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Natural Variation in the Vertical Distribution of Macrobenthic Invertebrates Within Sandy-Mud Habitats

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NATURAL VARIATION IN THE VERTICAL DISTRIBUTION
OF MACROBENTHIC INVERTEBRATES WITHIN SANDY-MUD HABITATS

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by

Amanda Maxemchuk-Daly

1998

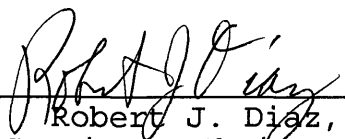
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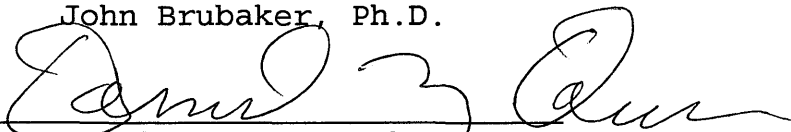
Master of Science


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Approved, March 1998


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Table of Contents

	page
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	v
LIST OF FIGURES	vi
ABSTRACT	viii
INTRODUCTION	1
STUDY SITE - THE YORK RIVER, VIRGINIA.	6
METHODS.	8
RESULTS	
Physical and Chemical Data.	12
General Biological Data.	15
Vertical Distribution.	17
Logistic Regression.	25
DISCUSSION.	35
CONCLUSIONS.	56
LITERATURE CITED.	60
TABLES.	65
FIGURES.	76
APPENDICES	
VITA	

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LIST OF TABLES

	page
Table 1. York River Sampling Sites - Physical Environmental Variables.65
Table 2. York River Biological Data.66
Table 3. York River Dominants.67
Table 4. Vertical Distribution of Dominants Within the Sediment Column.69
Table 5. Differences in the Vertical Distribution of Dominants Between the Upper and Lower Estuary. . .	.71
Table 6. Paired Comparisons of Vertical Distribution.72
Table 7. Variables Used In Logistic Regresssions to Determine Potential Explanation for Vertical Distribution Patterns.73
Table 8. Summary of Results from Logistic Regression Modeling of Vertical Distribution of Individuals and Biomass Within Estuarine Sandy-Mud.74

LIST OF FIGURES

	page
Figure 1. Diagram of Changes in Fauna and Sediment Structure along a Gradient of Organic Enrichment. . .	76
Figure 2. Study Site and Sampling Stations.	77
Figure 3. Principal Components Analysis of Physical Data. . .	78
Figure 4. York River Physical Environmental Parameters.	79
Figure 5. Cluster Analysis of Sites Based on Species Composition and Abundances.	81
Figure 6. York River Biological Parameters.	82
Figure 7. Vertical Distribution of Individuals Within the Top 10 cm of Sediment.	83
Figure 8. Vertical Distribution of Individuals Without <i>Leucon americanus</i>	84
Figure 9. Vertical Distribution of Annelids Within the Top 10 cm of Sediment.	85
Figure 10. Vertical Distribution of Biomass Within the Top 10 cm of Sediment.	86
Figure 11. Vertical Distribution of Biomass Without Bivalves. . .	87
Figure 12. Vertical Distribution of Annelid Biomass Within the Top 10 cm of Sediment.	88
Figure 13. Observed vs Expected Vertical Distributions of Individuals Within the Top 10 cm of Sediment All Variables Modeled.	89
Figure 14. Observed vs Expected Vertical Distributions of Individuals Within the Top 10 cm of Sediment Physical Variables Modeled	90
Figure 15. Observed vs Expected Vertical Distributions of Individuals Within the Top 10 cm of Sediment Biological Variables Modeled.	91
Figure 16. Observed vs Expected Vertical Distributions of Individuals Within the Top 10 cm of Sediment Feeding Modes Modeled.	92
Figure 17. Observed vs Expected Vertical Distributions of Individuals Within the Top 10 cm of Sediment Living Positions Modeled.	93

Figure 18. Observed vs Expected Vertical Distributions
of Biomass Within the Top 10 cm of Sediment
All Variables Modeled.94

Figure 19. Observed vs Expected Vertical Distributions
of Biomass Within the Top 10 cm of Sediment
Biological Variables Modeled.95

Figure 20. Observed vs Expected Vertical Distributions
of Annelid Biomass Within the Top 10 cm of Sediment
All Variables Modeled.96

Figure 21. Observed vs Expected Vertical Distributions
of Annelid Biomass Within the Top 10 cm of Sediment
Physical Variables Modeled.97

Figure 22. Observed vs Expected Vertical Distributions
of Annelid Biomass Within the Top 10 cm of Sediment
Biological Variables Modeled.98

ABSTRACT

Benthic macroinfauna are used worldwide to assess human impact in aquatic environments. However, interpretation of metrics derived from macrobenthic data for evaluating estuarine environmental conditions can be complicated by the influence of natural variables such as salinity, water depth, and sediment grain size on benthic communities. An understanding of how non-anthropogenic environmental variability affects infauna is key to the successful use of any benthic assessment method.

One metric that has been used for assessing the extent of anthropogenic effects on coastal ecosystems is the vertical distribution of infauna within the sediment column. How organisms are distributed within the sediment provides important information on ecosystem function, potentially reflecting food availability to higher trophic levels, sediment and pollutant transport processes, and nutrient cycles. This study has investigated the influence of salinity, sediment organic content, community composition, organism sizes, community trophic structure, and other physical and biological variables on how macrobenthos are distributed vertically within estuarine sandy-mud. No changes in vertical distribution of abundance or biomass were observed along the estuarine gradient, even though there were changes in community composition. How deep macrobenthic organisms live in the sediment appeared to be influenced by or related to water depth, sediment organic carbon content and quality, organism abundances, sizes of organisms, and life-history and trophic structure of the community. Trends in and models of vertical distribution patterns are discussed.

INTRODUCTION

The utility of macrobenthos for environmental assessment is well documented. One parameter of macrobenthic community structure that is indicative of community health as related to environmental stress is the distribution of macrofauna within the sediment column. How deep organisms live within sediments has important implications for food availability to higher trophic levels, oxygenation and reworking of sediments, sediment transport, biogeochemical processes, and the fate and transport of pollutants and organic material (see Diaz and Schaffner 1990 for a review).

As the benthic environment becomes more impacted by humans, macroinfauna become more concentrated in the upper layers of sediment. A shallowing of the infaunal distribution can be related to two factors:

- 1) Changes in the species composition of the community from longer-lived, deeper-dwelling, equilibrium species to shallower, short-lived, opportunistic and stress tolerant species (Pearson and Rosenberg 1978; Weston 1990).
- 2) Changes in the behavior of organisms as they try to avoid environmental stress (Diaz et al. 1992).

If a shallowing of the infauna is manifested as a change in community composition, the taxonomic diversity and the functional complexity of the community usually decrease, as well (Pearson and

Rosenberg 1978).

The best documented cases of pollution-induced changes in the vertical distribution of macrofauna within estuarine sediments are related to organic enrichment and sediment hypoxia (Pearson and Rosenberg 1978; Weston 1990; Diaz and Rosenberg 1995). Less impacted macrobenthic communities are dominated by larger, long-lived, deep-dwelling species (Rhoads and Boyer 1982; Warwick 1986). Along an increasing gradient of organic enrichment, macrobenthic assemblages change from a species-rich community with a high diversity of living positions, feeding groups, functional roles, and life-histories to a shallow, species-poor community dominated by smaller sedentary, opportunistic, deposit-feeding species (Figure 1) (Pearson and Rosenberg 1978). Weston (1990) also demonstrated a loss of deep-dwelling biomass with increasing organic enrichment; but because deeper-dwelling fauna were numerically sparse at relatively unenriched sites, there was little effect on vertical abundance profiles. Sanders et al. (1980) demonstrated that after defaunation of estuarine sediments following an oil spill, the substrate was initially colonized by shallow-dwelling opportunistic species. Sediments that are chronically contaminated by petroleum hydrocarbons are characterized by shallow communities that are restricted to surface sediment layers (0-5 cm) (Diaz et al. 1993). Dauer (1993) and Dauer et al. (1992) have shown that low dissolved oxygen and sediment contamination in the lower Chesapeake Bay resulted in macrobenthic communities characterized by shallow-dwelling

opportunistic species and a decrease in deep-dwelling biomass, as well. Hypoxia and anoxia events cause a shallowing of the sediment redox potential discontinuity (RPD), forcing the benthic community to concentrate in surface sediment layers (Ankar and Jansson 1973; Pearson and Rosenberg 1976). A shallowing of the infauna is not always the result of changes in species composition of macrobenthic assemblages. Diaz et al. (1992) demonstrated that short-term reductions in dissolved oxygen can cause the resident infauna to move to the sediment surface in response to the stress.

Studies investigating natural changes in the vertical distribution of macrobenthos within the sediment column are necessary for understanding the effects of the benthic community on sediment biogeochemical processes and benthic-pelagic coupling, designing benthic sampling programs, and using vertical distribution as a measure of environmental health. Dauer et al. (1987) demonstrated that macrofauna penetrate deeper in sand than in mud, and Dauer (1993) showed that communities in higher salinity habitats (>5 ppt) have a higher percentage of deeper-dwelling biomass. Hines and Comtois (1985) and Schaffner (1990) demonstrated seasonal changes in vertical distribution profiles, and differences associated with population size structure. Seasonal differences in vertical distributions are most likely related to recruitment events, as smaller individuals will not penetrate into the sediments as deep as larger individuals (Clavier 1984; Diaz et al. 1992). Organism abundances, species richness, and penetration depth of macroinfauna have also been positively

correlated with the presence of some large, bioturbating, deep burrow-dwelling organisms in the community (Flint and Kalke 1986; Schaffner 1990). Lastly, individuals within a species, most likely those which are adults, appear to "prefer" a particular depth range within the sediment (Sun and Dong 1985; Weston 1990).

In this study, an attempt was made to better understand the natural variability of infaunal distributions within sandy mud habitats of a relatively unimpacted estuary. Sandy-mud sediments are very common in estuaries, making the communities associated with them very important to ecosystem function. The high percent silt and clay of these habitats binds readily to organic compounds and other toxicants and is positively correlated with sediment organic content (Boesch 1971; Dauer et al. 1989; EPA 1991). Understanding the natural dynamics of these habitats is, therefore, useful for environmental monitoring programs which may focus on the assessment of communities in more fine-grained sediments where exposure to anthropogenic stress will most likely be greatest. Some of the factors investigated for explaining natural variation in the distribution of macrobenthic invertebrates within these sediments included organism behavior, physical environmental variability, variations in basic community measures, community trophic structure, and living positions.

Hypotheses tested included:

H_{01} : Estuarine organisms do not exhibit fidelity to a particular depth range within the sediment column.

- H₀₂: The vertical distribution of a species does not change between different salinity habitats (i.e. there are not behavioral differences within a species between different salinity habitats when anthropogenic stress is relatively low).
- H₀₃: The vertical distribution of community abundance and biomass is not different across salinity (i.e. changes in community composition do not cause changes in vertical distribution profiles when anthropogenic stress is relatively low).
- H₀₄: The vertical distribution of macrobenthic assemblages cannot be explained by natural physical environmental factors such as salinity, water depth, or sediment organic content/quality.
- H₀₅: The vertical distribution of macrobenthic assemblages cannot be explained by community measures such as the abundance, number of species, or sizes of organisms that make up the community.
- H₀₆: The vertical distribution of infauna cannot be explained by trophic structure or living positions of organisms that make up macrobenthic communities.

Pearson and Rosenberg (1976, 1978) defined 2 cm to be the maximum depth of penetration of transitional macrobenthic assemblages between grossly polluted and more stable minimally

impacted assemblages. Pioneer species which colonize and dominate disturbed environments usually construct tubes 1-2 cm long near the sediment surface (Rhoads et al. 1985). Therefore, this study focused on understanding the natural variation in vertical distribution patterns of organisms relative to this sediment depth. Patterns were only analyzed to a depth of 10 cm in the sediment because studies have shown that the majority of individuals in estuaries are found in the top 10 cm of sediment (Holme 1964; Lie and Pamatmat 1965; Rosenberg 1974; Meyers 1977; Spies and Davis 1979; Clavier 1984; Hines and Comtois 1985; Rhoads et al. 1985; Sun and Dong 1985; Flint and Kalke 1986; Dauer et al. 1987; Dauer et al. 1989; Schaffner et al. 1987; Weston 1990). Even in deeper marine habitats, most individuals and biomass can be collected in the first 10 cm of the sediment column (Jumars and Hessler 1976; Richardson et al. 1985). In freshwater habitats, maximum penetration is even shallower (Alekperov 1984). Once natural patterns are understood better, vertical distributions may be used more effectively for assessing environmental health.

STUDY SITE - THE YORK RIVER, VIRGINIA

The study was conducted in the York River, a subestuary in the lower Chesapeake Bay (Figure 2). The mainstem of the York River is about 35 miles long, covers an area of 29.86 mi² (77.4 km²), and drains an area of 2650 mi² (Virginia Water Control Board 1991). Its bathymetry is mostly shoals less than 9 m deep with a natural central channel, 9-25 m deep (Pritchard 1967). The shoals consist

of muddy sand, and mud is found in the channel (Pritchard 1967). Sampling sites had depths ranging from 6-18 m (mean=10 m) and were characterized by sandy mud.

The York River is classified as a moderately stratified estuary (Pritchard 1967), with periodic destratification events (Haas 1977). Salinity along the estuary generally ranges from 5-26 ppt, and annual temperature ranges from 2-32° C (Virginia Water Control Board 1991). The tide range averages 0.7 m. Tidal currents in the lower estuary only reach a maximum of about 0.3 m/s, but tidal currents in the upper estuary are much stronger, reaching as high as 0.8 m/s in the channel (Schaffner 1997).

The York River watershed is largely rural and relatively unaffected by industrial activity. The estuary receives a total of 584 tons of nitrogen and 91 tons of phosphorus annually. There are four point sources of pollution along the estuary: a paper pulp mill at confluence of the Pamunkey and Mattaponi Rivers; a Naval Weapons Station in the lower estuary just above the York River bridge; an oil refinery in the lower estuary below the York River bridge; and an electricity generation plant, also in the lower estuary below the York River bridge. The presence of the oil refinery has contributed to the low levels of PAHs in the sediments. Non-point sources of pollution include agriculture and residential sanitary systems. Most (~65%) organic input is from non-point sources (Virginia Water Control Board 1991; Dauer et al. 1989).

The lower York River predictably experiences short-term

hypoxia at depths > 9 m during the summer (Diaz et al. 1992). This has not caused a significant change in benthic community health as reflected in community abundance, biomass and composition (Dauer et al. 1992; Dauer 1993).

METHODS

Benthic samples were collected from 24 randomly selected sites (Figure 2) between May 29 and June 2, 1992. The coordinates and water depth of each site are provided in Appendix A. Only sandy-mud habitats were sampled, as determined by rubbing some of the sediment sampled between two fingers.

Three samples were taken at each site using 225 cm² Wildco box core. The penetration depth of the sampling device was generally 20 cm. A subsample was obtained from each of the first two box cores at each station for sediment grain size and organic content analyses. These subsamples were taken from the top 5 cm of sediment with a 2.5 cm diameter core tube, maintained on ice, and then frozen until analyses were performed. Every box core was subsampled with a 10 cm long 8.8 cm diameter (60.8 cm²) PVC core, which was sectioned into two strata (0-2 and 2-10 cm) to determine vertical distribution patterns of organisms within the sediment column. The top 2 cm of each subcore was sieved through a 0.5 mm mesh nested in a 0.25 mm mesh. The 0.25 mm sieve was used to collect smaller and newly recruited individuals. The 2-10 cm portion of the subcore and the remainder of the box core were sieved through a 0.5 mm mesh. Material retained on each sieve was

fixed in a 10% solution of buffered formalin containing rose bengal stain to facilitate sorting.

In the lab, organisms were sorted, identified to the lowest practical taxonomic level, and counted. Selected dimensions were measured on all individuals (Appendix B). A different dimension was measured for each species, and dimensions were selected based on what was thought to be the least variable and easiest to measure. Whole individuals were dried to constant weight at 55° C (24-48 hr) and ashed for four hours at 550° C. Ash-free dry weights were calculated from the data, and size-weight relationships were determined. Sample biomasses were estimated using the size-weight regressions obtained. This method provided a more accurate estimate of sample biomass. Usually when macrobenthic samples are processed, some organisms are fragmented and body parts are lost, causing biomass to be underestimated if it is measured directly. When size-weight regressions could not be determined for a species due to inadequate data, ash-free dry weights for the organisms were added directly to sample biomass.

Biological data collected for each box core sample included species composition and abundances, biomass:abundance ratios, the number of individuals retained on a 0.5 mm mesh (abundance), the number of individuals retained on a 0.25 mm mesh (small individuals/recruits), the number and biomass of organisms in each vertical stratum (0-2 and 2-10 cm) retained on a 0.5 mm mesh, trophic structure (numbers of predators, omnivores, filter feeders, surface deposit-feeders, subsurface deposit-feeders, interface

feeders - organisms that switch between filter feeding and deposit feeding from surface sediments), and living positions of organisms (i.e. burrowing, tube-dwelling, or free-living). The classification of organisms into living position and feeding mode was based on the literature and is outlined in Appendix C.

Spatial and temporal variability in estuarine macrobenthic communities is high, and data sometimes needs to be standardized to make comparisons between sites and/or over time. All vertical distribution data was standardized to proportions of abundances and biomass in the top 10 cm of the sediment column that were found in the top 2 cm for comparability between stations.

Physical and chemical data collected for each station included water depth and salinity 1 m from the bottom (collected at the time of sampling), distance from Tue Marsh Light at the mouth of the York River (estimated from nautical charts; a surrogate for the salinity continuum), apparent color depth of the RPD as determined from sediment profile photographs (Diaz et al. 1993; Rhoads and Germano 1982, 1986) (average of three photographs from each station), organic carbon and organic nitrogen content of the sediment, the atomic carbon:nitrogen (C:N) ratio, and sediment grain size distribution. Biological reworking of the sediments was also noted in sediment profile photographs. Dissolved oxygen was not measured because sampling was conducted before the annual hypoxia event. Organic carbon and organic nitrogen analyses were performed using a Carlo Erba microanalyzer following vapor-phase acidification (Hedges & Stern 1984). The atomic C:N ratio was then

calculated to provide an indication of organic quality. Sediment grain size analysis was performed by wet sieving samples with a 63 um mesh to remove the sand fraction and pipetting the remaining sediment to determine the silt (4 phi - 8 phi) and clay (>8 phi) fractions (Folk 1974).

Numerical classification (cluster analysis) and ordination (principal components analysis) techniques were used to assess similarities between sites sampled. Cluster analysis was performed on species and abundance data using the Bray-Curtis similarity coefficient and flexible sorting with a cluster intensity coefficient $\beta = -0.25$. Organism abundances were log-transformed to reduce the effects of dominance (Boesch 1977). Principal components analysis was performed on physical and chemical data to group stations based on physical and chemical variables and infer which of the environmental variables measured may be influencing organism distributions.

Univariate analyses of physical and biological variables were performed to determine significant differences between different station groups. Trends in the physical, chemical and biological data along the length of the estuary were assessed by linear regression analysis. Transformations were applied as appropriate.

A Mann-Whitney Rank Sums test was used to compare vertical distribution of abundances and biomass between the upper and lower estuary, and Wilcoxon Signed Rank Tests were used to determine differences in abundance within a species between surface (0-2 cm) and deeper (2-10 cm) sediment layers. Chi-square analysis of the

relative abundances of individuals in the top 2 cm and in 2-10 cm of sediment were performed to determine differences in the vertical distribution of dominant species between the upper and lower estuary. Wilcoxon paired sample tests were applied to determine if selected groups of organisms had a significant influence on vertical distribution patterns observed.

Lastly, stepwise logistic regressions were performed on abundance data and stepwise general regressions were performed on biomass data to determine which recorded variables may explain patterns of vertical distribution within the top 10 cm of the sediment column and to formulate models explaining vertical distribution patterns. Actual data was used for formulating logistic regression models. General linear models were developed using arcsine square root-transformed proportions of biomass in surface sediment layers.

RESULTS

Physical and Chemical Data

The Principal Components Analysis revealed that there are two station groups that differ in their physical and chemical parameters (Figure 3). Stations 1-6 and 8-10 fell into a lower estuary, polyhaline (18-30 ppt salinity) group, and stations 7 and 11-24 fell into an upper estuary, mesohaline (5-18 ppt salinity) group. The first two principal components explained 72% of the variability in the data. In descending order of importance, salinity, atomic carbon:nitrogen ratios, water depth, and sediment

carbon content (principal component I) together were most responsible for differences between stations, explaining 50% of the variability. Silt and clay content of the sediment, depth of the RPD, and sediment carbon content (principal component II) together were of secondary importance. Station 7 was probably grouped with the upper estuary stations due to its slightly lower organic quality, shallower water depth, and higher sediment organic carbon content as compared with other lower estuary stations. Its C:N ratio was 9.87 while the other lower estuary stations ranged from 6.58-8.94, organic carbon content of the sediment was 18.44 mg/g as opposed to 7.53-17.95 mg/g, and sandy mud habitat at this station was in 7.3 m of water, which is slightly shallower than the range of 8.8-18.0 m for the other lower estuary stations.

Physical and chemical data for all sampling sites are presented in Table 1 and Appendix D. Salinity throughout the York River at the time of sampling ranged from about 5-24 ppt, low mesohaline to low polyhaline based on the Venice system of classification (Remane and Schlieper 1971). Water depth of the sample stations ranged from 5-18 m, and decreased significantly with distance from the mouth of the estuary as the target habitat became shallower (Figure 4a; $p=0.0027$, $r^2=0.34$). The difference in water depth between upper estuary station group and lower estuary station group was also significant ($t=3.69$, $p=0.0013$).

As expected, the sediment habitat sampled was similar throughout the estuary, averaging 76% silt and clay and 24% sand ($sd=12.8\%$). There was a significant decrease in the percent silt

and clay content of the sediment up estuary (Figure 4b; $p=0.0462$, $r^2=0.18$) and a significant difference silt and clay content of the sediment between the upper and lower estuary station groups ($T=154.0$; $p=0.0111$). Due to the nature of muddy sediments, the depth of the apparent color RPD was expected to be consistently shallow throughout the sandy-mud habitat. The average depth of the RPD was 0.7 cm and ranged from 0.1-2.3 cm. No significant trend was observed along the length of estuary (Figure 4c; $p=0.2504$), and there was no difference in depth of the RPD between the upper and lower estuary groups ($t=-1.28$; $p=0.2138$).

Organic carbon and organic nitrogen content of the sediment both increased significantly with increasing distance from the mouth of the estuary (Figure 4d and 4e; $p_{\text{carbon}} < 0.0001$, $r_{\text{carbon}}^2 = 0.51$; $p_{\text{nitrogen}} = 0.0073$, $r_{\text{nitrogen}}^2 = 0.28$). This trend was expected due to the greater industrial and terrestrial inputs further upstream. Sediment carbon throughout the estuary ranged from 7.53-27.36 mg/g ($\bar{x}=19.32$) and sediment nitrogen ranged from 0.9-3.16 mg/g ($\bar{x}=2.42$). Sediment carbon was significantly higher at the upper estuary stations as compared with the lower estuary stations ($T=69.0$; $p=0.0012$). However, sediment nitrogen was not significantly different between the upper and lower estuary station groups ($t=-2.00$; $p=0.0581$), most likely because of the low nitrogen content of the sediment at station 17 (0.90 mg/g). The atomic carbon:nitrogen ratio ranged from 6.58-10.82 mg/g ($\bar{x}=9.27$), and there was a significant increase in the C:N ratio with increasing distance from the mouth of the estuary (Figure 4f; $p=0.0001$, $r^2=0.50$), indicating

that organic quality decreased and sediment organic material became more refractory. Organic quality at lower estuary stations was significantly higher than that at the upper estuary stations ($T=70.0$; $p=0.0014$).

There was a general lack of biological sedimentary structures such as feeding voids and burrows in the sediment profile photographs. The apparent color RPD was consistently shallow, and sediment strata appeared to be undisturbed. This trend was more apparent for the upper estuary stations than for the lower estuary stations.

General Biological Data

Seventy-six taxa, most at the species level, were identified in the 9,664 individuals collected from the York River sandy-mud habitat (Appendix E). Annelids comprised 55% of the organisms, followed by arthropods which accounted for 22% (only 1 species was non-crustacean). Mollusks made up 9% of the total number of organisms collected, most being bivalves. Organisms collected were typical of those collected from the York River during previous studies (Boesch et al. 1976; Diaz 1984; Zobrist 1988; Diaz et al. 1992; Dauer et al. 1989).

The cluster analysis defined two distinct station groups based on species composition and abundances (Figure 5). Stations were divided into polyhaline (18-30 ppt) and mesohaline (5-18 ppt) assemblages, and stations within each group generally exhibited 45% similarity or higher in species composition and abundance (see

Appendix F for similarity matrix). Even though stations 11 and 12 were grouped with the lower estuary stations in the cluster analysis, evaluation of species composition revealed that these two stations could have been classified as either upper or lower estuary stations.

General biological data are presented in Table 2. The data presented only represent organisms retained on a 0.5 mm mesh. The number of organisms collected in each 225 cm² sample ranged from 16-192 (\bar{x} =69). Due to the high variability in abundances along the length of the estuary, no significant trend was observed (Figure 6a; $p=0.2336$). However, abundances were significantly higher in the lower estuary as compared with the upper estuary ($T=162.0$; $p=0.0326$). The number of species collected at each station ranged from 9-39, and decreased significantly with distance up estuary (Figure 6b; $p<0.0001$, $r^2=0.58$). The number of species peaked at the break between the polyhaline and mesohaline reaches of the river, and there were significantly more species collected in the lower estuary ($t=6.22$; $p<0.0001$). Lastly, organism biomass per sample ranged from 0.700-18.77 mg ash-free dry weight (\bar{x} =6.99). (Length-weight regressions that could be calculated are presented in Appendix G.) No significant trend along the estuary was observed (Figure 6c; $p=0.6518$), and there was no difference between upper and lower estuary stations ($t=0.188$; $p=0.8526$). In the mesohaline reaches of the York River, the tellinid bivalve *Macoma balthica* contributed to most of the biomass and biomass variability observed. When these larger-bodied

organisms were eliminated from biomass estimates, the biomass per station decreased significantly along the length of the estuary (Figure 6d; $p=0.0006$, $r^2=0.42$), and biomass at lower estuary stations was significantly higher than at upper estuary stations ($t=3.61$; $p=0.0015$).

Numerical dominants were defined as those taxa which contributed greater than 2% of all organisms collected. The dominant organism throughout the estuary was the cumacean *Leucon americanus*, although most of the dominants were annelid polychaetes. Several community dominants were similar for the upper and lower estuary. However, the relative dominance and importance of species differed. Those organisms that comprised 80% of the community for the upper estuary, lower estuary, and both the upper and lower reaches combined are listed in Table 3a-c. The degree of dominance was higher for the lower salinity reaches of the estuary, fewer species accounting for a higher percentage of individuals, while the distribution of abundances across species was more even for the higher salinity community. At least eleven species contributed to 75% of total numbers of individuals in the lower estuary, while only about five contributed to 75% of total abundance in the upper estuary.

Vertical Distribution

The first two hypotheses tested were 1) whether infaunal species exhibited a preference for a particular depth range in the sediment, and 2) whether there were differences in the vertical

distribution of a species between habitats. Because many of the species collected did not occur in high enough abundances in the subcores to assess differences in vertical distribution patterns between habitats, only the dominant species in the estuary were analyzed.

Table 4a-c presents the relative percentages of the dominant species collected in the 0-2 cm and 2-10 cm depth strata. Only organisms collected on a 0.5 mm mesh were considered because the 2-10 cm depth stratum was not processed with a 0.25 mm mesh. About half of the dominants in the lower estuary reaches appeared to utilize the top 2 cm of sediment more, while most of the others utilized the 2-10 cm sediment depths more. In the upper estuary, only one species, *Leucon americanus*, utilized surface sediments more than the deeper sediment layers. This indicated a more even distribution of organisms within the sediment column in the polyhaline reaches. The surface deposit-feeding cumacean *Leucon americanus* is epibenthic and was found almost exclusively in surface sediments. The deep-dwelling bivalve *Macoma balthica* and *Tubificoides* spp. oligochaetes are generally found deeper than 10 cm (Dauer et al. 1989), and the few individuals collected in the subcores were probably younger, smaller organisms.

Species were tested for significant differences in abundance distributions between the two depth strata by Wilcoxon Signed Rank Tests. Some tests were not performed due to low abundances or because the species was not found throughout the estuary. The subsurface deposit-feeding polychaetes *Leitoscoloplos* spp.,

Clymenella torquata and *Notomastus latericeus*, deep-burrowing predatory nemerteans, and the larger-bodied filter/surface deposit-feeding polychaete *Paraprionospio pinnata*, all of which have life spans of one year or greater, were generally found in deeper sediment layers. The polychaetes *Mediomastus* spp., *Streblospio benedicti*, *Sigambra tentaculata*, and *Glycinde solitaria* did not have significantly higher abundances in one depth stratum over the other. *Mediomastus* spp. and *S. benedicti* seemed to be more abundant in surface sediments, but differences were not significant due to variability between stations. *S. tentaculata* and *G. solitaria* are both motile, free-burrowing predators, and their distributions were variable. Both were found in approximately equal abundances in the 0-2 and 2-10 cm sediment layers. The smaller-bodied, short-lived, opportunistic, surface deposit-feeding polychaetes *Mediomastus* spp., *Asabellides oculata* and *S. benedicti* all appeared to occur in higher abundances in surface sediments. So, it appears that vertical distribution patterns of the York River dominants are generally related to body size and/or life history strategy, living position, and feeding mode.

Vertical distribution profiles for most dominant species were the same between station groups (upper vs. lower estuary) (Table 5). Only *Mediomastus* spp. and *Streblospio benedicti* showed differences in vertical distribution across habitats. Both populations were significantly deeper in the upper estuary.

The third hypothesis tested was whether there were differences in vertical distribution patterns of abundance and biomass between

polyhaline and mesohaline communities. Figure 7 shows the proportion of individuals in the top 2 cm of the sediment column relative to the top 10 cm of sediment throughout the York River. No individuals were collected from the top 2 cm of sediment at station 18, possibly due to a recent or continuous physical disturbance at this station. None of the physical variables appeared to be unusual for this type of habitat. Station 18 was one of the shallowest stations, however, and therefore more prone to physical disturbance and the swift tidal currents in the upper York River. Sediment profile images revealed that the sediments were less compact, resulting in higher penetration of the camera into the sediment, indicating that sediments may have recently been suspended. Lowest organism abundances occurred at station 18, most of the organisms collected were burrowers (65%), and only four organisms were collected in all three subcores, also suggesting that this station was recently or continuously disturbed.

The vertical distribution of individuals along the York River estuary was highly variable. Variability between stations was significantly higher in the upper estuary relative to the lower estuary ($F=11.09$, $p<0.001$). Spatial variation in benthic abundances was generally higher in the upper estuary, as well. At lower estuary polyhaline stations, 32-68% of the individuals collected in the top 10 cm of sediment were found in the upper (0-2 cm) sediment layers ($\bar{x}=52.2\%$, $sd=10.4\%$). At upper estuary mesohaline stations, 0-88% of the individuals were found in the upper sediment layers ($\bar{x}=47.7\%$, $sd=28.9\%$). There was no

significant difference in the vertical distribution of individuals between the upper and lower estuary communities ($T=129.5$, $p=0.810$).

Further investigation of the large variation between stations in the upper estuary indicated that the variation in the abundances of the surface-dwelling cumacean, *Leucon americanus*, was the main cause for the large fluctuations in the proportion of individuals found in the top 2 cm of sediment. *L. americanus* was present in extremely high numbers in the mesohaline portion of the York River, but its distribution was also very patchy. When *L. americanus* was eliminated from the analysis (Figure 8), there was a significant difference in the mean percentage of individuals in surface sediments between the upper ($\bar{x}=20.5\%$) and lower ($\bar{x}=51.0\%$) estuary ($t=5.07$, $p<0.0001$), and a significant decrease in the proportion of individuals found in surface sediments along the length of the estuary ($p=0.0020$, $r^2=0.36$). Between station variability in the percentage of individuals in the top 2 cm of sediment was also still significantly different between the two communities. However, the difference between the upper ($sd=17.6\%$) and lower ($sd=10.6\%$) reaches was not as large ($F=5.57$, $p<0.01$). *L. americanus* was the top dominant in the upper estuary, making up 30.2% of total abundances, but was only the 11th dominant in the lower estuary, making up 2.0% of total abundances. It is an epibenthic crustacean which takes refuge by burrowing into the very surface layers of sediment, and was the only organism present in significantly higher abundances in surface sediments (0-2 cm) relative to deeper sediment layers in the mesohaline community. A

pairwise comparison of proportions of individuals in surface sediment with and without *L. americanus* indicated that the cumacean had significant effects on vertical distribution patterns of the mesohaline community ($t=4.13$; $p=0.0012$), while the vertical distribution of the polyhaline community was unaffected (Table 6a; $W=15.0$, $p=0.0625$). Therefore, abundances of this dominant organism had a very large influence on the vertical distribution patterns of individuals in the upper estuarine community.

The dominant group of organisms in both communities was the annelids. Annelids made up 73% of abundances in the lower estuary polyhaline community and 40% of abundances in the upper estuary mesohaline community. The vertical distribution of annelids is presented in Figure 9. When only the annelid component of the benthic community was considered, 49.8% (sd=10.9%) of the individuals in the top 10 cm of sediment were found in surface layers (0-2 cm) in the lower estuary, and only 11.6% (sd=12.6%) were found in surface layers in the upper estuary, indicating that the majority of annelid species in the upper estuary live deeper in the sediments. This trend was supported in the previous analysis of vertical distribution patterns which indicated that *L. americanus* was the only organism present in higher abundances in surface sediments relative to deeper sediment layers. The proportion of annelids in surface sediments was significantly higher in the polyhaline reaches than the mesohaline reaches ($T=194.5$, $p<0.0001$), and there was a significant decrease in the proportion of surface-dwelling annelids along the length of the

estuary ($p < 0.0001$, $r^2 = 0.52$). A pairwise comparison of vertical distribution patterns of the whole community with annelid vertical distributions showed significant differences for the upper estuary stations but not for the lower estuary stations (Table 6a; $T_{\text{lower}} = 36.5$, $p_{\text{lower}} = 0.098$; $T_{\text{upper}} = 90.0$, $p_{\text{upper}} = 0.0005$). Results indicated that annelids were not largely responsible for organism abundances in surface sediment layers in the mesohaline reaches of the estuary.

Like the vertical distribution of individuals, the vertical distribution of community biomass along the York River was highly variable (Figure 10). The proportion of biomass in the top 10 cm of sediment found in 0-2 cm ranged from 6-53% in the lower estuary ($\bar{x} = 31.7\%$, $sd = 19.2\%$) and from 0-63% in the upper estuary ($\bar{x} = 27.1\%$, $sd = 19.5\%$). There was no significant difference in the vertical distribution of biomass or between station variability between the upper and lower estuary station groups ($T = 133.0$, $p = 0.661$; $F = 1.622$, $p = 0.409$).

The bivalve *Macoma balthica* was a dominant organism in the upper estuary. Because of its larger body size and biomass and deeper living position, its influence on vertical distribution patterns was analyzed. Eliminating bivalve biomass from the analysis of biomass distribution within the top 10 cm of sediment had little influence on results (Figure 11). The proportion of biomass in the top 2 cm of sediment increased slightly at a few stations, however, the differences in vertical distribution between the upper and lower estuary still were not significant. Pairwise

comparisons of the vertical distribution of community biomass with and without bivalves indicated that bivalves did have a significant effect on vertical distribution patterns in the upper estuary (Table 6b; $T=28.0$, $p=0.0156$), and significantly contributed to deeper biomass.

Again, because annelids dominated the upper and lower estuary communities, the distribution of annelid biomass within the sediment column was analyzed separately (Figure 12). An average of 26.7% (sd=18.8%) of annelid biomass in the top 10 cm of sediment was found in surface layers (0-2 cm) at lower estuary polyhaline stations, and an average of only 7.9% (sd=10.6%) was found in surface sediments at upper estuary mesohaline stations. Vertical distribution patterns between the upper and lower estuary were significantly different ($T=171.0$, $p=0.0077$), and the proportion of annelid biomass found in 0-2 cm of sediment decreased significantly along the length of the estuary ($p=0.0070$, $r^2=0.29$), just as annelid abundances did. Pairwise comparisons between community biomass distributions and annelid biomass distributions indicated that in the lower estuary the proportion of biomass in surface sediment layers was not significantly affected when non-annelid taxa were eliminated from the analysis. However, proportions of biomass in surface sediments in the upper estuary were significantly lower when only annelids were considered (Table 6b; $T_{\text{lower}}=14.0$, $p_{\text{lower}}=0.193$; $T_{\text{upper}}=84.0$, $p_{\text{upper}}=0.0046$).

Regression Models

In an attempt to explain factors which may be influencing vertical distribution patterns in the York River, the relative proportions of abundance and biomass in the 0-2 and 2-10 cm depth strata were regressed on physical and biological variables measured. Models of the distribution of individuals predicted expected patterns such that:

$$\log(p_{0-2\text{cm}}/p_{2-10\text{cm}}) = \text{intercept} + x_1 \cdot \text{var}_1 + x_2 \cdot \text{var}_2 + \dots + x_n \cdot \text{var}_n$$

where $p_{0-2\text{cm}}$ and $p_{2-10\text{cm}}$ are the proportions of individual or biomass found in the top 2 cm of sediment and in 2-10 cm of sediment and var_1 through var_n are the environmental parameters measured and tested for entry into the models. Models of the distribution of biomass predicted expected patterns such that:

$$\arcsine(\sqrt{p_{0-2\text{cm}}}) = \text{intercept} + x_1 \cdot \text{var}_1 + x_2 \cdot \text{var}_2 + \dots + x_n \cdot \text{var}_n$$

Models were formulated for the whole estuary as well as for the upper and lower estuary communities.

Physical variables tested for entry into the models included the dummy variable group (GP), which separated upper from lower estuary stations (tested for models of the whole estuary only), distance from the mouth of the estuary (DIST), which may be a surrogate for the salinity gradient or other gradients along the length of the estuary, water depth (DEP), organic carbon content of the sediment (C), and the atomic ratio of organic carbon to organic nitrogen (C:N), which indicates organic quality. Organic nitrogen content of the sediment was not tested because it was highly correlated with organic carbon. Percent silt and clay content of

the sediment was not tested because this variable was controlled for by sampling sandy-mud habitat only. Results of the grain size analysis indicated that samples collected could acceptably be classified in this category (Shepard 1954; Ranasinghe et al. 1992). Lastly, depth of the RPD was not tested. Depth of the RPD was less than 2 cm at all stations except station 14 (2.3 cm). This means that the influence of this variable would be within the top 2 cm of sediment, and samples were sectioned at 2 cm.

Biological variables tested included the dummy variable group (GP) which separated upper from lower estuary communities (tested for models of the whole estuary only), the number of species collected in each 10 cm subcore (SPP), the number of macrofauna collected on the 0.25 mm sieve (SM), which may indicate recruitment of smaller individuals to the community, the total number of organisms collected in each 10 cm subcore retained on a 0.5 mm sieve (N), the total number of organisms collected in the 0-2 cm fraction of each sample retained on a 0.5 mm sieve (NTOP; tested for biomass models of the whole community only), the total number of organisms collected in the 2-10 cm fraction of each sample (NBOT; tested for biomass models of the whole community only), the mean weight per individual collected in the 0-2 cm fraction of each sample retained on a 0.5 mm sieve (XWTTOP; tested for biomass models of the whole community only), the mean weight per individual collected in the 2-10 cm fraction of each sample (XWTBOT; tested for biomass models of the whole community only), and SMAN, NAN, NANTOP, NANBOT, XWTANTOP, and XWTANBOT which are the

equivalents of the previous six variables for the annelid portion of the community (tested for annelid biomass models only). Feeding groups tested for entry into models of vertical distribution of community abundances included the number of predators (P), omnivores (O), filter feeders (FF), surface deposit-feeders (SDF), subsurface deposit-feeders (SSDF), and interface feeders (organisms that alternately filter feed and feed on surface sediments) collected in each 10 cm subcore. Living positions tested included numbers of burrow-dwelling (B), tube-dwelling (T), free-living/actively burrowing (FL), and epibenthic (E) organisms collected in each 10 cm subcore. Table 7 provides a concise list of all variables tested for entry into the models.

When the log odds of individuals in the top 2 cm of sediment was regressed on both physical and biological variables, the best model obtained contained explanatory variables which entered into the model at or below the 0.1 significance level ($p=0.0001$) such that:

$$\log(p_{0-2}/p_{2-10}) = 3.43 - 0.71*GP + 0.05*DIST - 0.33*C:N \\ - 0.001*N + 0.01*SM - 0.06*SPP.$$

However, when observed and expected proportions in 0-2 cm were plotted together with the 95% confidence interval (Figure 13a), the data fit the model very poorly. Because the dummy variable group entered significantly into the model, separate analyses were conducted for the upper and lower estuary station groups, as different variables may influence vertical distributions of organisms between the two communities. The best model for the

lower estuary included explanatory variables which entered at or below the 0.2 significance level, such that:

$$\begin{aligned} \log(p_{0-2}/p_{2-10}) = & 4.25 + 0.20*DIST - 0.18*DEP \\ & - 0.22*C - 0.01*SM \quad (p=0.0003). \end{aligned}$$

The best model for the upper estuary contained explanatory variables which entered at or below the 0.1 significance level such that:

$$\begin{aligned} \log(p_{0-2}/p_{2-10}) = & 8.08 - 0.23*DEP - 0.63*C:N \\ & - 0.02*N + 0.02*SM \quad (p=0.0001). \end{aligned}$$

The fit of the data to the models obtained through separate analyses was much better, as more data points fell within the 95% confidence interval of values predicted by the model, and the data followed the trend of the model better (Figure 13b). However, the model for the upper estuary still did not explain vertical distributions of organisms within the sediment very well.

Because the physical environment has such a large influence on biological variables, separate logistic regressions were run on the physical and biological variables. The dummy variable "group" was tested as both a physical and biological variable, representing either the polyhaline and mesohaline reaches of the estuary or the upper and lower estuary communities respectively. When proportions of individuals in the 0-2 and 2-10 cm depth strata at all stations were regressed on physical variables, the best model contained those variables which entered at or below the 0.1 significance level, such that:

$$\log(p_{0-2}/p_{2-10}) = 2.04 - 0.49*GP + 0.04*DIST - 0.07*DEP -$$

$$0.018 * C:N \quad (p=0.001).$$

Again, because the data fit the model so poorly (Figure 14a) and because the dummy variable group was significant, the vertical distribution patterns in upper and lower estuary were analyzed separately. The best model for the lower estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p0-2/p2-10) = 3.26 + 0.19 * DIST - 0.18 * DEP - 0.18 * C \quad (p=0.0005).$$

The best model for the upper estuary contained variables which entered at the 0.05 significance level such that:

$$\log(p0-2/p2-10) = 15.75 - 0.45 * DEP - 1.22 * C:N \quad (p=0.0001).$$

The data fit the model very well for the lower estuary but fit the model for the upper estuary poorly (Figure 14b).

When vertical distribution patterns at all stations were regressed on the biological variables, the best model obtained contained variables entering at or below the 0.05 significance level such that:

$$\log(p0-2/p2-10) = 0.51 - 0.01 * N + 0.01 * SM - 0.03 * SPP \quad (p=0.0001).$$

The data fit the model poorly (Figure 15a), and although the dummy variable group did not enter significantly into the model, individual analyses for the upper and lower estuary were still conducted. No significant model which contained only biological variables was obtained for the lower estuary. The model for the upper estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p0-2/p2-10) = 0.14 - 0.02 * N + 0.02 * SM \quad (p=0.0001).$$

This provided the best data fit of all the models for the upper estuary, being the only one that actually followed the same trend as the data (Figure 15b).

The analysis of the vertical distribution of dominants indicated that the depth in the sediment column at which organisms are found may be related to living position (i.e. tube-dweller, burrow-dweller, active burrower or epibenthic) and feeding mode (i.e. filter-feeder, surface deposit-feeder, subsurface deposit-feeder or predator). Therefore, proportions of individuals in 0-2 and 2-10 cm depth strata were regressed on functional groups. When vertical distribution patterns were regressed on feeding mode, the best model contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = 1.00 - 0.42*P - 0.60*FF - 0.33*SDF + 0.23*SSDF - 0.52*I \quad (p=0.0001).$$

The data fit the model very poorly (Figure 16a). When separate analyses were performed for the upper and lower estuary, the best model obtained for the lower estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = 0.06 + 0.37*P - 0.61*O + 0.73*FF - 0.20*SDF - 0.08*SSDF \quad (p=0.0001).$$

The best model for the upper estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = -1.73 + 0.37*P - 0.63*FF - 0.09*SDF + 0.20*SSDF \quad (p=0.0001).$$

Conducting separate analyses for the upper and lower estuary did not provide better models for explaining trends in the

data (Figure 16b). In fact, trends were actually opposite of what the models predicted, and some correlations of vertical distribution patterns with functional groups were opposite of what was expected.

When vertical distribution patterns were regressed on living positions, the best model for the whole estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = -1.15 + 0.27*B - 0.07*T - 0.10*E \quad (p=0.0001).$$

Once again, the data fit the model very poorly (Figure 17a), and separate analyses were performed for the upper and lower estuary stations. The best model for the lower estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = 0.12 + 0.01*B - 0.001*T \quad (p=0.0001).$$

The best model for the upper estuary contained variables which entered at or below the 0.05 significance level such that:

$$\log(p_{0-2}/p_{2-10}) = 0.17 - 0.01*B - 0.01*E \quad (p=0.0001).$$

Again, developing separate models for the upper and lower estuary did not improve the predictive value of the models (Figure 17b). Data trends were opposite of what was predicted by the models, and some correlations were opposite of what was expected.

Stepwise general linear regressions were run on transformed proportions of biomass in 0-2 cm of sediment to determine which variables may be influencing vertical distribution patterns of macrobenthic biomass within the top 10 cm of sediment. All models developed contained only variables which entered at or below the 0.05 significance level.

The model with both physical and biological variables was

$$\arcsine(\sqrt{p0-2}) = 1.0541 - 0.0226*C + 0.0226*NTOP - 0.0359*NBOT$$

$$(p < 0.0001, r^2 = 0.34).$$

The fit was mediocre and but better for lower than upper estuary stations (Figure 18a). The separate model for lower estuary was:

$$\arcsine(\sqrt{p0-2}) = 0.8265 - 0.0276*NBOT \quad (p = 0.0038, r^2 = 0.28).$$

The model for the upper estuary was:

$$\arcsine(\sqrt{p0-2}) = 0.0534 + 0.0227*NTOP - 0.0387*NBOT$$

$$(p = 0.0008, r^2 = 0.32).$$

The predictive value of the models did not improve when separate models were formulated for the two communities (Figure 18b).

Again, physical and biological variables were analyzed separately because of possible interactions. When proportions of biomass in 0-2 cm of sediment were regressed on physical variables, no model was significant. When vertical biomass was regressed on biological variables, the model developed was:

$$\arcsine(\sqrt{p0-2}) = 0.5455 + 0.0203*NTOP - 0.0275*NBOT$$

$$(p < 0.0001, r^2 = 0.29).$$

The data fit to the model was mediocre (Figure 19a). When the upper and lower estuary were analyzed separately, the model obtained for the lower estuary was:

$$\arcsine(\sqrt{p0-2}) = 0.8265 - 0.0276*NBOT \quad (p < 0.0038, r^2 = 0.28).$$

The model for the upper estuary was:

$$\arcsine(\sqrt{p0-2}) = 0.5336 + 0.0227*NTOP - 0.0378*NBOT$$

$$(p=0.0008, r^2=0.32).$$

The fit of the data to the two separate models was not improved (Figure 19b). In fact, data fit was worse.

Because annelids dominated both the upper and lower estuary communities, vertical distribution patterns of their biomass were modeled separately. When both physical and biological variables were modeled, the model developed was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) &= 0.5210 - 0.2755*GP + 0.0176*NANTOP \\ &- 0.0204*NANBOT + 0.7662*XWTANTOP - 0.2030*XWTANBOT \\ &(p<0.0001, r^2=0.72). \end{aligned}$$

The model predicted vertical distribution of annelid biomass fairly well (Figure 20a). The dummy variable group (GP) was significant, so mesohaline and polyhaline communities were analyzed separately in an attempt to improve the model. The model obtained for the lower estuary was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) &= 0.7334 + 0.0157*NANTOP - 0.0290*NANBOT \\ &+ 0.9952*XWTANTOP - 0.4554*XWTANBOT \\ &(p<0.0001, r^2=0.73). \end{aligned}$$

The model for the upper estuary was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) &= 0.0101 + 0.0419*NANTOP + 0.6628*XWTANTOP \\ &(p<0.0001, r^2=0.82). \end{aligned}$$

Both models developed predicted vertical distribution patterns better than the model for the whole estuary (Figure 20b).

When only physical variables were modeled for explaining patterns in the vertical distribution of annelid biomass, only the dummy variable group (GP) entered into the model significantly such that:

$$\arcsine(\sqrt{p0-2}) = 0.4770 - 0.308*GP \text{ (} p < 0.0008, r^2 = 0.17 \text{)}.$$

As expected, the model had no predictive value (Figure 21a). When patterns in the upper and lower estuary were analyzed separately, no significant models could be developed.

When only biological variables were modeled, the model obtained was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) = & 0.5210 - 0.2755*GP + 0.0176*NANTOP \\ & - 0.0204*NANBOT + 0.7662*XWTANTOP - 0.2030*XWTANBOT \\ & \text{(} p < 0.0001, r^2 = 0.72 \text{)}. \end{aligned}$$

The predictive value of the model was good (Figure 22a). The dummy variable group (GP) entered significantly into the model, so independent models for the upper and lower estuary were developed.

The model developed for the lower estuary was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) = & 0.7334 + 0.0157*NANTOP - 0.0290*NANBOT \\ & + 0.9952*XWTANTOP - 0.4554*XWTANBOT \\ & \text{(} p < 0.0001, r^2 = 0.73 \text{)}. \end{aligned}$$

The model for the upper estuary was:

$$\begin{aligned} \arcsine(\sqrt{p0-2}) = & 0.0101 + 0.0419*NANTOP + 0.6628*XWTANTOP \\ & \text{(} p < 0.0001, r^2 = 0.82 \text{)}. \end{aligned}$$

Again, developing separate models improved their value for predicting vertical distribution patterns of annelid biomass (Figure 22b).

Variables which entered significantly into the models developed and general correlations are summarized in Table 8. Generally, the proportion of surface-dwelling organisms increased along the estuary (DIST) in the polyhaline reaches. There were more organisms deeper in the sediment column at greater water depths (DEP). In the lower estuary, the proportion of shallow-dwelling organisms decreased with increasing organic quality (C:N). As expected, where in the sediment organisms were found was related to body size. The proportion of individuals in surface sediments (0-2 cm) was positively correlated with the abundance of smaller individuals retained on a 0.25 mm mesh (SM and SMAN). There was also a positive correlation of surface-dwelling biomass with the mean weight per individual in 0-2 cm of sediment (XWTTOP and XWTANTOP) and a negative correlation of surface-dwelling biomass with the mean weight per individual in 2-10 cm of sediment (XWTBOT and XWTANBOT). Biomass distributions were correlated with abundances of organisms in each depth range. Relative proportions of shallow biomass increased as the number of individuals in surface sediments (NTOP and NANTOP) increased, and decreased as the number of deeper organisms increased (NBOT and NANBOT). Throughout the estuary, the proportion of individuals in surface sediments decreased as the number of species (SPP) increased.

DISCUSSION

The attempt to target sandy-mud habitat for this study was successful. The difference in sediment type between the upper and

lower estuary station groups, and the decrease in the percent silt and clay content of the sediment was not considered to be great enough to influence benthic community composition (Ranasinghe et al. 1992). Because the RPD in finer sediments is naturally low, there was not significant variation in the RPD across sampling sites. Therefore, other physical and chemical variables were largely responsible for the differences between station groups and the changes in community observed.

Results of the cluster analysis were in keeping with Boesch's (1971) finding that while faunal changes along the length of the York River estuary are gradual and follow an overlapping continuum of assemblages, there is a sharp discontinuity between the polyhaline and mesohaline reaches. Because of this sharp change in community composition, it was reasonable to conduct other analyses which compared and contrasted communities in each region of the estuary, as well as for the entire estuary. Even though the cluster analysis placed sites 11 and 12 in the lower estuary station group, the principal components analysis placed stations 11 and 12 with the upper estuary group. Since it is the physical environmental variables that ultimately drive organism distributions, all other analyses between the upper and lower estuaries were conducted with stations 11 and 12 as upper estuary stations.

Before beginning any discussion of vertical distribution patterns, it must be pointed out that many macrobenthic species do not have fixed living positions, but rather move up and down in

their tubes and burrows within the sediment column. Although macroinfauna may show fidelity to sediment depth ranges (Sun and Dong 1985; Weston 1990), it is not suggested that organisms are restricted to the depth in the sediment at which they were found.

Vertical distribution profiles were similar for the polyhaline and mesohaline communities of the York River estuary. The proportions of individuals and biomass in the top 10 cm of sediment that were found in the surface sediment layers was the same for both the upper and lower estuary. This indicated that a change in the species composition and abundances of a community does not necessarily lead to changes in vertical distribution profiles.

Variability in vertical distribution patterns was higher for the upper estuary, and the organisms influencing vertical distribution patterns were different. Differences in variability between the upper and lower estuary were caused by lower abundances of organisms and numbers of species in the mesohaline community, and the higher degree of dominance in the mesohaline community. One organism was largely responsible for variability in the vertical distribution patterns for the upper estuary. The epibenthic crustacean *Leucon americanus* was the only organism found in significantly higher abundances in 0-2 cm of sediment relative to the 2-10 cm depth stratum. It also exhibited high spatial variability in abundances. Being the top dominant in the mesohaline community, making up 30% of the total abundance, *L. americanus* was responsible for patterns of vertical distribution observed in the upper estuary. Individuals in the polyhaline

community were more evenly distributed over species, and spatial variations in abundances were lower, so vertical distribution patterns observed could not be attributed to any one species.

Abundances of *L. americanus* have also been shown to have a large influence on the vertical distribution of organisms within the sediments of the James River estuary in the lower Chesapeake Bay (Schaffner et al. 1987). Populations of *L. americanus* exhibit high seasonal variability. Abundances peak in the spring and are lowest in the summer in polyhaline habitats, and peak in the winter in mesohaline habitats (Boesch et al. 1976). Because of the higher degree of dominance in the mesohaline portion of the York River, and because *L. americanus* was the top dominant in the upper estuary, mesohaline vertical distribution patterns are expected to vary seasonally. This in turn would result in seasonal variation in food availability to organisms which consume the cumaceans and in the bioturbation of surface sediments caused by these organisms.

In many cases, vertical distribution of biomass within the sediment column can follow a very different pattern from abundance. One or two large individuals can have an overwhelming effect on biomass, especially in less stressed communities where individuals have the opportunity to grow to larger sizes. Variability in biomass patterns was high throughout the estuary. The high variability in the vertical distribution of biomass in the upper estuary was caused in part by the spatial variability of *L. americanus* and in part by the occurrence of the larger-bodied deep-dwelling bivalve *Macoma balthica* in some samples. As already

mentioned, *L. americanus* was the only dominant found in higher abundances in surface sediment layers relative to deeper sediment layers. As many as 150 *L. americanus* (~2200/m²) were collected at one station (0.5 mm mesh). All other dominants were significantly more abundant in the 2-10 cm depth stratum. Therefore, at stations where *L. americanus* was found in low abundances, the majority of community biomass was deeper in the sediment.

The presence of deep-dwelling bivalves caused proportions of biomass in deeper sediment strata to be higher, as well. The influence of *M. balthica* on vertical biomass patterns, however, was not as large as would be expected. Even though the deep-dwelling tellinid bivalve *Macoma balthica* was a dominant in the upper reaches of the estuary, elimination of bivalve biomass from the analysis did not affect results as greatly as expected. *M. balthica* is generally found deeper than 10 cm in the sediment, and the majority of the population was not sampled with the subcores used for determining vertical distribution patterns. So, although studies have shown that the majority of individuals occurs within the top 10 cm of sediment (Holme 1964; Lie and Pamatmat 1965; Rosenberg 1974; Meyers 1977; Spies and Davis 1979; Clavier 1984; Hines and Comtois 1985; Rhoads et al. 1985; Sun and Dong 1985; Flint and Kalke 1986; Dauer et al. 1987; Dauer et al. 1989; Schaffner et al. 1987; Weston 1990), deep-dwelling biomass may be unaccounted for by only sampling to this depth (Weston 1990; Dauer 1993). While low numbers of organisms live in sediments deeper than 10 cm, the organisms which dwell at greater depths are usually

larger individuals which contribute significantly to community biomass.

Patterns of vertical distribution observed for annelid abundances and biomass were similar, possibly indicating low within-station variability in annelid size and body weight throughout the estuary. The lower proportions of annelid biomass in surface sediments in the upper estuary relative to the lower estuary was at least in part due to differences in body size. Many of the numerically dominant annelids in the lower estuary were smaller-bodied, shallow-dwelling species, while those in the upper estuary were larger-bodied, deeper-dwelling species. Annelids contributed significantly to deep-dwelling organisms throughout the estuary, but only contributed significantly to deep-dwelling biomass in the upper estuary. This is because only one organism was found in higher proportions in surface sediment layers in the upper estuary, and that organism was the crustacean *Leucon americanus*. All dominant annelids in the upper estuary were more abundant in deeper sediment layers. Therefore, the cumacean *L. americanus* was responsible for surface-dwelling biomass while annelids were largely responsible for deeper-dwelling biomass. In the lower estuary, many dominant annelids were found in surface sediments, and therefore made a significant contribution to both surface and deep-dwelling biomass.

Vertical distribution patterns within a species were generally the same across salinity habitats. Differences in vertical distribution patterns could indicate a change in behavior between

habitats as a result of changes in the physical environment and/or changes in the associated community which may lead to differential habitat utilization. Differences could also be due to size structure, as smaller individuals usually live at shallower sediment depths. Only *Mediomastus* spp. and *Streblospio benedicti* had significantly different vertical distribution profiles between the upper and lower estuary. The reason for the differences was not investigated. However, the most likely explanation is the change in the physical environment between the upper and lower estuary. The upper York River experiences very swift tidal currents (up to 0.8 m/s) (Schaffner 1997). Higher current speeds and bedload transport could prevent colonization of surface sediments by many species, which could also explain why only one species is found in higher abundances in surface sediments relative to deeper sediment layers. Intraspecific changes in behavior in response to changes in habitat or community composition that would alter vertical distribution patterns cannot be verified or negated based on the results obtained. *S. benedicti* is normally restricted to the top 2 cm of sediment due to its small size and its feeding behavior. However, this surface deposit-feeder may withdraw into the bottom of its tube during periods of high current speed to avoid being swept away and return to the sediment surface to feed when tidal currents are slower in order to feed. Further investigation is necessary to test this hypothesis.

Weston (1990) demonstrated that within a single estuarine habitat and for a single season, most species show a high degree of

fidelity to a depth range within the sediment, even along a gradient of increasing organic enrichment. Other studies have also shown that different species demonstrate a preference for a particular depth range (Sun and Dong 1985). Hines and Comtois (1984) and Schaffner (1990) showed that individuals within a species may change living positions between seasons. However, this seasonal variability is most likely related to recruitment events, as new recruits colonize surface sediments and probably take time to move into their preferred living positions. In this study, results indicate that most species do not change living positions across salinity habitats, which generally supports previous conclusions that different species may exhibit a preference for a depth position within the sediment column, regardless of their physical and/or biological environment.

However, vertical distribution patterns of dominant species in the York River differed somewhat from those observed in sandier Chesapeake Bay sediments (Schaffner 1990) and in other estuaries (Weston 1990). Tubificid oligochaetes in the York River sandy-mud habitat were generally deeper than those in the mainstem Chesapeake Bay fine sand habitat, possibly due to the presence of different species in each of the two habitats (neither study identified them to the species level). *Mediomastus* spp. was found predominantly deeper in the sediments in the upper York River and Puget Sound (Weston 1990), but was found in higher abundances in surface sediments in the lower York River and the mainstem Chesapeake Bay (Schaffner 1990). On the continental shelf, *M. ambiseta* has been

found from the surface sediments to the deepest sediment layers (Sun and Dong 1985). The majority of *Paraprionospio pinnata* collected from the York River were found in deeper sediment strata, while the mode for the mainstem bay was in the 0-2 cm depth range (Schaffner 1990), possibly due to the presence of large numbers of smaller individuals/new recruits. *P. pinnata* in the Elizabeth River muds were more shallow-dwelling, as well (Diaz et al. 1993). Approximately equal proportions of *Glycinde solitaria* were found in the 0-2 and 2-10 cm depth horizons in the lower York River, higher proportions of *G. solitaria* were found in the deeper strata of the upper York River, and the modal depth in the mainstem bay was 0-2 cm (Schaffner 1990). Patterns of vertical distribution for dominants in the York River were similar to those observed for organisms collected from the Rhode River, a subestuary of the Chesapeake Bay (Hines and Comtois 1985). For all other York River dominants not mentioned, either the species were not dominant in the other studies, or vertical distribution patterns for the spring sampling season were similar. The differences observed between the York River sandy-mud and other estuaries/habitats may be due to differences in community composition which may cause differential habitat partitioning, differences in sediment type, or differences in other environmental variables which may influence vertical distribution patterns.

Most models developed for explaining vertical distribution patterns were highly significant ($p=0.0001$). However, most were not very effective for predicting patterns observed. Many times,

the data for which the models were calibrated were not even within the 95% confidence interval or one standard deviation of the values predicted by the model, and data trends did not always follow the same patterns as the models. This may be because there were other parameters influencing vertical distribution patterns that weren't measured and/or because there was such high variability in the odds of organisms being found in surface sediment layers (0-2 cm). Even still, strong generalizations about how physical and biological variables may influence the distribution of organisms within estuarine sediments could be made.

There were differences in the models developed for explaining vertical distribution patterns between the two station groups (habitats/communities) in the estuary. The relative magnitude of influence of variables across habitats was also different. The dummy variable group (GP) entered significantly into many models developed for the whole estuary, indicating significant differences in patterns between the upper and lower estuary community. Also, the data generally fit the models better when the two station groups were analyzed separately. Physical variables best explained the vertical distribution of individuals within the sediment column for the lower estuary polyhaline community. A combination of physical and biological variables explained patterns of vertical distribution of individuals most effectively for the upper estuary mesohaline community. Biomass distribution within the sediment column in both communities was best explained by biological variables.

Vertical distribution patterns for the York River dominants seemed to be related to living positions, life history strategies, feeding modes, and body sizes of organisms. Models indicated that vertical distribution patterns were related to body size. However, none of the models developed for explaining vertical distributions of individuals based on living positions and feeding modes were good at predicting data trends. Data fit the models very poorly, and some correlations were opposite of what was expected. Again this may be due to a combination of the variability in the odds that an individual will be found in the top 2 cm of sediment and the fact that trophic structure or living position alone are not enough to explain where in the sediment column an organism will be found.

Work done by Pearson and Rosenberg (1978) and Gaston (1992) has indicated that there should be a significant correlation between vertical distributions of macrofauna within sediments and community trophic structure. As expected, the influence of motile, free-living organisms (FL) on vertical distribution patterns was variable. Because these organisms actively move through the sediment and can be found at various sediment depths, this variable did not enter significantly into any of the models. However, predators (P), which are also motile, were expected to be found where there were more prey items. Higher densities of organisms occurred in the surface sediment layers, but the dominant predators, *Glycinde solitaria* and *Sigambra tentaculata*, did not show the same pattern, possibly because they were actively avoiding

the sampling gear. Yet models did generally predict that there should be more predators in surface sediments. It has been suggested that organisms penetrate deeper into the sediment when there are more suspension/filter feeders and less when there is a dominance of deposit-feeders (Pearson and Rosenberg 1978). However, because filter-feeders range from shallow-dwelling, opportunistic polychaetes to deep-dwelling bivalves the influence of filter-feeding (FF) organisms on vertical distributions should actually be variable. As expected, penetration depth was negatively correlated with filter-feeders in the lower estuary where the majority of filter-feeders are smaller polychaetes and positively correlated with filter-feeding organisms in the upper estuary where the majority of filter-feeders are deep-dwelling bivalves. Correlations of vertical distribution patterns with deposit-feeding macrofauna depend on whether the organisms are surface or subsurface deposit-feeders. The proportion of individuals in surface sediments was expected to be positively correlated with the number of surface deposit-feeders (SDF) and negatively correlated with the number of sub-surface deposit-feeders (SSDF). Also, the proportion of shallow-dwelling organisms was expected to be correlated with epibenthic organisms. Models, however, generally predicted the opposite of these three trends. Further investigation of the data is necessary to explain why data did not follow trends predicted by the models and why the models predicted trends opposite of what was expected. It is possible that the size structure of organisms needs to be factored into the

model, as larger organisms generally live deeper in the sediment column, or the physical sediment dynamics of the benthos precluded the effect of functional groups on vertical distributions.

Depth of the RPD was not a concern in this study because it was less than 2 cm deep at almost all stations. A shallowing of the RPD, which is usually related to increased sediment organic content and decreased dissolved oxygen concentrations, has been shown to force the majority of infauna to move toward the sediment-water interface and cause mortality of more sensitive species (Ankar and Jansson 1973; Pearson and Rosenberg 1978; Dauer et al. 1989). Because horizontal partitioning for this study was at 2 cm, influences on the macrobenthos due to a shallow RPD could not be assessed. Caution must be taken when making assessments of the vertical distribution of macrobenthos in areas where the RPD is naturally shallow because sulfidic, anaerobic sediments will generally cause the depth of penetration of macroinfauna to be naturally low, as well. This may in part explain the high proportions of organisms observed in surface sediment layers in the York River estuary. Some species, however, may be able to avoid the effects of reducing sediments and porewater by constructing tubes and burrows that keep them removed from this type of environment. The proportion of deeper-dwelling individuals in the polyhaline community increased towards the mouth of the estuary. This supports conclusions from other studies that the periodic short-term hypoxia in the lower estuary has not adversely affected the community (Diaz et al. 1992; Dauer 1993). If the community had

been affected by these events, a general shallowing of the community should have occurred towards the mouth of the estuary where the effects of hypoxia events is more severe.

The increase in the proportion of deep-dwelling organisms with increasing water depth in the lower estuary and the decrease in surface-dwelling organisms with decreasing organic quality in the upper estuary may be related to related to increasing tidal current speed. In the lower estuary, current speeds are higher in the deeper channels, and in the upper estuary, current speed increases with distance from the mouth of the estuary (and as organic quality decreases). Higher current speeds may be causing organisms to move deeper into the sediment to avoid physical disturbance. It is unlikely that the trends observed in any way reflect on food availability or quality because organisms do not occur in high enough abundances to compete for resources and sediment organic content is not low enough to be limiting.

The decrease in shallow-dwelling organisms and increase in deep-dwelling biomass with increasing organic carbon and organic quality is not in keeping with traditional enrichment models which predict a shallowing of the infauna with increased sediment organic content. This suggests that at "natural" background levels, a slight increase in organic carbon may lead to an increase in abundance and biomass of deeper-dwelling organisms related to higher food availability.

The proportion of individuals in surface sediments was positively correlated with smaller organisms, as expected. The

smaller organisms represented smaller-bodied opportunistic species and new recruits, both of which concentrate in upper sediment layers. Recruitment and mortality patterns in temperate estuaries such as the York River are strongly seasonal, and have a profound effect on community structure (Boesch et al. 1976). It appears that recruitment patterns may have a significant effect on vertical distribution patterns, as well.

Larger individuals generally live deeper in the sediments. The evolution of longer life spans and larger body size is correlated with deeper living positions, because deeper-dwelling organisms are less susceptible to predation and physical disturbance (Pianka 1978). The correlation of vertical biomass distribution with abundances indicated that increased abundances were responsible for increased biomass in both the 0-2 and 2-10 cm depth horizons. Body size also significantly affected changes in biomass in surface sediments. Surface-dwelling biomass increased as the mean size of surface-dwelling organisms increased and decreased as the mean size of deeper-dwelling organisms increased.

The proportion of individuals in surface sediments was negatively correlated with abundance. There was also a negative correlation between shallow-dwelling individuals and the number of species present. Both trends may be an indication that the number of deeper-dwelling species and their abundances increase more rapidly than the number of shallow-dwelling and opportunistic species and their abundances under conditions of minimal impact.

A physical environmental variable that was not measured that

should have been modeled was maximum tidal current speed at each station. Tidal currents in the York River are very strong and are suspected of being responsible for preventing many organisms from colonizing surface sediments at upper estuary stations. Rhoads et al. (1985) and Schaffner et al. (1987) demonstrated that the vertical sediment structure of marine and estuarine environments characterized by low deposition rates is controlled by biological activity. Areas of the seabed where sedimentation rates are 3-4 cm/yr., areas of high erosion, areas that alternate between episodes of high erosion and high deposition, and areas where physical reworking of the sediments is continuous are dominated by physical sedimentary structures, exhibit low bioturbation (Rhoads et al. 1985; Schaffner et al. 1987), and support shallow-dwelling communities dominated by small polychaetes (Rhoads et al. 1985; Sun and Dong 1985). However, communities in areas of higher deposition (>5.4 cm/yr.) generally have fewer individuals in surface sediments (0-5 cm). Many estuaries experience high rates of deposition and low bedload transport due to restricted flow regimes, and it would seem that characteristic sedimentary profiles would be dominated by physical processes. The York River benthos is subjected to high tidal currents, which results in dominance by physical processes and a shallow-dwelling community, as well (Schaffner 1997). Estuaries are generally dominated by shallow-dwelling, stress-tolerant or opportunistic species because they are controlled by physical processes (Burbanck et al. 1956; Sanders et al. 1963; Tenore 1972; Biggs and Cronin 1981; Levinton 1982; Schaffner et al.

1987). This would explain the general lack of sedimentary structures such as feeding voids and burrows, the absence of organisms from one of the upstream stations, and the low proportions of most species in surface sediments at upestuary stations. The high rates of physical sediment transport in the York River are likely responsible for the generally shallow-dwelling, stress-tolerant community. These two factors combined would also explain the low occurrence of biological structures in the sediment profile images and the shallow RPD. The influence of the biota on sediment reworking is small, and rates of burial of contaminants and nutrients is likely to be low.

The depth of biological sediment reworking and oxygenation increases as macrofauna penetrate deeper into the sediment (Flint and Kalke 1986). This is especially true when most of the larger, deeper-dwelling individuals are either active burrowers or head-down deposit feeders. Deep-dwelling bivalves probably do not have as much of an effect on sediments at depth. A shallow community dominated by surface deposit feeders or filter/suspension feeding organisms does not process sediments up to great depths, and biogeochemical processes influenced by sediment reworking are slower.

Although proportional distributions of organisms within the sediment column did not change between habitats, total abundances and species composition did change. Therefore, while the depth to which organisms affected sediment processes may not have changed, the relative magnitude and type of effects most likely did,

depending on the functional groups and activity of the organisms present. Where organism abundances are higher, the effects of macrobenthos on sediment transport and biogeochemical processes is probably greater. However, this may not be the case if the activity rates of organisms are low. The nature of effects would depend on whether the dominant species were bioturbators, biodepositors, surface deposit-feeders, subsurface deposit-feeders, burrow-dwellers, tube-dwellers, etc. (Diaz and Schaffner 1990).

A shallow-dwelling community also suggests that the availability of infauna to higher trophic levels may increase. Species which live in tough tubes, can quickly retract deep into the sediment, or live deeper in the sediment are less preyed upon than species which live near or on the sediment surface (Virnstein 1979). For example, the shallow-dwelling *Streblospio benedicti* is an important prey species in the York River (Virnstein 1979). *Paraprionospio pinnata* has also been shown to be an important prey species; the deep-dwelling capitellid *Heteromastus filiformis*, the active burrowing polychaetes *Glycinde solitaria*, *Nereis succinea* and *Scoloplos robustus* were moderately important; and tubificid oligochaetes, and adult deep-dwelling tellinid bivalves were not important (Virnstein 1979). Virnstein (1979) also showed that juveniles were more susceptible to predation because they recruit to surface sediments.

When environmental stress causes alterations in macroinfaunal behavior but not community structure, more tolerant demersal feeding fish may change their feeding habits to take advantage of

macrobenthic organisms that move to the sediment surface to avoid stress (Diaz et al. 1992; Nestlerode 1995). However, changes in community structure to smaller, more shallow-dwelling organisms may not necessarily result in greater energy transfer to higher trophic levels. The amount of trophic transfer would depend on whether or not the consumers feed selectively on macrofaunal species (Boesch 1982). A greater understanding of the relationship between macroinfaunal vertical distribution profiles and energetics requires further investigation.

Studies have shown that the depth to which organisms penetrate the sediment can indicate environmental quality. As sediments become more impacted, macroinfauna become more concentrated in the upper layers of sediment (Ankar and Jansson 1973; Pearson and Rosenberg 1978; Weston 1990; Dauer et al. 1992; Diaz et al. 1992; Dauer 1993; Diaz et al. 1993). However, in habitats like the mesohaline York River where there is naturally high spatial variability in the vertical distribution of organisms within sediments due to high spatial variation in the community, and vertical distribution patterns are controlled by fewer species, using this community metric for assessments becomes problematic. The potential seasonal variability caused by seasonal variations in the abundance of a top dominant could confound assessments as well, if sampling is conducted over multiple seasons.

It has also been demonstrated that some relatively unstressed estuarine communities can be dominated by shallow-dwelling, long-lived species (Dauer 1993). When considering only the top 10 cm of

sediment, the York River could be considered to be intermediately impacted. On average, approximately equal proportions of individuals and biomass were found in the upper 2 cm and 2-10 cm depth horizons. On a volumetric basis, this would mean that there were more shallow-dwelling organisms/biomass than deep-dwelling organisms/biomass for this portion of the sediment column. The York River estuary, however, endures relatively low anthropogenic impact.

Patterns of vertical distribution also may not always be predictable. This was seen in the differences in vertical distribution patterns of *Mediomastus* spp. and *Streblospio benedicti* between the upper and lower estuary and differences in the vertical distribution of dominants between studies. Individuals may also change their position in the sediment column to avoid stress (Diaz et al. 1992). Lastly, a large recruitment of new individuals to an area can cause an apparent shallowing of the benthos. Organisms that are newly settled have not had the opportunity to move into their preferred living positions or respond to local conditions, and may not be good indicators of sediment quality.

While vertical distribution patterns are useful indicators of environmental quality, there is a potential that this metric will fail to lead to accurate classification of impact levels. It is therefore necessary to consider other additional community measures to accurately evaluate environmental conditions. Using more than one approach to assess macrobenthic communities is always advisable.

Sampling programs throughout the world should also consider sampling to sediment depths greater than 10 cm to collect deep-dwelling organisms, which are indicative of community health. The 10 cm long PVC core used for this study to sample for vertical distribution analysis missed most of the population of the deep-dwelling bivalve *Macoma balthica*. Adult *M. balthica* have been found at sediment depths as great as 40 cm in the mesohaline reaches of the Chesapeake Bay and its tributaries (Hines and Comtois 1985). Other species that may be missed by sampling protocols which use a relatively shallow sampler include other bivalves (Spies and Davis 1979; Clavier 1984; Hines and Comtois 1985; Weston 1990), specifically those with longer siphons, echiurans (Weston 1990), sipunculans (Weston 1990), the polychaete *Heteromastus filiformis*, which is most abundant below 15 cm (Rhoads et al. 1985) and penetrates the sediment at least as deep as 35 cm (Hines and Comtois 1985), maldanid polychaetes (Clavier 1984; Rhoads et al. 1985), the polychaetes *Notomastus tenuis*, *Polydora brachycephala* (5-20 cm; Weston 1990), *Melinna palmata*, *Hyalinoecia bilineata*, and *Nephtys hombergii* (Clavier 1984), *Banantolla americana* (5-20 cm; Weston 1990), the crab *Pinnixa schmitti* (0-20 cm; Weston 1990), other burrowing crustaceans (Rice and Chapman 1971), and ophiuroids (Rhoads et al. 1985). Most of these species are abundant and ubiquitous estuarine endemics.

Other factors for explaining vertical distribution patterns of macrobenthos still need to be investigated. Some questions that need to be addressed are inspired by work done with meiofauna. It

has been shown that meiofaunal densities decrease precipitously with increasing sediment depth (Rao 1987; Vicente 1990). This decline is directly correlated with decreasing sediment porewater and organic carbon (Vicente 1990). Such relationships may not exist for the macrobenthos, however, as living position does not necessarily reflect where the organisms obtain their food from. Organisms that build tubes and burrows also do not depend on the amount of space between sediment particles to provide living space. However, sediment compaction may prevent sediment penetration, and this hypothesis should be investigated. No attempt has been made here to correlate vertical distribution patterns of macrofauna and meiofauna for two reasons. First, the importance of meiofauna as a food source for macrofauna has not been proven (Rao 1987). Secondly, most of the macrobenthos collected from the York River sandy mud sediments were deposit feeders, not predators, and consumption of meiofauna would be incidental.

Another aspect of vertical distribution patterns of macroinfauna that still needs to be investigated is diel variations. It is possible that organisms migrate within the sediment column over a 24 hour period to feed, as most food occurs within surface sediments or in the sediment column, or retreat to avoid predation. Daily migratory patterns may be related either to tidal cycles or circadian cycles.

CONCLUSIONS

General vertical distribution patterns of individuals and

biomass in the top 10 cm of sediment of the York River did not change along the estuarine gradient. However, species composition did change between the polyhaline and mesohaline community. A single species, *Leucon americanus*, was largely responsible for driving vertical distribution patterns in the upper estuary mesohaline community. It was the only organism which contributed significantly to abundances and biomass in surface sediment layers. Annelids in the upper mesohaline community were responsible for most of the deep-dwelling abundance and biomass, and the bivalve *Macoma balthica* contributed significantly to deep dwelling biomass, as well. Due to the higher abundances and lower dominance of organisms in the lower estuary polyhaline community, vertical distribution patterns could not be attributed to any one species. However, annelids dominated the lower estuary community, and the body sizes, life history strategies, and feeding modes of the dominant species were in part responsible for patterns observed.

Vertical distribution patterns of most dominant species within the estuary did not change between the upper mesohaline and lower polyhaline communities. Only *Mediomastus* spp. and *Streblospio benedicti* showed differences. Both had significantly higher proportions of individuals in deeper sediment layers in the upper estuary and significantly higher proportions of individuals in surface sediment layers in the lower estuary. The low proportions of individuals of these species in surface sediments in the upper estuary was probably caused by increased tidal current speeds which precluded colonization of surface sediments. Whether there are

changes in behavior within a species across salinity habitats when anthropogenic stress is relatively low is inconclusive.

Although the value of models developed for predicting vertical distributions of individuals and biomass was low, most models were highly significant and provided a strong indication of general trends. Patterns of vertical distribution could be explained by water depth, organic carbon content of the sediment, organic quality, organism sizes, organism abundances, and numbers of species. It also appeared that where organisms reside in the sediment column is related to living position (i.e. tube-dwelling, burrow-dwelling, free-living, epibenthic), life history strategy, and feeding mode (i.e. filter-feeding, predatory, surface deposit-feeding, subsurface deposit-feeding). No useful models could be developed, however, using functional group data.

Under conditions of minimal impact, vertical distribution patterns are driven by the dominant organisms in the community and their biological characteristics. Estuarine communities are ultimately influenced by the physical environment, therefore vertical distribution patterns are also correlated with physical environmental variables.

Vertical distribution patterns may not change across habitats, but community composition and abundances change. Therefore, the depth to which the sediment is affected by the community may remain the same across communities, but the relative magnitude and nature of effects may differ depending on the activity rates and feeding modes of the different species. The general decrease in abundances

and numbers of species, and increase in dominance and spatial variability in communities may complicate evaluations of environmental quality based on vertical distribution patterns in upper reaches of estuaries. Assessments are complicated by high spatial variation in vertical distribution patterns and larger control of these patterns by fewer species. It is therefore necessary to use multiple benthic community metrics to make accurate environmental assessments.

Further investigation is necessary to better understand patterns of vertical distribution of macrobenthos within the sediment column. Studies need to be conducted on: 1) the sizes of individuals and their relationship to feeding modes at various sediment depths; 2) the effects of life history structure on vertical distribution of individuals and biomass within sediments; 3) the effects of tidal current speed on vertical distribution patterns; 4) the effects of sediment compaction on penetration of organisms into the sediment; 5) correlations in vertical distribution patterns between macrobenthic and meiobenthic communities; 6) diel variations in vertical distribution patterns of organisms within sediments; and 7) changes in living positions over a tidal cycle, to name a few. Such studies would provide more insight on the effects of vertical distribution patterns on macrobenthic community function and the utility of vertical profiles as a metric for environmental assessment.

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VITA

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The author was born on August 20, 1969 in Trenton, N.J. She attended Rutgers University in New Brunswick, N.J. where she was awarded a B.S. degree in environmental science from Cook College in May 1991. She began her masters work in September 1991 at the Virginia Institute of Marine Science as a research assistant to Dr. Robert J. Diaz. She has also held full-time positions as a bioassay scientist, a teacher, and a senior laboratory technician with various employers in New Jersey during the course of her studies.

TABLE 1. YORK RIVER SAMPLING SITES - PHYSICAL ENVIRONMENTAL VARIABLES Trends are based on linear regression of parameters on distance from the mouth of the estuary. Differences between the upper and lower estuary were determined by t-test or Mann-Whitney U test as appropriate.

Parameter	Measurements	Trend	Difference Between Upper and Lower Estuary
Salinity	5-24 ppt	↓ upestuary	not tested
Water Depth	5-18 m	↓ upestuary	significant (p=0.0013)
Sediment Granulometry	mean=76% silt and clay (sd=12.6%)	↓ upestuary	significant (p=0.0111)
Depth of the Sediment Redoxcline	mean=0.7 cm (0.1-2.3)	None	not significant
Sediment Organic Carbon	19.32 mg/g (7.53-27.36)	↑ upestuary	significant (p=0.0012)
Sediment Organic Nitrogen	2.42 mg/g (0.9-3.16)	↑ upestuary	not significant
Atomic C:N Ratio	9.27 (6.58-10.82)	↑ upestuary	significant (p=0.0014)

Table 2. YORK RIVER BIOLOGICAL DATA Numbers in the table are on a per station basis, and only represent those organisms retained on a 0.5 mm mesh. Trends are based on linear regression of parameters on distance from the mouth of the estuary. Differences between the upper and lower estuary were determined by t-test or Mann-Whitney U test as appropriate. AFDW = Ash-free dry weight.

Parameter	Measurements	Trend	Difference Between Upper and Lower Estuary
Number of Organisms per Sample	mean=69 (16-192)	none	significant (p=0.0326)
Total Number of Species	mean=24 (9-39)	↓ upestuary	significant (p<0.0001)
Biomass per Sample	mean=6.99 mg AFDW (0.70-18.77)	none	not significant
Biomass per Sample Without Bivalves	mean=4.89 mg AFDW (0.38-11.62)	↓ upestuary	significant (p=0.0015)

Total Number of Organisms Collected: 9,664
Minimum Number of Species Collected: 76
Annelids: 55% **Crustaceans:** 22% **Mollusks:** 9% **Others:** 14%
 Dominance was higher in the upper reaches of the estuary. Fewer species contributed to 75% of the individuals collected (5 in the upper estuary vs. 11 in the lower estuary). Organisms collected from the York River estuary were typical of those collected during previous studies (Boesch et al. 1976; Diaz 1984; Zobrist 1988; Diaz et al. 1992).

TABLE 3. YORK RIVER DOMINANTS

A) NUMERICALLY DOMINANT SPECIES IN THE YORK RIVER ESTUARY

Species/Taxon	Total Abundance	% of Total	Cum. %
<i>Leucon americanus</i> (C)	822	16.7	16.7
<i>Tubificoides</i> spp. (O)	573	11.6	28.3
<i>Mediomastus</i> spp. (P)	541	11.0	39.3
<i>Leitoscoloplos</i> spp. (P)	393	8.0	47.3
<i>Paraprionospio pinnata</i> (P)	379	7.7	55.0
<i>Macoma baltica</i> (B)	336	6.8	61.8
<i>Streblospio benedicti</i> (P)	186	3.8	65.6
<i>Asabellides oculata</i> (P)	164	3.3	68.9
<i>Sigambra tentaculata</i> (P)	155	3.2	72.1
<i>Glycinde solitaria</i> (P)	123	2.5	74.6
<i>Caprella equilibra</i> (C)	119	2.4	77.0
<i>Notomastus latericeus</i> (P)	114	2.3	79.3
Nemertinea	111	2.3	81.6

B) NUMERICALLY DOMINANT SPECIES IN THE LOWER YORK RIVER ESTUARY

Species/Taxon	Total Abundance	% of Total	Cum. %
<i>Mediomastus</i> spp. (P)	488	20.4	20.4
<i>Leitoscoloplos</i> spp. (P)	248	10.4	30.8
<i>Paraprionospio pinnata</i> (P)	227	9.5	40.3
<i>Asabellides oculata</i> (P)	157	6.6	46.9
<i>Streblospio benedicti</i> (P)	146	6.1	53.0
<i>Sigambra tentaculata</i> (P)	141	5.9	58.9
<i>Notomastus latericeus</i> (P)	109	4.6	63.5
<i>Caprella equilibra</i> (C)	107	4.5	68.0
Nemertinea	85	3.6	71.6
<i>Clymenella torquata</i> (P)	54	2.3	73.9
<i>Leucon americanus</i> (C)	49	2.0	75.9

TABLE 3. (CONTINUED)

C) NUMERICALLY DOMINANT SPECIES IN THE UPPER YORK RIVER ESTUARY

Species/Taxon	Total Abundance	% of Total	Cum. %
<i>Leucon americanus</i> (C)	770	30.2	30.2
<i>Tubificoides</i> spp. (O)	527	20.7	50.9
<i>Macoma baltica</i> (B)	332	13.0	63.9
<i>Paraprionospio pinnata</i> (P)	152	6.0	69.9
<i>Leitoscoloplos</i> spp. (P)	145	5.7	75.6
<i>Glycinde solitaria</i> (P)	80	3.1	78.7
<i>Phoronis</i> spp.	63	2.5	81.2
<i>Mediomastus</i> spp. (P)	53	2.1	83.3
<i>Pseudeurythoe paucibranchiata</i> (P)	51	2.0	85.3

B=Bivalve

C=Crustacean

O=Oligochaete

P=Polychaete

Phoronis spp. is from the phylum Phoronida

**TABLE 4. VERTICAL DISTRIBUTION OF DOMINANTS
WITHIN THE SEDIMENT COLUMN**

**A) VERTICAL DISTRIBUTIONS OF DOMINANT SPECIES
THROUGHOUT THE YORK RIVER ESTUARY**

Species/Taxon	% in 0-2 cm	% in 2-10 cm
<i>Leucon americanus</i> *	96.0	4.0
<i>Tubificoides</i> spp. ^{NT}	-	most > 10 cm
<i>Mediomastus</i> spp. ^{NS}	65.2	34.8
<i>Leitoscoloplos</i> spp.*	8.5	91.5
<i>Paraprionospio pinnata</i> *	19.0	81.0
<i>Macoma balthica</i> ^{NT}	-	most > 10 cm
<i>Streblospio benedicti</i> ^{NS}	48.1	51.9
<i>Asabellides oculata</i> ^{NT}	80.6	19.4
<i>Sigambra tentaculata</i> ^{NS}	48.5	51.5
<i>Glycinde solitaria</i> ^{NS}	48.6	51.3
<i>Caprella equilibra</i> ^{NT}	-	-
<i>Notomastus latericeus</i> *	12.7	87.3
Nemertinea ^{NT}	5.9	94.1

**B) VERTICAL DISTRIBUTIONS OF DOMINANT SPECIES
IN THE LOWER YORK RIVER ESTUARY**

Species/Taxon	% in 0-2 cm	% in 2-10 cm
<i>Mediomastus</i> spp. ^{NS}	68.3	31.7
<i>Leitoscoloplos</i> spp.*	11.5	88.5
<i>Paraprionospio pinnata</i> ^{NS}	23.4	76.6
<i>Asabellides oculata</i> *	82.0	18.0
<i>Streblospio benedicti</i> ^{NS}	72.9	27.1
<i>Sigambra tentaculata</i> ^{NS}	50.0	50.0
<i>Notomastus latericeus</i> ^{NS}	16.7	83.3
<i>Caprella equilibra</i> ^{NT}	-	-
Nemertinea*	7.1	92.9
<i>Clymenella torquata</i> ^{NT}	22.2	77.8
<i>Leucon americanus</i> *	100.0	0.0

TABLE 4. (CONTINUED)

C) VERTICAL DISTRIBUTIONS OF DOMINANT SPECIES
IN THE UPPER YORK RIVER ESTUARY

Species/Taxon	% in 0-2 cm	% in 2-10 cm
<i>Leucon americanus</i> *	95.6	4.4
<i>Tubificoides</i> spp. ^{NT}	-	most > 10 cm
<i>Macoma baltica</i> ^{NT}	4.8	95.2 (most > 10 cm)
<i>Paraprionospio pinnata</i> ^{NT}	0.0	100.0
<i>Leitoscoloplos</i> spp.*	3.3	96.7
<i>Glycinde solitaria</i> ^{NS}	33.3	66.7
<i>Phoronis</i> spp. ^{NT}	-	-
<i>Mediomastus</i> spp. ^{NS}	20.0	80.0
<i>Pseudeurythoe paucibranchiata</i> ^{NT}	-	-

*Indicates significant difference in abundance between the 0-2 and 2-10 depth strata.

^{NS} No significant difference in abundance between the 0-2 and 2-10 depth strata.

^{NT} Not tested

Caprella equilibra and *Pseudeurythoe paucibranchiata* were not present in high enough numbers in sub-cores to determine their vertical distributions. *Caprella equilibra*, however, is an epibenthic species.

No *Tubificoides* spp. or *Phoronis* spp. were present in the subcores, therefore their vertical distribution could not be determined. *Tubificoides* spp. are generally found deeper than 10 cm in the sediment.

TABLE 5.
DIFFERENCES IN THE VERTICAL DISTRIBUTION
OF DOMINANTS BETWEEN THE
UPPER AND LOWER ESTUARY

Species/Taxon	X ²	Conclusion
<i>Leucon americanus</i>	0.156	No significant difference
<i>Tubificoides</i> spp.	1.436	No significant difference
<i>Mediomastus</i> spp.	7.595	Significantly deeper in the upper estuary
<i>Leitoscoloplos</i> spp.	0.758	No significant difference
<i>Paraprionospio pinnata</i>	0.990	No significant difference
<i>Macoma baltica</i>	-	Not tested because are generally deeper than 10 cm
<i>Streblospio benedicti</i>	25.570	Significantly deeper in the upper estuary
<i>Asabellides oculata</i>	-	Not enough individuals collected from the upper estuary
<i>Sigambra tentaculata</i>	0.011	No significant difference
<i>Glycinde solitaria</i>	3.252	No significant difference
<i>Caprella equilibra</i>	-	Not enough individuals collected
<i>Notomastus latericeus</i>	0.253	No significant difference
<i>Phoronis</i> spp.	-	Not enough individuals collected from the lower estuary

X²_{0.05,1} = 3.84

TABLE 6. PAIRED COMPARISONS OF VERTICAL DISTRIBUTION Paired comparisons were made for each station to test if vertical distributions of individuals and biomass were different for various components of the community relative to the whole community. Significant differences indicated that component of the community was a driving force in vertical distribution patterns.

A)

Abundances

Comparison	Whole Estuary	Lower Estuary	Upper Estuary
Annelids Only	proportion in top 2 cm relative to the top 10 cm significantly lower (p<0.0001)	no significant difference (p=0.098)	proportion in top 2 cm relative to the top 10 cm significantly lower (p=0.0005)
Community Without <i>Leucon</i>	proportion in top 2 cm relative to the top 10 cm significantly lower (p<0.0001)	no significant difference (p=0.625)	proportion in top 2 cm relative to the top 10 cm significantly lower (p=0.0012)

B)

Biomass

Comparison	Whole Estuary	Lower Estuary	Upper Estuary
Annelids Only	proportion in top 2 cm relative to the top 10 cm significantly lower (p=0.0018)	no significant difference (p=0.193)	proportion in top 2 cm relative to the top 10 cm significantly lower (p=0.0046)
Community Without Bivalves	proportion in top 2 cm relative to the top 10 cm significantly higher (p=0.0098)	no significant difference (p=1.0000)	proportion in top 2 cm relative to the top 10 cm significantly higher (p=0.0156)

TABLE 7.
 VARIABLES USED IN LOGISTIC REGRESSIONS
 TO DETERMINE POTENTIAL EXPLANATIONS
 FOR VERTICAL DISTRIBUTION PATTERNS

Physical	Biological
*GP=Group; a dummy variable which separates upper from lower estuary stations DIST=Distance from the mouth of the estuary, which may represent a salinity gradient or other gradients DEP=Water depth C=Organic carbon content of the sediment C:N=Atomic ratio of organic carbon to organic nitrogen, which indicates organic quality	*GP=Group; a dummy variable which separates upper from lower estuary communities SPP=The # of species collected in each sample SM=The # of macrofauna collected on the 0.25 mm sieve, which may indicate recruitment LG=The total # of organisms collected in each sample (0.5 mm sieve) **NTOP=The total # of organisms collected in the 0-2 cm fraction of each sample (0.5 mm sieve) **NBOT=The total # of organisms collected in the 2-10 cm fraction of each sample **XWTTOP=The mean weight per individual collected in the 0-2 cm fraction of each sample (0.5 mm sieve) **XWTBOT=The mean weight per individual collected in the 2-10 cm fraction of each sample ***SMAN, LGAN, NANTOP, NANBOT, XWTANTOP, XWTANBOT
Living Positions	
B=Burrow dwelling T=Tube dwelling FL=Free-living and actively moves through the sediment E=Epibenthic	
Feeding Modes	
P=Predator O=Omnivore FF=Filter feeder SDF=Surface deposit feeder SSDF=Subsurface deposit feeder I=Interface feeder (filter feeds and feeds on surface sediments)	

*Tested for entry into models for the whole estuary only.

**Tested for entry into community biomass models only.

***Represent same biological variables for annelids. Tested for entry into annelid biomass models only.

TABLE 8.
SUMMARY OF RESULTS FROM REGRESSION MODELING
OF THE VERTICAL DISTRIBUTION
OF INDIVIDUALS AND BIOMASS WITHIN ESTUARINE SANDY-MUD

Variables in the table were those that had a significant correlation with the proportion of individuals and biomass within the top 2 cm of sediment.

A) Vertical Distribution of Individuals

Model Variables	York River	Lower Estuary	Upper Estuary	Significance (p)
<i>Physical & Biological</i>	-GP +DIST -C:N -N +SM -SPP	+DIST -DEP -C -SM	-DEP -C:N -N +SM	Estuary=0.0001 Lower=0.0003 Upper=0.0001
<i>Physical Only</i>	-GP +DIST -DEP -C:N	+DIST -DEP -C	-DEP -C:N	Estuary=0.001 Lower=0.0005 Upper=0.0001
<i>Biological Only</i>	-LG +SM -SPP	No model	-LG +SM	Estuary=0.001 Lower=none Upper=0.0001

B) Vertical Distribution of Biomass

Model Variables	York River	Lower Estuary	Upper Estuary	Significance (p)
<i>Physical & Biological</i>	-C +NTOP -NBOT	-NBOT	+NTOP -NBOT	Estuary<0.0001 Lower=0.0038 Upper=0.0008
<i>Physical Only</i>	No Model	No Model	No Model	
<i>Biological Only</i>	+NTOP -NBOT	-NBOT	+NTOP -NBOT	Estuary<0.0001 Lower=0.0038 Upper=0.0008

TABLE 8. (CONTINUED)

C) Vertical Distribution of Annelid Biomass

Model Variables	York River	Lower Estuary	Upper Estuary	Significance (p)
<i>Physical & Biological</i>	-GP +NANTOP -NANBOT +XWTANTOP -XWTANBOT	+NANTOP -NANBOT +XWTANTOP -XWTANBOT	+NANTOP +XWTANTOP	Estuary<0.0001 Lower<0.0001 Upper<0.0001
<i>Physical Only</i>	-GP	No Model	No Model	Estuary=0.0008
<i>Biological Only</i>	-GP +NANTOP -NANBOT +XWTANTOP -XWTANBOT	+NANTOP -NANBOT +XWTANTOP -XWTANBOT	+NANTOP +XWTANTOP	Estuary<0.0001 Lower<0.0001 Upper<0.0001

D) The Influence of Functional Groups on the Vertical Distribution of Individuals

Model Variables	York River	Lower Estuary	Upper Estuary	Significance (p)
<i>Feeding Groups</i>	-P -FF -SDF +SSDF -I	+P -O +FF -SDF -SSDF	+P -FF -SDF +SSDF	Estuary=0.0001 Lower=0.0001 Upper=0.0001
<i>Living Positions</i>	+B -T -E	-B -E	-B -T	Estuary=0.001 Lower=0.0001 Upper=0.0001

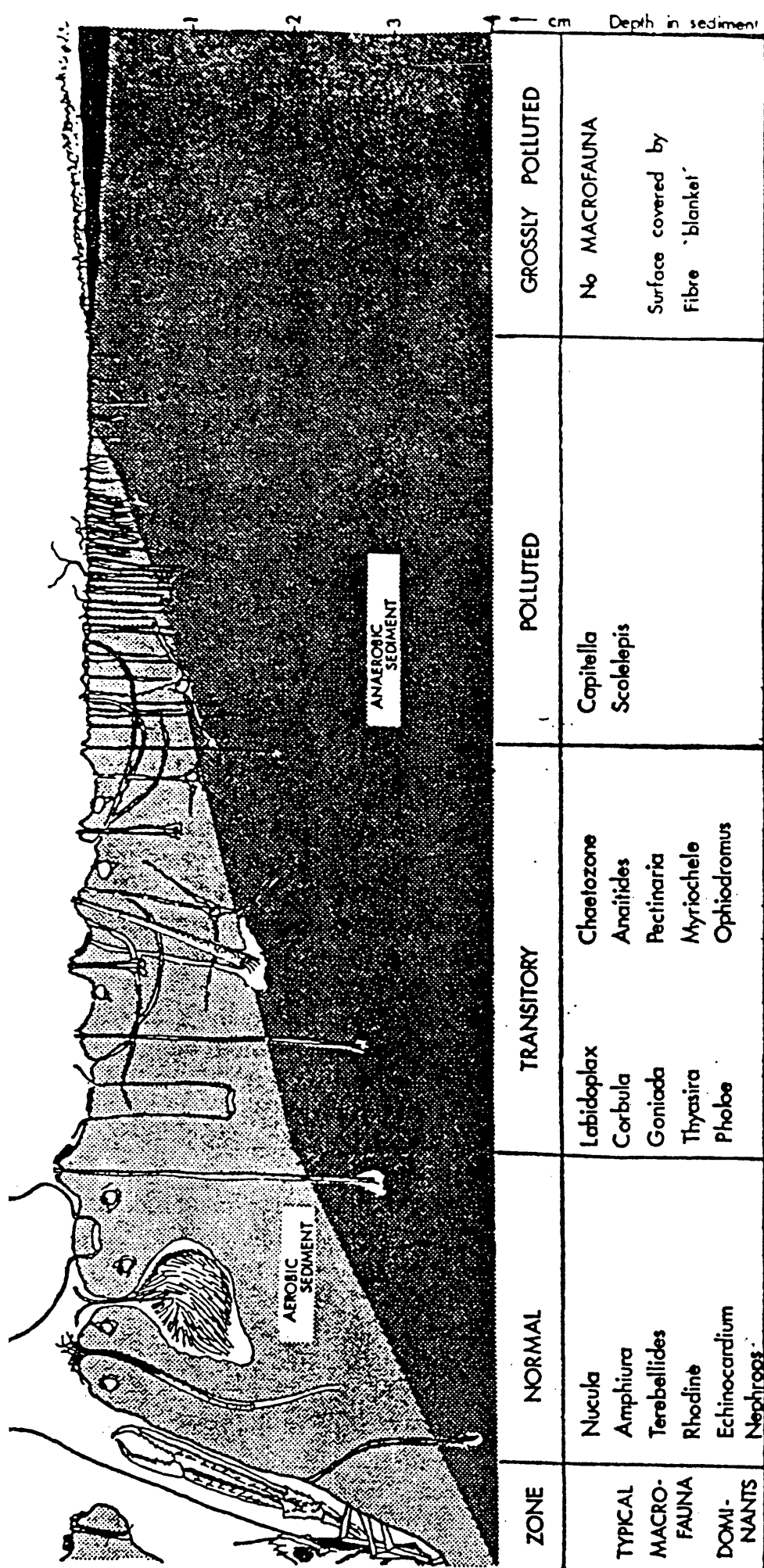
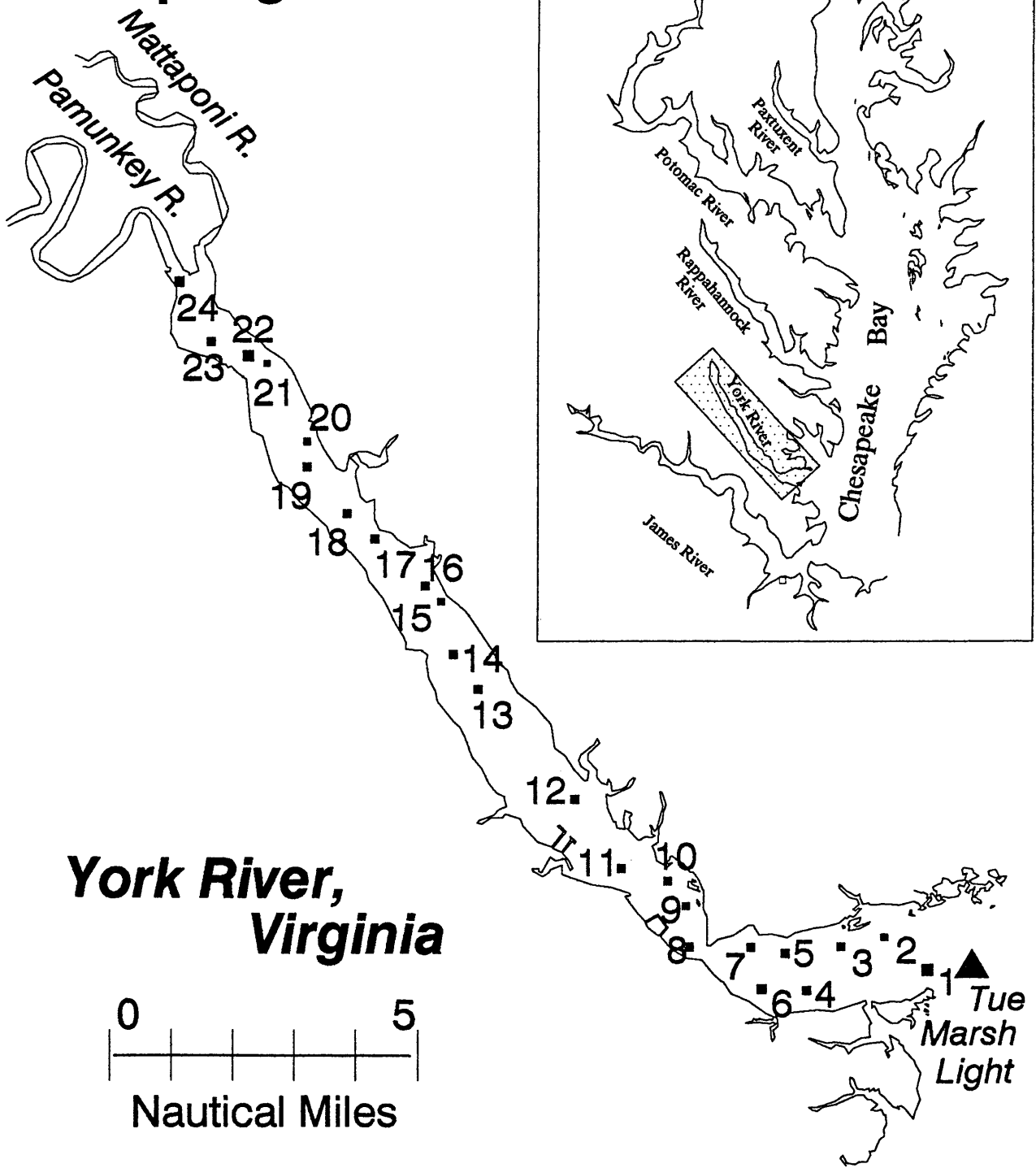


Diagram of changes in fauna and sediment structure along a gradient of organic enrichment (from Pearson & Rosenberg, 1976).

Figure 1.

Figure 2. Study Site and Sampling Stations

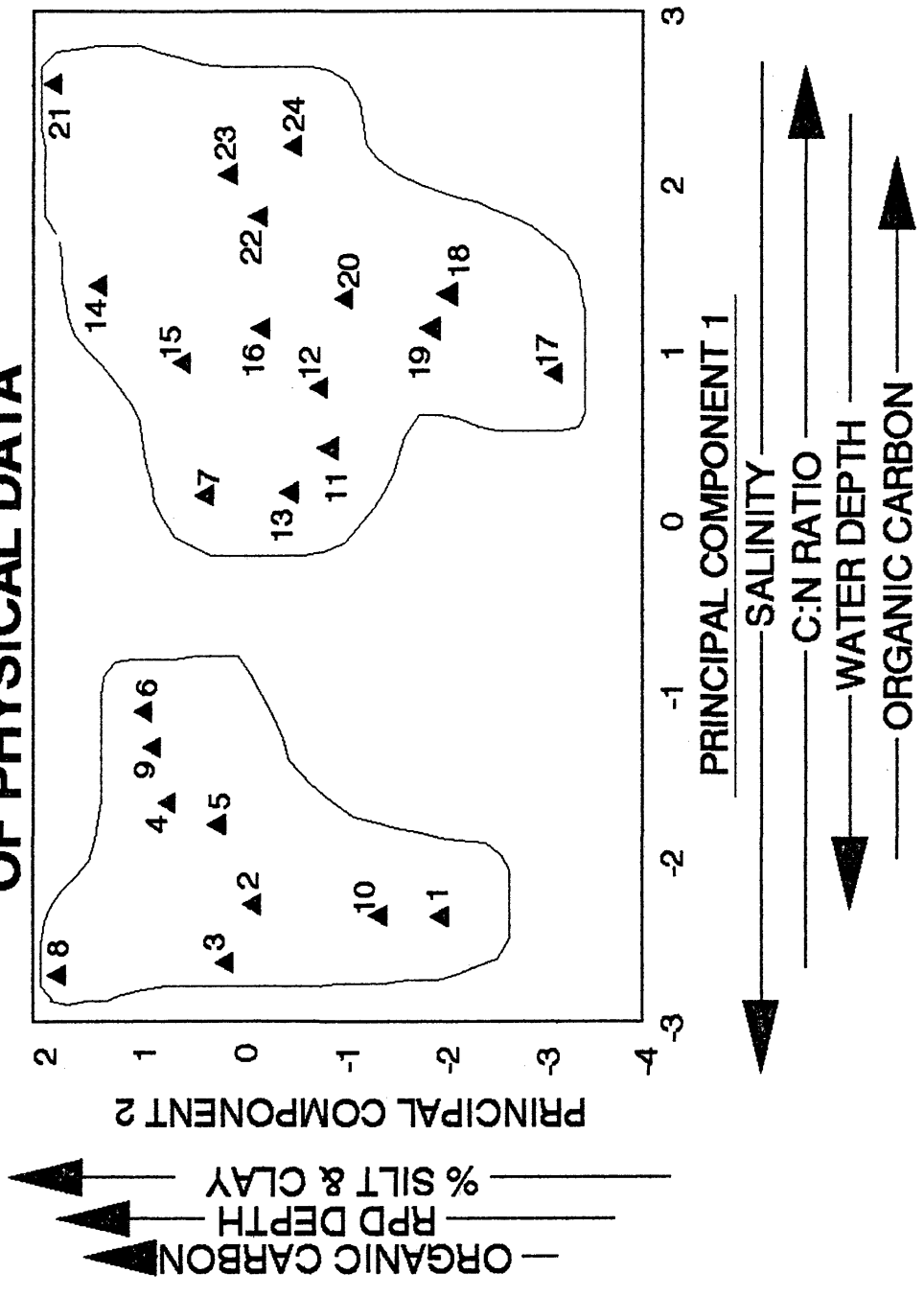


**York River,
Virginia**

0 5
Nautical Miles

Tue
Marsh
Light

Figure 3.
PRINCIPAL COMPONENTS ANALYSIS
OF PHYSICAL DATA



The length of each arrow indicates the relative magnitude of influence by each physical parameter on station clusters. Arrow direction indicates an increasing gradient.

Figure 4. YORK RIVER PHYSICAL ENVIRONMENTAL PARAMETERS

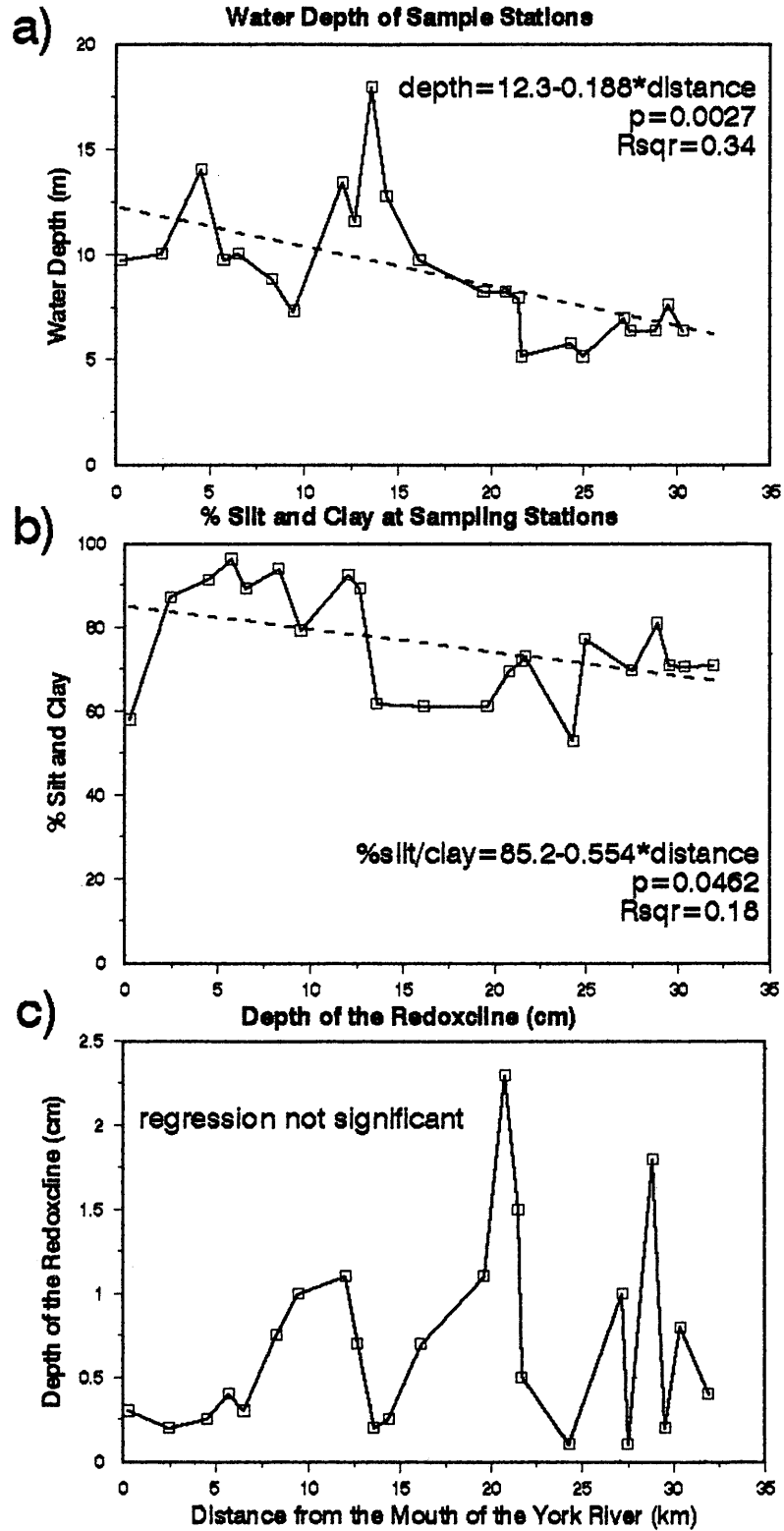


Figure 4. (continued)

YORK RIVER PHYSICAL ENVIRONMENTAL PARAMETERS

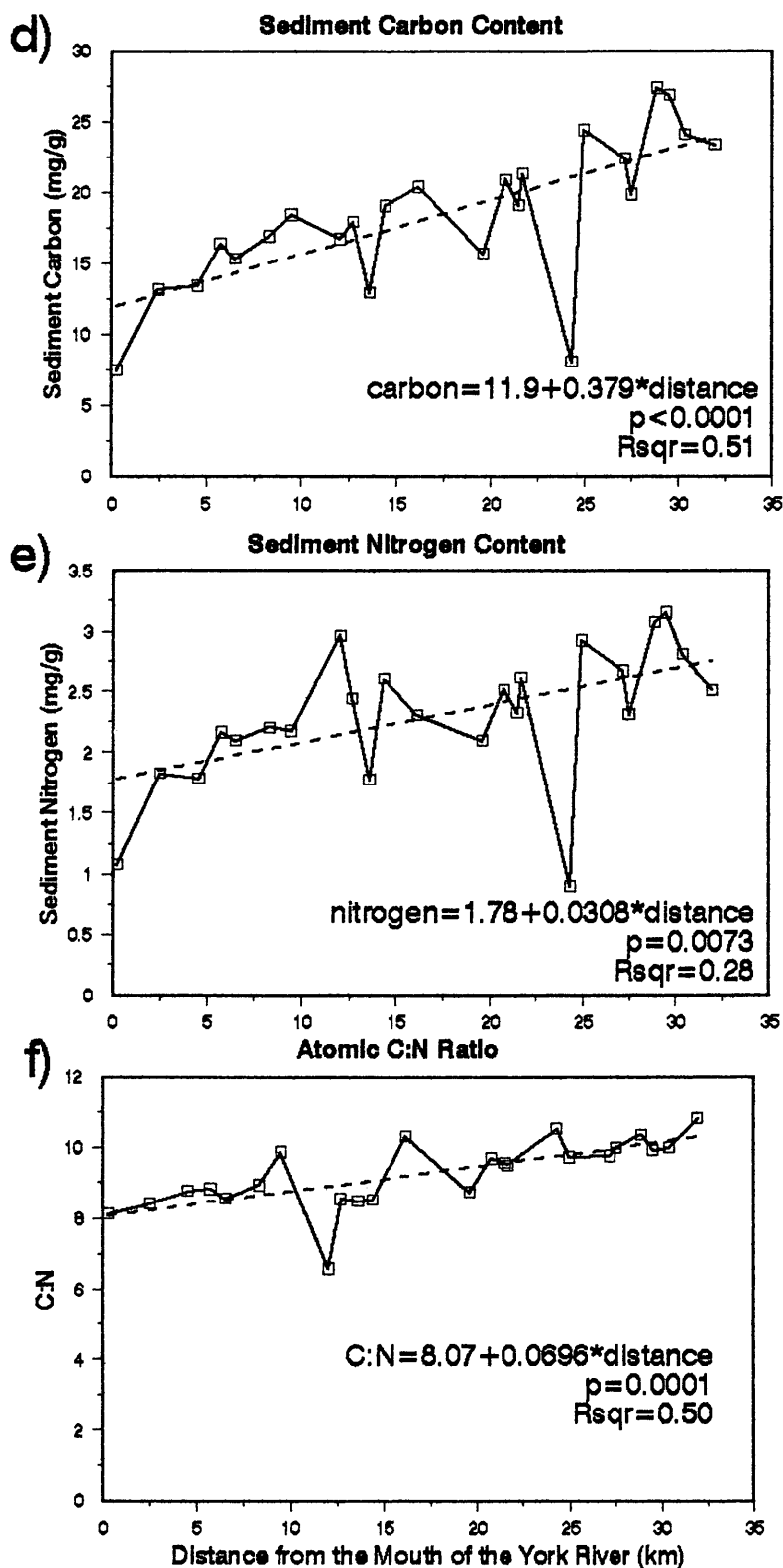


Figure 5.
CLUSTER ANALYSIS OF SITES
BASED ON SPECIES COMPOSITION AND ABUNDANCES

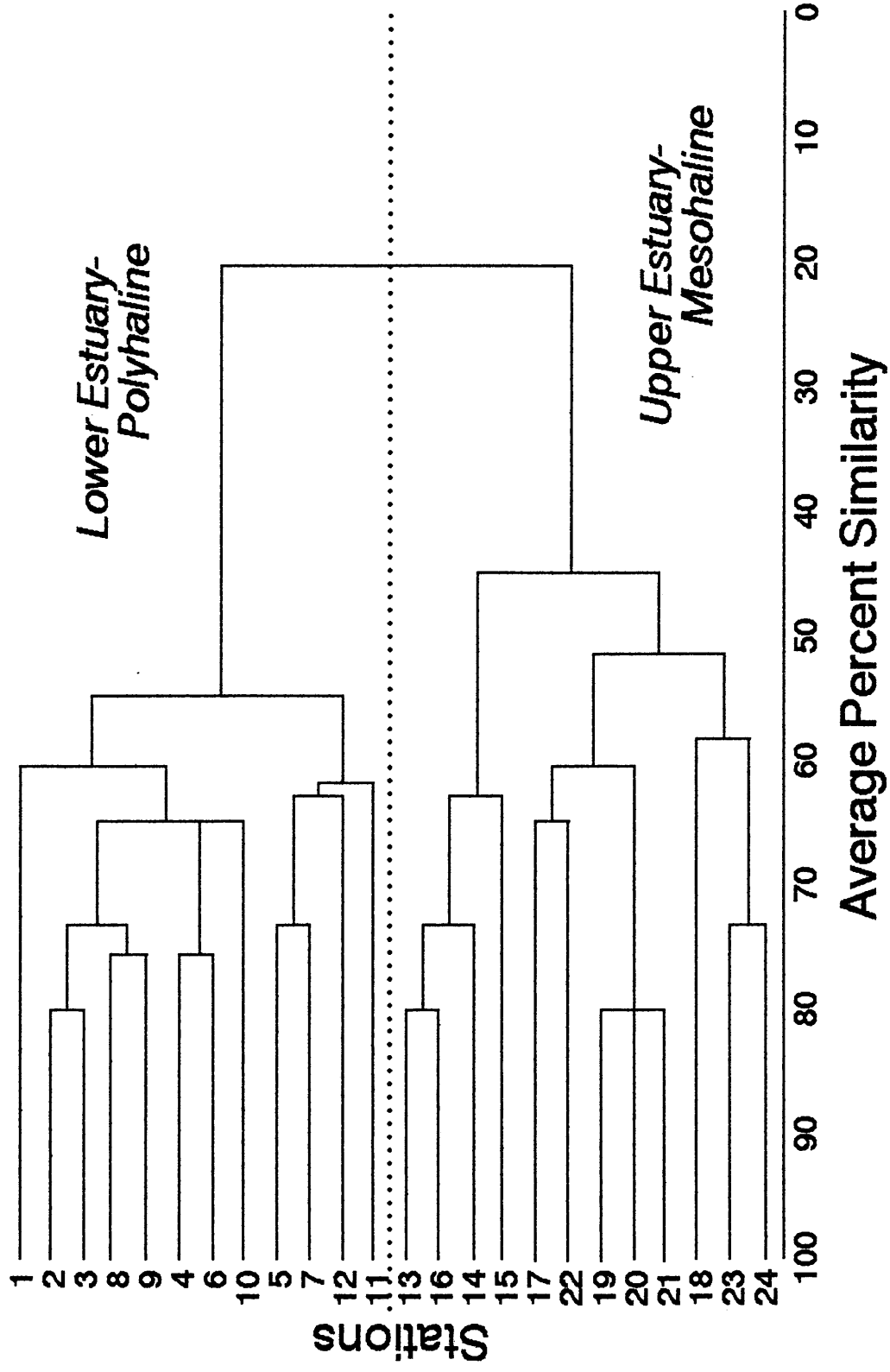
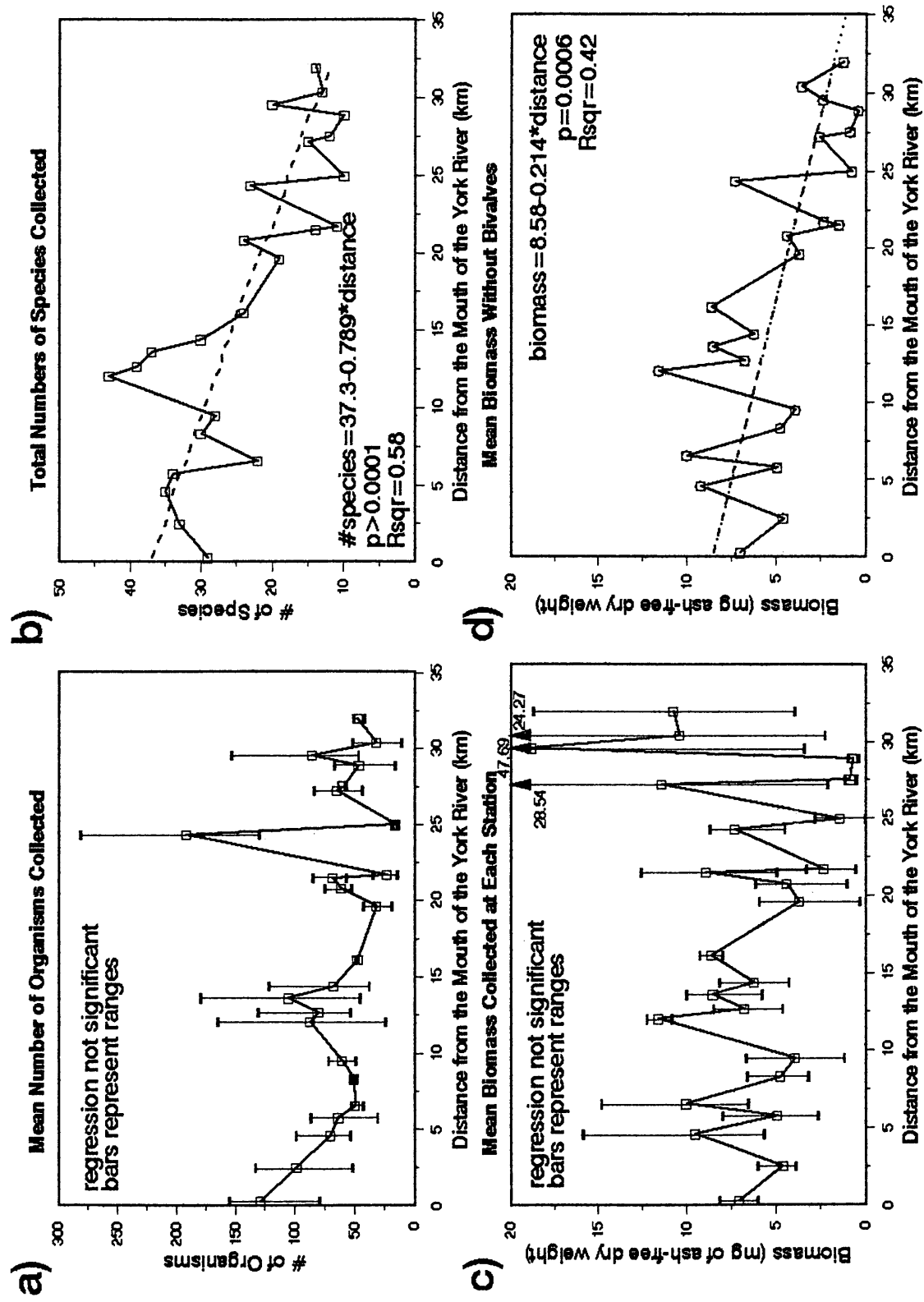
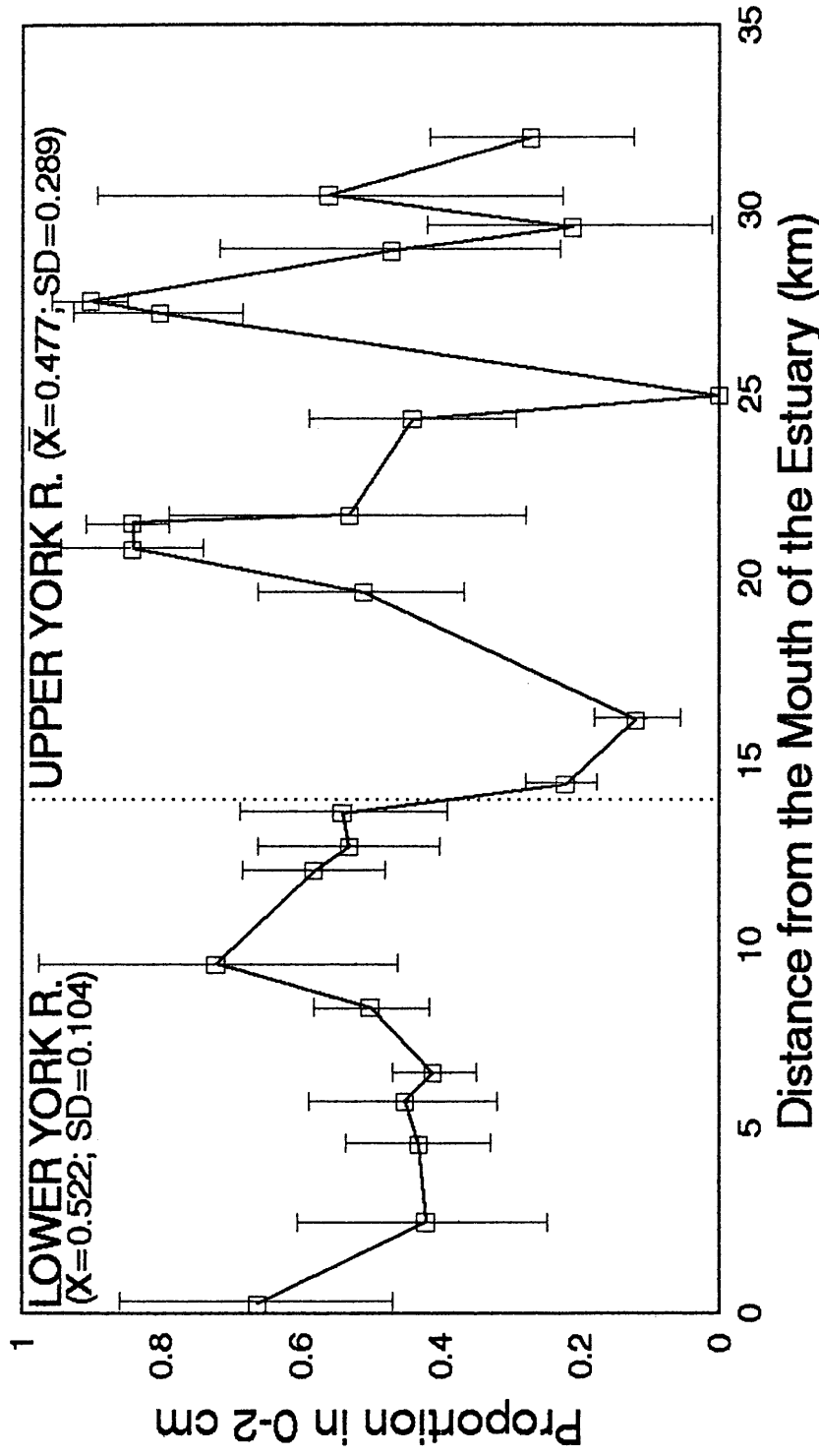


Figure 6. YORK RIVER BIOLOGICAL PARAMETERS

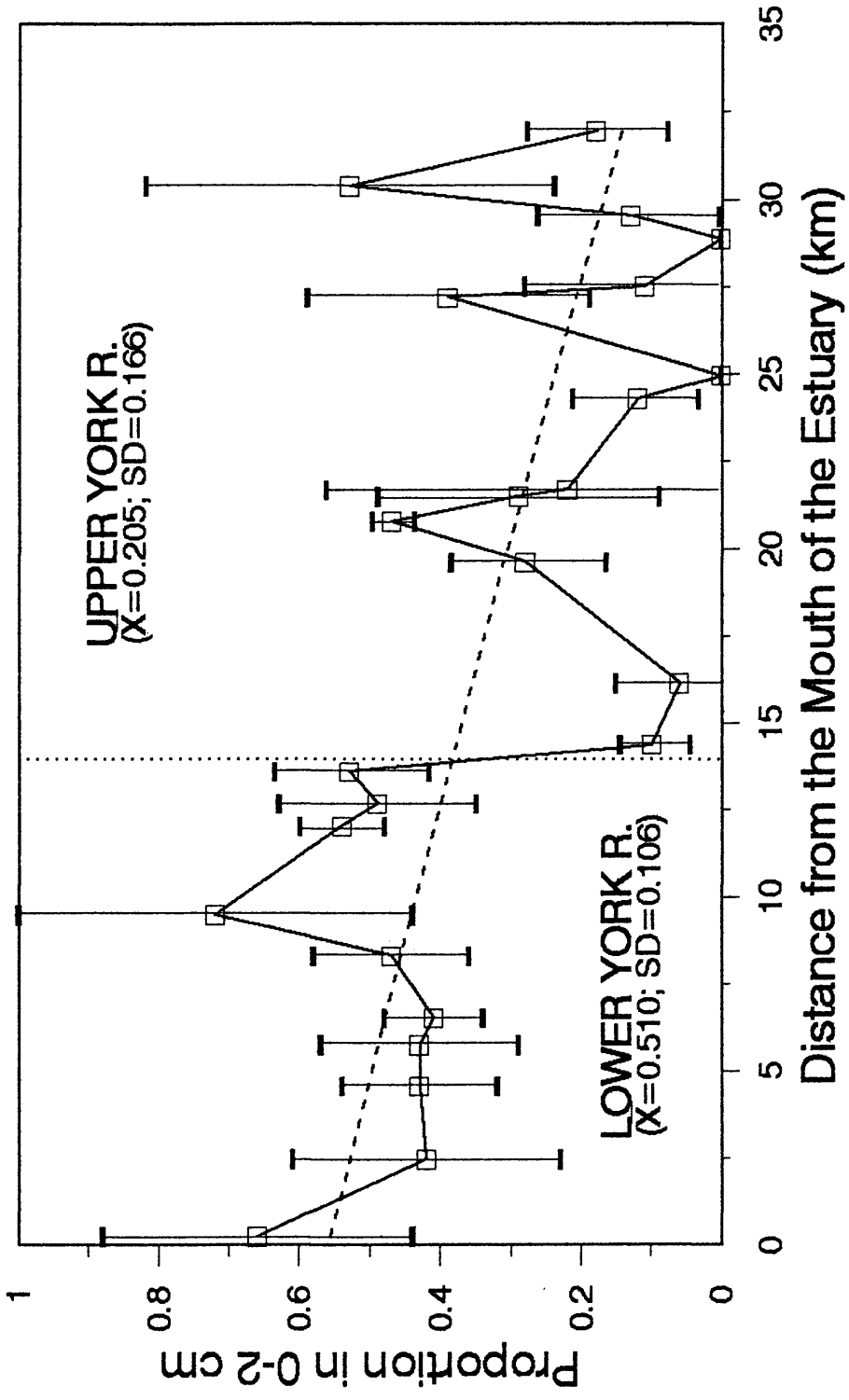


**Figure 7.
VERTICAL DISTRIBUTION OF INDIVIDUALS
WITHIN THE TOP 10 CM OF SEDIMENT**



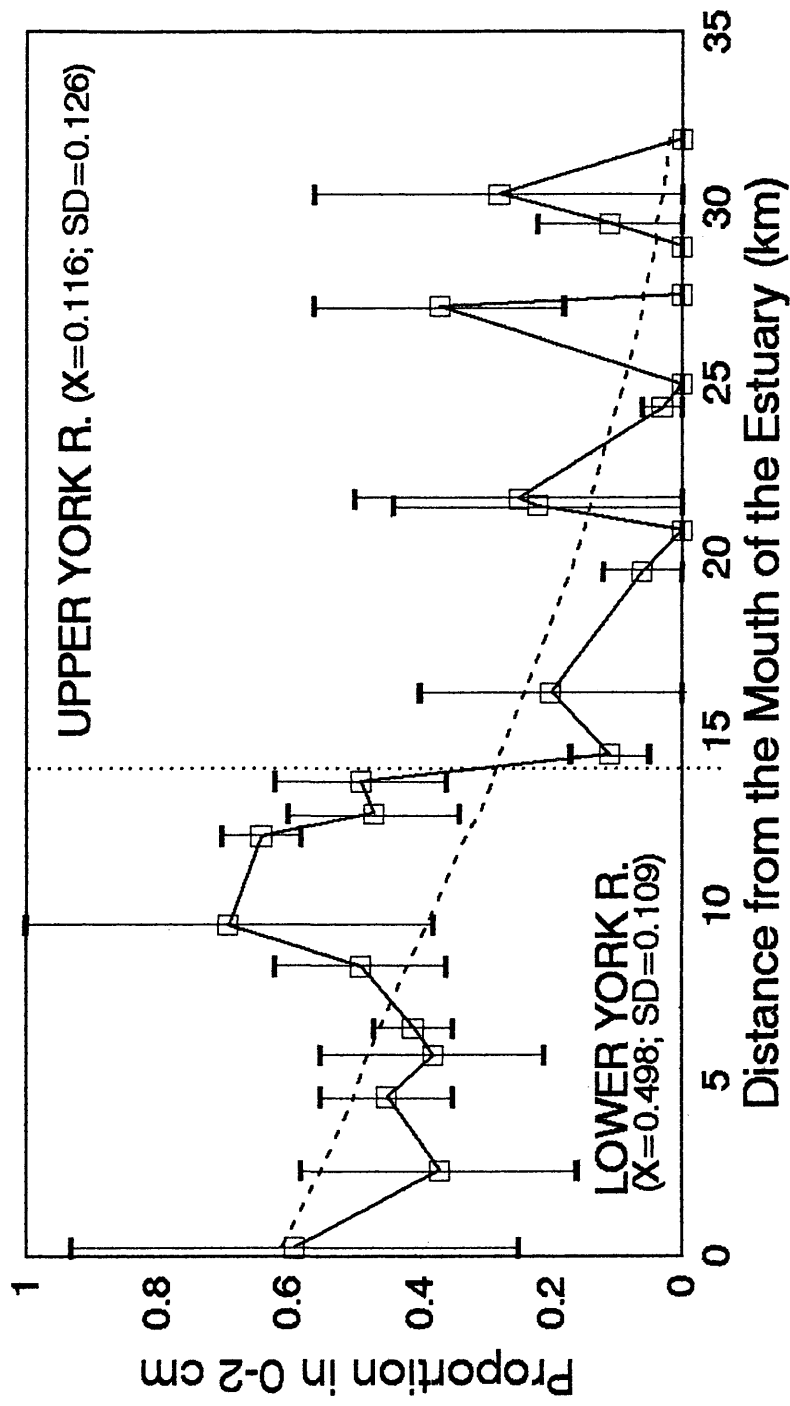
Note: Bars represent standard error.
 No significant trend along the estuary was observed.
 Upper and lower estuary were not significantly different ($T=129.5$, $p=0.81$).
 Between station variability was significantly higher for the upper estuary ($F=11.09$, $p<0.001$)

Figure 8.
VERTICAL DISTRIBUTION OF INDIVIDUALS
WITHOUT LEUCON AMERICANUS



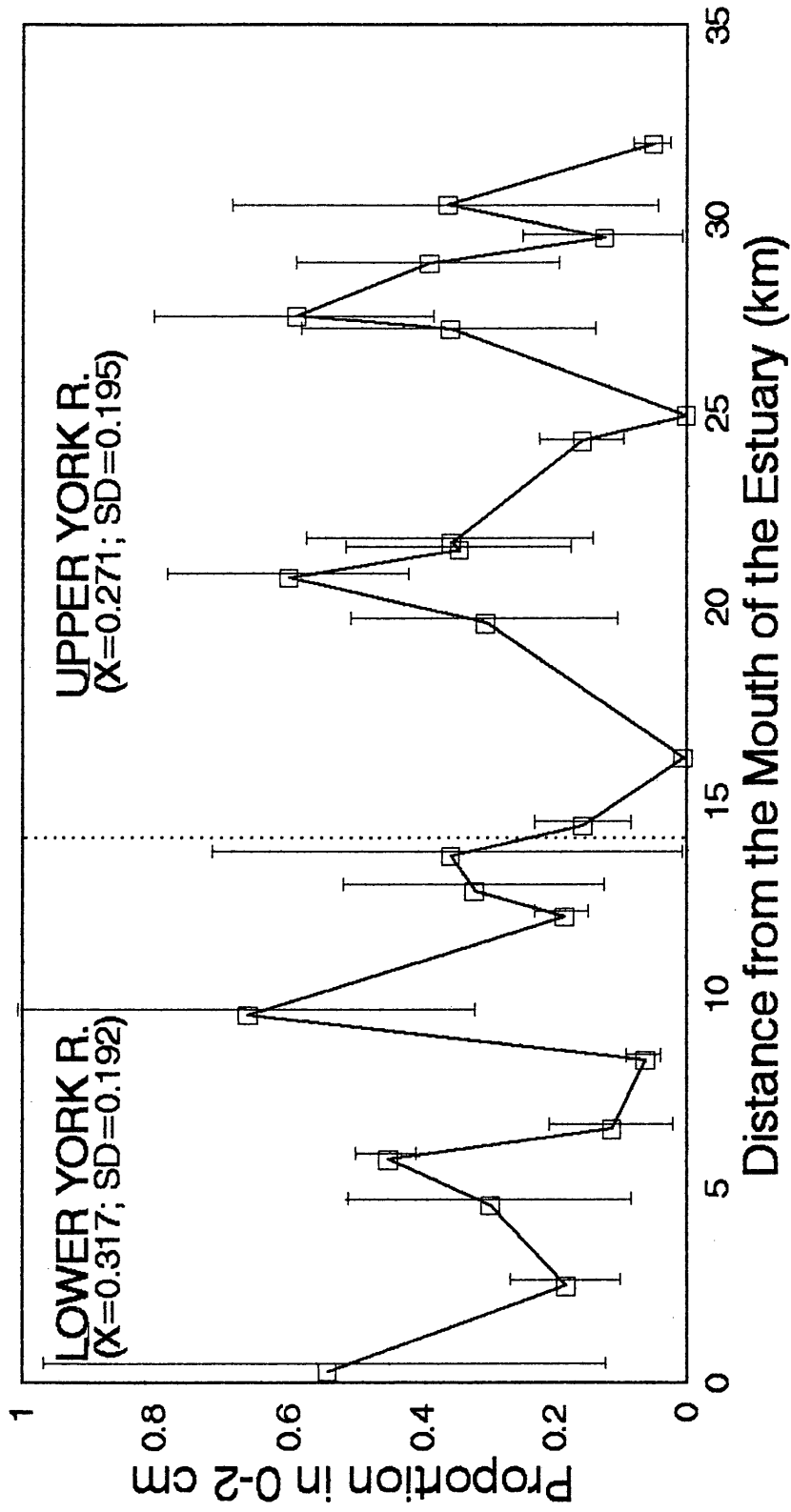
Note: Bars represent standard error.
 $\text{asin}(\text{proportion}) = 33.7 - (0.798 * \text{distance})$; $R_{sq} = 0.36$, $p = 0.002$
Upper and lower estuary were significantly different ($t = 5.07$, $p < 0.0001$).

Figure 9.
VERTICAL DISTRIBUTION OF ANNELIDS
WITHIN THE TOP 10 CM OF SEDIMENT



Note: Bars represent standard error.
 $\text{asin}(\text{proportion}) = 0.900 - (0.024 * \text{dist})$; $\text{Rsqr} = 0.52$, $p < 0.0001$
 Upper and lower estuary were significantly different ($T = 194.5$, $p < 0.0001$).

Figure 10.
VERTICAL DISTRIBUTION OF BIOMASS
WITHIN THE TOP 10 CM OF SEDIMENT

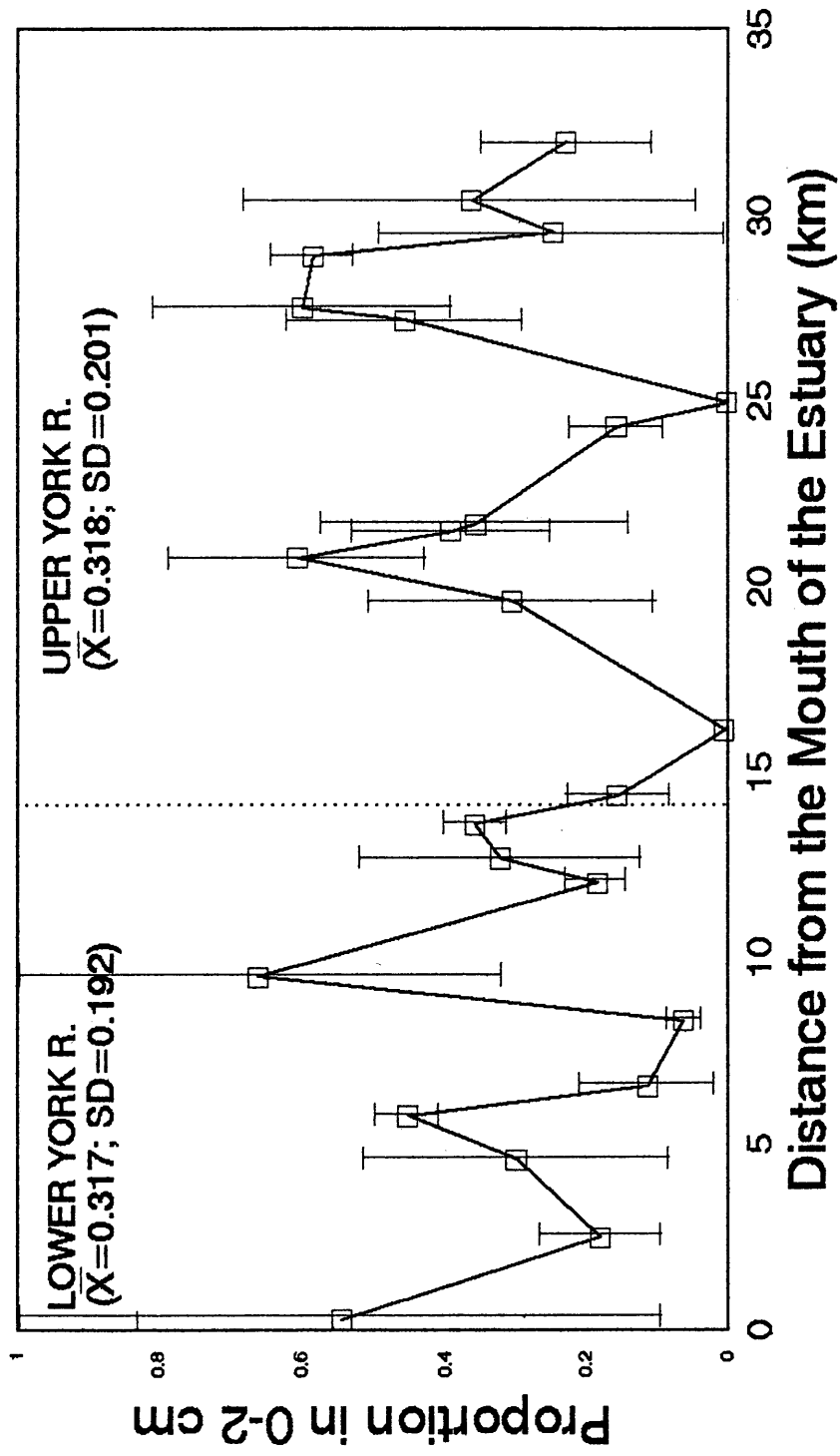


Note: Bars represent standard error.

No significant trend along the estuary was observed.

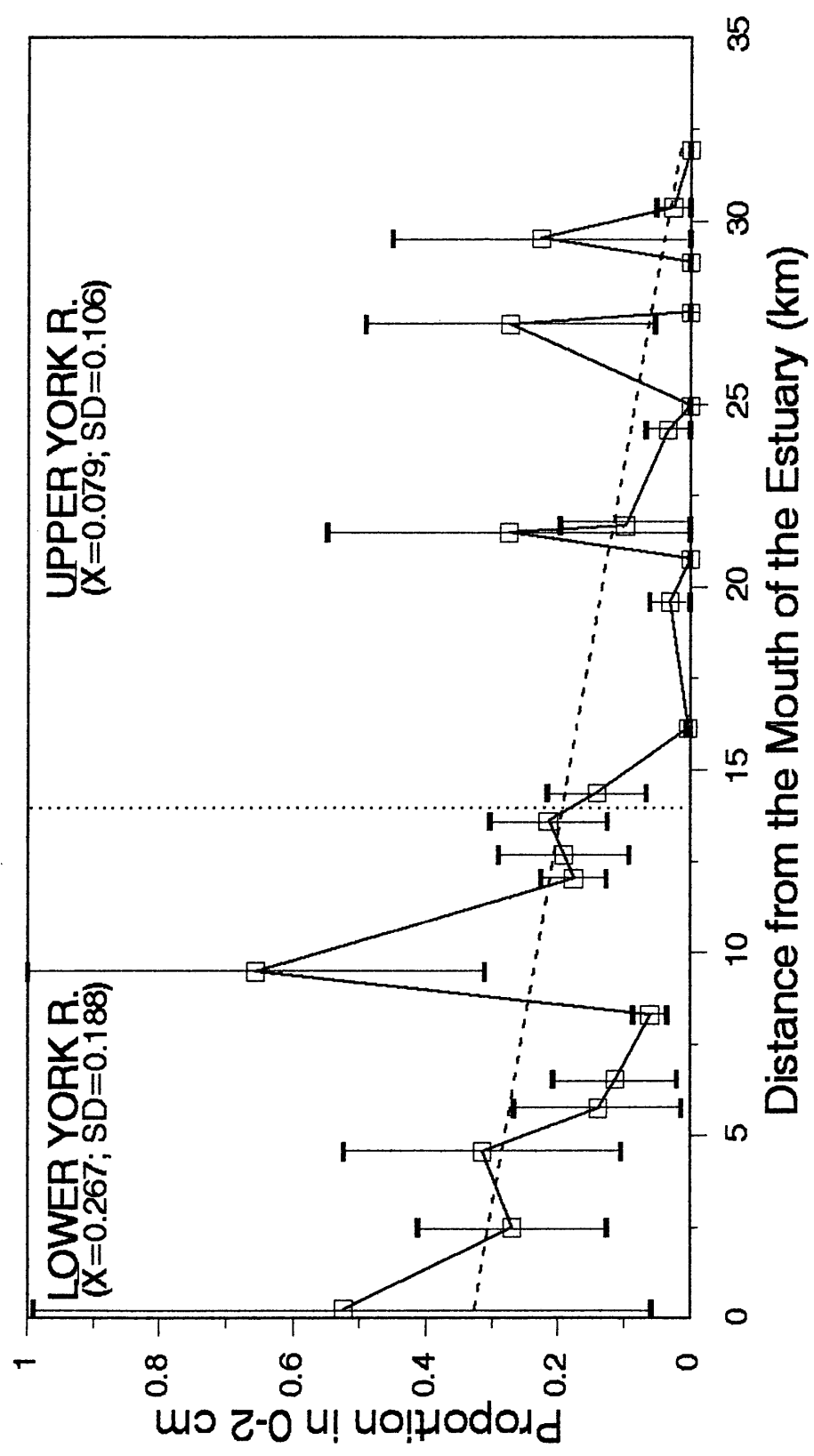
Upper and lower estuary were not significantly different ($T=133.0, p=0.661$).

Figure 11.
VERTICAL DISTRIBUTION OF BIOMASS
WITHOUT BIVALVES



Note: Bars represent standard error.
 No significant trend along the estuary was observed.
 Upper and lower estuary were not significantly different ($t=-0.008, p=0.99$).

Figure 12.
VERTICAL DISTRIBUTION OF ANNELID BIOMASS
WITHIN THE TOP 10 CM OF SEDIMENT



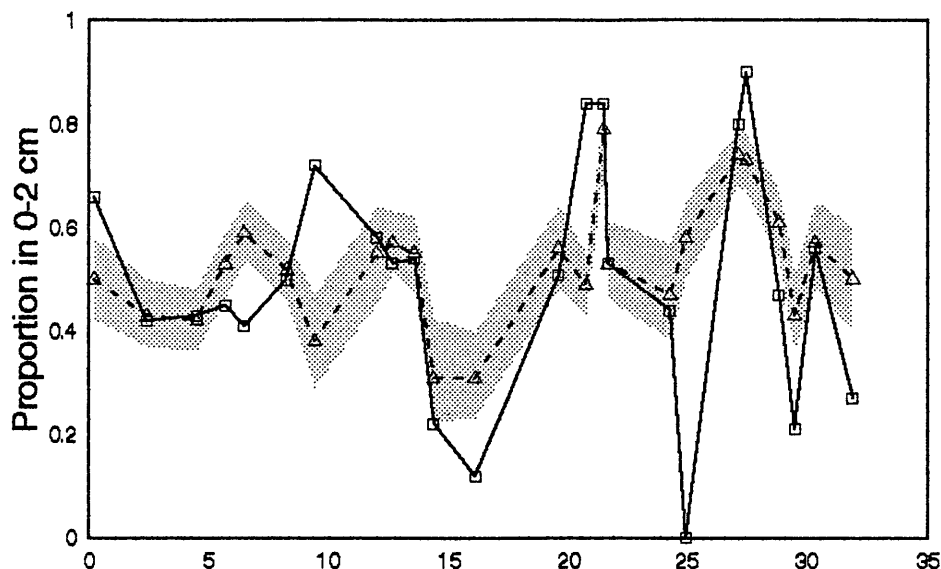
Note: Bars represent standard error.
 $\text{asin}(\text{proportion}) = 19.2 - (0.573 \cdot \text{dist})$; $R_{\text{sqr}} = 0.29$, $p = 0.007$
 Upper and lower estuary were significantly different ($\Gamma = 171.0$, $p = 0.0077$).

Figure 13.

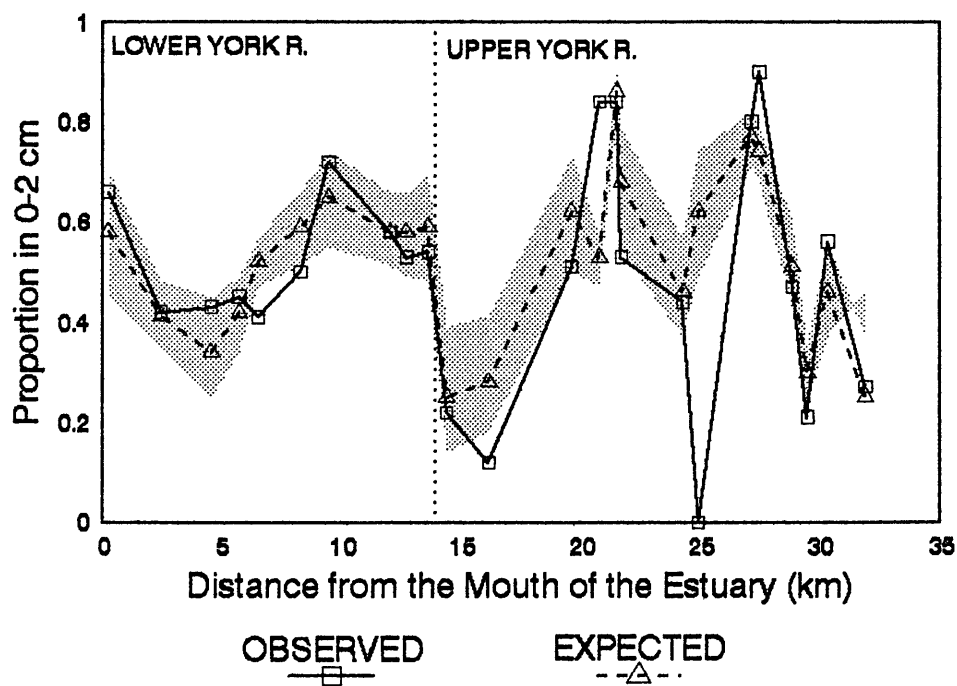
OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF INDIVIDUALS
WITHIN THE TOP 10 CM OF SEDIMENT

ALL VARIABLES MODELED

A) Model for whole estuary



B) Models for Lower and Upper Estuary

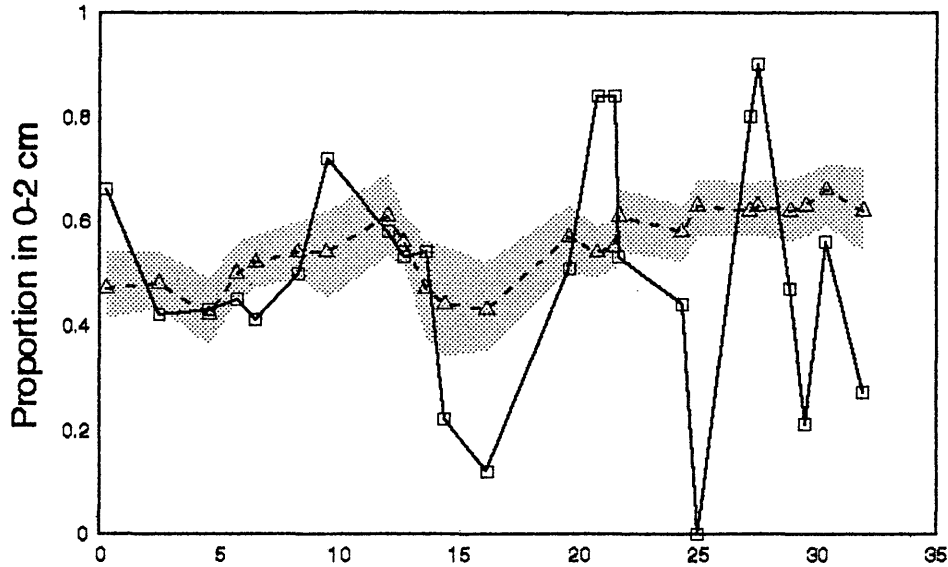


Note: Shaded areas represents the 95% confidence interval for models.

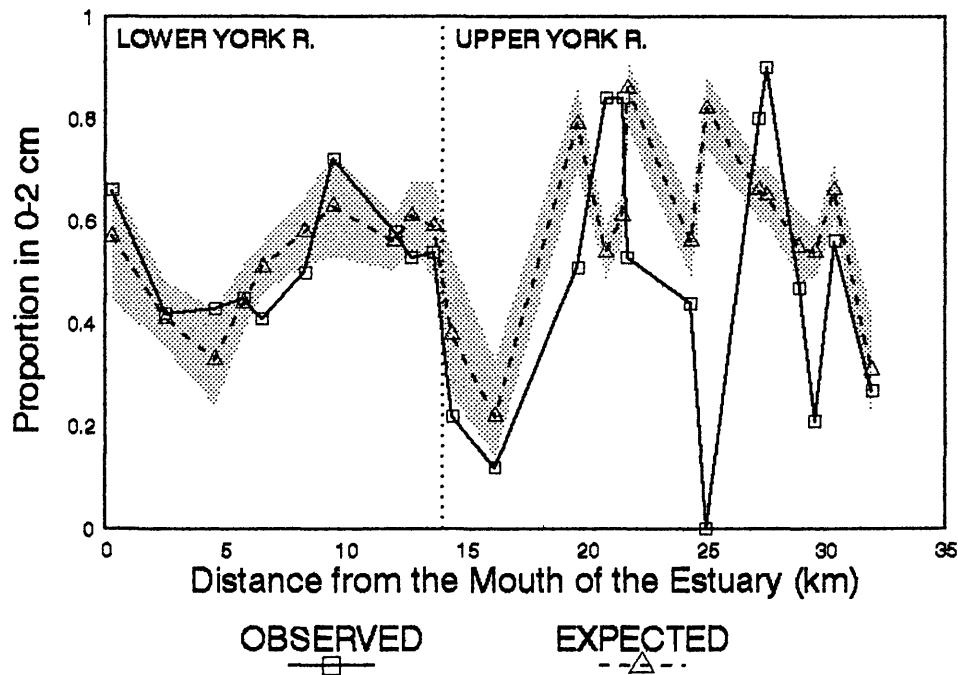
Figure 14.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF INDIVIDUALS WITHIN THE TOP 10 CM OF SEDIMENT PHYSICAL VARIABLES MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

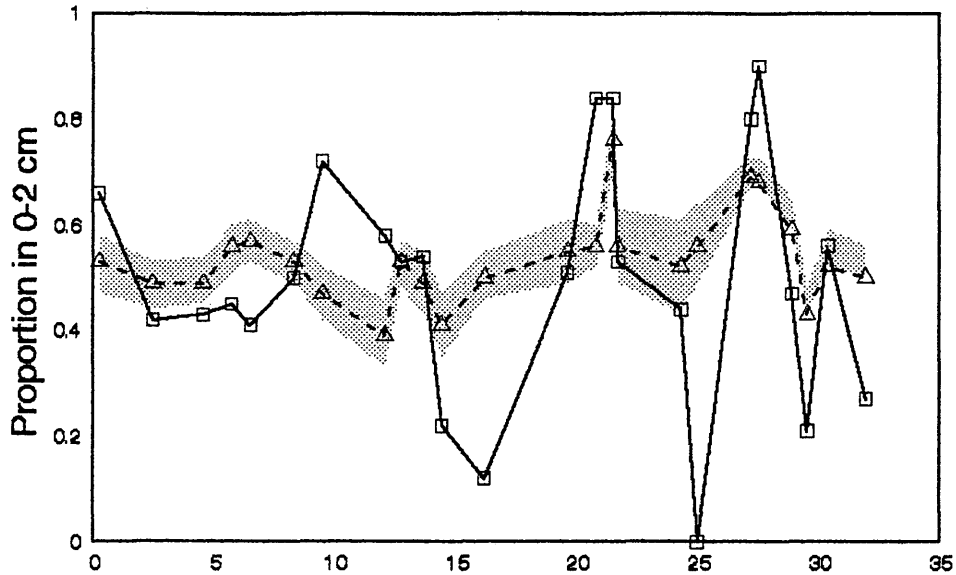


Note: Shaded areas represents the 95% confidence interval for models.

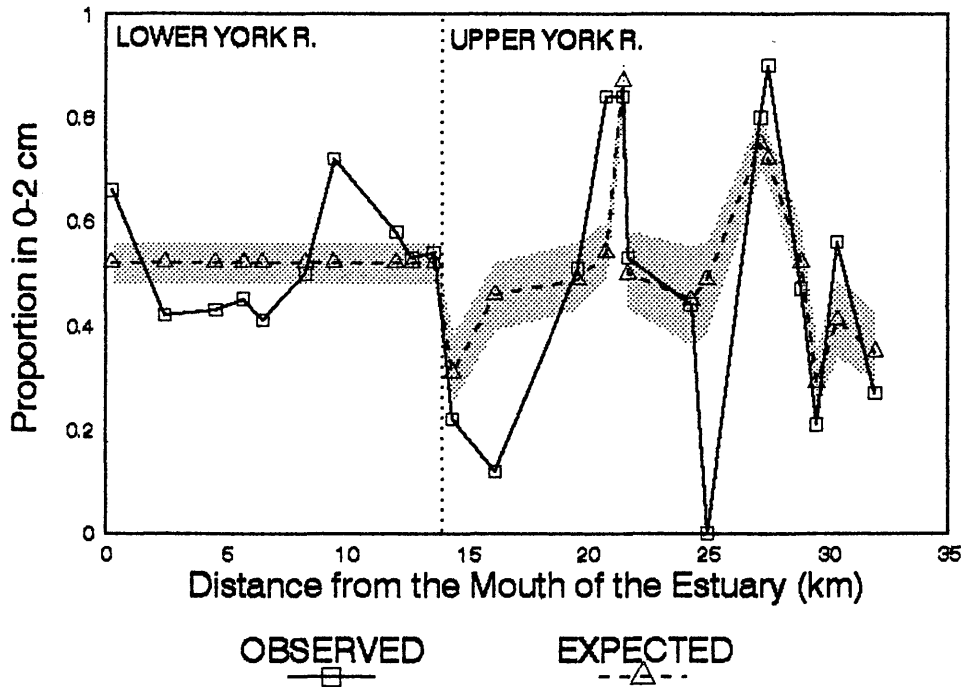
Figure 15.

**OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF INDIVIDUALS
WITHIN THE TOP 10 CM OF SEDIMENT
BIOLOGICAL VARIABLES MODELED**

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

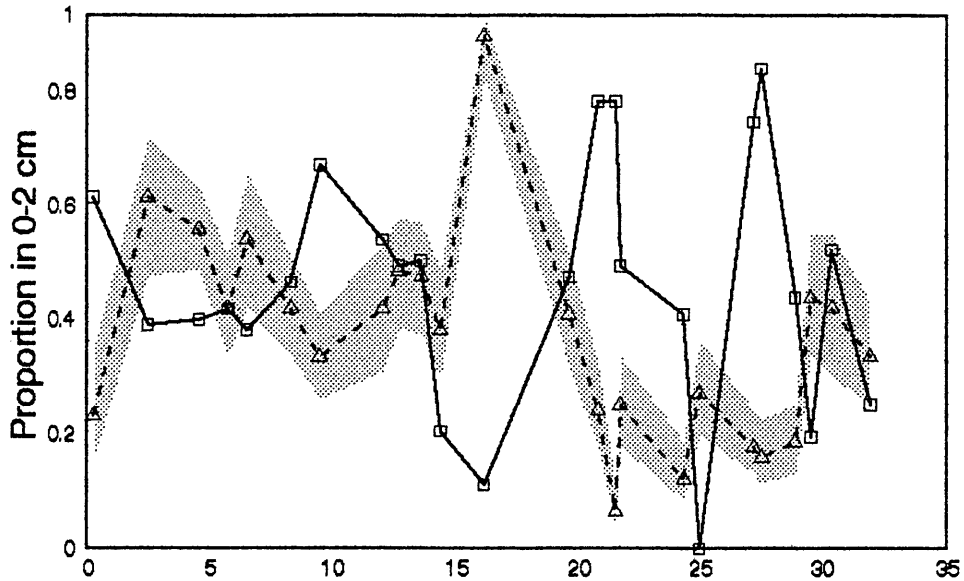


Note: Shaded areas represents the 95% confidence interval for models.

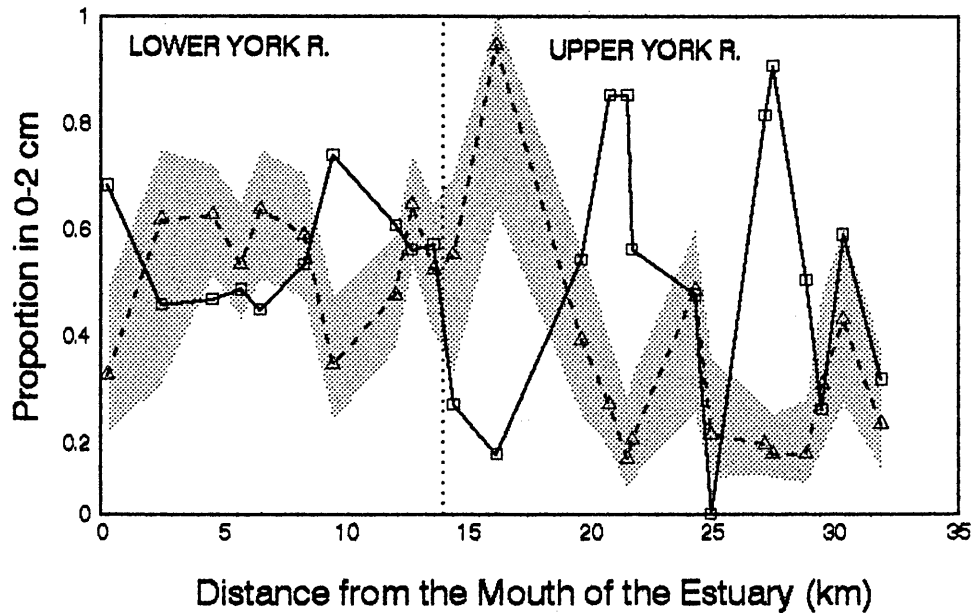
Figure 16.

**OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF INDIVIDUALS
WITHIN THE TOP 10 CM OF SEDIMENT
FEEDING MODES MODELED**

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary



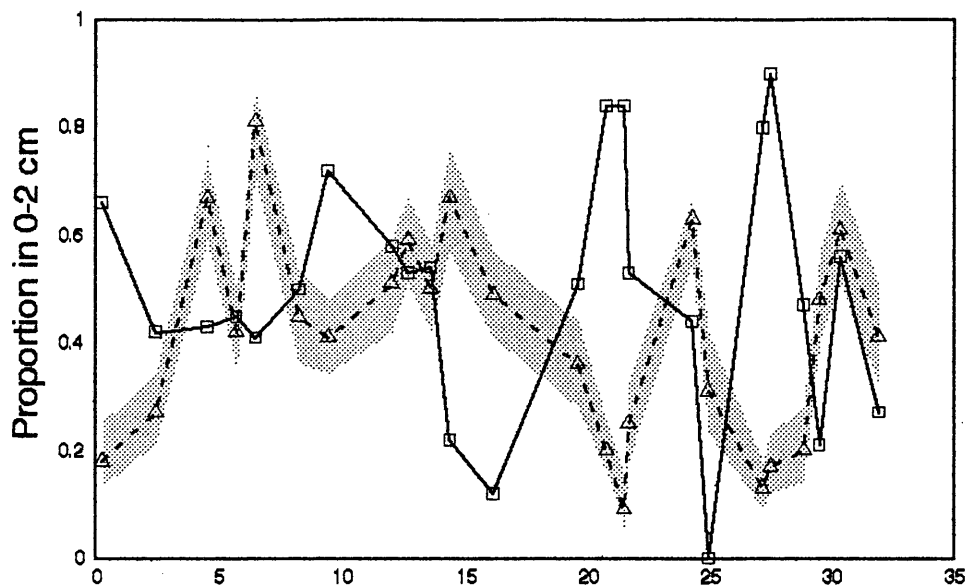
OBSERVED EXPECTED

Note: Shaded areas represents the 95% confidence interval for models.

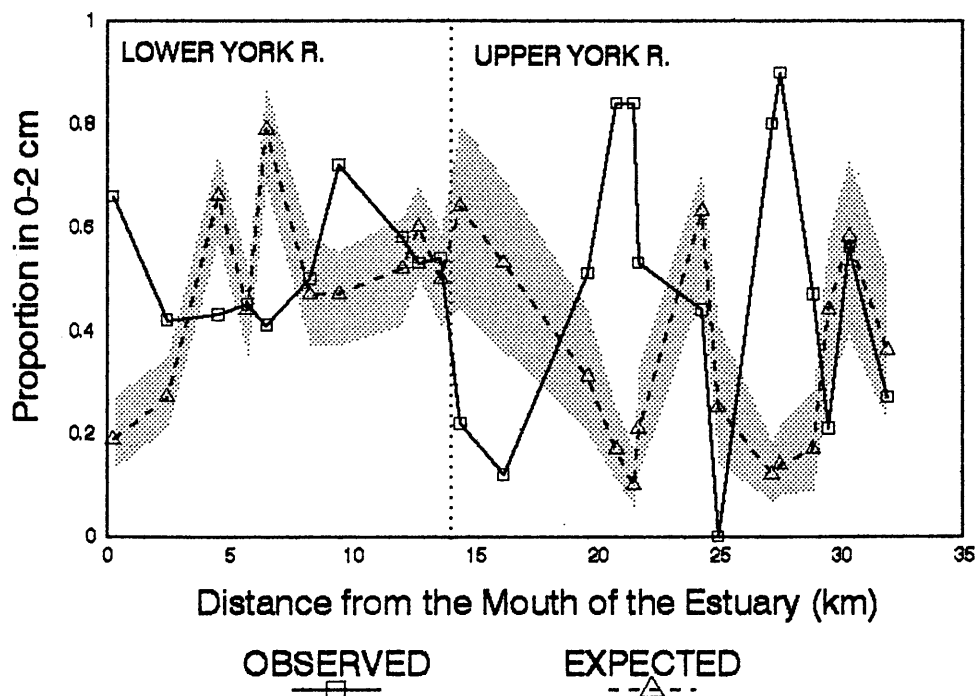
Figure 17.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF INDIVIDUALS WITHIN THE TOP 10 CM OF SEDIMENT LIVING POSITIONS MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

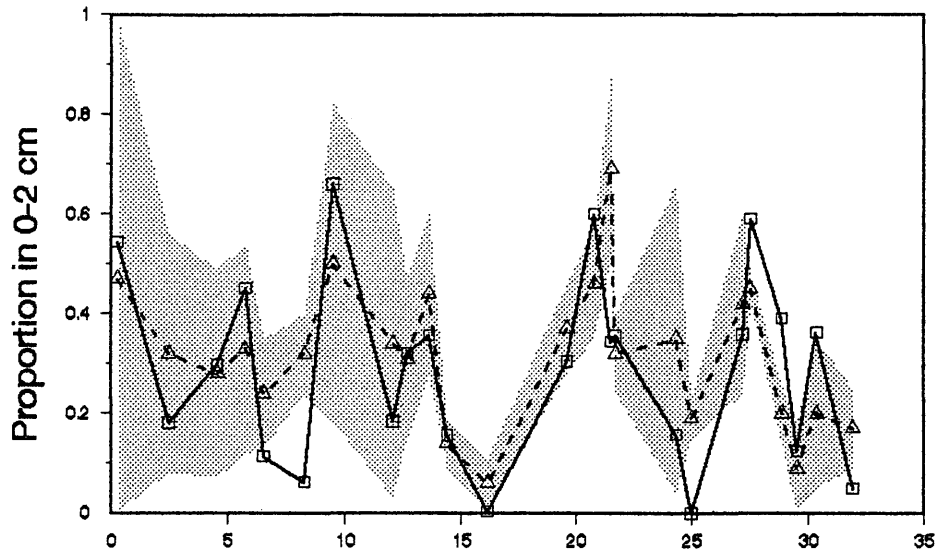


Note: Shaded areas represents the 95% confidence interval for models.

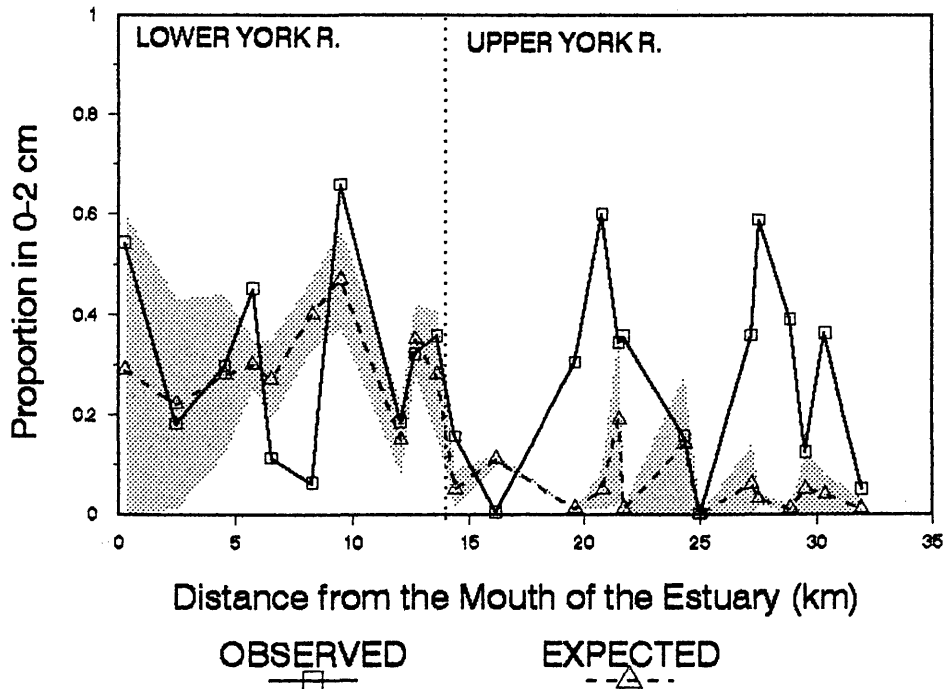
Figure 18.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF BIOMASS WITHIN THE TOP 10 CM OF SEDIMENT ALL VARIABLES MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

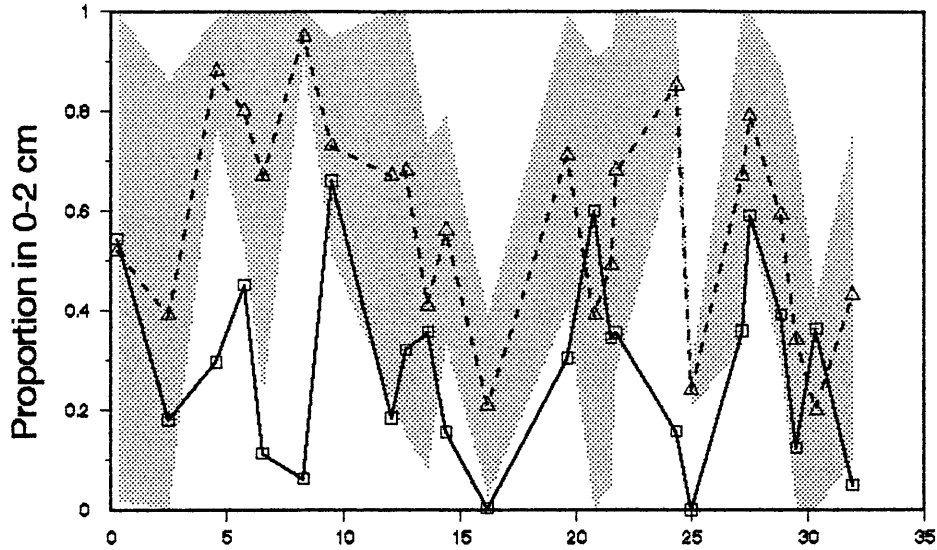


Note: Shaded areas represent one standard deviation of the expected mean.

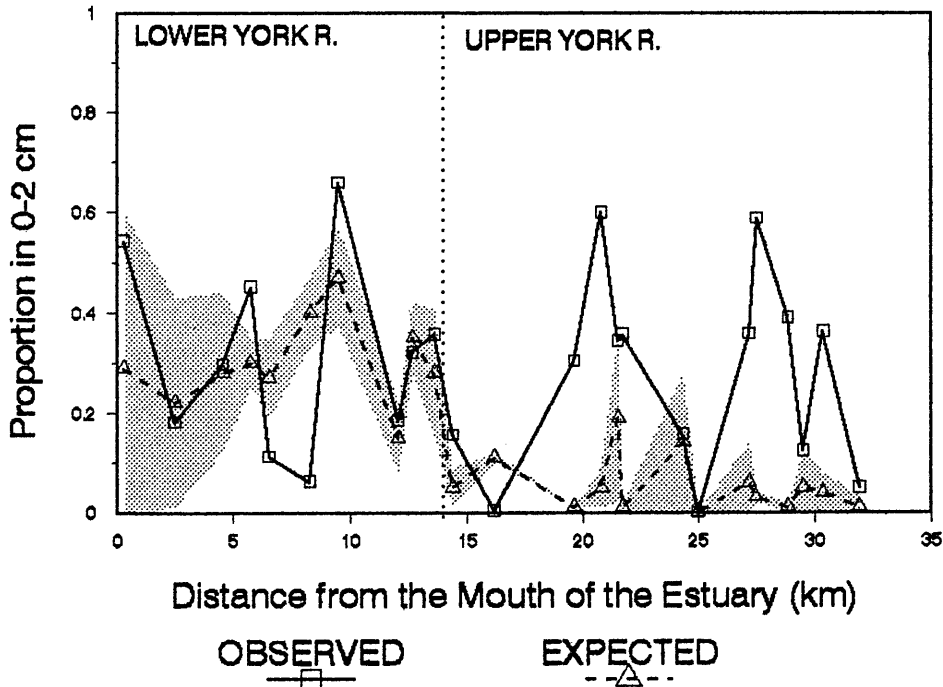
Figure 19.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF BIOMASS WITHIN THE TOP 10 CM OF SEDIMENT BIOLOGICAL VARIABLES MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

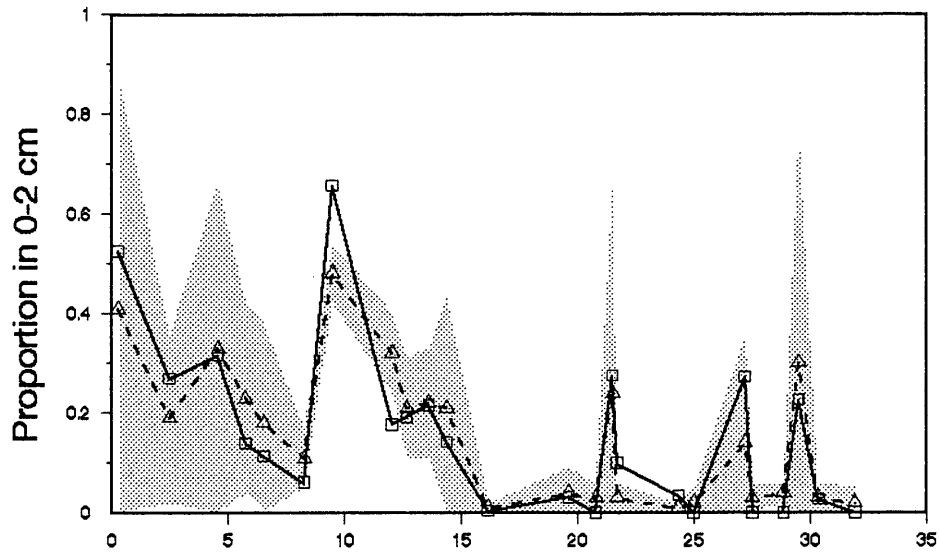


Note: Shaded areas represent one standard deviation of the expected mean.

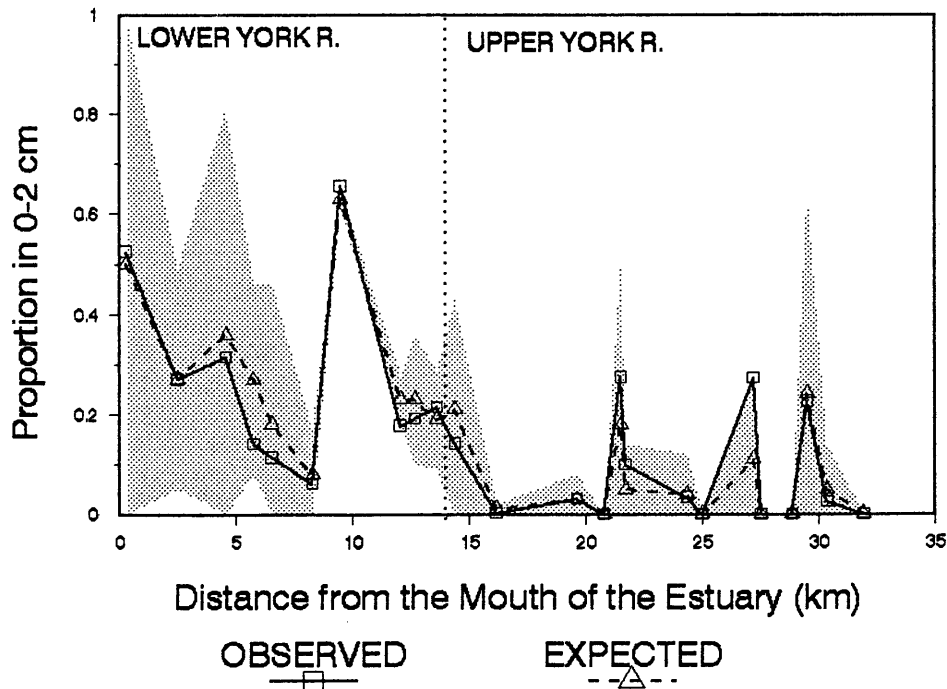
Figure 20.

**OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS
OF ANNELID BIOMASS WITHIN THE TOP 10 CM OF SEDIMENT
ALL VARIABLES MODELED**

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary



Distance from the Mouth of the Estuary (km)

OBSERVED
—□—

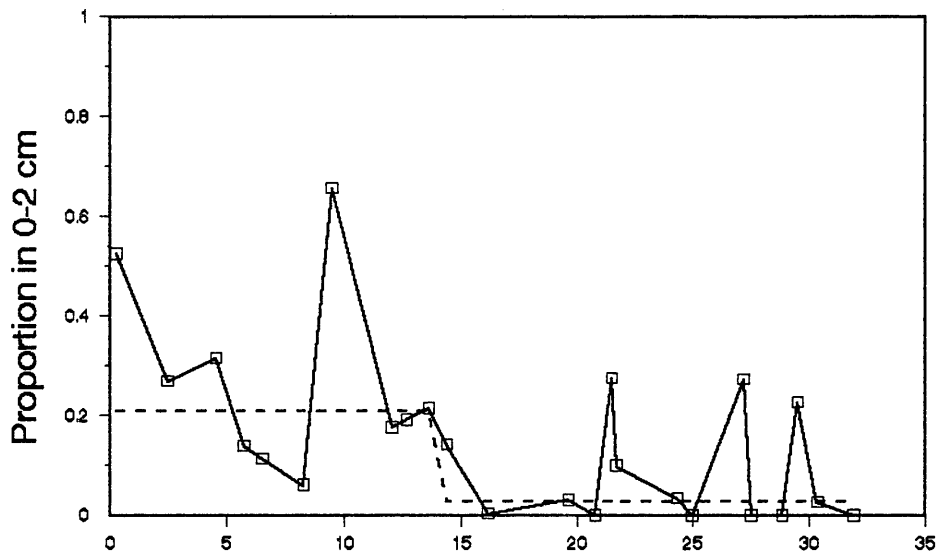
EXPECTED
--△--

Note: Shaded areas represent one standard deviation of the expected mean.

Figure 21.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF ANNELID BIOMASS WITHIN THE TOP 10 CM OF SEDIMENT PHYSICAL VARIABLES MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary

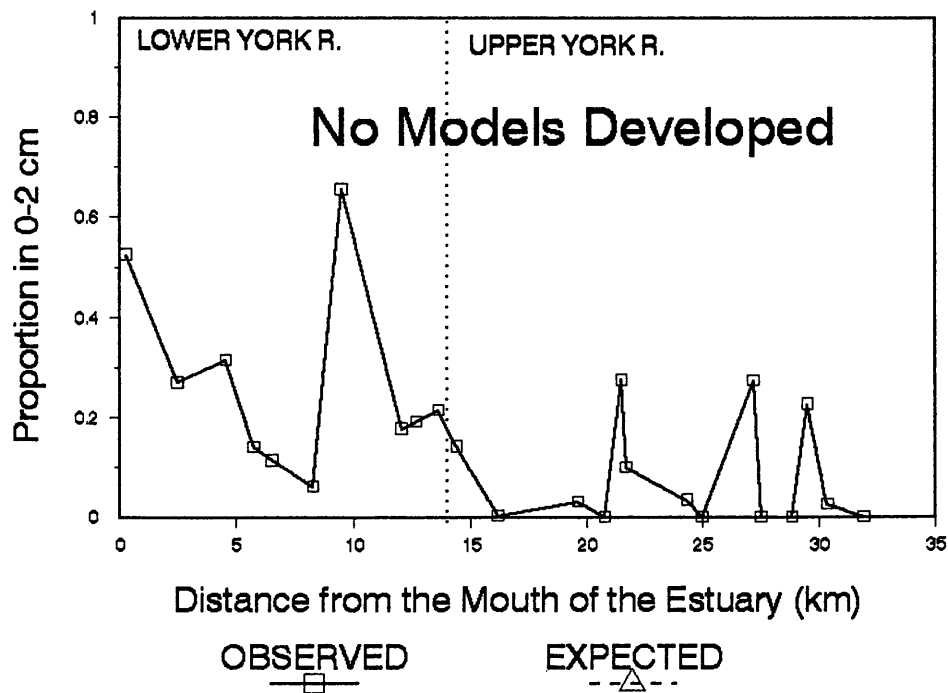
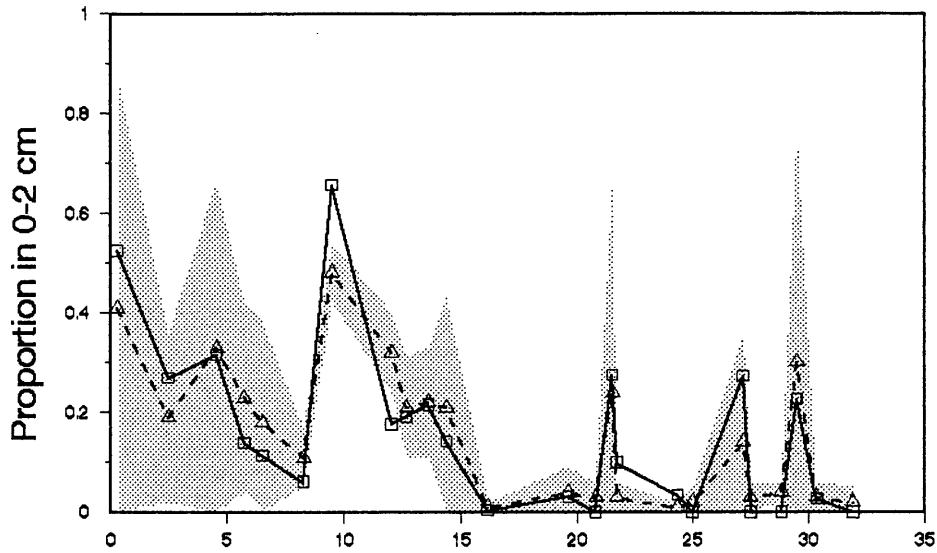


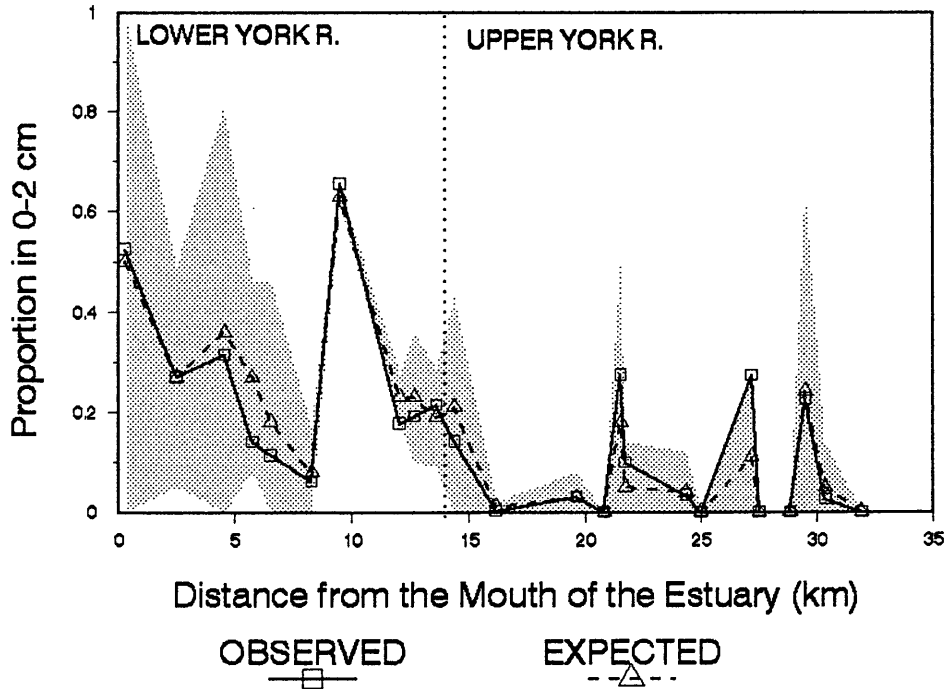
Figure 22.

OBSERVED VS EXPECTED VERTICAL DISTRIBUTIONS OF ANNELID BIOMASS WITHIN THE TOP 10 CM OF SEDIMENT BIOLOGICAL VARIABLES MODELED

A) Model for Whole Estuary



B) Model for Lower and Upper Estuary



Note: Shaded areas represent one standard deviation of the expected mean.

APPENDIX A

**Loran Coordinates and Mean Low Water Depths
For York River Sampling Stations**

Station	West Longitude	North Latitude	Depth (ft)
1	27304.45	41448.06	33
2	27312.21	41451.64	32
3	27315.92	41444.46	47.5
4	27317.50	41435.68	33
5	27321.42	41443.10	33
6	27325.55	41433.43	30
7	27337.50	41445.10	50
8	27339.74	41455.13	38
9	27345.80	41462.39	59
10	27351.30	41464.30	42
11	27360.70	41480.00	32
12	27377.60	41594.20	32
13	27383.50	41523.60	27
14	27387.10	41531.40	26
15	27387.80	41533.10	17
16	27401.40	41554.60	19
17	27405.30	41556.20	17
18	27403.40	41558.4	25
19	27417.40	41577.90	23
20	27417.7	41582.00	21
21	27425.70	41596.10	21
22	27429.20	41601.70	25
23	27435.30	41604.70	19
24	27442.24	41622.34	24

APPENDIX B

Dimensions of Each Species Measured
For Determining Size-Weight Relationships
in York River Macrobenthic Organisms

Organism	Dimension Measured
<i>Anadara</i> spp. (B)	Maximum shell width from hinge to opposite edge
<i>Asabellides oculata</i> (P)	Maximum width of 3rd setiger
Caprellid Amphipods	Length along dorsal midline of head and first two segments
<i>Cirratulus</i> spp. (P)	Maximum width of 1st setiger
<i>Cistena gouldii</i> (P)	Maximum width across operculum
<i>Clymenella torquata</i> (P)	Maximum width of 4th setiger
<i>Cyathura polita</i> (P)	Total length
Decapod Crustaceans	Maximum carapace width
<i>Edotea triloba</i> (I)	Total length
<i>Eteone heteropoda</i> (P)	Maximum width across head
Gammarid Amphipods	Length along dorsal midline of head and first three segments
Gastropods	Total shell length
<i>Glycinde solitaria</i> (P)	Maximum width of 3rd setiger
<i>Glycera</i> spp. (P)	Maximum width of 3rd setiger
<i>Harmathoe extenuata</i> (P)	Maximum width of 3rd setiger
<i>Leucon americanus</i> (C)	Carapace length
<i>Macoma balthica</i> (B)	Maximum shell width from hinge to opposite edge
<i>Macoma mitchelli</i> (B)	Maximum shell length
<i>Mediomastus</i> spp. (P)	Maximum width of 3rd setiger
<i>Mercenaria mercenaria</i> (B)	Maximum shell width from hinge to opposite edge
<i>Micrura ruber</i> (N)	Width across collar
<i>Mulinia lateralis</i> (B)	Maximum shell width from hinge to opposite edge

Organism	Dimension Measured
Mysidacean Crustaceans	Carapace length
<i>Nephtys incisa</i> (P)	Maximum width of 4th setiger
<i>Nereis succinea</i> (P)	Maximum width of peristomium
<i>Ogyrides limnicola</i> (C)	Carapace length
<i>Paraprionospio pinnata</i> (P)	Maximum width of 5th setiger
<i>Pseudeurythoe paucibranchiata</i> (P)	Maximum width of 3rd setiger
<i>Scoloplos</i> spp. (P)	Maximum width of 4th setiger
<i>Sigambra tentaculata</i> (P)	Maximum width of 3rd setiger
<i>Squilla empusa</i> (C)	Carapace length
<i>Streblospio benedicti</i> (P)	Maximum width of 2nd setiger
<i>Stylochus elipticus</i> (N)	Total length
Tubificid Oligochaetes	Length of segments 2-6

B = Bivalve
 C = Crustacean
 I = Isopod
 N = Nemertean
 P = Polychaete

APPENDIX C

Living Positions, Motility and Feeding Modes
of Organisms Collected from the York River

Organism	Feeding Mode	Motility	Living Position	Reference
<i>Acteocina canaliculata</i> (Gastropoda)	O	M	E	37
<i>Acteon punctostriatus</i> (Gastropoda)	C	M	E	44
<i>Ampelisca</i> spp. (Amphipoda)	I	LM	T	25, 36
<i>Anadara</i> spp. (Bivalvia)	SD	M	B	19, 41
<i>Ancistrosyllis jonesi</i> (Polychaeta)	C	M	B	16, 23
<i>Asabellides oculata</i> (Polychaeta)	SD	S	T	16
<i>Bhawania heteroseta</i> (Polychaeta)	C, P-O	M	B	16, 37
<i>Branchiostoma</i> spp. (Cephalochordata)	SD	M	B	7
Capitellidae (Polychaeta)	SSD	M	B, T	16, 23, 37
<i>Caprella</i> spp. (Amphipoda)	I	M	E	9, 10
<i>Cerabratulus lactea</i> (Nemertinea)	C, P-O	M	B	11, 18
Cirratulidae (Polychaeta)	SD	LM	B	16, 23, 37
<i>Cistena gouldii</i> (Polychaeta)	SSD	M	T	16, 23, 37
<i>Clymenella torquata</i> (Polychaeta)	SSD	S	T	16, 23, 37
<i>Corophium</i> spp. (Amphipoda)	I	LM	T	4, 24, 26, 27
<i>Cyathura polita</i> (Isopoda)	O	M	B	8, 13

Organism	Feeding Mode	Motility	Living Position	Reference
<i>Diopatra cuprea</i> (Polychaeta)	O	LM	T	16
<i>Echiura</i>	SD	S	B	3
<i>Edotea triloba</i> (Isopoda)	SD	M	B	28
<i>Eteone heteropoda</i> (Polychaeta)	C	M	E	16
<i>Gammarus</i> spp. (Amphipoda)	I	M	E	4, 14, 22
<i>Glycera americana</i> (Polychaeta)	P-O	M	B	16, 21, 23
<i>Glycinde solitaria</i> (Polychaeta)	C	M	B	23, 37
<i>Gyptis brevipalpa</i> (Polychaeta)	P-O	M	B	23, 37
<i>Harmathoe extenuata</i> (Polychaeta)	P-O	LM	E	16
<i>Heteromastus</i> spp. (Polychaeta)	SSD	M	B	23, 37
<i>Idotea balthica</i> (Isopoda)	H, D, O	N	E	30, 34
<i>Lepidonotus squamata</i> (Polychaeta)	P-O	LM	E	16
<i>Leucon americanus</i> (Crustacea)	SD	M	E	3, 37
<i>Listriella</i> spp. (Amphipoda)	O	M	C	37
<i>Loimia medusa</i> (Polychaeta)	SD	S	T	23, 37
<i>Lyonsia hyalina</i> (Bivalvia)	FF	M	E	29, 32
<i>Macoma balthica</i> (Bivalvia)	I	LM	B	5, 20
<i>Macoma mitchelli</i> (Bivalvia)	I	LM	B	5, 20
<i>Mediomastus</i> spp.	SSD	M	T	16, 37

Organism	Feeding Mode	Motility	Living Position	Reference
<i>Mercenaria mercenaria</i> (Bivalvia)	FF	LM	B	15,36,40
<i>Micropholis atra</i> (Ophiuroidea)	SSD	S	B	37
<i>Micrura ruber</i> (Nemertinea)	C,P-O	M	B	11,37,18
<i>Mitrella lunata</i> (Gastropoda)	P	M	E	31
<i>Mulinia lateralis</i> (Bivalvia)	F	S	E	37
<i>Mysis</i> spp. (Crustacea)	F	M	E	3,38
<i>Nassarius trivittatus</i> (Gastropoda)	O	M	E	37
Nemertinea	P-O	M	B	11,18
<i>Neopanope sayi</i> (Crustacea)	P	M	E	13,19
<i>Nephtys</i> spp. (Polychaeta)	P-O	M	B	16,37
<i>Nereis succinea</i> (Polychaeta)	O	LM	E	16,21,37
<i>Notomastus</i> spp. (Polychaeta)	SSD	M	B	37
<i>Odostomia bisaturalis</i> (Gastropoda)	C	M	E	34,42
<i>Odostomia egonia</i> (Gastropoda)	P-O	M	E	37
<i>Ogyrides limnicola</i> (Crustacea)	I	M	B	19,43
<i>Parametopella cypris</i> (Amphipoda)	I	M	E	2,4,17
<i>Parapleustes</i> spp. (Amphipoda)	I	M	E	2,17
<i>Paraprionospio pinnata</i> (Polychaeta)	I	LM	B	12,23,37
<i>Phoronis</i> spp. (Phoronida)	FF	S	T	37

Organism	Feeding Mode	Motility	Living Position	Reference
<i>Pinnixa</i> spp. (Crustacea)	F	M	B	43
<i>Polydora ligni</i> (Polychaeta)	I	LM	T	12, 16, 37
<i>Prionospio cirrifera</i> (Polychaeta)	I	LM	T	16, 37
<i>Pseudeurythoe paucibranchiata</i> (Polychaeta)	P-O	M	B	23, 37
Pycnogonida (Arthropoda)	C	M	E	3
<i>Saccoglossus kowaleski</i> (Hemichordata)	SSD	S	B	37
<i>Sabellaria vulgaris</i> (Polychaeta)	FF	S	T	16
Sabellidae (Polychaeta)	FF	S	T	16
<i>Scoloplos</i> spp. (Polychaeta)	SSD	M	B	16
<i>Sigambra tentaculata</i> (Polychaeta)	P-O	M	B	23, 37
<i>Spiophanes bombyx</i> (Polychaeta)	I	LM	T	12, 16
<i>Squilla</i> spp. (Crustacea)	P	M	B	3
<i>Stenothoe minuta</i> (Amphipoda)	I	M	E	3, 17
<i>Streblospio benedicti</i> (Polychaeta)	I	LM	T	12, 16, 23
<i>Stylochus elipticus</i> (Turbellaria)	P	M	E	33
Syllidae (Polychaeta)	C	M	E	16
<i>Tubificoides</i> spp. (Oligochaeta)	SSD	M	B	1, 6, 39
Turbellaria	P	M	E	33
<i>Turbonilla interupta</i> (Gastropoda)	P-O	M	E	37
Xanthidae	P	M	E	13, 19

Feeding Modes:

C = Carnivore

D = Detritovore

FF = Filter-Feeder

H = Herbivore

I = Interface Feeder (may filter feed or deposit feed on surface sediments)

O = Omnivore

P = Predator

P-O = Predator/Omnivore

SD = Surface Deposit-Feeder

SSD = Sub-Surface Deposit-Feeder

Motility:

LM = Low Motility

M = Motile

S = Sedentary

Living Positions:

B = Burrowing

C = Commensal

E = Epibenthic/Epizoic

T = Tube-Dwelling

Note: The combination of high motility and burrow-dwelling indicates that the organism actively burrows through the sediment.

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APPENDIX D

**Physical and Chemical Parameters
of York River Sampling Sites**

Station	Distance from Mouth (km)	% Silt & Clay	Depth of RPD (cm) *	Sediment Carbon (mg/g)	Sediment Nitrogen (mg/g)	C:N
1	0.261	58.0	0.30	7.53	1.08	8.13
2	2.482	87.2	0.20	13.19	1.83	8.41
3	4.572	91.4	0.25	13.45	1.79	8.77
4	5.748	96.2	0.40	16.43	2.17	8.83
5	6.531	89.1	0.30	15.39	2.10	8.55
6	8.295	94.0	0.75	16.93	2.21	8.94
7	9.471	79.2	1.00	18.44	2.18	9.87
8	12.018	92.4	1.10	16.75	2.97	6.58
9	12.671	89.1	0.70	17.95	2.45	8.55
10	13.585	61.7	0.20	12.95	1.78	8.49
11	14.369		0.25	19.08	2.61	8.53
12	16.133	61.1	0.70	20.41	2.31	10.31
13	19.594	61.2	1.10	15.74	2.10	8.74
14	20.770	69.6	2.30	20.93	2.52	9.69
15	21.488	71.9	1.50	19.12	2.33	9.57
16	21.684	73.1	0.50	21.35	2.62	9.51
17	24.297	52.9	0.10	8.13	0.90	10.54
18	24.950	77.2		24.43	2.93	9.73
19	27.171		1.00	22.42	2.68	9.76
20	27.497	69.8	0.10	19.87	2.32	9.99
21	28.869	81.0	1.80	27.36	3.08	10.36
22	29.522	71.0	0.20	26.87	3.16	9.92
23	30.371	70.7	0.80	24.12	2.82	9.98
24	31.939	71.1	0.40	23.38	2.52	10.82

*Average of three measurements.

APPENDIX E

APPENDIX F

APPENDIX G

Length-Weight Regressions

<u>Species</u>	df	(total N)	R ²	Equation
Acteocina canaliculata	15	17	.44	W=.06555L ^{1.87}
Anadara spp.	5	7	.89	W=.2554L ^{1.94}
Asabellides oculata	11	153	.87	W=.235L ^{2.37} (linear)
Corophium spp.	11	23	.71	W=.116L ^{3.58}
Edotea triloba	12	23	.79	W=.03183L ^{1.67}
Eteone heteropoda	18	81	.69	W=20.949L ^{3.64} (linear)
Gammarid amphipods	18	56	.81	W=.1402L ^{1.66}
Glycera spp.	5	8	.96	W=2.8481L ^{3.41} (linear)
Glycinde solitaria	14	22	.68	W=23.421L ^{2.66}
Leitoscoloplos spp.	28	80	.80	W=2.082L ^{2.00}
Leucon americanus	42	306	.45	W=.08904L ^{2.10}
Macoma balthica	144	244	.96	W=.0009215L ^{3.65}
Macoma mitchelli	20	24	.87	W=.00755L ^{2.79}
Mulinia lateralis	6	8	.97	W=.05753L ^{2.12}
Ogyrides limnicola	27	30	.69	W=.03198L ^{3.12}
Paraprionospio pinnata	16	27	.92	W=1.775L ^{3.00}
Pseudeurythoe paucibranchiata	17	23	.68	W=.2157L ^{6.84}
Streblospio benedicti	12	189	.96	W=1.86L ^{3.75}
Turbonilla and Odostomia spp.	5	7	.89	W=.0257L ^{2.49}