; Pihl et al. 1992). This dichotomy creates site-specific macrobenthic communities that are influenced by local biological and physical parameters and tributary- or estuary-specific nekton communities influenced by larger-scale processes that are relatively uniform from creek-to-creek through time (Pacheco 1962; Weinstein 1983). Following suit, nekton were collected at the sites concurrently with the caging study (Schaffner, *unpub*) and during the subsequent Summer of 2007 (Gillett and Schaffner 2008) using baited traps and castnetting. There were similar densities of *L. xanthurus*, *C. sapidus*, *Fundulus heteroclitus*, and *Trinectes maculatus* at all 4 of the sites and densities were similar to previous data collected at similar sites (Cicchetti 1998; Fabrizio and Montane 2007; Weinstein 1983). Given this even distribution of nekton across the sites, the differences in nekton utilization of the macrobenthos at each of the sites should be due to the differences in macrobenthic community structure, more so than differing levels of potential predatory pressure.

As briefly mentioned above and detailed in Hines et al. (1990), the benthivoric nekton of Chesapeake Bay comprise a guild with diverse taxonomic composition, feeding style, and life history.

During the Summer of 2006 while the caging experiment was being conducted, abundance of *L. xanthurus*, *F. heteroclitus*, and *C. sapidus* were similar, but the total and per capita biomass dominant of the benthivoric nekton guild was *C. sapidus* at Thorntons, Chisman, and Sarah creeks (nekton were not sampled at Catlett Islands in 2006). As such, it is likely that *C. sapidus* exerted greater predation pressure on the benthic community than the other components of the benthivoric nekton guild. This would give the predation pressure that was measured a more "crab-like" signature than "fish-like" and explain why the most of the production consumed was that of bivalves, as they are thought to be one of the preferred prey items of *C. sapidus* (Hines et al. 1990; Seitz et al. 2001; Seitz et al. 2005).

Across all 4 of the sites through July, August, and September, the predominant trend was towards greater production in the fully caged treatments; whether considering total community production or that of the component taxa. This pattern suggests that almost all of the macrobenthos that occur in the mesohaline portions of Chesapeake Bay can serve as a food source to the suite of benthivoric nekton, which are all considered to be relatively generalist feeders, capable of prey-switching (Hines et al. 1990; Seitz et al. 2001). The notable exception to this general pattern were filter- and deposit-feeding amphipods.

There was greater production of amphipods in the ambient sediments exposed to benthivoric nekton than in the protected sediments, even though many gut-content studies have observed amphipods as an important component of the estuarine benthivoric nekton diet (e.g., Chao and Musick 1977; Horvath 1997). This discrepancy may have been a function of the timing of the cage placement. The largest and most consistent examples of amphipod 2° production were at Catlett Islands, which consisted primarily of *L. plumulosus*, a species that broods its young and establishes communities by active migration or transport in the benthic boundary layer. There were relatively few amphipods at either the Catlett Islands or Thorntons Creek sites at the beginning of this experiment when the cages were deployed, so the amphipods migrated/recruited to the sites between the Spring and July sampling events (Appendix 2). As very few amphipods were collected in the cages, it appears that full cages may have limited their access to the sediments inside the cages. If so, the experimental design would not detect the utility of amphipod production to benthivoric nekton,

Contrary to expectations, the utilization of macrobenthos by benthivoric nekton was not predictably related to habitat quality as measured in this study. Much like the outcome of other experiments looking at

predatory impacts on macrobenthic community structure, when a system is not extremely degraded multiple macrobenthic communities are potentially possible in similar environmental settings due to variation in larval pool or the local environment, and this seems to be especially true in the shallow water portions of estuaries (Schaffner and Gillett, *in prep*; Seitz 1996). There were a number of trends in the data, but many of the results were not statistically significant due to the patchiness of the fauna relative to the size of the sampling device. As a result, any subtle patterns of nekton predation of macrobenthos would be lost in the variance. The one pattern that was most clearly evident through all of the various taxonomic and feeding guild iterations of the analyses was that the tellinid bivalves *Macoma balthica*, *M. tenta*, and *M. mitchelli* were the most productive and most utilized group of macrofauna by the nekton.

All 3 species of *Macoma* are common estuarine endemics found throughout the mesohaline to polyhaline portions of Chesapeake Bay (Boesch 1977; Holland et al. 1987) but they are also relatively sensitive to the hypoxia and the toxic compounds that often accompany eutrophication (Brylawski 2008; Gray et al. 2002; Long et al. 2008). As such, *M. balthica* abundance and biomass are incorporated into the B-IBI and MAIA benthic indices (Llansó et al. 2002; Weisberg et al. 1997) that are used to assess benthic community quality in the Mid-Atlantic US. When conditions are favorable, these tellinid bivalves can be the biomass dominant in the shallow waters of estuaries, reaching >15 g AFDM m^{-2} standing stock biomass in some sites (Schaffner et al. 2008). Though they can live relatively deep in the sediment, often > 20 cm deep (Hines and Comtois 1985; Schaffner et al. 1987), *Macoma* spp position their siphons near the sediment-water interface to feed and respire. This makes them vulnerable to non-lethal siphon nipping by the whole suite of benthivoric nekton and to excavation and consumption by larger *C. sapidus*. Gut-content studies from Chesapeake Bay almost always show a considerable amount of food material in the stomachs of benthivoric fishes and crabs to be siphons or shell fragments of *Macoma* spp. (Chao and Musick 1977; Derrick and Kennedy 1997; Hines et al. 1990; Horvath 1997).

The macrobenthic community at Chisman Creek, where production was dominated by the bivalves *Macoma* spp. and *Mulinia lateralis*, consistently experienced the highest degree of predation through July, August, and September, at both shallow and deep sediment depths, and across multiple taxa. In addition to the bivalves, the omnivorous and carnivorous polychaetes (including *Neanthes succinea*) were significantly preyed upon as well. Chisman Creek was not the highest quality site as determined simply by B-IBI score,

as the Chesapeake Bay Program would, or in the PCA conducted in this study, but it was not particularly degraded either. Across the spectrum of the sites that were sampled, Chisman Creek had mid-level species diversity and richness, but high abundance and biomass, which suggests that there was a greater number of potential types of prey items for the nekton. However, there was still a strong selection for the bivalves and this reinforces the importance of bivalves to the diet of the benthivoric nekton guild, particularly when that guild is dominated by *C. sapidus* as it is in the shallow waters of Chesapeake Bay. Furthermore, the large amounts of bivalve production may serve as an attractant for nekton, as previous studies have suggested that *C. sapidus* use a density-dependent searching strategy and will stay in area if there is high prey density available (Clark et al. 2000; Lipcius and Hines 1986; Seitz et al. 2001). The high levels of predation experienced by non-bivalve fauna living at both shallow and deep sediment depths at Chisman Creek suggests that benthivoric nekton, in their searching patterns, come across habitats with high bivalve densities, they stay there, and in the process feed upon the other fauna there. In other habitats where the bivalve densities are not as high, there will likely be some consumption of all the fauna, but the nekton may move on.

As an example, Thorntons Creek was the highest quality site that was sampled, but total community production did not show any statistically significantly utilization of the macrobenthic community by the nekton as a food source. Like at Chisman Creek, there was significant consumption of bivalves where they were present, but they were not as uniformly distributed in Thorntons Creek as in Chisman Creek. Production at Thorntons Creek was consistently dominated by large polychaetes (*Loimia medusa*, *Clymenella torquata*, and *Leitoscolopolis fragilis*), which were preyed upon, but the results were not significant due in part to the patchy distribution throughout the site. Two additional aspects of the Thorntons Creek site may have secondarily contributed to the muted impact of predation on the different components of the macrobenthic community production, especially the polychaetes. The high species diversity, especially polychaetes, presented an increased number of prey items to the nekton, preventing them from focusing on a given taxon and the higher sand content of the sediments likely provides more protection from excavation than the much muddier sediments at the other sites (e.g., Lipcius and Hines 1986; Seitz et al. 2001).

The Catlett Islands site was another moderate-to-high quality site that was similar to the Chisman Creek site based on both B-IBI and multivariate approaches, but the production of the macrobenthic community was not used by the nekton as much as at Chisman Creek. Community 2° production at Catlett Islands was more evenly distributed among amphipods, polychaetes, and bivalves, but the data indicate that there was little nekton consumption of this production. No significant differences between ambient and caged sediments were consistently observed, but unlike Sarah Creek, which was relatively depauperate, the underlying cause was typically equivalent amounts of production in both treatments. The lack of a predation upon a community that should have been desirable (e.g., *Macoma* spp., *Neanthes succinea*), suggests that some other, uncharacterized process within the nekton communities in the region of Catlett Islands (e.g., cannibalism/predation, recruitment, fishing pressure) was the underlying influence on predation, not macrobenthic community structure.

Sarah Creek was one of the two sites where there was significantly greater production of the entire macrobenthic community in the fully caged samples than those exposed to nekton, despite the degraded nature of the site. As noted earlier, the one potential cage effect that may have influenced the study was the greater amounts of benthic chl *a* in fully caged sediments than ambient sediments, which indicates a greater amount of microphytobenthos or deposited phytoplankton on the sediment surface. A closer inspection of the data (Fig. 6) shows that this result was driven primarily by the Sarah Creek samples from early in the experiment. The community there was comprised of shallow deposit-feeding and omnivorous polychaetes and oligochaetes; taxa that can utilize microphytobenthos and sediment organic matter as food source (Gillett et al. 2007; Chapter 4). Consequently, one cannot fully attribute the differences in macrobenthic production at Sarah Creek to the exclusion of predatory nekton and must allow that there may have been some degree of fertilization of at least shallow deposit-feeding oligochaetes and capitellid polychaetes, which have reproductive patterns conducive to rapidly responsive population booms to fresh organic matter inputs (e.g., Gillett et al. 2007; Marsh et al. 1989). Furthermore, at the three other sites, oligochaete production was greater in ambient sediments or equivalent between the two treatments, which suggests that the oligochaetes likely do not serve as a desirable or easily detectable prey item to nekton found at the sites. The small size of the oligochaetes found in this study (*Limnodriloides anxius*, *Tubificoides heterochaetus*, and *T. brownae*) likely make them hard to detect by any of the benthivoric nekton encountered at these

sites, with the possible exception of spot, *L. xanthurus*. These sciaenids gulp mouthfuls of sediment, straining out any potential food items with its gill rakers (Chao and Musick 1977) and should encounter and subsequently consume oligochaetes.

Predation Patterns Among Faunal Groups – Beyond the site-specific effects on the relationship between nekton on macrobenthic production , there also were autecological trends that persisted across the sites. Based upon living-position within the sediment one could easily assume that there should not be significant consumption of deep-deposit feeding production by benthivoric nekton. The depth at which these fauna, primarily *H. filiformis* and *L. fragilis* in this study, live and feed drastically reduces the probability of them being detected by predators. However, there were consistent trends in the data that show greater production inside the cages despite no difference in TOC or TN in the sediment (the best measures of their food source). Hines et al. (1990) have shown, that beyond the direct effects of consumption, benthivoric nekton can have an indirect effect on the macrobenthos via of the bioturbation that occurs while they are searching for prey items. This type of bioturbation, which would be prevented by the predator exclusion, should disrupt and inhibit the feeding galleries of deep-deposit feeders, which might account for the reduced production observed in the ambient sediments. There is also the potential to smother small surface dwelling fauna like *S. benedicti* (e.g., Hinchey et al. 2006; McCann and Levin 1989; Rhoads and Young 1970). This type of indirect, predator related mortality could account for the significantly greater production of *S. benedicti* in caged sediments observed at the higher quality sites. Interestingly, bioturbation that would negatively affect deep-dwelling deposit-feeders and small interface-feeders like *S. benedicti* does not negatively affect shallow-dwelling fauna like oligochaetes and amphipods, which have evolved to handle sediment disturbance and burial common in the top layer of the sediment-water interface (Hinchey et al. 2006).

From the macrobenthic feeding-guild perspective, there was a degree of agreement between the *apriori* hypotheses on size and motility of macrobenthos and how the benthivoric nekton consumed production. The guilds that consistently showed statistically significant impacts from benthivoric nekton were filter-feeders (with the exception of *L. plumulosus*) and interface-feeders; taxa that live at or near the sediment-water interface and are relatively non-motile, as well as omnivores and carnivores, large, motile fauna that move on or near the sediment surface. These behaviors are likely responsible for making them

more desirable to nekton as a prey item, but many of the species that comprise these groups are also sensitive to eutrophic, chemical, and physical stressors. In contrast, the small size of shallow deposit-feeders probably protects them from nekton as discussed above. Deep deposit-feeders, which are typically large and therefore desirable prey items, were not preyed upon because they live deep enough in the sediment to avoid detection and excavation, though they did appear to be sensitive to indirect impacts of bioturbation from the nekton.

CONCLUSIONS

Previous work has shown that as habitat quality decreases in the shallow water portions of estuaries, the overall magnitude of secondary production decreases thereby limiting the amount of food available to benthivoric nekton (Chapter 2; Sardá et al. 1996). The current work suggests that the kinds of taxa that comprise the production are also important and can further limit nekton feeding, affecting functioning of the ecosystem. Results from this study demonstrate that the feeding behaviors of benthivoric nekton are influenced by the composition of a macrobenthic community and that they selectively prey upon some taxa more than others, but these dynamics were not predicted solely by the habitat quality. In the shallow waters of Chesapeake Bay, the blue crab *C. sapidus* is the biomass dominant of the benthivoric nekton guild so these results are likely biased towards their behavior. Thus there was strong and consistent consumption of macrobenthic production at those sites that had large amounts of bivalve production. These bivalves, though more tolerant than some taxa, are still sensitive to the stressors related to eutrophication and their disappearance from a macrobenthic community may limit the utility of a given system as a feeding ground to the nekton. This is yet another example of how eutrophication may not directly harm benthivoric nekton, but indirectly limits their food sources and possibly their growth and other aspects of the nekton life cycle. That being said, population-level processes on the nekton themselves (e.g., predation, recruitment, fishing pressure) also have an impact on the utilization of the macrobenthos as a food source, as suggested by the Catlett Islands example.

One of the most important reasons to measure 2° production is to understand the role of macrobenthic production in the food web of an ecosystem; to determine how much organic matter is consumed by the macrobenthos and also how much they potentially provide for subsequent trophic levels. In measuring macrofaunal production that was protected from predators, an estimate can be made of 2° production rates not influenced by predation. The difference between the maximum production rate and that measured in the ambient sediments represents a better estimate of the 2° production that is consumed by subsequent trophic levels than traditional empirical estimates of 2° production and provides a better estimate of how much of the total 2° production is consumed and how much is retained in the benthic

system. These types of data should be valuable for the modeling of benthic-pelagic food webs whether the benthos are treated as a single unit or divided into trophic or taxonomic components.

The goal of this study was to determine if and how the composition of a given macrobenthic community, which is in part related to habitat quality, influences the utility of that community to benthivoric nekton as a food source. The relationship was far less robust than the relatively strong relationship between sediment quality and macrobenthic community structure. This illustrates one of the difficulties associated with the concept of habitat quality. The quality of a given system as perceived by the feeding of benthivoric nekton appears to be different than how it is typically assessed by scientists and ecosystem managers. In the shallow waters of Chesapeake Bay, where the composition of the benthivoric nekton guild is skewed towards *C. sapidus*, benthic communities composed of preferred prey items of the crab had the greatest utility as a food source and therefore, of the highest quality. The anthropocentric view of habitat quality is more broadly defined because of the numerous services provided by the estuary and the stakeholders invested in them. Consequently, the standard, approach of evaluation of estuarine habitat quality only did a moderate job of capturing the "nektonic perspective". Rectifying the two scales of habitat quality valuation will be an important task in the future as researchers try to integrate estuarine productivity at multiple trophic levels into habitat assessment and ecosystem management practices.

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Sources of Unpublished Data

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Personal Communications

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Table 1. A list of all macrobenthic taxa collected during this study and the feeding guilds to which they were assigned.

Filter-Feeders

Aligena elevata
Demonax microphthalmus
Gemma gemma
Geukensia demissa
Ischadium recurvum
Leptocheirus plumulosus
Mulinia lateralis
Mya arenaria
Ostracoda
Phoronis sp.
Potamilla neglecta
Spiochaetopterus oculatus
Tagelus plebius

Grazers

Americamysis almyra
Americamysis bigelowi
Cumacea
Cyclaspis varians
Edotea triloba
Gastropoda
Leucon americanus
Listriella barnardi
Listriella clymenellae
Melita nitida
Mysidae
Rithropanopeus harrisii

Shallow Deposit-Feeders

Corophium ascheruscium
Corophium simile
Limnodriloides anxius
Mediomastus ambiseta
Paranais litoralis
Tubificidae
Tubificoides brownae
Tubificoides heterochaetus
Tubificoides motei
Tubificoides wasselli

Deep Deposit-Feeders

Capitella capitata
Capitella jonesi
Capitomastus aciculatus
Clymenella torquata
Heteromastus filiformis
Leitoscoloplos fragilis
Pectinaria gouldi

Omnivores

Cyathura polita
Insecta
Laeonereis culveri
Leptochelia rapax
Neanthes succinea

Carnivores

Eteone heteropoda
Glycera dibranchiata
Glycinde solitaria
Hesionidae
Nemertean
Parahesione luteola
Podarke obscura
Podarkeopsis levifuscina
Turbellaria

Bivalve Interface-Feeders

Macoma balthica
Macoma mitchelli
Macoma tenta

Non-Bivalve Interface-Feeders

Loimia medusa
Melinna maculata
Paraprionospio pinnata
Polydora cornuta
Samythella elongata
Spionidae
Streblospio benedicti

Table 2. Pairwise comparisons from Analysis of Similarity (ANOSIM) of square-root transformed Bray Curtis similarities from **CH** - Chisman Creek, **CI** - Catlett Islands, **SA** - Sarahs Creek, and **ST** - Thorntons Creek in Spring, July, August, and September. The higher the R-value from 0 - 1, the greater the dissimilarity between sites. Probability of each R-value is presented, with an α=0.05.

Pairwise Comparison	R-Statistic	Probability
CH vs ST	0.615	0.001
CH vs SA	0.505	0.001
CH vs CI	0.458	0.001
ST vs SA	0.830	0.001
ST vs CI	0.758	0.001
SA vs CI	0.854	0.001

Global R-Statistic = 0.661, p = 0.001

Table 3a. Output of the 3-way ANOVA for environmental and community parameters testing for cage effects including: sample size, degrees of freedom (model, error), r^2, overall model f-statistic and probability, as well as the probability of each treatment variable, the significant interaction terms (**S**=site, **M**=month, and **T**=cage type). *Post hoc* analyses are presented for each treatment effect: Cage Effect, the type of cage that was different than ambient samples in a Dunnett's test; for the Site Effect, an underline implies similarity of least squared means between sites (α=0.05) **CH**=Chisman Creek, **CI**=Catlett Islands, **SA**=Sarahs Creek, and **ST**=Thorntons Creek. Note that since the month term was not significant in any of the analyses, no post hoc comparisons were done. ‡ one benthic chl a sample was lost in processing

Table 3b. Detailed post-hoc least squared means comparison of the significant interaction terms, where an underline implies similarity of months or cage-type within a given site or month (α=0.05). **J**=July, **A**=August, **S**=September, **O**=ambient, **P**=partial-cage, and **F**=full-cage

a

Parameter	N	d.f.	r^2	f-stat	model p	Cage Treatment	Month	Site	Interaction Terms	Cage Effect ($\mu_{ij} \neq$ ambient)	Month Effect	Site Effect
Arcsine Sqrt Sand Content (% by mass)	108	7, 100	0.801	57.65	<0.0001	0.1062	0.6010	<0.0001		-	-	ST CH SA CI
Arcsine Sqrt Silt Content (% by mass)	108	7, 100	0.818	64.19	<0.0001	0.2758	0.7337	<0.0001		-	-	CI SA CH ST
Arcsine Sqrt Clay Content (% by mass)	108	7, 100	0.714	35.69	<0.0001	0.0132	0.5178	<0.0001		-	-	SA CI CH ST
Log_{10} Benthic Chlorophyll a (mg m^{-2})	107‡	7, 99	0.400	9.42	<0.0001	0.0007	0.9497	<0.0001		Full	-	ST SA CI CH
Sediment Total Organic Carbon (% by mass)	108	7, 100	0.757	44.43	<0.0001	0.0870	0.5120	<0.0001		-	-	SA CH CI ST
Sediment Total Nitrogen (% by mass)	108	7, 100	0.757	44.42	<0.0001	0.0265	0.4282	<0.0001		-	-	SA CH CI ST
Shannon Weiner Diversity (H')	108	19, 88	0.559	5.86	<0.0001	0.1567	0.2219	<0.0001	S*M S*T	-	-	ST CI CH SA
Species Richness (S)	108	17, 90	0.719	13.52	<0.0001	0.0332	0.0759	<0.0001	S*T M*T	Full	-	ST CH CI SA
Pielou's Evenness (J')	108	19, 88	0.467	4.05	<0.0001	0.0297	0.4661	0.0188	S*M S*T	-	-	CI SA ST CH

b

Parameter	Site*Month Interaction				Site*Cage Interaction				Month*Cage Interaction		
	Thorntons Creek	Chisman Creek	Catlett Islands	Sarahs Creek	Thorntons Creek	Chisman Creek	Catlett Islands	Sarahs Creek	July	August	September
Shannon-Weiner Diversity (H')	S A J	A S J	A S J	J A S	O P F	P O F	P F O	P F O			
Species Richness (S)					P O F	F P O	F O P	P F O	P O F	F P O	P F O
Pielou's Evenness (J')	S A J	S A J	A S J	J A S	O P F	O P F	P F O	P F O			

Figure 1. The four sampling sites located in the mesohaline portions of southwestern Chesapeake Bay. The inset shows the location of the region on the eastern coast of the United States.

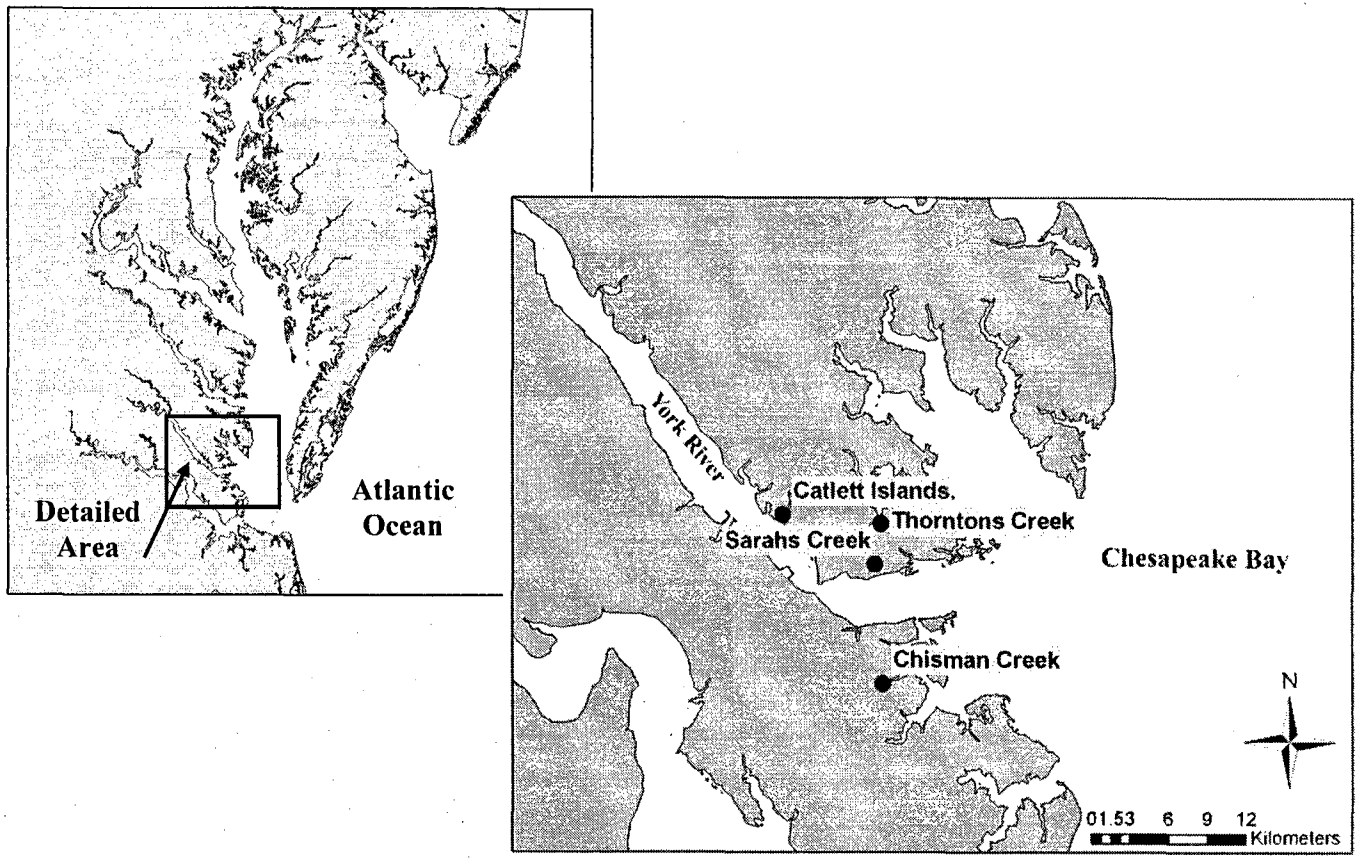

Detailed
Area
Atlantic
Ocean
York River
Catlett Islands.
Thorntons Creek
Sarahs Creek
Chesapeake Bay
Chisman Creek
N
01.53 6 9 12
Kilometers

Figure 2. **a**. A side-view of a partial- and full-cage. **b**. A top-view of a partial- and full-cage.

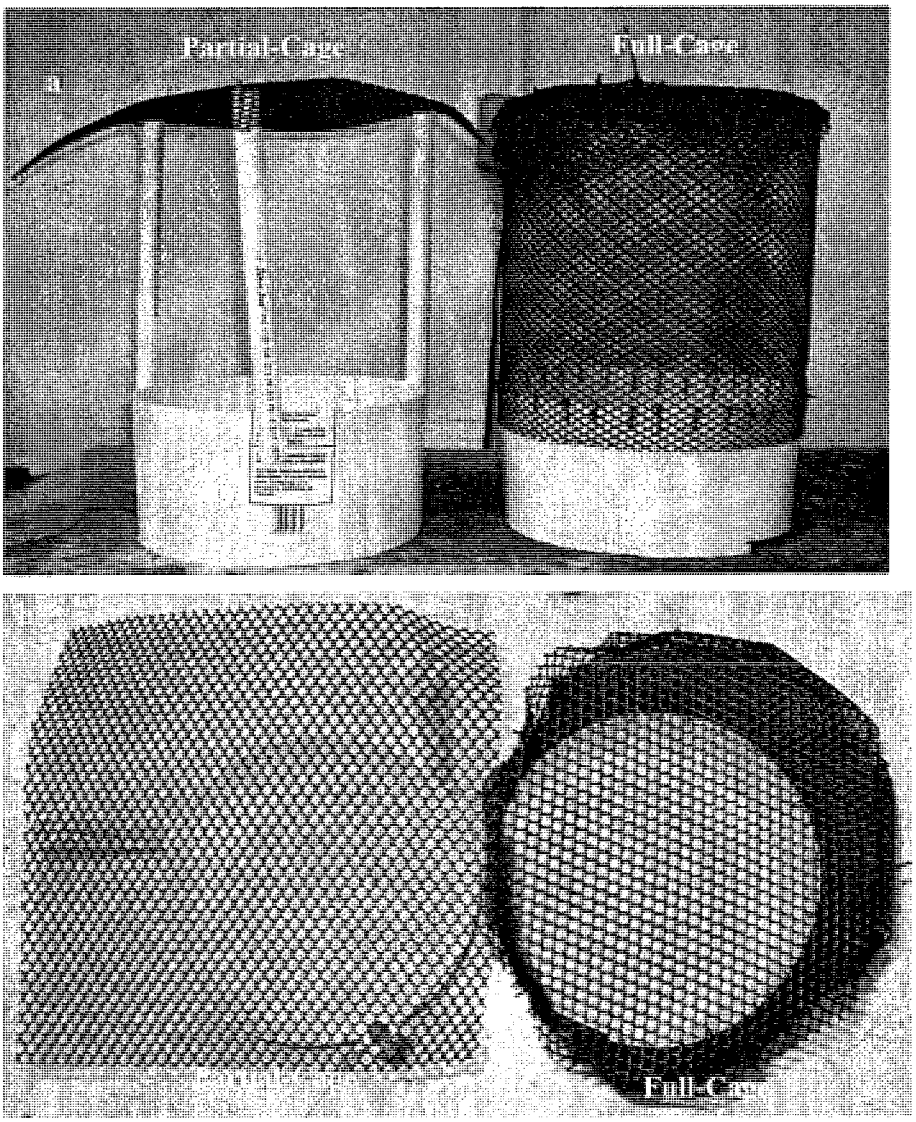

Partial-Cage
Full-Cage
a
Full-Cage

Figure 3. Principal components analysis (PCA) of habitat quality metrics at each of the 4 sites in Spring, July, August, and September arrayed along PC1 and PC2. PC1 accounted for 70.7% of variance and PC2 accounted for 16.3%. The Eigenvectors contributing to PC1 and PC2 of each degradation metric in the analysis, multiplied by 10 for ease of plotting, are superimposed over the plot to show the contribution of each metric to the overall PCA.

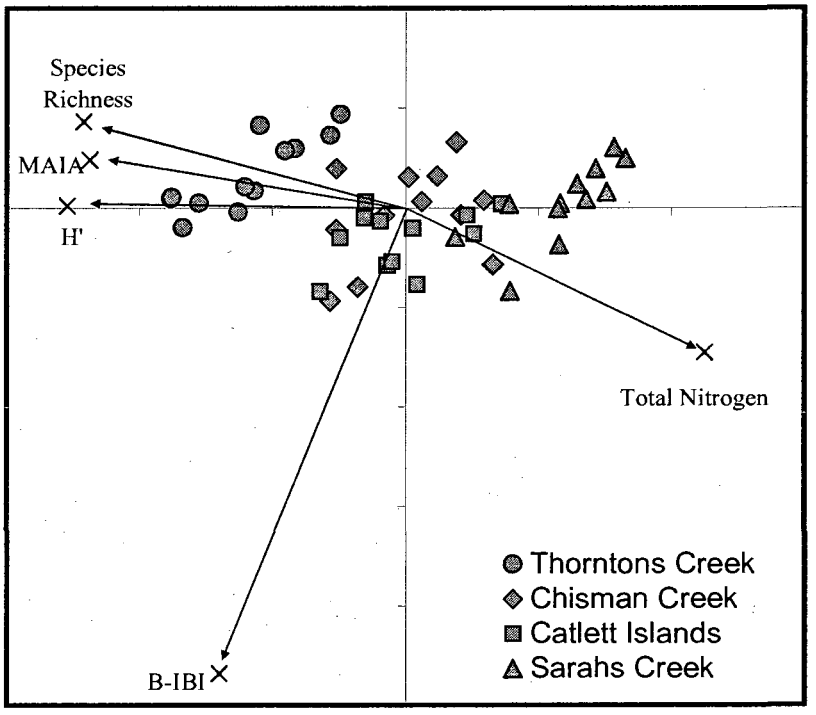

Species
Richness
MAIA
H'
Total Nitrogen
B-IBI
Thorntons Creek
Chisman Creek
Catlett Islands
Sarahs Creek

Figure 4. A multi-dimensional scaling (MDS) plot of square root-transformed Bray-Curtis similarities of benthic community samples from the ambient sediments presented with overall stress value. Smaller stress values, which range from 0.0 – 1.0, indicate greater confidence in the pattern. The encircled samples show the statistically distinct communities determined by a pair-wise comparison of sites with ANOSIM (full details in Table 2).

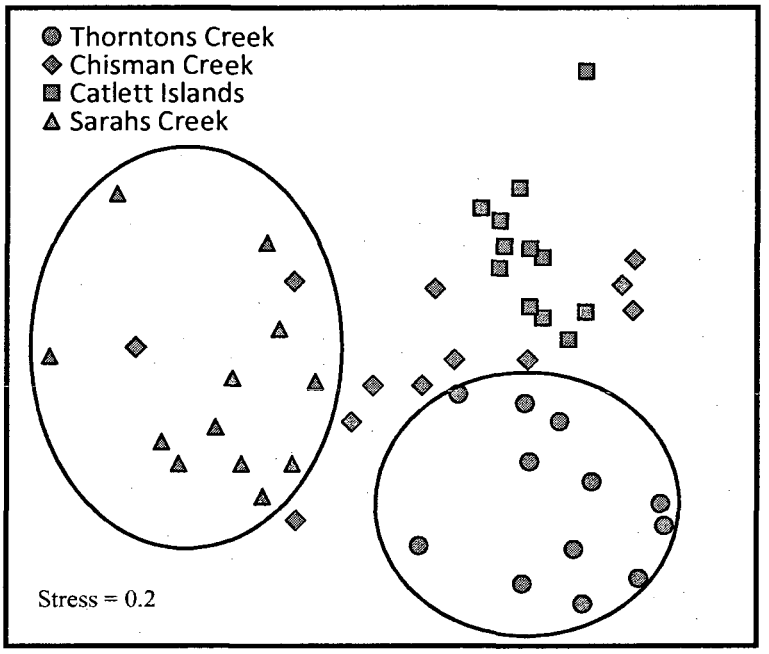

Thorntons Creek
Chisman Creek
Catlett Islands
Sarahs Creek
Stress = 0.2

Figure 5. Sediment composition as **a** mean %sand content, **b** mean %silt content, and **c** mean %clay content in ambient, partially and fully caged samples from the initial Spring sampling through September. Error bars are +/- one standard error of the mean. Spring samples were not analyzed in 3-way ANOVA but are included here to provide context to the subsequent measurements.

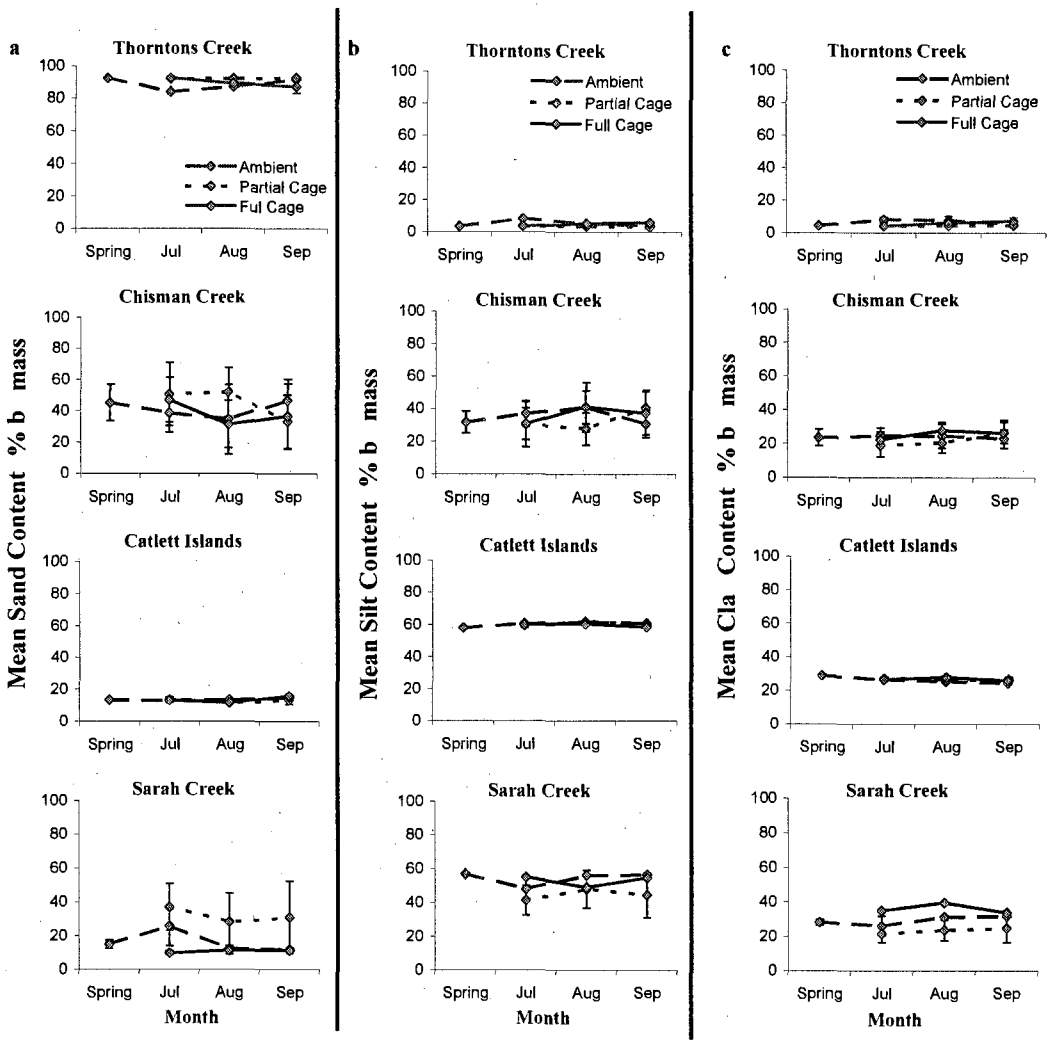

a
b
c
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Ambient
Partial Cage
Ful Cage
Full Cage
Mean Sand Content % b mass
Mean Silt Content % b mass
Mean Cla Content % b mass
Spring
Jul
Aug
Sep
Month
0
20
40
60
80
100

Figure 6. Sediment parameters **a** mean benthic chlorophyll *a*, **b** mean total organic carbon content, and **c** mean total nitrogen content in ambient, partially and fully caged samples from the initial Spring sampling through September. Error bars are +/- one standard error of the mean. Spring samples were not analyzed in 3-way ANOVA but are included here to provide context to the subsequent measurements.

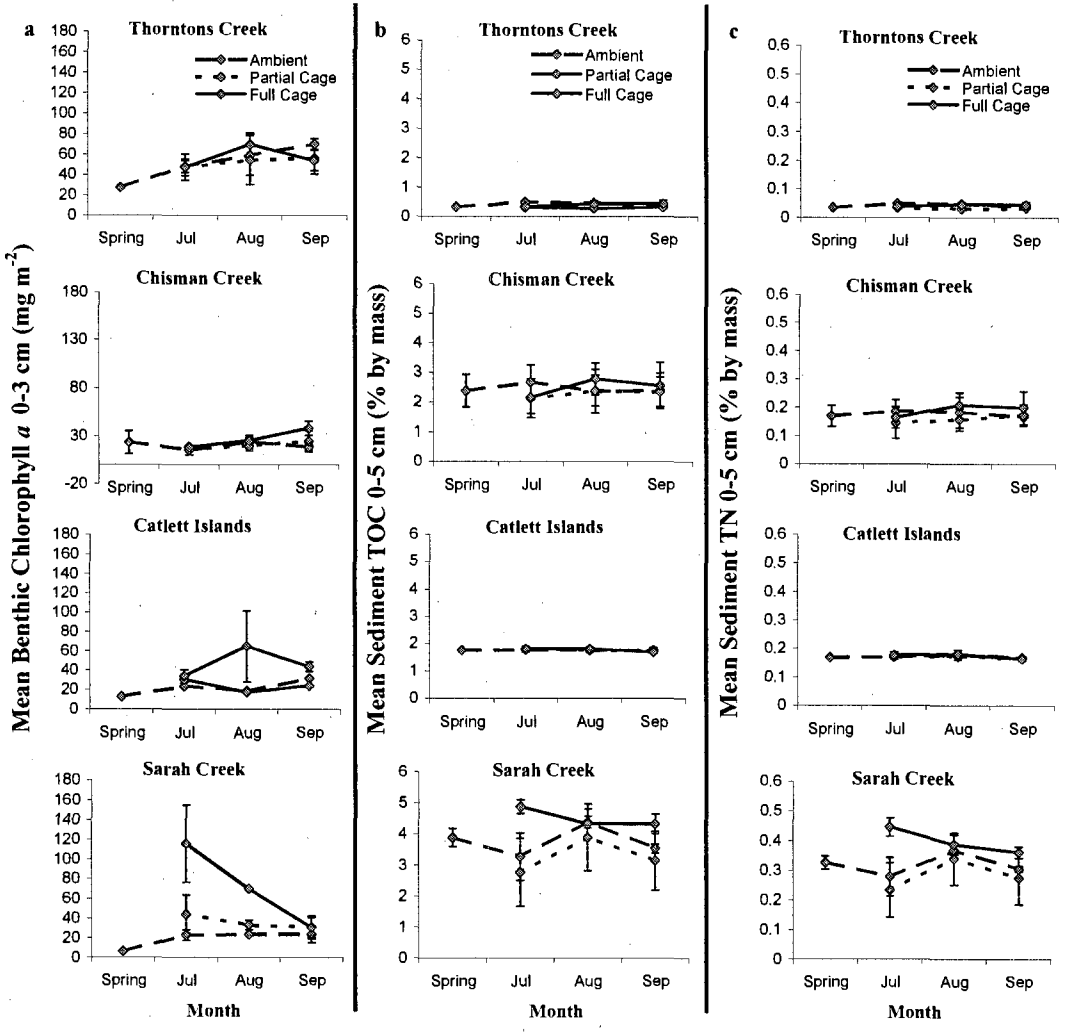

a
b
c
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Ambient
Partial Cage
Full Cage
Mean Benthic Chlorophyll a 0-3 cm (mg m-2)
Mean Sediment TOC 0-5 cm (% by mass)
Mean Sediment TN 0-5 cm (% by mass)
Spring
Jul
Aug
Sep
Month

Figure 7. Macrobenthic community structure as **a** mean Shannon-Weiner species diversity (H'), **b** mean species richness (S), and **c** mean Pielou's Evenness (J') in ambient, partially and fully caged samples from the initial Spring sampling through September. Error bars are +/- one standard error of the mean. Spring samples were not analyzed in 3-way ANOVA but are included here to provide context to the subsequent measurements.

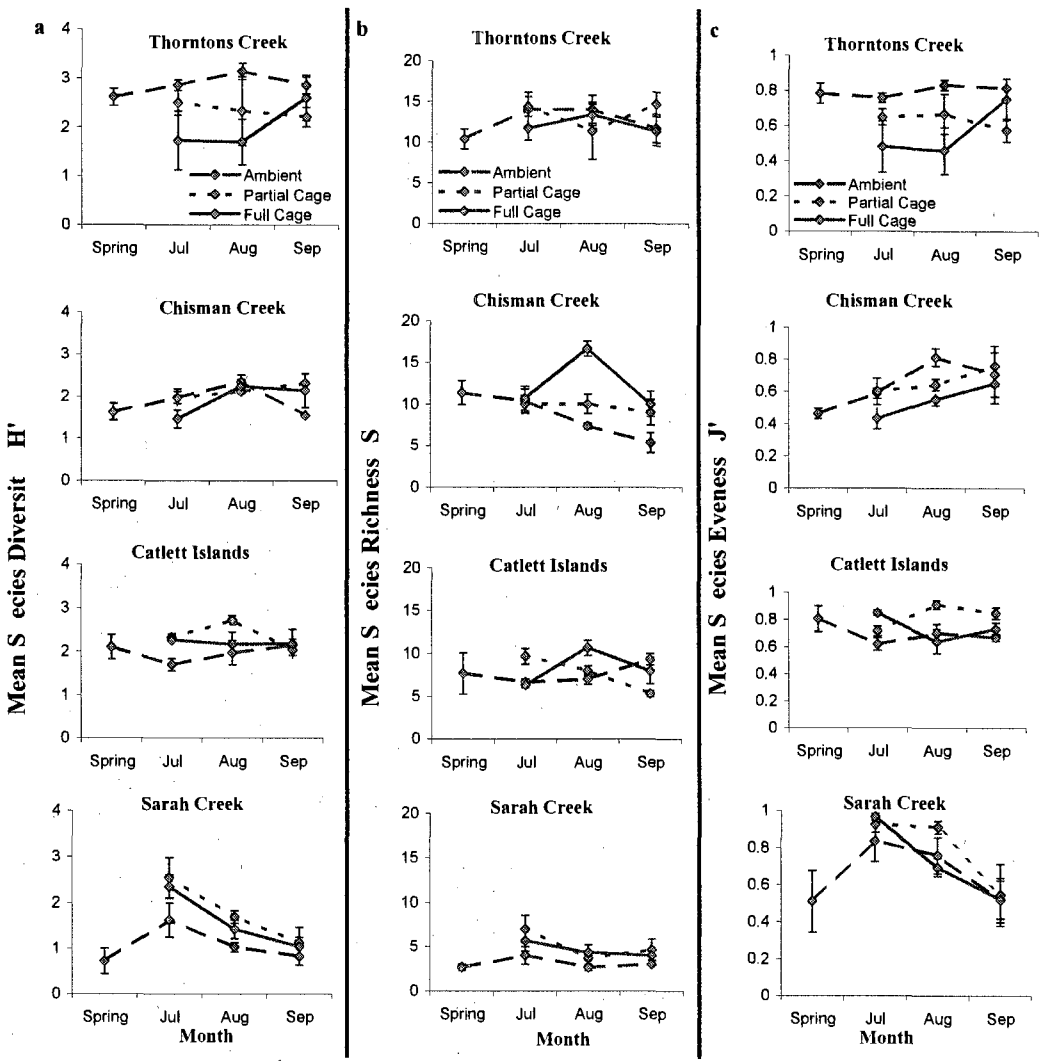

a
b
c
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Ambient
Partial Cage
Full Cage
Spring
Jul
Aug
Sep
Month
Mean S ecies Diversit H'
Mean S ecies Richness S
Mean S ecies Eveness J'

Figure 8. The difference in mean total community 2° production in the fully caged sediments minus that in the ambient sediments at the 4 sites from July through September. Bars above the x-axis indicate greater production in the fully caged sediments and bars below the x-axis indicate greater production in the ambient sediments. An asterisk above a given bar indicates a value significantly different than 0 in the contrast of $\log_{10}$ transformed production between full-cage and ambient samples in the site*cage-type interaction of a 2-way ANOVA (α=0.05). Diamonds represent the mean total community 2° production from the ambient samples, +/- one standard error of the mean.

Macrobenthic Production
(mg AFDM m-2 d-1)
140
120
100
80
60
40
20
0
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
*
*
Greater in Ambient
Greater in Full-Cage

Figure 9. The difference in mean 2°production in the fully caged sediments minus that in the ambient sediments of **a** amphipods, **b** bivalves, **c** nemerteans, **d** oligochaetes, and **e** polychaetes at the 4 sites from July through September. Bars above the x-axis indicate greater production in the fully caged sediments and bars below the x-axis indicate greater production in the ambient sediments. An asterisk above a given bar indicates a value significantly different than 0 in the contrast of $\log_{10}$ transformed production between full-cage and ambient samples in the site*cage-type interaction of a 2-way ANOVA (α=0.05). Diamonds represent the mean 2° production from the ambient samples, +/- one standard error of the mean.

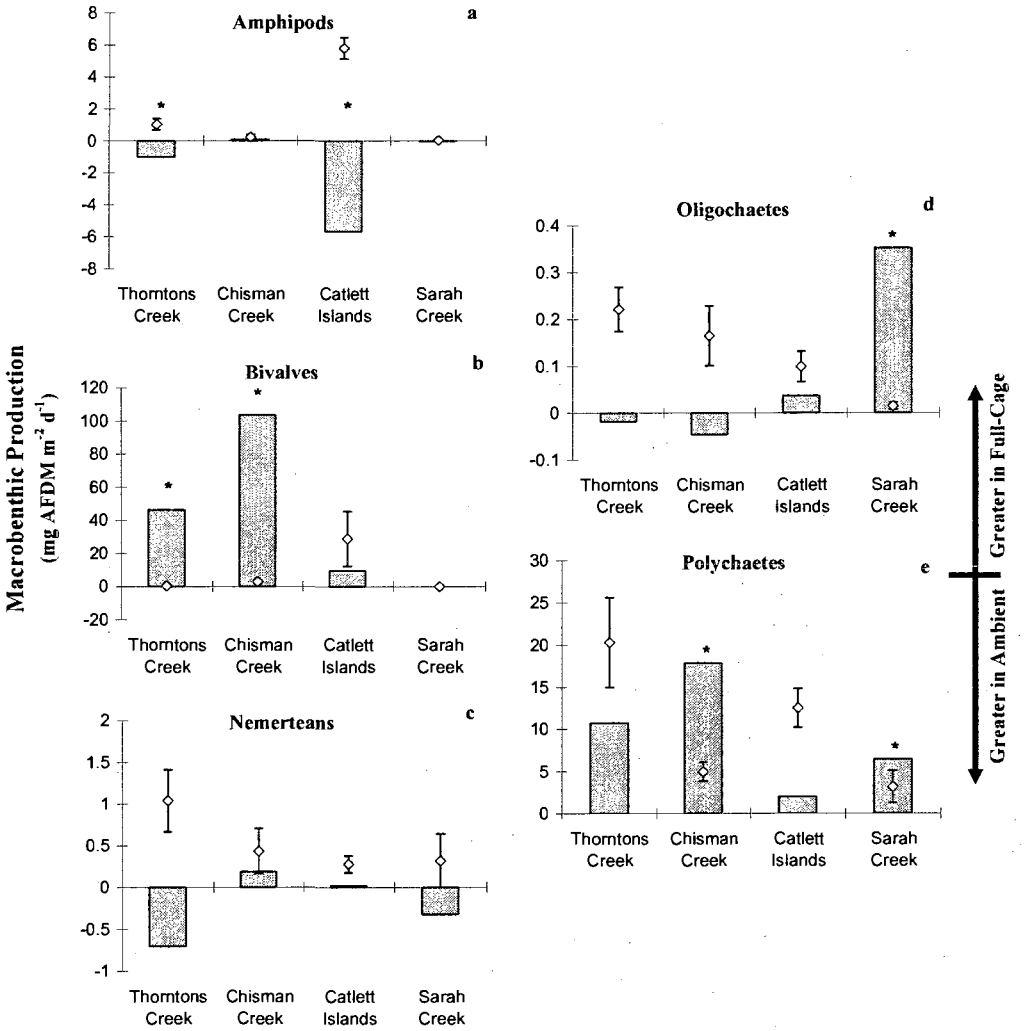

Macrobenthic Production
(mg AFDM m-2 d-1)
Amphipods
a
Bivalves
b
Nemerteans
c
Oligochaetes
d
Polychaetes
e
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Greater in Full-Cage
Greater in Ambient

Figure 10. The difference in mean 2°production in the fully caged sediments minus that in the ambient sediments of **a** *Macoma* spp., **b** *Heteromastus filiformis*, **c** *Leptocheirus plumulosus*, **d** *Neanthes succinea*, and **e** *Streblospio benedicti* at the 4 sites from July through September. Bars above the x-axis indicate greater production in the fully caged sediments and bars below the x-axis indicate greater production in the ambient sediments. An asterisk above a given bar indicates a value significantly different than 0 in the contrast of $\log_{10}$ transformed production between full-cage and ambient samples in the site*cage-type interaction of a 2-way ANOVA (α=0.05). Diamonds represent the mean 2° production from the ambient samples, +/- one standard error of the mean.

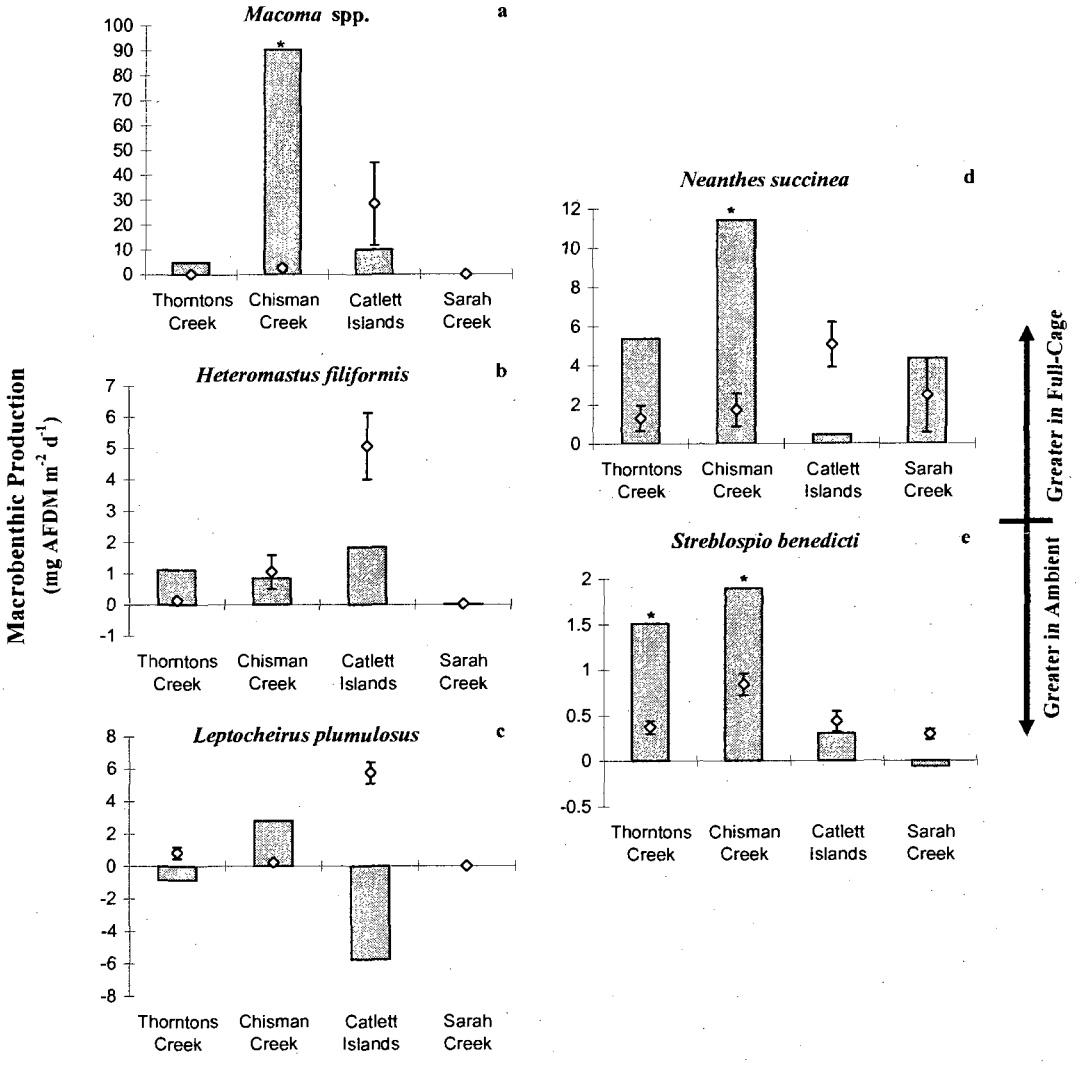

Macoma spp.
a
Heteromastus filiformis
b
Leptocheirus plumulosus
c
Neanthes succinea
d
Streblospio benedicti
e
Macrobenthic Production
(mg AFDM m-2 d-1)
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Greater in Full-Cage
Greater in Ambient

Figure 11. The difference in mean community 2°production in the fully caged sediments minus that in the ambient sediments of **a** fauna in 0-5 cm below the sediment-water interface and **b** fauna below 5 cm at the 4 sites from July through September. Bars above the x-axis indicate greater production in the fully caged sediments and bars below the x-axis indicate greater production in the ambient sediments. An asterisk above a given bar indicates a value significantly different than 0 in the contrast of $\log_{10}$ transformed production between full-cage and ambient samples in the site*cage-type interaction of a 2-way ANOVA (α=0.05). Diamonds represent the mean 2° production from the ambient samples, +/- one standard error of the mean.

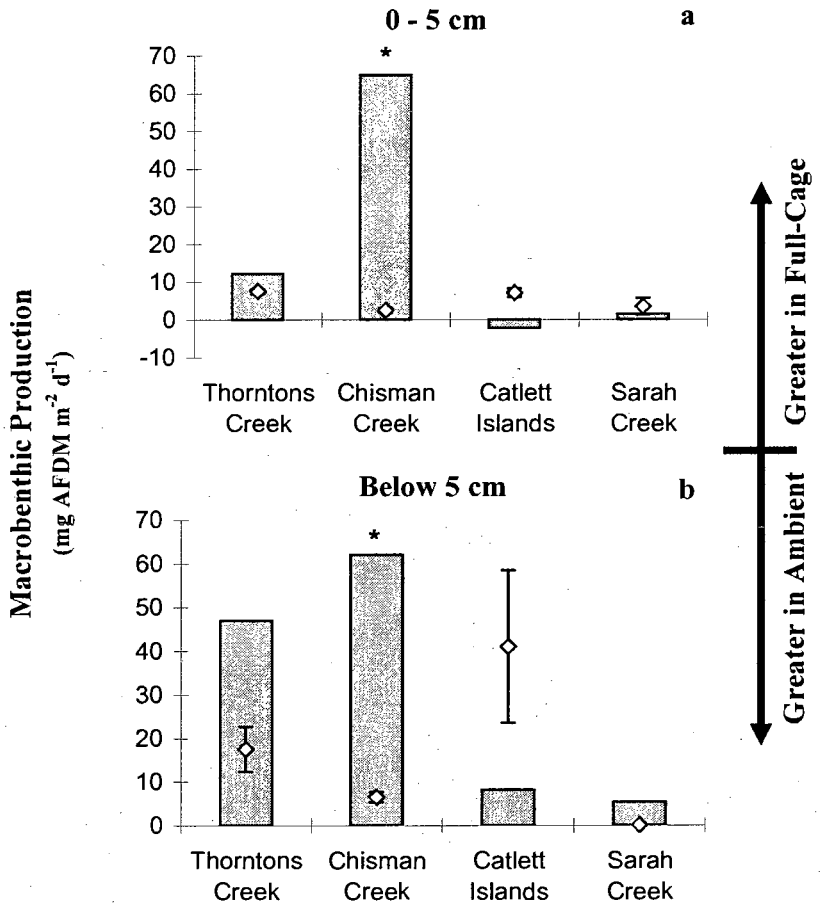
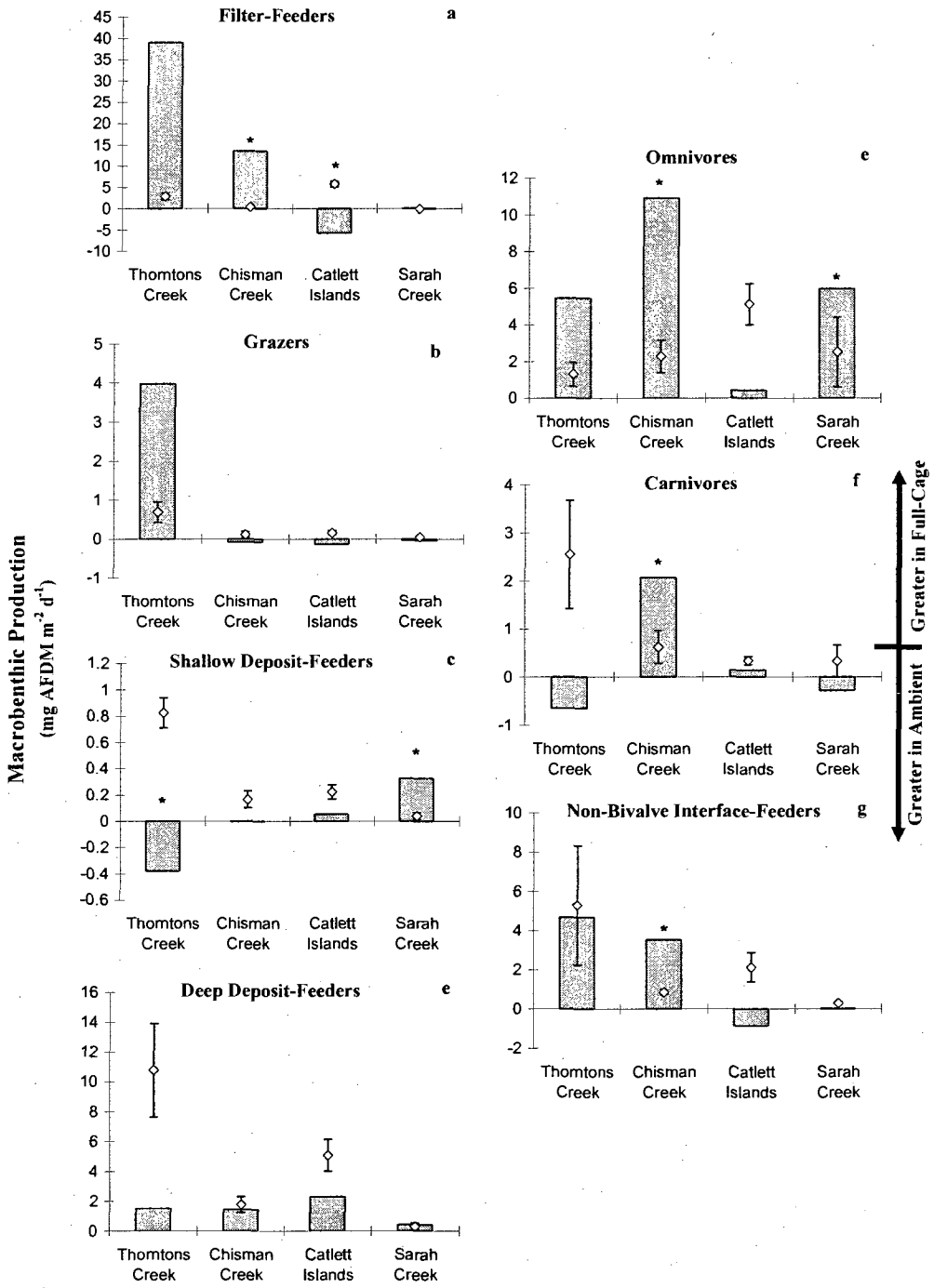

0 - 5 cm
a
70
60
50
40
30
20
10
0
-10
*
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Below 5 cm
b
70
60
50
40
30
20
10
0
*
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Macrobenthic Production
(mg AFDM m-2 d-1)
Greater in Full-Cage
Greater in Ambient

Figure 12. The difference in mean 2°production in the fully caged sediments minus that in the ambient sediments of **a** filter-feeders, **b** grazers, **c** shallow deposit-feeders, **d** deep deposit-feeders, **e** omnivores, **f** carnivores, and **g** non-bivalve interface-feeders at the 4 sites from July through September. As noted in the text, bivalve interface-feeders are equivalent to *Macoma* spp., which are depicted in figure 10a. Bars above the x-axis indicate greater production in the fully caged sediments and bars below the x-axis indicate greater production in the ambient sediments. An asterisk above a given bar indicates a value significantly different than 0 in the contrast of $\log_{10}$ transformed production between full-cage and ambient samples in the site*cage-type interaction of a 2-way ANOVA (α=0.05). Diamonds represent the mean 2° production from the ambient samples, +/- one standard error of the mean.


Macrobenthic Production
(mg AFDM m-2 d-1)
Filter-Feeders
a
Grazers
b
Shallow Deposit-Feeders
c
Deep Deposit-Feeders
e
Omnivores
e
Carnivores
f
Non-Bivalve Interface-Feeders
g
Thorntons Creek
Chisman Creek
Catlett Islands
Sarah Creek
Greater in Full-Cage
Greater in Ambient

Appendix 1. Mean (n=3) secondary production rates of the samples collected at the 4 sample sites in Spring, July, August, and September from ambient, partially caged, and fully caged sediments

Site	Month	Cage Type	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
	Spring	Ambient	11.17	3.9
		Ambient	26.91	6.5
	July	Partial Cage	21.32	5.6
		Full Cage	61.00	21.9
Thorntons		Ambient	33.98	13.1
Creek	August	Partial Cage	21.43	13.9
		Full Cage	163.38	122.0
		Ambient	12.84	5.0
	September	Partial Cage	32.38	5.0
		Full Cage	25.54	15.5
	Spring	Ambient	67.35	41.1
		Ambient	6.78	2.3
	July	Partial Cage	38.40	22.4
		Full Cage	31.71	5.9
Chisman		Ambient	13.66	1.5
Creek	August	Partial Cage	13.00	5.9
		Full Cage	156.82	37.7
		Ambient	6.05	2.0
	September	Partial Cage	45.14	20.3
		Full Cage	202.46	104.9
	Spring	Ambient	19.67	9.9
		Ambient	72.30	48.0
	July	Partial Cage	66.75	42.7
		Full Cage	76.10	62.0
Catlett		Ambient	44.93	24.8
Islands	August	Partial Cage	19.98	4.0
		Full Cage	68.76	24.6
		Ambient	25.50	4.1
	September	Partial Cage	21.26	11.0
		Full Cage	15.69	7.6
	Spring	Ambient	1.52	0.3
		Ambient	3.02	1.8
	July	Partial Cage	4.25	0.9
		Full Cage	8.25	3.3
Sarah		Ambient	0.80	0.3
Creek	August	Partial Cage	4.66	4.3
		Full Cage	10.06	8.2
		Ambient	7.30	6.7
	September	Partial Cage	7.68	6.5
		Full Cage	11.82	4.7

Appendix 2. Mean (n=3) secondary production rates of amphipods, bivalves, nemerteans, oligochaetes, and polychaetes from the samples collected at the 4 sample sites in Spring, July, August, and September from ambient, partially caged, and fully caged sediments

Site	Month	Cage Type	Taxon	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Thorntons Creek	Spring	Ambient	Amphipod	0.45	0.2
			Bivalve	0.28	0.2
			Nemertean	0.44	0.4
			Oligochaete	0.15	0.1
			Polychaete	8.93	4.2
Thorntons Creek	July	Ambient	Amphipod	0.25	0.1
			Bivalve	0.20	0.2
			Nemertean	2.24	0.6
			Oligochaete	0.24	0.1
			Polychaete	22.58	5.7
		Partial Cage	Amphipod	0.13	0.1
			Bivalve	1.50	0.9
			Nemertean	0.61	0.6
			Oligochaete	0.14	0.1
			Polychaete	18.06	6.1
		Full Cage	Amphipod	0.00	0.0
			Bivalve	18.87	14.7
			Nemertean	0.94	0.5
			Oligochaete	0.04	0.0
			Polychaete	32.17	7.6
Thorntons Creek	August	Ambient	Amphipod	0.66	0.4
			Bivalve	0.74	0.7
			Nemertean	0.25	0.3
			Oligochaete	0.30	0.1
			Polychaete	30.70	12.2
		Partial Cage	Amphipod	0.31	0.2
			Bivalve	0.15	0.2
			Nemertean	0.71	0.7
			Oligochaete	0.17	0.1
			Polychaete	16.91	10.1
		Full Cage	Amphipod	0.00	0.0
			Bivalve	118.89	104.7
			Nemertean	0.00	0.0
			Oligochaete	0.32	0.1
			Polychaete	38.41	19.3
Thorntons Creek	September	Ambient	Amphipod	2.17	0.5
			Bivalve	0.44	0.3
			Nemertean	0.62	0.3
			Oligochaete	0.13	0.0
			Polychaete	7.59	4.6
		Partial Cage	Amphipod	0.60	0.2
			Bivalve	0.32	0.2
			Nemertean	0.84	0.5
			Oligochaete	0.07	0.0
			Polychaete	29.52	4.3
		Full Cage	Amphipod	0.00	0.0
			Bivalve	2.41	1.4
			Nemertean	0.07	0.1
			Oligochaete	0.25	0.1
			Polychaete	22.50	15.4

Site	Month	Cage Type	Taxon	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Chisman Creek	Spring	Ambient	Amphipod	15.20	1.7
			Bivalve	44.59	39.8
			Nemertean	0.00	0.0
			Oligochaete	0.08	0.0
			Polychaete	7.20	2.4
Chisman Creek	July	Ambient	Amphipod	0.20	0.2
			Bivalve	0.19	0.2
			Nemertean	0.59	0.6
			Oligochaete	0.34	0.1
			Polychaete	4.95	2.1
		Partial Cage	Amphipod	0.56	0.3
			Bivalve	31.06	23.8
			Nemertean	0.00	0.0
			Oligochaete	0.20	0.1
			Polychaete	4.89	0.4
		Full Cage	Amphipod	0.64	0.6
			Bivalve	19.76	5.3
			Nemertean	0.34	0.3
			Oligochaete	0.12	0.0
			Polychaete	10.66	4.2
Chisman Creek	August	Ambient	Amphipod	0.49	0.5
			Bivalve	7.13	1.5
			Nemertean	0.07	0.1
			Oligochaete	0.15	0.1
			Polychaete	5.51	2.6
		Partial Cage	Amphipod	0.00	0.0
			Bivalve	1.59	0.8
			Nemertean	0.00	0.0
			Oligochaete	0.08	0.0
			Polychaete	11.05	6.5
		Full Cage	Amphipod	0.15	0.1
			Bivalve	127.03	35.9
			Nemertean	1.54	1.2
			Oligochaete	0.16	0.1
			Polychaete	27.69	4.1
Chisman Creek	September	Ambient	Amphipod	0.00	0.0
			Bivalve	0.78	0.6
			Nemertean	0.66	0.7
			Oligochaete	0.00	0.0
			Polychaete	4.46	2.0
		Partial Cage	Amphipod	0.11	0.1
			Bivalve	36.47	19.2
			Nemertean	0.52	0.3
			Oligochaete	0.04	0.0
			Polychaete	7.88	1.9
		Full Cage	Amphipod	0.15	0.1
			Bivalve	172.20	86.9
			Nemertean	0.00	0.0
			Oligochaete	0.08	0.0
			Polychaete	30.03	17.8

Site	Month	Cage Type	Taxon	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Catlett Islands	Spring	Ambient	Amphipod	3.85	2.2
			Bivalve	2.31	2.3
			Nemertean	0.96	1.0
			Oligochaete	0.08	0.0
			Polychaete	11.32	6.1
Catlett Islands	July	Ambient	Amphipod	5.71	1.0
			Bivalve	50.36	49.1
			Nemertean	0.19	0.2
			Oligochaete	0.04	0.0
			Polychaete	15.89	2.8
		Partial Cage	Amphipod	5.01	1.7
			Bivalve	52.23	45.2
			Nemertean	0.91	0.5
			Oligochaete	0.11	0.0
			Polychaete	8.00	1.9
		Full Cage	Amphipod	0.28	0.0
			Bivalve	63.82	57.9
			Nemertean	0.00	0.0
			Oligochaete	0.16	0.1
			Polychaete	11.84	4.2
Catlett Islands	August	Ambient	Amphipod	4.01	0.5
			Bivalve	29.11	19.6
			Nemertean	0.40	0.2
			Oligochaete	0.09	0.1
			Polychaete	11.22	5.6
		Partial Cage	Amphipod	0.20	0.2
			Bivalve	4.97	4.3
			Nemertean	0.07	0.1
			Oligochaete	0.15	0.0
			Polychaete	14.18	6.4
		Full Cage	Amphipod	0.00	0.0
			Bivalve	44.39	17.0
			Nemertean	0.35	0.3
			Oligochaete	0.09	0.0
			Polychaete	23.67	10.1
Catlett Islands	September	Ambient	Amphipod	7.65	0.8
			Bivalve	6.67	3.9
			Nemertean	0.25	0.2
			Oligochaete	0.16	0.1
			Polychaete	10.47	3.9
		Partial Cage	Amphipod	0.02	0.0
			Bivalve	11.63	11.3
			Nemertean	0.40	0.3
			Oligochaete	0.01	0.0
			Polychaete	9.19	3.1
		Full Cage	Amphipod	0.00	0.0
			Bivalve	6.97	7.0
			Nemertean	0.55	0.5
			Oligochaete	0.16	0.1
			Polychaete	8.02	4.0

Site	Month	Cage Type	Taxon	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Sarah Creek	Spring	Ambient	Amphipod	0.14	0.1
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.00	0.0
			Polychaete	1.15	0.3
Sarah Creek	July	Ambient	Amphipod	0.08	0.1
			Bivalve	0.04	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.02	0.0
			Polychaete	2.57	1.6
		Partial Cage	Amphipod	0.00	0.0
			Bivalve	0.06	0.0
			Nemertean	0.06	0.1
			Oligochaete	0.01	0.0
			Polychaete	3.55	0.6
		Full Cage	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.12	0.1
			Polychaete	8.01	3.3
Sarah Creek	August	Ambient	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.01	0.0
			Polychaete	0.68	0.3
		Partial Cage	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.16	0.1
			Polychaete	4.40	4.3
		Full Cage	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.06	0.0
			Polychaete	9.92	8.2
Sarah Creek	September	Ambient	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.97	1.0
			Oligochaete	0.01	0.0
			Polychaete	6.21	5.8
		Partial Cage	Amphipod	0.00	0.0
			Bivalve	0.66	0.7
			Nemertean	0.16	0.2
			Oligochaete	0.40	0.4
			Polychaete	6.17	5.5
		Full Cage	Amphipod	0.00	0.0
			Bivalve	0.00	0.0
			Nemertean	0.00	0.0
			Oligochaete	0.92	0.6
			Polychaete	10.90	5.3

Appendix 3. Mean (n=3) secondary production rates of selected species from the samples collected at the 4 sample sites in Spring, July, August, and September from ambient, partially caged, and fully caged sediments

Site	Month	Cage Type	Scientific Name	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Thorntons Creek	Spring	Ambient	*Heteromastus filiformis*	3.27	3.0
			Leptocheirus plumulosus	0.38	0.2
			Macoma spp.	0.20	0.2
			Neanthes succinea	0.00	0.0
			Streblospio benedicti	0.63	0.3
Thorntons Creek	July	Ambient	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.05	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	2.91	1.7
			Streblospio benedicti	0.50	0.2
		Partial Cage	*Heteromastus filiformis*	0.82	0.8
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.42	0.2
			Neanthes succinea	0.07	0.1
			Streblospio benedicti	0.90	0.2
		Full Cage	*Heteromastus filiformis*	0.66	0.2
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	3.02	2.7
			Neanthes succinea	0.20	0.1
			Streblospio benedicti	2.01	1.1
Thorntons Creek	August	Ambient	*Heteromastus filiformis*	0.20	0.1
			Leptocheirus plumulosus	0.45	0.4
			Macoma spp.	0.73	0.7
			Neanthes succinea	0.43	0.2
			Streblospio benedicti	0.26	0.1
		Partial Cage	*Heteromastus filiformis*	0.59	0.6
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	0.00	0.0
			Streblospio benedicti	0.78	0.5
		Full Cage	*Heteromastus filiformis*	1.74	1.1
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	10.89	8.7
			Neanthes succinea	17.50	15.2
			Streblospio benedicti	3.02	1.0
Thorntons Creek	September	Ambient	*Heteromastus filiformis*	0.25	0.2
			Leptocheirus plumulosus	2.13	0.5
			Macoma spp.	0.12	0.1
			Neanthes succinea	0.65	0.6
			Streblospio benedicti	0.37	0.1
		Partial Cage	*Heteromastus filiformis*	1.20	1.2
			Leptocheirus plumulosus	0.17	0.1
			Macoma spp.	0.01	0.0
			Neanthes succinea	0.08	0.1
			Streblospio benedicti	1.27	0.2
		Full Cage	*Heteromastus filiformis*	1.47	1.3
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	1.94	1.5
			Neanthes succinea	2.72	1.4
			Streblospio benedicti	0.73	0.6

Site	Month	Cage Type	Scientific Name	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Chisman Creek	Spring	Ambient	*Heteromastus filiformis*	1.44	1.2
			Leptocheirus plumulosus	15.57	1.8
			Macoma spp.	44.49	39.8
			Neanthes succinea	0.98	1.0
			Streblospio benedicti	2.10	0.2
Chisman Creek	July	Ambient	*Heteromastus filiformis*	0.52	0.2
			Leptocheirus plumulosus	0.20	0.2
			Macoma spp.	0.19	0.2
			Neanthes succinea	1.47	1.5
			Streblospio benedicti	1.06	0.1
		Partial Cage	*Heteromastus filiformis*	1.81	0.8
			Leptocheirus plumulosus	0.58	0.3
			Macoma spp.	31.00	23.8
			Neanthes succinea	0.00	0.0
			Streblospio benedicti	1.11	0.4
		Full Cage	*Heteromastus filiformis*	1.44	1.1
			Leptocheirus plumulosus	0.65	0.7
			Macoma spp.	19.69	5.4
			Neanthes succinea	4.08	2.2
			Streblospio benedicti	2.38	0.5
Chisman Creek	August	Ambient	*Heteromastus filiformis*	2.61	1.3
			Leptocheirus plumulosus	0.50	0.5
			Macoma spp.	7.07	1.5
			Neanthes succinea	1.89	1.8
			Streblospio benedicti	0.86	0.2
		Partial Cage	*Heteromastus filiformis*	1.43	0.8
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	1.38	0.9
			Neanthes succinea	6.22	6.1
			Streblospio benedicti	1.63	0.7
		Full Cage	*Heteromastus filiformis*	2.07	2.0
			Leptocheirus plumulosus	0.09	0.1
			Macoma spp.	111.88	31.8
			Neanthes succinea	12.86	2.3
			Streblospio benedicti	5.53	1.3
Chisman Creek	September	Ambient	*Heteromastus filiformis*	0.07	0.1
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.65	0.6
			Neanthes succinea	1.89	1.9
			Streblospio benedicti	0.65	0.3
		Partial Cage	*Heteromastus filiformis*	1.75	1.3
			Leptocheirus plumulosus	0.05	0.0
			Macoma spp.	36.40	19.2
			Neanthes succinea	3.82	3.2
			Streblospio benedicti	0.46	0.4
		Full Cage	*Heteromastus filiformis*	2.22	1.5
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	110.18	66.1
			Neanthes succinea	23.12	15.6
			Streblospio benedicti	0.43	0.3

Site	Month	Cage Type	Scientific Name	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Catlett Islands	Spring	Ambient	*Heteromastus filiformis*	8.38	4.8
			Leptocheirus plumulosus	3.92	2.3
			Macoma spp.	2.31	2.3
			Neanthes succinea	0.82	0.8
			Streblospio benedicti	0.40	0.3
Catlett Islands	July	Ambient	*Heteromastus filiformis*	5.27	1.1
			Leptocheirus plumulosus	5.82	1.0
			Macoma spp.	50.36	49.1
			Neanthes succinea	7.35	0.6
			Streblospio benedicti	0.34	0.1
		Partial Cage	*Heteromastus filiformis*	2.15	1.3
			Leptocheirus plumulosus	5.12	1.7
			Macoma spp.	52.23	45.2
			Neanthes succinea	4.56	2.3
			Streblospio benedicti	0.37	0.1
		Full Cage	*Heteromastus filiformis*	6.48	3.4
			Leptocheirus plumulosus	0.10	0.1
			Macoma spp.	63.82	57.9
			Neanthes succinea	5.01	2.2
			Streblospio benedicti	0.18	0.0
Catlett Islands	August	Ambient	*Heteromastus filiformis*	5.98	3.1
			Leptocheirus plumulosus	4.09	0.5
			Macoma spp.	29.11	19.6
			Neanthes succinea	4.33	2.9
			Streblospio benedicti	0.15	0.0
		Partial Cage	*Heteromastus filiformis*	7.01	4.5
			Leptocheirus plumulosus	0.20	0.2
			Macoma spp.	4.97	4.3
			Neanthes succinea	6.53	3.3
			Streblospio benedicti	0.18	0.0
		Full Cage	*Heteromastus filiformis*	9.42	3.3
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	44.39	17.0
			Neanthes succinea	10.98	5.7
			Streblospio benedicti	1.57	0.7
Catlett Islands	September	Ambient	*Heteromastus filiformis*	4.20	1.6
			Leptocheirus plumulosus	7.81	0.8
			Macoma spp.	6.67	3.9
			Neanthes succinea	3.76	1.9
			Streblospio benedicti	0.84	0.1
		Partial Cage	*Heteromastus filiformis*	3.23	0.5
			Leptocheirus plumulosus	0.03	0.0
			Macoma spp.	11.63	11.3
			Neanthes succinea	4.26	3.4
			Streblospio benedicti	0.21	0.1
		Full Cage	*Heteromastus filiformis*	5.11	3.6
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	6.97	7.0
			Neanthes succinea	0.83	0.1
			Streblospio benedicti	0.49	0.2

Site	Month	Cage Type	Scientific Name	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Sarah Creek	May	Ambient	*Heteromastus filiformis*	0.08	0.1
			Leptocheirus plumulosus	0.07	0.1
			Macoma spp.	0.00	0.0
			Neanthes succinea	0.00	0.0
			Streblospio benedicti	1.10	0.3
Sarah Creek	July	Ambient	*Heteromastus filiformis*	0.05	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.04	0.0
			Neanthes succinea	1.73	1.1
			Streblospio benedicti	0.17	0.1
		Partial Cage	*Heteromastus filiformis*	0.07	0.1
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	2.40	1.2
			Streblospio benedicti	0.15	0.1
		Full Cage	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	5.92	3.7
			Streblospio benedicti	0.00	0.0
Sarah Creek	August	Ambient	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	0.00	0.0
			Streblospio benedicti	0.34	0.1
		Partial Cage	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	4.41	4.4
			Streblospio benedicti	0.14	0.0
		Full Cage	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	9.85	8.4
			Streblospio benedicti	0.38	0.1
Sarah Creek	September	Ambient	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	5.99	6.0
			Streblospio benedicti	0.41	0.0
		Partial Cage	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.66	0.7
			Neanthes succinea	5.65	5.7
			Streblospio benedicti	0.49	0.2
		Full Cage	*Heteromastus filiformis*	0.00	0.0
			Leptocheirus plumulosus	0.00	0.0
			Macoma spp.	0.00	0.0
			Neanthes succinea	5.52	5.5
			Streblospio benedicti	0.33	0.2

Appendix 4. Mean (n=3) secondary production rates of the different macrobenthic feeding guilds from the samples collected at the 4 sample sites in Spring, July, August, and September from ambient, partially caged, and fully caged sediments

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Thorntons Creek	Spring	Ambient	Bivalve Interface-Feeders	0.20	0.2
			Carnivores	1.18	0.7
			Deep Deposit-Feeders	5.56	4.1
			Filter-Feeders	2.30	1.5
			Grazers	0.03	0.0
			Non-Bivalve Interface-Feeders	0.78	0.4
			Omnivores	0.30	0.2
			Shallow Deposit-Feeders	0.81	0.3
Thorntons Creek	July	Ambient	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	5.48	2.8
			Deep Deposit-Feeders	13.06	4.0
			Filter-Feeders	1.72	0.9
			Grazers	0.45	0.2
			Non-Bivalve Interface-Feeders	2.56	1.9
			Omnivores	2.85	1.7
			Shallow Deposit-Feeders	0.79	0.1
		Partial Cage	Bivalve Interface-Feeders	0.42	0.2
			Carnivores	1.04	0.4
			Deep Deposit-Feeders	13.64	7.1
			Filter-Feeders	1.54	0.9
			Grazers	0.31	0.0
			Non-Bivalve Interface-Feeders	2.95	1.0
			Omnivores	0.55	0.4
			Shallow Deposit-Feeders	0.80	0.2
		Full Cage	Bivalve Interface-Feeders	3.02	2.7
			Carnivores	1.05	0.5
			Deep Deposit-Feeders	16.17	6.1
			Filter-Feeders	16.72	16.1
			Grazers	8.31	8.2
			Non-Bivalve Interface-Feeders	14.90	12.7
			Omnivores	0.19	0.1
			Shallow Deposit-Feeders	0.50	0.3
Thorntons Creek	August	Ambient	Bivalve Interface-Feeders	0.73	0.7
			Carnivores	0.66	0.4
			Deep Deposit-Feeders	14.63	7.4
			Filter-Feeders	2.31	0.4
			Grazers	1.23	0.7
			Non-Bivalve Interface-Feeders	12.92	7.9
			Omnivores	0.42	0.2
			Shallow Deposit-Feeders	1.09	0.1
		Partial Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	1.94	0.7
			Deep Deposit-Feeders	13.31	10.3
			Filter-Feeders	4.04	2.4
			Grazers	0.49	0.3
			Non-Bivalve Interface-Feeders	1.02	0.4
			Omnivores	0.00	0.0
			Shallow Deposit-Feeders	0.60	0.2
		Full Cage	Bivalve Interface-Feeders	10.89	8.7
			Carnivores	4.55	4.3
			Deep Deposit-Feeders	12.82	5.8
			Filter-Feeders	108.54	107.8
			Grazers	5.43	5.3
			Non-Bivalve Interface-Feeders	3.16	1.0
			Omnivores	17.29	15.1
			Shallow Deposit-Feeders	0.52	0.2

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Thorntons Creek	September	Ambient	Bivalve Interface-Feeders	0.12	0.1
			Carnivores	1.51	0.8
			Deep Deposit-Feeders	4.65	4.3
			Filter-Feeders	4.58	1.8
			Grazers	0.38	0.2
			Non-Bivalve Interface-Feeders	0.36	0.1
			Omnivores	0.64	0.6
			Shallow Deposit-Feeders	0.59	0.2
		Partial Cage	Bivalve Interface-Feeders	0.01	0.0
			Carnivores	1.51	0.3
			Deep Deposit-Feeders	25.06	3.6
			Filter-Feeders	1.92	1.0
			Grazers	0.49	0.2
			Non-Bivalve Interface-Feeders	2.69	1.3
			Omnivores	0.08	0.1
			Shallow Deposit-Feeders	0.48	0.2
		Full Cage	Bivalve Interface-Feeders	1.94	1.5
			Carnivores	0.11	0.1
			Deep Deposit-Feeders	7.86	5.5
			Filter-Feeders	0.54	0.4
			Grazers	0.24	0.1
			Non-Bivalve Interface-Feeders	11.81	10.6
			Omnivores	2.74	1.3
			Shallow Deposit-Feeders	0.31	0.1
Chisman Creek	Spring	Ambient	Bivalve Interface-Feeders	44.49	39.8
			Carnivores	0.97	0.6
			Deep Deposit-Feeders	3.10	1.1
			Filter-Feeders	15.53	1.7
			Grazers	0.06	0.0
			Non-Bivalve Interface-Feeders	2.16	0.1
			Omnivores	0.97	1.0
			Shallow Deposit-Feeders	0.08	0.0
Chisman Creek	July	Ambient	Bivalve Interface-Feeders	0.19	0.2
			Carnivores	0.94	0.9
			Deep Deposit-Feeders	2.09	0.8
			Filter-Feeders	0.45	0.2
			Grazers	0.02	0.0
			Non-Bivalve Interface-Feeders	1.06	0.0
			Omnivores	1.60	1.6
			Shallow Deposit-Feeders	0.34	0.1
		Partial Cage	Bivalve Interface-Feeders	31.00	23.8
			Carnivores	0.42	0.2
			Deep Deposit-Feeders	3.21	0.1
			Filter-Feeders	0.79	0.3
			Grazers	0.08	0.1
			Non-Bivalve Interface-Feeders	1.09	0.4
			Omnivores	1.61	1.5
			Shallow Deposit-Feeders	0.20	0.1
		Full Cage	Bivalve Interface-Feeders	19.69	5.4
			Carnivores	0.50	0.4
			Deep Deposit-Feeders	4.06	1.9
			Filter-Feeders	0.87	0.7
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	2.42	0.4
			Omnivores	4.01	2.2
			Shallow Deposit-Feeders	0.12	0.0

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Chisman Creek	August	Ambient	Bivalve Interface-Feeders	7.07	1.5
			Carnivores	0.17	0.1
			Deep Deposit-Feeders	2.63	1.2
			Filter-Feeders	0.55	0.5
			Grazers	0.31	0.2
			Non-Bivalve Interface-Feeders	0.85	0.2
			Omnivores	1.93	1.7
			Shallow Deposit-Feeders	0.15	0.1
		Partial Cage	Bivalve Interface-Feeders	1.38	0.9
			Carnivores	0.21	0.0
			Deep Deposit-Feeders	3.11	1.8
			Filter-Feeders	0.22	0.1
			Grazers	0.29	0.0
			Non-Bivalve Interface-Feeders	1.60	0.6
			Omnivores	6.12	6.0
			Shallow Deposit-Feeders	0.08	0.0
		Full Cage	Bivalve Interface-Feeders	111.88	31.8
			Carnivores	5.52	0.5
			Deep Deposit-Feeders	3.35	1.8
			Filter-Feeders	15.39	7.9
			Grazers	0.02	0.0
			Non-Bivalve Interface-Feeders	7.65	2.1
			Omnivores	12.80	2.3
			Shallow Deposit-Feeders	0.22	0.0
Chisman Creek	September	Ambient	Bivalve Interface-Feeders	0.65	0.6
			Carnivores	0.75	0.7
			Deep Deposit-Feeders	0.58	0.4
			Filter-Feeders	0.13	0.1
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.64	0.3
			Omnivores	3.30	1.7
			Shallow Deposit-Feeders	0.00	0.0
		Partial Cage	Bivalve Interface-Feeders	36.40	19.2
			Carnivores	0.86	0.5
			Deep Deposit-Feeders	3.30	1.7
			Filter-Feeders	0.11	0.1
			Grazers	0.13	0.1
			Non-Bivalve Interface-Feeders	0.48	0.3
			Omnivores	3.76	3.1
			Shallow Deposit-Feeders	0.10	0.1
		Full Cage	Bivalve Interface-Feeders	110.18	66.1
			Carnivores	1.55	1.1
			Deep Deposit-Feeders	1.64	1.3
			Filter-Feeders	18.97	21.6
			Grazers	0.06	0.1
			Non-Bivalve Interface-Feeders	2.28	1.4
			Omnivores	17.06	14.1
			Shallow Deposit-Feeders	0.11	0.1
Catlett Islands	Spring	Ambient	Bivalve Interface-Feeders	2.31	2.3
			Carnivores	0.99	1.0
			Deep Deposit-Feeders	8.27	4.8
			Filter-Feeders	3.85	2.2
			Grazers	1.16	0.9
			Non-Bivalve Interface-Feeders	2.19	1.2
			Omnivores	0.81	0.8
			Shallow Deposit-Feeders	0.10	0.0

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Catlett Islands	July	Ambient	Bivalve Interface-Feeders	50.36	49.1
			Carnivores	0.21	0.2
			Deep Deposit-Feeders	5.20	1.1
			Filter-Feeders	5.71	1.0
			Grazers	0.11	0.1
			Non-Bivalve Interface-Feeders	3.42	2.0
			Omnivores	7.25	0.6
			Shallow Deposit-Feeders	0.04	0.0
		Partial Cage	Bivalve Interface-Feeders	52.23	45.2
			Carnivores	1.25	0.7
			Deep Deposit-Feeders	2.12	1.3
			Filter-Feeders	5.01	1.7
			Grazers	0.49	0.2
			Non-Bivalve Interface-Feeders	1.02	0.7
			Omnivores	4.50	2.3
			Shallow Deposit-Feeders	0.14	0.0
		Full Cage	Bivalve Interface-Feeders	63.82	57.9
			Carnivores	0.03	0.0
			Deep Deposit-Feeders	6.39	3.3
			Filter-Feeders	0.10	0.1
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.47	0.3
			Omnivores	4.95	2.2
			Shallow Deposit-Feeders	0.34	0.1
Catlett Islands	August	Ambient	Bivalve Interface-Feeders	29.11	19.6
			Carnivores	0.49	0.2
			Deep Deposit-Feeders	5.90	3.0
			Filter-Feeders	4.01	0.5
			Grazers	0.09	0.1
			Non-Bivalve Interface-Feeders	0.61	0.4
			Omnivores	4.46	2.8
			Shallow Deposit-Feeders	0.27	0.0
		Partial Cage	Bivalve Interface-Feeders	4.97	4.3
			Carnivores	0.08	0.1
			Deep Deposit-Feeders	7.50	4.1
			Filter-Feeders	0.20	0.2
			Grazers	0.09	0.1
			Non-Bivalve Interface-Feeders	0.21	0.0
			Omnivores	6.76	3.4
			Shallow Deposit-Feeders	0.18	0.0
		Full Cage	Bivalve Interface-Feeders	44.39	17.0
			Carnivores	0.64	0.3
			Deep Deposit-Feeders	10.73	4.6
			Filter-Feeders	0.08	0.1
			Grazers	0.09	0.1
			Non-Bivalve Interface-Feeders	1.62	0.7
			Omnivores	10.99	5.6
			Shallow Deposit-Feeders	0.22	0.1

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Catlett Islands	September	Ambient	Bivalve Interface-Feeders	6.67	3.9
			Carnivores	0.33	0.1
			Deep Deposit-Feeders	4.14	1.6
			Filter-Feeders	7.65	0.8
			Grazers	0.29	0.0
			Non-Bivalve Interface-Feeders	2.35	0.6
			Omnivores	3.71	1.9
			Shallow Deposit-Feeders	0.36	0.1
		Partial Cage	Bivalve Interface-Feeders	11.63	11.3
			Carnivores	0.59	0.3
			Deep Deposit-Feeders	3.18	0.5
			Filter-Feeders	0.02	0.0
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.27	0.1
			Omnivores	5.46	2.7
			Shallow Deposit-Feeders	0.10	0.1
		Full Cage	Bivalve Interface-Feeders	6.97	7.0
			Carnivores	0.80	0.6
			Deep Deposit-Feeders	5.04	3.6
			Filter-Feeders	0.07	0.1
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	1.74	0.5
			Omnivores	0.82	0.1
			Shallow Deposit-Feeders	0.27	0.1
Sarah Creek	Spring	Ambient	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.02	0.0
			Deep Deposit-Feeders	0.08	0.1
			Filter-Feeders	0.06	0.1
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	1.06	0.3
			Omnivores	0.15	0.1
			Shallow Deposit-Feeders	0.08	0.1
Sarah Creek	July	Ambient	Bivalve Interface-Feeders	0.04	0.0
			Carnivores	0.01	0.0
			Deep Deposit-Feeders	0.61	0.6
			Filter-Feeders	0.00	0.0
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.16	0.1
			Omnivores	1.79	1.0
			Shallow Deposit-Feeders	0.10	0.1
		Partial Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.16	0.1
			Deep Deposit-Feeders	0.99	0.6
			Filter-Feeders	0.08	0.1
			Grazers	0.08	0.1
			Non-Bivalve Interface-Feeders	0.14	0.1
			Omnivores	2.45	1.3
			Shallow Deposit-Feeders	0.01	0.0
		Full Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.09	0.1
			Deep Deposit-Feeders	2.16	1.2
			Filter-Feeders	0.08	0.1
			Grazers	0.04	0.0
			Non-Bivalve Interface-Feeders	0.06	0.1
			Omnivores	5.70	3.6
			Shallow Deposit-Feeders	0.12	0.1

Site	Month	Cage Type	Feeding Guild	Mean Production (mg AFDM m^{-2} d^{-1})	Standard Error
Sarah Creek	August	Ambient	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.00	0.0
			Deep Deposit-Feeders	0.34	0.3
			Filter-Feeders	0.02	0.0
			Grazers	0.08	0.1
			Non-Bivalve Interface-Feeders	0.34	0.2
			Omnivores	0.00	0.0
			Shallow Deposit-Feeders	0.01	0.0
		Partial Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.00	0.0
			Deep Deposit-Feeders	0.01	0.0
			Filter-Feeders	0.02	0.0
			Grazers	0.08	0.1
			Non-Bivalve Interface-Feeders	0.14	0.0
			Omnivores	4.24	4.2
			Shallow Deposit-Feeders	0.16	0.1
		Full Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.02	0.0
			Deep Deposit-Feeders	0.03	0.0
			Filter-Feeders	0.06	0.0
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.28	0.1
			Omnivores	7.12	7.2
			Shallow Deposit-Feeders	0.04	0.0
Sarah Creek	September	Ambient	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.99	1.0
			Deep Deposit-Feeders	0.00	0.0
			Filter-Feeders	0.00	0.0
			Grazers	0.08	0.0
			Non-Bivalve Interface-Feeders	0.42	0.0
			Omnivores	5.77	5.8
			Shallow Deposit-Feeders	0.01	0.0
		Partial Cage	Bivalve Interface-Feeders	0.66	0.7
			Carnivores	0.28	0.3
			Deep Deposit-Feeders	0.01	0.0
			Filter-Feeders	0.00	0.0
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.53	0.2
			Omnivores	5.80	5.4
			Shallow Deposit-Feeders	0.40	0.4
		Full Cage	Bivalve Interface-Feeders	0.00	0.0
			Carnivores	0.06	0.1
			Deep Deposit-Feeders	0.00	0.0
			Filter-Feeders	0.00	0.0
			Grazers	0.00	0.0
			Non-Bivalve Interface-Feeders	0.55	0.2
			Omnivores	10.29	5.1
			Shallow Deposit-Feeders	0.92	0.6

Chapter IV

Natural Abundance ^{13}C and ^{15}N Isotopes of Shallow, Subtidal Estuarine Macrobenthos and Their Relation to Habitat Quality

For potential submission to Estuaries and Coasts

ABSTRACT

Natural abundance ^{15}N and ^{13}C stable isotopes were used to characterize microphytobenthos, seston, bulk sediment, macrobenthic consumers, and benthivoric nekton during the late Spring and Summer at a series of shallow subtidal sites in Chesapeake Bay, USA that comprised a gradient in eutrophication-driven habitat degradation. Despite the shallow depth and presence of microphytobenthos, results indicate that the majority of the community likely relied upon a mix of organic matter sources processed in part by bacteria. In general, the trophic relationships among macrofaunal feeding guilds were consistent through time and relatively insensitive to habitat degradation. There was some evidence for prey switching by omnivorous macrofauna and benthivoric nekton however, which would affect trophic structure and complexity of the food web. Shallow subtidal benthic food webs are poorly characterized compared to their intertidal counterparts and appear to be less dependent on microphytobenthos than intertidal habitats, despite similar types of component fauna.

INTRODUCTION

Benthic macrofauna are an important component of estuarine food webs. In these complex systems, they serve as a conduit or link between the multitude of primary or bacterial/detrital producers and subsequent trophic levels. This process is interesting to ecologists and insight into the underlying mechanisms is key for effective management of estuarine ecosystems. The organic matter in estuaries comes from autochthonous sources (e.g., microphytobenthos, phytoplankton, salt marsh plants) and allochthonous sources (upland plants, riverine/up stream primary production) that are directly consumed by metazoans or enter the microbially-mediated detrital food web (Seitzinger et al. 2002; Cloern 1996; MacIntyre et al. 1996; Heip et al. 1995; Kennish 1986). Most nekton cannot directly utilize this organic matter or the subsequent bacterial/detrital production and rely on macrobenthos for access to these energy sources. The benthic macrofauna of estuaries and the coastal ocean comprise a wide array of feeding modes. A healthy, non-disturbed benthic community typically consists of fauna that can exploit organic matter from the water column, from detritus, bacteria, microphytobenthos, macroalgae associated with the sediment, as well as other fauna (Gaudênci and Cabral 2007; Diaz and Schaffner 1990; Commito and Ambrose 1985; Fauchald and Jumars 1979). Macrofauna provide a broad base of support for estuarine food webs because they are prey items for numerous species of nekton and birds (Finn et al. 2008; Hines et al. 1990; Virnstein 1979; Chapter 3). Macrobenthos may be more susceptible to environmental perturbations than their predators due to their association with the sediment and their limited mobility (e.g., Peterson et al. 1996; Schwinghamer 1988; Warwick 1988; Bilyard 1987).

Over recent decades benthic ecologists have demonstrated that environmental perturbations lead to relatively predictable changes in macrobenthic community structure (Gray et al. 2002; Weisberg et al. 1997; Rhoads et al. 1978; Pearson and Rosenberg 1978). Water column eutrophication and the accumulation of excess organic matter in the sediment change trophically and taxonomically complex

communities populated with a range of sizes and lifespans to simplified communities dominated by short-lived, opportunistic fauna, typically annelids (e.g., spionid or capitellid polychaetes, oligochaetes) and crustaceans (amphipods) (Diaz et al. 2008; Gaston et al. 1998; Pearson and Rosenberg 1978). These shifts in community structure have multiple consequences for the functioning of the benthos, including reduced community 2° production (Chapter 2) and changes in the suitability of the macrobenthos as prey items to benthivoric nekton (Chapter 3). Additionally, shifts in the trophic structure of a macrobenthic community may result in changes in the types of organic matter that are utilized by the macrobenthos and therefore support subsequent trophic levels.

Given their relatively small sizes and cryptic lifestyles, direct monitoring of the feeding habits of different species of macrofauna is difficult, especially *in situ* (e.g., Clough and Lopez 1993; Sanchez-Mata et al. 1993; Gaston 1987; Fauchald and Jumars 1979). An alternative approach is to measure the ratios of naturally occurring isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in organic matter pools and in macrobenthic consumers. Stable isotopes have been used for the last 20+ years to investigate the trophic relationships between fauna and their food sources (e.g., Post 2002; Peterson 1999; Deegan and Garritt 1997), nutrient inputs/pollution (Bannon and Roman 2008; Tucker et al. 1999; McClelland and Valiela 1998), and a number of other applications, in a variety of aquatic and marine ecosystems. The semi-conservative nature of the isotopic ratio at the molecular level makes it possible to use them as tracers of organic matter through a food web. Natural variation in the ratio of heavy to light C and N in organic matter is created by enzymatic differences in carbon fixation (C3 vs. C4 photosynthesis) (Lajtha and Marshall 1994; Fogel et al. 1992), the isotope ratio of the dissolved inorganic carbon (DIC) pool fixed during photosynthesis (Chanton and Lewis 1999; Michener and Schell 1994; Libes 1992), and nitrogen cycling (Tucker et al. 1999; Wada and Hattori 1991).

Of particular importance to food web studies and understanding consumer/producer relationships, is that the ratio of heavy to light isotopes in organic matter is altered by digestion and excretion processes, referred to as trophic fractionation. The degree of fractionation is different for different elements, but these rates are relatively well understood predictable. For a mix of tissues across a variety of organisms the values that are currently accepted are 3.4‰ (isotopic ratio notation, defined in methods, below) for N and 1.0‰ for C (Fry 2006; Yokoyama et al. 2005; Post 2002; Peterson 1999). There are, however, tissue-

specific and ontogenetic changes in the fractionation rate for both C and N and as such, it is important to use standardized sampling routines that take into account size/age and tissue type, if possible (e.g., Yokoyama et al. 2005; O'Reilly et al. 2002; Hentschel 1998).

Previous studies have used stable isotopes to determine the relative importance of different organic matter pools in supporting estuarine benthic food webs (e.g., Choy et al. 2008; Carmichael et al. 2004; Chanton and Lewis 2002, Deegan and Garritt 1997). Results have generally shown that upland detritus is relatively unimportant, with microphytobenthos or phytoplankton (depending upon whether the fauna are benthic or pelagic feeders) serving as the primary organic matter sources across a variety of study sites. Epiphytic algae associated with seagrasses (Douglass 2008; Melville and Connolly 2005; Kharlamenko et al. 2001) and salt marsh plants (Currin et al. 2003; Deegan and Garritt 1997; Kwak and Zedler 1997) are also relatively important in supporting resident fauna within these habitats.

Despite the limited spatial-scope of these studies, which focus primarily on intertidal habitats or intertidal organic matter pools (e.g., Choy et al. 2008; van Oevelen et al. 2006; Deegan and Garritt 1997; Currin et al. 1995; Couch 1989), the resultant patterns are often generalized over the entire estuary (i.e., subtidal areas) (e.g., Nadon and Himmelman 2006). Furthermore, most previous isotopic studies of subtidal macrobenthic food webs have focused on phytoplankton and bulk sediment as potential food sources, rarely even mentioning microphytobenthos, even though they may be in shallow water (e.g., Nordström et al. 2009; Carmichael et al. 2004; McClelland and Valiela 1998).

In order to address these generalizations and to better characterize the structural components of shallow, subtidal food webs, natural abundance ratios of stable ^{13}C and ^{15}N isotopes were measured in the macrobenthic fauna, their food sources, and their nektonic predators at a series of sites characterized by varying degrees of anthropogenic influence and alteration of habitat quality, due primarily to nutrient-supported eutrophication, in Chesapeake Bay, USA. The primary goal was to provide baseline information on the diet of macrobenthic fauna during a very productive time of year (Spring through late Summer) in shallow subtidal estuarine systems, where the sediment surface is in the photic zone, as these are relatively poorly characterized systems. The secondary goal was to concurrently determine if the changes in macrobenthic community structure (e.g., trophically and functionally simplified communities with decreases in habitat quality) and production (e.g., reduced production with decreases in habitat quality) that

have previously been observed (Chapter 2; Chapter 3) resulted in changes in the utilization of organic matter by the macrobenthos, or the trophic relationships among the component fauna and their nektonic predators. These changes represent a potential breakdown in the functioning of benthic-pelagic food webs in estuaries such that organic matter is respired or buried and therefore, remains in the estuary (e.g., Bishop et al. 2007).

MATERIALS AND METHODS

Study Sites – Sites in the high mesohaline portions of Chesapeake Bay, USA (Fig. 1) were selected to comprise a gradient of habitat quality and eutrophication-related impacts (Schaffner and Gillett, in prep). The five sites that that were sampled, arrayed from best to worst, are: Thorntons Creek, VA; Chisman Creek, VA; Catlett Islands, VA (a National Estuarine Research Reserve System site); Sarah Creek, VA; and Atlantic Woods Creek (a Chesapeake Bay Program Region of Concern [www.chesapeakebay.net]). At each site, a relatively sheltered, depositional habitat, typically in a tidal creek, was chosen for sampling to maximize the effects of upland related anthropogenic stressors while minimizing those of natural physical disturbances like waves or erosion on macrobenthic community structure and organic matter utilization (e.g., Holland et al. 2004; Schaffner et al. 2008). All benthic samples were collected at a constant depth (between 0.5 and 0.75 m below mean-low-water), so as to keep potential light exposure constant and minimize the potential for exposure to hypoxic/anoxic conditions. Water and nekton samples were collected in nearby areas that were not disturbed during the process of collecting benthic samples.

Sample Collection – The trophic relationships between organic matter pools and consumers are not static and are likely to change over relatively short periods of time as environmental conditions (e.g., salinity, temperature, light penetration) change (Nordström et al. 2009; Cloern et al. 2002). To account for this variation sites were sampled 4 times each: Spring (late April-early June), July, August, and September 2006. Macrobenthos were collected by scooping sediments to a depth of approximately 10 cm, which were sieved in ambient water on a 500-μm sieve. Material retained on the sieve was placed on ice until returned to the laboratory where live animals were removed from detrital matter. Animals were placed in filtered seawater for 4-5 hours to allow them to clear their lower digestive tracts, after which they were identified to the lowest possible taxonomic level. For most taxa, individuals had to be pooled to obtain enough material for analysis (~ 1 mg dry mass); when sufficient material was available replicate pooled-samples were created. Nekton were collected only once from Chisman, Sarah, and Thorntons creeks in June or July 2006 using either a 4.3-m diameter, 9.5-mm bar mesh monofilament cast net and baited crab traps (bait was kept segregated from the nekton). Juvenile and year-1 fishes and crabs were targeted, as they are the size classes most likely to consistently use the shallow water habitats (e.g., Ross 2003; Ruiz et al. 1993). Of the

specimens kept for analysis, fishes were typically <8-cm fork length and crabs were <10-cm carapace width. After identification, crabs were placed directly on ice and fish were euthanized with a 250 mg L^{-1} solution of tricaine methanesulfonate (MS222) before being placed on ice. Claw muscle was removed from crabs and skinless, side muscle fillets of the fish were removed for analysis.

Eight samples for microphytobenthos were collected to a depth of 3 mm with a 12-mm i.d. core. Microphytobenthos was isolated from the sediment using the density gradient method (Hamilton et al. 2005; Blanchard et al. 1990). In summary, two cores were pooled (creating 4 replicates) into 50-mL centrifuge tubes with 20 mL of HS-40 Ludox colloidal silica, vortexed for 1 min., and centrifuged 15 min at 4500 rpm. This process left the microphytobenthic cells suspended in the supernatant and the sediment as a pellet in the bottom of the tube. The supernatant was poured through a 63-μm mesh nitex mesh to remove large detrital particles and then vacuum-filtered onto a pre-combusted GF/A filter (1.6 μm pore size), which was subsequently rinsed with distilled water to remove any excess silica or salt. Bulk sediment was collected as 3 replicate 25-mm i.d. cores taken to a depth of 10 cm, which were subsequently divided into 0–2-cm, 2–6-cm, and 6–10-cm sections. Note that no 0–2-cm samples were collected from Chisman and Thorntons creeks in the Spring sampling. The 6–10-cm sections were only analyzed from Thorntons Creek samples, as the organic matter usage of Maldanid polychaetes, which commonly reside deeper than 5 cm in the sediment, was of interest, but they were only found at Thorntons Creek. Three replicate 1-L samples of ambient surface water were collected with acid-washed polycarbonate bottles for seston analysis. Water samples were vacuum filtered on pre-combusted GF/F (0.7 μm pore size) filters until the filter was nearly clogged, typically 200 – 400 mL, and then rinsed with distilled water.

After collection, all samples were kept frozen at -80°C to minimize bacterial decomposition until they were prepared for stable isotopic analysis (Sweeting et al. 2004; Ponsard and Amlou 1999). Upon thawing, macrobenthos and nekton samples were dried at 60°C for at least 48 hours, ground to fine powder, and approximately 1 mg of material was sealed in an aluminum capsule. For some macrobenthic samples additional preparation was needed before drying: after thawing, tissue was removed from the shells of large bivalves, while small bivalves and crustaceans (e.g., amphipods and isopods) were acidified with 10% HCl to remove the inorganic carbon contained in their shells and carapaces, which may not reflect the

isotopic ratio of their diet (e.g., Carabel et al. 2006; Yokoyama et al. 2005). After shell removal or acidification, the material was dried, ground, weighed, and processed as above. Bulk sediment samples were acidified with 10% HCl, freeze dried at -20°C, and between 11 and 60 mg (depending upon the bulk C:N ratio of the sediment) were sealed in aluminum capsules. Filters containing microphytobenthos and seston samples were acidified with 10% HCl, dried at 60°C for at least 48 h, and packed into aluminum capsules.

Isotope ratios of ^{13}C:^{12}C and ^{15}N:^{14}N for each sample were determined at the Stable Isotope Facility, University of California , Davis using a PDZ Europa ANCA-GSL elemental analyzer that combusts the samples and a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) to measure the isotope ratios. Results are presented as deviations from standards expressed as $\delta^{13}C$ and $\delta^{15}N$, which are calculated as

$$\delta X = [(R_{sample} - R_{Standard})/R_{standard}] \times 1000$$

where X = ^{13}C or ^{15}N measured in ‰ and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard for C was Peedee Belemnite (PDB) and atmospheric N_2 (Air) for N. Machine accuracy was 0.3‰ for $\delta^{15}N$ and 0.2‰ for $\delta^{13}C$.

Data Analysis –Inferences about the relationships between the various organic matter pools, the macrobenthic consumers, and benthivoric nekton (when available) for each site and month were made by visual inspection of scatter plots of $\delta^{15}N$ and $\delta^{13}C$ values. Interpretations about utilization of a given organic matter pool by a consumer was made by adjusting consumer values of $\delta^{15}N$ by –3.4‰ and $\delta^{13}C$ by –1.0‰ to account for trophic fractionation of the organic matter consumed (Fry 2006; Post 2002).

Spatial and temporal variability in the $\delta^{15}N$ and $\delta^{13}C$ values of organic matter pools in estuaries is well documented (e.g., Cloern et al. 2002; Deegan and Garritt 1997) and of potential importance to this study is the influence of sewage and septic tank outputs, which can lead to eutrophication-driven habitat degradation and have microbially enriched $\delta^{15}N$ values (Bannon and Roman 2008; Tucker et al. 1999; McClelland and Valiela 1998). As such, differences in the $\delta^{15}N$ and $\delta^{13}C$ ratios of the organic matter pools (0–2, 2–6, and 6–10-cm bulk sediment fractions, microphytobenthos, and seston) among sites and months were assessed using a 2-way analysis of variance (ANOVA) where the $\delta^{15}N$ ratio was the response variable

with site (Thorntons Creek, Chisman Creek, Catlett Islands, Sarah Creek, and Atlantic Woods Creek) and month (Spring, July, August, and September) as the treatment variables. The 2–6-cm fraction of the bulk sediment was only compared among sites, because there was no within-site replication at all of the sites for each sampling event. Similarly, the 6–10-cm fraction was only compared among months, as only Thorntons Creek samples were analyzed. Post-hoc (α=0.05) comparisons of the classes in each treatment were made between unprotected least square means or, when an entire treatment class was missing, contrasts of the site*month interaction term, as there was more concern with minimizing Type II than Type I errors (Milliken and Johnson 2009; Littell et al. 2002; Day and Quinn 1989) given the exploratory nature of this study.

Only a limited number of individual species of macrofauna were consistently collected at each site during the four sampling dates. In order to make site-to-site comparisons of $\delta^{15}N$ and $\delta^{13}C$ values possible, the species were pooled into feeding guilds recognized by most benthic ecologists based upon life history and personal observations (Gaudêncio and Cabral 2007; Weisberg et al. 1997; Gaston 1987; Fauchald and Jumars 1979): filter-feeders, non-bivalve interface-feeders, bivalve interface-feeders, shallow deposit-feeders, deep deposit-feeders, carnivores, omnivores, or benthivoric nekton. The feeding guild approach to classifying organisms provides information on both feeding habits and living position in the sediment, which should influence the utilization of different organic matter pools. See Chapter 2 for a description of each feeding guild and the Appendix for which guild the taxa were assigned.

It was assumed that there would be differences in the isotopic ratios of the carbon and nitrogen pools at each of the sampling sites (e.g., Fry 2006; Cloern et al. 2002; Post 2002) and therefore to truly compare the effects of habitat quality on the trophic relationships and organic matter utilization by the estuarine fauna, the $\delta^{13}C$ and $\delta^{15}N$ ratios of each faunal sample had to be corrected for this variability (e.g., Anderson and Cabana 2007; Post 2002). As such, the $\delta^{13}C$ and $\delta^{15}N$ ratios for each organism were normalized by subtracting the mean $\delta^{13}C$ or $\delta^{15}N$ of the bulk sediment 0–2-cm fraction (when available) for each site and month from the respective values of the fauna. The 2–6-cm fraction ratios had to be used for Chisman and Thorntons creeks in the Spring, as no 0–2-cm sections were collected. These sediment values were used under the assumption that they would represent the best integration of all the different organic matter

sources in the system and provided a reasonable baseline against which the feeding guilds could be compared.

The adjusted $\delta^{13}C$ and $\delta^{15}N$ ratios for each feeding guild were compared using a 2-way ANOVA with the isotopic ratio as the response variable and site and month as the treatment variables. Post-hoc comparisons of the classes in each treatment were made among unprotected least square means (α=0.05). There was not enough material to do month-to-month comparisons of $\delta^{13}C$ and $\delta^{15}N$ ratios of the shallow deposit-feeders or benthivoric nekton, so they were only analyzed in a 1-way ANOVA with site as the treatment variable. These, and all of the 1- and 2-way ANOVA analyses, were done with SAS v9.2.

RESULTS

Spatial and Temporal Comparisons – Based on the 2-way ANOVAs, there were significant spatial (site-to-site) and temporal (month-to-month) differences in the $\delta^{15}N$ and $\delta^{13}C$ ratios within all of the organic matter pools, with the exception of the 6-10-cm fraction of the bulk sediment (Table 1). The significant spatial differences within the organic pools was not related to the degradation gradient, but the organic matter from Catlett Islands was consistently more enriched in ^{15}N and ^{13}C compared to the other sites (Table 1a). There were fewer temporal differences within the organic matter pools; only the 0–2-cm bulk sediment and microphytobenthos had significantly different isotopic values among the four months. The most ^{15}N-enriched values of both the microphytobenthos and bulk sediments were consistently measured in the September samples. This may be indicative of a greater dependence on recycled N and the importance of coupled nitrification-denitrification at the end of the of bacterial and 1° production summer growing season (e.g., Epstein 1997; Sander and Kalff 1993). However, the 0-2-cm bulk sediment from Spring – when there should be deposition of fresh 1° production relatively deplete in ^{15}N – and September – when there is no deposition – were similar and more enriched than July and August. Seston was the only organic matter pool that showed significant temporal differences in $\delta^{13}C$ values, with August samples being the most enriched. There was a significant interaction between site and month terms in the ANOVA model for the $\delta^{15}N$ ratios of 0–2-cm fraction of bulk sediment, the microphytobenthos, and the $\delta^{13}C$ ratios of the seston because the month-to-month differences within some sites followed a different patterns than at others (Table 1b).

Given the site and month differences among the organic mater pools, adjustments of the $\delta^{13}C$ and $\delta^{15}N$ ratios of the macrobenthic feeding guilds for the changes in the baseline $\delta^{13}C$ and $\delta^{15}N$ for each site and month were appropriate. Consequently, any differences observed in the analyses result from feeding by the fauna, not the isotopic differences in the organic matter at each site through the sampling period. Among the different feeding guilds, the $\delta^{13}C$ values of deep deposit-feeding macrofauna were the only isotopic values that showed significant response by month, though there was no clear separation of any of

the four months from each other. In contrast, there were significant site-to-site differences in both $\delta^{15}N$ and $\delta^{13}C$ across the different feeding guilds (Table 2).

The post-hoc analyses of the ANOVAs illustrate that the site-to-site differences in $\delta^{13}C$ and $\delta^{15}N$ values were not related to the habitat quality gradient (Table 2). Furthermore, there was little consistency in the site-to-site patterns within each of the feeding guilds, though some feeding guilds had clear differences or similarities in isotopic values among sites. As an example, filter-feeders had similar $\delta^{15}N$ values at the three sites where they were collected (Chisman Creek, Catlett Islands, and Thorntons Creek). The $\delta^{13}C$ values were similar between Catlett Islands and Chisman Creek, both of which were more enriched than those from Thorntons Creek, suggesting that they were feeding at similar trophic levels, probably seston and the phytoplankton component, detailed below, but of different origin. In contrast, there were distinct differences in the $\delta^{15}N$ and $\delta^{13}C$ values of the omnivorous and carnivorous (only $\delta^{13}C$) macrofauna among all of the sites, indicating they may have been feeding at different trophic levels (i.e. grazing vs. predation among omnivores) and selecting different types of prey items among the different sites. The only consistent trend among the sites was that the different feeding guilds from Atlantic Woods Creek, with the exception of the bivalve interface-feeders, had the most enriched $\delta^{13}C$ values and they were significantly different than the other sites (Table 2).

Organic Matter-Consumer Relationships – As there was minimal monthly variation within the different feeding guilds of macrobenthos and nekton, bi-plots of the $\delta^{15}N$ and $\delta^{13}C$ of the organic matter sources, macrofauna, and nekton sampled from the fives sites are presented as mean values across the four months for ease of interpretation (Fig 2). The $\delta^{15}N$ and $\delta^{13}C$ values for each of the individual species that comprise the feeding guilds across all sites and months are available for comparison in Appendix 1. The use of feeding guilds for classifying the macrofauna makes it easier to compare the different sampling sites and will make these data more useful to investigators in other estuarine systems with different species pools. However, changes in the individual species that comprise the feeding guilds were instructive in explaining some of the feeding guild patterns that were observed (Fig. 3).

When accounting for trophic fractionation (3.4‰ for $\delta^{15}N$ and 1.0‰ for $\delta^{13}C$), the fauna (as either feeding guilds or individual taxa) and the measured organic matter pools showed little overlap. Most of the

organisms were enriched in ^{15}N relative to the organic matter sources, as would be expected, but they were also enriched in ^{13}C beyond the average trophic fractionation value. This implies that some of the fauna were feeding upon other or additional organic matter beyond the seston, microphytobenthos, and bulk sediment. Possible food sources are locally produced phytoplankton or sediment bacteria associated with autochthonous and allochthonous detritus. For reference, hypothetical estimates of $\delta^{15}N$ and $\delta^{13}C$ values for locally produced phytoplankton, sediment bacteria, and the marsh grass *Spartina alterniflora* are plotted in Figures 2 and 3. The values that were used as reference points were either directly from reported values or based upon published relationships between isotopic values and other environmental parameters: for phytoplankton – $\delta^{13}C$ values were based upon the range of salinities measured at the sites (Table 3) and the salinity-DIC/phytoplankton isotopic value relationships of Chanton and Lewis (1999), while $\delta^{15}N$ values for phytoplankton at each site were taken from the mean seston values (+/- S.E.); sediment bacteria – $\delta^{13}C$ values were estimated from bacterial (iso- and anteiso-branched 15:0) polyunsaturated fatty acids isotopic values reported in a survey of studies from unvegetated and C4 plant marsh sediments with 5 – 10% TOC (Bouillon and Boschker 2006), which were in turn adjusted by adding 4‰ to account for the fractionation of lipid synthesis (Van Der Meer et al. 1998; Canuel et al. 1997; Blair et al. 1985) to create an estimate for whole bacteria. Sediment bacteria $\delta^{15}N$ estimates were bound by the range of $\delta^{15}N$ that were measured for all bulk sediment samples (+/- the standard error) at each site; *Spartina alterniflora* – $\delta^{13}C$ values were taken range of values for leaves reported in the literature, as *S. alterniflora* fixes carbon from the atmosphere (Canuel et al. 1997; Deegan and Garritt 1997; Currin et al. 1995), while $\delta^{15}N$ for *S. alterniflora* was bound by the mean (+ S.E.) $\delta^{15}N$ observed among all the microphytobenthos measured at a given site.

As would be expected *a priori*, there was considerable range in the $\delta^{15}N$ values of the macrobenthos at each site, with carnivorous macrofauna (when they were present) having the highest values, while filter- and interface-feeding taxa had the lowest values (Fig 2). Carnivores typically had $\delta^{15}N$ ratios 2 to 3‰ greater than, but similar $\delta^{13}C$ ratios to, smaller fauna such as shallow deposit-feeders and non-bivalve interface-feeders (Fig 2). Thus, shallow deposit-feeders and non-bivalve interface-feeders may serve as prey items to carnivores. The position of omnivores in relation to other taxa and the organic matter sources was less consistent among the sites relative to strict carnivores. At three sites (Chisman Creek, Catlett

Islands, and Atlantic Woods Creek) omnivores had relatively enriched $\delta^{15}N$ values and were similar to carnivores, suggesting a greater importance of carnivory than deposit-feeding/grazing while those collected from Thorntons and Sarah creeks were more depleted, suggesting a reduced importance of carnivory (Fig 2; Table 2). The omnivores from Sarah and Thorntons creeks had similar $\delta^{13}C$ and $\delta^{15}N$ values to the deposit- and interface-feeding taxa at their sites, which further reinforces the notion that the omnivores functioned more as primary, than secondary consumers at these 2 sites (one of the highest quality and one of the lowest).

Neanthes succinea was the only omnivore that was consistently collected across all of the sites and during most months (Appendix). By comparing the absolute and relative positions of *N. succinea* in ^{15}N and ^{13}C space across the five sites (Fig 3), it is clear that differences in its and the other ominvores' feeding habits were related to differences at the sampling site, not changing species composition within the feeding guild. At Thorntons and Sarah creeks, *N. succinea* and other omnivore species, with the exception of the isopod *Cyathura polita*, have isotopic values that suggest they fed upon microphytobenthos and bulk sediment. The individuals from Chisman Creek and Catlett Islands appear to have fed predominantly on other fauna (Fig 3). The *N. succinea* from the degraded Atlantic Woods Creek site could not be clearly interpreted to have been functioning as grazers/deposit feeders or carnivores.

An unexpected result was that the $\delta^{15}N$ values of the deep and shallow deposit-feeding taxa were nearly as enriched as to those of carnivores and omnivores. These taxa (e.g., *Heteromastus filiformis*, *Leitoscolopolis fragilis*, or *Limnodriloides anxius*) are non-carnivorous (Clough and Lopez 1993;Giere and Pfannkuche 1982; Fauchald and Jumars 1979), but had $\delta^{15}N$ values enriched beyond what would be expected based upon the trophic fractionation from any of the bulk sediment measurements. The enriched $\delta^{15}N$ values could be indicative of these fauna feeding on sources of recycled N and possibly bacteria involved in coupled nitrification-denitrification at the oxic/anoxic boundary (e.g., Jensen et al. 1994; Jenkins and Kemp 1984), facilitated by macrofaunal burrowing into anoxic sediments and circulating oxygenated water in the process (e.g., Wu et al. 2003; Schaffner et al. 2001; Aller and Aller 1998). This pattern is further supported when the individual species of deep deposit-feeders are considered (Fig 3). At Thorntons Creek the shallow and deep deposit-feeding guilds were more diverse than other sites and

consisted of capitellid (*H. filiformis* and *Mediomastus ambiseta*) and maldanid (*Clymenella torquata*) polychaetes (*C. torquata* was collected only at Thorntons Creek). Maldanids are known to gather organic matter from surface sediments into their tubes that extend centimeters below the surface (Levin et al. 1997; Dobbs and Whitlach 1982) and in this study they had similar $\delta^{13}C$ and $\delta^{15}N$ values to fauna that fed at the sediment surface. In contrast, the capitellids typically feed, near or below the oxic-anoxic boundary, (Hines and Comtois 1985; Fauchald and Jumars 1979). Consistent with this, they had the most enriched $\delta^{15}N$ values seen among deposit-feeders from the other sites (Fig. 3).

The highest trophic level fauna included in the study were benthivoric fishes and crabs (e.g., *Callinectes sapidus*, *Leiostomus xanthurus*, or *Trinectes undulatus*). When trophic fractionation was taken into account, benthivoric nekton from Chisman and Thorntons creeks had similar isotopic values to a variety of the macrobenthic fauna collected during the same time and in previous months (Fig. 2). Likely prey items included interface-feeding bivalves (e.g., *Macoma balthica*), which are thought to be the preferred prey items (e.g., Seitz et al. 2001; Chao and Musick 1977; Chapter 3), as well as carnivores, omnivores and non-bivalve interface-feeders (e.g., *Loimia medusa* at Thorntons Creek). Closer inspection shows that at these two higher habitat quality sites there were some differences in the potential interactions of the nekton and the macrobenthos. At Thorntons Creek, the nekton had similar $\delta^{13}C$ and $\delta^{15}N$ values to many of the carnivorous macrofauna, implying that they shared similar prey items among the other macrofauna present, but at Chisman Creek there was a separation of the nekton and carnivorous macrobenthos isotopic values, suggesting a segregation of prey items between the two types of predators (Figs. 2 & 3). Conversely, at the more degraded Sarah Creek site there was a distinct separation of the nekton from the macrobenthos, both as potential prey items or competing consumers. The nekton $\delta^{13}C$ and $\delta^{15}N$ values were not similar to the macrobenthos collected during the same month, nor those collected from the previous months, which was interpreted to mean that the nekton were feeding on fauna from other locations.

DISCUSSION

The primary goal of this study was to provide basic diet information on the macrobenthos of shallow subtidal estuarine habitats, which are distinctly different and relatively understudied in comparison to intertidal and deeper subtidal regions. To achieve this, the natural abundance of stable ^{13}C and ^{15}N isotopes in a number of different organic matter pools, macrobenthic taxa, and benthivoric nekton were measured at a series of sites through the high mesohaline portions of the Chesapeake Bay ecosystem. The secondary goal was to determine if the impacts of eutrophication on macrobenthic community composition could be detected as changes in the relationships of the components in shallow subtidal estuarine food webs. This study provides spatial and temporal replication during a period of high growth and productivity (Spring-Summer), combined with taxonomic rigor and a wide base of organic matter pools. Furthermore, the feeding guild approach to analysis and classification of the fauna will facilitate comparisons with systems other than Chesapeake Bay.

The macrobenthos and nekton that were sampled had isotopic signatures that were less variable than their food sources. Temporal changes in the isotopic values of the organic matter pools is relatively well documented (e.g., Nordström et al. 2009; Cloern et al. 2002). These changes reflect environmental variability and high turnover rates compared to those of the macrobenthos and nekton (Cahoon 1999; Edgar 1990; Diaz and Schaffner 1990), whose isotopic ratios integrate the diet over time (Currin et al. 2003; O'Reilly et al. 2002; Hentschel 1998). In particular, the $\delta^{15}N$ values of the organic matter pools were more temporally variable than the $\delta^{13}C$, with the exception of the seston. The $\delta^{15}N$ values did not have a distinct temporal trend like Nordström et al. (2009) observed; instead the $\delta^{15}N$ values increased and decreased throughout the sampling period. This is likely indicative of relatively consistent DIC sources, compared to episodic inputs of dissolved and particulate nitrogen to the systems, which are then quickly consumed and reworked by the fauna and the microbes, successively enriching the ^{15}N content. These pulses of fresh, relatively ^{15}N deplete organic matter could have been in the form of Spring and Autumn phytoplankton blooms or runoff from heavy rain events (Fry 2006; Michener and Schell 1994). The monthly differences in the isotopic values of the seston, which were not consistent across sites, is likely due to localized rainfall

and tidal/estuarine circulation altering the isotopic value of local water column DIC, as well as delivery of material produced elsewhere. Such short-term, relatively unpredictable changes in the isotopic values reinforces the idea that it is important to repeatedly measure organic matter pools or have an understanding of the inherent variability (e.g., Cloern et al. 2002) in order to adequately characterize the base of estuarine food webs.

There has been an ongoing debate in the ecological literature over the relative importance of autochthonous (e.g., phytoplankton, microphytobenthos, SAV) versus allochthonous production (e.g., salt marsh and upland detritus, riverine inputs) in supporting the rich array of 2° and higher organismal production in estuaries and coastal oceans. Usually this argument breaks down along the lines of methodological approach: 1.) those researchers who conduct isotopic (natural abundance or tracer additions) analyses of the fauna and their potential food sources tend to conclude that autochthonous production, especially that of the microphytobenthos and epiphytic algae, is important (Choy et al. 2008; Galván et al. 2008; van Oevelan et al. 2006; Kharlamenko et al. 2001; Herman et al. 2000), though see Nadon and Himmelman (2006); and 2.) those researchers who conduct mass-balance or energetic studies tend to conclude that autochthonous production is important, but it must be supplemented by allochthonous/detrital sources of organic matter (Kneib 2003; Baird et al. 1991).

The isotopic data from this study did not show a clear and consistent contribution of the microphytobenthos to the shallow deposit-feeding (e.g., oligochaetes and small capitellid polychaetes) or the interface-feeding (spiond polychaetes, tellinid bivalves) macrofauna. It would be expected that these two feeding guilds would consume a considerable amount of microphytobenthic organic matter given their feeding styles (Levin et al. 1997; Clough and Lopez 1993; Lopez and Levinton 1987; Giere and Pfannkuche 1982; Pohlo 1982; Fauchald and Jumars 1979). The samples of microphytobenthos collected in this study were relatively deplete in ^{13}C compared to values observed in previous studies (e.g., Buchsbaum et al. 2009; Currin et al. 1995; Couch 1989) and more deplete than the fauna that were collected. Regardless, the author is confident in the accuracy of those microphytobenthic isotopic values and, therefore their apparent trophic disconnect from the macrofauna. A majority of isotopic measurements of microphytobenthos in the literature are from intertidal populations and the degree of tidal inundation can influence the source of the DIC to the microphytobenthos (i.e., porewater vs. water column), which in part

dictates the $\delta^{13}C$ value (Currin et al. 2003). Currin et al. (2003) observed differences in $\delta^{13}C$ values of microphytobenthos along a tidal inundation gradient, with samples from the marsh platform being more enriched than those from the adjacent berm, which in turn were more enriched than the present subtidal samples. Furthermore, subtidal estuarine microphytobenthos grow under lower light levels than intertidal populations, which will influence photosynthetic rates and subsequently cause greater isotopic fractionation of carbon (Fogel et al. 1992). As a consequence, other sources of organic matter beyond the microphytobenthos must be considered when determining how the benthic food webs of subtidal estuaries are supported.

The Contribution of Salt Marsh Detritus – Like much of the Virginia portion of Chesapeake Bay, there was 3 – 4 m of fringing *Spartina alterniflora* marsh in the littoral zone of all of the creeks where samples were collected. *Spartina alterniflora* is a C_4 plant, which typically has $\delta^{13}C$ values ranging from -15 to -12‰ while alive or dead (Canuel et al. 1997; Deegan and Garritt 1997; Currin et al. 1995), a $\delta^{13}C$ ratio that would bound all of the fauna that were collected. Organic matter from these marshes was observed in the sediments at all sites. However, few of the collected macrofauna are expected to directly consume the large pieces of salt marsh detritus, but instead consume bacteria and fungi associated with the detrital material (Jumars 1993; Lopez and Levinton 1987), though see Kenworthy et al. (1989). The degree of isotopic fractionation by bacteria and fungi is not well understood, though most bacteria are thought to fractionate ^{13}C less than 1‰ from their organic matter sources (Bouillon and Boschker 2006; Boschker and Middelburg 2002). There are few field-based collections for bacterial isotopic values in the literature, but Bouillon and Boschker (2006) presented a survey of bacteria-specific polyunsaturated fatty acid isotopic values collected in field studies, which can be subsequently adjusted by 4‰ to account for fractionation differences between whole bacteria and only their fatty acids (Van Der Meer et al. 1998; Canuel et al. 1997; Blair et al. 1985). When these data are overlaid on the faunal data (Figs 2 and 3), they are in a range such that the bacterial carbon may be a reasonable food source given both the isotope ratios and life history of the macrofauna collected in this study, especially the deposit- and interface-feeding taxa. These feeding guilds are thought to selectively remove bacteria that coat sediment/detrital particles they ingest (Hymel and Plante 2000; Cheng and Lopez 1991; Cammen 1980), with the caveat that the fauna likely incorporate

more material from bacteria than just the fatty acids and therefore would potentially incur slightly different values from the compound-specific ones.

The Contribution of Phytoplankton – Another potential organic matter source to these systems is phytoplankton. Samples of seston were collected from the water column, which presumably contained phytoplankton, but given the relatively depleted $\delta^{13}C$ of the samples, likely also contained upland particulate organic matter and resuspended sediment. As such, the seston as collected was not an ideal representation of solely the phytoplankton at the sites, but can be considered representative of the material available to the filter and interface-feeding fauna. As an example, when adjusted for trophic fractionation, amphipod and bivalve filter-feeders had similar $\delta^{13}C$ and $\delta^{15}N$ ratios to their respective seston measurements, though the filter-feeding phoronids and anthozoans did not.

Based upon the relationships between salinity and $\delta^{13}C$ ratios of DIC/phytoplankton (Chanton and Lewis 1999), the phytoplankton grown at the sample sites should have had a $\delta^{13}C$ value between -22 and -20‰ based upon salinities of 15 to 20 psu (Table 5). The hypothetical, locally produced phytoplankton $\delta^{13}C$ ratios in this range (overlaid on Figs 2 & 3) would overlap with many of the macrofauna collected at the study sites, particularly the filter-feeding anthozoans and phoronids. These fauna do not appear to be supported by the mix of organic matter sources that the seston samples represented; possibly indicating their ability to selectively remove only phytoplankton cells from the water column. With the exception of those taxa, many of the other macrofauna that were collected do not have a mechanism to collect phytoplankton from the water column and would instead have to obtain the organic matter after it is deposited to the sediment surface and incorporated into the system (e.g., Marsh and Tenore 1990), possibly after bacterial processing.

The Influence of Habitat Quality – The data from this study indicate there was some degree of prey/organic matter switching within a feeding guild among sites but with relative fidelity through time. In high mesohaline estuaries, natural history would suggest that the carnivorous, omnivorous, interface-feeding macrofauna, as well as benthivoric nekton would have the greatest potential to switch among food sources with different trophic positions as relative density of their food sources changed in relation to habitat quality (Riisgård and Kamermans 2001; Seitz et al. 2001; Taghon et al. 1980). The omnivores and

shallow deposit-feeders showed the most distinct differences among sites. These differences, however, were not tightly coupled to the environmental quality at the site, as diets of fauna from degraded sites like Sarah Creek were often similar to those in relatively non-degraded site.

When the $\delta^{15}N$ ratios of consumers were adjusted for the temporal and spatial differences in the organic matter that was collected, omnivores from Sarah Creek and Thorntons Creek appeared to have functioned as primary consumers (i.e., grazing or deposit feeding) and as secondary consumers (i.e., carnivores) at Catlett Islands and Atlantic Woods Creek. These differences could not be linked to the degree of degradation at a site because both feeding styles were observed at both degraded and relatively non-degraded sites. Shallow deposit-feeders also showed distinct differences in $\delta^{15}N$ ratios, which were likely related to the changes in species composition linked to habitat quality. Specimens from a degraded site (Sarah Creek) had the more ^{15}N enriched isotope values, while the least degraded site (Thorntons Creek) had the more depleted values. This is indicative of a greater importance of aged, recycled organic matter at the degraded site, where the shallow deposit feeding guild was composed of taxa that are more resistant to low dissolved oxygen and sulfides (*Capitomastus aciculatus* and *Limnodriloides anxius*) than those (*Mediomastus ambiseta*) at less degraded sites (Gray et al. 2002; Weisberg et al. 1997; Theede 1973). This tolerance possibly allows the shallow deposit feeders at the degraded site to access anoxic sediments and the bacteria/detritus located there, which likely have higher denitrification rates (e.g., Schaffner et al. 2008).

The benthivoric nekton collected in this study present an additional set of problems in interpreting the contribution of various organic matter sources to their diet. Given the integrative nature of the stable isotopic ratios in tissue combined with the lifespan and movement of the nekton, it is difficult to draw links between nekton and fauna from specific habitat. These problems are further exacerbated when mobile fauna presented with a spatially heterogeneous mixture of potential prey items as in systems like the tidal creeks that were sampled (e.g., Gillett et al. 2007; Metcalfe 2005; Holland et al. 2004). Isotopic similarities/dissimilarities observed between nekton from the degraded and non-degraded sites provides an illustration of this point. Previous studies have shown that benthivoric predators will remain within area if high densities of suitable prey are continuously encountered (Seitz et al. 2001; Clark et al. 2000; Lipcius

and Hines 1986). The benthic communities of Thorntons and Chisman creeks were composed of the preferential prey items of the nekton, but not the community from Sarah Creek (Chapter 3). The isotopic values of the nekton from Thorntons and Chisman creeks indicate their dietary preferences for local macrofauna from relatively non-disturbed communities (e.g., Deegan and Garritt 1997). Conversely, the nekton collected from Sarah Creek were dissimilar to the local macrofauna and had isotopic values that likely reflect a greater contribution of prey items from other locations.

The isotopic data suggest that habitat quality is not the only force structuring food web interactions in shallow water portions of the estuary (e.g., Chapter 3). Site-specific differences in the macrobenthic community structure, related in part to habitat quality, but also to natural macrobenthic population dynamics affected food web structure. At Chisman Creek, a mid-quality habitat where production of the macrobenthic community was dominated by bivalves (Chapter 3), the isotopic data show that the carnivorous macrofauna and the nekton appear to have fed on different prey items. These differences were likely because bivalves were present and available to the nekton, while the predatory macrofauna (e.g., nemerteans and goniadid or phyllodocid polychaetes) are not capable of feeding on post-juvenile bivalves (Fauchald and Jumars 1979; McDermott 1976). In contrast, macrobenthic production at Thorntons Creek (a high quality site) was dominated by polychaetes and less by bivalves than at Chisman Creek (Chapter 3). In that situation, the nekton and the carnivorous macrofauna had similar isotopic values and were likely preying upon the same group of polychaetes and crustaceans. Though there is only evidence from two sites, these data provide an example of how the presence of significant amounts of key prey species in a community can have direct influence on the structure and functional redundancy of the benthic-pelagic food webs in shallow water estuarine habitats. When the bivalves were present, the food web could be characterized to have had greater resource usage diversity among the higher trophic levels, but when they were not present all of the predatory fauna were focused on one resource only.

CONCLUSIONS

At the outset of this study, the goals were to use stable carbon and nitrogen isotopes to investigate the position of the macrobenthos in the relatively cryptic and complex food web of shallow subtidal estuarine sites and to determine if changes in macrobenthic community structure and composition related to habitat quality would lead to changes in their position. Based upon the isotopic values of the organic matter that were collected and those reported in the literature, it seems very unlikely that any one organic matter source supports the production of the macrofauna in shallow subtidal, depositional habitats like those that were sampled. These data indicate that both autochthonous and allochthonous organic matter sources are important to the community. While it was initially expected that the microphytobenthos would be an important source of organic matter in these systems, almost all of the primary consumers that were sampled had isotopic values indicative of feeding upon a mixture of locally produced phytoplankton and microphytobenthos, as well as imported organic matter from the adjacent uplands and salt marshes; all of which has likely undergone some degree of bacterial decomposition. These animals are, in turn, consumed by other macrofauna and nekton, which represent a vector for transport of the mix of organic matter in shallow water, near-shore systems to other parts of the estuary and coastal ocean via migration or consumption by subsequent predators.

Furthermore, at most sites the patterns of organic matter utilization by the macrobenthos was insensitive to the degree of habitat degradation. The exception was the extremely disturbed Atlantic Woods Creek, which had few species due to the effects of sediment toxicity and eutrophication. There were some changes along the gradient of habitat quality that were likely mediated by the changes in species composition of the macrobenthic community, but overall, the macrobenthic communities and their components were surprisingly similar to each other from an isotopic viewpoint. There was a greater separation between the isotopic values of the organic matter pools that were measured and the macrobenthic community at the degraded sites than at the relatively non-degraded ones, but the relationships of the different types of fauna to each other was relatively consistent across the sites. The sediments in these muddy, depositional systems are rich in organic matter and the bacterial community integrates all of that matter from the water column and the sediment. It could be argued that this acts as a

near-inexhaustible supply of food to the macrofauna, which may be augmented by freshly deposited phytoplankton or living microphytobenthos and probably accounts for the lack of temporal variation in the isotopic values of the biota in spite of considerable temporal variability of the singular organic matter pools. In the future, compound-specific isotope analysis or enrichment-level tracer techniques may be better approaches to determine the importance of bacteria and detritus to the fauna.

The isotopic results from this study have allowed fore the creation of a basic structural framework for a shallow subtidal, estuarine benthic food web, identify the major components and an understanding of the trophic relationships within the macrobenthos and the nekton. These data can be put into functional perspective if they are combined with quantitative measure of 1° and 2° production that provide a magnitude of material flow in each diet relationship and the productivity and functioning of the ecosystem as a whole (e.g., Choy et al. 2009; Maier and Simenstad 2009; Hagy 2002). The isotope-derived relationships among organic matter pools and different fauna are valuable though, in determining the fate of the organic matter in the benthos.

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Table 1a. Summary of the 2-way analysis of variance of the $\delta^{15}N$ and $\delta^{13}C$ ratios of the different organic matter pools with site and month as the treatment variables. Presented are sample size, model r^2, model and error degrees of freedom, and overall F-values and *p*-values, as well as the *p*-values based upon type III sums of squares for each treatment and the interaction term, where applicable. *Post-hoc* comparisons of the two treatments are presented and arrayed from most enriched to most deplete. An underline indicates similarity at an α=0.05. Least square means were used when all treatment levels were present and directed contrasts were used when they were not. Site abbreviations arrayed from highest to lowest habitat quality: **ST** = Thorntons Creek, **CH** = Chisman Creek, **CI** = Catlett Islands, **SA** = Sarahs Creek, **AW** = Atlantic Woods Creek. Month abbreviations: **Sp** = Spring, **J** = July, **A** = August, and **S** = September. Note that sediment from 6-10cm and 2-6cm were only analyzed as 1-way ANOVAs as detailed in the text..

Table 1b. *Post-hoc* comparisons of the Site*Month interactions of $\delta^{15}N$ and $\delta^{13}C$ ratios of the organic matter pools at the five sample sites. Month abbreviations are arrayed from most enriched to most deplete and an underline indicates similarity of *post-hoc* least square means comparisons at α=0.05. Month abbreviations are the same as above.

a

Response Variable	Organic Matter Pool	N	r^2	d.f.	F-value	*p*-value	Site Treatment	Month Treatment	Interaction	Site Effect	Month Effect
$\delta^{15}N$	Bulk Sediment 0-2 cm	51	0.854	17, 33	11.32	<0.0001	<0.0001	0.0152	0.0131	CI SA ST AW CH	S Sp J A
	Bulk Sediment 2-6 cm	23	0.782	4, 18	11.40	<0.0001	<0.0001	-	-	CI SA ST CH AW	
	Bulk Sediment 6-10 cm (ST Only)	8	0.245	3, 4	0.43	0.7411	-	0.7411	-		
	Seston (0.7μm)	53	0.426	7, 45	4.76	0.0005	0.0023	0.0095	-	CI CH SA ST AW	S A J Sp
	Microphytobenthos	63	0.742	18, 44	7.02	<0.0001	0.0185	0.0014	<0.0001	CI SA AW CH ST	S A Sp J
$\delta^{13}C$	Bulk Sediment 0-2 cm	51	0.865	7, 43	39.21	<0.0001	<0.0001	0.7275	-	CI ST SA CH AW	
	Bulk Sediment 2-6 cm	23	0.915	4, 18	48.75	<0.0001	<0.0001	-	-	CI ST SA CH AW	
	Bulk Sediment 6-10 cm (ST Only)	8	0.467	3, 4	1.17	0.4251	-	0.4251	-		
	Seston (0.7μm)	53	0.981	18, 34	98.66	<0.0001	<0.0001	<0.0001	<0.0001	CI SA AW ST CH	A J S Sp
	Microphytobenthos	63	0.583	7, 55	10.97	<0.0001	<0.0001	0.4657	-	CI SA ST AW CH	

b

Response Variable	Organic Matter Pool	Interaction Terms: Thorntons Creek	Chisman Creek	Catlett Islands	Sarahs Creek	Atlantic Woods Creek
$\delta^{15}N$	Bulk Sediment 0-2 cm	J A S	J S A	S J Sp A	S Sp A J	S Sp A J
	Microphytobenthos	A Sp S J	S J A	S A Sp J	J Sp A S	Sp A S J
$\delta^{13}C$	Seston (0.7μm)	A J S Sp	J A S Sp	A J S Sp	A S Sp J	Sp S J

Table 2. Summary of the 2-way analysis of variance of the adjusted $\delta^{15}N$ and $\delta^{13}C$ ratios of the different macrobenthic feeding guilds with site and month as the treatment variables where enough samples were collected. Presented are sample size, model r^2, model and error degrees of freedom, model F-value and *p*-value, as well as the *p*-values based upon type III sums of squares for each treatment. *Post-hoc* comparisons of the two treatments are presented and arrayed from most enriched to most deplete. An underline indicates similarity at an α=0.05. Least square means were used when all treatment levels were present and directed contrasts were used when they were not. Site abbreviations arrayed from highest to lowest habitat quality: **ST** = Thorntons Creek, **CH** = Chisman Creek, **CI** = Catlett Islands, **SA** = Sarahs Creek, **AW** = Atlantic Woods Creek. Month abbreviations: **Sp** = Spring, **J** = July, **A** = August, and **S** = September. Note that filter-feeders and nekton were only analyzed as 1-way ANOVAs, as not enough material was collected for replicates for months.

Response Variable	Feeding Guild	N	r^2	d.f.	F-value	*p*-value	Site Treatment	Month Treatment	Site Effect	Month Effect
Site and Month Adjusted $\delta^{15}N$	Filter-Feeders	27	0.095	5, 21	0.44	0.8127	0.4901	0.8478	-	-
	Non-Bivalve Interface-Feeders	34	0.451	7, 26	3.05	0.0176	0.0381	0.1274	AW CH CI ST SA	-
	Bivalve Interface-Feeders	21	0.566	6, 14	3.04	0.0406	0.0160	0.7074	CI CH AW ST	-
	Shallow Deposit-Feeders	5	0.971	1, 3	100.05	0.0021	0.0021		SA ST	
	Deep Deposit-Feeders	43	0.364	6, 36	3.43	0.0088	0.0024	0.3999	CH CI SA ST	-
	Omnivores	54	0.546	7, 46	7.93	<0.0001	<0.0001	0.7208	CI CH AW ST SA	-
	Carnivores	49	0.285	7, 41	2.34	0.0418	0.0256	0.5604	AW CH CI ST SA	-
	Benthivoric Nekton	20	7.26	2, 17	7.26	0.0053	0.0053		CH SA ST	
Site and Month Adjusted $\delta^{13}C$	Filter-Feeders	27	0.605	5, 21	6.43	0.0009	0.0004	0.0793	CH CI ST	-
	Non-Bivalve Interface-Feeders	34	0.610	7, 26	5.80	0.0004	<0.0001	0.7932	AW CH CI SA ST	-
	Bivalve Interface-Feeders	21	0.419	6, 14	1.78	0.1976	0.1565	0.3516	-	-
	Shallow Deposit-Feeders	5	0.765	1, 3	9.78	0.0522	0.0522		-	
	Deep Deposit-Feeders	43	0.401	6, 36	4.01	0.0036	0.0222	0.0036	SA CH ST CI	Sp S J A
	Omnivores	54	0.883	7, 46	49.41	<0.0001	<0.0001	0.2389	AW SA CH CI ST	-
	Carnivores	49	0.726	7, 41	15.49	<0.0001	<0.0001	0.1079	AW CH ST SA CI	-
	Benthivoric Nekton	20	0.2975	2, 17	3.60	0.0497	0.0497		SA CH ST	

Table 3 Water quality measurements collected at each sample site. Values are the means of 3 samples taken approximately mid-way between the sediment and water surface approximately 2-3 hrs after low tide. * = CTD was malfunctioning at Atlantic Woods in August, so temperature was measured with a mercury thermometer and salinity with a hand-held refractometer. # = Low salinity due to heavy rainfall in the Sarahs Creek watershed the previous evening

Site	Month	Water Temperature (C)	Salinity (psu)	Dissolved Oxygen (mg L^{-1})
Thorntons Creek	Spring	15.40	16.9	7.40
	July	31.60	19.4	6.96
	August	30.93	16.3	5.53
	September	27.30	15.7	7.90
Chisman Creek	Spring	21.13	16.0	5.58
	July	32.40	17.1	11.95
	August	26.30	21.3	6.81
	September	27.60	14.2	3.54
Catlett Islands	Spring	26.43	17.6	5.90
	July	30.37	20.2	7.16
	August			
	September	28.67	18.1	7.85
Sarahs Creek	Spring	21.40	17.2	7.84
	July	24.43	#0.9	3.78
	August	31.77	21.4	6.02
	September	22.83	19.7	3.90
Atlantic Woods Creek	Spring	22.07	19.4	8.79
	July	28.83	18.9	4.97
	August	*27.5	*24	
	September	24.23	17.2	4.58

Figure 1. Chesapeake Bay, USA showing the sites where samples were collected. The inset figure shows the Northwest Atlantic coast and the location of Chesapeake Bay in the Mid-Atlantic United States.

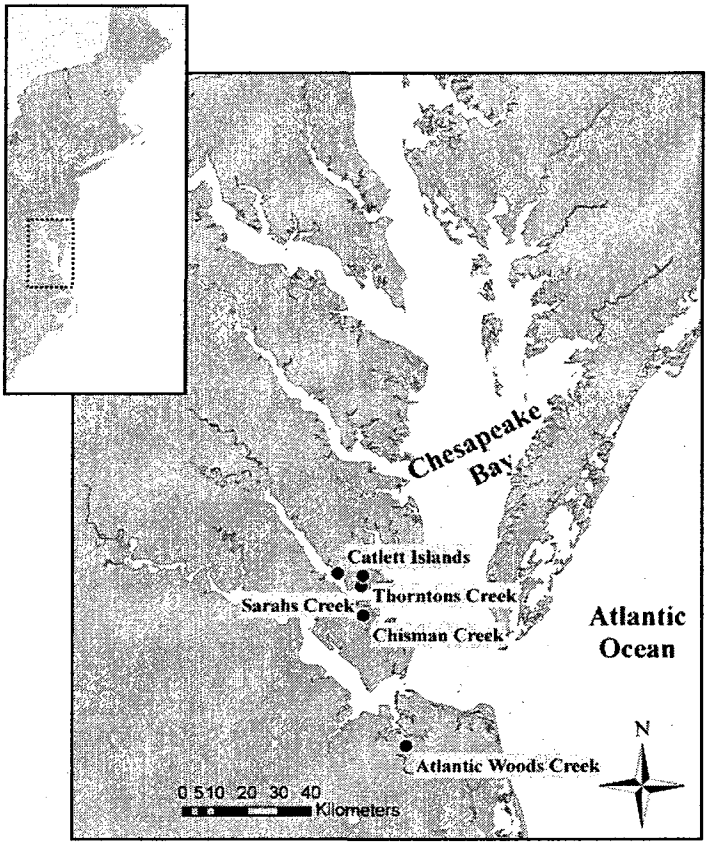
Chesapeake Bay
Catlett Islands
Thorntons Creek
Sarahs Creek
Chisman Creek
Atlantic Ocean
Atlantic Woods Creek
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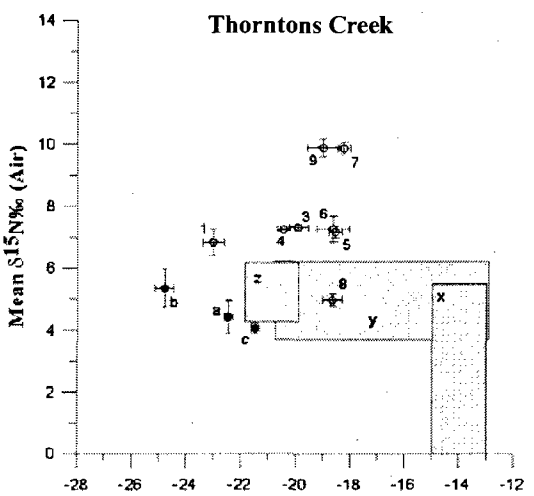
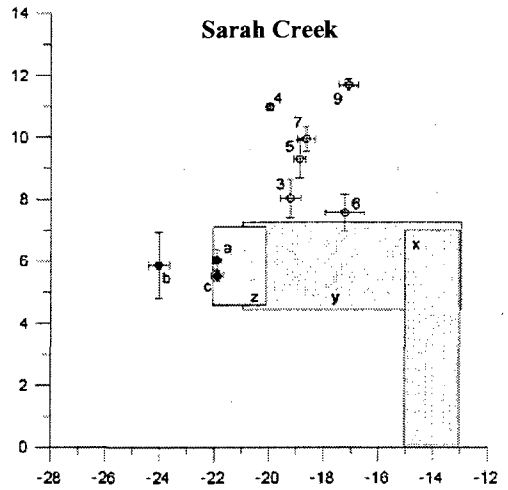
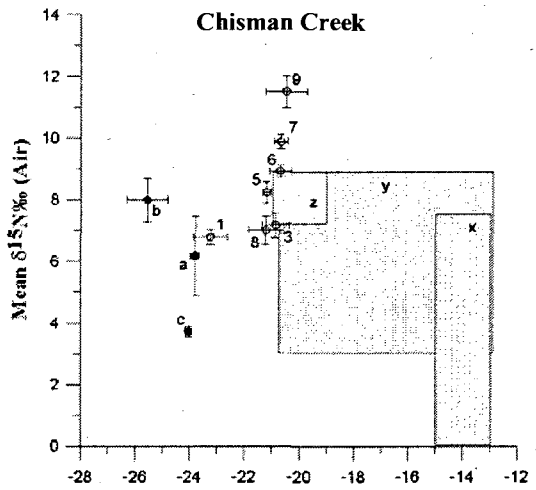
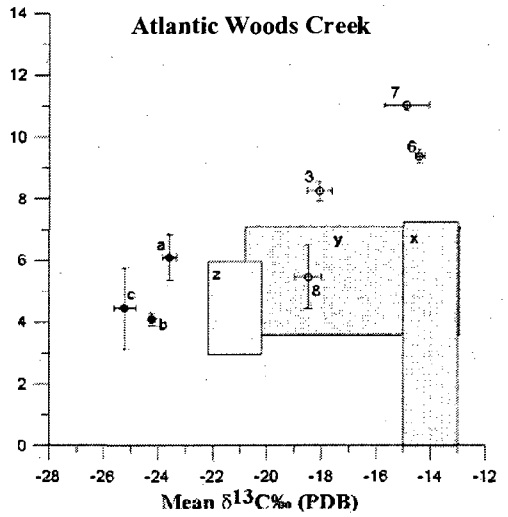
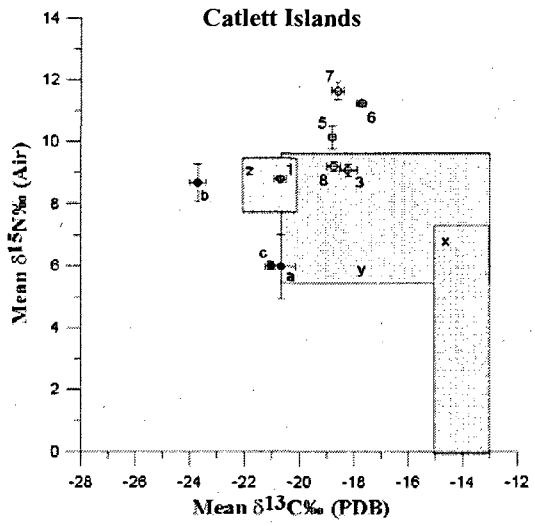
Figure 2. Mean (+/- S.E.) $\delta^{13}C$ and $\delta^{15}N$ values of Spring, July, August, and September sampling events combined for each feeding guild and organic matter pool. Estimates of other potentially important organic matter sources, which were not sampled in the current study, are plotted as shaded boxes. * - *S. alterniflora* $\delta^{13}C$ values from Canuel et al. (1997), Deegan and Garritt (1997), and Currin et al. (1995), $\delta^{15}N$ bound by measured maximum microphytobenthic values; † - Sediment bacteria $\delta^{13}C$ values from polyunsaturated fatty acids in Bouillon and Boschker (2006) adjusted by 4‰, $\delta^{15}N$ bound by standard errors of all measured organic matter pools; § - Phytoplankton $\delta^{13}C$ estimated from salinity-DIC-phytoplankton relationships in Chanton and Lewis (1999), $\delta^{15}N$ bound by the standard error of the seston measurements







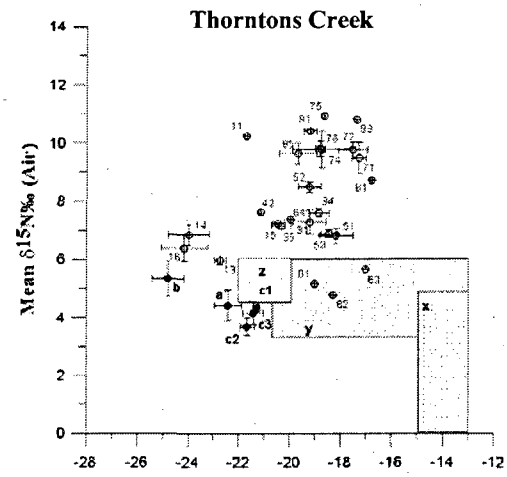


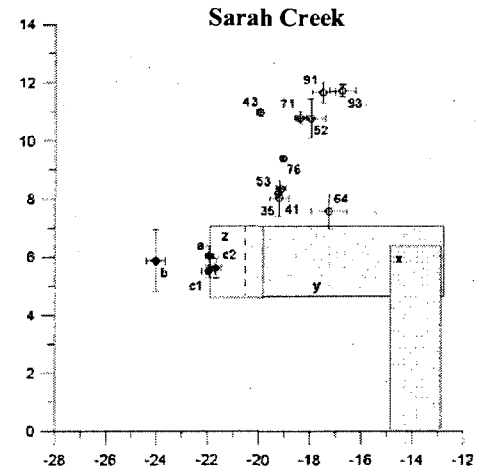


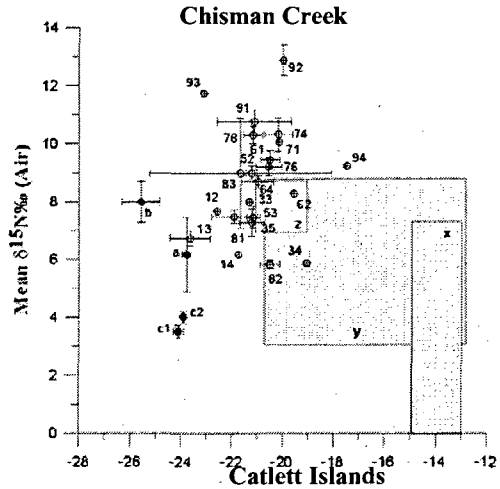
Feeding Guild Key

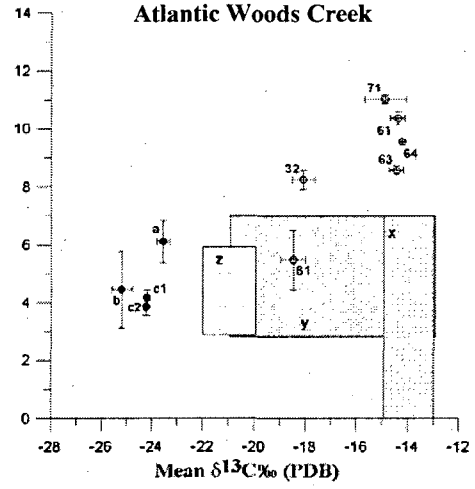
1 - Filter-Feeders
3 - Non-Bivalve Interface-Feeders
4 - Shallow Deposit-Feeders
5 - Deep Deposit-Feeders
6 - Omnivores
7 - Carnivores
8 - Bivalve Interface-Feeders
9 - Benthivoric Nekton
a - Microphytobenthos
b - Seston
c - Bulk Sediment
x - Spartina alterniflora*
y - Sediment Bacteria†
z - Calculated Phytoplankton§

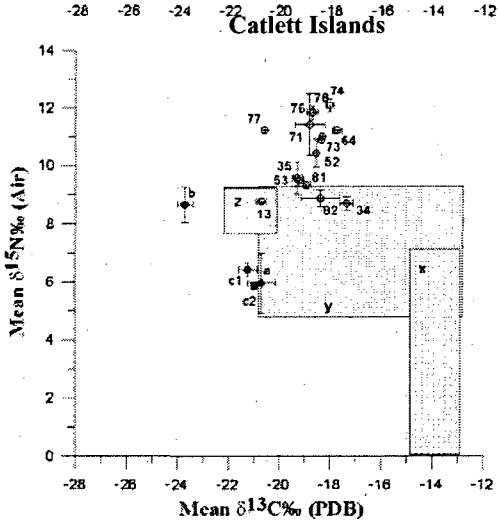
Figure 3. Mean (+/- S.E.) $\delta^{13}C$ and $\delta^{15}N$ values of Spring, July, August, and September sampling events combined for each taxon and organic matter pool. Estimates of other potentially important organic matter sources, which were not sampled in the current study, are plotted as shaded boxes. *, †, and § - estimated values are the same as noted in caption for Figure 2. Macrofauna with the same first digit in the key are from the same feeding guild (e.g., 1_ – filter-feeders, 3_ – non-bivalve interface-feeders, etc.) as plotted in Figure 2.











Species Key

11 - Anthozoa
12 - *Gemma gemma*
13 - *Leptocheirus plumulosus*
14 - *Mulinia lateralis*
15 - *Phoronis* spp.
16 - *Tagelus plebius*
31 - Ampharetidae
32 - *Hobsonia florida*
33 - *Polydora* sp.
34 - *Paraprionospio pinnata*
35 - *Streblospio benedicti*
41 - *Capitomastus aciculatus*
42 - *Mediomastus ambiseta*
43 - *Limnodriloides anxius*
51 - *Clymenella torquata*
52 - *Heteromastus filiformis*
53 - *Leitoscolopolis fragilis*
61 - *Cyathura polita*
62 - *Edotea triloba*
63 - *Laeonereis culveri*
64 - *Neanthes succinea*
71 - *Eteone heteropoda*
72 - *Glycera dibranchiata*
73 - *Glycera* sp.
74 - *Glycinde soliteria*
75 - Phyllodocida
76 - Nemertean
77 - Nemertean sp1
78 - *Podarkeopsis levifucina*
81 - *Macoma balthica*
82 - *Macoma* spp.
83 - *Macoma tenta*
91 - *Callinectes sapidus*
92 - *Fundulus heteroclitus*
93 - *Leiostomus xanthurus*
94 - *Palaemonetes pugio*
95 - *Trinectes maculatus*
a - Microphytobenthos
b - Seston
c1 - Bulk Sediment 0-2 cm
c2 - Bulk Sediment 2-6 cm
c3 - Bulk Sediment 6-10 cm
x - *Spartina alterniflora*[*]
y - Sediment Bacteria[†]
z - Calculated Phytoplankton[§]

Appendix Mean (standard error) $\delta^{13}C$ and $\delta^{15}N$ ‰ for all of the macrobenthos, nekton, and organic matter pools collected from each site. Feeding guild abbreviations: **BIF**-bivalve interface-feeder, **CA**-carnivore, **DDF**-deep deposit-feeder, **FF**-filter-feeder, **NBIF**-non-bivalve interface-feeder, **OM**-omnivore, and **SDF**-shallow deposit-feeder

Scientific Name	Feeding Guild	Thorntons Creek							
		Spring		July		August		September	
		Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$
Organic Matter									
Bulk Sediment 0-2 cm				-21.2 (0.2)	4.5 (0.1)	-20.8 (0.04)	4.4 (0.2)	-21.7 (0.2)	4.1 (0.2)
Bulk Sediment 2-6 cm		-21.3 (0.1)	4.3 (0.4)	-22.1	2.5	-20.9	5.0	-21.4	4.1
Bulk Sediment 6-10 cm		-20.9 (0.3)	3.8 (0.07)	-21.3 (0.09)	4.1 (0.7)	-21.9 (0.3)	3.1 (1.1)	-22.3 (1.0)	3.6 (0.1)
Microphytobenthos		-22.5 (0.1)	5.1 (1.0)	-22.0 (0.2)	2.6 (1.2)	-21.8 (0.1)	6.2 (0.3)	-23.1 (0.1)	3.6 (0.2)
Seston		-26.3 (0.2)	3.2 (1.8)	-24.6 (0.07)	5.0 (0.6)	-23.1 (0.2)	7.4 (0.1)	-24.9 (0.2)	5.5 (0.5)
Macrobenthos									
Ampharetidae	NBIF			-19.9	7.3				
Anthozoa	FF	-21.7	10.2						
Capitomastus aciculatus	SDF								
Clymenella torquata	DDF	-17.2	6.3	-19.4	7.0			-17.7	7.0
Cyathura polita	OM	-16.7	8.7						
Edotea triloba	OM								
Eteone heteropoda	CA	-17.1 (0.6)	10.2 (0.08)			-17.4	7.9	-17.4	9.3
Gemma gemma	FF								
Glycera dibranchiata	CA			-18.0 (0.1)	9.4 (0.00)			-16.4	10.3
Glycera sp.	CA								
Glycinde soliteria	CA	-18.2 (0.1)	10.4 (0.05)	-19.0 (0.3)	9.8 (0.04)	-19.1	8.6	-19.0	9.6
Heteromastus filiformis	DDF	-18.5	8.8			-20.0	8.3	-19.0	8.2
Hobsonia florida	NBIF								
Phyllodocida	CA	-18.6	10.9						
Laeonereis culveri	OM					-17.0	5.6		
Leitoscolopolis fragilis	DDF	-17.2 (0.4)	6.9 (0.2)	-18.8 (0.05)	6.4 (0.01)	-19.4 (0.1)	7.0 (0.3)	-18.4 (0.3)	6.9 (0.05)
Leptocheirus plumulosus	FF	-23.2	5.7	-22.5	6.3	-22.2	6.0	-22.8	5.7
Limnodriloides anxius	SDF								
Macoma balthica	BIF	-19.0	5.1						
Macoma tenta	BIF								
Macoma s pp.	BIF	-18.2	4.7						
Mediomastus ambiseta	SDF			-20.2	7.2	-20.6	7.2		
Mulinia lateralis	FF	-24.7	6.4	-23.1	7.2				
Neanthes succinea	OM	-17.1	7.1	-19.4 (1.6)	6.6 (1.1)	-20.8	7.5	-19.2 (0.4)	7.9 (0.5)
Nemertean	CA	-18.9	10.3	-19.4	10.4				
Phoronis spp.	FF							-21.1	7.6
Podarkeopsis levifucina	CA								
Polydora sp.	NBIF								
Prionospio pinnata	NBIF	-18.4	7.4	-19.2	7.7				
Streblospio benedicti	NBIF	-19.0	7.3	-21.2	7.3	-20.2 (0.4)	7.0 (0.2)	-20.8	7.0
Tagelus plebius	FF	-25.0	5.9			-23.2	6.8		
Nekton									
Calinectes sapidus				-18.7 (1.1)	9.7 (0.6)				
Fundulus heteroclitus									
Leiostomus xanthurus				-17.3	10.8				
Palaemonetes pugio									
Trinectes undulatus				-19.6 (0.7)	9.6 (0.3)				

Scientific Name	Feeding Guild	Chisman Creek							
		Spring		July		August		September	
		Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$
Organic Matter									
Bulk Sediment 0-2 cm				-23.8 (0.3)	3.7 (0.2)	-24.0 (0.2)	3.3 (0.5)	-24.4 (0.3)	3.4 (0.4)
Bulk Sediment 2-6 cm		-24.0 (0.1)	4.2 (0.3)	-23.7	3.4	-23.6	4.0	-23.8	3.8
Bulk Sediment 6-10 cm									
Microphytobenthos				-24.2	3.6	-24.0 (0.1)	3.1 (1.2)	-23.3 (0.1)	9.8 (0.5)
Seston		-28.9 (0.08)	7.2 (0.5)	-22.7 (0.01)	8.5 (1.2)	-23.8 (0.08)	5.1 (0.1)	-26.7 (0.2)	11.0 (0.5)
Macrobenthos									
Ampharetidae	NBIF								
Anthozoa	FF								
Capitomastus aciculatus	SDF								
Clymenella torquata	DDF								
Cyathura polita	OM	-20.5	10.4	-21.8	9.7	-20.2	9.3	-19.8 (0.1)	8.8 (0.1)
Edotea triloba	OM					-19.5	8.2		
Eteone heteropoda	CA	-20.1	10.0						
Gemma gemma	FF					-22.5	7.6		
Glycera dibranchiata	CA								
Glycera sp.	CA								
Glycinde soliteria	CA	-20.7	10.8			-19.6	9.7		
Heteromastus filiformis	DDF			-21.3 (0.4)	8.6 (0.3)	-21.1	9.2	-21.0	9.3
Hobsonia florida	NBIF								
Phyllodocida	CA								
Laeonereis culveri	OM								
Leitoscolopolis fragilis	DDF	-21.3 (0.2)	7.8 (0.7)			-21.4	7.2	-20.4	6.9
Leptocheirus plumulosus	FF	-24.9 (0.06)	6.9 (0.05)	-22.3	7.0			-21.1	5.6
Limnodriloides anxius	SDF								
Macoma balthica	BIF	-22.4 (1.2)	7.1 (0.00)	-23.0	8.0			-19.7	7.6
Macoma tenta	BIF	-21.6 (3.5)	8.9 (1.9)						
Macoma s pp.	BIF			-21.3	6.4	-21.3	5.7	-19.9 (0.2)	5.6 (0.07)
Mediomastus ambiseta	SDF								
Mulinia lateralis	FF					-21.7	6.1		
Neanthes succinea	OM	-22.7	8.6	-22.5 (0.1)	8.7 (0.4)	-19.7 (0.2)	8.1 (0.5)	-18.9 (0.1)	9.0 (0.01)
Nemertean	CA	-20.7	9.3	-21.9	9.9			-19.7 (0.07)	8.7 (0.02)
Phoronis spp.	FF								
Podarkeopsis levifucina	CA	-20.8 (0.1)	10.3 (0.3)	-22.2	10.9			-20.6	9.6
Polydora sp.	NBIF	-21.2	7.9						
Prionospio pinnata	NBIF							-19.0	5.8
Streblospio benedicti	NBIF	-21.6	8.5	-22.4	7.4	-20.3	6.7	-20.4	6.4
Tagelus plebius	FF								
Nekton									
Calinectes sapidus				-21.1 (1.4)	10.7 (0.3)				
Fundulus heteroclitus				-19.9 (0.08)	12.8 (0.5)				
Leiostomus xanthurus				-23.0	11.7				
Palaemonetes pugio						-17.4	9.2		
Trinectes undulatus									

Scientific Name	Feeding Guild	Catlett Islands							
		Spring		July		August		September	
		Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$
Organic Matter									
Bulk Sediment 0-2 cm		-21.2 (0.3)	5.5 (0.1)	-20.8 (0.06)	6.0 (0.3)	-20.9 (0.03)	5.5 (0.1)	-20.7 (0.06)	6.2 (0.1)
Bulk Sediment 2-6 cm		-20.8	5.9	-22.2	7.0	-20.9	6.1	-20.7	6.5
Bulk Sediment 6-10 cm									
Microphytobenthos		-19.6 (2.0)	4.1 (0.7)	-21.0 (0.3)	3.5 (1.1)	-21.2	8.3	-21.0 (0.2)	10.2 (0.4)
Seston		-24.3 (0.1)	7.5 (0.7)	-23.6 (0.1)	7.0 (1.1)	-21.7 (0.07)	9.8 (0.9)	-24.3 (0.07)	10.7 (0.1)
Macrobenthos									
Ampharetidae	NBIF								
Anthozoa	FF								
Capitomastus aciculatus	SDF								
Clymenella torquata	DDF								
Cyathura polita	OM								
Edotea triloba	OM								
Eteone heteropoda	CA			-18.2	11.0				
Gemma gemma	FF								
Glycera dibranchiata	CA								
Glycera sp.	CA	-18.3	10.9						
Glycinde soliteria	CA			-18.1	11.5	-17.7 (0.01)	12.4 (0.2)	-18.3	11.9
Heteromastus filiformis	DDF	-18.4 (0.01)	9.2 (1.2)	-18.3 (0.04)	10.9 (0.08)	-18.5 (0.09)	11.2 (0.1)	-18.7 (0.07)	10.9 (0.03)
Hobsonia florida	NBIF								
Phyllodocida	CA								
Laeonereis culveri	OM								
Leitoscolopolis fragilis	DDF	-19.0	9.3	-19.5	9.2	-18.5	11.7	-19.6 (0.01)	8.8 (0.2)
Leptocheirus plumulosus	FF	-21.0 (0.1)	8.6 (0.08)	-20.0 (0.01)	8.8 (0.1)	-19.8 (0.1)	8.8 (0.04)	-21.3 (0.1)	8.8 (0.1)
Limnodriloides anxius	SDF								
Macoma balthica	BIF			-18.6	9.7	-19.0 (0.1)	9.2 (0.06)		
Macoma tenta	BIF								
Macoma s pp.	BIF	-17.6	8.5					-19.1	9.1
Mediomastus ambiseta	SDF								
Mulinia lateralis	FF								
Neanthes succinea	OM	-17.3 (0.2)	10.9 (0.2)	-17.3 (0.2)	11.3 (0.1)	-17.8 (0.3)	11.4 (0.08)	-18.2 (0.2)	11.2 (0.08)
Nemertean	CA	-20.5	11.2	-18.3	13.0	-18.3 (0.8)	11.1 (2.2)	-20.1	10.3
Phoronis spp.	FF								
Podarkeopsis levifucina	CA	-18.2	12.4			-18.5 (0.05)	11.4 (0.1)	-19.2	12.0
Polydora sp.	NBIF								
Prionospio pinnata	NBIF	-16.3	7.8	-17.0 (0.3)	8.8 (0.7)	-17.0	8.8	-18.0 (0.09)	8.8 (0.2)
Streblospio benedicti	NBIF	-19.4 (0.1)	9.5 (0.1)	-18.8	9.0	-18.6	8.9	-19.4 (0.1)	9.9 (0.06)
Tagelus plebius	FF								
Nekton									
Calinectes sapidus									
Fundulus heteroclitus									
Leiostomus xanthurus									
Palaemonetes pugio									
Trinectes undulatus									

Scientific Name	Feeding Guild	Sarah Creek							
		Spring		July		August		September	
		Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$
Organic Matter									
Bulk Sediment 0-2 cm		-21.7 (0.2)	6.0 (0.1)	-22.7 (0.8)	4.6 (0.1)	-21.9 (0.5)	5.2 (0.2)	-21.4 (0.1)	6.1 (0.2)
Bulk Sediment 2-6 cm		-21.3	6.1	-22.2	4.8	-21.8	5.2	-21.2	6.2
Bulk Sediment 6-10 cm									
Microphytobenthos		-22.4 (0.03)	6.7 (0.2)	-21.0 (0.4)	6.9 (1.0)	-21.8 (0.1)	5.3 (0.4)	-22.3 (0.06)	5.0 (0.4)
Seston		-24.3 (0.1)	5.6 (3.6)	-25.1 (0.2)	3.2 (0.9)	-21.6 (0.02)	6.3 (0.7)	-24.1 (0.09)	8.3 (0.2)
Macrobenthos									
Ampharetidae	NBIF								
Anthozoa	FF								
Capitomastus aciculatus	SDF					-19.1 (0.1)	8.3 (0.04)		
Clymenella torquata	DDF								
Cyathura polita	OM								
Edotea triloba	OM								
Eteone heteropoda	CA	-18.5	10.1					-17.4	11.4
Gemma gemma	FF								
Glycera dibranchiata	CA								
Glycera sp.	CA								
Glycinde soliteria	CA								
Heteromastus filiformis	DDF	-18.1	10.5			-18.6	10.9		
Hobsonia florida	NBIF								
Phyllodocida	CA								
Laeonereis culveri	OM								
Leitoscolopolis fragilis	DDF					-19.2	8.1		
Leptocheirus plumulosus	FF								
Limnodriloides anxius	SDF	-20.1	11.0			-19.8 (0.06)	10.9 (0.00)		
Macoma balthica	BIF								
Macoma tenta	BIF								
Macoma s pp.	BIF								
Mediomastus ambiseta	SDF								
Mulinia lateralis	FF								
Neanthes succinea	OM			-15.8	6.3	-17.9 (0.03)	8.1 (0.02)		
Nemertean	CA					-19.0 (0.01)	9.4 (0.04)		
Phoronis spp.	FF								
Podarkeopsis levifucina	CA								
Polydora sp.	NBIF								
Prionospio pinnata	NBIF								
Streblospio benedicti	NBIF	-18.1	9.2			-19.5 (0.04)	6.9 (0.2)	-19.6	8.9
Tagelus plebius	FF								
Nekton									
Calinectes sapidus						-17.4 (0.4)	11.6 (0.3)		
Fundulus heteroclitus									
Leiostomus xanthurus						-16.7 (0.5)	11.7 (0.2)		
Palaemonetes pugio									
Trinectes undulatus									

Scientific Name	Feeding Guild	Atlantic Woods Creek							
		Spring		July		August		September	
		Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$	Mean $\delta^{13}C$	Mean $\delta^{15}N$
Organic Matter									
Bulk Sediment 0-2 cm		-24.3	4.7	-24.3 (0.2)	3.5 (0.5)	-24.2 (0.1)	3.7 (0.1)	-24.0 (0.09)	5.0 (0.04)
Bulk Sediment 2-6 cm				-24.2	3.5	-24.0	3.5	-24.3	4.4
Bulk Sediment 6-10 cm									
Microphytobenthos		-23.7 (0.3)	8.9 (0.4)	-23.5 (1.1)	4.1 (1.9)	-22.1	5.2	-23.7 (0.2)	4.4 (0.2)
Seston		-24.2 (0.07)	3.4 (2.4)	-26.2 (0.2)	3.8 (2.5)			-24.4 (0.1)	6.3 (2.5)
Macrobenthos									
Ampharetidae	NBIF								
Anthozoa	FF								
Capitomastus aciculatus	SDF								
Clymenella torquata	DDF								
Cyathura polita	OM	-13.5	11.2	-15.6 (0.4)	9.7 (0.2)	-14.0 (0.05)	10.2 (0.01)	-14.1 (0.2)	10.5 (0.4)
Edotea triloba	OM								
Eteone heteropoda	CA	-15.7	11.1					-14.0	10.8
Gemma gemma	FF								
Glycera dibranchiata	CA								
Glycera sp.	CA								
Glycinde soliteria	CA								
Heteromastus filiformis	DDF								
Hobsonia florida	NBIF	-17.9	8.6	-18.8	7.6			-17.3	8.4
Phyllodocida	CA								
Laeonereis culveri	OM	-14.9 (0.6)	9.0 (0.1)	-14.3 (0.4)	8.2 (0.1)	-13.3 (0.2)	8.9 (0.04)	-14.6 (0.1)	8.0 (0.05)
Leitoscolopolis fragilis	DDF								
Leptocheirus plumulosus	FF								
Limnodriloides anxius	SDF								
Macoma balthica	BIF	-18.4 (0.4)	5.4 (1.0)						
Macoma tenta	BIF								
Macoma s pp.	BIF								
Mediomastus ambiseta	SDF								
Mulinia lateralis	FF								
Neanthes succinea	OM			-14.2	9.5				
Nemertean	CA								
Phoronis spp.	FF								
Podarkeopsis levifucina	CA								
Polydora sp.	NBIF								
Prionospio pinnata	NBIF								
Streblospio benedicti	NBIF								
Tagelus plebius	FF								
Nekton									
Calinectes sapidus									
Fundulus heteroclitus									
Leiostomus xanthurus									
Palaemonetes pugio									
Trinectes undulatus									

Chapter V:

Overall Conclusions and Implications

SUMMARY CONCLUSIONS

In the preceding chapters, three studies investigated the effects of altered habitat quality on different functional components of food webs in shallow subtidal environments of Chesapeake Bay. Within this productive ecosystem shallow subtidal habitats are important for many ecologically and economically important biota, but they are also relatively sensitive to anthropogenic disturbances. These habitats, and similarly their food webs, are not discrete units unto themselves. They are part of the larger and more complex estuarine ecosystems and also link to the coastal ocean. Thusly, the research focused on shallow subtidal estuarine habitats for both practical and philosophical reasons.

A variety of autochthonous and allochthonous organic matter pools found at the base of the food web in estuaries are consumed by macrobenthos. Results from Chapter 4 illustrate that there was relatively little impact of decreasing habitat quality on those relationships, except for the most extreme cases of eutrophication and contamination (Atlantic Woods Creek site). Along a gradient of habitat quality, there was relatively consistent dependence of the macrobenthos on a mix of organic matter sources, with the indication that bacterially processed material may have a greater importance to the diet of the macrobenthos than in more commonly studied intertidal communities. The apparent lack of a relationship between habitat quality and macrobenthic consumption of organic matter has two likely causes: 1.) the functional redundancy of bacterial and microphytobenthic communities makes them a consistently present organic matter source in the photic subtidal zone; 2.) the sediments of shallow water depositional environments are naturally rich in organic matter, more so than could be consumed by the macrobenthos, so there is always a supply of organic matter for those species capable of utilizing it. The conclusions I have drawn from this portion of my work are somewhat at odds with a large component of the stable isotope literature, which stresses the importance of fresh microphytobenthic production supporting

macrofauna. Much of the previous work has been done in intertidal habitats where microphytobenthic production is presumably greater due to increased irradiance. My data suggest that the sediment food web may function quite differently in the subtidal zone. Consequently, future research might focus on a comparative, natural abundance stable isotope study of benthic food webs along a gradient of tidal inundation from the marsh platform → intertidal flat → shallow subtidal → deep subtidal habitats to rectify the apparent differences in the importance of different organic matter pools to the production of macrofauna.

Macrobenthos have a well-documented structural response to changes in habitat quality and the accumulation of sediment organic matter. There has been, however, little evidence to link structural changes to the function of the macrobenthos. In Chapter 2, I presented results that demonstrate a complex relationship between 2° production of the macrofauna and eutrophication/habitat quality. Either fertilization or degradation may result, depending upon the environmental setting. In depositional environments of the saline estuary, macrobenthic production decreased with decreasing habitat quality, which I hypothesize was a function of changes in the species composition of the macrobenthic community related to habitat quality, rather than conspecific changes in the production rates in habitats of differing quality. In the tidal freshwater estuary, there was a less conclusive pattern, but the trend was towards increases in the degree of eutrophication and degradation leading to increased 2° production. These dichotomous responses between similarly depositional habitats in the saline and tidal freshwater parts of the estuary are likely related to the different types of fauna that reside there. The most productive taxa found in the saline portions of the estuary tend to be bivalves, whicht are relatively sensitive to toxic reduced compounds that accumulate in the sediment under eutrophication In contrast, tidal freshwater systems are populated by taxa the are resistant to low oxygen and reduced compounds and can feed upon sediment organic matter and bacteria (i.e., oligochaetes and chironomids).

As detailed in Chapter 3, mobility and relatively sophisticated sensory capabilities limit the direct, impacts of eutrophication on nektonic communities to only the most extreme cases. The impacts of eutrophic degradation on nekton are primarily indirect, and realized through their feeding on benthic fauna. However, my experiments demonstrated that the predation pressure exerted by the nekton on the

macrobenthic community did not follow the gradient in habitat quality that I sampled. Instead, the nekton appear to have been attracted to habitats rich in bivalve production, especially those of the genus *Macoma*, and stayed in those habitats feeding on many other taxa in the process. The distribution of the bivalves did not correspond to the habitat quality gradient, with the highest levels of production and predation, at a mid-quality site. This pattern suggests that population dynamics, or habitat preferences of the bivalves were not captured in my assessment of habitat quality and may be just as important in determining the utility of different systems and macrobenthic communities as food sources to the nekton of Chesapeake Bay.

Considered together, my results show a negative impact of eutrophication on the functioning of depositional, shallow estuarine habitats. There is a loss in the 2° productivity of the system, which represents a loss in food available for subsequent trophic levels. Additionally this may indicate a loss in the amount of primary/detrital production that is transported through the food web and is therefore buried or respired through the microbial loop. Changes in productivity are probably less related to changes in the food sources to the macrobenthos relative to changes in the community structure, including those related to the stress-tolerance or feeding guilds of the component taxa. This loss in productivity to subsequent trophic levels is further exacerbated by the observation that some benthivoric nekton (e.g., blue crabs *Callinectes sapidus*) have relatively narrow profiles of what are desirable or detectable prey items and these are not found in degraded benthic communities. As such, the degraded habitats not only have reduced production compared to non-degraded ones, but that production is in the form of taxa less desirable to most predators (i.e., a trophic cul-de-sac).

These changes in productivity and utility of the fauna as vector for organic matter transport represent a fundamental breakdown in the functioning and services of this component of the ecosystem. From an energetics and functional network perspective, the role of a food web is the transformation and dispersal of energy and materials through an ecosystem (and into other, adjacent ecosystems, as well). The loss of this ecosystem function can, consequently, have a myriad of effects on the different uses of estuarine ecosystems: social, economic, and ecological. A convenient example, which is also particularly relevant to Chesapeake Bay, is the desire of both scientists and ecosystem managers to move towards the establishment of ecosystem-scale management of fisheries resources; a recognition of the interconnectedness of many commercially exploitable species and their food sources. To take this

approach, is to implicitly recognize that the suitability of the environment to the fauna will be nearly as important as the interaction of the component taxa in the food web of the ecosystem.

In my research, I developed relationships between the productivity of a system to the Chesapeake Bay benthic index of biotic integrity (B-IBI), an assessment tool currently being used to monitor and assess the quality or integrity of benthic habitats on an estuarine-wide scale. Though my study was limited in spatial scope, i.e. just in shallow water, it sets the groundwork for an added dimension to how habitat assessment is currently done in Chesapeake Bay by incorporating estimates of community function in addition to structural measures. Some further testing of these concepts across the whole estuary would allow managers to start predicting the amounts of food available for benthivoric nekton and how this would influence nektonic production in a fashion that is sensitive to changes in habitat quality.

Another potential concern for natural resource managers highlighted by this research is the possible path of recovery from eutrophic to healthy conditions in Chesapeake Bay. My 2° production data suggest that there is a differential response in benthic communities of the saline estuary to eutrophic enrichment: stimulation of community 2° production with increasing organic matter inputs in non-depositional habitats populated with filter-feeding fauna or a decline in 2° production in depositional habitats. It therefore stands to reason that, if eutrophication trends were reversed, there may be a similarly differential response in the recovery trajectory of the communities: an increase in 2° production as conditions improve and community structure changes in depositional habitats, but a decline in production at non-depositional habitats as the communities lose their organic matter subsidy. At present, all benthic habitats in Chesapeake Bay are managed uniformly under the Chesapeake 2000 Agreement among the states in the estuary's watershed and the potential for habitat-specific differential recoveries could lead to unexpected results (i.e., reduced overall benthic productivity) depending upon the net-result of productivity changes in both depositional and non-depositional habitats.

The final implication of my work that I would like to highlight concerns how habitat quality is typically measured and evaluated in estuaries and coastal oceans. In Chapter 1, I briefly discussed a number of approaches to measuring stressors and their effects in the environment. The present standard used by many state and federal agencies are based upon multi-metric indices of biotic condition like the

Chesapeake Bay B-IBI used by the Chesapeake Bay Program (also used in my work). The central reasons for their widespread and relatively successful usage are that they incorporate multiple lines of evidence describing potentially complex biotic communities while condensing this information into an understandable index that enables easy communication of overall condition to scientists, politicians, and the lay-public alike. These indices are a tool that, by design, provides a broad definition of habitat quality that works adequately for the multiple resource-users of the estuary and coastal zone. In some cases, it may do an excellent job of capturing a specific resource-user's needs or definition of quality, but not for others. My dissertation research demonstrated that the Chesapeake Bay B-IBI captured the productivity of the entire macrobenthic community quite well, which would be of benefit to a scientist with an intellectual interest in maximizing organic matter processing and food web functioning. My predator exclusion experiment, however, showed that the B-IBI and similar approaches did not do a very good job of capturing the value of a given habitat to the benthivoric nekton, which would be important to a fisheries manager concerned with maximizing ecologically sustainable landings from the estuary.

The ideal habitat quality assessment tool should be one that is still capable of evaluating habitat from a broad perspective, incorporating the needs of many resource-users, but can also be deconstructed to provide user-specific evaluations that address specific management goals, as well as providing some information on the causative forces (e.g., eutrophication, toxic chemicals, physical disturbances, or some combination of multiple stressors) of habitat degradation. The state of the science in estuarine ecology is sophisticated enough to begin to address these challenges, but I think it is more than a scientific problem. Building these kinds of management tools will require a collaboration of scientists, lawmakers, environmental mangers, and resource-users to attempt to incorporate and accurately measure the varied systems of habitat valuation of each group. The adoption of this type of approach would represent a significant step forward to an ecologically relevant and socially responsive management of the coastal zone.

VITA

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