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Organism -sediment interactions: The role of seabed dynamics in structuring the mesohaline York River macrobenthic community

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ORGANISM-SEDIMENT INTERACTIONS:
THE ROLE OF SEABED DYNAMICS IN STRUCTURING THE MESOHALINE YORK RIVER MACROBENTHIC COMMUNITY

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In Partial Fulfillment

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by

Elizabeth Kathleen Hinchey

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment

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DEDICATION

To my parents, Martha and Frank, and my siblings, Molly and Frank,
for all of their encouragement, humor, and love

and

To the amazing Janet Nestlerode,
for making everything fun

TABLE OF CONTENTS

CHAPTER 2: AN EVALUATION OF ELECTRODE INSERTION TECHNIQUE FOR MEASUREMENT OF REDOX POTENTIAL IN ESTUARINE SEDIMENTS

CHAPTER 3: TEMPORAL AND SPATIAL VARIATION IN THE SPRING RECRUITMENT OF MACROBENTHOS IN THREE MESOHALINE SUBENVIRONMENTS OF THE YORK RIVER SUBESTUARY OF CHESAPEAKE BAY

CHAPTER 4: BENTHIC COMMUNITY STRUCTURE AND SECONDARY PRODUCTION IN MAJOR SUBENVIRONMENTS OF THE MESOHALINE YORK RIVER SUBESTUARY

CHAPTER 5: RESPONSES OF ESTUARINE INVERTEBRATES TO SEDIMENT BURIAL: THE IMPORTANCE OF MOBILITY AND LIFESTYLE

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LIST OF TABLES

Table Page

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

LIST OF FIGURES

CHAPTER 4

CHAPTER 5

ABSTRACT

Estuaries are dynamic physical environments. The stability of the sediment-water interface is influenced by sources and rates of sediment delivery and physical reworking of sediments by currents, tides, waves and biology, but effects of disruption of this interface on benthic biology are poorly resolved.

For this study, I investigated effects of prevalent gradients in seabed disturbance processes and associated seabed characteristics on estuarine benthic community structure and function in the mesohaline York River, a tributary of Chesapeake Bay, USA. I used a variety of approaches to characterize the seabed, including sediment grain size, sediment water content, maximum depth of ^{7}Be, depth of the oxidized sediment layer, profiles of sediment Eh, physical structure of the sediment, sediment chlorophyll *a*, and sediment organic content. Differences in magnitude of deposition and subsequent reworking of sediments by physical processes were documented among the five benthic subenvironments sampled (south shoal, secondary channel, main channel flank, main channel, and north shoal).

Temporal and spatial variations in spring recruitment were observed among subenvironments sampled weekly for recruits: the south shoal, secondary channel and main channel flank. Total recruitment was greatest in the main channel flank, which experienced the highest sediment deposition, and was limited in the secondary channel, which had the strongest tidal currents. The five benthic subenvironments sampled for patterns of community structure and estimates of secondary production were dominated by estuarine opportunist species. Total abundance was greatest in the north shoal, which experienced minimal deposition and physical reworking of sediment. Biomass and secondary production estimates were driven by presence of deep-dwelling bivalves, and were greatest in subenvironments that experienced deposition. These results suggest that variations in seabed characteristics across relatively small spatial scales can influence estuarine benthic community structure and function.

Laboratory experiments were conducted to further elucidate the effect of sediment deposition on estuarine organism survival. Species representing both infaunal and epifaunal taxa ranged from highly susceptible to highly tolerant of burial by sediment. Survival was a function of organism motility, residence depth and perhaps physiological adaptations. Small, shallow-dwelling juveniles of some common estuarine species were highly tolerant of burial.

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ORGANISM-SEDIMENT INTERACTIONS: THE ROLE OF SEABED DYNAMICS IN STRUCTURING THE MESOHALINE YORK RIVER MACROBENTHIC COMMUNITY

GENERAL INTRODUCTION

Estuaries are challenging environments for resident benthic organisms, owing to high levels of environmental stresses associated with seasonal and tidal changes of many physical factors, including temperature, dissolved oxygen, turbidity and salinity (Deaton and Greenberg 1986, Platell and Potter 1986, Holland et al. 1987). Furthermore, the seabed in which the benthic organisms reside is itself a dynamic habitat, subject to variable sources and rates of sediment delivery and physical reworking by currents, tides, waves, and biology (Nichols and Biggs 1985, Hall 1994, Schaffner et al. 2001, Sousa 2001). Thus, estuaries are dominated by relatively few species that have evolved the complex adaptations necessary for survival in the highly variable estuarine habitat (Deaton and Greenburg 1986).

The extent to which macrobenthic communities influence estuarine function via their role in sediment modification and trophic transfer depends on factors such as species composition, abundance, size, motility and residence depth. While it is recognized that these demographic factors are often correlated with estuarine gradients of salinity and dissolved oxygen (Boesch 1977, Dauer et al. 1987, Holland et al. 1987, Dauer et al. 1993), the importance of seabed dynamics and physical sediment disturbance regimes for infaunal community structure and function remains poorly resolved (Ólafsson et al. 1994, Schaffner et al. 2001). In highly energetic estuaries and large river mouth systems, such as the Bay of Fundy, the Columbia River estuary, and the Amazon and

Changjiang Rivers, frequent, intense physical disturbance of the seabed occurs which causes impoverishment of benthic macrofauna assemblages (Rhoads et al. 1985, Aller and Aller 1986, Jones et al. 1990, Aller and Stupakoff 1996, Wildish and Kristmanson 1997). The importance of less dramatic variations in seabed dynamics for benthic community structure and function in microtidal estuaries is not as well documented, but limited evidence suggests that processes associated with turbidity maxima formation and sediment disturbance can cause depauperate benthic assemblages (Le Bris and Glemarec 1996, Schaffner et al. 2001).

Recent investigations in the upper York River, Virginia, have demonstrated that it is a tidally-energetic microtidal estuary characterized by frequent physical mixing of the fine-grained seabed (Dellapenna 1999, Dellapenna et al. 1998, 2001, Friedrichs et al. 2000, Lin and Kuo 2001, Schaffner et al. 2001, Kniskern and Kuehl in review). The documentation of physical mixing of the upper 25 cm of the seabed on fortnightly time scales by Dellapenna and colleagues (Dellapenna 1999, Dellapenna et al. 1998, 2001) sparked a series of investigations to better understand the time scales and sources of this seabed disturbance (Friedrichs et al. 2000, Lin and Kuo 2001, Kniskern and Kuehl in review) as well as the implications of seabed mixing for organic matter and contaminant transport and fate (Arzayus et al. 2002). Schaffner et al. (2001), in a review of estuarine benthic community structure and function along the York River-lower Chesapeake Bay estuarine gradient, highlighted the potential for impoverishment of benthic communities in the upper York River, driven by the high degree of seabed disturbance observed in this region of the system.

Within upper York River, Dellapenna (1999), Dellapenna et all (1998, 2001), and Kniskern and Kuehl (in review) documented that major benthic subenvironments, delineated by bathymetry and across-estuary location, were subject to differences in the frequency and magnitude of sediment disturbance across relatively short spatial and often temporal scales. The effect of seadbed disturbance on macrobenthic communities operating along these short spatial and temporal scales was an unknown, but potentially important, structuring force. Thus, I proposed to conduct an interdisciplinary investigation of organism-sediment interactions in the subenvironments of the upper York River, requiring not only collections of the macrobenthic animals, but identification of seadbed disturbance regime via geological and biogeochemical indicators of sediment disturbance.

Objectives

In this dissertation, I examine the effects of seabed characteristics and sediment disturbance regime on community structure and function in macrobenthic infaunal communities in the York River, Chesapeake Bay, USA. I use a combination of interdisciplinary field surveys and laboratory experiments to investigate the role of seabed dynamics in influencing macrobenthic recruitment, community structure, diversity, and secondary production.

In Chapter 1, I describe cross-estuary variation in physical seabed characteristics and disturbance regimes of major benthic subenvironments in the mesohaline York River subestuary during spring 1999. Based on investigations by Dellapenna et al. (1998, 2001) and knowledge of strong tidal velocities in the upper York River (Friedrichs et al.

2000, Schaffner et al. 2001), I hypothesized that a spring-neap cycles of seabed disturbance would be evident in subenvrionments characterized by strong tidal currents (secondary channel, main channel flank, main channel). The shallow, exposed south shoal was predicted to be subject to disturbance by episodic wind events and the shallow, protected north shoal was predicted to be the least energetic and least disturbed subenvironment. I used a variety of tools to characterize the seabed, including sediment grain size, sediment water content, maximum depth of ^{7}Be, depth of the oxidized sediment layer, shape of Eh profiles, physical structure of the sediment, sediment chlorophyll *a*, and sediment organic content. This habitat characterization was required to assess the role of seabed disturbance events in structuring patterns of infaunal recruitment (Chapter 3), and macrobenthic community abundance, diversity and secondary production (Chapter 4).

Although a fortnightly time scale of disturbance was not detected in any of the subenvironments, consistent differences in seabed dynamics were documented among the subenvironments. The south shoal was characterized by some deposition and physical reworking of the upper few cm of the seabed. The secondary channel experienced cycles of deposition and erosion in the upper few cm of the seabed, but displayed longer-term evidence of significant deposition and erosion. Deposition and longer-term sediment accumulation were the predominant processes in the main channel flank, likely due to sediment trapping associated with overlying lateral convergence zones. The main channel was depositional during the study, but sediments preserve a longer-term record of deposition and erosion. The north shoal subenvironment was non-depositional and was the most stable subenvironment sampled.

In Chapter 2, I investigate potential biases associated with two long-standing methods of measuring redox potential (Eh) with electrodes in sediment cores. During the course of my field study, I observed that when the electrodes are inserted laterally into the sediment through silicone-sealed ports in acrylic corers, resulting Eh values are 10-100 mV more positive than when electrodes are inserted vertically into the sediment without using ports. I present results of experiments conducted to test the hypotheses that presence of the silicone plug around the electrode shaft or possibly sulfilde poisoning was the cause of the discrepancy in Eh measurement. The results suggest that both insertion methods are subject to potential bias due to either the silicone effect (lateral insertion) or sulfide poisoning (vertical insertion), however the silicone effect is primarily responsible for the discrepancy in measurement by generating artificially positive Eh values.

In Chapter 3, I compare springtime recruitment patterns of the dominant mesohaline macrobenthic species across the different benthic subenvironments characterized in Chapter 1. Sampling was conducted in the spring because it is the time when many of the dominant species of the mesohaline macrobenthic community exhibit peak recruitment (Diaz 1984, Zobrist 1998) and maximum production (Marsh and Tenore 1990), and is also a time of significant seabed processes such as deposition and tidally-driven erosion (Schaffner et al. 2001). Spatial and intra-annual temporal differences in recruitment were observed among subenvironments at both the community and species level. There was a trend of increased abundance of total recruits, driven by the numerical dominant of the recruitment assemblage, *Streblospio benedicti,* in the subenvironment characterized by the highest deposition and long-term sediment accumulation (main channel flank) relative to the south shoal and secondary channel subenvironments. The differences in recruitment abundance and biomass patterns suggest that variations in seabed characteristics across relatively small spatial scales can influence benthic community structure.

In Chapter 4, I compare macrobenthic community structure and secondary production across the different benthic subenvironments characterized in Chapter 1. The macrobenthic assemblages were dominated by estuarine opportunists and were low in diversity. Macrobenthic abundance was highest in the subenvironment characterized by the least deposition and physical reworking of sediments (north shoal). Abundance was reduced in subenvironments characterized by deposition and physical reworking of the upper seabed. Patterns of biomass and secondary production were driven primarily by large individuals of the biomass dominant, the bivalve *Macoma balthica.* Even when disturbance regime restricted abundances of juvenile opportunistic species in surface sediments, large *M. balthica* were often present at depth in the sediments and contributed to high biomass and secondary production.

In Chapter 5, I discuss the results of stressor-reponse experiments conducted to further elucidate the effect of sediment burial on estuarine infaunal and epifaunal invertebrate species. The experiments compared survival rates of juvenile and adults of five species exhibiting different motility modes and residence depths subjected to varying overburden stress via burial by sediment. Rather than being solely a function of life stage or body size, species-specific response to burial varies as a function of motility, living position, and physiological tolerance of anoxic conditions while buried. I conclude that some benthic species (*Macoma balthica, Leptocheirus plumulosus, Crassostrea virginica*) exhibit mechanical and physiological adaptations that may allow them to survive deposition events of the magnitude commonly encountered in estuarine environments.

Overall, differences in community structure and function were observed among benthic subenvironments of the upper York River that are closely located within the same major estuarine salinity regime, but that are subject to different patterns of hydrodynamics, seabed dynamics, and longer-term sediment accumulation. Although a suite of physical and biological factors likely interacts to influence the observed patterns in recruitment, community structure and production we documented, the potential role of seabed disturbance as a major factor in structuring the upper York River macrobenthic community can not be discounted given the limited spatial scale of this study.

CHAPTER 1

CROSS-ESTUARY VARIATION IN SEABED CHARACTERISTICS AND SEDIMENT DISTURBANCE REGIMES IN THE MESOHALINE YORK RIVER SUBESTUARY

Abstract

Physical processes vary spatially and temporally in an estuary, resulting in gradients in seabed characteristics and sediment disturbance processes. We documented distinct across-estuary differences in seabed characteristics of five major benthic subenvironments (south shoal, secondary channel, main channel flank, main channel, north shoal) of the mesohaline York River subestuary of Chesapeake Bay, USA. A variety of approaches were used to characterize the seabed, including: sediment x-radiographs, profiles of sediment redox values, percent water content, chlorophyll *a*, maximum depth penetration of ^{7}Be, sediment organic content, and grain size. The south shoal subenvironment was characterized by some deposition and physical reworking of the upper few cm of the seabed. The secondary channel experienced cycles of deposition and erosion in the upper few cm of the seabed, but displayed longer-term evidence of significant deposition and erosion. Deposition and longer-term sediment accumulation were the predominant processes in the main channel flank, likely due to sediment trapping associated with overlying lateral convergence zones. The main channel was depositional during the study, but sediments preserve a longer-term record of deposition and erosion. The north shoal subenvironment was non-depositional and represents the most stable subenvironment sampled. Previous studies in the upper York River documented deep physical mixing of the seabed on tidal cycles, but the subenvironments we sampled in spring 1999 did not show discernable spring-neap tidal patterns of disturbance. Drought-induced changes in the distribution of the salinity field that reduce the intensity and variability of the local turbidity maxima provide a mechanism for

seasonal to annual system-wide shifts in the seabed disturbance regime in the upper York River estuary.

Introduction

In estuaries, stability of the sediment-water interface is affected by the sources and rates of sediment delivery and physical reworking of sediments due to currents, tides, waves, and biology (Nichols and Biggs 1985, Schaffner et al. 2001). Sediments are transported into estuaries from both the river and ocean, and are directly input via bank erosion. In many estuaries, convergent transport processes associated with estuarine circulation and tidal asymmetry in velocity and stratification lead to zones of sediment trapping within the estuary (Nichols et al. 1991, Dalrymple et al. 1992, Geyer 1993, Friedrichs et al. 1998). Fine sediments may be retained even when there is strong potential for physical reworking, and these sediments may be eroded and transported many times prior to permanent burial (Sanford 1992, Dellapenna et al. 1998). Resuspension of unconsolidated, muddy estuarine seabeds can be great enough to form near-bottom estuarine turbidity maxima decoupled from the classical estuarine turbidity maxima located near the upstream limit of salt intrusion (Uncles et al. 1994, Friedrichs et al. 1999, Lin and Kuo 2001).

The forcing factors that control seabed dynamics vary significantly along and across an estuary and temporally within a given region (Ward 1985, Wright et al. 1987, Dalrymple et al. 1992, Schaffner et al. 2001), giving rise to gradients in sediment disturbance processes and associated seabed characteristics (Nichols and Biggs 1985, Schaffner et al. 1987, Nichols et al. 1991, Dellapenna et al. 1998, Dellapenna 1999, Kniskern and Kuehl in review). In lower Chesapeake Bay, Wright et al. (1987) observed spatial variability in benthic flow regimes and seabed conditions over short distances (5 to 10 km) that were sufficient to cause corresponding variations in boundary layer dynamics and sediment transport. Dellapenna and colleagues (Dellapenna 1999, Dellapenna et al. 1998, 2001) and Schaffner et al. (2001) documented differences in seabed mixing and accumulation rates related to the strength of physical versus biological controls on mixing in across-estuary subenvironments in the York River, USA, and along the York River-Chesapeake Bay estuarine gradient. In the Columbia River estuary, high current velocities in the deep channels relative to protected bays result in major differences in sediment type and bedload movement along and across the system (Jones et al. 1990). Woodruff et al. (2001) documented rapid rates of sediment deposition and remobilization characterized by a high degree of spatial variability during and following the spring freshet in the Hudson River estuary. In the Tamar and Weser estuaries, easily erodable bed sediment is suspended, transported and deposited on intratidal time scales by tidal currents (Graberman et al. 1997).

Seabed dynamics have important implications for a variety of physical and biological processes. Formation and preservation of strata are influenced by the physical mixing of sediments, which can reset sedimentary structures through cycles of erosion and deposition of varying intensity (Nittrouer and Sternberg 1981, Dellapenna et al. 1998). Sediment resuspension and fluidization of muds can reset sediment redox boundaries, resulting in efficient remineralization of deposited organic matter (Aller 1998) and enhanced release of sediment-bound trace elements (Shaw et al. 1994). Contaminant accumulation, transport and fate are also strongly coupled to seabed dynamics, as particle-bound organic contaminants are subject to the same forces controlling fine particle dynamics (Olsen et al. 1993). Deposition can concentrate sediment-bound contaminants in the sediments, while sediment resuspension can liberate some contaminants from sediments and porewaters (Mitra et al. 1999). Macrobenthic community structure and function can also be impaired by physical disturbance of the seabed (Aller and Stupakoff 1996, Schaffner et al. 2001), resulting in impoverished faunal assemblages with decreased abundance, secondary production and diversity.

While geologists typically focus on time-scales of years to decades or longer, knowledge of the recent disturbance history of a seabed is required for correct interpretation of many key ecological and biogeochemical processes occurring in energetic estuarine environments (Mitra et al. 1999, Schaffner et al. 2001, Arzayus et al. 2002). Resolution of sediment dynamics on spatial and temporal scales relevant to processes such as macrobenthic larval settlement (Ólafsson et al. 1994) and seasonal organic matter inputs (Shaw et al. 1994) would further enhance our understanding of estuarine function. To support investigations of ecological and biogeochemical processes, the objective of this study was to examine cross-estuary spatial and temporal (weekly) variations in near-surface seabed dynamics of mesohaline York River benthic subenvironments, through characterization and comparison of physical seabed characteristics.

Materials and Methods

Study region

The study region was in the York River subestuary of Chesapeake Bay, USA. The York River is a partially mixed coastal plain estuary located on the bay's western shore. It is considered microtidal, with a spring tidal range < 1 m (Bender 1987). General descriptions of the York River environmental setting are given in Dellapenna et al. (1998)

and Schaffner et al. (2001). Bottom water salinity of 10 - 20 ppt and bottom water temperature of 2-28 °C are characteristic for this reach of the estuary. The infaunal community in the mesohaline York River is relatively depauperate, and is dominated by small annelids, peracarid crustaceans, and bivalves (Boesch 1977, Schaffner et al. 2001, Chapters 3 and 4).

Field sampling

Fifteen permanent stations were sampled for sediments weekly (on consecutive spring and neap tides) from 1 April - 21 May 1999 and again on 21 June 1999, from a 2.5 x 22 km area (Figs. 1 and 2). The relationship of sampling dates to the spring-neap tidal cycle is given in Figure 3. Sampling was conducted during a time of predicted maximum physical forcing, owing in part to the interaction of perigean spring tides with high river discharge rates that occur during spring periods of high freshwater inflow, and also to the greater potential for storms to occur relative to summer months (Friedrichs et al. 1999, Schaffner et al. 2001, Kniskern and Kuehl in review). One spring tide sampling date (17 May) occurred 1 day after a northeast storm. Only one secondary channel station (SC10) was missed due to rough sea conditions on 20 April.

The stations established a range of across-estuary subenvironments that were designated south shoal, secondary channel, and main channel flank (Fig. 2). The rationale for sampling the south shoal and secondary channel subenvironments was based on previous research in the upper York River system that revealed differences in sources of physical energy and resulting effects on the seabed between these subenvironments (Dellapenna et al. 1998, Dellapenna 1999, Schaffner et al. 2001). The depth difference between these subenvironments (mean depths for this study: south shoal = 2.5 m, secondary channel = 4.8 m) results in greater bottom tidal current speeds at the secondary channel relative to the south shoal (Huzzey and Brubaker 1988, Schaffner 1997) and increased potential for wind-driven wave orbital velocity to impact the seabed at the south shoal (Sanford 1992, Schaffner 1997). Thus, it was predicted that seabed dynamics at the secondary channel would vary on time scales related to spring-neap tidal cycles due to greater strength of tidal currents here, and vary on episodic time scales related to occurrence of wind events at the south shoal. The main channel flank stations were originally intended to be located in the south shoal and secondary channel, however presence of a relict oyster reef prohibited sample collection at the original randomly stratified station locations, resulting in selection of five stations upriver of the secondary channel. The resulting sampling effort across subenvironments was: 4 stations in the south shoal, 6 stations in the secondary channel, and 5 stations in the main channel flank.

In an attempt to sample muddy, undisturbed sites in the York River as controls, we conducted nearshore sampling of five permanent stations on the north shoal (Figs. 1 and 2). The north shoal has little to no sediment accumulation (Dellapenna 1999). As these stations were too shallow (mean depth < 1.5 m) to be sampled with the research vessel used for the other stations, four sampling cruises were conducted at approximately monthly intervals (6 April, 7 May, 3 June, 24 June 1999) using a smaller boat. Two of the north shoal sites were located near the mouths of tidal creeks, and three were located in near shore bays (Fig. 1).

In addition, two spring tide cruises (13 May and 18 June, 1999) were conducted to investigate sediment dynamics in the main channel subenvironment. These 12 permanent main channel sites were located slightly farther downstream than the other, more frequently sampled subenvironments (Figs. 1 and 2), in an area of the river where strong currents, fluid mud layers, and estuarine turbidity maxima had been previously documented (Friedrichs et al. 1999, Lin and Kuo 2001, Schaffner et al. 2001).

Methodological approach

A variety of tools were used to describe the physical characteristics of the seabed in each subenvironment. X-radiographs of sediment cores were used to characterize the sedimentary fabric and seabed disturbance signatures. General interpretations of features are as in Schaffner et al. (1987), Dellapenna et al. (1998), and Dellapenna (1999). Strata formed through physical mixing exhibit sediment packets separated by hiatal (erosional) surfaces. Physical laminations are indicative of deposition. Biological reworking of sediments, such as burrow formation or tube construction increases as physical sediment disturbance decreases. X-radiographs can provide evidence to determine the role of biological vs. physical mixing in a core and denote long-term changes in each, but alone provide little insight into the rates of processes (Schaffner et al. 1987). By coupling x-radiographs with other surface sediment characterization methods and employing a weekly sampling regime, short-term interactions among erosion, deposition, and biogenic reworking might be resolved.

Profiles of sediment redox potential (mV) were generated from cores to document existence of highly oxidized layers of sediment that are assumed to be present only when muddy sediments are bioturbated or have been recently mobilized by physical disturbance (Schaffner et al. 2001). Profiles of sediment water content and chlorophyll *a* (chl *a*) were also used to determine recent mixing history of sediments. For a given grain size, sediments that have been recently deposited are less compacted, as evidenced by higher water contents than undisturbed sediments (Dellapenna et al. 1998). As there is not enough light penetration in subtidal upper York River sediments to support benthic microalgal production, any chl *a* present in the sediments is derived from sedimentation of planktonic algae or lateral transport from shallows (Malone et al 1986). Presence of chl *a* at depth in sediment (half life ~23 d) indicates recent deposition or mixing of sediments (Sun et al. 1994). Sediment organic content (TOC, TN) was also measured in the surface sediments to index sediment lability, which is another indication of recent deposition of organic matter (Canuel and Zimmerman 1999). Low sediment C:N ratios (6-8) indicate presence of labile organic matter such as sedimenting phytodetritus in sediments (Marsh and Tenore 1990), whereas higher C:N ratios (20-60) are attributed to the presence of older refractory organic matter such as that derived from salt marsh detritus (Valiela 1995). At some stations on some dates penetration depth of the short-lived radioisotope ^{7}Be ($t_{1/2}$ =53 d) was determined to estimate depth of short-term deposition and/or mixing (Schaffner et al. 1987, Dellapenna et al. 1998, 2001). ^{7}Be is introduced into the water column by atmospheric deposition and is scavenged readily by particles in the water column. Due to the short half life of this isotope, it can be assumed that ^{7}Be found below the sediment-water interface is a result of recent deposition or bioturbation (Dibb and Rice 1989). Subenvironments exhibiting deep ^{7}Be sediment penetration depths are interpreted as being depositional or recently physically mixed when there is no evidence of bioturbation (Dellapenna et al. 1998, 2001, Knistern and Kuehl in review).

Sample collection

At the south shoal, secondary channel, main channel flank, and main channel stations, sediments were collected with a Gray O'Hara box core (625 cm^2 area, 50 cm maximum length). For the north shoal stations, sediment cores were collected by hand by snorkeling, with the same acrylic subcores that were used to remove sediments for the various analyses from the box core (described below).

In the field, three acrylic subcores were removed from each box core for sampling of various parameters. Sediment from a 15.2 cm (i.d.) subcore was extruded upward and sliced into 1 cm increments. The sediment from the 0-1, 1-2, 2-3, 3-4, 4-5, 10-11, and 15-16 cm increments was apportioned for analyses of sediment water content, grain size, TOC and TN, chl *a*, and ^{7}Be presence. Sediments for water content, organic content and chl *a* content were frozen at –80 °C for later determination; sediments for grain size were refrigerated until analyzed. A 10.2 cm (i.d.) subcore was removed for determination of a downcore profile of sediment redox potential. A rectangular subcore (11.5 x 60 x 2 cm) was removed and x-rayed to examine physical and biogenic structures. From each box core, sediment surface temperature was measured with a thermometer, and salinity of water overlying the sediment was measured with a refractometer.

Laboratory analyses

Sediment x-radiographs were made using Kodak Industrex Redipack™ film and a Dinex 120-F X-ray unit set at 3mA and 60 kV. Exposure times were 45-60 s (Dellapenna et al. 1998). Sediment water content was estimated by weight loss of wet sediment samples oven-dried at 60 °C for approximately 3 d or until dry (not corrected for salt content). Sediment percent sand, silt and clay composition was determined following standard sieving and pipette analysis procedures described in Folk (1980) after addition of sodium hexametaphosphate as a dispersant. When data are expressed as mud, this equals the combined silt and clay fractions. Organic content was determined with an EA 1108 CHNS-O elemental analyzer (Fisons Corp.) after acidification with 10% HCl to remove carbonates (Hedges and Stern 1984). Sediment chl *a* samples were analyzed spectrophotometrically following the procedures of Pinckney et al. (1994), modified by Neubauer (2001). Collection of sediments for organic content and chl *a* commenced on 13 April 1999, two weeks into the study.

Profiles of redox potential (measured as Eh) were generated for subcores collected from the south shoal, secondary channel flank, secondary channel and main channel flank on 7 May, 10 May and 17 May, from the main channel on 13 May, and from the north shoal on 3 June and 24 June, 1999. Measurements were made immediately after collection by inserting a platinum electrode (3-mm long, 0.5 mm wide) vertically down through the sediment surface (Moore et al. 1993, Chapter 2). Voltage readings were recorded at 1 cm intervals, beginning 0.5 cm above the sediment water interface. The resulting redox potential was read on a Beckman model 220 portable pH-millivolt meter connected to a saturated calomel electrode suspended in the water overlying the subcore. Values were corrected to the hydrogen reference electrode scale by adding + 244 mV to each measurement (Bagander and Niemisto 1978). Calibration of the electrodes was verified by measuring the redox potential of quinhydrone dissolved in buffers of pH 4 and 7 (Bohn 1971). Electrodes were cleaned prior to use and after each profile by scouring with a non-chlorinated cleansing powder and wiping with a deionized water-soaked tissue.

^{7}Be was measured using either a semi-planar intrinsic germanium detector, a coax detector, or a well detector coupled with a multichannel analyzer. For the coax and intrinsic germanium detectors, samples were homogenized, packed wet, sealed into 70 ml Petri dishes and counted for ~24 h (Dellapenna et al. 1998). For the well detector, samples were homogenized, dried, ground and sealed into 12 ml vials and counted for ~24 h. The ^{7}Be data must be viewed as ancillary, as penetration depths were not determined for all subenvironments on each sampling date, and for a number of cores the maximum penetration depth of <1 cm is an estimate (Table 1). In these cores, the 0-1 cm surface sediment layer was not counted, therefore it is unknown if ^{7}Be was absent from the 0-1 cm layer or indeed present to a depth of 1 cm. Absence of ^{7}Be in the 1-2 cm layer of these cores constrains the maximum penetration depth of ^{7}Be to <1 cm.

Statistical analyses

We tested for differences in mean sediment water content (0-5 cm), chl *a* (0-5 cm), percent mud (0-1 cm), organic content (0-1 cm) and maximum depth of oxidized sediments with 1-way Model I ANOVAs. All data were checked for normality with a Shapiro-Wilks test (Zar 1999) and for homogeneity of variance with a Cochran's test (Underwood 1997). Percent mud content data were transformed (X^2) prior to analysis. When significant differences in the sediment parameters were detected among subenvironments, Tukey *post hoc* comparison tests were performed.

Statistics were performed using PC SAS version 8.0 (SAS Institute, Cary, NC).

Results

General physical setting. Surface sediment temperature increased during the course of the study from approximately 13 °C in early April to approximately 24 °C in late June 1999 (Appendix I). Differences in mean sediment temperatures among the subenvironments were < 3 °C on a given sampling date. Mean salinity (averaged across all subenvironments sampled on a given date) increased from ~ 12 ppt in early April to ~ 20 ppt in late June 1999 (Appendix I). Data for near-bottom (1 m) current speed during the month of April 1999 for the secondary channel is provided by Kniskern and Kuehl (in review), who deployed moored Inner Ocean S4 current meters from 26 January to 26 April, 1999. They measured bottom currents ranging from 5-40 cm/s during neap tides and 40-70 cm/s during spring tides, which is in agreement with other near-bottom current measurements previously recorded in the secondary channel (Schaffner et al. 2001).

Seabed characteristics. We found no significant spring-neap changes in x-radiograph appearance, sediment grain size, sediment water content, sediment Eh, sediment chl *a*, or sediment organic content during the study. Therefore, for each subenvironment, representative x-radiographs and grand mean data for sediment grain size, sediment water content, sediment Eh, sediment chl *a*, and sediment organic content are presented. Time series data for grain size and organic content of the surface sediments (0-1 cm) and profiles of sediment water content, sediment Eh, and sediment chl *a* (0- 15 cm) comprise Appendix II.

X-radiographs. In general, x-radiographs exhibited distinct sediment stratigraphic patterns across subenvironments (Fig. 4). Although some episodic depositional events, characterized by well preserved primary physical laminations in surface sediments, were noted for some subenvironments (discussed below), consistent spring-neap variations in x-radiograph appearance were not observed at any of the subenvironments sampled.

The south shoal x-radiographs showed relatively mottled sediments overlain by 1-5 cm of mm-scale physical laminations (Fig. 4). Bioturbation by live burrow-dwelling *Macoma balthica* bivalves and tube building *Loimia medusa* polychaetes was apparent in many of the south shoal x-radiographs, indicating a lack of recent sediment disturbance of deeper sediment layers.

X-radiographs from the secondary channel exhibited 2-3 cm of fine laminations, indicating recent deposition. These laminations were over unstructured and/or bioturbated units of sediment 5-20 cm thick, interspersed by physical laminations and hiatal surfaces, which indicate a complex history of past erosion and deposition events. Laminations at depth were distorted by *Macoma balthica* burrows and tubes of large *Loimia medusa*, and live *Macoma balthica* were often present in the cores.

Physical features dominated sediment structure in the main channel flank. Packages of mm- to cm-thick laminae (in 10 cm-thick units) were present throughout the cores, suggesting the occurrence of frequent tidal forcing. These laminae often appear less-distinct downcore, perhaps due to bioturbation processes such as burrow formation. Live *Macoma balthica* were present in many of the cores. Hiatal surfaces were visible in some x-radiographs, but were generally less prevalent in the main channel flank than in the secondary channel.

With the exception of the four most downstream stations, x-radiographs from the main channel were similar in appearance on the two sampling dates. The eight upstream main channel stations yielded x-radiographs characterized by sediment with packages of cm-scale laminations, indicating sediment deposition. Laminations were less distinct downcore as the result of bioturbation. Compared with the secondary channel, hiatal surfaces did not appear until deeper depths in cores. X-radiographs of the next two downstream main channel stations revealed mottled looking cores, with no distinct laminations preserved, just massively undulated and/or bioturbated erosional contacts.

Density changes in x-radiographs of the two most downstream main channel stations in May reveal that sediments become consolidated at depths of approximately 10 cm. In these cores, a layer of relatively unstructured sediment was situated over packets of laminated sediments, each 10 cm thick. In x-radiographs from June, sediments appeared more homogeneous. Physical laminations were absent, and animal burrows and shell fragments were observed.

North shoal x-radiographs were characterized by burrows and mottling, reflecting bioturbation, with no preservation of physical stratification below 2 cm, if at all. They often resembled the x-radiographs of Frey et al. (1989) for tidal creek-margin sediments, and usually revealed a muddy sand layer with detritus overlying root-mottled sediment composed of dead *Spartina alterniflora*.

Sediment grain size. Surface sediments in the south shoal, secondary channel flank, secondary channel and main channel were consistently muddy, with grain sizes ranging from silty clays to clayey silts (Fig. 5). Main channel flank surface sediments were also muddy and primarily composed of silty clay (Fig. 5). Grand mean percent mud contents for the study period were highest for the south shoal (95%), main channel flank (98%) and main channel (93%) subenvironments (Fig. 6), with the secondary channel having a lower mud content of 89% (Fig. 6). Stations in this subenvironment spanned a wider range of mud contents (83-97%), with the cores containing coarser surface sediments primarily collected from one station (Fig. 5). Compared to the other subenvironments, the north shoal was the least muddy, with a grand mean percentage of 41% mud in surface sediments (Fig. 6). North shoal grain sizes ranged from sandy to clayey sand to sand-silt-clay, depending on station (Fig. 5).

Sediment water content. Surface sediments in the main channel flank contained water contents that were higher than in all other subenvironments except the main channel, with values of 70 % water to a depth of 15 cm (Tables 3 and 4, Fig. 7). This percent mud content of main channel flank surface sediments was also significantly greater than in all other subenvironments except the main channel (Tables 3 and 4, Fig. 6). Water content profiles for the muddy south shoal and secondary channel subenvironments show that sediments deeper than 5 cm generally contained water contents on the order of 55-60 %.

The slope break in water content profile for the main channel was subtle, with mean values in near-surface sediments of approximately 70%, and values at depths > 5 cm of approximately 65%. North shoal surface sediments had the lowest water contents, which can be attributed to the lack of deposition and coarser grain sizes encountered in this subenvironment (Tables 3 and 4, Fig. 5). During core extrusion in the field, a high level of sediment compaction relative to the other subenvironments was noted at north shoal stations. It was not possible to obtain a long core from the station that was the most compacted, therefore in this case nominal values of percent water content from the deepest layer sampled were substituted for missing values. The large standard error of the grand mean percent water content at north shoal is due to the larger variation in grain size between stations relative to the other subenvironments.

Sediment Eh. Mean depth of oxidized sediments (>0 mV) ranged from 3 to 7 cm among subenvironments. Differences in oxidized depth among subenvironments were not significant (Tables 3 and 4), but there was a trend for the deepest oxidized sediments to occur at the main channel flank (Fig. 8), the subenvironment characterized by the finest sediment and highest water content (Figs. 6 and 7). Redox profiles at the south shoal and secondary channel exhibited steeper declines with depth than did the main channel flank redox profile. The north shoal exhibited a trend of negative Eh values in near-surface sediments, with values of –100 mV recorded at depths of only 6.5 cm (Fig. 8).

Sediment chl a. Grand mean chl *a* abundance in near-surface sediments (0-5 cm) did not differ among subenvironments during the study (Tables 3 and 4), however the slopes of the profiles exhibited different trends (Fig. 9). Mean chl *a* values in the top 5 cm of main channel flank sediments were relatively uniform, and chl *a* values at the other subenvironments tended to decrease more rapidly with depth in the upper 5 cm (Fig. 9).

Sediment organic content. TOC abundance in surface sediments (0-1 cm) was highest in the main channel flank subenvironment, with a grand mean of ~ 3.0 % (Tables 3 and 4,

Fig. 10a). TN abundance in surface sediments was significantly greater in the main channel and main channel flank subenvironments (Tables 3 and 4, Fig. 10b). Elemental ratios expressed on a molar basis ($C:N_a$) were calculated from the TOC and TN concentration data. North shoal sediments contained the most refractory organic matter, as indicated by the highest sediment $C:N_a$ (grand mean of 15.3; Tables 3 and 4, Fig. 10a). The main channel surface sediments contained the lowest $C:N_a$ (10.5) sampled (Tables 3 and 4, Fig. 10a), which indicates that this subenvironment contained the most labile organic matter. Sediment $C:N_a$ of the remaining subenvironments were intermediate between the north shoal and main channel subenvironments, with grand mean values of approximately 12.5.

^{7}Be. Although the data are limited, ^{7}Be maximum penetration depths indicate that recently deposited sediments were present on a number of sampling dates throughout the sampling period (Table 1). The deepest penetration of ^{7}Be to 6 cm was observed at the main channel flank. ^{7}Be was found to 4 cm at both the south shoal and main channel, and to 2 cm at the secondary channel and north shoal. Replicate samples were not always available to assess spatial variability in a subenvironment; spatial variability is indicated for dates when multiple samples were counted in the main channel flank, main channel, and north shoal subenvironments.

Discussion

The upper York River subenvironments sampled in spring 1999 did not show discernable spring-neap patterns of sediment disturbance despite expectations based on previous studies. Although a temporal pattern of sediment disturbance was not observed, we documented consistent differences in seabed characteristics among subenvironments. These results indicate that physical forcing acts to differentially structure seabed characteristics across the estuary.

The main channel flank experienced the greatest amount of sediment accumulation of the five sampled subenvironments, based on the criteria we used. This subenvironment had the finest sediment grain size, the deepest depth of oxidized sediments (7 cm), highest sediment water contents both in the surface and at depth, ^{7}Be depths up to 6 cm, elevated surface sediment TOC and TN abundances, low C:N$_a$, and x-radiographs with thick layers of physical laminations (Table 2). Channel flanks are recognized as often being depositional estuarine subenvironments (Nichols 1972, Byrne et al. 1982). In the upper York River, it is hypothesized that near-bed convergence associated with lateral circulation processes drives sediment deposition on the main channel flank (C. Friedrichs, pers. comm.). Sediment transport in the main channel is greater on the flood tide, whereas sediment transport in the secondary channel is greater on the ebb tide (Friedrichs et al. 2000, Scully and Friedrichs in review). This hydrodynamic pattern is expected in an estuary with both a main channel and a shallower secondary channel or lateral shoal (Friedrichs and Hamrick 1996). Coriolis force in an estuarine channel in the northern hemisphere causes flow at the surface to turn toward the right ("surface Ekman layer") and flow at the bottom to turn toward the left ("bottom Ekman layer"), creating lateral convergence zones between main and secondary channels (Friedrichs and Valle-Levinson 1998). Therefore, the dominant nearbed lateral sediment transport pathway in the main channel is toward the secondary channel (maximum on flood tide) and the dominant near-bed lateral sediment transport pathway in the secondary channel is toward the main channel (maximum on ebb tide), resulting in deposition on the main channel flank. Kniskern and Kuehl (in review) similarly suggest that convergence due to lateral circulation is the explanation for high sediment accumulation in upslope regions of the secondary channel flank, which in turn can cause episodic sediment slumping when slopes become unstable.

The south shoal was also a depositional subenvironment. Surface sediments were composed of silty-clays, and water content profiles at this site indicate that the muddy sediments were more compacted than in the main channel flank. ^{7}Be was present to a depth of 4 cm on the one date it was measured. Oxidized sediments were present to a depth of 6 cm. Underneath the relatively shallow depth (1-5 cm) of physically reworked sediments, sediment structure was relatively mottled from week to week and often was bioturbated. Kniskern and Kuehl (in review) suggest two possible explanations for the mottled appearance of sediments in their south shoal x-radiographs. One is that the shallow bathymetry of this subenvironment renders it susceptible to wind-wave disturbance, which would disturb laminations and thus obscure any evidence of short-term erosion/deposition events from the sediment record. The other is that sediment deposition in this subenvironment occurs en masse without generation of laminations. Despite their observation that up to 31 cm deposition occurred during neap tides in this subenvironment, Kniskern and Kuehl (in review) recorded only one deposition event in their x-radiographs (7 April 1999) that contained 10 cm of laminations; their other neap x-radiograph (6 March 1999) did not record deposition. In our study, no differences in x-radiograph or sediment geochemistry profiles were observed after a northeast storm, suggesting that wind-wave energy was not controlling sediment structure in the south shoal subenvironment during spring 1999. The mottled nature of sediments may have been caused by wind-wave disturbance or deposition of sediments en masse at a date that preceded this study. Biotic reworking by large bivalves and polychaetes was frequently observed in the south shoal x-radiographs, but it is unlikely that this produced the homogeneous subsurface sediment, since estimated rates of bioturbation in this region of the estuary are low (Dellapenna et al. 1998, Schaffner et al. 2001).

Sediment characteristics suggest that the secondary channel is a highly dynamic subenvironment, subject to variable, perhaps erosional, physical forcing interspersed with depositional events. X-radiograph appearance together with grain sizes composed of a mixture of sand-silt-clay, suggest that fine sediments deposited in this subenvironment are subsequently winnowed away by tidal currents. ^{7}Be data and water content, Eh and chl *a* profiles suggest that physical reworking is limited to the top 3-5 cm in this subenvironment during our observational period.

The main channel subenvironment is depositional, as indicated by fine grain sizes, elevated water contents, high organic contents, high sediment chl *a* values, and ^{7}Be penetration depths up to 4 cm. X-radiographs generally appear laminated throughout their length, with primary sediment structures well preserved at depth. The presence of some interspersed bioturbated layers throughout the core suggests that there may be a time lag between deposition events that allow for colonization by organisms (Schaffner et al. 1987, Kniskern and Kuehl in review). The presence of oxidized sediments to a depth of only 3 cm suggests that any recent physical reworking events were restricted to this depth.

Attempts to sample low-energy stations in the north shoal subenvironment that also contained fine-grained sediments proved difficult, as predicted by earlier sampling in this subenvironment by Dellapenna (1999). The facies model proposed by Dellapenna (1999) that relates lithofacies pattern to estuary morphology and energy regime suggests that this subenvironment is non-depositional, therefore it was not surprising that habitats containing muddy sediments (>80 % mud) could not be located. Our five north shoal stations were composed of coarser sediments, ranging from muddy sands to sands, and often contained an abundance of detritus owing to their proximity to tidal creeks. The x-radiographs from this subenvironment were not physically structured, and often displayed bioturbation. ^{7}Be was only found at depth on one occasion, and it is possible that its presence at 2 cm was a result of bioturbation. Bioturbation could also account for presence of oxidized sediments to depth of 4 cm. The north shoal sediments were more reducing overall (< –100 mV at 6 cm), as redox values declined more rapidly with depth than at the other subenvironments.

Earlier work in the upper York River by Dellapenna and colleagues (Dellapenna 1999, Dellapenna et al. 1998, 2001) revealed that the seabed in this system was subject to frequent, deep physical mixing. In the secondary channel, physical mixing of the upper 25 cm of the seabed was observed to occur on fortnightly time scales, due to the formation of transient sedimentary furrows during neap tides and their infilling and destruction on subsequent spring tides (Dellapenna et al. 2001). These observations, in conjunction with knowledge of strong tidal energy in the upper York River operating on an unconsolidated, easily erodable fine-grained seabed, led to the prediction that spring-neap differences in disturbance regime would be observed during our intensive study. Despite predictions, spring-neap differences in disturbance regime were not detected in spring 1999. Use of multiple techniques for documenting disturbance in conjunction with weekly sampling on consecutive spring and neap tides (which also encompassed a windy storm event) ensured we were appropriately poised to sample the seabed to document any potential disturbance.

The existence of a severe drought that reduced the intensity and variability of the turbidity maxima during the course of this study could explain why less sediment disturbance was documented in spring 1999 relative to earlier surveys during exceptionally wet years (1995-1998) by Dellapenna (1999). USGS discharge data for the Mattaponi and Pamunkey Rivers reflect the 1999 drought, with low river flow into the York River observed (USGS 2002). Variations in river flow change the salinity field and, indirectly, shift the location of the turbidity maxima in the York River by tens of kilometers. Wetter seasons favor greater turbidity down-estuary as the frontal trapping zone migrates seaward (Lin and Kuo 2001). Kniskern and Kuehl (in review) further postulate that the secondary channel could receive less sediment when a secondary turbidity maximum is present downstream, thus potentially limiting formation of sedimentary furrows.

Acknowledgments

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Table 1. Maximum ^{7}Be Penetration Depths (cm) in Upper York River Subenvironments.

Subenvironment	**Dates (month/day/year) of samples collected for ^{7}Be measurement**	**Maximum ^{7}Be penetration depth (cm)**
South shoal	04/01/99	4
	04/20/99	<1 *
	06/21/99	<1 *
Secondary channel	04/13/99	2
	04/20/99	<1 *
	04/27/99	<1 *
	05/03/99	2
	05/17/99	<1 *
	06/21/99	<1 *
Main channel flank	04/08/99	<1 * , <1 *, 4
	04/13/99	2
	04/20/99	<1 *
	04/27/99	6
	05/10/99	<1 *, 3
	05/17/99	<1 *, 2
	05/21/99	<1 *, <1 *
	06/21/99	<1 *
Main channel	05/13/99	0, 3
	06/18/99	4, 4
North shoal	05/07/99	<1 *, <1 *
	06/03/99	<1 *, <1 *, <1 *
	06/24/99	<1 *, 2

Dates with more than one ^{7}Be maximum penetration depth display data from sediments collected at multiple stations in the subenvironment. The <1 cm depths are labeled with an asterisk to indicate that this depth is a maximum estimate, as the 0-1 cm fraction for these cores was unfortunately not counted for ^{7}Be presence. Thus, it is possible that ^{7}Be was present in the surface sediment layer but its actual existence is unknown.

Table 2. Summary of measured seabed parameters (grand means with ranges of means in parentheses) for the different subenvironments during the study period of 1 April 1- 21 June, 1999. Depths are actual depths sampled.

Subenvironment	south shoal	secondary channel	main channel flank	main channel	north shoal
Station depth	2.5 m (1.8-3)	4.8 m (3.8-5.8)	3.4 m (2.5-3.8)	11.2 m (8.5-14)	1.5 m (1.5-1.5)
Water content (%) 0-5 cm	65 (63-70)	65 (60-67)	73 (73-76)	68 (56-81)	48 (24-76)
Mud content (%) 0-1 cm	95 (92-96)	88 (83-97)	98 (96-99)	93 (93-93)	43 (37-48)
Depth of 0 mV Eh	6 cm (4.5-11.5)	4.5 cm (3.5-13.5)	7 cm (5.5-12.5)	3 cm (1-6.5)	4 cm (4-4)
Max. depth of ^{7}Be	4 cm (<1 - 4)	2 cm (<1 - 2)	6 cm (<1 - 6)	4 cm (0-4)	2 cm (<1 –2)

X-radiograph appearance	fine surface laminations (0-5 cm) over mottled with some bioturbation	laminations and hiatal surfaces interspersed with 5-20 cm of bioturbated units	mm-cm thick packets of laminations throughout cores; bioturbation at depth	mm-cm thick packets of laminations throughout cores; bioturbation at depth	mottled or bioturbated
Chl *a* (μg g^{-1} wet sed) 0-5 cm	2.7 (1.8-4.1)	2.6 (1.9-3.4)	3.0 (1.8-5.4)	4.4 (4.1-4.7)	2.4 (0.9-3.7)
TOC (%) 0-1 cm	2.28 (2.02-2.57)	2.29 (1.97-2.5)	2.98 (2.75-3.16)	2.48 (2.23-2.73)	2.10 (1.71-2.33)
$C:N_a$ 0-1 cm	12.6 (11.7-13.6)	12.3 (11.8-12.9)	12.4 (11.6-13.3)	10.48 (10.4-10.6)	15.3 14.6-16.0

Table 3. Results of 1-way ANOVAs tests for differences among subenvironment in select sediment parameters. *P* values < 0.05 are in bold.

Source (DF)	SS	MS	F	P
Percent mud				
subenvironment (4)	193x10^6	48.5x106	248.76	**0.0001**
error (31)	6.04x10^6	0.19x10^6		
Percent water				
subenvironment (4)	2327.070	581.760	144.81	**0.0001**
error (31)	124.540	4.018		
Chl *a*				
subenvironment (4)	6.066	1.516	1.63	0.1995
error (24)	22.343	0.931		
Depth of oxidized layer				
subenvironment (4)	38.667	9.667	0.66	0.6370
error (7)	102	14.571		
TOC				
subenvironment (4)	287.342	71.836	15.97	**0.0001**
error (24)	0.864	0.032		
TN				
subenvironment (4)	4.487	1.122	25.26	**0.0001**
error (24)	1.066	0.044		
$C:N_a$				
subenvironment (4)	31.544	7.886	24.69	**0.0001**
error (24)	7.665	0.319		

Table 4. Results of Tukey multiple comparisons for differences in sediment parameters across subenvironment. First column lists subenvironment, second column indiactes subenvironment comparison for which a significant difference in mean was detected (*P* <0.05). Subenvironment abbreviations: SS= south shoal; SC= secondary channel; MCF= main channel flank; C= main channel; NS= north shoal.

Percent mud

subenvironment	significant difference
SS	SC, MCF, NS
SC	SS, NS
MCF	SS, SC, NS
C	NS
NS	all

Percent water

subenvironment	significant difference
SS	MCF, NS
SC	MCF, NS
MCF	SS, SC, NS
C	SC, NS
NS	all

TOC

subenvironment	significant difference
SS	MCF, C
SC	MCF, C
MCF	all
C	MCF
NS	MCF

TN

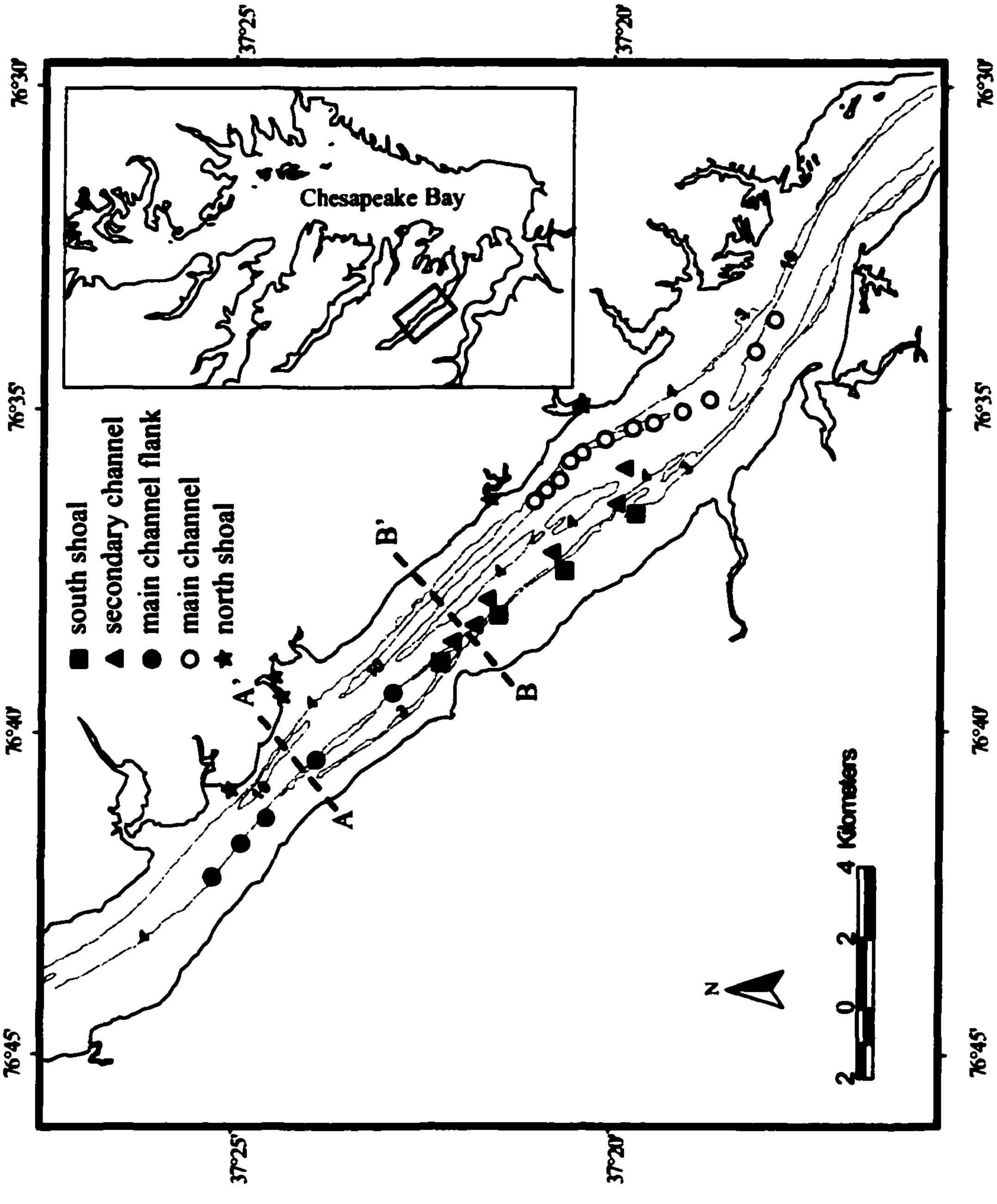
subenvironment	significant difference
SS	MCF
SC	MCF
MCF	SS, SC, NS
C	SS, SC, NS
NS	all

Table 4. (Continued)

$C:N_a$

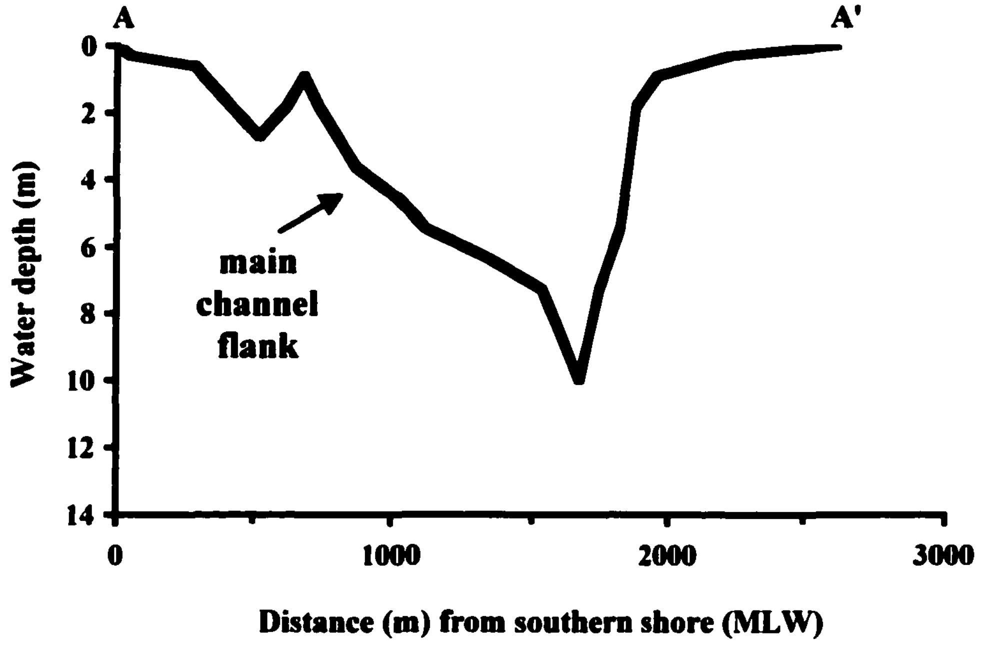
subenvironment	significant difference
SS	C, NS
SC	C, NS
MCF	C, NS
C	all
NS	all

Fig. 1. The upper York River estuary study area, showing station locations in each sunbenvironment and depth contours of 3, 4, and 10 m. Transect lines (A-A' and B-B') indicate locations of the cross sections depicted in Fig. 2.



76°30'
76°35'
76°40'
76°45'
37°25'
37°20'
Chesapeake Bay
■ south shoal
▲ secondary channel
● main channel flank
○ main channel
★ north shoal
A
A'
B
B'
N
2 0 2 4 Kilometers

Fig. 2. Cross-sectional profiles of two upper York River transects (A-A') and (B-B'), depicting locations of the sampled subenvironments. The profiles show change in bathymetry along the transects, expressed as distance from the southern shore (MLW).


A
A'
Water depth (m)
0
2
4
6
8
10
12
14
main channel flank
0
1000
2000
3000
Distance (m) from southern shore (MLW)

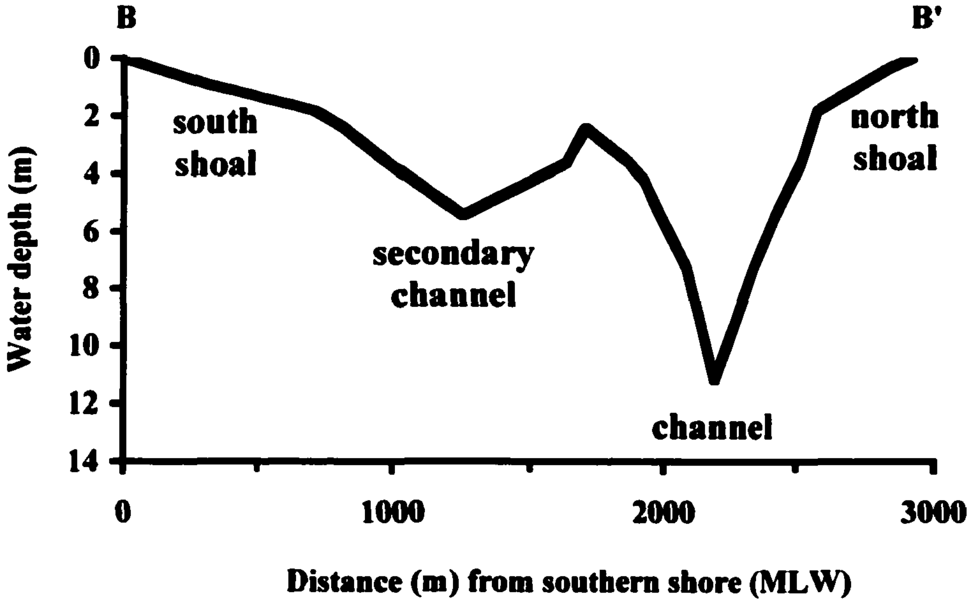

B
B'
Water depth (m)
0
2
4
6
8
10
12
14
south shoal
secondary channel
channel
north shoal
0
1000
2000
3000
Distance (m) from southern shore (MLW)

Fig. 3. Graph of NOAA predicted tide height (cm) in the upper York River, corrected for Clay Bank location for 1 March through 30 June, 1999. Sampling dates are indicated, along with dates of perigean spring tides and a northeasterly storm.

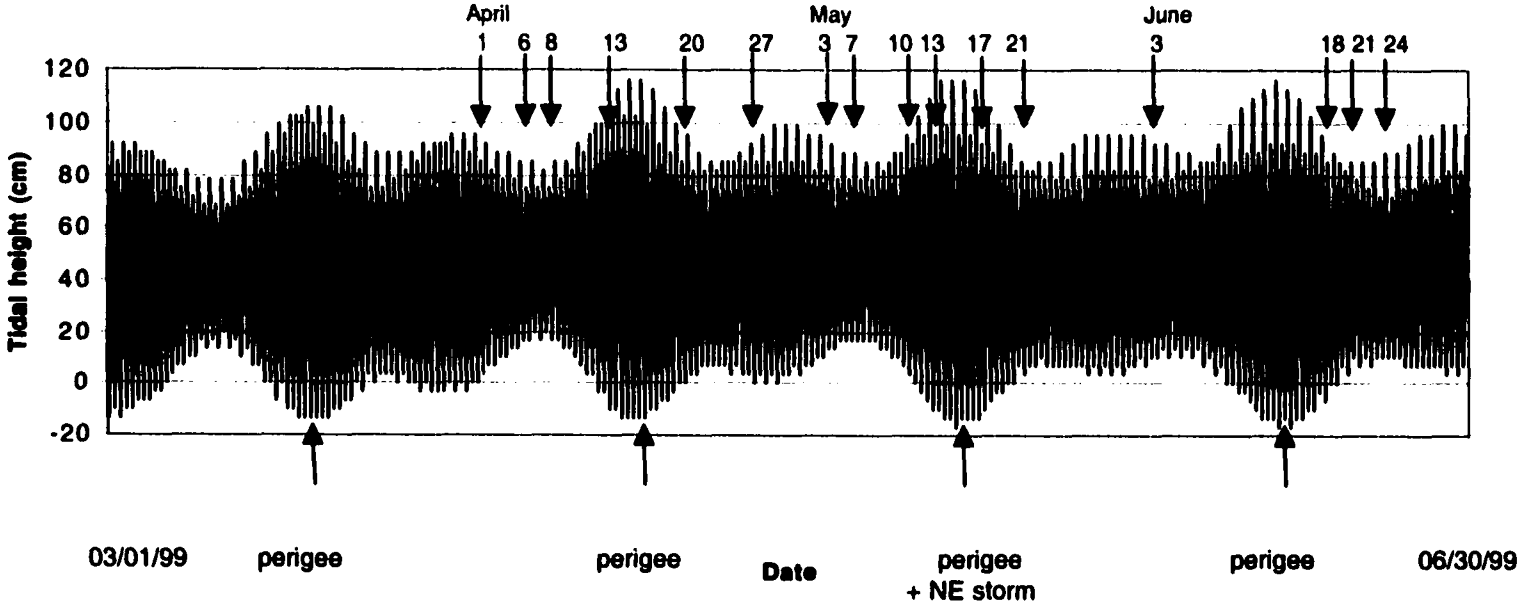

April
1
6
8
13
20
27
May
3
7
10
13
17
21
June
3
18
21
24
120
100
80
60
40
20
0
-20
Tidal height (cm)
03/01/99
perigee
perigee
Date
perigee
+ NE storm
perigee
06/30/99

Fig. 4. Representative x-radiographs of sediment cores for the five subenvironments sampled. Abbreviations as follows: erosional surface (er); laminations (l); bivalve (b).

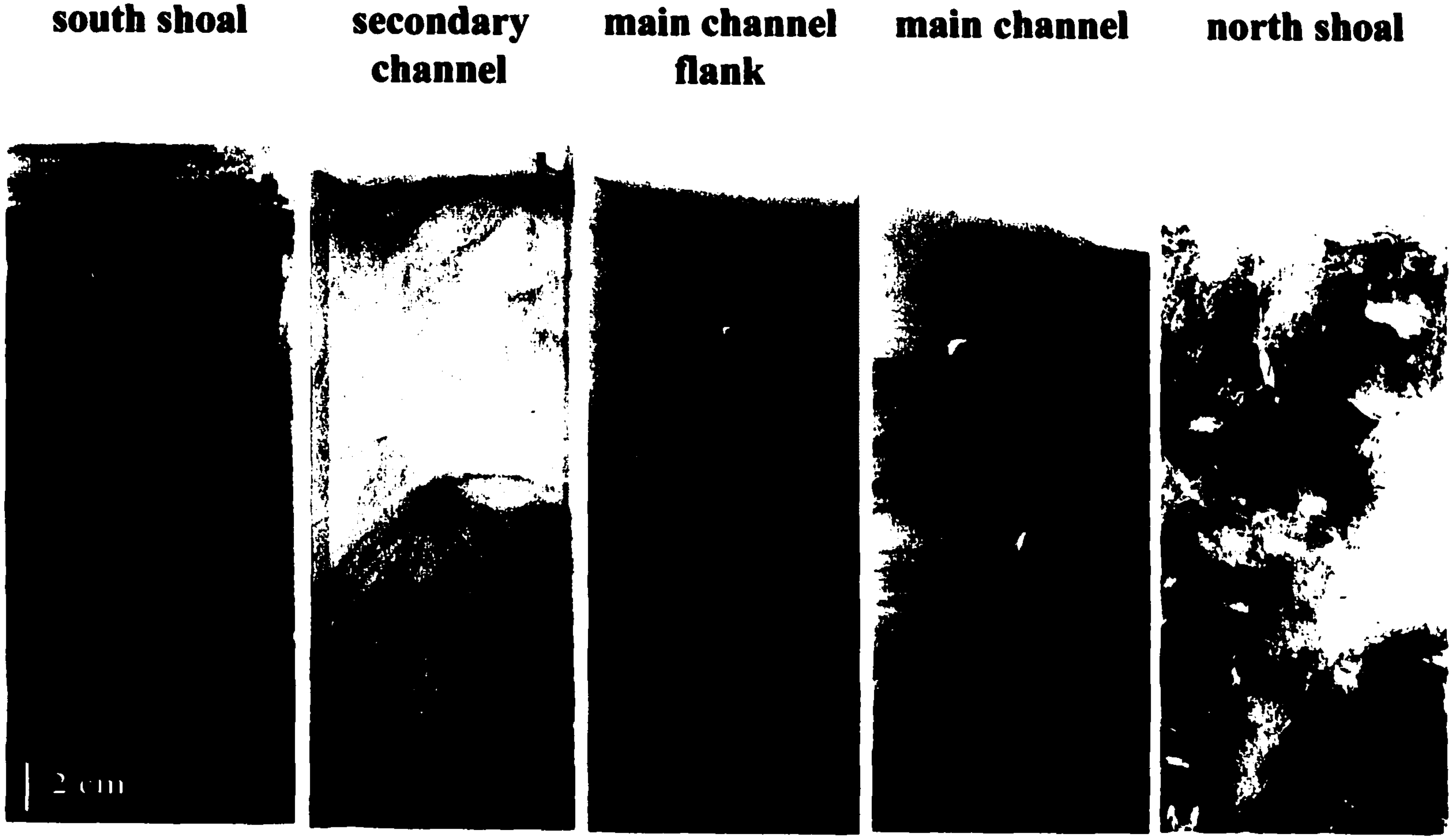
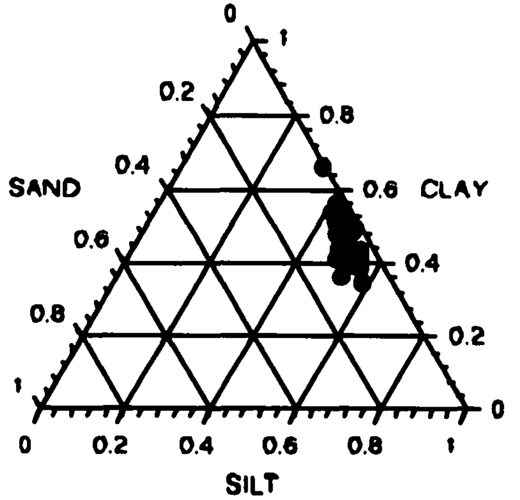
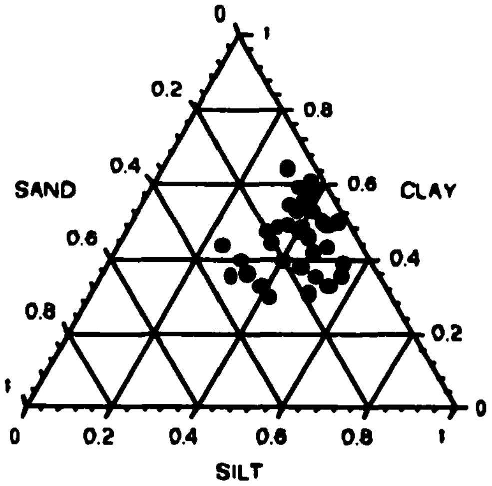

south shoal
secondary channel
main channel flank
main channel
north shoal
2 cm

Fig. 5. Ternary diagrams showing the distribution of grain sizes in surface sediment (0-1 cm) for each subenvironment.

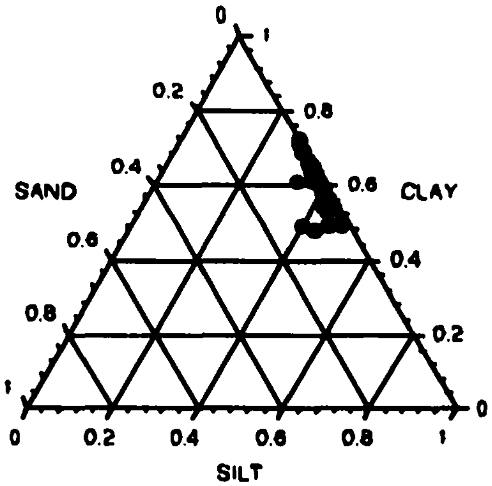
south shoal



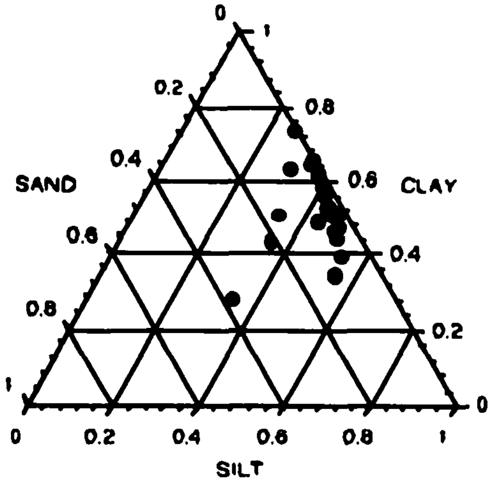
secondary channel



main channel flank



main channel



north shoal

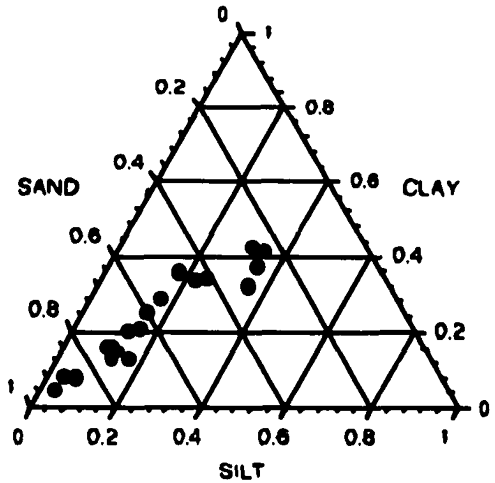


Fig. 6. Grand mean percent mud (= silt + clay) content (± SE) in surface sediments (0-1 cm) for each subenvironment. Subenvironment abbreviations as follows: SS= south shoal; SC= secondary channel; MCF= main channel flank; C= main channel; NS= north shoal.

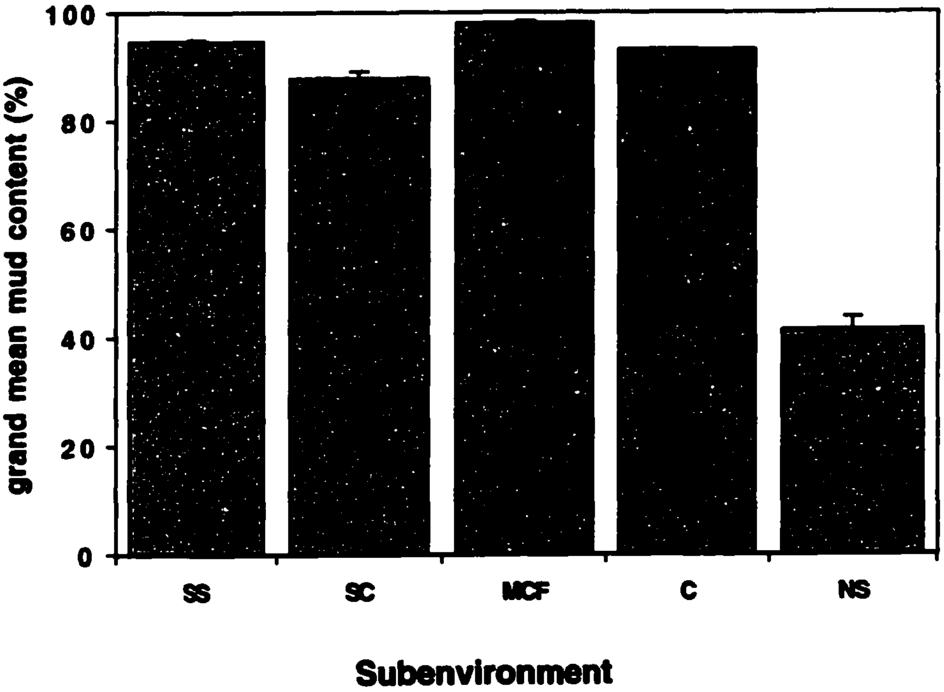

100
80
60
40
20
0
grand mean mud content (%)
SS
SC
MCF
C
NS
Subenvironment

Fig. 7. Profiles of grand mean sediment water content percent (± SE) with depth for cores from each subenvironment. Subenvironment abbreviations as in Fig. 6.

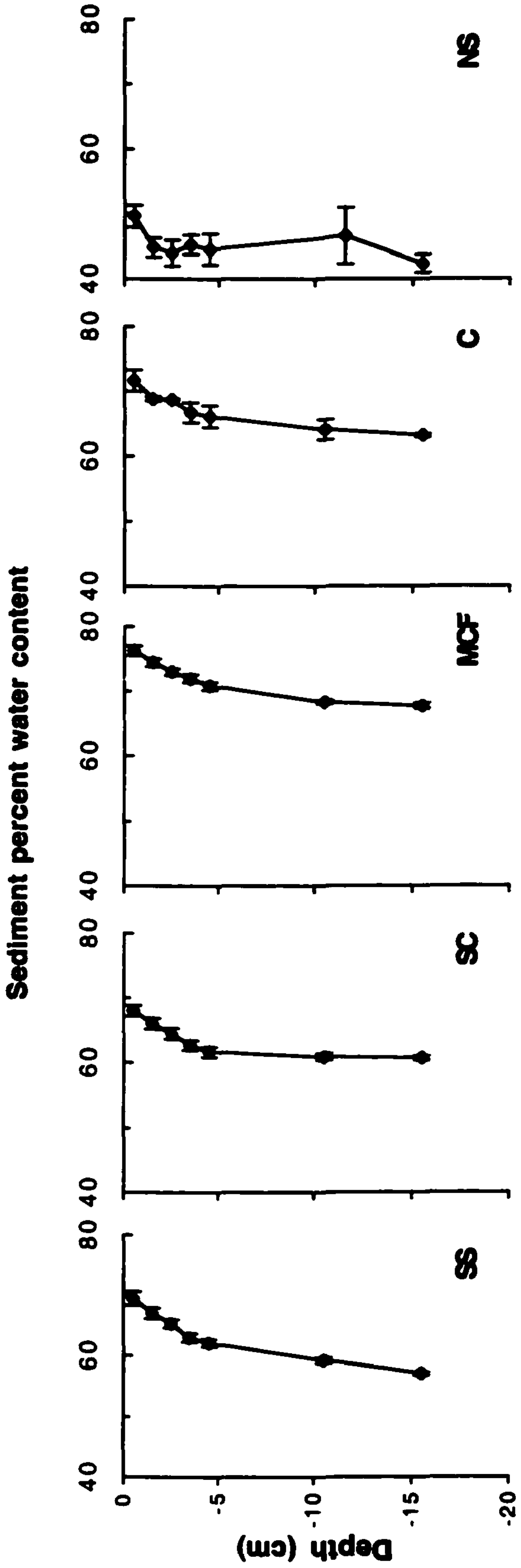

Sediment percent water content
40
60
80
NS
C
MCF
SC
SS
0
-5
-10
-15
-20
Depth (cm)

Fig. 8. Profiles of grand mean sediment Eh (mV) values (± SE) with depth for cores from each subenvironment. Dashed horizontal line in each panel designates depth in sediment at which Eh values cross the 0 mV threshold. Subenvironment abbreviations as in Fig. 6.

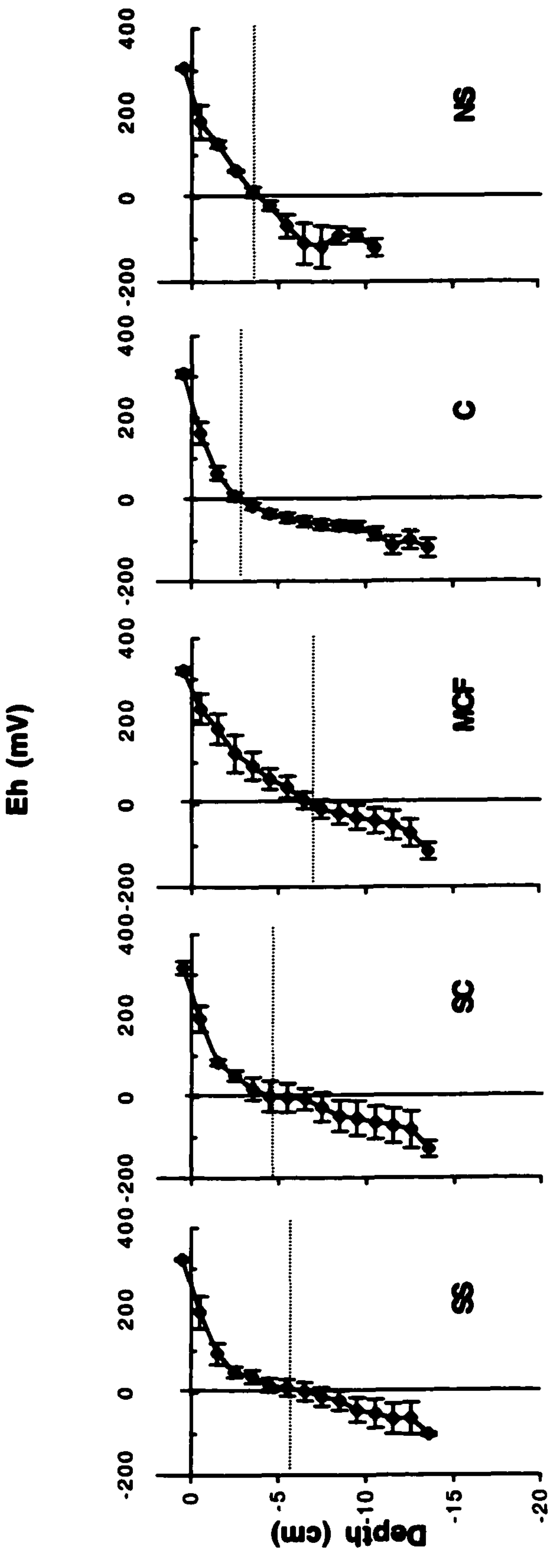

Eh (mV)
-200
0
200
400
Depth (cm)
0
-5
-10
-15
-20
NS
C
MCF
SC
SS

Fig. 9. Profiles of grand mean μ chl *a*/g wet sediment weight (± SE) with depth for cores from each subenvironment. Subenvironment abbreviations as in Fig. 6.

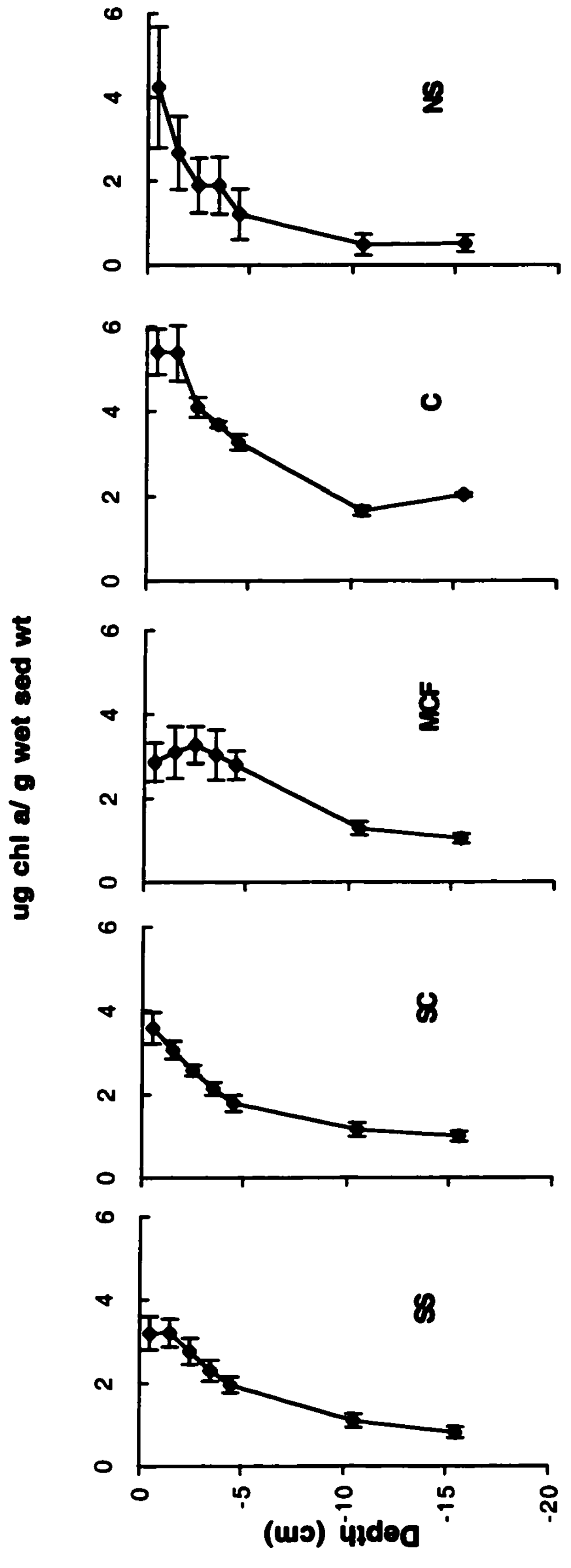
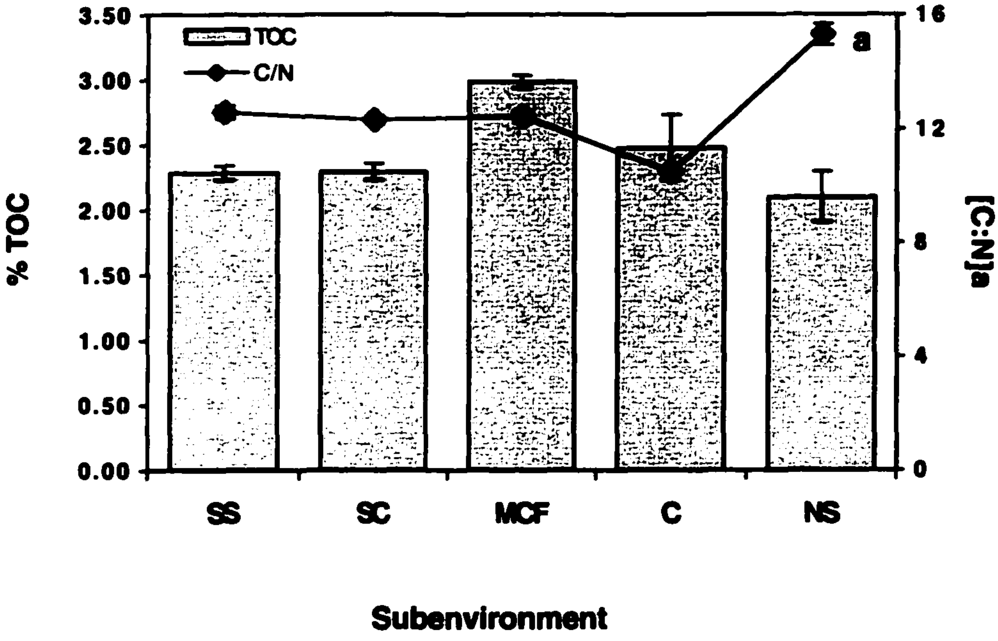
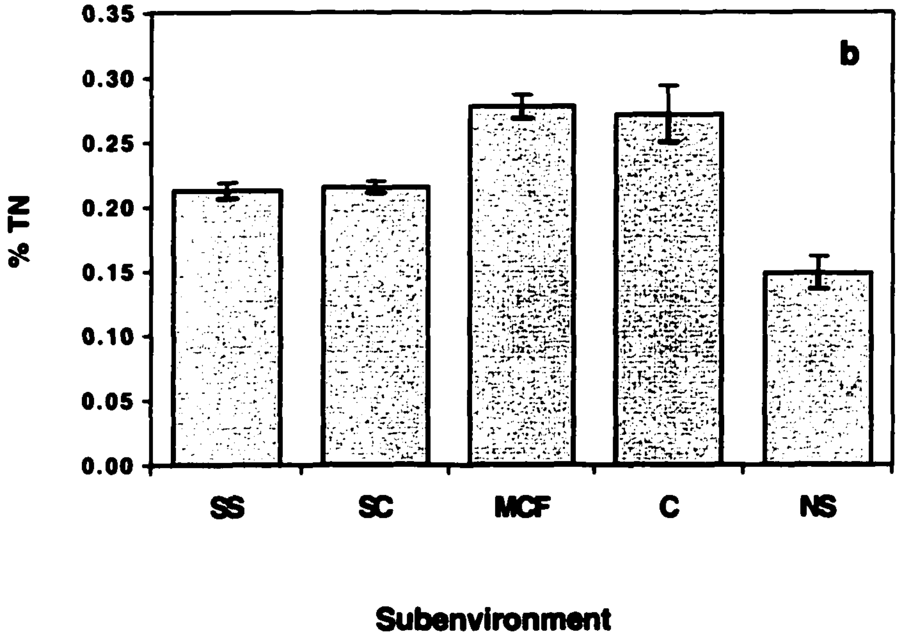

ug chl a/ g wet sed wt
Depth (cm)
0
-5
-10
-15
-20
0
2
4
6
NS
C
MCF
SC
SS

Fig. 10. a) Grand mean sediment organic carbon content (percent dry weight basis) and C:N_a in surface sediment (0-1 cm) for the different subenvironments. Error bars are ± SE. b) Grand mean sediment nitrogen content (percent dry weight basis) in surface sediment (0-1 cm) for the different subenvironments. Error bars are ± SE. Subenvironment abbreviations as in Fig. 6.


TOC
C/N
a
% TOC
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
16
12
8
4
0
[C:N]a
SS
SC
MCF
C
NS
Subenvironment


b
% TN
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
SS
SC
MCF
C
NS
Subenvironment

CHAPTER 2

AN EVALUATION OF ELECTRODE INSERTION TECHNIQUES FOR MEASUREMENT OF REDOX POTENTIAL IN ESTUARINE SEDIMENTS

This note will be submitted to Limnology & Oceanography: Methods with the authors E.K. Hinchey and L.C. Schaffner

Abstract

Eh measurements are commonly used to characterize redox potentials of sediments in freshwater, marine and estuarine studies, due to the relative ease and rapidity of data collection. In our studies of fine-grained estuarine seabeds, we observed that measured Eh values of intact sediment cores were influenced by different electrode insertion techniques. Profiles of sediment Eh generated via lateral insertion of electrodes through silicone-filled ports in acrylic cores were systematically more positive (on the order of 10 to 100 mV) than profiles generated via vertical insertion of electrodes downward through the sediment-water interface of the same cores. A review of the literature indicated that both insertion techniques are routinely used by researchers to measure Eh, but no discrepancy in output has previously been reported. This note summarizes our investigations of Eh measurement generated via both techniques on field-collected cores, and describes three experiments conducted to determine if the cause of the discrepancy in output was due to electrode poisoning by sulfides or due to the presence of the silicone plug around the electrode. Both insertion techniques were found to be subject to potential biases. Thus, we urge caution and consideration of these potential biases when using either technique.

Introduction

For over half a century, sediment redox profiles (measured as Eh) have been used widely as a means by which to approximate the depth of the oxidized zone in sediments. A number of valuable reviews describe the use of Eh as an operational parameter in marine, estuarine and freshwater sediments, as well as on electrode design and Eh measurement technique (Zobell 1946, Hayes et al. 1958, Fenchel 1969, Whitfield 1969, Hargrave 1972). Sediment redox potential is most commonly measured by inserting an inert metal electrode (usually platinum) into the sediment, in conjunction with a reference electrode used to form a complete cell (Zobell 1946, Whitfield 1969). Whitfield (1969), in his seminal paper on use of Eh as an operational parameter in estuarine studies, proposed Eh measurement as a simple, rapid means by which to characterize and map the redox potential of estuarine sediments. Measurement of sediment Eh via electrodes is substantially quicker than chemical analyses of the redox couples, the technology is relatively inexpensive, and data can be generated rapidly shipboard.

The scientific literature is replete with field and lab studies in which sediment redox potential has been measured (Table 1). In these studies, two methods were described for electrode insertion into intact sediment cores: vertical insertion down through the sediment-water interface and lateral insertion through ports, usually filled with silicone sealant. In initial studies of redox profiles in estuarine sediments, we observed that profiles of sediment Eh generated via lateral insertion of electrodes through silicone-filled ports in acrylic cores were systematically more positive (on the order of 10 to 100 mV) than profiles generated via vertical insertion of electrodes downward through the sediment-water interface of the same cores. Thus, the same sediment layer could be could be classified as oxidized or reduced, depending on method of electrode insertion. This discrepancy has not been documented by previous researchers, presumably because only one insertion technique was used for Eh measurement in each study.

During vertical insertion, the electrode is embedded in sediment for the duration of the profile (typically 30 to 60 min). During exposure to reducing sediments, the electrode could be poisoned by sulfides, a phenomenon that produces erroneous negative Eh values (Whitfield 1969). An electrode inserted laterally through ports should be less prone to sulfide poisoning because it is removed from the sediment and exposed briefly to air in between measurements. Effect of the presence of the silicone plug around the electrode shaft has not been previously documented however. In this note, we present the findings of our investigations into the effects of electrode insertion technique on sediment redox profiles, and caution researchers generating sediment redox profiles to be aware of the potential biases inherent in each method.

Materials and Methods

Subtidal sediment cores (grain size composed of >90 % mud) were collected from the York River (Virginia, USA) estuary with a Gray O'Hara box core (625 cm^2 area, 50 cm maximum length). An acrylic (9-cm i.d., 0.4-cm wall thickness) core was removed from each box core. Additional cores were hand-collected from a salt marsh. Profiles of redox potential (measured as Eh, in mV) were determined for cores using a platinum electrode inserted both laterally and vertically. For lateral insertion, a platinum electrode (2 cm long, 0.5 mm wide) was inserted through silicone-filled ports at 1-cm increments along the side of the core, beginning 0.5 - 1 cm above the sediment-water interface. For vertical insertion, a platinum electrode (3-mm or 2 cm long, 0.5 mm wide) was inserted down through the sediment surface with voltage readings taken at 1 cm intervals, beginning 0.5 cm above the sediment-water interface. For both insertion techniques, the resulting redox potential was read on a Beckman model 220 portable pH-millivolt meter connected to a saturated calomel electrode suspended in the water overlying the core. Readings at each depth interval were accepted when the rate of change was less than 0.5 mV in 8 s. Values were corrected to the hydrogen reference electrode scale by adding + 244 mV to each measurement (Bagander and Niemisto 1978). Calibration of the electrodes was verified by measuring the redox potential of quinhydrone dissolved in buffers of pH 4 and 7 (Bohn 1971). Electrodes were cleaned prior to use and after each profile by scouring with a non-chlorinated cleansing powder and wiping with a deionized water-soaked tissue. Cleansing the electrode with an abrasive scouring powder is preferable to acid cleaning, as it results in more reproducible measurements (Davis 1974).

Two experiments were conducted to determine if the more negative Eh values observed during vertical electrode insertion were a function of the time that the electrode spends in reducing sediment prior to measurement. In the first experiment, a series of trials was performed in which cores were initially profiled via standard vertical and lateral electrode insertion techniques, followed by rapid plunging of electrodes vertically through the sediment surface to specified depths in the same core prior to recording the mV output. Plunges were conducted with electrodes that were cleaned as described above prior to insertion ($n = 3$) and with electrodes that were conditioned by exposure to reducing conditions deep in a core for 30 to 60 min and not cleaned in any way prior to reinsertion (n = 8). Trials were conducted on three field-collected cores held in a laboratory incubator at ambient temperature (T= 21 °C) for 0 to5 d.

In the second experiment, trials were conducted in which overlying sediments were removed to expose deeper sediments prior to Eh measurement, thereby allowing the electrode to be inserted directly into subsurface sediments without having to first pass through a reducing sediment column which could poison the electrode. Cores were initially profiled via standard vertical and lateral insertion of electrodes, and then extruded in 3 cm increments and the overlying sediment removed. Each time a layer of sediment was removed, an electrode was directly inserted 1.5 cm into the top or side (without passing through silicone-filled side ports of the acrylic core) of the remaining sediment column. The reference electrode was suspended in a seawater-filled depression created in the surface sediment (away from the electrode insertion area). This experiment utilized two field-collected cores that were stored in laboratory flow-through aquaria at ambient temperature (T= 21 °C) for 14 and 19 d.

A third experiment was conducted to determine if the presence of the silicone plug itself was responsible for the more positive Eh readings generated via lateral insertion of electrodes through silicone-filled side ports. A 4 mm-long silicone plug, created by punching out the silicone from a side port in the acrylic core, was placed at the base of the shaft of a 2 cm-long platinum electrode. This electrode was then vertically inserted into a reducing sediment surface in a salt marsh core, exposed by extruding and removing the top 3 cm of surface sediment. To mimic the scenario of lateral insertion, the silicone plug was rendered flush with the sediment-water interface upon electrode insertion, such that 1.6 cm of the electrode shaft was embedded in the sediment and 4 mm of the shaft was embedded in silicone. The reference electrode was suspended in a small saltwater-filled acrylic core (2 cm-i.d.) inserted into the surface sediment. Trials were also conducted using a 2-cm long electrode not embedded in a silicone plug and inserted to a depth of 2 cm such that the entire electrode shaft was embedded in the sediment. Twelve measurements were performed for both configurations, in an alternating fashion. The electrode was cleaned prior to each measurement, and for each trial a new, undisturbed area the sediment surface was chosen for insertion.

Profiles generated on experimental cores held in the laboratory are likely to differ from the profiles that would have been generated if readings were done directly after collection in the field due to alterations of microbial processes that no doubt occur during extended storage in the laboratory. However, characterization of field Eh conditions was not the purpose of these experiments.

Results

Electrodes inserted laterally through silicone-filled ports consistently yielded profiles that were more positive (on the order of 10-100 mV) than profiles generated via vertical insertion (Fig. 1a). To evaluate differences in methods, we compared values at two depths (-7 cm, -10 cm) for each profile generated. We found a significant effect of insertion method on measured Eh (two-way ANOVA; n = 19 cores; F = 59.72, $P < 0.0001$). Depth of measurement was not significant and there was no interaction. Profiles produced via lateral insertion often did not cross the 0 mV threshold. Values generated via vertical insertion had more negative Eh values at depth and exhibited less variability than values generated via lateral insertion.

Results of the electrode plunging experiments (Fig. 1b) show that the Eh values generated via vertical insertion of clean electrodes directly to a depth of ~ 15 cm in the sediment cores were intermediate between values generated via standard vertical and lateral electrode insertion methods, but closer to vertical values. Eh values generated via plunges of cleaned electrodes were, in general, less negative than values generated via plunges with conditioned electrodes. Conditioned electrodes plunged to a depth of ~15 cm resulted in Eh values that closely approximated values generated via the incremental vertical insertion method.

In the core extrusion experiments, measurements of Eh in extruded sediments were consistently more negative throughout the cores than measurements generated via lateral insertion of electrodes through ports (Fig. 1c). At sediment depths of 13.5 to 15 cm, vertical and lateral measurements of Eh in extruded sediments yielded more positive Eh values than those generated via standard, incremental vertical insertion. A consistent relationship of Eh measurements in extruded sediments relative to the incremental vertical insertion method was not observed in core depths less than 12 cm. In trials at these depths, vertical and lateral measurements of Eh in extruded sediments ranged from values that were 0.5 to 75 mV more negative to 14.7 to 113 mV more positive than Eh values generated via incremental vertical insertion.

The presence of the silicone plug around the electrode shaft produced significantly more positive Eh values (mean ± SE = 69.4 ± 14.0 mV) than those measured by an electrode without the silicone plug (mean ± SE = 19.7 ± 14.3 mV; $P < 0.0215$, unpaired *t*-test).

Discussion

Comparison of sediment Eh values in field-collected cores via vertical and lateral platinum electrode insertion techniques, in conjunction with results of laboratory experiments, indicates that method of electrode insertion influences the shape of the sediment redox profile generated. Both of the widely used electrode insertion techniques are subject to potential biases.

Our results indicate that embedding 4 mm of an electrode shaft in the silicone plug during lateral insertion causes more positive Eh values to result than when no plug was present. The interference of the silicone is supported by results of the sediment extrusion experiments and by comparison of Eh values generated both with and without a silicone plug attached to the electrode shaft. Given our results, it seems likely that atmospheric oxygen contacts the electrode through small junctions between the silicone plug and the electrode using this method.

Results of the plunging experiments and sediment extrusion experiments (for the deepest extruded core depths only, in this case ~15 cm) suggest that during the incremental vertical insertion technique electrode poisoning by hydrogen sulfide can occur near the bottom of the profile, although this appears to be a less serious problem than the silicone effect (Fig 1b). Thus, the incremental vertical insertion technique likely produces excessively negative redox values when the electrode is embedded in reducing sediments for long periods of time (30 min to 1 hr). Hargrave (1972) noted that the reproducibility of Eh measurements in cores of profundal lake sediment was low (±80 mV) unless the electrode was cleaned between series of profiles.

To obtain the most accurate measurements of Eh, it would be preferable either to clean the electrode after each depth measurement prior to reinserting it to the next depth (in a new zone of sediment to avoid sampling a disturbed zone) or to extrude successive core depths and perform measurements in newly exposed sediment. Both techniques will increase processing time of a core and extrusion will preclude multiple measurements through time in a single core.

When addressing electrode limitations, early researchers emphasized the usefulness of redox profiles as a relative measure rather than an exact measure of reduction in the samples (Teal and Kanwisher 1961, Whitfield 1969). The depth transition of oxidized to reduced sediment conditions can be better constrained when Eh profiles are coupled with measurement of porewater constituents such as nutrients, sulfides, pH, and alkalinity (Giblin et al. 1997, Hopkinson et al. 1999) or indicators of recent sediment disturbance including radioisotope profiles and x-radiograph appearance (Hinchey and Schaffner, unpublished). We conclude that redox profiles generated via either electrode insertion method should be interpreted cautiously, with the potential limitations of each method carefully considered, especially when profiles are not generated in conjunction with other sediment parameters.

Acknowledgements

We thank Andrew Draxler, Randy Chambers, Christopher Earnhart, Robert Diaz, Kenneth Moore, Elizabeth Canuel, Krisa Arzayus, Carl Friedrichs and the participants of the 2001 US EPA Eh Workshop in Narragansett, RI for valuable discussions on measuring Eh in estuarine sediments. Comments from Emmett Duffy, Steve Kuehl and Cindy Van Dover greatly improved the manuscript. Funding was provided by a grant from the International Women's Fishing Association and a Craig Smith Educational Scholarship granted by the Virginia Institute of Marine Science.

Table 1. Summary of studies in which redox potential was measured on intact sediment cores via vertical or lateral insertion of platinum electrodes. Studies in which sediments were subsampled, homogenized and transferred to stoppered jars (Zobell 1946, Whitfield 1969) or plexiglass slides (Bagander and Niemisto 1978) prior to measurement were not included.

Reference	Locality	Insertion method	Probe length, diameter	Remarks
Hayes et al. 1958	lake	vertical	1cm, 2 mm	multiple electrode (spiral arrangement of 12 electrodes that penetrate to different depths in the sediment)
Teal and Kanwisher 1961	salt marsh	vertical	n/a, 7 mm	
Fenchel 1969	coastal Danish waters	vertical	n/a, 0.7 mm	
Hargrave 1972	eutrophic lake	vertical	1 mm, 0.2 mm	
Revsbech et al. 1980	coastal Danish waters	vertical	n/a, n/a	assumed same as Fenchel 1969
Jørgensen and Revsbech 1989	Baltic and North Sea	vertical	5 mm, 0.6 mm	assumed same as Fenchel 1969

Table 1. (Continued)

Smayda 1990	oligotrophic, acidic lake	vertical	n/a, n/a (60 mm^2 area)	
Forester and Graf 1992	North Sea	vertical	n/a, n/a (25 mm^2 area)	multiple electrode (lateral arrangement of 10 electrodes that penetrate to different depths in the sediment)
Draxler 1995; Davis et al. 1998	sewage dump site, New York Bight	vertical	4 mm, 6 mm	electrode was first equilibrated with the sediment at 10 cm in the grab, then with the overlying water
Moore et al. 1993	estuarine SAV beds	vertical	5 mm, 0.8 mm	
Giblin et al. 1997	Boston Harbor	vertical	n/a, n/a	
Laima et al. 1998	Danish fjord	vertical	2 mm, 0.5 mm	
Meijer and Avnimelech 1999	fish pond	vertical	n/a, 0.5 mm	
This study	York River estuary	vertical	2 cm and 3 mm, 0.5 mm	
Schindler and Honick 1971	fish pond	lateral	n/a, 0.18 mm	ports filled with silicone sealant

Table 1. (Continued)

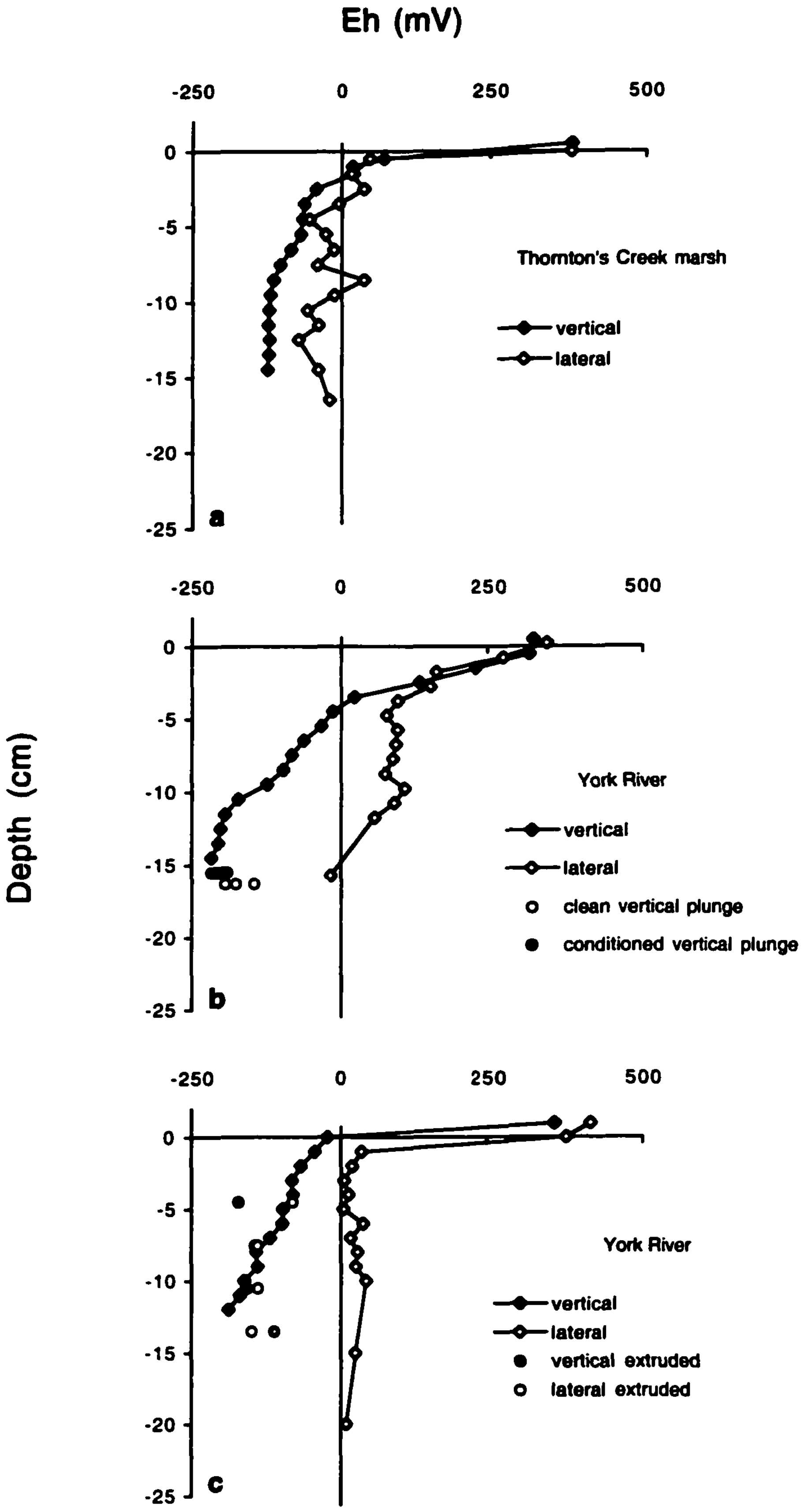
Davis 1974	lake	lateral	1 cm, 0.4 mm	ports covered by an unspecified material
Koepfler and Kator 1986	York River estuary	lateral	n/a, 0.5 mm	ports filled with silicone sealant
Wigand et al. 1997	tidal freshwater SAV beds	lateral	n/a, n/a	ports covered with duct tape and pierced with electrode
Rosenberg et al. 2001	hypoxic fjord	lateral	1.5 cm, 1 mm	ports filled with silicone sealant; 10 electrodes inserted simultaneously into sediment at 1 cm increments
Arzayus et al. 2002	York River estuary	lateral	2 cm, 0.5 mm	ports filled with silicone sealant
This study	York River estuary; salt marsh	lateral	2 cm, 0.5 mm	ports filled with silicone sealant

Fig 1. Sediment Eh values from field-collected cores illustrate the variation resulting from different methods of electrode insertion. For all panels, "vertical" designates profiles generated via insertion of a 3 mm-long (panels a, c) or 2 cm-long (panel b) platinum electrode vertically down through the sediment column and "lateral" designates profiles generated via insertion of a 2 cm-long platinum electrode horizontally through silicone-sealed ports drilled in the acrylic core. The total number of cores comprising each trial is indicated after each legend entry below, but only one representative profile is shown for each trial.

a. Sediment Eh profiles generated via vertical and lateral electrode insertion. N = 19 cores.

b. Comparison of sediment Eh profiles generated via vertical and lateral electrode insertion to sediment Eh values generated by rapidly plunging clean and conditioned electrodes vertically down through the sediment column to 14.5 cm (not stopping at 1 cm increments). Data points for the conditioned plunges are offset by 1.0 cm on the depth axis and data points for the clean plunges are offset by 2.3 cm on the depth axis for clarity. N = 3 cores.

c. Comparison of sediment Eh profiles generated via vertical and lateral electrode insertion to sediment Eh values generated in extruded core surfaces. "Vertical extruded" designates values generated via vertical insertion of a 3 mm-long platinum electrode into surface sediment that was extruded to a specified depth, sliced and exposed. "Lateral extruded" designates values generated via horizontal insertion of a 2-cm long platinum electrode into the extruded sediment at a specified depth (not through side ports of the acrylic core). N = 2 cores.


Eh (mV)
Depth (cm)
-250
0
250
500
0
-5
-10
-15
-20
-25
a
Thornton's Creek marsh
vertical
lateral
b
York River
vertical
lateral
clean vertical plunge
conditioned vertical plunge
c
York River
vertical
lateral
vertical extruded
lateral extruded

CHAPTER 3

TEMPORAL AND SPATIAL VARIATION IN THE SPRING RECRUITMENT OF MACROBENTHOS IN THREE MESOHALINE SUBENVIRONMENTS OF THE YORK RIVER SUBESTUARY OF CHESAPEAKE BAY

Abstract

Environmental variables that structure recruitment of benthic organisms to the seabed are far from resolved, despite the fact that recruitment is essential for population maintenance and strongly effects benthic community structure and trophic dynamics in estuaries. We studied temporal and spatial variations in spring recruitment of macrobenthos in a mesohaline estuary among major benthic subenvironments, which are known to differ in respect to seabed characteristics, depositional regime and salinity. Spatial and intra-annual temporal differences in recruitment were observed among subenvironments at both the community and species level. There was a trend of increased abundance of total recruits, driven by the numerical dominant of the recruitment assemblage, *Streblospio benedicti*, in an area characterized by high deposition and long-term sediment accumulation (flank of the main channel) relative to areas characterized by lower deposition rates and physical mixing of surface sediments (south shoal and secondary channel subenvironments). Although the numerically dominant taxa that comprised the recruitment assemblage are classified as euryhaline opportunists, differences in abundance and biomass patterns suggest that variations in seabed characteristics across relatively small spatial scales can influence benthic community structure. Our study also highlights the importance of frequent sampling using small screen sizes (125 µm and 250 µm) to track recruitment pulses accurately.

Introduction

Recruitment is an ecological process that has important effects on seasonal and long-term dynamics of estuarine soft-sediment benthic communities (Hall 1994, Ólafsson et al. 1994). Factors influencing recruitment success are numerous and can be divided into pre- and post-settlement processes, operating over a range of temporal and spatial scales (reviewed by Ólafsson et al. 1994, Todd 1998). Successful recruitment of benthic organisms is known to be subject to pre-settlement processes including, but not limited to, larval supply to the substratum (Gaines and Bertness 1993), substratum electivity by larvae (Butman 1987, Woodin et al. 1995), passive accumulation and dispersion by settling larvae (Palmer 1988, Snelgrove and Butman 1994, Snelgrove 1994), and post-settlement processes such as predation (Peterson 1979, Ambrose 1984).

Temporal variation in recruitment is commonplace in marine environments and is related to the combined effects of life history characteristics of reproducing organisms (Diaz 1984), food availability that provides nutritional resources for reproducing organisms (Marsh and Tenore 1990), and species interactions such as competition and predation (Peterson 1979, Wilson 1981). Spatial variation in recruitment occurs in relation to gradients in chemical, biological and physical environmental parameters such as salinity (Kalke and Montagna 1991), sediment grain size and organic content (Butman and Grassle 1992), sedimentation disturbance history (Zajac and Whitlatch 1982, Woodin et al. 1995), and hydrodynamic regimes (Snelgrove 1994).

Recent investigations of the York River estuary identified major benthic subenvironments that differ in respect to the local hydrodynamic forcing and associated physical bed disturbance and sediment deposition (Dellapenna et al. 1998, Dellapenna et al. 2001, Schaffner et al. 2001, Kniskern and Kuehl in review, Chapter 1). While the implications of seabed disturbance on sediment facies formation (Dellapenna et al. 1998, Dellapenna 1999, Kniskern and Kuehl in review), contaminant fate (Dellapenna et al. 1998, Arzayus et al. 2002), and organic matter degradation (Arzayus et al. 2002) in the York River are recognized, the effect of disturbance regime on the resident benthic community has not been well-studied.

In this study, we compared short-term (weekly) macrobenthic species recruitment patterns among three benthic subenvironments in the upper York River: south shoal, secondary channel and main channel flank. Fauna that recruit to the benthic population via pelagic larvae or via post-settlement dispersal of juveniles are initially restricted to shallow residence depths in the sediment (Llansó 1992, Woodin et al. 1995). These new recruits and juveniles living near the sediment-water interface are generally predicted to be the most strongly affected by physical disturbance processes (Wilson 1981, Brenchley 1982, Emerson 1989, Bonsdorff et al. 1995). Thus, our objective was to determine if patterns of abundance and biomass of recruiting macrobenthic species could be explained by the small-scale gradients in hydrodynamically-forced seabed characteristics and dynamics observed among the south shoal, secondary channel and main channel flank subenvironments. This project was conducted in the spring because it is the time when many of the dominant species of the York River macrobenthic community exhibit peak recruitment (Diaz 1984, Zobrist 1988).

Materials and methods

Study region

The study region encompassed ~ 34 km^2 of the upper York River, a subestuary of Chesapeake Bay, Virginia, USA (Fig. 1). General descriptions of the environmental setting are given in Dellapenna et al. 1998, Schaffner et al. 2001, and Chapter 1. Bottom water salinity of 10 - 20 ppt and bottom water temperature of 2-28 °C are characteristic for this reach of the estuary. The study region does not suffer hypoxia or anoxia during the summer, as is observed farther downstream (Pihl et al. 1992). The infaunal community in the mesohaline York River is relatively depauperate, and is dominated by small annelids, peracarid crustaceans, and bivalves (Boesch 1977, Schaffner et al. 2001).

Subenvironment characteristics

Fifteen permanent stations were established in three subenvironments (Figs. 1 and 2), designated south shoal (4 stations), secondary channel (6 stations), and main channel flank (5 stations). The subenvironments were sampled weekly (on consecutive spring and neap tides) from 1 April - 21 May, 1999 and again on 21 June, 1999. A summary of the physical characteristics of each subenvironment based on results of this study and previous investigations are presented in Table 1, with differences in physical characteristics among subenvironments attributed to both their along- and across-estuary locations. Salinity and sediment temperature increased at all subenvironments from April to June. Salinity was lowest at the main channel flank in April and early May, due to the more upstream location of this subenvironment relative to the south shoal and the secondary channel. Sediment temperatures were comparable across subenvironments on all dates.

Sediment deposition occurred all subenvironments during the study, however distinct seabed characteristics and dynamics have been documented for each subenvironment (Chapter 1). The south shoal is characterized by tidally- or wave-driven cycles of erosion and deposition in the upper few centimeters of the seabed, the secondary channel is characterized by cycles of erosion and deposition in the upper few to 10's of cm of the seabed, and the main channel flank is characterized by the highest rates of deposition with evidence of longer-term sediment accumulation (Chapter 1).

Infaunal sampling

At each station, sediment was collected with a Gray O'Hara box corer (625 cm^2 area, 50 cm maximum length). Infauna were sampled with a 9.0 cm (i.d.) acrylic core (64 cm^2 surface area). From each core, sediment surface temperature was measured with a thermometer, and salinity of water overlying the sediment was measured with a refractometer. Additional cores were remove from each box core for the determination of the seabed characteristics presented in Table 1 (methods described in Chapter 1).

On each sampling date, the 0-1 cm and 1-2 cm depth intervals of sediment from the core were extruded in the field and immediately fixed in buffered 10% formalin containing Rose Bengal stain. Prior to extrusion, water overlying the sediment core was drawn off and passed through a 125 µm sieve. Any animals in the sieve were washed into to the 0-1 cm sample jar using 125 µm- filtered seawater.

Laboratory methods

In the laboratory, the 0-1 and 1-2 cm fractions were sieved on nested 500-250-125 μm screens. Use of the 125 μm screen ensured collection of the earliest benthic life stages of the dominant local macrobenthic infaunal organisms, termed early juveniles (Zobrist 1988), while the 250 μm screen retained the late juveniles (Zobrist 1988). The 500 μm screen retained adult organisms, which are outside the scope of this study. Macrobenthic organisms were identified to the lowest taxonomic level possible (usually species) and enumerated. Previously determined values of ash-free dry weight (AFDW) individual^{-1} for York River taxa (Schaffner and Hinchey, unpublished) were used to convert abundances to AFDW for species in each size class. Briefly, these AFDW values were determined by oven-drying formalin-fixed specimens at 60°C for a minimum of 48 h and ashing at 550°C for 4 h. An average AFDW individual $^{-1}$ was determined for each size class of taxa. Total biomass for each size class of taxon was calculated by multiplying the total taxon abundance in each size class by the average taxon AFDW individual $^{-1}$ in each size class.

Statistical analyses

We tested for differences in abundance and biomass of total recruits and abundance of the five dominant taxa among stations with repeated measures analysis of variance (RANOVA), using date and subenvironment as factors after combining the data for size classes. All data were checked for normality with a Shapiro-Wilks test (Zar 1999), for homogeneity of variance with a Cochran's test (Underwood 1997), and for Type H covariances with sphericity tests (Sokal and Rohlf 1981). Abundance data were transformed by log (X+1) or square root (X + 0.5) and total biomass data were transformed by $X^{0.3}$ using a Box-Cox power transformation (Sokal and Rohlf 1981) prior to analysis. Although total recruit abundance and biomass data did not meet the assumption of homogeneity of variance, even after transformation, an RANOVA was performed on these data, as ANOVA is robust even when data display considerable heterogeneity of variance (Zar 1999). Non-significant outcomes of the F-ratio test are still reliable results when homogeneity of variance is violated, however significant results should be interpreted using a lower probability level for significance tests (Underwood 1981). Thus, we used a more conservative probability level of < 0.01 for all tests. Transformed abundance data for the dominant taxa met the assumption of homogeneity of variance, but were not normally distributed. Again, RANOVAs were performed for these data as ANOVA is also robust to non-normality (Underwood 1981). When significant differences in abundance and total biomass were detected for the factor of date, 1-way ANOVAs followed by Tukey *post hoc* tests were performed for each subenvironment to enable identification of significant peaks in abundance. Statistics were analyzed using PC SAS version 8.0 (SAS Institute, Cary, NC). The relationship between abundance and biomass is linear for individual species due to the method of biomass conversion, and therefore biomass is not separately evaluated for each species.

Similarity of species composition and abundance among subenvironments was determined by calculation of group-averaged Bray-Curtis similarity measures followed by hierarchical cluster analysis using the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package. Abundance data were square-root transformed prior to analysis to down-weight the importance of the highly abundant species, so that similarities are also based on values of mid-range species (Clarke and Warwick 2001).

Results

Patterns of abundance

A total of 25 species in the recruiting size classes were collected at the mesohaline York River subenvironments during this study. A full listing of the species collected and abundances is provided in Appendix III. A subset of 5 taxa accounted for > 90% of abundance of the total fauna collected (Table 2). Of these, two are polychaetes that recruit via pelagic larvae: the spionid *Streblospio benedicti* and the capitellid *Mediomastus ambiseta*. Together, *S. benedicti* and *M. ambiseta* accounted for ~ 75 % of total individuals collected during the study, and the majority of recruits were collected on the 250 μm screen (~64 and ~80%, respectively). The other three dominant taxa were tubificid oligochaetes (*Tubificoides* spp., grouped together because immature individuals are indistinguishable), an unidentified species of Turbellaria, and the cumacean crustacean *Leucon americanus*. *Tubificoides* spp. and Turbellaria hatch from eggs deposited directly into the sediment, and *L. americanus* recruits via direct development in which benthic juveniles are released from brood pouches in adult females. The oligochaetes and *L. americanus* were primarily collected on the 250 μm screen (~86 and 97%, respectively), while a larger percentage of Turbellaria (63%) was collected on the 125 μm screen. Overall, the majority of recruiting individuals of the dominant taxa and of the total fauna collected in the 125 µm and 250 µm fractions was retained on the 250 µm screen (~70% and ~ 71%, respectively; Table 2, Fig. 3).

There was a significant effect of date but not subenvironment on total abundance of recruits collected in spring 1999 (Table 3). A peak in abundance was detected at the south shoal, beginning on 13 April, and at the main channel flank, beginning on 20 April (Table 4, Fig. 3). These peaks occurred 3 days before (south shoal) and 4 days after (main channel flank) a strong spring tide on 16 April. No significant changes in total abundance through time were observed at the secondary channel (Table 4, Fig. 3).

Abundance of *S. benedicti* did not statistically differ among subenvironments (Table 3), but there was an apparent trend of increased abundance of this polychaete species at the main channel flank (Fig. 4). The peaks in *Streblospio benedicti* abundance varied among subenvironments. Recruitment peaked earlier at the south shoal and main channel flank (20 April) relative to the secondary channel (27 April) (Table 5, Fig. 4). *Mediomastus ambiseta* abundance was significantly lower at the main channel flank than at the south shoal or secondary channel (Table 3, Fig. 5). No recruitment peaks of this species were detected (Table 6). Abundance of *Tubificoides* spp. did not statistically differ among subenvironments (Table 3). A significant peak in *Tubificoides* spp. abundance was observed at the secondary channel beginning on 17 May, consistent with the trends in the other subenvironments (Table 7, Fig. 6). Abundance of Turbellaria was highly variable and did not differ significantly among subenvironments or through time (Table 3, Fig. 7). *Leucon americanus* abundance did not differ among subenvironments (Table 3), but a significant peak in abundance was detected on 13 April at the south shoal, with a trend of somewhat later peaks at the secondary channel and main channel flank (20 April) (Table 8, Fig. 8).

Community analyses

Hierarchical clustering delineated 10 major station groups with species assemblages ranging from 35 to 75% similarity (Fig. 9). The station groups reflect both differences among subenvironments and temporal changes in the species assemblages during the course of the study. For example, station groups 1-3 are primarily composed of south shoal and secondary channel stations sampled from the early (group 1) to middle (group 3) dates of the study. Main channel flank stations mostly clustered together with some south shoal or secondary channel stations in station groups 4-7, again with some grouping by date apparent (collection dates varied). Station groups 6-10 included collections from the later part of the study.

Patterns of biomass

There was a significant effect of date but not subenvironment on total recruit biomass (Table 9). Peaks in biomass at the south shoal (beginning 13 April) and the main channel flank (beginning 20 April) tracked the total abundance peaks in these subenvironments (Table 10, Fig. 10). A biomass peak was detected at the secondary channel on 27 April (Table 10, Fig. 10). Organisms in the 250 um size class accounted for ~ 96 % of the total biomass (Fig. 10). Owing to its high abundance, *Streblospio benedicti* was the biomass dominant at all subenvironments (Fig. 11), followed by *Mediomastus ambiseta* (Fig. 12). Despite being the third most abundant species, the contribution of *Tubificoides* spp. to total community biomass (Fig. 13) was lessened due to its lower mean biomass individual $^{-1}$ value than mean biomass individual $^{-1}$ values measured for Turbellaria (Fig. 14) or *Leucon americanus* (Fig. 15).

Discussion

In the upper York River, recruiting macrobenthic organisms colonized surface sediments of three benthic subenvironments that are known to be characterized by different local hydrodynamic forcing of the seabed and different rates of sediment reworking and accumulation. Overall, the temporal variation in species abundance we observed was expected, as bursts in population abundances of opportunistic species resulting from juvenile recruitment are the norm in estuaries (Diaz 1984, Holland et al. 1987, Zobrist 1988, Marsh and Tenore 1990). We found no strong evidence for variations in recruitment patterns that reflected a spring-neap tidal cycle, despite the fact that peaks in larval abundance are often tied to lunar periodicity (Olive 1984), a phenomenon that has been documented for a polychaete species in the polyhaline York River (Seitz and Schaffner 1995). Single peaks in total taxa abundance at both the south shoal and main channel flank did roughly coincide with a strong spring tide on 16 April, which could reflect increased larval supply during this spring tide. Peaks in abundance were not observed during any other spring tide event however.

The two polychaete species that reproduce via pelagic larvae displayed different recruitment patterns during this study. *Streblospio benedicti* settled in a pulse over a relatively short (< 8 week) time period, which is typical for this species in the polyhaline York River (Diaz 1984, Zobrist 1988) and other Chesapeake Bay tributaries (Holland et al. 1987, Marsh and Tenore 1990). Its settlement appears to have been delayed in the secondary channel, perhaps due to strong tidal currents. *Mediomastus ambiseta* displayed continuous recruitment throughout the study, a pattern also observed for this species in the polyhaline York River (Diaz 1984). The taxa that hatch from eggs laid in sediment also displayed different recruitment patterns. *Tubificoides* spp., known to exhibit summer recruitment peaks in the York River (Diaz 1984), peaked in abundance in late May, whereas Turbellaria abundance was consistent through time. *Leucon americanus* juvenile abundance in sediments is likely strongly tied to the presence of adult females, for although this species is motile, dispersal capability by taxa that brood their young is generally considered to be lower than in taxa that release planktonic larvae.

The dominant polychaetes in this study are classified as widespread "euryhaline opportunists" that are characteristically abundant in salinities of 10-20% (Boesch 1977). The difference in salinity observed in April and May between the main channel flank and the two more downstream subenvironments could have influenced polychaete recruitment patterns. Both *Streblospio benedicti* and *Mediomastus ambiseta* are often the community dominants in meso-polyhaline reaches of estuaries throughout the east coast (Diaz 1984, Llansó 1992) and the Gulf of Mexico (Mannino and Montagna 1997, Butts and Lewis 2002). It is possible that larvae or recently settled juveniles of *S. benedicti* thrive at lower salinities and those of *M. ambiseta* thrive at higher salinities. Of the dominant species in this study, *S. benedicti* and *M. ambiseta* are the species expected to have the greatest dispersal ability owing to their planktonic larval stages. *Streblospio benedicti* also commonly dominates benthic assemblages in the lower mesohaline reaches of Chesapeake Bay tributaries (Schaffner et al. 1987, Marsh and Tenore 1990). If salinity was important in determining patterns observed, *M. ambiseta* abundance might be reduced at the main channel flank due to slightly lower salinity (Table 1) relative to other subenvironments, but it is unlikely that *S. benedicti* abundance would be reduced at the south shoal or secondary channel due to salinity effects.

The main channel flank is the most depositional of the subenvironments sampled during the study (Table 1, Chapter 1), and there was a trend of highest abundance of *Streblospio benedicti* juveniles in this subenvironment. Enhanced settlement of larvae of macrobenthic organisms in microdepositional environments has been shown experimentally in flume studies and in other field studies, as larvae are transported and deposited by near-bed hydrodynamics in a manner similar to sediment sorting (Butman 1987, Butman 1989, Snelgrove 1994). Over the relatively short distances between subenvironments, there is no obvious reason to expect along-channel distance to cause differing larval supply of *Streblospio benedicti* to the three subenvironments. The main differences driving the trend of enhanced recruitment at the main channel flank is hypothesized to be the localized sediment deposition due to near-bed flow convergence associated with lateral circulation (Chapter 1). Thus, our results suggest that *S. benedicti* larvae may have been "deposited" along with the suspended sediment.

Differential predation by demersal predators acting across the subenvironments was not likely a primary factor controlling abundance of newly recruiting organisms, as the dominant epibenthic predators in the system, including blue crabs (*Callinectes sapidus*), spot (*Leiostomus xanthurus*) and hogchoaker (*Trinectes maculatus*) typically do not enter the estuary until late May (Lipcius and Van Engel 1990, Seitz 1996). While predation by infaunal predators such as Turbellaria, Nemertea, and glycerid polychaetes can not be discounted, Turbellaria were the only group of predators occurring in large numbers and their abundance was comparable across subenvironments.

The high abundance of juveniles retained on 250 and 125 µm screens during this study emphasize the importance of using small sieve sizes and a high- frequency sampling regime to accurately sample recruiting species of macrobenthic organisms. Our results also demonstrate significant variability in recruitment density and biomass at relatively small across- and along-estuary spatial scales. Thus, studies and monitoring programs that utilize larger sieve sizes and/or restrict sampling to relatively few sites or dates within an estuary are at risk of failing to accurately sample recruiting juveniles. Omission of this life stage can compromise estimations of post-settlement growth rates and secondary production (Schaffner et al. 2002, Chapter 4).

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Table 1. Grand means of physical parameters (with ranges of means in parentheses) for the different subenvironments during the study period of 1 April - 21 June, 1999. Depths are actual depths sampled. n = number of stations sampled in each subenvironment per date. Seabed classification based on the physical parameters presented below, appearance of x-radiographs (Chapter 1) results of previous investigations.

Subenvironment & seabed classification	Depth (m)	Salinity (ppt)	Sediment temp (°C)	Mud content (%) 0-1 cm	TOC (%) 0-1 cm	$C:N_a$ 0-1cm	Chl *a* ($\mu g\ g^{-1}$ wet sed) 0-5 cm	Depth of 0 mV Eh (cm)	Maximum depth of ^7Be (cm)
south shoal n = 4 tidally- or wave-driven cycles of deposition and erosion in surface sediments	2.5 (1.8-3.0)	16 (13-20)	17 (13-23)	95 (92-96)	2.3 (2.0-2.6)	12.6 (11.7-13.6)	3.2 (2.1-5.3)	6	4
secondary channel n = 6 tidally-driven cycles of deposition and erosion in surface sediments	4.8 (3.8-5.8)	17 (16-21)	16 (13-22)	88 (83-97)	2.3 (2.0-2.5)	12.3 (11.8-12.9)	3.6 (2.6-5.3)	4.5	2
main channel flank n = 5 high deposition, long-term sediment accumulation	3.4 (2.5-3.8)	14 (10-19)	16 (13-22)	98 (96-99)	3.0 (2.8-3.2)	12.4 (11.6-13.3)	2.9 (1.6-5.0)	7	6

Table 2. Numerically dominant species, accounting for >90 % of abundance in the 250 µm and 125 µm size fractions. N is summed total number of individuals collected in the 250 µm and 125 µm size fractions. Major taxa are: (P) Polychaeta; (O) Oligochaeta; (T) Turbellaria; (C) Cumacea.

Species	N	% on 250 µm	% on 125 µm	% of total N
Streblospio benedicti (P)	5535	64.2	35.8	49.1
Mediomastus ambiseta (P)	2937	80.3	19.7	26.1
Tubificoides spp. (O)	793	85.8	14.2	7.0
Turbellaria (T)	749	37.4	62.6	6.6
Leucon americanus (C)	571	96.8	3.2	5.1
Total N (dominants)	10585	70.1	29.9	93.9
Total N (all species)	11272	70.9	29.1	100.0

Table 3. Results of 1-way repeated measures ANOVAs (RMANOVAs) testing differences in abundance of taxa over 10 sampling dates. *P* values ≤ 0.01 are in bold.

Source (DF)	SS	MS	F	*P*
Total abundance:				
subenvironment (2)	5.42	2.71	0.38	0.6926
date (9)	483.08	53.68	11.54	**<0.0001**
subenvironment*date (18)	77.06	4.28	0.92	0.5572
error (90)				
Streblospio benedicti				
subenvironment (2)	3.01	1.50	3.31	0.0790
date (9)	49.44	5.49	27.58	**<0.0001**
subenvironment*date (18)	5.53	0.25	1.26	0.2321
error (90)				
Mediomastus ambiseta				
subenvironment (2)	152.80	76.40	12.08	**0.0022**
date (9)	70.87	7.87	7.09	**<0.0001**
subenvironment*date (18)	21.57	1.20	1.08	0.3860
error (90)				
Tubificoides spp.				
subenvironment (2)	1.45	0.73	3.95	0.0545
date (9)	10.07	1.12	8.80	**<0.0001**
subenvironment*date (18)	2.79	0.15	1.22	0.2647
error (90)				
Turbellaria				
subenvironment (2)	0.60	0.28	3.99	0.0531
date (9)	1.20	0.14	1.20	0.3076
subenvironment*date (18)	2.20	0.12	1.08	0.3876
error (90)				
Leucon americanus				
subenvironment (2)	0.94	0.47	1.54	0.2612
date (9)	8.91	0.99	10.12	**<0.0001**
subenvironment*date (18)	3.41	0.19	1.94	0.0220
error (90)				

Table 4. Results of Tukey multiple comparison tests for differences in total abundance of recruits across dates, grouped by subenvironment. The first column of each table lists each sampling date, the second column indicates dates for which a significant difference in abundance was detected ($P < 0.05$). Sampling dates as follows: 1 April (1); 8 April (2); 13 April (3); 20 April (4); 27 April (5); 3 May (6); 10 May (7); 17 May (8); 21 May (9); 21 June (10). NS= no significant difference among dates.

South Shoal

Date	Dates for which significant difference detected
1	3,4,5
2	3,4
3	1,2,9,10
4	1,2,9,10
5	1,10
6	NS
7	NS
8	NS
9	3,4
10	3,4,5

Secondary Channel

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	NS
5	NS
6	NS
7	NS
8	NS
9	NS
10	NS

Main Channel Flank

Date	Dates for which significant difference detected
1	5
2	NS
3	NS
4	10
5	1,10
6	10
7	NS
8	NS
9	NS
10	4,5,6

Table 5. Results of Tukey multiple comparison tests for differences in total abundance of *Streblospio benedicti* recruits across dates, grouped by subenvironment. The first column of each table lists sampling date, the second column indicates dates for which a significant difference in abundance was detected ($P < 0.05$). Sampling dates as in Table 4. NS= no significant difference among dates.

South Shoal

Date	Dates for which significant difference detected
1	2,3,4,5,6,7,9
2	1,4,10
3	1,8,10
4	1,2,8,9,10
5	1,8,10
6	1,10
7	1,10
8	3,4,5
9	1,4,10
10	2,3,4,5,6,7,9

Secondary Channel

Date	Dates for which significant difference detected
1	3,4,5,6,7,8,9
2	4,5,6,7,10
3	1,5,6,10
4	1,2,10
5	1,2,3,8,9,10
6	1,2,3,9,10
7	1,2,10
8	1,5,10
9	1,5,6,10
10	2,3,4,5,6,7,8,9

Main Channel Flank

Date	Dates for which significant difference detected
1	4,5,6,7
2	10
3	10
4	1,10
5	1,10
6	1,10
7	1,10
8	10
9	NS
10	2,3,4,5,6,7,8

Table 6. Results of Tukey multiple comparison tests for differences in total abundance of *Mediomastus ambiseta* recruits across dates, grouped by subenvironment. The first column of each table lists sampling date, the second column indicates dates for which a significant difference in abundance was detected ($P < 0.05$). Sampling dates as in Table 4. NS= no significant difference among dates.

South Shoal

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	NS
5	NS
6	NS
7	NS
8	NS
9	NS
10	NS

Secondary Channel

Date	Dates for which significant difference detected
1	10
2	NS
3	10
4	10
5	NS
6	10
7	NS
8	NS
9	NS
10	1,3,4,6

Main Channel Flank

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	NS
5	NS
6	NS
7	NS
8	NS
9	NS
10	NS

Table 7. Results of Tukey multiple comparison tests for differences in total abundance of *Tubificoides* spp. recruits across dates, grouped by subenvironment. The first column of each table lists sampling date, the second column indicates dates for which a significant difference in abundance was detected (P< 0.05). Sampling dates as in Table 4. NS= no significant difference among dates.

South
Shoal

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	NS
5	NS
6	NS
7	NS
8	NS
9	NS
10	NS

Secondary
Channel

Date	Dates for which significant difference detected
1	8,9,10
2	8,9,10
3	8,9,10
4	8
5	8
6	NS
7	8
8	1,2,3,4,5,7
9	1,2,3
10	1,2,3

Main
Channel
Flank

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	8
5	NS
6	NS
7	NS
8	4,10
9	NS
10	8

Table 8. Results of Tukey multiple comparison tests for differences in total abundance of *Leucon americanus* recruits across dates, grouped by subenvironment. The first column of each table lists sampling date, the second column indicates dates for which a significant difference in abundance was detected ($P < 0.05$). Sampling dates as in Table 4. NS= no significant difference among dates.

South Shoal

Date	Dates for which significant difference detected
1	3,4,5
2	3,4,5
3	1,2
4	1,2,7,8,10
5	1,2
6	NS
7	4
8	4
9	NS
10	4

Secondary Channel

Date	Dates for which significant difference detected
1	5
2	5
3	5
4	8
5	1,2,3,8,9
6	NS
7	NS
8	4,5
9	5
10	NS

Main Channel Flank

Date	Dates for which significant difference detected
1	5
2	NS
3	NS
4	NS
5	1
6	NS
7	NS
8	NS
9	NS
10	NS

Table 9. Results of 1-way repeated measures ANOVAs (RMANOVAs) testing differences in total biomass of taxa over 10 sampling dates. *P* values ≤ 0.01 are in bold.

Source (DF)	SS	MS	F	*P*
Total abundance:				
subenvironment (2)	0.0015	0.0008	1.23	0.3317
date (9)	0.0323	0.0036	10.62	**<0.0001**
subenvironment*date (18)	0.0097	0.0005	1.60	0.0766
error (90)				

Table 10. Results of Tukey multiple comparison tests for differences in total biomass of recruits across dates, grouped by subenvironment. The first column of each table lists each sampling date, the second column indicates dates for which a significant difference in abundance was detected ($P < 0.05$). Sampling dates as follows: 1 April (1); 8 April (2); 13 April (3); 20 April (4); 27 April (5); 3 May (6); 10 May (7); 17 May (8); 21 May (9); 21 June (10). NS= no significant difference among dates.

South Shoal

Date	Dates for which significant difference detected
1	3,4
2	NS
3	8, 9, 10
4	1, 10
5	10
6	NS
7	NS
8	3
9	3
10	3,4,5

Secondary Channel

Date	Dates for which significant difference detected
1	NS
2	NS
3	NS
4	NS
5	9, 10
6	9, 10
7	10
8	NS
9	5, 6
10	5, 6, 7

Main Channel Flank

Date	Dates for which significant difference detected
1	4, 5, 6, 7
2	NS
3	NS
4	1, 10
5	1,10
6	1, 10
7	10
8	NS
9	NS
10	4,5,6, 7

Fig. 1. The upper York River estuary study area, showing station locations in each subenvironment and depth contours of 3, 4, and 10 m. Transect lines (A-A' and B-B') indicate locations of the cross sections depicted in Fig. 2.

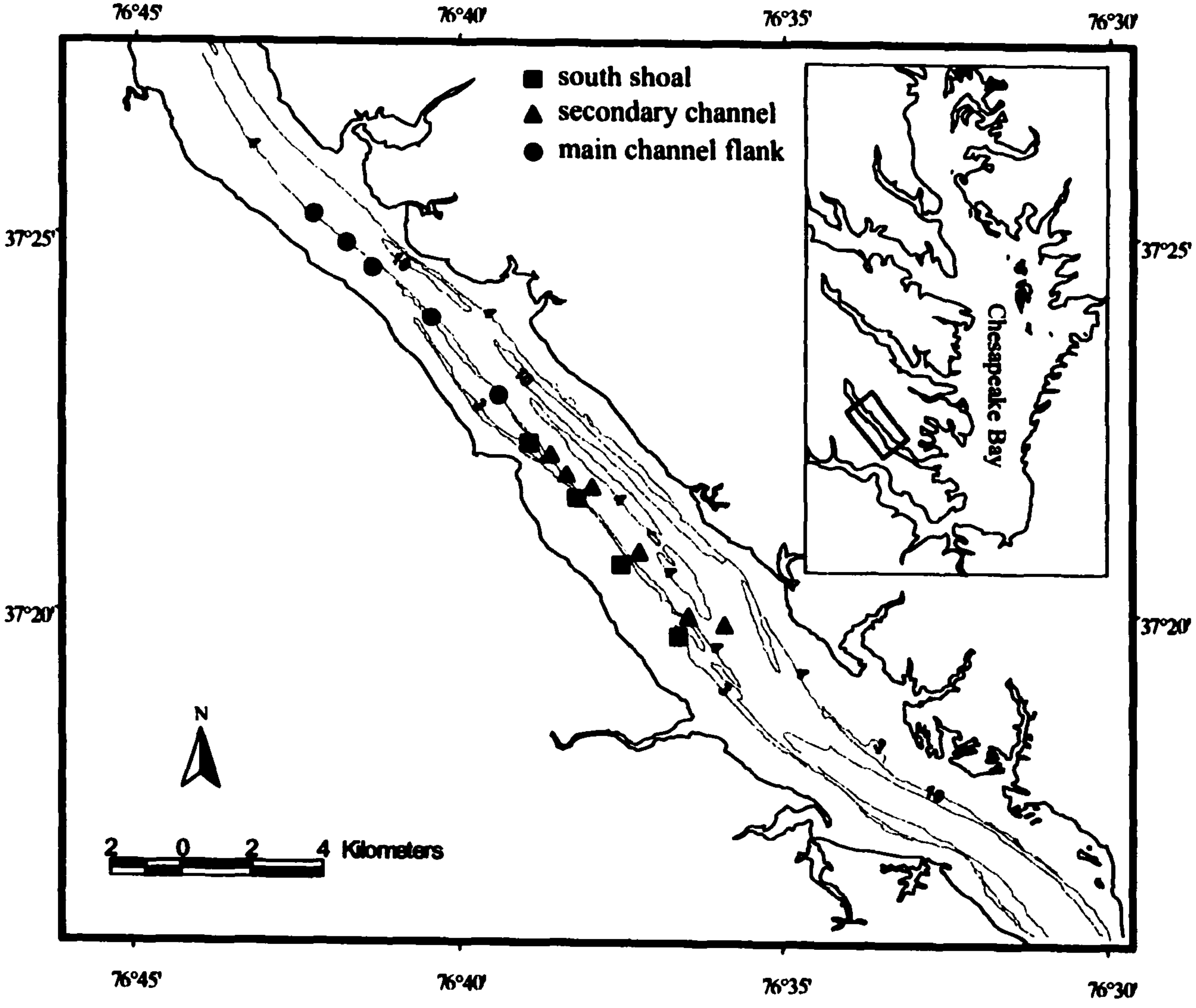
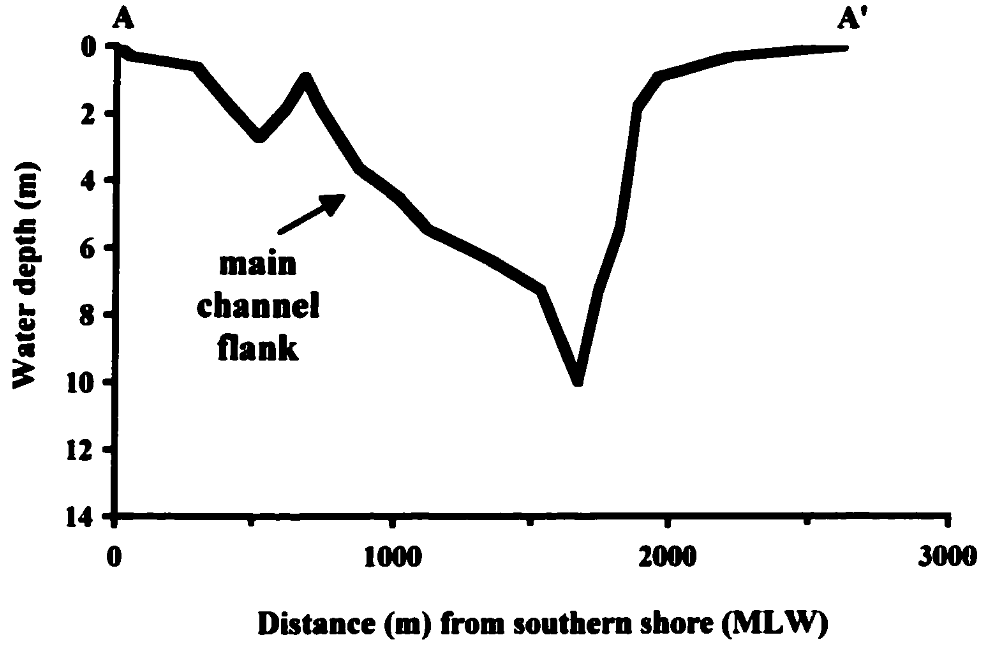
76°45'
76°40'
76°35'
76°30'
37°25'
37°20'
■ south shoal
▲ secondary channel
● main channel flank
Chesapeake Bay
N
2 0 2 4 Kilometers

Fig. 2. Cross-sectional profiles of two upper York River transects (A-A') and (B-B'), depicting locations of the sampled subenvironments. The profiles show change in bathymetry along the transects, expressed as distance from the southern shoreline (MLW).


A
A'
0
2
4
6
8
10
12
14
Water depth (m)
main
channel
flank
0
1000
2000
3000
Distance (m) from southern shore (MLW)

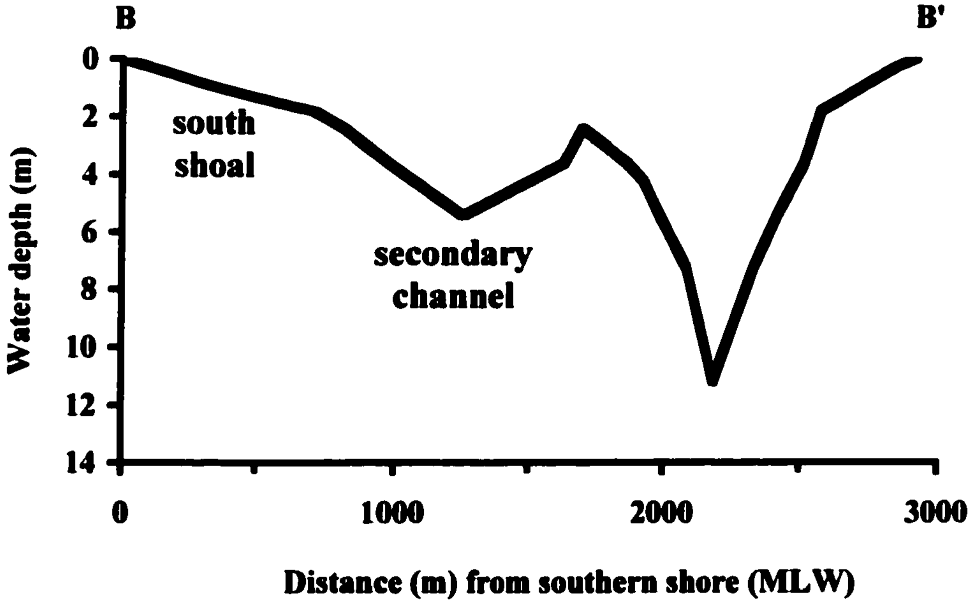

B
B'
0
2
4
6
8
10
12
14
Water depth (m)
south
shoal
secondary
channel
0
1000
2000
3000
Distance (m) from southern shore (MLW)

Fig. 3. Abundance (mean ± SE) of all organisms retained on 125 μm and 250 μm screens.

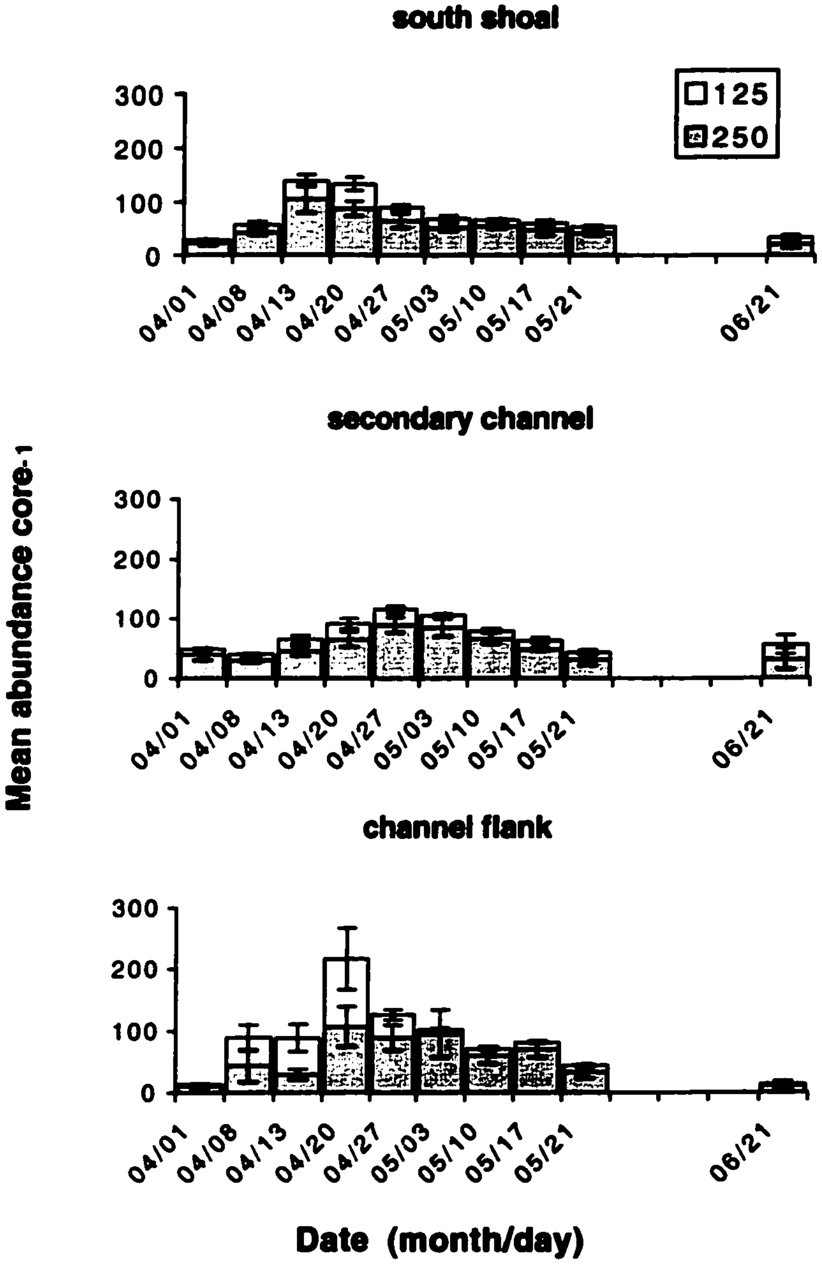

south shoal
300
200
100
0
□125
▨250
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
300
200
100
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
300
200
100
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean abundance core-1
Date (month/day)

Fig. 4. Abundance (mean ± SE) of *Streblospio benedicti* retained on 125 μm and 250 μm screens.

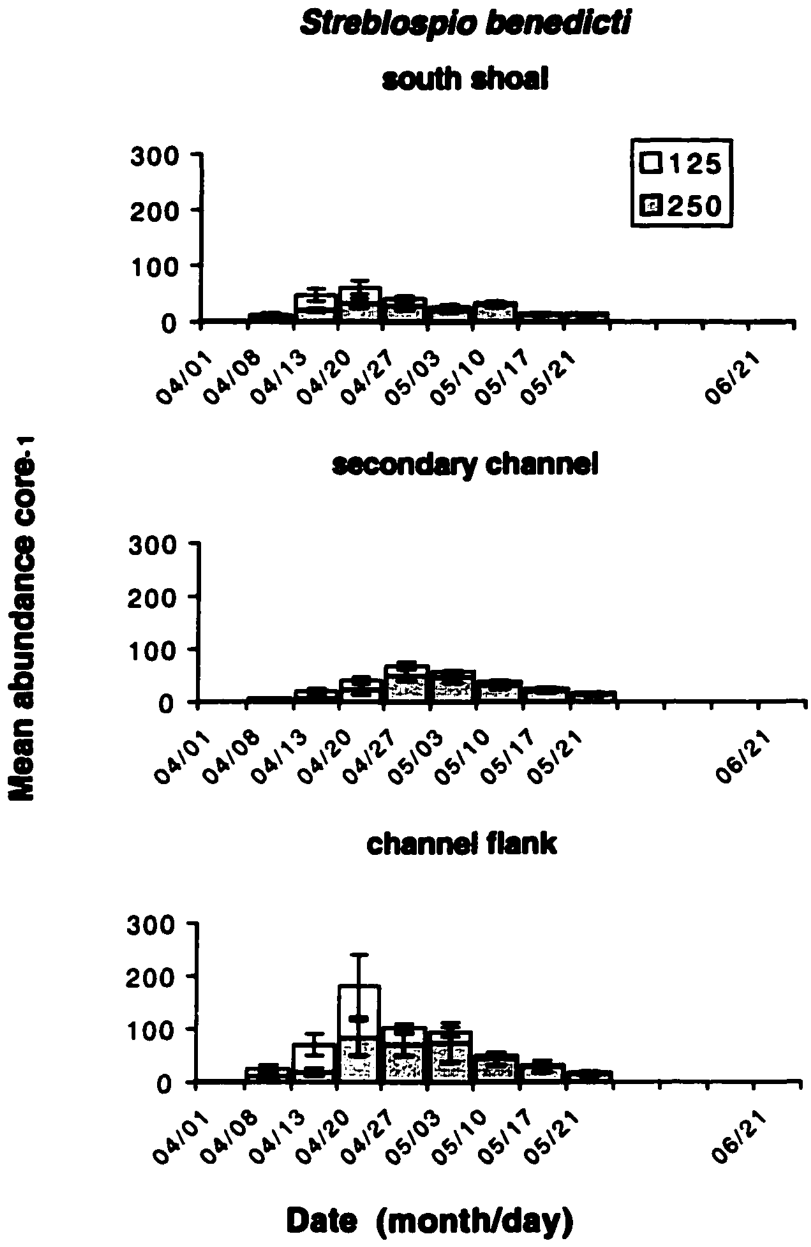

Streblospio benedicti
south shoal
secondary channel
channel flank
300
200
100
0
□125
▨250
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean abundance core-1
Date (month/day)

Fig. 5. Abundance (mean ± SE) of *Mediomastus ambiseta* retained on 125 μm and 250 μm screens.

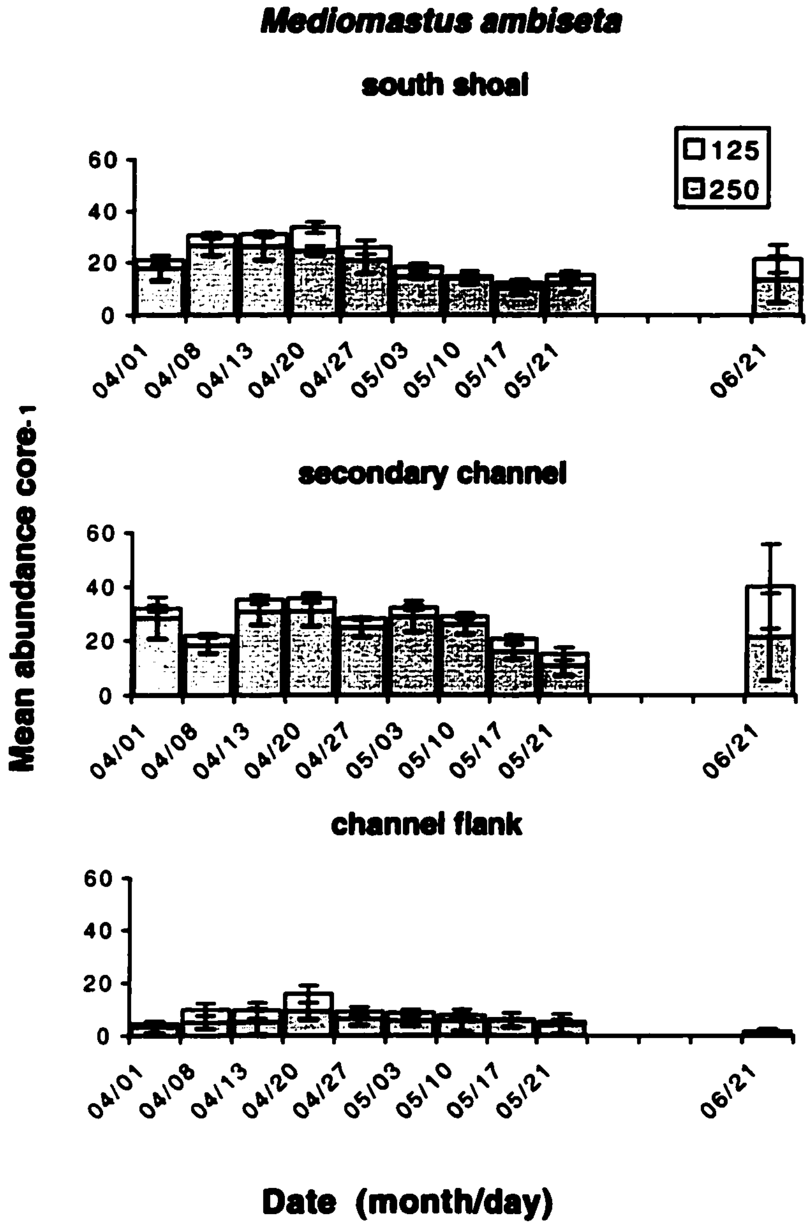

Mediomastus ambiseta
south shoal
secondary channel
channel flank
125
250
0
20
40
60
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean abundance core-1
Date (month/day)

Fig. 6. Abundance (mean ± SE) of *Tubificoides* spp. retained on 125 μm and 250 μm screens.

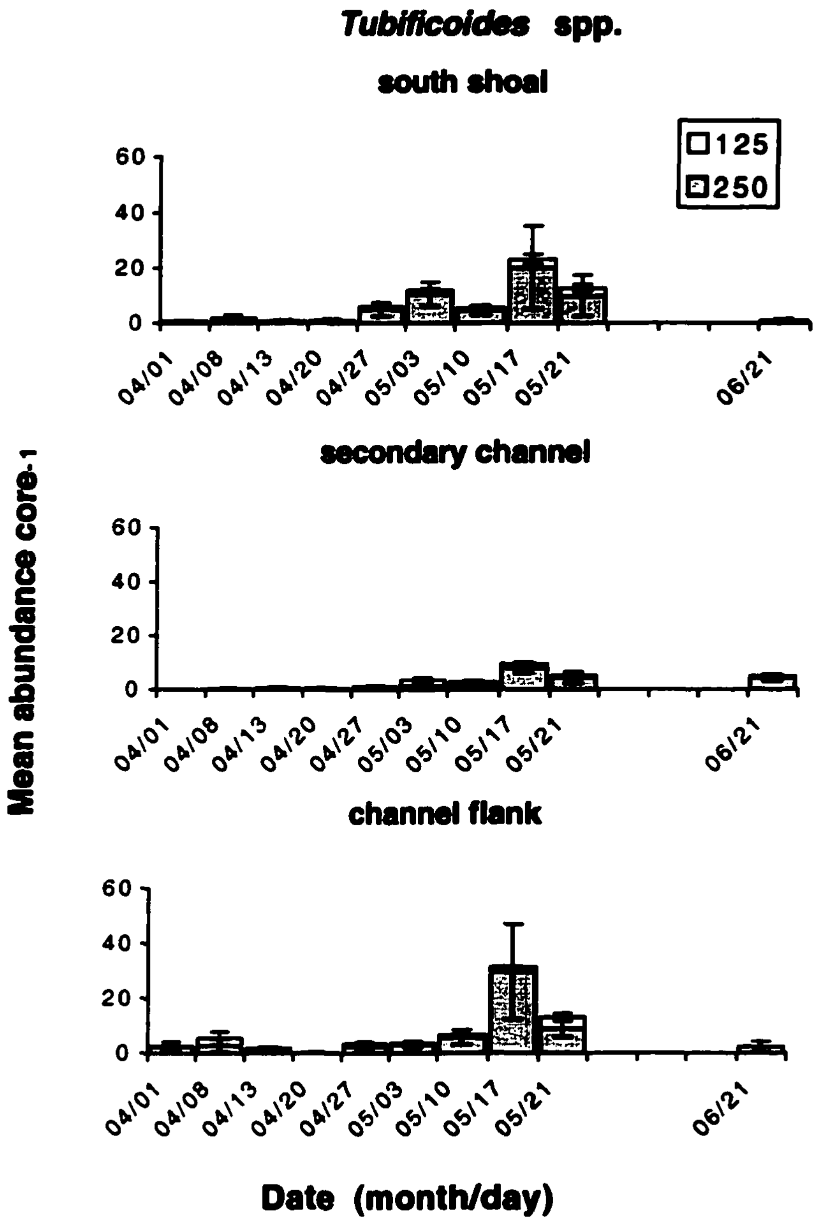
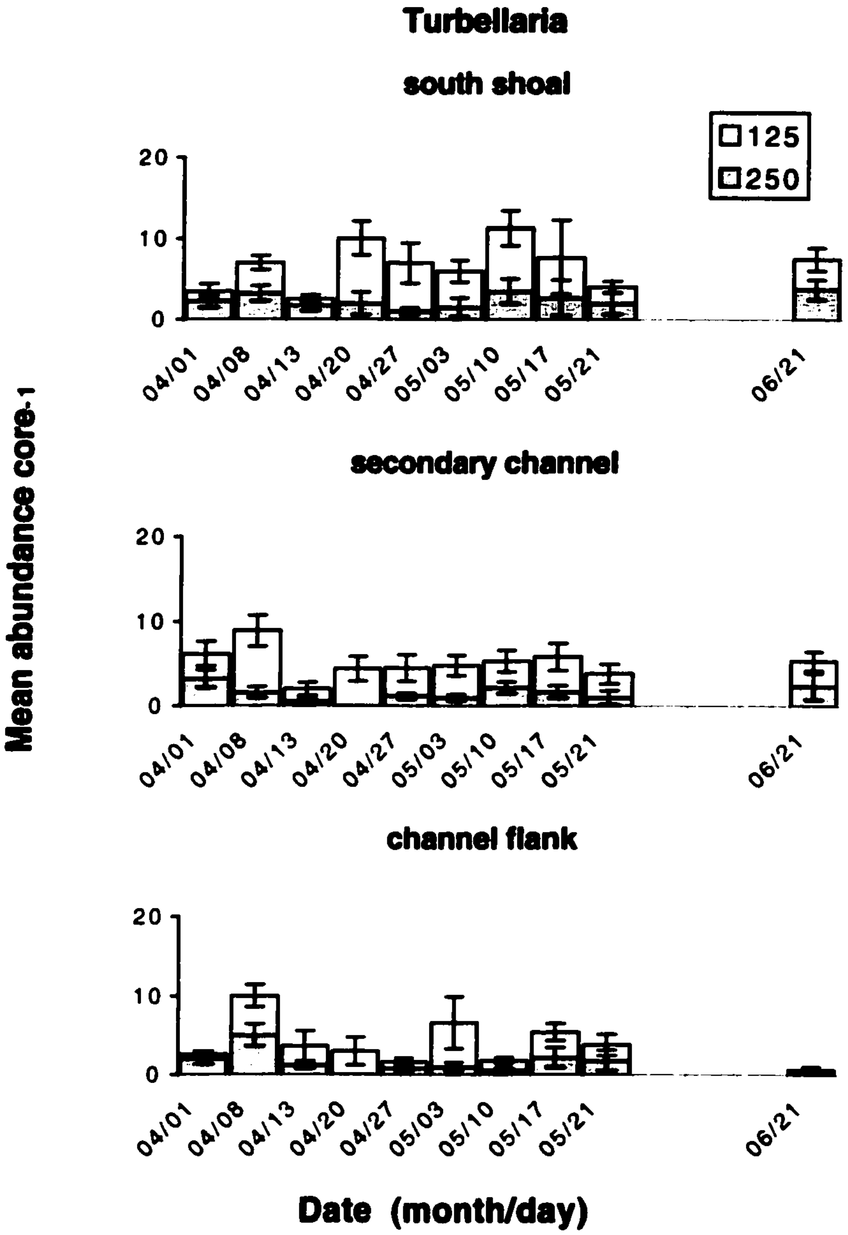

Tubificoides spp.
south shoal
125
250
60
40
20
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
60
40
20
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
60
40
20
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean abundance core-1
Date (month/day)

Fig. 7. Abundance (mean ± SE) of Turbellaria retained on 125 µm and 250 µm screens.



Turbellaria
south shoal
□125
□250
20
10
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
20
10
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
20
10
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean abundance core-1
Date (month/day)

Fig. 8. Abundance (mean ± SE) of *Leucon americanus* retained on 125 μm and 250 μm screens.

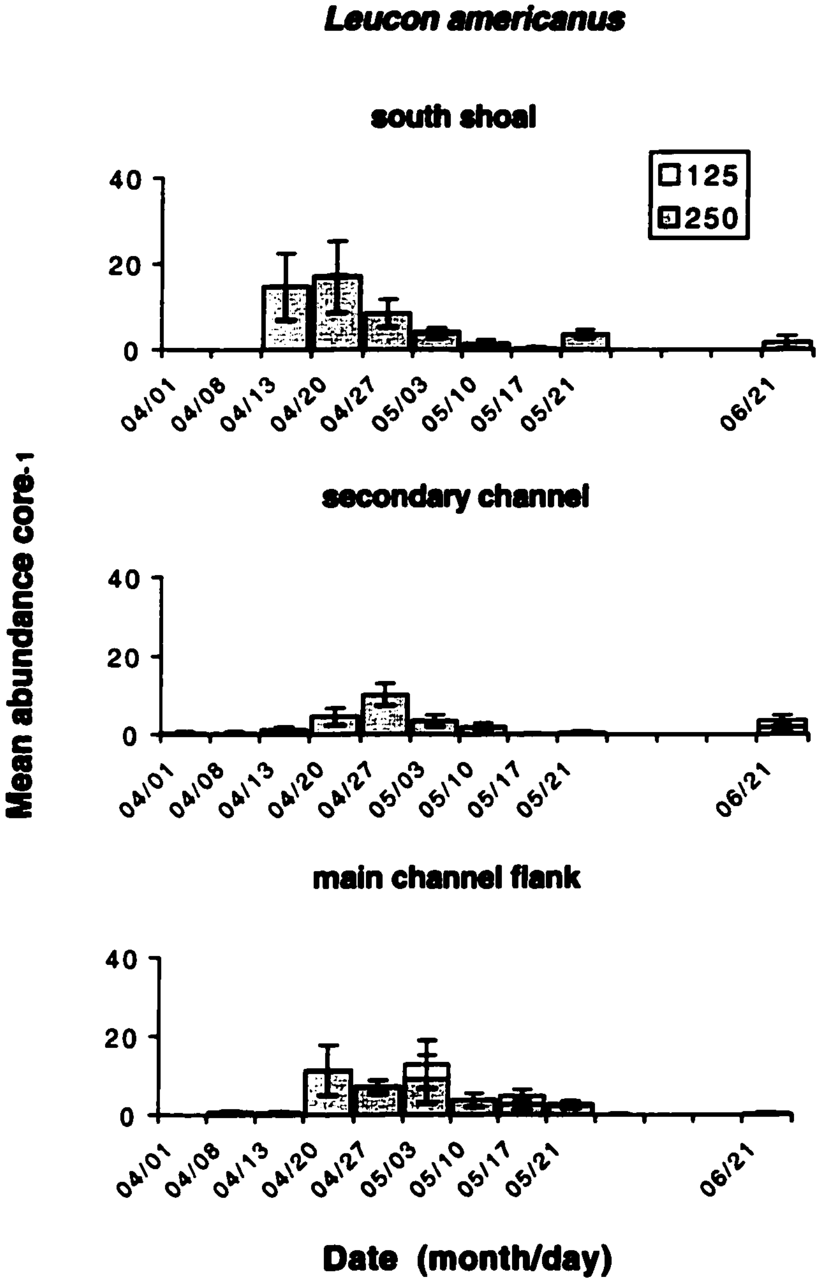

Leucon americanus
south shoal
□125
▨250
40
20
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
main channel flank
Mean abundance core-1
Date (month/day)

Fig. 9. Hierarchies resulting from clustering of stations using Bray-Curtis similarities. Subenvironment abbreviations are as follows: SS = south shoal, SC = secondary channel, MF = main channel flank. Dates as in Table 4.

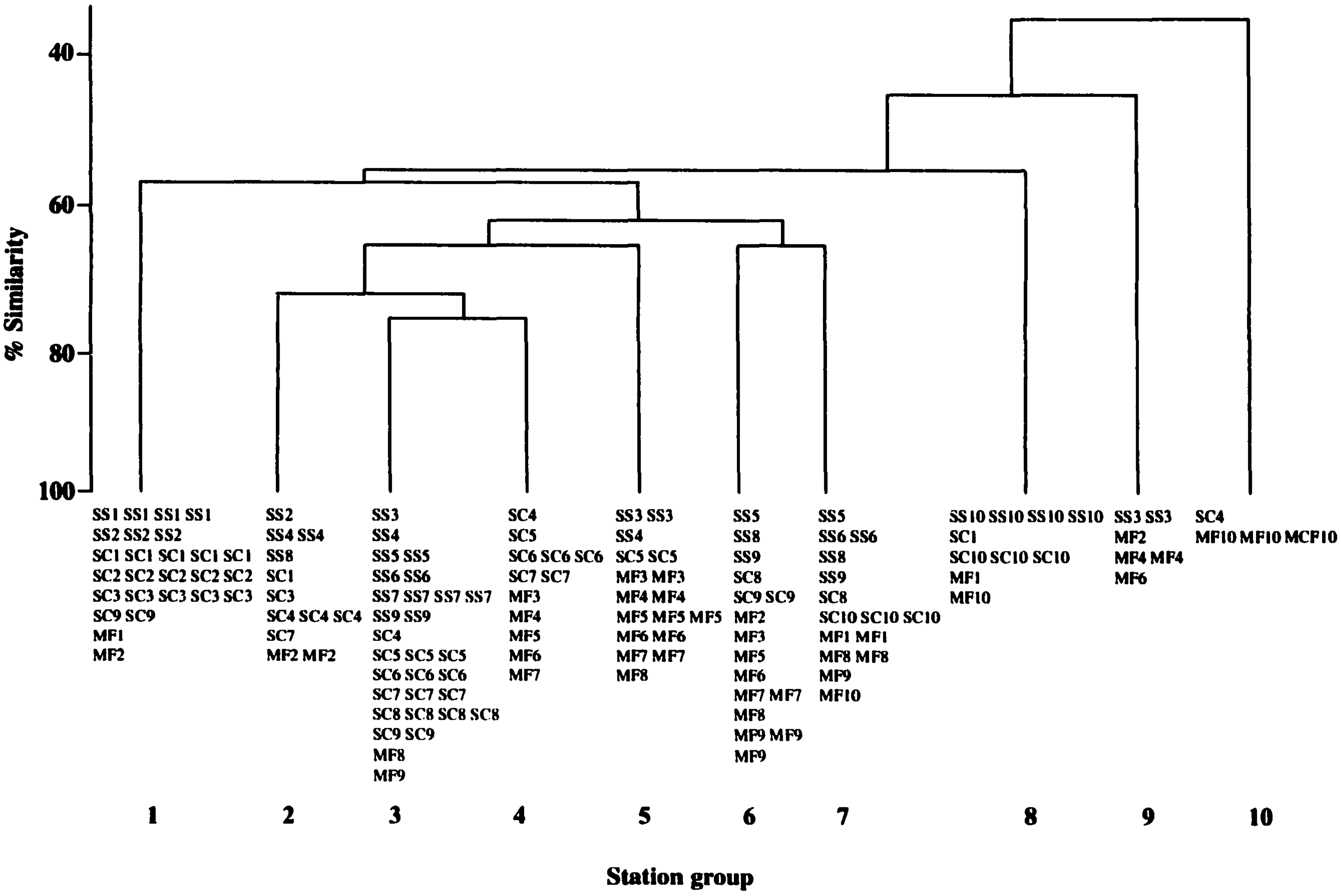

% Similarity
40
60
80
100
SS1 SS1 SS1 SS1
SS2 SS2 SS2
SC1 SC1 SC1 SC1 SC1
SC2 SC2 SC2 SC2 SC2
SC3 SC3 SC3 SC3 SC3
SC9 SC9
MF1
MF2
SS2
SS4 SS4
SS8
SC1
SC3
SC4 SC4 SC4
SC7
MF2 MF2
SS3
SS4
SS5 SS5
SS6 SS6
SS7 SS7 SS7 SS7
SS9 SS9
SC4
SC5 SC5 SC5
SC6 SC6 SC6
SC7 SC7 SC7
SC8 SC8 SC8 SC8
SC9 SC9
MF8
MF9
SC4
SC5
SC6 SC6 SC6
SC7 SC7
MF3
MF4
MF5
MF6
MF7
SS3 SS3
SS4
SC5 SC5
MF3 MF3
MF4 MF4
MF5 MF5 MF5
MF6 MF6
MF7 MF7
MF8
SS5
SS8
SS9
SC8
SC9 SC9
MF2
MF3
MF5
MF6
MF7 MF7
MF8
MF9 MF9
MF9
SS5
SS6 SS6
SS8
SS9
SC8
SC10 SC10 SC10
MF1 MF1
MF8 MF8
MF9
MF10
SS10 SS10 SS10 SS10
SC1
SC10 SC10 SC10
MF1
MF10
SS3 SS3
MF2
MF4 MF4
MF6
SC4
MF10 MF10 MCF10
1
2
3
4
5
6
7
8
9
10
Station group

Fig. 10. Biomass (mean AFDW ± SE) of all organisms retained on 125 µm and 250 µm screens.

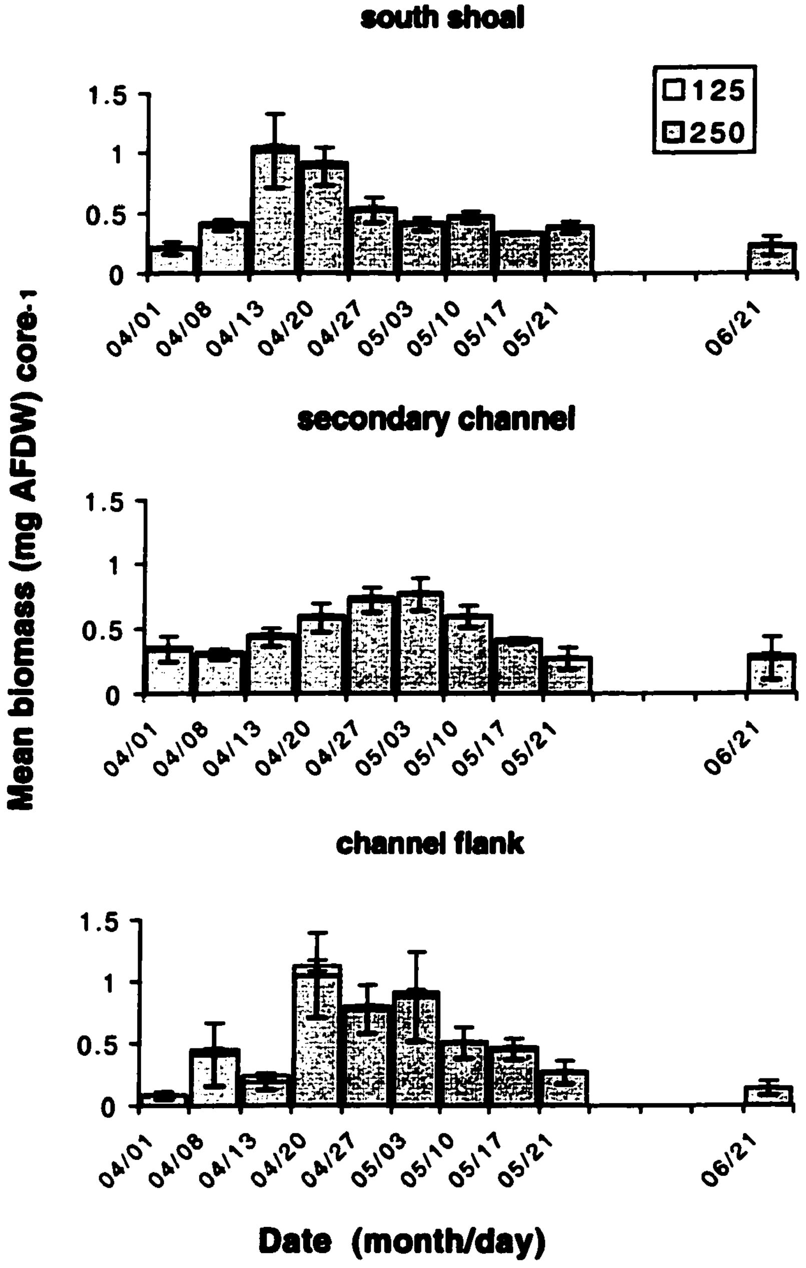

south shoal
▢125
▨250
1.5
1
0.5
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
1.5
1
0.5
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
1.5
1
0.5
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean biomass (mg AFDW) core-1
Date (month/day)

Fig. 11. Biomass (mean AFDW ± SE) of *Streblospio benedicti* retained on 125 μm and 250 μm screens.

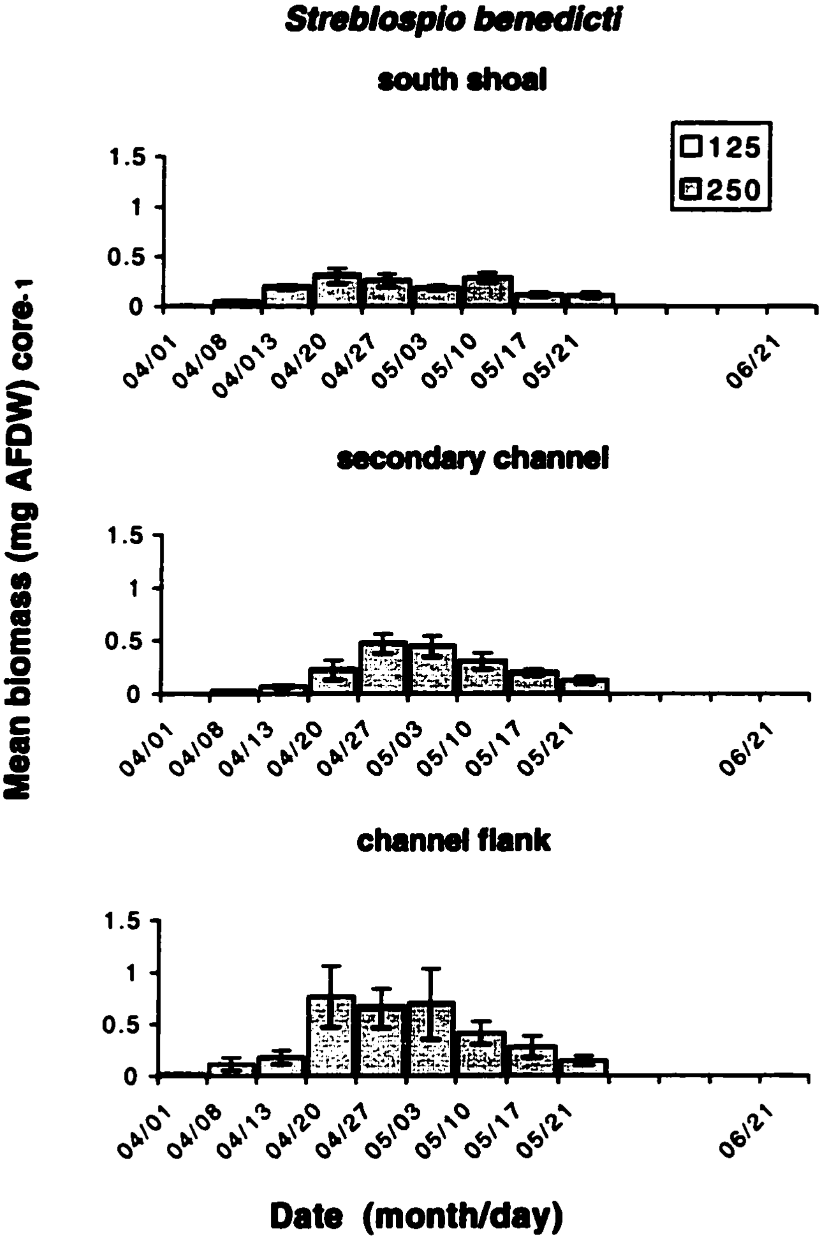
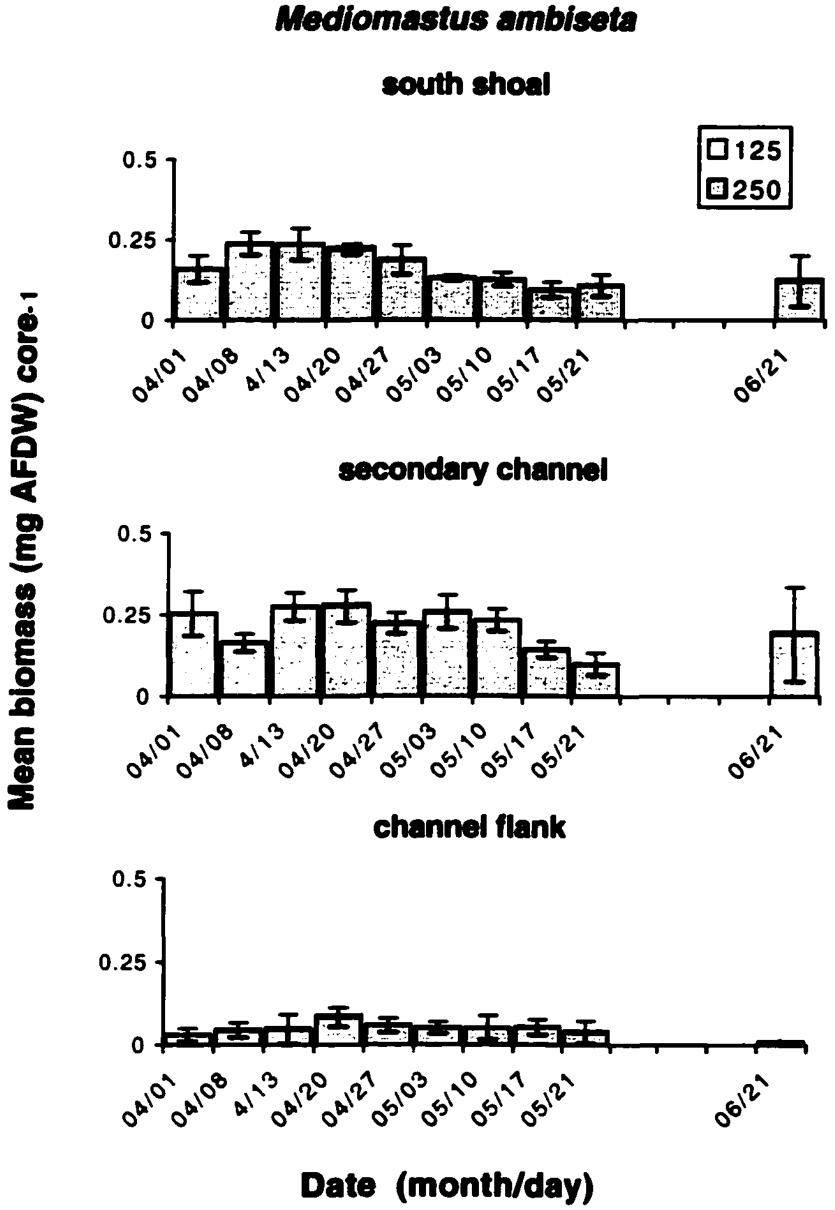

Streblospio benedicti
south shoal
□125
▨250
1.5
1
0.5
0
04/01
04/08
04/013
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
1.5
1
0.5
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
1.5
1
0.5
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean biomass (mg AFDW) core-1
Date (month/day)

Fig. 12. Biomass (mean AFDW ± SE) of *Mediomastus ambiseta* retained on 125 µm and 250 µm screens.



Mediomastus ambiseta

south shoal

secondary channel

channel flank

Fig. 13. Biomass (mean AFDW ± SE) of *Tubificoides* spp. retained on 125 μm and 250 μm screens.

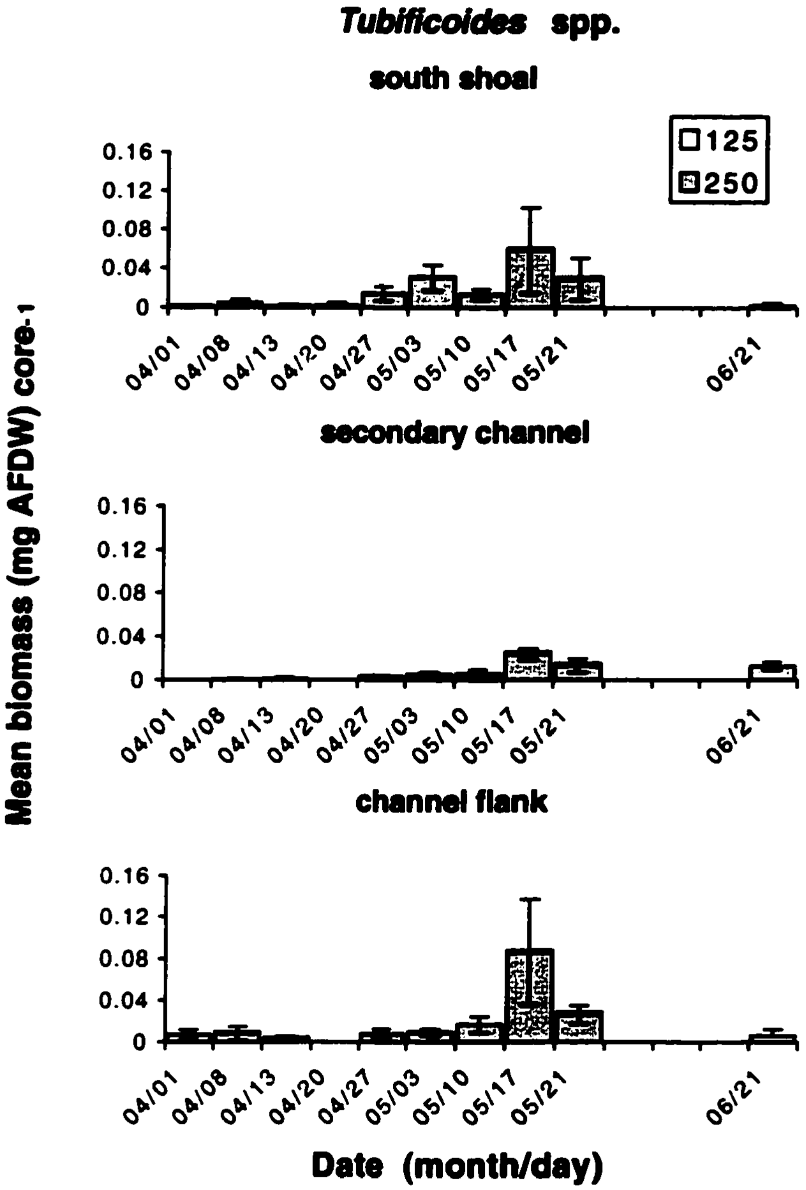

Tubificoides spp.
south shoal
secondary channel
channel flank
□125
▨250
0.16
0.12
0.08
0.04
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean biomass (mg AFDW) core-1
Date (month/day)

Fig. 14. Biomass (mean AFDW ± SE) of Turbellaria retained on 125 μm and 250 μm screens.

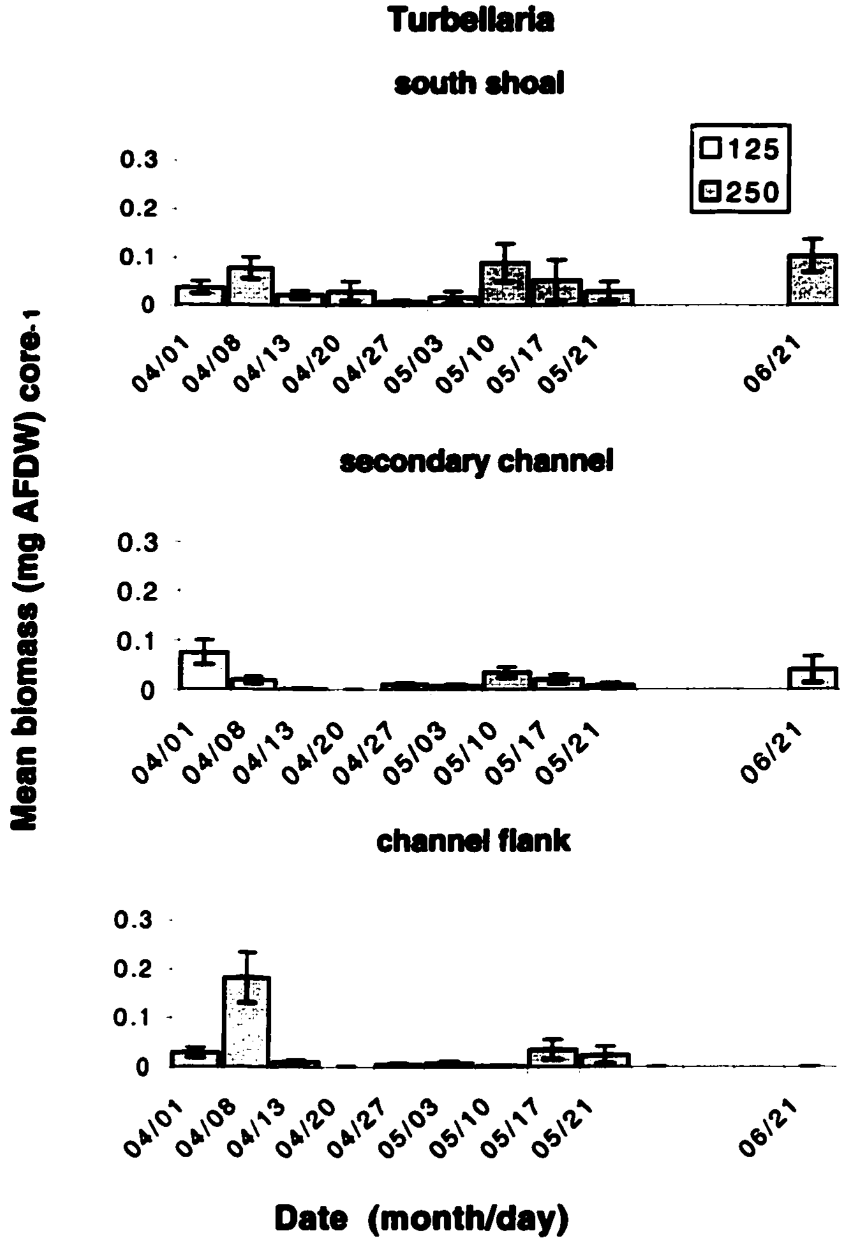
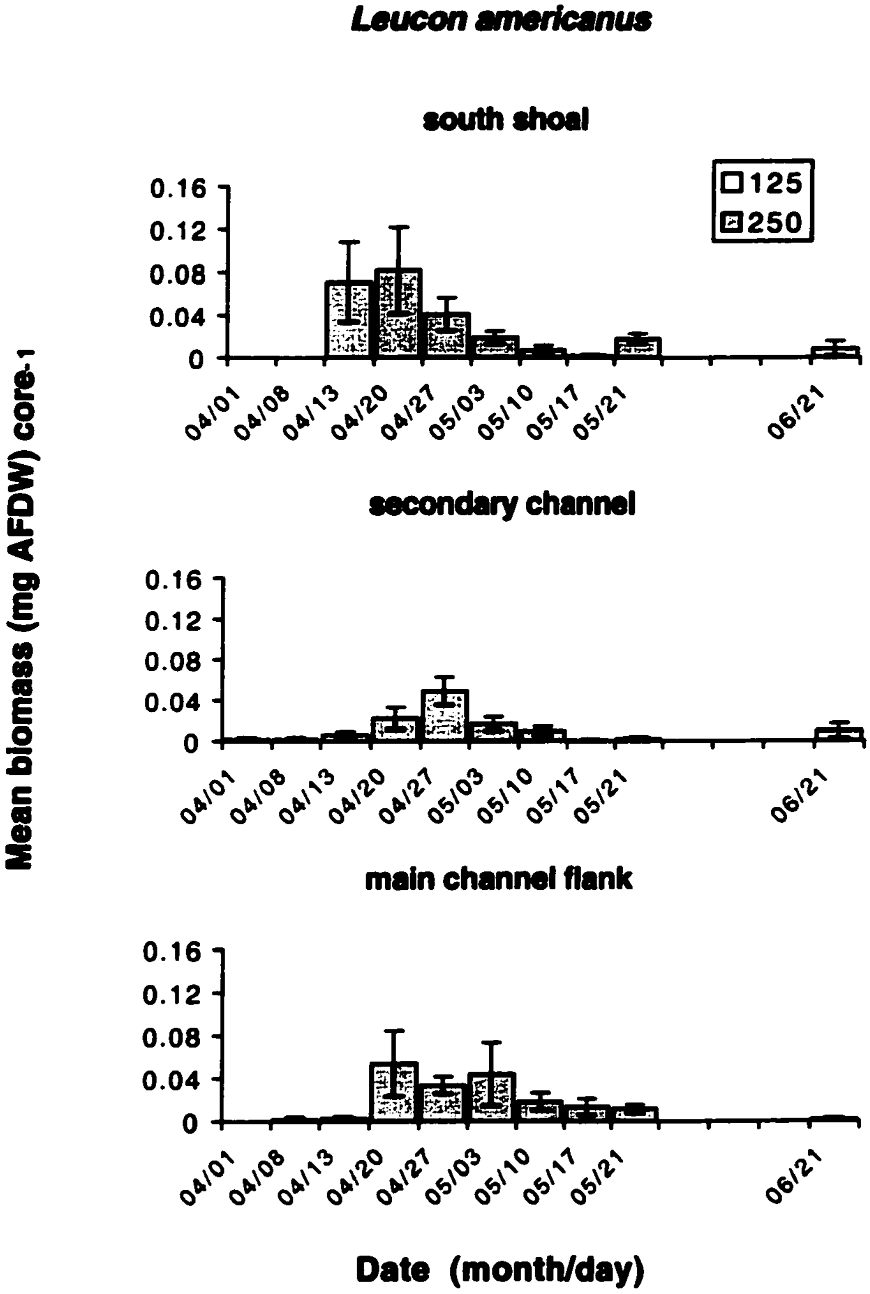

Turbellaria
south shoal
125
250
0.3
0.2
0.1
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
secondary channel
0.3
0.2
0.1
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
channel flank
0.3
0.2
0.1
0
04/01
04/08
04/13
04/20
04/27
05/03
05/10
05/17
05/21
06/21
Mean biomass (mg AFDW) core-1
Date (month/day)

Fig. 15. Biomass (mean AFDW ± SE) of *Leucon americanus* retained on 125 μm and 250 μm screens.



Leucon americanus

south shoal

secondary channel

main channel flank

CHAPTER 4

BENTHIC COMMUNITY STRUCTURE AND SECONDARY PRODUCTION IN MAJOR SUBENVIRONMENTS OF THE MESOHALINE YORK RIVER SUBESTUARY OF CHESAPEAKE BAY

Abstract

Strong associations exist between estuarine benthic community structure, benthic function and environmental gradients. In estuaries, environmental gradients often vary over relatively short temporal and spatial scales, and have been shown to influence benthic community structure and secondary production. We investigated these relationships in a mesohaline estuary among major benthic subenvironments known to differ with respect to seabed characteristics and physical energy regime. Although the macrobenthic assemblages we sampled were characterized by estuarine opportunists and were low in diversity, differences in species abundances and composition were observed across subenvironments. Macrobenthic abundance was highest in the subenvironment characterized by the least deposition and physical reworking of sediments (north shoal). Abundance was reduced in subenvironments characterized by deposition and physical reworking of the upper seabed. Patterns of biomass and secondary production were driven primarily by large individuals of the biomass dominant, the bivalve *Macoma balthica*. Even when disturbance regime restricted abundances of juvenile opportunistic species in surface sediments, large *M. balthica* were often present at depth in the sediments and contributed to high biomass and secondary production. This study emphasizes the importance of including juvenile organisms in calculations of secondary production and of sampling across a range of subenvironments to encompass the variation in community parameters that occur over relatively small distances within the mesohaline estuary.

Introduction

Macrobenthic invertebrates are important components of estuarine ecosystems, as their feeding, burrowing, growth and respiration activities often have major effects on estuarine function (Diaz and Schaffner 1990, Schaffner et al. 2001). Bioturbation by benthic organisms enhances remineralization of organic matter by increasing the depth of the redoxcline in sediments (Aller 1994, Aller and Aller 1998). Bioturbation and biodeposition influence contaminant transport and fate by mixing, burying or liberating contaminants or concentrating them in the food chain (Schaffner et al. 1997, Thompson and Schaffner 2000). Benthic organisms are important food items for demersal predators including fish and crabs (Virnstein 1977, Hines et al. 1990) and estuarine fishery yield is often linked directly or indirectly to benthic secondary production (Baird and Ulanowicz 1989, Diaz and Schaffner 1990). Furthermore, benthic community structure and secondary production estimates are used in monitoring studies as indicators of environmental degradation (Waters 1977, Holland et al. 1987, Weisberg et al. 1997) and as tools for evaluating habitat resource value (Fredette and Diaz 1986).

The extent to which benthic communities modify the sediment or influence trophic transfer depends on factors such as species composition, abundance, size, motility, and residence depth. Benthic community structure and function is correlated with a suite of environmental gradients (Dauer et al. 1987, Holland et al. 1987, Platell and Potter 1996, Schaffner et al. 2001). Factors known to influence estuarine macrobenthic community structure include salinity (Boesch 1977, Schaffner et al. 2001), dissolved oxygen (Dauer et al. 1993, Diaz and Rosenberg 1995), sediment parameters such as grain size and organic content (Boesch 1973, Rhoads 1974), sedimentation rate (Rhoads et al. 1978) and hydrodynamic regimes (Warwick and Uncles 1980, Wildish and Kristmanson 1997, Schaffner et al. 2001, Zajac 2001). In general, diversity and abundance decrease up-estuary (Boesch 1977), while biomass and production patterns may be more complicated (Schaffner et al. 2001).

Results of our work (Chapter 1) and that of previous investigators have delineated benthic subenvironments with distinct across-estuary differences in physical forcing, seabed dynamics, and sediment accumulation regimes across relatively small spatial scales in the York River subestuary of Chesapeake Bay. While the response of benthic communities to major gradients of environmental variables in estuaries is well established, local gradients in hydrodynamics and physical processes have generally not been addressed, but could be equally important in structuring communities. The objective of this study was to compare patterns of macrobenthic community abundance, biomass, secondary production and diversity among major benthic subenvironments in the mesohaline York River estuary to determine if community structure reflected documented variations in across-estuary seabed characteristics (Chapter 1).

Materials and Methods

Study region

The study region encompassed ~ 55 km^2 of the upper York River, a subestuary of Chesapeake Bay, Virginia, USA (Fig. 1). General descriptions of the environmental setting are given in Dellapenna et al. 1998, Schaffner et al. 2001, and Chapter 1. Bottom water salinity of 10 - 20 ppt and bottom water temperature of 2 - 28 °C are characteristic for this reach of the estuary. The study region does not suffer hypoxia or anoxia during the summer, as is observed further downstream (Pihl et al. 1992). The infaunal community in the mesohaline York River is relatively depauperate, and is dominated by small annelids, peracarid crustaceans, and bivalves (Boesch 1977, Schaffner et al. 2001).

Seabed characteristics

Using a variety of tools to characterize the seabed, including grain size, sediment water content, maximum depth of ^{7}Be, depth of the oxidized layer, physical structure of the sediment, sediment chlorophyll *a* and organic content, we documented consistent differences in physical characteristics of the seabed among upper York River subenvironments sampled in April – June 1999 (Table 1, Chapter 1). These differences were attributed to the along- and across-estuary location of the subenvironments. The south shoal, secondary channel, main channel flank and main channel were characterized by variations in short-term sediment deposition and physical reworking rates of near-surface sediments and longer-term sediment accumulation. The south shoal experienced deposition and physical reworking of the upper few centimeters of the seabed during this study. The secondary channel was characterized by cycles of erosion and deposition in the upper few centimeters of the seabed, with longer-term evidence of significant erosion and deposition, possibly associated with tidal currents. Sediment accumulation was the predominant process in the main channel flank, likely due to sediment trapping associated with overlying lateral convergence zones. The main channel was depositional during the study, but evidence of longer-term erosion and deposition is recorded in the seabed, and this subenvironment experiences the strongest tidal currents.

The north shoal was non- depositional, and sediments in this subenvironment are the most stable in the system.

Infaunal sampling

Permanent stations were established in five major subenvironments of the upper York River, Chesapeake Bay, USA (Figs. 1 and 2): south shoal, secondary channel, main channel flank, main channel, and north shoal. Sampling was conducted in the spring because it is the time when many of the dominant species of the mesohaline macrobenthic community exhibit peak recruitment (Diaz 1984, Zobrist 1988) and maximum production (Marsh and Tenore 1990), and is also a time of significant seabed processes such as new deposition associated with the spring freshet and tidally-driven sediment transport processes (Dellapenna et al. 1998, Friedrichs et al. 2000, Schaffner et al. 2001). For this study, the south shoal, secondary channel and main channel flank subenvironments were sampled on 20 April, 21 May, and 21 June 1999; the north shoal was sampled on 7 May and 24 June 1999; the main channel was sampled on 13 May and 18 June 1999.

At the south shoal, secondary channel, main channel flank and main channel, sediment was collected with a Gray O'Hara box core (625 cm^2 area, 50 cm maximum length). Infauna were sampled with a 9.0 cm (i.d.) acrylic core (64 cm^2 surface area). For the north shoal stations, sediment was collected by hand via snorkeling, using an acrylic core. Additional cores were remove from each box core, or collected in the immediate vicinity of the faunal core in the case of the north shoal, for the determination of the seabed characteristics presented in Table 1 (methods described in Chapter 1). For each core, sediment surface temperature was measured with a thermometer, and salinity of water overlying the sediment was measured with a refractometer.

On each date, the 0-1 cm, 1-2 cm and 2-5 cm depth intervals of sediment from the core were extruded in the field and immediately fixed in buffered 10% formalin containing rose bengal stain. Prior to extrusion, water overlying the sediment core was drawn off and passed through a 125 µm sieve. Animals retained in the sieve were washed into the 0-1 cm sample jar using 125 µm- filtered seawater. The 5-10 cm, 10-15 cm and > 15 cm depth intervals were sieved on 500 µm screens in the field before fixation. In this region of the estuary, only bivalves are generally found in the > 15 cm depth fraction (Schaffner et al. 1987), and they were retained by visual sorting of the materials remaining after the sediment was washed through a 500 µm screen in the field.

Laboratory analyses

In the laboratory, the 0-1 and 1-2 cm fractions were sieved on nested 500-250-125 µm screens, and the 2-5 cm samples were sieved on nested 500-250 µm screens. Use of the 125 µm screen ensured collection of the earliest benthic life stages of the dominant macrobenthic infaunal organisms in the York River community (early juveniles), while the 250 µm screen retained the late juveniles (Zobrist 1988, Llansó 1992). The 500 µm screen retains most adult organisms. Macrobenthic organisms in all depth fractions were identified to the lowest taxonomic level possible (usually species) and enumerated. Ash-free dry weight (AFDW) was measured for each taxon retained on 500 µm screens as ash-free dry weight (AFDW) by oven-drying at 60°C for a minimum of 48 h and ashing at 550°C for 4 h. For organisms retained on the 250 µm and 125 µm screens, previously determined AFDW values individual^{-1} for York River taxa (Schaffner and Hinchey, unpublished) were used to convert abundances to AFDW biomass.

Community production in each subenvironment was calculated using the model of Edgar (1990):

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

in which P = daily average production in µg d^{-1}, B = AFDW biomass (µg), and T = water temperature in °C. This model, calculated from the published production rates of 41 marine and estuarine invertebrate species ranging in size from 10^{-5} g to 1 g and valid for temperatures from 5-30 °C, is proven effective for estimating benthic community production in Chesapeake Bay (Hagy 2001). For each sample, we determined production separately for the combined juvenile size classes (125 µm + 250 µm) and adults (500 µm) using the equation above and then summed the two size class production values into a total production value. Production values were converted to mg AFDW m^{-2} d^{-1} for this study.

Species richness, diversity and evenness indices were calculated for each subenvironment on each sampling date using the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package. The two estimates of diversity calculated were the Simpson index ($1-\lambda$) and the Shannon index (H', using $\log_2$). The Simpson index is the probability that any two individuals from a sample, chosen at random, are from different species, with larger values corresponding to more diverse assemblages. The Simpson index is the preferred diversity measure to use for this study because it is relatively unbiased with respect to sample size (Lande 1996). H' is dependent on sampling effort and on the actual number of species in a community (Lande 1996). *H'* is also insensitive to rare species (Clarke and Warwick 2001). Despite its inherent bias, *H'* was calculated because of its widespread reporting in marine and estuarine studies.

We tested for differences in total community abundance and biomass between the five subenvironments for the May and June sampling dates using a 2-factor Model 1 (fixed factor) AVOVA with the factors date and location (subenvironment). We tested for differences in richness, diversity and evenness among subenvironments using 1-way ANOVAs. Data were transformed by log (X + 1) to satisfy assumptions of the parametric tests, tested using a Shapiro-Wilk test of normality (Zar 1999) and Bartlett's test of homogeneity of variance (Underwood 1997). Multiple comparisons between means were subsequently performed with Tukey Studentized Range tests.

Similarity of species composition and abundance among subenvironment was determined by calculation of group-averaged Bray-Curtis similarity measures followed by hierarchical cluster analysis using the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package. Abundance data were square-root transformed prior to analysis to down-weight the importance of the highly abundant species, so that similarities are also based on values of mid-range species (Clarke and Warwick 2001).

Results

Physical characteristics

Salinity and sediment temperature increased from April to June (Appendix I). Lowest mean salinity (14 ppt) was measured at the main channel flank, the most upstream subenvironment, and the highest mean salinity (21 ppt) was at measured at the main channel, the most downstream subenvironment. Among the subenvironments, the salinity range was 6 ppt in May, but only 3 ppt in June. A range of 5 ppt is a common daily range at a fixed location in this region of the York River (Schaffner et al. 2001).

Patterns of total abundance and biomass among subenvironments

A total of 41 species were collected during this study (Appendix IV). A subset of 11 species or species groups accounted for > 95% of the abundance and > 90% of the biomass of the total fauna collected (Table 2). Comprising this assemblage were seven polychaete species (*Mediomastus ambiseta*, *Streblospio benedicti*, *Glycinde solitaria*, *Heteromastus filiformis*, *Eteone heteropoda*, *Paraprionospio pinnata* and *Nereis succinea*), one oligochaete species group (*Tubificoides* spp., grouped together because immature individuals are indistinguishable), an unidentified species of Turbellaria, the cumacean *Leucon americanus*, and the bivalve *Macoma balthica*.

In April, mean total abundance at the south shoal, secondary channel and main channel flank ranged between ~150 and 300 individuals core^{-1}. In May, mean total abundance was significantly greater at the north shoal than at the south shoal, secondary channel and main channel flank (Tables 3 and 4, Fig. 3a), exceeding 500 individuals core^{-1}. This large abundance was primarily attributed to high densities of the polychaete *Streblospio benedicti* (~1100 individuals) collected at one station (Fig. 4). May mean abundance at the other subenvironments was < 200 individuals core^{-1}, with macrofaunal abundance at the channel significantly greater than at the secondary channel and main channel flank. In June, mean total abundance at the north shoal was again significantly greater than at the south shoal, secondary channel and main channel flank (Tables 3 and 4, Fig. 3a), driven by high densities of *Tubificoides* spp. and Turbellaria in the cores (Fig. 4). Mean abundance at the channel was also high in June (> 350 individuals core^{-1}, driven largely by high densities of *Mediomastus ambiseta)* and was significantly greater than at the secondary channel and main channel flank (Figs. 3a and 4).

Presence or absence of large specimens of the bivalve *Macoma balthica*, the biomass dominant in the study, was primarily responsible for driving the spatial and temporal patterns we observed in biomass (Figs. 3b and 4). Despite the high mean total abundance at the north shoal in May (Fig. 3a), biomass was significantly lower here than at the south shoal and main channel flank (Tables 3 and 4, Fig 3b). The abundant taxa at the north shoal in May (primarily *Streblopsio benedicti*, *Eteone heteropoda*, *Tubificoides* spp. and Turbellaria) have lower AFDW individual^{-1} relative to large *M. balthica*, which were present at depth at the south shoal and main channel flank at this time. In June, the channel also displayed low biomass, despite high mean abundance. This was due to dominance of the channel assemblage by small *Mediomastus ambiseta* and absence of large adult taxa (*M. balthica* and the polychaetes *Nereis succinea* and *Paraprionospio pinnata*), which were present at the south shoal and north shoal during this time.

Depth distribution patterns of total abundance and biomass

There was a trend of greater total abundance of organisms at sediment depths less than 2 cm, where juveniles (retained on 125 μm and 250 μm screen sizes) often constituted greater than 50% of the total abundance (Fig. 5). A trend of shallow overall distribution of abundance was apparent at the secondary channel, which consistently had a low abundance of organisms at depths below 2 cm. Biomass displayed the opposite pattern, with the bulk of the biomass occurring at depths below 2 cm, largely driven by adult organisms retained on 500 μm screens, primarily large *Macoma balthica* (Fig. 6). For the south shoal, secondary channel and main channel flank, greater abundance of *M. balthica* in April translated into greater biomass at depth.

Diversity

Diversity at the main channel flank, measured by both *H'* and the Simpson index, was significantly lower in April compared to the south shoal and secondary channel subenvironments (Tables 5 and 6, Fig. 7). In May and June, months when all five subenvironments were sampled, diversity measured by both *H'* and the Simpson index did not vary across subenvironment. When *H'* is calculated using data for organisms retained on 500 μm screens only (the screen size most often used by monitoring programs), mean diversity ranged from 1.9-2.7. When data for all screen sizes are included, mean diversity ranged from 1.7-2.6 (Fig. 7).

Evenness in May was significantly lower at the north shoal than at the south shoal and secondary channel, and evenness in June was significantly lower in the main channel than at the main channel flank. Species richness at the north shoal was significantly greater than for any other subenvironment in May, and was significantly greater than only the main channel flank in June.

Community analyses

Hierarchical cluster analysis revealed that species composition and abundance among the south shoal, secondary channel and main channel flank subenvironments displayed similarities of 45 to 70% in April, and distinct station groups could be discerned for the main channel flank subenvironment versus the south shoal and secondary channel (Fig. 8). In May, the station groups based on species composition and abundance among all five subenvironments displayed similarities of 40 to 70%, and distinct station groups were discerned for each subenvironment (Fig. 9). In June, station groups were 35 to 75% similar, and distinct station groups were discerned for the main channel flank, main channel and north shoal (Fig. 10). The south shoal and secondary channel subenvironments formed a mixed station group in June.

Secondary production

As with biomass, large specimens of the bivalve *Macoma balthica* were primarily responsible for driving the spatial and temporal patterns we observed in secondary production among subenvironments (Fig. 11). Along with a few individuals of its congener *M. mitchelli*, *M. balthica* accounted for 18 to 87 % of the total calculated production at the subenvironments during our study. At the north shoal and main channel, juveniles (organisms in the 125 µm and 250 µm size classes) contributed almost 20% of the total production in May and June, compared with < 10% in the other subenvironments (Fig. 12).

Discussion

We observed differences in community structure and function among benthic subenvironments of the upper York River that are closely located within the same major estuarine salinity regime, but that are subject to different patterns of hydrodynamics, seabed dynamics, and longer-term sediment accumulation. In general, the main channel, an energetic subenvironment characterized by strong tidal currents and considerable sediment transport (Friedrichs et al. 2000, Lin and Kuo 2001, Schaffner et al. 2001), had the lowest abundance and the lowest production. The north shoal subenvironment, which was the most stable benthic habitat sampled, had the highest abundance of shallow surface dwellers and occasional large individuals of *M. balthica*, which resulted in increased production relative to the channel. Abundances of shallow-dwelling infauna at the south shoal, secondary channel and main channel flank subenvironments, which experienced higher deposition and more frequent sediment reworking rates, were depressed relative to the north shoal subenvironment. Although a suite of physical and biological factors likely influences the patterns we documented, the potential role of seabed disturbance as a major factor in structuring the upper York River macrobenthic community can not be discounted given the limited spatial scale of this study.

Salinity has been shown to play a major role in determining large-scale patterns of species distribution along the York River-lower Chesapeake Bay estuarine gradient and in other estuarine systems worldwide (Boesch 1977, Schaffner et al. 2001), with a species minimum occurring between 5 and 8 ppt. Salinity stress limits the regional species pool in the York River to approximately 40 species in the upper York estuary, with the 15% isohaline generally regarded as the upestuary limit of marine euryhaline species (Boesch

1977, Schaffner et al. 2001). All subenvironments we studied were populated by the same, reduced species pool of euryhaline opportunists (*sensu* Boesch 1977), that typically dominate the mesohaline benthic assemblages of the Chesapeake Bay ecosystem. Cluster analyses revealed that the stations in the different subenvironments displayed distinct patterns of species abundance and composition. Despite the importance of salinity in structuring benthic communities along the estuarine gradient, our work supports the hypothesis proposed by Schaffner et al. (2001) that seabed dynamics exert significant local effects on benthic communities in this and other coastal ecosystems.

Shannon *H'* diversity values measured in the upper York River subenvironments were low, ranging from 1.9- 2.7 for the 500 µm size class. These values are less than characteristic diversity values measured in non-impacted high mesohaline mud communities in Chesapeake Bay and its tributaries (where $H' > 3$ for the 500 µm size class), and often border or equal diversity values of communities classified as impacted ($H' < 2$ for the 500 µm size class) (Weisberg et al. 1997). Due to the limited regional species pool of estuarine macrofauna (Deaton and Greenberg 1986), disturbed benthic habitats in this system are characterized by depauperate benthic communities exhibiting depressed abundance and, often, low biomass. Decreased macrofaunal abundance and biomass that results in a shift toward microfaunal-dominated communities have been similarly observed for large, dynamic river mouths such as the Amazon and Chainghang Rivers, where bottom disturbance is severe (Rhoads et al. 1985, Aller and Stupakoff 1996). *Macoma balthica* is an exception to the trend of decreased biomass in the York River, as the subenvironments characterized by sediment deposition and surface disturbance are often populated by adults of this species. This species, which has motile juveniles capable of migrating up through ~ 20 centimeters of deposited sediment (Chapter 5) and adults that can reside up to 40 cm deep in the sediment, appears to be resilient to sediment disturbance, and can grow to adulthood in this system (Schaffner et al. 2001).

Both settlement and post-settlement processes could be directly generating the differences in abundance we observed among subenvironments. In a companion study of recruitment dynamics for this region of the York River (Chapter 3), we documented different trends in the magnitude and timing of settlement among subenvironments, with a strong recruitment pulse occurring in the main channel flank region, which is characterized by the highest short-term deposition and long term accumulation. Unfortunately, time-series recruitment data for that study did not include the main channel or north shoal environment. The stable nature of the sediment-water interface of the north shoal subenvironment could render it a likely candidate habitat for source populations of larvae and juveniles of resident invertebrate species, a phenomenon that should be investigated further.

Factors indirectly related to difference in physical energy regimes across subenvironments could also drive the patterns observed. Food availability did not appear to be a major determinant of organism abundance or production among stations. Many of the resident species in the York River mesohaline species assemblage are deposit feeders, dependent on sedimentary organic matter, and productive populations existed at the north shoal, where the organic matter in surface sediments was most refractory (Chapter 1).

Differential predation by demersal predators across the subenvironments seems unlikely, as the dominant demersal predators in the system, including blue crabs

(*Callinectes sapidus*), spot (*Leiostomus xanthurus*), and hogchoaker (*Trinectes maculatus*), typically only begin entering this region of the estuary in late May to early June (Lipcius and Van Engel 1990, Seitz 1996). Predation by infaunal predators was not investigated, but its importance can not be overlooked.

The differences in abundance, biomass and production we documented between the physically stable north shoal subenvironment and the tidally energetic channel subenvironment have important implications for monitoring and production studies. Historically, channel sites have most often been selected as monitoring stations in the Chesapeake Bay region. As this study shows, benthic surveys should take into consideration the wide variation in community structure and function that can occur across relatively small spatial scales by sampling more than one subenvironment. Appropriate sampling gear and technique is also essential to accurately estimate secondary production. Presence of the biomass dominant, *Macoma balthica*, was often responsible for a large percentage (up to 87%) of the total community production. Thus, to correctly estimate production in estuarine systems, the sampling gear used must be able penetrate deep enough into the sediment to collect adults.

The early life stages of benthic assemblages were also observed to contribute significantly to overall secondary production estimates in some locales, especially when large bivalves were absent. The important contribution of juvenile organisms to production has been documented for two infaunal polychaetes in the York River – Chesapeake Bay system. Rapidly growing juveniles of *Loimia medusa* in the lower York River accounted for 36% of the annual secondary production of this species at a shallow subtidal site (Seitz and Schaffner 1995). Production by juvenile *Chaetopterus* *variopedatus* in the subtidal lower Chesapeake Bay accounted for 17% of total production in a low recruitment year and 105% of total production in a high recruitment year (Thompson and Schaffner 2001). Note that production estimates for these large polychaetes were determined using the increment summation method (Downing and Rigler 1984), in which production calculations are based on visual identification of cohorts in size-frequency histograms of biomass plotted through time, and not simply the summed total AFDW per taxa. Nonetheless, they are provided here as examples to show the importance of including juveniles in estimates of total production. Benthic monitoring protocols that call for use of a 500 μm or larger screen to retain organisms from the sediment can significantly underestimate the abundance of most species via failure to capture the rapidly growing, highly productive, juvenile stages. As a result, community abundance and secondary production are likely significantly underestimated during the spring and fall periods of heavy recruitment (Schaffner et al. 2002).

Acknowledgments

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Table 1. Summary of physical characteristics of the subenvironments. Values presented are means. Sediment parameters measured in surface sediments (0-1 cm). N= number of stations sampled in each subenvironment per date; nd= no data; A= April; M= May; J= June. Note that the main channel and the north shoal subenvironments were not sampled in April. Seabed classification based on the physical parameters presented below, appearance of x-radiographs (Chapter 1) results of previous investigations.

Subenvironment & seabed classification	Depth (m) (range)	Salinity (ppt)			Sediment temp. (°C)			Mud content (%)			TOC (% dry wt.)			C:N$_a$			Chl *a* (μg chl *a* g sed^{-1})		
		A	M	J	A	M	J	A	M	J	A	M	J	A	M	J	A	M	J
south shoal (n=4) tidally- or wave-driven cycles of deposition and erosion in surface sediments	2.5 (1.8-3)	16	17	20	13	23	21	96	94	93	2.4	2.3	2.8	13.2	13.6	12.1	2.6	3.3	4.3
secondary channel (n=6) tidally-driven cycles of deposition and erosion in surface sediments	4.8 (3.8-5.8)	17	16	21	13	22	21	86	89	87	2.2	2.2	2.8	12.9	13.4	11.8	2.8	2.8	4.9
main channel flank (n=5) high depsoition, long-term accumulation	3.4 (2.5-3.8)	14	15	19	13	22	22	99	98	97	2.2	2.0	3.0	13.4	13.0	12.0	1.6	2.2	4.6
main channel (n=12) strong tidal currents, longer term cycles of deposition and erosion	11.2 (8.5-14.0)		21	21		21	22		93	93		2.2	2.7		10.4	10.6		6.0	4.9
north shoal (n=5) stable sediment-water interface	1.5 (1.5-1.5)		16	20		nd	26		37	48		2.2	2.3		15.0	16.0		1.4	6.0

Table 2. Dominant species, accounting for >96 % of the total abundance and >92% of total biomass (all size fractions summed). N is number of individuals collected. Major taxa are: (P) Polychaeta; (O) Oligochaeta; (T) Turbellaria; (C) Cumacea; (B) Bivalvia.

Species	N	% of total abundance	% of total biomass
Mediomastus ambiseta (P)	6197	38.3	2.5
Streblospio benedicti (P)	4549	28.1	3.8
Tubificoides spp. (O)	2310	14.3	0.6
Leucon americanus (C)	1026	6.3	0.4
Turbellaria (T)	798	4.9	1.3
Glycinde solitaria (P)	161	1.0	0.5
Heteromastus filiformis (P)	157	1.0	2.2
Eteone heteropoda (P)	156	1.0	0.3
Paraprionospio pinnata (P)	117	0.7	2.5
Nereis succinea (P)	99	0.6	9.5
Macoma balthica (B)	97	0.6	68.4
Cumulative percent		96.7	92.0
Total abundance, biomass		15471	2.0 g AFDW

Table 3. Results of ANOVA tests for differences in total community abundance and AFDW biomass among subenvironment and among dates (May and June). *P* values < 0.05 are in bold.

Source (DF)	SS	MS	F	*P*
Total abundance				
subenvironment (4)	3.0376	0.7593	9.83	**<0.0001**
date (1)	0.0441	0.0441	0.57	0.4531
location * date (4)	0.3556	0.0889	1.15	0.3427
error (54)	4.1701	0.0772		
Total biomass				
subenvironment (4)	0.0569	0.0142	10.41	**<0.0001**
date (1)	0.0010	0.0010	0.74	0.3919
location * date (4)	0.0063	0.0016	1.15	0.3430
error (54)	0.0738	0.0014		

Table 4. Results of Tukey post-hoc comparison tests for differences in total community abundance and AFDW biomass among subenvironment and among dates (May and June). *P* values < 0.05 are in bold.

Source (DF)	SS	MS	*F*	*P*
Total abundance				
subenvironment (4)	3.0376	0.7593	9.83	**<0.0001**
date (1)	0.0441	0.0441	0.57	0.4531
location * date (4)	0.3556	0.0889	1.15	0.3427
error (54)	4.1701	0.0772		
Total biomass				
subenvironment (4)	0.0569	0.0142	10.41	**<0.0001**
date (1)	0.0010	0.0010	0.74	0.3919
location * date (4)	0.0063	0.0016	1.15	0.3430
error (54)	0.0738	0.0014		

Table 5. Results of 1-way ANOVAs tests for differences among subenvironment in species richness *(S)*, diversity *(H'* and 1-λ), and eveness (*J'*). *P* values < 0.05 are in bold.

Source (DF)	SS	MS	F	P
April				
Species richness *(S)*:				
subenvironment (2)	28.110	14.050	2.01	0.1797
error (11)	76.750	6.977		
Shannon's Index *(H')*:				
subenvironment (2)	2.067	1.033	52.42	**0.0001**
error (11)	0.217	0.020		
Simpson Index (1-λ):				
subenvironment (2)	0.218	0.109	34.44	**0.0000**
error (11)	0.035	0.003		
Eveness *(J')*:	0.067	0.034	4.10	**0.0466**
subenvironment (2)	0.090	0.008		
error (11)				
May				
Species richness *(S)*:				
subenvironment (4)	95.800	23.950	6.24	**0.0011**
error (11)	76.750	6.977		
Shannon's Index *(H')*:				
subenvironment (4)	0.477	0.119	1.45	0.2444
error (11)	2.217	0.082		
Simpson Index (1-λ):				
subenvironment (4)	0.061	0.015	2.06	0.1135
error (11)	0.199	0.007		
Eveness *(J')*:	0.179	0.045	4.26	**0.0084**
subenvironment (4)	0.283	0.010		
error (11)				

Table 5. (Continued)

Source (DF)	SS	MS	F	P
June				
Species richness *(S):*				
subenvironment (4)	0.178	0.044	3.17	**0.0292**
error (11)	0.378	0.014		
Shannon's Index *(H'):*				
subenvironment (4)	19.78	4.945	1.38	0.2664
error (11)	96.592	3.577		
Simpson Index (1-λ):				
subenvironment (4)	0.265	0.066	2.07	0.1128
error (11)	0.864	0.032		
Eveness *(J'):*	0.423	0.106	4.54	**0.0062**
subenvironment (4)	0.628	0.232		
error (11)				

Table 6. Results of Tukey *post-hoc* comparison tests for differences in species richness (S), diversity (*H'* and *1-λ*), and evenness (*J'*) among subenvironments in April, May, and June. Underlined subenvironments and those with underlines that overlap are not statistically different. Means were considered significantly different at $P < 0.05$.

April					
Species richness (*S*)	SS	SC	MCF		
Shannon's Index (*H'*)	SS	SC	MCF		
Simpson Index (1-λ)	SS	SC	MCF		
Evenness (*J'*)	SS	SC	MCF		
May					
Species richness (*S*)	SS	SC	MCF	C	NS
Shannon's Index (*H'*)	SS	SC	MCF	C	NS
Simpson Index (1-λ)	SS	SC	MCF	C	NS
Evenness (*J'*)	SS	SC	MCF	C	NS
June					
Species richness (*S*)	MCF	SS	SC	C	NS
Shannon's Index (*H'*)	SS	SC	MCF	C	NS
Simpson Index (1-λ)	SS	SC	MCF	C	NS
Evenness (*J'*)	MCF	SS	SC	NS	C

Fig. 1. The upper York River estuary study area, showing station locations in each subenvironment and depth contours of 3, 4, and 10 m. Transect lines (A-A' and B-B') indicate locations of the cross sections depicted in Fig. 2.

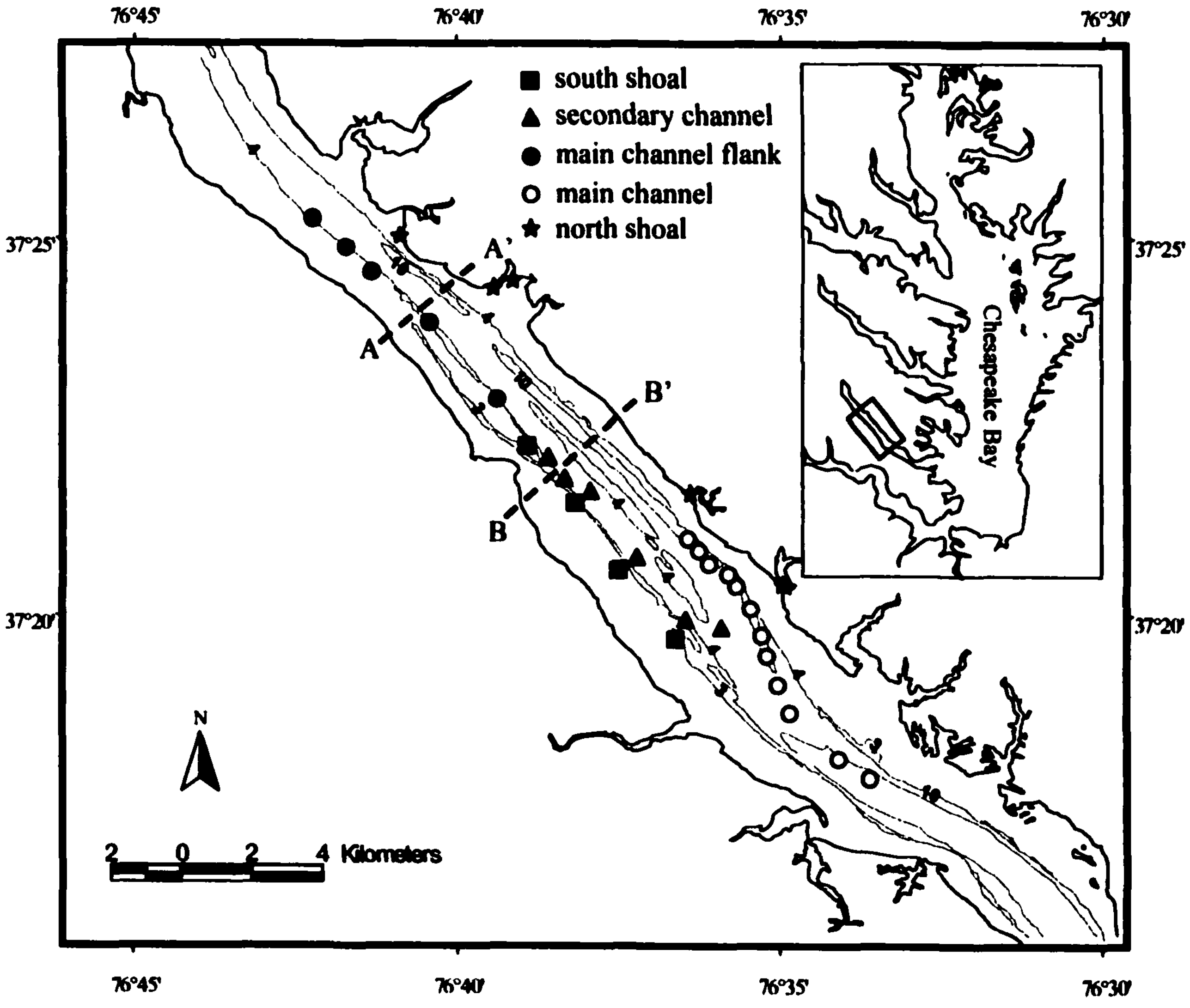
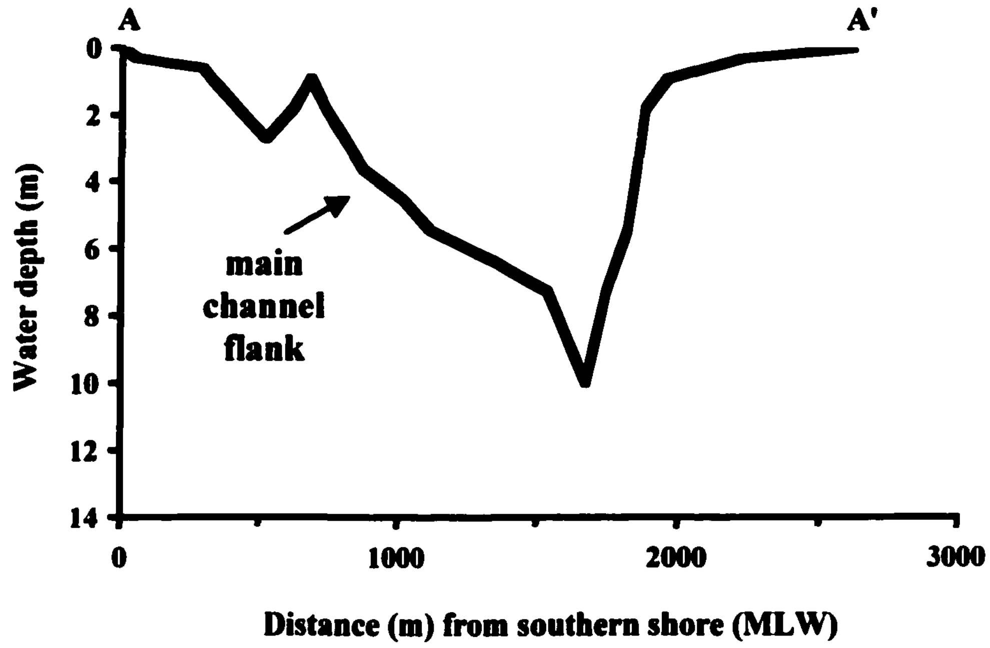

76°45'
76°40'
76°35'
76°30'
37°25'
37°20'
■ south shoal
▲ secondary channel
● main channel flank
○ main channel
★ north shoal
Chesapeake Bay
A'
A
B'
B
N
2 0 2 4 Kilometers

Fig. 2. Cross-sectional profiles of two upper York River transects (A-A') and (B-B'), depicting locations of the sampled subenvironments. The profiles show change in bathymetry along the transects, expressed as distance from the southern shoreline (MLW).


A
A'
Water depth (m)
0
2
4
6
8
10
12
14
main channel flank
0
1000
2000
3000
Distance (m) from southern shore (MLW)

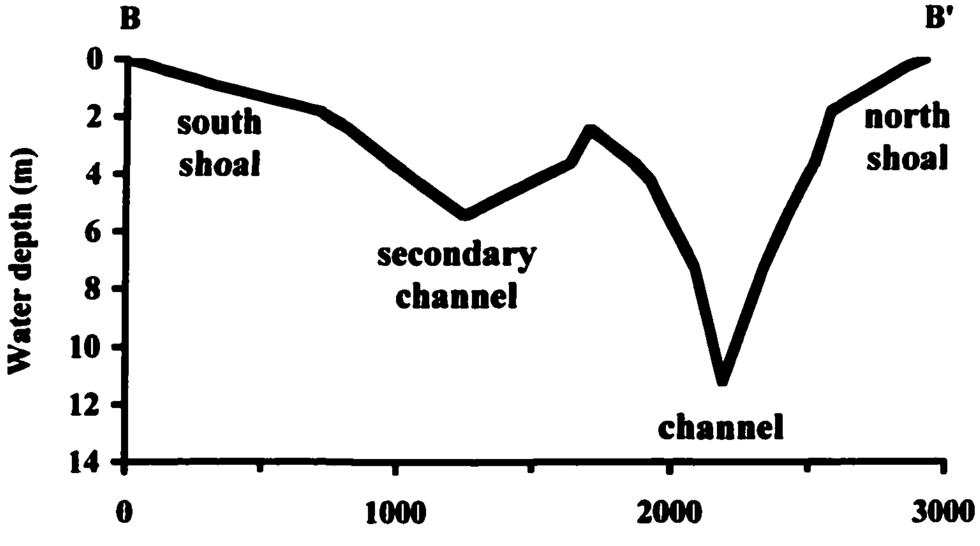
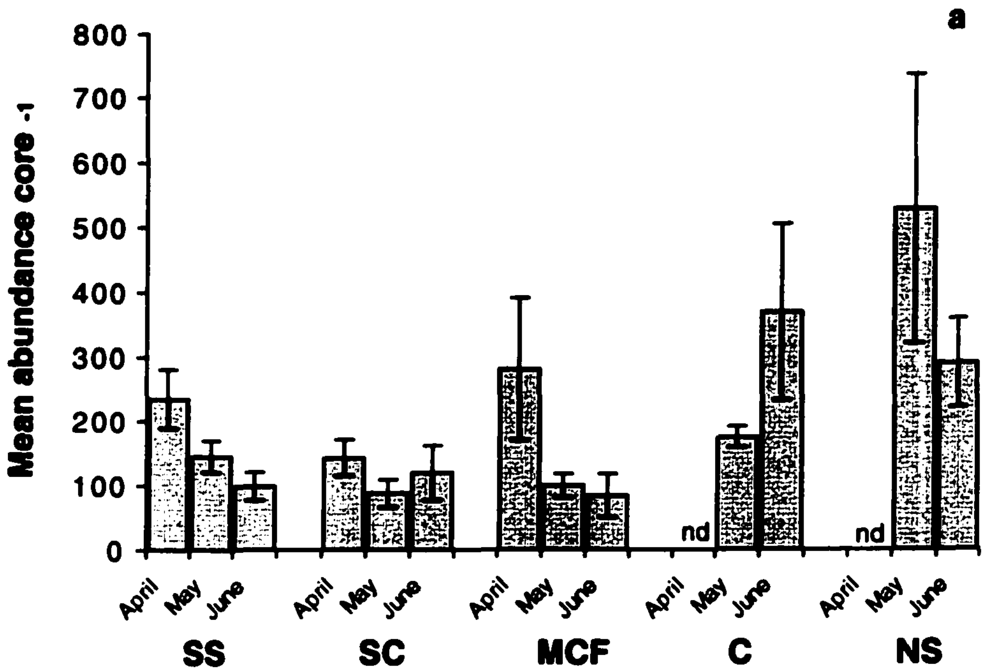

B
B'
Water depth (m)
0
2
4
6
8
10
12
14
south shoal
secondary channel
channel
north shoal
0
1000
2000
3000
Distance (m) from southern shore (MLW)

Fig. 3. a, b) Mean macrobenthic abundance (mean per core ± SE) and mg AFDW biomass (mean per core ± SE) for the different subenvironments sampled. Data represent sums of all size classes (125 µm, 250 µm, 500 µm). Subenvironment abbreviations as follows: SS= south shoal, SC= secondary channel; MCF= main channel flank; C= main channel; NS= north shoal. April data were collected 20 April at the south shoal, secondary channel, and main channel flank only. May data were collected 21 May at the south shoal, secondary channel, and main channel flank, 13 May at the main channel, and 7 May at the north shoal. June data were collected 21 June at the south shoal, secondary channel, and main channel flank, 18 June at the main channel, and 24 June at the north shoal. Nd= no data.


a
Mean abundance core -1
800
700
600
500
400
300
200
100
0
nd
nd
April
May
June
SS
SC
MCF
C
NS

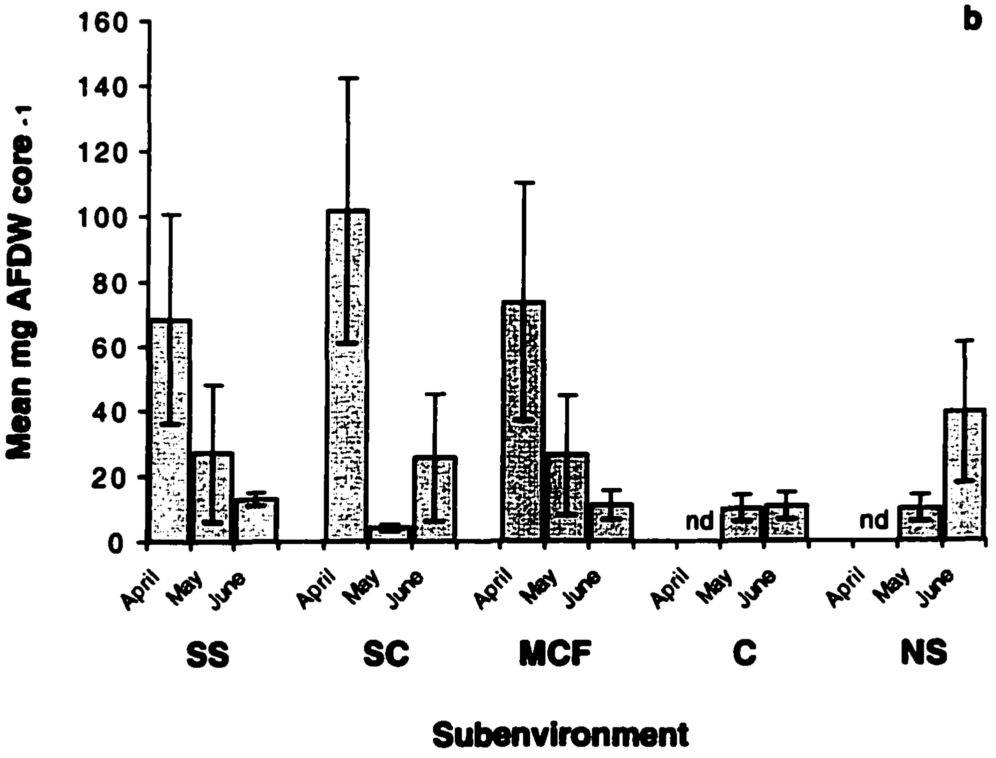

b
Mean mg AFDW core -1
160
140
120
100
80
60
40
20
0
nd
nd
April
May
June
SS
SC
MCF
C
NS
Subenvironment

Fig. 4. Abundance (mean per core ± SE) of the numerical and biomass dominants in this study in the different subenvironments. Station abbreviations and sampling dates as in Fig. 3 caption. * = no data.

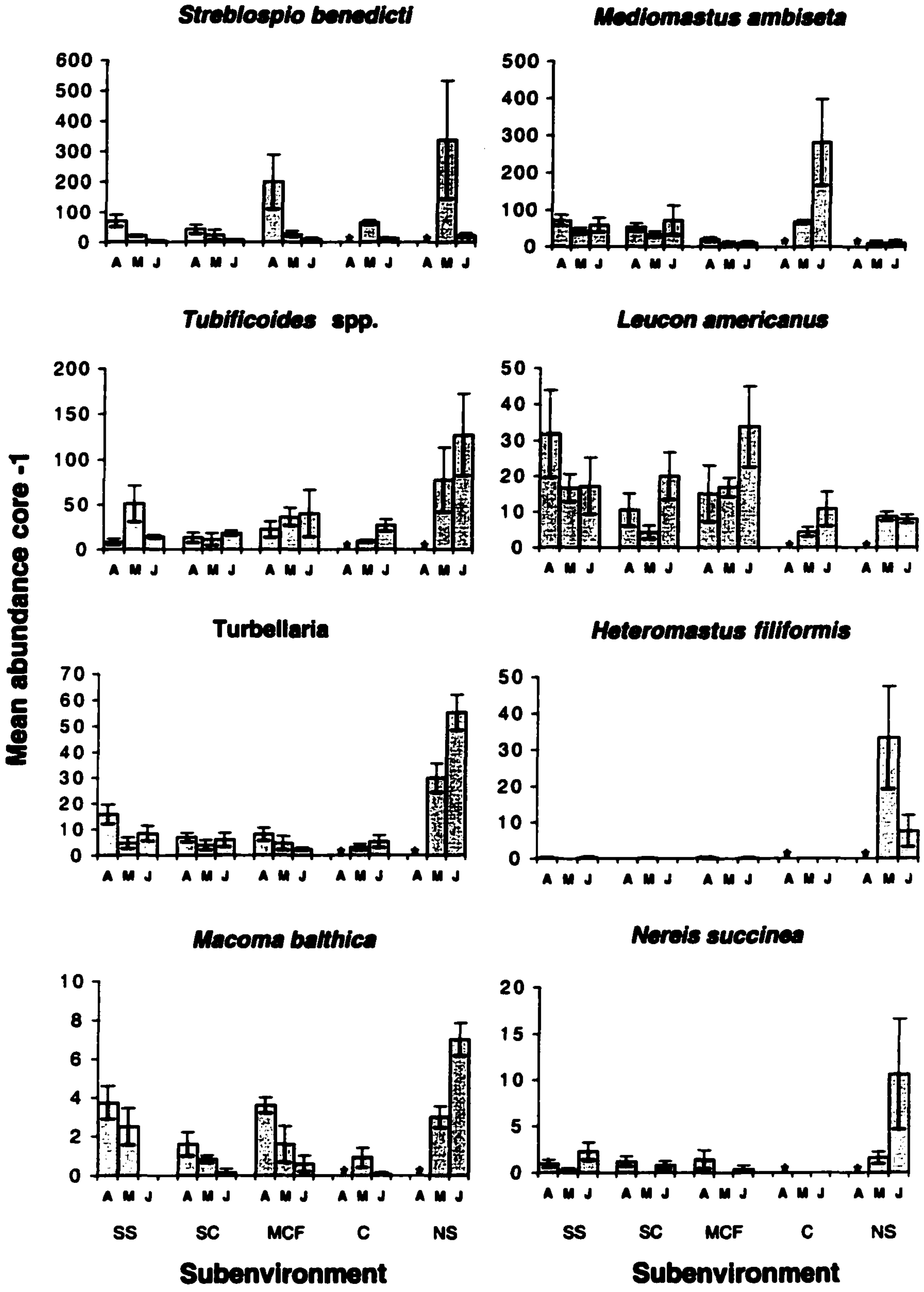

Streblospio benedicti
600
500
400
300
200
100
0
Mediomastus ambiseta
500
400
300
200
100
0
Tubificoides spp.
200
150
100
50
0
Leucon americanus
50
40
30
20
10
0
Turbellaria
70
60
50
40
30
20
10
0
Heteromastus filiformis
50
40
30
20
10
0
Macoma balthica
10
8
6
4
2
0
Nereis succinea
20
15
10
5
0
A M J
Mean abundance core -1
SS
SC
MCF
C
NS
Subenvironment

Fig. 5. Mean macrobenthic abundance by size class and depth fraction in each subenvironment. Dashed line drawn to indicate 2 cm depth. Station abbreviations and sampling dates as in Fig. 3 caption.

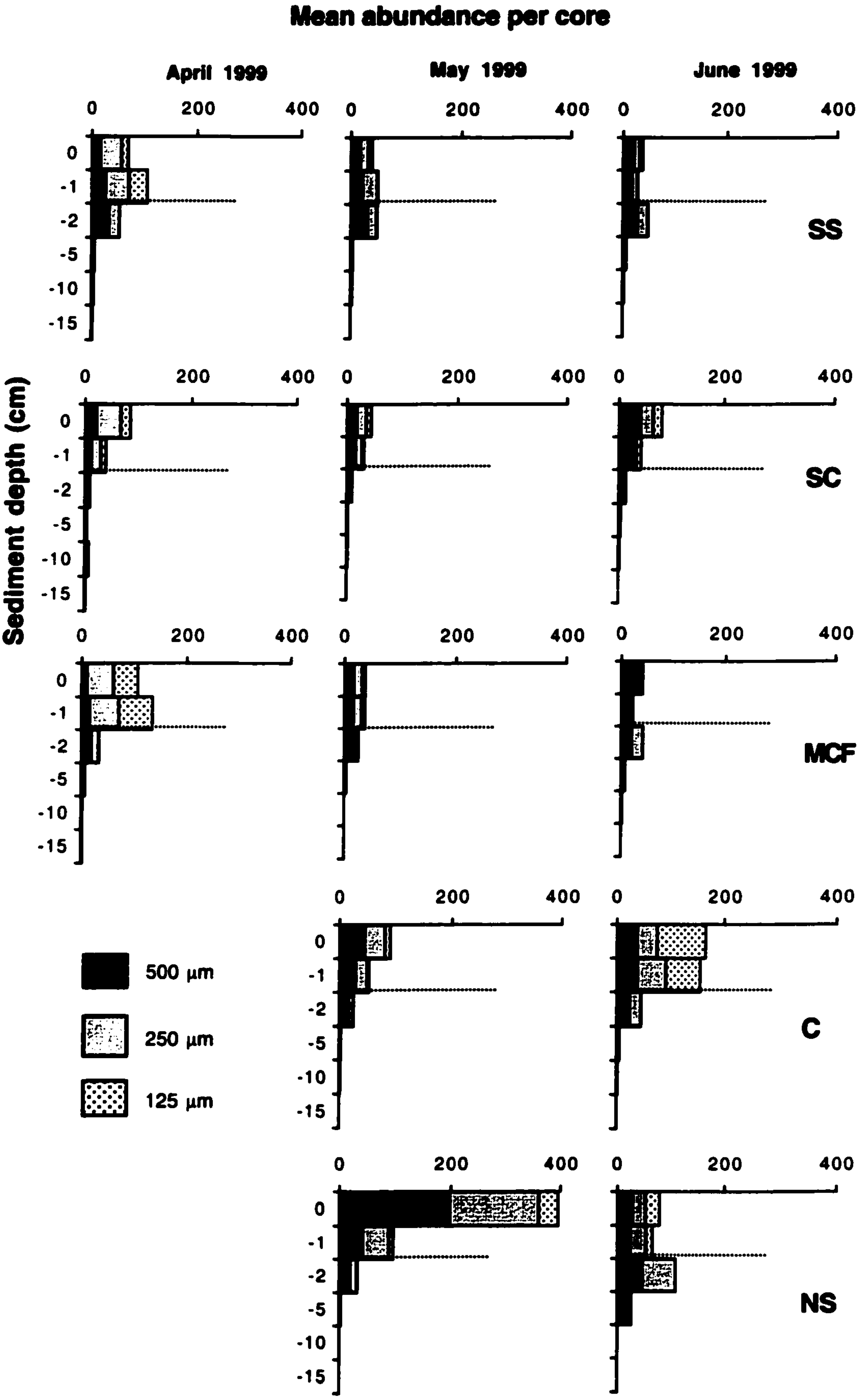

Mean abundance per core
April 1999
May 1999
June 1999
0
200
400
Sediment depth (cm)
0
-1
-2
-5
-10
-15
SS
SC
MCF
C
NS
500 µm
250 µm
125 µm

Fig. 6. Mean macrobenthic biomass (mg AFDW) by size class and depth fraction in each subenvironment. Dashed line drawn to indicate 2 cm depth. Station abbreviations and sampling dates as in Fig. 3 caption. Due to the small biomass values for the 250 µm and 125 µm size classes relative to the 500 µm size class, bars for the 250 µm and 125 µm size classes are not visible.

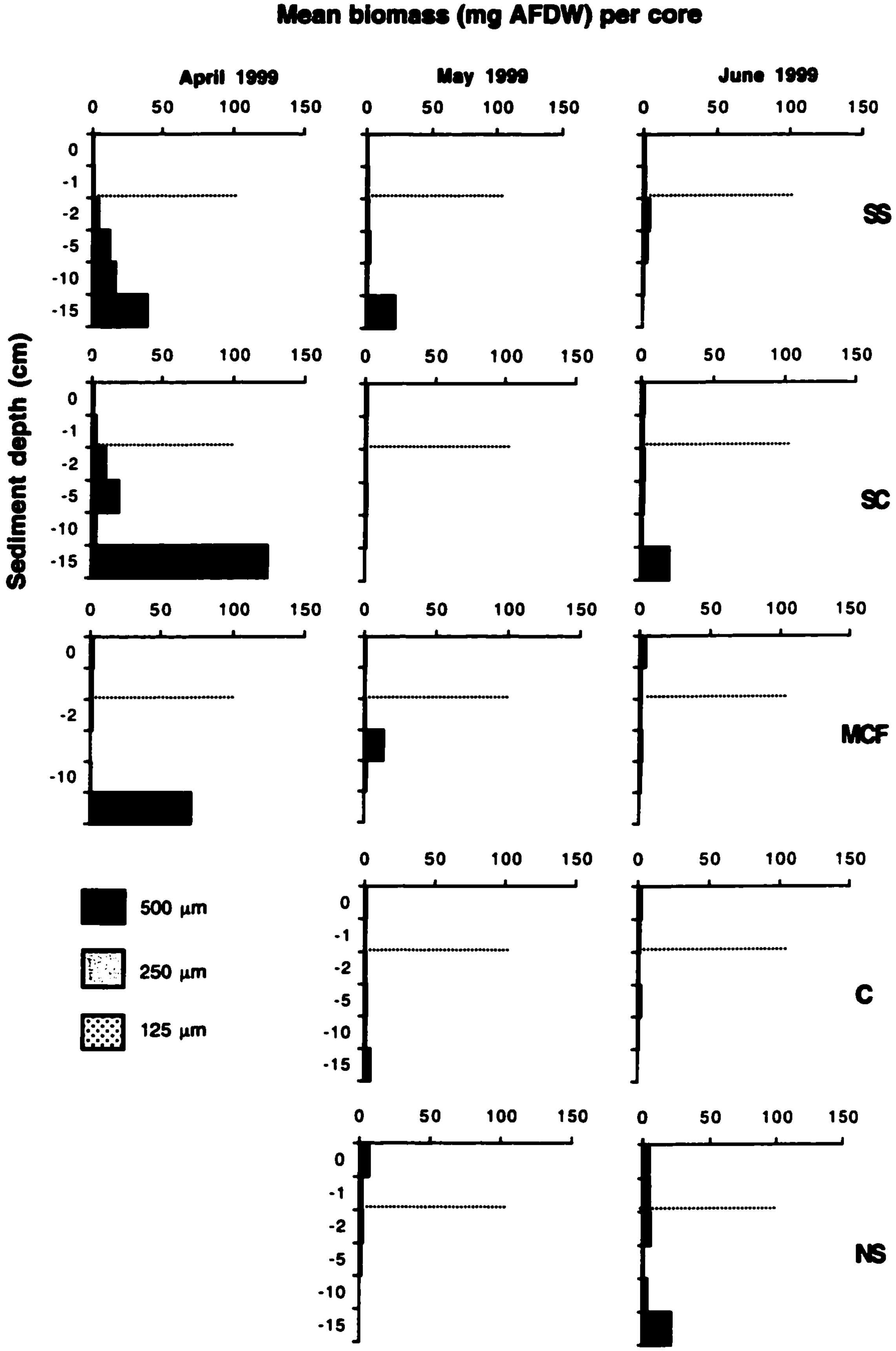

Mean biomass (mg AFDW) per core
April 1999
May 1999
June 1999
0 50 100 150
Sediment depth (cm)
0
-1
-2
-5
-10
-15
SS
SC
MCF
C
NS
500 µm
250 µm
125 µm

Fig. 7. Species richness (number of species, *S*), Shannon's diversity (*H'*), Simpson's index (1-λ), and Pielou's evenness (*J'*) for each subenvironment. Station abbreviations and sampling dates as in Fig. 3 caption. Nd= no data.

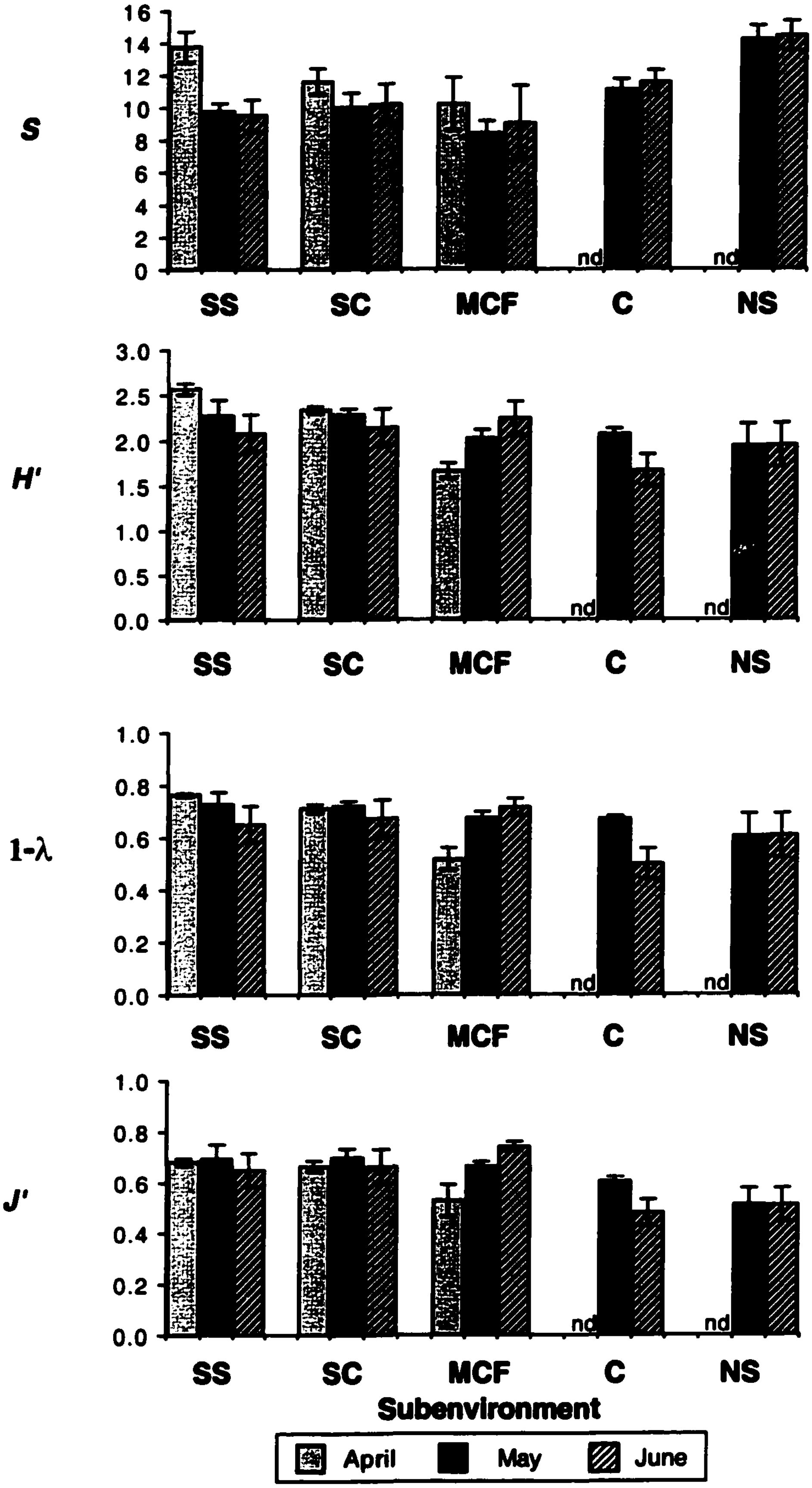

S
16
14
12
10
8
6
4
2
0
nd
nd
SS
SC
MCF
C
NS
H'
3.0
2.5
2.0
1.5
1.0
0.5
0.0
nd
nd
SS
SC
MCF
C
NS
1-λ
1.0
0.8
0.6
0.4
0.2
0.0
nd
nd
SS
SC
MCF
C
NS
J'
1.0
0.8
0.6
0.4
0.2
0.0
nd
nd
SS
SC
MCF
C
NS
Subenvironment
April
May
June

Fig. 8. Hierarchies resulting from clustering of April stations using Bray-Curtis similarities. Subenvironment abbreviations as in Fig. 3 caption.

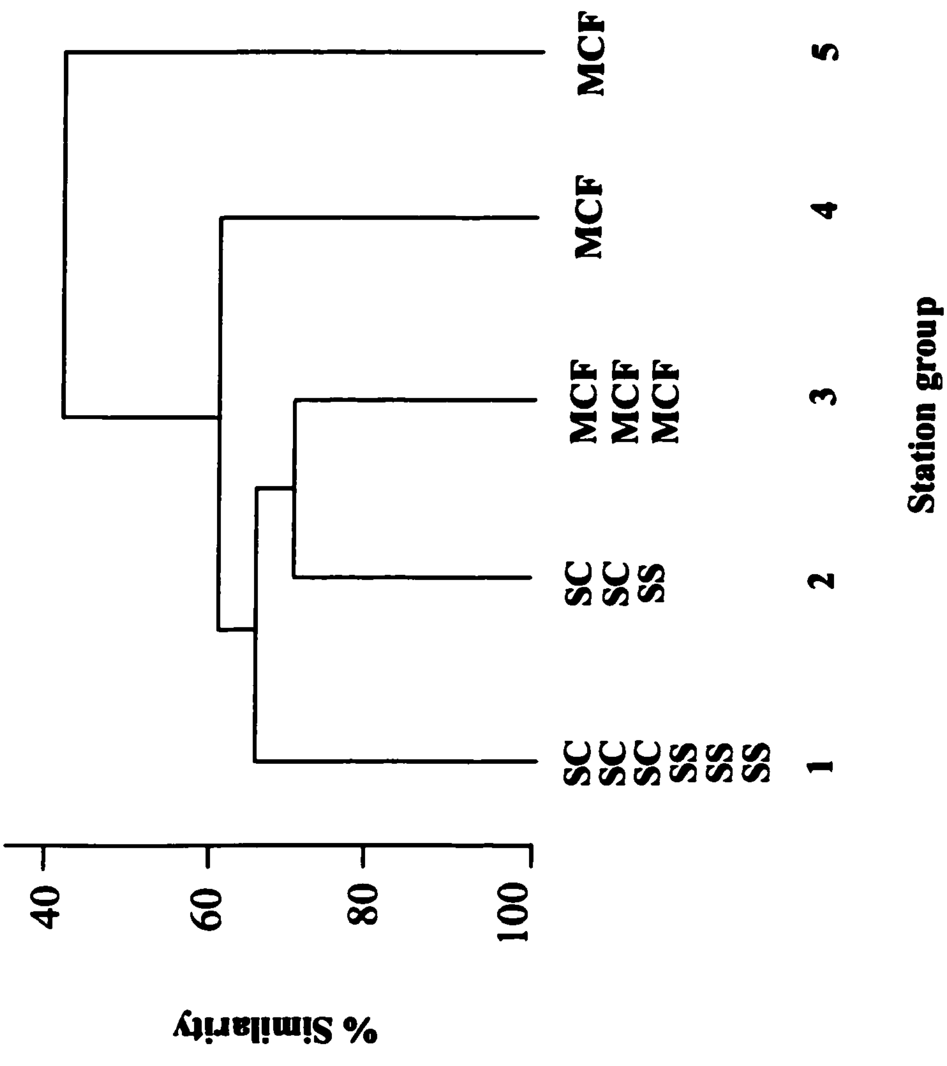

% Similarity
40
60
80
100
SC SC SC SS SS SS
SC SC SS
MCF MCF MCF
MCF
MCF
1
2
3
4
5
Station group

Fig. 9. Hierarchies resulting from clustering of May stations using Bray-Curtis similarities. Subenvironment abbreviations as in Fig. 3 caption.

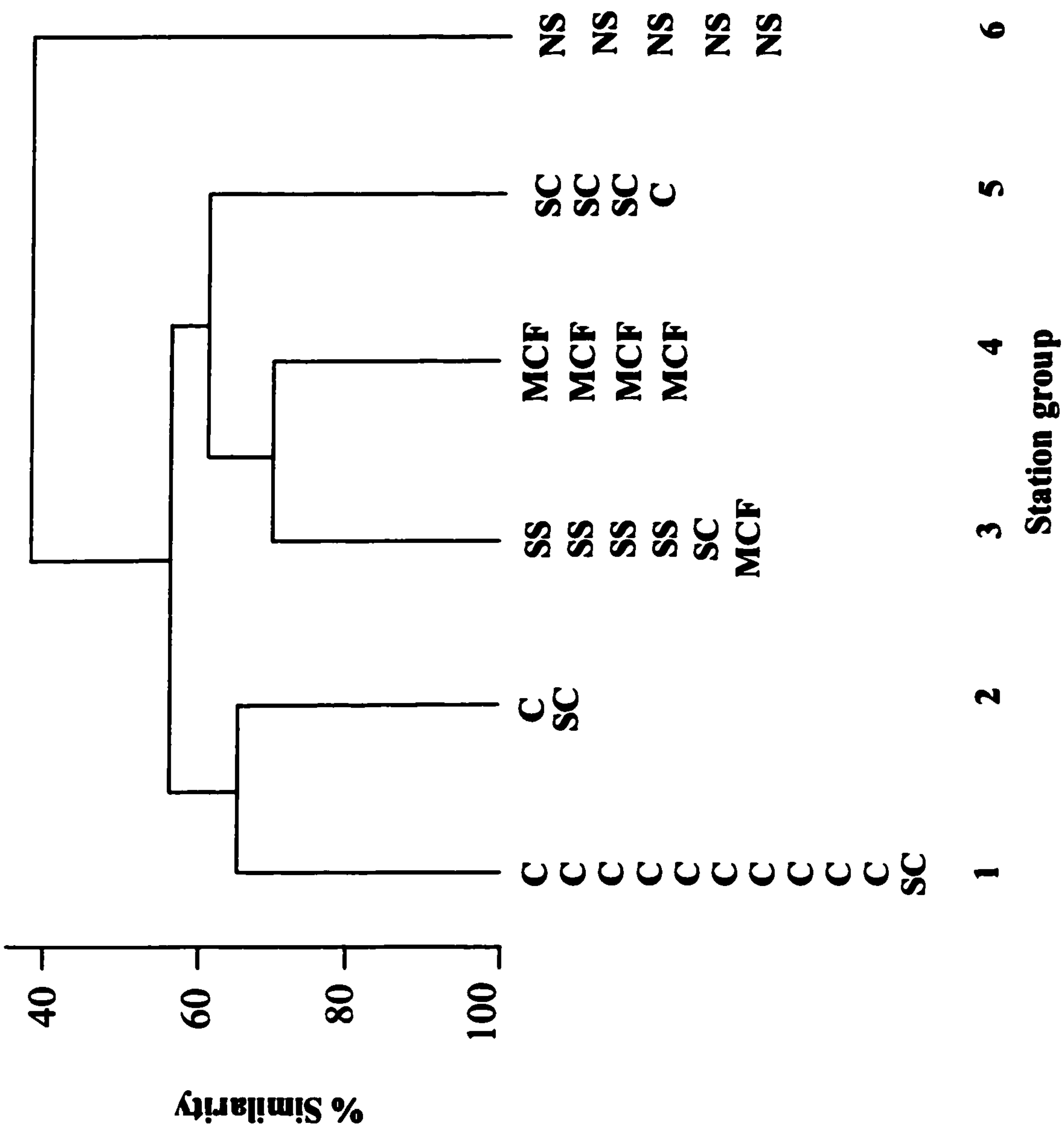

% Similarity
40
60
80
100
C C C C C C C C C C SC
C SC
SS SS SS SS SC MCF
MCF MCF MCF MCF
SC SC SC C
NS NS NS NS NS
1
2
3
4
5
6
Station group

Fig. 10. Hierarchies resulting from clustering of June stations using Bray-Curtis similarities. Subenvironment abbreviations as in Fig. 3 caption.

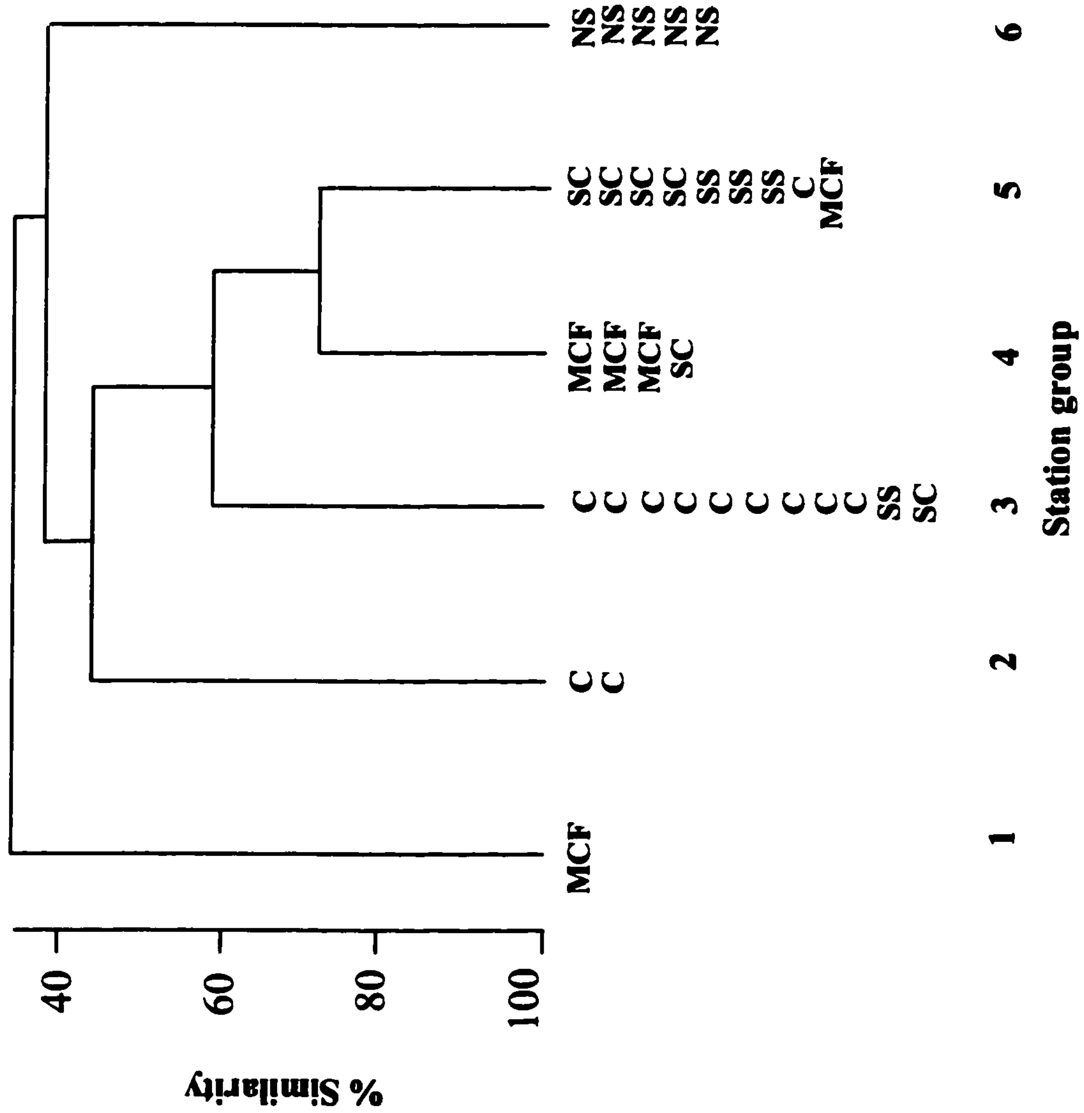
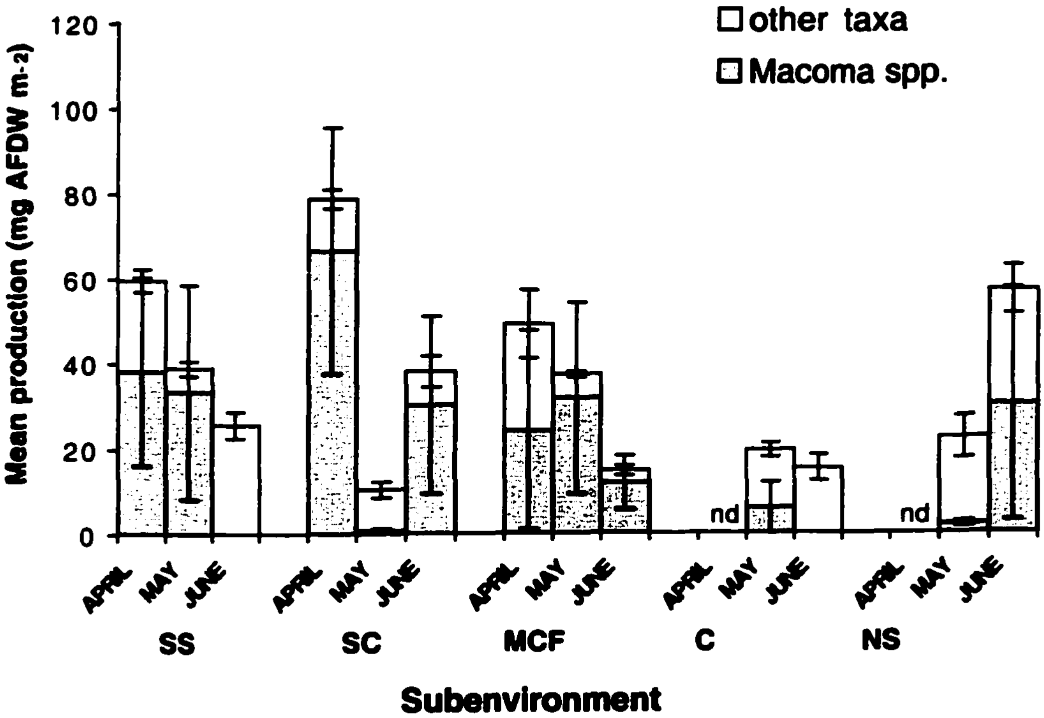
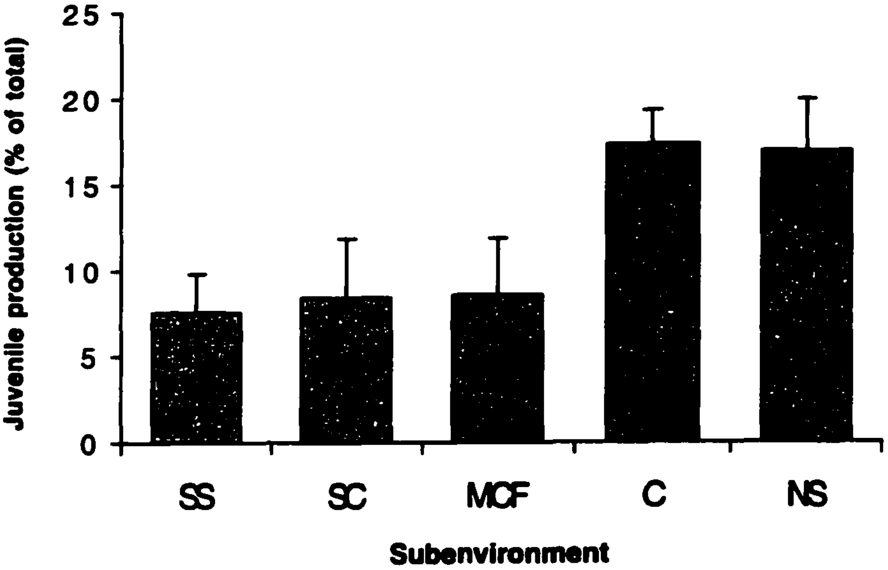

% Similarity
40
60
80
100
MCF
C C
C C C C C C C SS SC
MCF MCF MCF SC
SC SC SC SC SS SS SS C MCF
NS NS NS NS NS
1
2
3
4
5
6
Station group

Fig. 11. Mean production (mg AFDW m^{-2} ± SE) in each subenvironment, with proportion attributed to *Macoma balthica* and *M. mitchelli* production vs. production of remaining taxa indicated. Station abbreviations and sampling dates as in Fig. 3 caption. Nd= no data.



other taxa
Macoma spp.
Mean production (mg AFDW m-2)
120
100
80
60
40
20
0
nd
nd
APRIL
MAY
JUNE
SS
SC
MCF
C
NS
Subenvironment

Fig. 12. Percentage of total production (mean mg AFDW m^{-2} ± SE) attributed to juvenile production (organisms retained on 125μm and 250 μm screens) in the different subenvironments pooled across the May and June sampling dates.


Juvenile production (% of total)
25
20
15
10
5
0
SS
SC
MCF
C
NS
Subenvironment

CHAPTER 5

RESPONSES OF ESTUARINE BENTHIC INVERTEBRATES TO SEDIMENT BURIAL: THE IMPORTANCE OF MOBILITY AND LIFESTYLE

This paper will be submitted to the Journal of Experimental Marine Biology and Ecology with the authors E.K. Hinchey, L.C. Schaffner, C. C. Hoar, B.W. Vogt, and L. P. Batte

Abstract

Estuarine infaunal organisms are frequently subjected to disturbance events caused by hydrodynamic processes that disrupt and move the sediment in which the animals reside. The responses of five estuarine species to sediment disturbance (burial) were compared in laboratory experiments. Overburden stress (kPa) was calculated to quantify the force exerted on organisms by sediment burial for 6 d. At the levels tested (0-16 kPa), increasing overburden stress did not significantly decrease survival or growth of juvenile burrowing bivalves, *Macoma balthica*. Survival of juveniles and adults of the tubiculous polychaete *Streblospio benedicti* and neonates of the burrow-forming amphipod *Leptocheirus plumulosus* declined exponentially with increasing overburden stress. The mean *S. benedicti* survival rate was 4% of the control at an overburden stress of ≈ 4 kPa (40.8 g force cm^{-2}), while an overburden stress of 12 kPa (122.4 g force cm^{-2}) was necessary to comparably reduce survival for *L. plumulosus*. Complete burial under 5 mm of sediment did not cause significant juvenile oyster (*Crassostrea virginica)* mortality. In contrast, the epifaunal tunicate *Molgula manhattensis* exhibited significant mortality when partially (one or two siphons exposed) or completely buried for 6 d under 5 mm of sediment. Rather than being solely a function of life stage or body size, species-specific response to burial varies as a function of motility, living position, and physiological tolerance of anoxic conditions while buried. We conclude that some benthic species exhibit mechanical and physiological adaptations that may allow them to survive deposition events of the magnitude commonly encountered in estuarine environments.

Introduction

Disturbance influences the structure and function of marine communities in a wide array of habitats (Picket and White 1985, Hall 1994, Sousa 2001). Physical sediment disturbance is a common feature of coastal environments because of their relatively shallow depths and physical energy inputs associated with tides, waves, storms and currents. In estuaries, sediments are effectively trapped by estuarine circulation processes, but may be eroded, transported and deposited many times before they accumulate below the actively reworked surface layer (Sanford 1992, Geyer 1993, Dellapenna et al. 1998, Schaffner et al. 2001). Thus, the sediment-water interface in estuarine ecosystems often is highly dynamic and resident organisms are faced with erosion, transport and deposition events of various magnitudes over various time scales. In addition, anthropogenic activities such as dredging and dredged material disposal are common and cause significant, although localized, sediment disturbance (Maurer et al. 1986, Hall 1994).

The mechanisms by which physical disturbance processes affect infaunal populations and communities remains poorly resolved (Ólafsson et al. 1994). Animals living near the sediment-water interface, especially new recruits and juveniles or sedentary epifauna, are generally predicted to be the most strongly affected (Wilson 1981, Brenchley 1982, Posey 1986, Emerson 1989, Bonsdorff et al. 1995) since this is where sediment reworking is most intense (Nittrouer and Sternberg 1981, Schaffner et al. 2001). Mortality during or soon after larval settlement has been shown to dictate recruitment success, which can profoundly influence community dynamics (Woodin et al. 1995). In addition to other major physical stressors, such as reduced or variable salinity and hypoxia, sediment instability may be a major factor affecting the composition and abundance of benthic communities in some estuaries (Schaffner et al. 2001).

We conducted laboratory experiments to compare the responses of five common estuarine species to simulated natural physical disturbances via burial events of various magnitudes. Test species, exhibiting a range of motility and residence depths, included juveniles of a motile, burrowing bivalve (*Macoma balthica*), neonates (1-3 d) of a motile burrow-building amphipod (*Leptocheirus plumulosus*), juveniles and adults of a relatively sedentary, tubiculous, polychaete (*Streblospio benedicti*), juveniles of an epifaunal, reef-forming bivalve (*Crassostrea virginica*), and adults of a sedentary epifaunal tunicate (*Molgula manhattensis*). The range of burial depths used in the experiment spanned the range of sediment deposition events observed on annual time scales in the estuarine system of the lower Chesapeake Bay - York River, USA (Dellapenna et al. 1998, Kniskern and Kuehl in review, Schaffner et al. 2001). Our objectives were to (1) assay burial-induced mortality of juvenile estuarine organisms, as this life stage is perceived to be more vulnerable than adults to sediment disturbance, and (2) compare burial-induced mortalities of selected infauna and epifauna, to test the prediction that epifauna are more vulnerable than infauna due to their sessile, epibenthic existence. Our results will provide further insight into the role of sediment disturbance via burial in structuring estuarine benthic communities.

Materials and Methods

Infauna

The infaunal bivalve species used in these experiments, ***Macoma balthica***, is the biomass dominant in the mesohaline York River (Schaffner et al. 2001) and is abundant in estuaries on both sides of the Atlantic (Beukema and Meehan 1985). Juveniles live near the sediment-water interface (0-10 cm), while adults can burrow as deeply as 40 cm into the sediment (Schaffner et al. 1987). Juveniles collected in March 2002 from a 1 m station in Queen's Creek (37° 16' N, 76° 39' W), a tributary of the York River, were held in a flow-through aquarium for two weeks prior to the experiment and fed marsh detritus. Water temperature and salinity at collection were 11° C and 14 ppt, respectively, and clams were gradually raised (<4° C/d; 1 ppt/d) to a holding temperature and salinity of 20° C and 17 ppt. Individuals were separated into 4 length classes (2.0 ≤ 2.9 mm; 3.0 ≤ 3.9 mm; 4.0 ≤ 4.9 mm; 5.0 ≤ 5.9 mm). Clams in the three largest classes were numbered with a permanent marker and re-measured after the experiment to determine growth rates.

The spionid polychaete *Streblospio benedicti*, one of the most abundant members of the spring benthic assemblage of Chesapeake Bay (Diaz and Schaffner 1990), was obtained in April 2001 from a 6 m deep site in the York River (37° 15' N, 76° 30' W) using a grab. Adult and juvenile worms retained on a 500 μm screen were held in a flow-through aquarium at 19° C and 20 ppt (which were also the temperature and salinity at collection) for one week prior to the experiment and fed as above.

The amphipod *Leptocheirus plumulosus*, was collected in October 2001 from Queen's Creek. Gravid females removed from the sediment were placed in a laboratory aquarium containing marsh detritus and held at 21.5° C and 26 ppt, which were also the collection temperature and salinity. After three days, neonates (≤ 3 d old) retained on a 250 μm screen were removed and immediately used for the experiment.

Epifauna

Juveniles of the oyster *Crassostrea virginica* (9-12 mm length) were obtained in December 2001 from the VIMS Oyster Hatchery at Gloucester Point, VA, and maintained in ambient, unfiltered flow-through conditions (18° C, 27 ppt) for 16 h prior to the experiment. The sedentary tunicate *Molgula manhattensis* was collected by hand from submerged rocks and oysters at Queen's Creek, VA in March 2002. Individuals, ranging from 24 mm to 34 mm wide and 22 to 36 mm long, were maintained in the laboratory for 5 days prior to the experiment, during which time temperature was gradually raised from 11° to 20° C (< 2°C elevation per day) and salinity was raised from 13 to 17 ppt (1 ppt/d). Tunicates were fed a 25 ml slurry of algal paste (*Thalassiosira weissflogii*) and TetraMin fish food every other day during acclimation and throughout the course of the experiment.

Experimental sediments

Sediment used in the experiments was collected from lower Chesapeake Bay (CB, 37° 15' N, 76° 09' S; 25% mud) and the York River, Virginia (YR, 37° 29' N, 76° 46' W; 87% mud). To remove large animals and debris prior to use, sediments were gently sieved through a 2 mm screen without introduction of additional water and then further defaunated by freezing at –80° C. Just prior to each experiment, sediments were diluted with sand-filtered seawater to achieve differing bulk densities (Table 1).

Bulk density (γ_{sat}) of the sediment introduced for burial was calculated by the method of Richards et al. (1974) where:

$$\gamma_{sat} = \frac{\text{wet sediment weight}}{\text{volume}}$$

Bulk density of sediment used for each treatment was measured 24 h after sediment addition to account for the effect of rapid dewatering. This 24 h bulk density value was used in the calculation of effective overburden stress (below).

Effective overburden stress ($\bar{p}$) was calculated from the equation of Richards et al. (1974):

$$\bar{p} = (\gamma_{sat}-\gamma_{sw})\, z$$

where γ_{sat} is the bulk density of saturated sediments, γ_{sw} is the bulk density of water comprising the pore fluid, and z is depth of burial. Overburden stress, in units of kiloPascals (kPa), was calculated in order to quantify the force exerted on organisms by sediment burial *sensu* Nichols et al. (1978). Note that the bulk density and overburden stress calculations presented in Nichols et al. (1978) were reported incorrectly. Thus, we utilized the original equations (above) from Richards et al. (1974) that were referenced in Nichols et al. (1978).

The two different sediment types (CB, 25% mud; YR, 87% mud) were used to generate a wider range of overburden stress, with the sandier sediments producing the greatest overburden stress per depth of sediment addition (Table 1). These distinct grain size classes exhibit differences in permeability and shear strength properties that could have ramifications for faunal respiration and burrowing in addition to the force imparted on organisms during burial. Permeability, the capacity of a porous material to transmit fluids such as oxygen-laden porewater, decreases as particle size decreases, and therefore muddier sediments are less permeable than sandy sediments (Friedman and Sanders 1978). Muddy sediments, due to the high cohesion of the clay particles, are more difficult for organisms to burrow into than sandy sediments (Siebold and Berger 1996). As overburden stress has been shown to be a critical factor regulating the survival of benthic organisms when buried in both field and laboratory experiments (Nichols et al. 1978), it was chosen an appropriate measure of burial intensity for this study.

Experimental design

Macoma experiment

Plastic graduated cylinders (1000 ml volume, 42 cm tall, 6 cm i.d.) were used as experimental containers for the *Macoma* experiment. Five centimeters of CB sediment was added to each container as a base layer. Sand-filtered seawater (20 °C, 17 ppt) was added to the containers to a height of 18 cm above the sediment, and aerated with bubble flow. After 6 d, 11 clams (one between 2.0 and 2.9 mm; five between 3.0 and 3.9 mm; four between 4.0 and 4.9 mm; 1 between 5.0 and 5.9 mm) were added to each container. All clams readily burrowed and were allowed to acclimate for 4 d prior to the beginning of the experiment. Each day after addition and throughout the experiment, clams were fed 10 ml of 35 μm-filtered marsh detritus to each container. Every other day, 80% of the water column in each cylinder (including controls) was drained and replaced with fresh filtered seawater. Fecal pellets and burrow openings were observed on the sediment surface in all microcosms during the acclimation period.

Five burial regimes were used in the experiment: no burial (NB), and three acute burial (AB) treatments using different amounts of muddy sand (bulk density 1.67 g/l). In addition, a series of replicates was sampled prior to the initiation of the experiment in order to establish survival rates during the acclimation period (NB_0). Experimental treatments were sampled 6 d after sediment introduction. Each treatment consisted of five replicate containers that were randomly distributed in the experimental array. On Day 0, sediment was added to the AB treatments as follows. The overlying water level was drained until 2 cm of water remained over the base layer of sediment. A slurry of CB sediment (bulk density 1.67 g/ml) was then introduced to each AB container. This was accomplished by gently pushing sediment through holes punched in the bottom of plastic cups that were positioned above the sediment-water interface. This method allowed for even distribution of sediment and no to minimal disruption of the sediment-water interface. The volume of sediment was adjusted for each treatment to allow for a mean deposition depth of 8.4, 14.7 or 24.6 cm (Table 1). No sediment was added to the NB treatment containers. The water in the NB treatments was reduced by 80% and replaced with freshly-filtered seawater. The water replacements were performed to reduce build-up of NH_4^+ concentrations in the containers. In preliminary trials with *Macoma*, *Streblospio* and *Leptocheirus* we determined that the NH_4^+ concentrations in our experiments were well below the levels considered harmful to *Leptocheirus* (Moore et al. 1997).

Clams recovered from NB_0 treatments on Day 0 were used to estimate handling and other sources of mortality prior to the initiation of the burial treatments. Clams from the NB and AB treatments were recovered on Day 6. In all treatments, individuals were removed by sieving, separated into live versus dead, and live individuals were measured for growth estimates.

Streblospio experiment

One-liter glass mason jars (15 cm tall; 7.5 cm i.d.) were used as experimental containers for the *Streblospio* experiment. A base layer of 1.5 cm of CB sediment was added to each container. As the maximum burial depth in this experiment (7.6 cm) did not leave adequate head space in the jars to ensure that all treatments would have a uniform overlying water depth, the containers were randomly assigned to one of two aquaria (72 cm long x 39 cm wide x 32 cm high) supplied with flow-through sand-filtered seawater (19 °C, 20 ppt). To ensure that the worms did not migrate out of the containers, a 500 um mesh screen was affixed to each jar using a rubber band. Aeration of the water column under the mesh was ensured via insertion of an air-flow bubbler through each mesh covering. One week after adding the base layer, five *Streblospio* were added to each microcosm. All worms rapidly burrowed into the sediment and constructed tubes within 24 h or less. Each day after addition and throughout the experiment, 10 ml of 35 µm-filtered marsh detritus was added to each container as a food source. For water changes, jars were temporarily removed from the aquaria and 80% of the water column was drained and replaced with fresh filtered seawater. During a 6 d acclimation period, fecal pellets and tube openings were observed on the sediment surface in all containers.

Seven burial regimes were used in the experiment: no burial (NB), and six acute burial (AB) treatments with different grain sizes (muddy sand vs mud) and water contents (65%, 54% and 32% water content by volume), resulting in six different experimental bulk densities (Table 1). In addition, a series of replicates was sampled prior to the initiation of the experiment in order to establish survival rates during the acclimation period (NB_0). Each treatment consisted of five replicate containers randomly distributed in the experimental array. Sediment was added to the containers by the method employed in the *Macoma* experiment. No sediment was added to the NB treatment. The NB and AB treatments were sampled after 6 d by gently rinsing the contents of each container through nested 500 and 250 µm sieves. All live worms were counted. No dead worms were recovered.

Leptocheirus experiment

Plastic graduated cylinders (1000 ml volume, 42 cm tall, 6 cm i.d.) were used as experimental containers for the *Leptocheirus* experiment. A base layer of 2 cm of CB sediment was added to each cylinder. Sand-filtered seawater (21.5 °C, 26 ppt) was added to the containers to a height of 15 cm above the sediment, and aerated with bubble flow. Four days after adding the base layer, nine *Leptocheirus* neonates were added to each microcosm. All amphipods burrowed into the sediment within 1 h. Every 2 d after addition and throughout the experiment, amphipods were fed by adding 9 ml of algal paste slurry (*Thalassiosira weissflogii*) to each container. Every 2 d throughout the experiment, 80% of the water column was drained and replaced with fresh filtered seawater. Amphipods were allowed to acclimate for 4 d prior to the experiment during which time we observed burrow openings on the sediment surface in all containers.

Five burial regimes were used in the experiment: no burial (NB), and four acute burial (AB) treatments using different amounts of muddy sand (bulk density 1.79g/ml), resulting in four different burial depths (Table 1). In addition, a series of replicates was sampled prior to the initiation of the experiment in order to establish survival rates during the acclimation period (NB_0). Each treatment consisted of five replicate containers randomly distributed in the experimental array. Sediment was added to the containers by the method used in the *Macoma* experiment. No sediment was added to the NB treatment. The NB and AB treatments were sampled after six days by gently rinsing the contents of each container through nested 250 and 125 µm sieves. All live and dead amphipods present were counted.

Crassostrea experiment

The experimental design for the epifauna burial experiments differed slightly from the previous experiments on infauna. As *Crassostrea* and *Molgula* are sessile species that commonly attach to a hard substrate, they can not migrate to avoid burial. Thus, minimal burial depths, on the order of mm's, were used in this experiment to determine if burial causes mortality in these species.

For the *Crassostrea* experiment, 0.9 L plastic containers (8 cm deep, 13 cm wide, 13 cm long) were used as containers. Twenty-four hours prior to the experiment, oysters were adhered to individual microscope slides with a drop of superglue affixed to their ventral side. One slide was placed flat on the bottom of each microcosm, which was filled with filtered York River seawater (22° C, 27 ppt) and supplied with trickle flow aeration. Every other day each oyster was fed 10 mg of algal paste (*Thalassiosira weissflogii*) and 80% of the water column was replaced.

After 24 h, 10 replicates were completely covered with 5 mm of YK sediment (high burial treatment), 10 replicates were completely covered with 2 mm of YK sediment (low burial treatment) and 10 control replicates were not buried. All replicates were randomly allocated. Containers were monitored throughout the experiment for presence of feeding activity (fecal pellet production) or ventilation (as evidenced by "cracks" in the sediment above the buried oyster). Six days after burial, the slides were removed from the containers and survival status of the oysters was recorded by counting the number of individuals with gaping valves. Any shell discoloration was also noted at this time. Oysters were maintained for three weeks in a flow-through aquarium to monitor for any post-experimental mortality.

Molgula experiment

One day prior to burial, 30 tunicates were added to individual containers, each of which consisted of a 550 ml plastic cup (12 cm tall, 9 cm i.d.) filled with filtered seawater (20° C, 17 ppt) and supplied with trickle-flow aeration. For each randomly allocated burial treatment, tunicates were propped upright while a slurry of 60 ml of York River mud and 60 ml of filtered seawater was added to each cup. Burial patterns differed, depending on size of each tunicate and length of its siphons. As a result, 8 replicates contained tunicates that were completely buried by 5 mm of sediment, 5 replicates contained a partially buried tunicate with its body buried under 5 mm of sediment but one siphon exposed, and 7 replicates contained a partially buried tunicate with its body buried under 5 mm of sediment and 2 siphons exposed. Ten replicates were not buried and served as controls. Six days after burial, tunicates were excavated from the sediment and survival status was assessed. Live tunicates were firm to the touch and siphons retracted when touched. Dead tunicates were quickly assessed, as they were soft, black in color, and partially decayed.

Statistical analyses

Macoma survival and growth data were analyzed by analysis of variance (Zar 1999). All data were examined for normality and homogeneity of variance and transformed to meet assumptions if necessary. Survival data for *Leptocheirus* and *Streblospio* were analyzed using a Cochran-Mantel-Haenszel Test (Agresti 1990) and survival data for *Crassostrea* and *Molgula* were analyzed using a Fisher's Exact Test (Agresti 1990). Experimental results were analyzed using PC SAS version 8.0 (SAS Institute, Cary, NC).

Results

Overburden Stress Effects on Infaunal Behavior and Survival

At the levels tested, increasing overburden stress did not significantly decrease survival of juvenile *Macoma* (ANOVA, df =3, 19; MSE = 0.1000; $F = 0.67$; $P > 0.5874$, Fig. 1). *Macoma* growth (measured as change in length over the course of the experiment) was also not significantly different between treatments (ANOVA, square root transformation: df = 3, 198; MSE = 0.26; F= 1.683; $P > 0.1720$). Survival was significantly reduced by overburden stress for both *Streblospio* (Cochran-Mantel-Haenszel Test, df = 1; $Q_{CMH} = 79.0570$; $P < 0.0001$) and *Leptocheirus* (Cochran-Mantel-Haenszel Test, df = 1; $Q_{CMH} = 104.0808$; $P < 0.0001$), with survival rate for these species following a trend of exponential decline with increasing overburden stress (Fig. 1). An overburden stress of ≈ 4 kPa reduced the mean *Streblospio* survival rate to 4%, while an overburden stress approximately three times this level (12 kPa) was necessary to comparably reduce survival for *Leptocheirus*.

Crassostrea mortality

Burial by up to 0.5 cm of sediment did not cause significant juvenile oyster mortality (Fisher's Exact Test; $P = 0.3333$). Survival rates were 100% for the no burial treatment, 90% for the low burial (0.2 mm) treatment and 100% for the high burial (0.5 mm) treatment (Table 2). In 7 low burial containers, the sediment above the buried oysters appeared disturbed (cracks in the sediment were visible), which we attributed to the oysters attempting to open their valves to ventilate. No sediment disturbance was visible in the high burial treatment. In the no burial treatments, 7 oysters produced fecal pellets. This was the only treatment in which we observed fecal pellet production. Interestingly, the shells of 70% of the oysters in the high burial treatment appeared discolored (black around the edges) at the end of the experiment. There was no post-experimental mortality.

Molgula mortality

Unlike the juvenile oysters, the tunicates suffered significant mortality due to both complete and partial burial under 5 mm of sediment (Fisher's Exact Test, $p = 3.994 \times 10^{-6}$). No tunicates survived complete or partial burial with one siphon exposed. Even with both siphons exposed at or above the sediment water interface, survival was reduced to 14%, as compared to 90% in the no burial controls (Table 2).

Behavior observations

During sediment dosing in the *Leptocheirus* experiment, some individual neonates were observed to swim upward through the sediment slurry as it was being deposited, thus maintaining their position at the sediment water interface. In the *Streblospio* experiment, direct migration of worms up through the deposited sediment layer was not observed. In all burial treatments, however, dead worms could be observed between the base layer and the new sediment surface, trapped along the sides of the containers and rapidly forming black, anoxic zones.

Discussion

We found highly variable responses of estuarine benthic organisms to sediment burial regimes that were designed to mimic natural deposition events observed in Chesapeake Bay. Species representing both infaunal and epifaunal taxa ranged from highly susceptible (e.g. *Streblospio benedicti, Molgula manhattensis*) to highly tolerant (*Macoma balthica, Crassostrea virginica*) to burial by sediment. In cases where mortality occurred in infauna, exponential declines in survival with increasing overburden stress were observed for species belonging to two different phyla. Despite predictions that small, shallow-dwelling newly-settled individuals would be especially susceptible to sediment disturbance, we found that juveniles of some common estuarine infaunal and epifaunal species were in fact highly tolerant of burial by sediment. Susceptibility of estuarine organisms to deposition events, rather than being entirely dictated by life stage or body size, may be more strongly influenced by behavioral factors such as motility and residence depth in the sediment, as well as physiological adaptations.

The more motile, rapid burrowing infauna exhibited greater survival after an acute burial event than did the sedentary infaunal species. We documented unanticipated high survival of *Macoma balthica* juveniles and *Leptocheirus plumulosus* neonates even at deep burial depths. These species are capable of rapid migration up through deposited sediment to establish contact with the new sediment-water interface, which is essential for respiration and feeding activities. Survival of juvenile and adult *Streblospio benedicti* was more drastically reduced in the face of increasing overburden stress. This tube-dwelling species is relatively sedentary compared to *Macoma* and *Leptocheirus*, and was less successful at establishing contact with the new sediment-water interface. It is unlikely that food limitation was responsible for the mortality observed in *Streblospio* and *Leptocheirus*, as both species have been observed to survive in the laboratory without food for > 6 d (B. Vogt and C. Hoar, pers. comm.).

Exponential declines in survival with increasing overburden stress were exhibited by both *Leptocheirus* and *Streblospio*, with *Streblospio* displaying a much steeper decline. There are several possible reasons for this non-linear relationship, which can be related to the potential occurrence of a state change in the fluid mud as overburden stress increased. One state change that could occurs a decrease in porosity and void ratio with depth due to increased consolidation of sediment under increasing overburden pressure (Seymour et al. 1996). The change in porosity with depth in the sediment can be expressed as:

$$\eta = \eta_0 e^{-\alpha d}$$

where η is porosity, α is a coefficient and d is depth below the sediment-water interface (Althy 1930). This relationship could have significant effects on buried organism survival for both physiological and mechanical reasons.

First, organisms are subject to respiratory stress upon burial, as molecular diffusion of oxygen into fine-grained sediments in the absence of advective flow, mixing or bioirrigation only occurs via molecular diffusion and is limited to a distance of 1-2 mm (Rhoads 1974). Thus, any oxygen present at depth in the containers would be restricted to that which was contained in porewater. Buried organisms unable to conduct anaerobic metabolism would depend on this oxygen-laden porewater as a source of respiratory oxygen during their migration up through the sediment. Increasing overburden stress ultimately results in a reduction of available oxygen-saturated porewater at depth via decreased porosity and permeability, and thus increases the probability that an organism will suffocate before it is able to establish contact with the new sediment-water interface. Laboratory experiments reveal that although *Streblospio* is relatively tolerant of severe hypoxia (adults can survive at reduced oxygen concentrations for two weeks), it is intolerant of anoxia (100% mortality after 2.3 d; LT_{50} (median mortality time) = 1.8 d); worms exposed to hypoxia and anoxia, however, both exhibited decreased burrowing activities (Llansó 1991). Comparable anoxia tolerance data for *Leptocheirus* are not available, however they can also be expected to be relatively intolerant of anoxia, as crustaceans are generally considered to be less tolerant than polychaetes to low oxygen stress (Diaz and Rosenberg 1995). *Leptocheirus* is a more rapid burrower than *Streblospio*, and thus some individuals were still able to migrate upward at low to intermediate levels of overburden stress, thereby avoiding respiratory stress caused by decreased porosity. *Macoma*, which did not suffer significant mortality with increasing overburden stress, is not only a rapid burrower, but is also extremely tolerant of anoxia ($LT_{50} \cong 10$ d at 20° C in experimental containers; Dries and Theede, 1974).

Decreased porosity could also elicit differences in survival via differentially diminishing the effectiveness of locomotion strategies employed by each taxa. *Streblospio*, as a tubiculous polychaete, has reduced parapodia relative to errant polychaetes, and burrows primarily via peristaltic contractions of its longitudinal and circular muscles. Increased sediment compaction could mechanically inhibit the ability of this soft-bodied creature to undulate via contractions. It is also possible that the increased pressure at higher burial depths could have resulted in lethal deformation/crushing of *Streblospio*. In contrast, *Leptocheirus* burrows head-first through the sediment via excavation of a cavity in the sediment with its well-developed walking legs. The well-developed legs, in conjunction with possession of a chitinous exoskeleton, may render the amphipod better adapted to migrate through compacted sediment and also to withstand any crushing pressures of increasing overburden stress than the soft-bodied *Streblospio*. In contrast, bivalves are generally highly adapted for a burrowing lifestyle, and *Macoma* easily migrates upward through the sediment via use of a muscular foot. The presence of valves also serves to protect the soft, vulnerable internal tissues from damage due to any direct mechanical crushing effects of overburden stress. Thus, in select species, overburden stress can cause mortality due to direct mechanical stress and indirect respiratory stress that ultimately impairs or inhibits migration upward through the deposited sediments.

As maintenance of contact with the sediment-water interface is essential for survival in many benthic organisms (Nichols et al. 1978, Brenchley 1981, Maurer et al. 1986), the variable susceptibility of infauna to sediment disturbance can influence community structure. This phenomenon is reflected by the zonation patterns of many natural benthic assemblages in energetic marine environments. In general, relatively sessile organisms living in permanent tubes or burrows are excluded from physically dynamic sediments where motile, burrowing organisms are favored (Oliver et al. 1980, Gaston 1987, Levin et al. 1994). In addition to direct mortality effects, sediment disturbance can also cause sublethal effects in organisms resulting from changes in quality and quantity of food supply (Wildish and Kristmanson 1997), inhibition of feeding (Levinton 1991, Miller et al. 1992) and injury from abrasion (Emerson 1989), for example. In conjunction with direct mortality, these effects can translate a higher susceptibility to disturbance into lowered secondary production (Emerson 1989, Schaffner et al. 2001), thus impacting benthic community function.

Our data also allow for a preliminary comparison of burial response of estuarine infaunal species with estuarine epifaunal species. Despite our prediction that epifauna would generally be more vulnerable to burial than infauna, we documented drastically different responses to burial for the two epifaunal species we tested. Given the sedentary living position of both species, their survival is not a function of motility or residence depth but likely determined by different responses to metabolic stress. *Crassostrea virginica* juveniles were able to survive short-term (6 d) burial under 0.2 to 0.5 cm of sediment, presumably by resorting to anaerobic metabolism while buried. Anoxia tolerance by juvenile oysters was documented in the laboratory by Widdows et al. (1989), who found that the LT_{50} for juveniles (16 mm shell height) under anoxia was approximately 6 d at 22°C, and 100% mortality occurred at 7d. *Crassostrea* mortality observed by Widdows et al. (1989) was higher than that encountered in this experiment, likely due to the fact that their juveniles were placed directly in chambers of anoxic water. Regardless, their results in combination with ours demonstrate that anoxia tolerance is a viable short-term survival strategy for juvenile oysters that are temporarily buried by siltation. Others have reported that high sediment deposition resulting in burial for longer periods of time can reduce recruitment and increase mortality of juvenile oysters in the field, however (MacKenzie 1983, Lenihan 1999).

Unlike *Crassostrea virginica*, *Molgula manhattensis* was highly susceptible to burial under 0.5 cm of sediment, suffering severe mortality in all burial treatments. Partial burial was as deleterious as complete burial. It is possible that individuals were smothered underneath the sediments, as gas exchange occurs across the body wall, in addition to the linings of the pharynx and the cloacal chamber (Brusca and Brusca 1990). It is also possible that immersion of the body in sediment could have interfered with the mechanics of tunicate pumping and caused suffocation. This species is not highly tolerant of hypoxic conditions, as calculated LT_{50} values for this species exposed to hypoxic water (oxygen concentrations of 0.5 mg O_2/l) are 5 d (95% confidence interval: 3.98-5.35 d, Sagasti et al. (2001)). Lack of a tolerance of sulfide accumulation in the sediments could be another factor contributing to *M. manhattensis* mortality, as organisms digging into (or buried under) sediment cannot avoid being exposed to high concentrations of sulfide (Hagerman 1998).

We have documented that species resilience to sediment disturbance in the form of overburden stress caused by burial varies as a function of species motility, residence depth and metabolic strategy. In our experiments, motile infaunal species were better adapted than a sedentary infaunal species to survive acute burial events. Likewise, a sessile epifaunal species with the ability to convert to anaerobic metabolism in the face of burial survived acute burial events better than a sessile epifaunal species that is an obligate aerobe. The responses of the five common estuarine species studied, chosen because they spanned a range of motility and living positions, provide insights useful in predicting which estuarine species would be most adversely affected by sediment deposition. Further experiments with additional species would compliment this study and enhance our understanding of estuarine species response to sediment burial. Knowledge of other effects of flow-mediated sediment disturbance on organisms, such as erosion, is also important in predicting how an estuarine benthic community responds to stress, and should be considered in future studies.

Acknowledgments

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Table 1. Burial regimes for the five experiments. CB indicates sediment collected from Chesapeake Bay; YK indicates sediment collected from upper York River. AB indicates acute burial; PB indicates partial burial; NB indicates no burial; NB_0 indicates no burial sampled at end of acclimation period. Percent water of dosing sediment is indicated. †depths measured after 24 hr.

Experiment	Treatment	Initial percent water (%)	Bulk density after 24 hr ($g\ ml^{-1}$)	Mean sediment addition† (cm)	Overburden stress (kPa)
Macoma					
	CB AB	37	1.67	24.58	15.98
	CB AB	37	1.67	14.70	9.56
	CB AB	37	1.67	8.36	5.43
	CB NB	--	--	0.00	0.00
	CB NB_0	--	--	0.00	0.00
Streblospio					
	CB AB	32	1.76	5.60	4.14
	CB AB	54	1.73	6.02	4.27
	CB AB	65	1.69	6.50	4.36
	CB NB	--	--	0.00	0.00
	YK AB	32	1.23	5.56	1.17
	YK AB	54	1.20	7.64	1.38
	YK AB	65	1.17	8.36	1.25
	YK NB	--	--	0.00	0.00

Table 1. (Continued)

Leptocheirus					
	CB AB	47	1.79	20.20	15.58
	CB AB	47	1.79	15.60	12.04
	CB AB	47	1.79	11.10	8.52
	CB AB	47	1.79	5.90	5.54
	CB NB	--	--	0.00	0.00
	CB NB_0	--	--	0.00	0.00
Crassostrea					
	YK AB	69	1.21	0.52	0.10
	YK AB	69	1.21	0.21	0.04
	YK NB	--	--	0.00	0.00
Molgula					
	YK AB	69	1.21	1.00	0.19
	YK PB	69	1.21	0.75	0.14
	YK NB	--	--	0.00	0.00

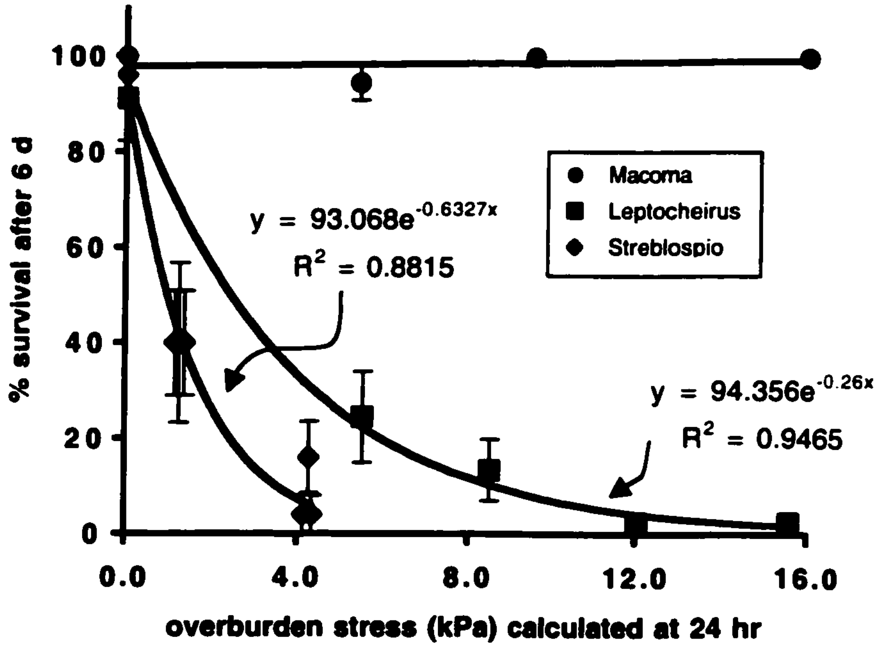
Table 2. Mean survival (with standard error) of the five species after 6 d of burial. CB indicates sediment collected from Chesapeake Bay; YK indicates sediment collected from upper York River. AB indicates acute burial, PB indicates partial burial (*Molgula* experiment only: 1 or 2 siphons exposed); NB indicates no burial; NB_0 indicates no burial sampled at end of acclimation period. N is number of individuals used in that treatment (total for all replicates). †Values in parentheses are mean burial depths.

Experiment	mean survival (SE)	N
Macoma		
CB AB (24.6 cm)†	100.00 (0.00)	55
CB AB (14.7 cm)†	100.00 (0.00)	55
CB AB (8.4 cm)†	94.55 (3.64)	55
CB NB	100.00 (0.00)	55
CB NB_0	100.00 (0.00)	55
Streblospio		
CB AB (6.5 cm)†	4.00 (4.00)	25
CB AB (6.3 cm)†	16.00 (7.48)	25
CB AB (5.8 cm)†	4.00 (4.00)	25
CB NB	96.00 (4.00)	25
YK AB (6.9 cm)†	40.00 (10.95)	25
YK AB (6.1 cm)†	40.00 (10.95)	25
YK AB (5.0 cm)†	40.00 (16.73)	25
YK NB	100.00 (0.00)	25
Leptocheirus		
CB AB (20.2 cm)†	2.22 (1.99)	45
CB AB (15.6 cm)†	2.22 (1.99)	45
CB AB (11.1 cm)†	13.33 (5.79)	45
CB AB (5.9 cm)†	24.44 (8.55)	45
CB NB	91.00 (7.95)	45
CB NB_0	93.33 (2.43)	45

Table 2. (Continued)

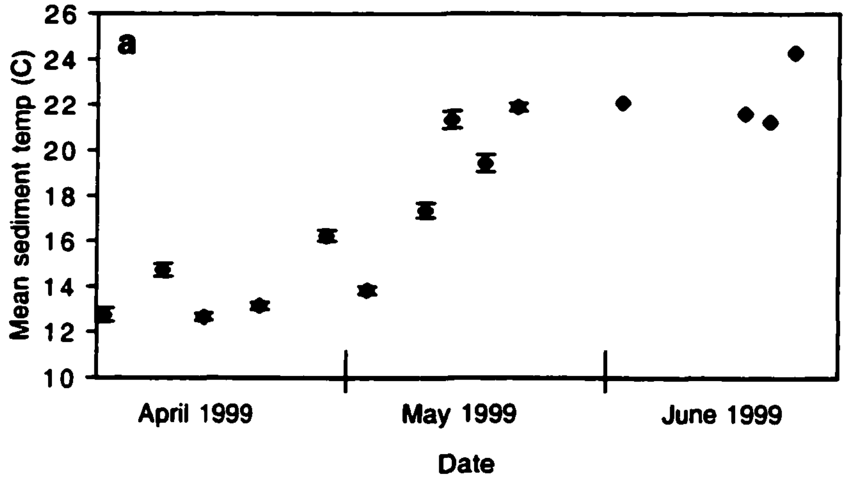
Crassostrea		
YK AB (0.52 cm)[†]	100.00 (0.00)	10
YK AB (0.21 cm)[†]	90.00 (10.00)	10
YK NB	100.00 (0.00)	10
Molgula		
YK AB (0.50 cm)[†]	0.00 (0.00)	8
YK PB (<0.50 cm)[†]	8.33 (8.33)	12
YK NB	90.00 (10.00)	10

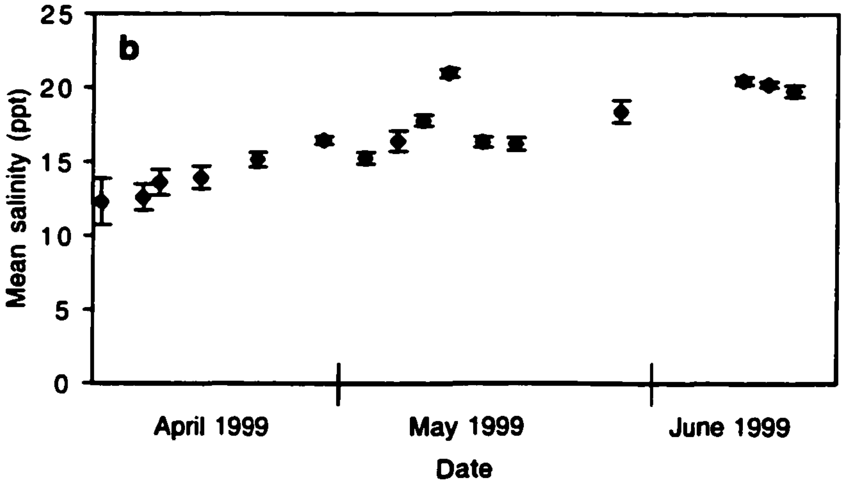
Fig. 1. Mean survival of *Macoma balthica, Leptocheirus plumulosus* and *Streblospio benedicti* after 6 d vs. overburden stress. Error bars = standard error of the mean.


100
80
60
40
20
0
% survival after 6 d
0.0
4.0
8.0
12.0
16.0
overburden stress (kPa) calculated at 24 hr
● Macoma
■ Leptocheirus
◆ Streblospio
y = 93.068e^-0.6327x
R^2 = 0.8815
y = 94.356e^-0.26x
R^2 = 0.9465

APPENDICES

Appendix I. a, b. Mean sediment temperature (°C) and mean salinity (ppt) recorded on each sampling date. Data are pooled across subenvironments. Error bars are standard errors.





Appendix II. Time series of measured sediment parameters

Percent mud content (= silt + clay fraction) in surface sediment layer (0-1 cm) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

Subenvironment	4/1/99 mean	4/8/99 mean	4/13/99 mean	4/20/99 mean	4/27/99 mean	5/3/99 mean	5/10/99 mean	5/17/99 mean	5/21/99 mean	6/21/99 mean	grand mean	std. error
south shoal	93.74	95.06	93.93	96.24	96.02	94.37	95.47	92.07	95.67	93.55	94.61	0.42
secondary channel	88.34	85.95	96.75	83.62	86.99	90.98	88.06	83.11	89.14	85.48	87.84	1.25
main channel flank	98.32	98.14	99.05	99.32	99.08	98.79	96.82	96.72	97.74	96.25	98.02	0.35

Subenvironment	5/13/99 mean	6/18/99 mean	grand mean	std. error
main channel	93.12	93.16	93.14	0.02

Subenvironment	4/6/99 mean	5/7/99 mean	6/3/99 mean	6/24/99 mean	grand mean	std. error
north shoal	41.47	36.85	39.03	48.07	41.35	2.43

Appendix II. Time series of measured sediment parameters (Continued)

Sediment water content (%) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

		4/1/99	4/8/99	4/13/99	4/20/99	4/27/99	5/3/99	5/10/99	5/17/99	5/21/99	6/21/99		
Subenvironment	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
south shoal	-0.5	70.99	67.31	64.62	72.44	74.91	67.51	71.66	71.69	69.54	64.01	69.47	1.12
	-1.5	67.50	64.45	63.96	67.99	71.02	66.85	68.23	70.36	67.57	62.30	67.02	0.87
	-2.5	64.36	62.63	65.88	63.50	69.33	64.73	67.71	66.89	65.25	62.89	65.32	0.69
	-3.5	61.31	60.98	62.71	62.91	68.08	62.15	64.48	62.35	62.40	62.23	62.96	0.64
	-4.5	61.20	60.98	64.03	62.51	65.87	60.25	60.72	59.58	62.85	62.75	62.07	0.60
	-10.5	58.51	58.92	58.84	59.19	56.44	59.77	61.85	59.60	59.04	60.42	59.26	0.44
	-15.5	57.26	57.30	56.08	57.10	55.43	58.23	56.70	57.29	57.23	57.63	57.02	0.25

	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
secondary channel	-0.5	66.74	69.15	64.87	67.43	69.52	66.94	73.44	67.02	69.86	65.45	68.04	0.80
	-1.5	65.95	66.35	60.02	66.85	69.12	64.66	68.28	65.65	67.88	65.49	66.02	0.80
	-2.5	66.31	64.81	60.95	67.87	68.27	62.07	65.17	64.18	64.59	60.82	64.50	0.83
	-3.5	65.43	64.96	58.88	63.99	62.57	58.70	64.35	62.36	63.49	61.87	62.66	0.74
	-4.5	64.35	63.87	58.87	64.38	59.19	58.25	62.00	60.78	63.71	61.12	61.65	0.75
	-10.5	60.64	61.37	58.82	60.72	60.83	57.91	61.93	61.78	62.24	62.72	60.90	0.48
	-15.5	59.81	60.29	59.91	59.87	61.91	60.59	61.77	59.14	61.16	62.06	60.65	0.32

	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
main channel flank	-0.5	74.88	78.39	78.65	73.02	80.57	74.49	77.35	75.56	75.37	74.36	76.26	0.75
	-1.5	73.78	74.32	77.99	71.94	73.12	75.14	77.30	73.69	73.56	73.75	74.46	0.59
	-2.5	71.43	70.28	74.38	72.01	75.21	73.11	74.74	73.22	71.29	74.09	72.98	0.53
	-3.5	70.15	70.26	71.37	69.24	73.94	72.09	74.26	71.76	72.05	74.50	71.96	0.57
	-4.5	68.26	69.58	69.00	69.16	71.06	72.17	74.05	70.31	72.41	72.01	70.80	0.58
	-10.5	68.14	68.78	68.94	67.86	67.60	66.60	70.11	68.65	68.32	68.10	68.31	0.29
	-15.5	67.12	68.15	65.16	65.85	68.05	67.67	69.20	68.26	68.47	69.08	67.70	0.42

Sediment water content (%) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

Subenvironment	depth (cm)	5/13/99 mean	6/18/99 mean	grand mean	std. error
main channel	-0.5	70.01	73.27	71.64	1.63
	-1.5	68.57	69.17	68.87	0.30
	-2.5	68.63	68.80	68.72	0.09
	-3.5	65.22	68.31	66.76	1.55
	-4.5	64.48	67.80	66.14	1.66
	-10.5	62.55	65.69	64.12	1.57
	-15.5	63.38	62.98	63.18	0.20

	depth (cm)	4/6/99 mean	5/7/99 mean	6/3/99 mean	6/24/99 mean	grand mean	std. error
north shoal	-0.5	52.15	49.20	45.14	52.22	49.68	1.67
	-1.5	49.20	44.37	43.61	42.22	44.85	1.52
	-2.5	49.49	42.54	40.13	43.64	43.95	1.99
	-3.5	49.61	43.05	44.40	44.10	45.29	1.47
	-4.5	51.50	43.30	40.55	42.79	44.54	2.40
	-10.5	59.35	44.89	41.48	40.71	46.61	4.34
	-15.5		43.71		40.86	42.28	1.42

Appendix II. Time series of measured sediment parameters (Continued)

Sediment Eh (mV) for each subenvironment. Means for each sampling date and grand mean for the study period are presented. Electrode was inserted vertically down through the sediment surface.

Subenvironment	depth (cm)	5/3/99 mean	5/10/99 mean	5/17/99 mean	grand mean	std. error
south shoal	0.5		322.83	316.60	322.83	3.11
	-0.5	237.05	150.68	104.43	193.86	38.87
	-1.5	135.15	52.40	69.45	93.78	25.23
	-2.5	70.30	30.63	32.13	50.46	12.98
	-3.5	63.43	14.13	17.95	38.78	15.83
	-4.5	44.63	-8.98	0.70	17.83	16.50
	-5.5	45.18	-22.23	4.23	11.48	19.61
	-6.5	38.00	-33.38	-19.35	2.31	21.83
	-7.5	23.40	-43.75	-42.10	-10.18	22.11
	-8.5	16.03	-55.08	-55.73	-19.53	23.81
	-9.5	6.58	-90.95	-72.80	-42.19	29.95
	-10.5	3.03	-105.08	-93.73	-51.03	34.30
	-11.5	-2.78	-124.65	-94.03	-63.71	36.60
	-12.5	1.05	-126.53	-97.05	-62.74	38.56
	-13.5		-101.65	-92.97	-101.65	3.54

	depth (cm)	5/3/99 mean	5/10/99 mean	5/17/99 mean	grand mean	std. error
secondary channel	0.5	349.60	303.03	300.67	317.77	15.93
	-0.5	202.90	239.72	131.08	191.23	31.90
	-1.5	92.50	88.90	70.10	83.83	6.94
	-2.5	69.15	55.93	28.00	51.03	12.13
	-3.5	53.15	37.48	-32.47	19.39	26.32
	-4.5	46.25	26.98	-71.77	0.49	36.55
	-5.5	38.50	24.17	-71.33	-2.89	34.47
	-6.5	24.95	15.60	-57.78	-5.74	26.16
	-7.5	16.25	3.17	-95.92	-25.50	35.41
	-8.5	12.65	-36.38	-118.57	-47.43	38.28
	-9.5	12.00	-38.00	-132.80	-52.93	42.46
	-10.5	3.20	-57.43	-136.72	-63.65	40.51
	-11.5	2.55	-74.47	-143.97	-71.96	42.31
	-12.5	4.20	-97.95	-151.12	-81.62	45.57
	-13.5		-105.07	-153.90	-129.48	19.94

	depth (cm)	5/3/99 mean	5/10/99 mean	5/17/99 mean	grand mean	std. error
main channel flank	0.5	334.55	309.60	319.20	321.12	7.27
	-0.5	228.74	292.18	166.92	229.28	36.16
	-1.5	203.54	229.60	110.42	181.19	36.17
	-2.5	133.88	192.72	38.06	121.55	45.07
	-3.5	113.23	135.38	24.92	91.18	33.74
	-4.5	89.56	79.88	10.24	59.89	24.98
	-5.5	60.70	71.66	-12.42	39.98	26.39
	-6.5	42.64	8.02	-24.48	8.73	19.38
	-7.5	30.60	-32.16	-34.12	-11.89	21.25
	-8.5	29.20	-36.96	-56.26	-21.34	25.88
	-9.5	25.48	-51.10	-69.18	-31.60	29.01
	-10.5	18.88	-62.52	-78.46	-40.70	30.14
	-11.5	16.42	-71.56	-97.44	-50.86	34.46
	-12.5	-9.60	-77.56	-123.22	-70.13	33.01
	-13.5		-90.60	-139.58	-115.09	20.00

Sediment Eh (mV) for each subenvironment. Means for each sampling date and grand mean for the study period are presented. Electrode was inserted vertically down through the sediment surface.

		5/13/99	
Subenvironment	**depth (cm)**	**mean**	**std. error**
main channel	0.5	307.41	7.76
	-0.5	162.65	26.66
	-1.5	64.54	16.66
	-2.5	7.02	9.74
	-3.5	-16.88	7.63
	-4.5	-35.39	8.77
	-5.5	-45.65	11.44
	-6.5	-54.48	12.26
	-7.5	-60.96	11.63
	-8.5	-64.59	10.21
	-9.5	-66.76	11.22
	-10.5	-84.73	14.82
	-11.5	-113.11	22.33
	-12.5	-100.41	21.06
	-13.5	-119.88	22.76

		5/7/99	6/24/99		
	depth (cm)	**mean**	**mean**	**grand mean**	**std. error**
north shoal	0.5	308.72	304.22	306.47	2.25
	-0.5	138.94	219.02	178.98	40.04
	-1.5	118.26	134.90	126.58	8.32
	-2.5	60.96	65.16	63.06	2.10
	-3.5	23.18	1.34	12.26	10.92
	-4.5	-8.20	-30.90	-19.55	11.35
	-5.5	-96.74	-42.18	-69.46	27.28
	-6.5	-157.65	-61.80	-109.73	47.93
	-7.5	-165.83	-68.93	-117.38	48.45
	-8.5	-71.73	-110.85	-91.29	19.56
	-9.5	-77.50	-104.30	-90.90	13.40
	-10.5	-139.35	-101.57	-120.46	18.89

Appendix II. Time series of measured sediment parameters (Continued)

Sediment chlorophyll *a* (µg chl *a* /g wet sediment weight) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

		4/13/99	4/20/99	4/27/99	5/3/99	5/10/99	5/17/99	5/21/99	6/21/99		
Subenvironment	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
south shoal	-0.5	2.06	2.28	2.57	2.47	5.34	3.36	3.25	4.31	3.20	0.40
	-1.5	2.49	2.09	3.18	2.41	4.87	3.76	2.89	4.08	3.22	0.34
	-2.5	1.76	2.03	2.08	2.76	4.08	2.89	2.54	4.05	2.78	0.31
	-3.5	1.99	1.48	2.11	1.77	3.45	2.53	1.90	3.21	2.30	0.25
	-4.5	1.43	1.44	1.81	1.85	2.86	1.70	1.92	2.68	1.96	0.19
	-10.5	0.97	0.79	0.28	1.27	1.31	1.46	0.91	1.75	1.09	0.16
	-15.5	0.85	0.86	0.00	1.07	0.87	1.12	0.56	1.20	0.82	0.14
	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
secondary channel	-0.5	2.87	2.58	2.76	4.00	5.33	3.46	2.83	4.86	3.59	0.37
	-1.5	2.72	2.94	2.35	3.40	3.83	3.22	2.35	3.79	3.07	0.21
	-2.5	2.53	2.45	2.44	2.73	3.02	2.31	2.08	3.10	2.58	0.12
	-3.5	2.30	2.41	1.65	2.81	2.28	1.40	2.12	2.16	2.14	0.16
	-4.5	2.42	1.92	0.80	2.35	2.08	1.32	1.80	1.65	1.79	0.19
	-10.5	2.03	1.28	0.37	1.35	1.21	1.10	0.96	0.95	1.16	0.16
	-15.5	1.34	1.13	0.38	1.45	0.98	0.82	0.87	1.01	1.00	0.12
	depth (cm)	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
main channel flank	-0.5	1.87	2.13	1.64	2.24	4.96	3.23	2.24	4.60	2.86	0.45
	-1.5	1.95	3.05	1.83	2.16	5.77	2.28	1.82	5.89	3.09	0.61
	-2.5	2.32	2.85	2.04	2.16	4.83	3.17	3.40	5.36	3.27	0.44
	-3.5	1.89	2.00	1.71	2.12	4.04	2.50	3.37	6.63	3.03	0.59
	-4.5	2.35	1.89	1.96	2.21	3.48	2.82	2.94	4.67	2.79	0.33
	-10.5	1.13	1.30	0.63	1.22	1.79	0.78	1.47	1.94	1.28	0.16
	-15.5	1.07	1.28	0.82	1.11	0.67	0.83	0.88	1.68	1.04	0.11

Sediment chlorophyll *a* (µg chl *a* /g wet sediment weight) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

Subenvironment	depth (cm)	5/13/99 mean	6/18/99 mean	grand mean	std. error
main channel	-0.5	5.95	4.87	5.41	0.54
	-1.5	6.02	4.73	5.37	0.65
	-2.5	4.34	3.87	4.10	0.24
	-3.5	3.62	3.77	3.69	0.08
	-4.5	3.45	3.09	3.27	0.18
	-10.5	1.54	1.76	1.65	0.11
	-15.5	2.08	1.99	2.04	0.05

	depth (cm)	5/7/99 mean	6/3/99 mean	6/24/99 mean	grand mean	std. error
north shoal	-0.5	1.36	5.36	5.98	4.23	1.45
	-1.5	1.24	2.50	4.26	2.67	0.88
	-2.5	0.81	1.79	3.07	1.89	0.66
	-3.5	0.56	2.29	2.82	1.89	0.68
	-4.5	0.29	1.01	2.34	1.21	0.60
	-10.5	0.17	0.29	0.98	0.48	0.25
	-15.5	0.72		0.32	0.52	0.20

Appendix II. Time series of measured sediment parameters (Continued)

Sediment organic content (% TOC, % TN, C:N$_a$) in surface sediment layer (0-1 cm) for each subenvironment. Means for each sampling date and grand mean for the study period are presented.

		4/13/99	4/20/99	4/27/99	5/3/99	5/10/99	5/17/99	5/21/99	6/21/99		
Subenvironment	parameter	mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
south shoal	% TOC	2.21	2.35	2.29	2.03	2.57	2.40	2.24	2.18	2.28	0.05
	% TN	0.21	0.21	0.23	0.18	0.24	0.23	0.19	0.21	0.21	0.01
	C:N$_a$	12.40	13.15	11.74	12.86	12.73	12.03	13.55	12.09	12.57	0.22

		mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
secondary channel	% TOC	2.50	2.26	2.39	2.45	2.39	2.13	2.24	1.97	2.29	0.06
	% TN	0.23	0.20	0.23	0.22	0.22	0.20	0.22	0.20	0.22	0.00
	C:N$_a$	12.62	12.91	12.16	11.96	12.46	12.13	12.37	11.76	12.30	0.13

		mean	mean	mean	mean	mean	mean	mean	mean	grand mean	std. error
main channel flank	% TOC	3.16	2.75	3.06	3.09	3.07	2.95	2.82	2.97	2.98	0.05
	% TN	0.30	0.24	0.31	0.25	0.29	0.29	0.25	0.29	0.28	0.01
	C:N$_a$	12.23	13.35	11.63	12.86	12.49	11.92	12.98	11.96	12.43	0.19

		5/13/99	6/18/99		
Subenvironment	parameter	mean	mean	grand mean	std. error
main channel	% TOC	2.23	2.73	2.48	0.25
	% TN	0.25	0.29	0.27	0.02
	C:N$_a$	10.41	10.55	10.48	0.07

		5/7/99	6/3/99	6/24/99		
Subenvironment	parameter	mean	mean	mean	grand mean	std. error
north shoal	% TOC	2.25	1.71	2.33	2.10	0.19
	% TN	0.16	0.12	0.17	0.15	0.01
	C:N$_a$	15.00	14.85	16.04	15.30	0.37

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