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Ecology of the benthos of the lower Chesapeake Bay (Maryland)

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ECOLOGY OF THE BENTHOS OF THE LOWER CHESAPEAKE BAY

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ECOLOGY OF THE BENTHOS OF THE LOWER CHESAPEAKE BAY

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

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

by
Linda C. Schaffner
1987

APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

Linda C. Schaffner

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This dissertation is dedicated to my husband Stephen and my dad. Their love and encouragement helped along the way.

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ABSTRACT

The spatially complex lower Chesapeake Bay estuary is characterized by a variety of bottom types and hydrodynamic regimes. To account for this physically-induced variability a benthic habitat delineation scheme was developed based on existing knowledge of physical and geological characteristics. Within the context of this scheme a series of studies were conducted to identify biotic response to and interactions with the physical, chemical and geological gradients that characterize the lower Chesapeake Bay. These studies characterized organism distribution and abundance patterns within the lower bay and identified processes controlling those patterns. The biological community of the polyhaline basin habitat, an area characterized by moderate tidal, but little wave-induced bottom disturbance was defined and described for the first time. This community is characterized by large tube and burrow builders, epifaunal and commensal organisms, shallowly-distributed, short-lived species and deeply-dwelling predators. The basin is also the preferred habitat of overwintering blue crabs and an area where biotic sediment reworking generally exceeds physical reworking. The results of these studies suggest that within the lower Chesapeake Bay estuarine system, the relative importance of biological versus physical processes in maintaining the structure and dynamics of estuarine benthic communities will be greatest in the basin habitat.

ECOLOGY OF THE BENTHOS OF THE LOWER CHESAPEAKE BAY

CHAPTER 1.

AN OVERVIEW OF THE DISSERTATION

INTRODUCTION

Considerable scientific attention has focused on estuaries because they are biologically productive habitats of commercial and recreational importance. Proximity to major population centers and relatively low flushing rates make most estuarine systems traps for fine sediments and therefore susceptible to pollution and eutrophication. While the accessibility of estuaries makes them easy to study, they are, unlike most shelf and deep sea environments, characterized by sharp physical and biological gradients. Formulation and testing of hypotheses regarding the mechanisms controlling benthic community structure and function depend on an adequate perception of organism response to both environmental heterogeneity and species interactions. As a first step, ecologists often infer a response from distribution patterns, however, the characteristic spatial and temporal variability in the estuary can make these patterns difficult to discern (Boesch, 1971; Boesch et al., 1976; Diaz, 1984; Holland, 1985; Holland et al., 1987). Overall, a meaningful evaluation of the relative importance of physical and biological processes in estuarine benthic community dynamics necessitates careful characterization of many potential sources of variation (eg. Holland et al., 1987)

Most early studies of the distribution and abundance patterns of benthic organisms in estuaries were done in Europe and South Africa (see reviews in Remane and Schlieper, 1971 for the Baltic Sea; Perkins, 1974 for British estuaries and Day, 1981 for the estuaries of South Africa). In 1967, Carriker published a perspective on estuarine ecology that included information from the few early studies done in estuaries of the United States. Clear relationships between organism distribution or patterns of diversity and the salinity gradient in estuaries and brackish seas were demonstrated in these early works (Remane, 1934; Remane and Schlieper, 1971). Estuaries were characterized as physically unstable habitats which are stressful to resident organisms (Burbanck et al., 1956; Sanders et al., 1963; Carriker, 1967). Concurrently with these estuarine studies, Sanders (1956, 1958) and others (see review in Rhoads, 1974) were documenting relationships between organism distribution patterns and sediment type in shallow water coastal areas. From his results in South African estuaries and other protected, but high salinity, coastal areas, Day (1959, 1964; Day and Morgans, 1956) showed that the distribution patterns of some organisms within the estuary were a function of sediment stability and a change in the hydrodynamic regime (moderation of energy input to the bottom relative to the adjacent shelf) rather than a function of the salinity gradient.

Until relatively recently, little was known about the physical and geological processes governing the distribution and abundance of benthic organisms in the main-stem of the lower Chesapeake Bay (ie. the Virginian waters). In the early 1960's sampling by Wass and others, funded by the U.S. Army Corps of Engineers, provided the first quantitative evaluation of benthic geological and biological patterns for a region of the bay near to the mouth of the Rappahannock River (Virginia Institute of Marine Science, 1967). Wass did not find strong relationships between sediment type and the distribution patterns of numerically dominant fauna at his study site (where salinities are transitional between meso- and polyhaline, ca. 13-20 ppt), but he did observe strong seasonal fluctuations in abundance, and he found that sandy areas contained more species and generally more individuals than muddy areas (based on individuals retained on a 500 um screen). The only previously published benthic biological investigations for the lower Chesapeake Bay were those of the United States Bureau of Fisheries (Cowles, 1930), but all faunal samples collected during that study utilized a beam trawl, which only poorly samples the infaunal benthos. However, Cowles did find some common estuarine species and the large tube-building polychaete <u>Chaetopterus variopedatus</u> in the main-stem of the lower bay.

During the late 1960's and early 1970's Boesch and others began a series of investigations to identify spatial and temporal patterns for fauna near the baymouth, in the Hampton Roads area and in the York River (Boesch 1971, 1973, 1977; Boesch et al., 1976a,b). Based on this work and reference to the results from other areas worldwide, Boesch generalized regarding benthic communities in the Chesapeake Bay. Specifically, for the polyhaline zone he stated that: 1) species are nearly individualistically distributed, with each species responding to environmental conditions, but not as part of a functioning unit, 2) most organisms in the polyhaline zone are euryhaline marine species that are more abundant in the estuary than they are on the adjacent shelf and 3) a group of short-lived, relatively opportunistic species (Boesch's 'euryhaline opportunists') are only sporadically abundant in the polyhaline zone, apparently being disfavored by biotic interactions with long-lived 'equilibrium' fauna (except in shallow or disturbed regions of the polyhaline zone).

The EPA sponsored Chesapeake Bay Program which began in the late 1970's provided significant research money for evaluation of geological and biological characteristics in the main-stem of both the upper (Maryland portion) and lower bay. As a result, surface sediment characteristics are now well documented (Byrne et al., 1982) and some insight regarding baywide faunal characteristics, particularly faunal depth distribution patterns was provided (Reinharz and O'Connell, 1981; Nilsen et al., 1982). These studies demonstrated that organisms in the lower bay represent a wide diversity of functional groups that occupy many living positions throughout the upper 15 to 30 cm of the sediment column.

A series of studies by investigators at Old Dominion University provided additional evidence regarding both temporal and spatial distribution patterns and community structure for benthic organisms in some shallow habitats in the main-stem of the lower bay (Ewing and Dauer, 1982; Tourtellotte and Dauer, 1983). They also analyzed a limited number of samples from deeper areas of the main-stem region (Dauer et al., 1984). Using a Shipek grab, which generally exhibits shallow sediment penetration, they were able to identify two distinct assemblages in the lower bay, a sand assemblage and a silty-sand assemblage. The dominants listed for their study include primarily shallow-living species and the maldanid Clymenella torquata.

An interdisciplinary investigation of benthic boundary layer characteristics and processes in the lower bay begun during the early 1980's produced a subenvironment classification scheme based on known or inferred hydrodynamic regimes and observed bottom types (Wright et al., 1987). Subenvironments ranging from relatively quiescent fringe embayments to high energy near-shore coastal areas were identified. Significantly, Wright et al. classified as distinct subenvironments the tributary mouths and main-stem areas of the bay because they are likely to be characterized by dissimilar hydrodynamic regimes. Subsequent investigations, conducted during the late winter of 1985, showed that the bay-stem plains subenvironment was characterized by tidally dominated flows coupled with a low amplitude, long period swell that appeared to emanate from the bay entrance (Boon et al., 1987). Similar analyses of data from the lower end of the York River show boundary layer flow to be tidally dominated with little evidence of wave-induced flow modifications (Wright, personal communication).

Extensive investigations to characterize the benthos of potential dredge material disposal sites and the surrounding regions of the main-stem of the lower bay began in November 1983 with funding supplied by the U.S. Army Corps of Engineers. In conjunction with the Benthic Boundary Layer Program (funded by the Commonwealth of Virginia), this investigation provided an important opportunity to evaluate biologic and geologic processes in the lower Chesapeake Bay.

Preliminary observations made during both of the latter studies suggested that some gaps in our knowledge of the biology and ecology of the benthos existed. For instance, detailed sampling of sediments in the lower bay by Byrne et al. (1982) indicated a higher level of spatial complexity and a higher diversity of bottom types in the lower bay main-stem than had previously been documented. Response of the benthos to these varying bottom types and to the hydrodynamic regimes characterizing subenvironments delineated by Wright et al. (1987) was unclear. Additionally, the polyhaline basin (ca. 18-28 ppt) or bay-stem plains region, an expansive area characterized by well sorted, silty-very fine sands not found elsewhere in the bay, had been sparsely sampled. Thus, it seemed an appropriate time to examine or re-examine benthic biological information for the lower Chesapeake Bay region and especially the polyhaline zone and then, given new findings, to reassess previous generalizations regarding the benthos of estuaries.

Specifically, this study had three major objectives. They were:

- Develop and test a benthic habitat delineation scheme for the lower Chesapeake Bay - tributary system based on existing knowledge of physical and geological characteristics and processes. (Chapters 2 and 3)
- Characterize the structure of the macrobenthic community at the Wolf Trap study site, an area located centrally within the polyhaline basin. (Chapter 4)
- Reassess generalizations regarding factors or processes governing the distribution and abundance of benthic organisms in the estuary with particular reference to the polyhaline estuary. (Chapters 2 - 4)

APPROACH

To develop a general scheme for studying and interpreting biological processes in the spatially complex lower bay I expanded and refined classification schemes previously presented for physical and geological processes. Benthic habitats in the lower bay - tributary system were delineated on the basis of existing physical and geological information as presented or summarized in Nichols (1972), Byrne et al. (1982) and Wright et al. (1987), 30 year averaged salinity trends (Stroup and Lynn, 1963) and reference to bathymetry as determined from navigation charts. Extensive quantitative benthic sampling on a bay-wide basis was not logistically feasible, so other methods were employed to evaluate the the usefulness of the scheme for investigations of benthic biological processes.

An integrated view of the physical, geological and biological processes operating within each subenvironment was obtained by examining patterns of biogenic sediment reworking, the types of organisms and biogenic structures present and the relative importance of biogenic versus physical reworking in 366 x-radiographs made from sediment cores collected between 1978 and 1986. With some knowledge of sediment accumulation rates, the potential sources of sediments, the types and magnitude of energy input to the bottom and general faunal characteristics it is possible to elucidate the rates of processes governing strata formation and the relative magnitude of each process. If biogenic structures were present in the original cores, records were preserved in x-radiographs making it easy to identify areas characterized by tube and lined-burrow builders, or areas where species excavate subsurface voids. The presence or absence of such structures aids in the interpretation of faunal ecological relationships because large tube and burrow builders and deep deposit-feeding species that excavate voids typify the later stages of community development (Rhoads et al., 1978). These organisms are members of what Boesch (1977) called the estuarine 'equilibrium' fauna. Short-lived, shallow-living 'opportunistic' species (eg. some capitellid and spionid polychaetes) generally build only thin walled, temporary tubes or small, unlined burrows which are difficult to see in x-radiographs. Thus, this part of my study provides insight into the applicability of the habitat delineation scheme in the identification of processes influenced by biological factors as well as in the identification of the processes that influence the distribution and abundance of differing types of benthic organisms.

To directly test the usefulness of the habitat delineation scheme as a means of predicting patterns of faunal abundance, dredge sampling for overwintering blue crabs, using a stratified random sampling design encompassing 94 stations, was conducted during the winter of 1985-86 in a portion of the main-stem that contains 3 of the major habitat types (shoals and spits, basin and channel). Blue crab sex ratios were also examined and crab abundance patterns through the winter were documented at two fixed sites.

To address my second major objective, I conducted a quantitative survey of the benthic fauna at the Wolf Trap study site, an area located centrally within the polyhaline basin of the lower Chesapeake Bay. Box cores for fauna, biomass and x-radiography were collected at fixed stations on 5 cruise dates during a 13 month period (November

1983 to November 1984). Sediment profile photographs were taken on the same sampling schedule. These samples, in conjunction with photographs and samples collected by divers between June 1984 and December 1986, were used to characterize faunal density and biomass, community composition and diversity, small-scale horizontal and vertical distribution patterns and spatial relationships among species.

Conclusions and insights from investigations addressing the first two objectives are used to evaluate some of the previous generalizations regarding the factors controlling the distribution and abundance patterns of estuarine organisms, particularly with respect to the polyhaline zone.

RESULTS AND DISCUSSION

Chapter 2

The delineation of habitats in the lower bay - tributary system resulted in the identification of 6 major subenvironments (=habitats, in the biological sense) and 6 major estuarine zones. The 6 major subenvironments are: 1) the shallow and generally high energy shoals and spits; 2) the deep channel areas, generally characterized by tidally scoured bottoms, but depositional flanks; 3) the troughs, deep holes that are not involved in any obvious circulation pathways; 4) the basin, an area characterized by moderate input of tidal energy; 5) fringe embayment areas that are relatively quiescent, and often sites of sediment accumulation and 6) the deep terrace, a relatively deep sandy area in the northern end of the lower bay that is apparently a relict feature from a lower stand of sea level. The characteristic and distinctly different sediment records as preserved in x-radiographs, demonstrate the varying contributions of physical, geological and biological processes in each subenvironment. Changes in the record that were concordant with the salinity gradient were also apparent when one subenvironment spanned a range of estuarine zones.

Biological mixing rates and the density of biogenic structures (tubes, burrows and voids) were highest in the polyhaline basin of the lower bay where dense populations of "conveyor-belt" maldanid polychaetes and other large, long-lived species are among the dominant organisms. This is also the area of the lower bay where average faunal biomass is highest. In fringe embayment habitats, where interface feeding organisms (eg. the tellinid bivalve Macoma balthica) can completely pelletize near-surface sediments, biotic mixing rates are also high, but because most mixing is attributable to Macoma, it is limited in vertical extent.

Sediment reworking and structuring processes in other habitats of the lower bay - tributary system are mostly physically controlled and biogenic structures are generally rare or absent. In the shoal and spit habitat the predominant features in radiographs were wave and current induced cross-bedding. The silty-fine sand sediments of channel flanks in the high salinity estuarine zones may be homogenized by biotic mixing, but the small, generally motile, fauna characterizing the muddier sediments found in channel environments in low salinity areas contribute little to sediment mixing processes. Similarly, biotic mixing is low and biogenic structures are rare in the muddy, but relatively high salinity trough environment adjacent to the polyhaline basin.

While a thorough understanding of physical, geological and biological processes within the estuary is necessary to adequately interprete the near-surface stratigraphic record this record contains much information about the physical environment with which the resident benthos are associated and information on how organisms rework or otherwise alter sediment structure. An important finding from this study is that tidal reworking of the silty, very fine sand basin sediments can result in physically laminated sediments at some times. However, the preponderance of radiographs from this habitat exhibiting mixed sediments indicates that relatively high rates of biotic mixing are likely to prevail during most seasons. It is now also clear that large tube-builders and other species that produce biogenic structures can be abundant where moderate tidal energy is characteristic, but that they are rare or absent when wave energy predominates or where the accumulation of fine silts and clays is high.

Chapter 3

Direct sampling of overwintering blue crabs in a portion of the lower bay that contains 3 of the major habitat types identified in the habitat delineation scheme (the trough and channel habitats were combined in this study) showed that the scheme is useful in predicting patterns of faunal abundance and distribution. During the study, crabs were most abundant in the basin. They were rare or absent in the shoal and spit habitat. A posteriori evaluations of abundance patterns showed that, at depths below 9 m, crabs were most abundant when sediments contained 40-80% sand, but were less common in coarser or finer sediments.

During this study, I also examined blue crab sex ratio patterns in each habitat and sex ratios and temporal patterns through the winter at two fixed sites located towards either the east (YSC) or west (WT) sides of the study area. Males were relatively more abundant at the WT fixed site and less abundant at the YSC fixed site, but no significant sex ratio differences were observed among major habitats. At the YSC site, crab abundances decreased during the winter, perhaps due to fishing pressure.

Within the context of the habitat delineation scheme and an increased understanding of benthic processes resulting from the study presented in Chapter 2, it was possible to identify a priori and, therefore, take into account many potential sources of variation. As a result, relationships between physical factors characterizing habitats and organism abundance and the spatial patterns of these relationships were elucidated. This information has important management implications for the blue crab, a species of commercial importance because it has enhanced our capabilities to assess and minimize the impacts of channel dredging and related activities on both the commercial fishery and the crab population.

Chapter 4

In Chapter 4, I present a detailed evaluation of characteristics and small scale spatial patterns for the fauna at the Wolf Trap study site, an area located centrally within the polyhaline basin habitat of the lower Chesapeake Bay. At least four major groups of organisms were among the dominants that characterized the basin community. These included 1) relatively large, long-lived and deeply distributed euryhaline marine species (ie. 'equilibrium' species), 2) small, short-lived and shallowly distributed euryhaline marine species (ie. 'opportunistic' species), 3) organisms that depend on structures for habitat including epifauna, co-inhabitants and commensals and 4) deeply-dwelling infaunal predators. Overall, the fauna at Wolf Trap includes species that are distributed among a wide range of functional groups with no clear domination by one group. The 'typical' estuarine situation of a fauna numerically dominated by short-lived, shallow-dwelling opportunists was not found in the basin habitat. However, while many of the species characterizing the Wolf Trap assemblage are long-lived, short-lived species were also present. Organisms were distributed throughout the sediment column. The availability of at least some of this living area is enhanced by the presence of Chaetopterus (especially above the sediment-water interface) and likely also by populations of Euclymene which increase the availability of oxygenated subsurface sediments through their feeding and pumping activities.

CONCLUSIONS

Given the results of this study it is possible to make some general conclusions and to reassess some of the generalizations regarding estuarine fauna and the processes governing the structure and dynamics of estuarine benthic communities. It is clear from the investigations of faunal distribution patterns and patterns of biotic reworking that the lower Chesapeake Bay includes numerous benthic habitats arranged in a spatially complex pattern. More than just simple correlations with salinity and sediment type are necessary to understand these patterns on both large and small scales. On a baywide basis, differing hydrodynamic regimes and the source and rate of sediment supply determine both the bed sediment type and the availability of different bottom types to the benthos. The subsequent utilization of these different habitats by species capable of inhabiting the estuary is then governed, in part, by species specific responses to these or related variables (eg. suspended load or the diffusion of oxygen into the sediment). Utilization is certainly also governed by species response to other environmental variables not addressed in this study (eg. dissolved oxygen, patterns of circulation). In most of the habitats of the lower bay - tributary system, physical processes are likely to dominate. However, in some habitats, particularly where large benthic organisms govern sediment reworking and sediment structuring processes (eg. the fringe embayment and basin habitats and the flanks of channels in higher salinity estuarine zones), the potential for intra-assemblage biotic interactions which alter distribution and abundance patterns of resident species seems high.

The distribution patterns of many epifaunal species in the basin of the lower bay are governed by the availability of the primary attachment sites - the tube tops of Chaetopterus. However, the availabilty of tube tops is governed by those processes that influence the distibution and abundance patterns of Chaetopterus and the physical and biological sediment reworking processes that change the relative height of sediments around the tube tops. As a result, a combination of biological and physical processes govern the patterns of distribution and abundance for the epifauna. It would be difficult to argue that physical processes alone account for these patterns. Similar arguments can be made for most of the organisms that live as co-inhabitants or commensals with the large tube and burrow-builders that are commonly found as components of the basin fauna. Thus, the generalizations which state or imply that estuaries are strictly physically-controlled habitats in which species are nearly individualistically distributed in response to physical conditions are not valid when the frame of reference includes the polyhaline basin of the lower Chesapeake Bay.

Many of the successful species (ie. those exhibiting high abundances and/or high standing stocks) in the basin of the lower bay are euryhaline marine species that are generally more abundant in the estuary than they are on the adjacent shelf. Indeed, many of these species are found in the Chesapeake Bay at densities which are higher than those reported from other estuarine and shallow coastal areas

(Boesch, 1979; Reid et al., 1979; Reid, 1979; Larsen et al., 1983; Knott et al., 1983; Van Dolah et al., 1979, 1983, 1984; Wildish et al., 1983; Shaw et al., 1982; Dauer et al., 1984). The Chesapeake Bay is a relatively productive estuary (Day, 1981; Boynton et al., 1982) and high primary production coupled with relatively high sediment stability and moderate salinities in the polyhaline basin may facilitate the success of the large sedentary tube-building polychaete _Chaetopterus_ and other euryhaline species.

Boesch (1977) suggested that euryhaline 'opportunists' and large, long-lived 'equilibrium' species should not coexist in the polyhaline lower bay and that the opprtunists should be abundant in the deeper areas of the polyhaline zone only when disturbance resulted in the exclusion of the equilibrium fauna. During 1983 and 1984 I found both groups among the dominants at the Wolf Trap study area. Observations and photographs from the spring through fall periods of three years (1984 to 1986) show recruitment of small tube-builders at the surface during early spring and summer when the large infaunal organisms are not rapidly feeding or otherwise reworking surface sediments.
Clearly, these species can coexist and the mechanisms of this coexistence deserve further consideration.

RECOMMENDATIONS

The lower Chesapeake Bay is large and logistically it is more difficult to study than the tributaries. However, because of the significant physical, geological and biological differences that exist between the main-stem and the tributaries, these two types of systems do not act as reasonable models for one another. Our present understanding of processes throughout the lower bay and especially in the main-stem remain limited. Especially needed are investigations of temporal trends and recruitment processes for the benthos. The processes governing patterns and levels of production in the water column and in the benthos and the links between these two components should be investigated because they determine the pathways of energy through the benthos to higher levels of the food chain. Physical processes governing circulation and stratification are poorly understood but studies of those processes will be necessary to evaluate the long term trends isalinity and dissolved oxygen that strongly influence the success of the benthos and the general resource value of the lower bay.

CHAPTER 2.

AN EVALUATION OF THE BIOLOGICAL AND PHYSICAL PROCESSES AFFECTING THE FORMATION OF RECENT ESTUARINE STRATIGRAPHY IN THE LOWER CHESAPEAKE BAY

ABSTRACT

Estuaries are characterized by sharp gradients in the physical, geological and biological processes that affect the formation of the near-surface stratigraphic record. Physical factors influencing strata formation include source and rate of sediment supply, and intensity and periodicity of hydrodynamic forcing. Important biotic characteristics include abundance and the types of organisms present. I documented the recent sediment record from more than 350 sites in the lower Chesapeake Bay and associated tributaries, ranging from muddy, tidal-freshwater areas to the sandy bay mouth. In low salinity areas sediments were physically structured when sediment accumulation was rapid, but biotic reworking was occasionally important in areas of fluctuating deposition or erosion-deposition cycles. Biological mixing predominated in high salinity areas even when areas were characterized by moderate to rapid accumulation and strong tidal currents but was less important where physical reworking due to oceanic or wind waves was intense. A posteriori allocation of radiographs to subenvironment categories aided in the identification of patterns of variation. Change within subenvironments was gradual and concordant with the estuarine gradient. Cross-estuary gradients in stratigraphy were steep, reflecting rapid changes in biological and physical/geological processes and the interactions of these processes in adjacent subenvironments.

INTRODUCTION

Estuaries, unlike most shelf and deep sea environments, exhibit relatively sharp spatial and temporal gradients in physical, geological, and biological processes. Formation of the recent stratigraphic record results from the interactions of many of these processes (Moore and Scruton, 1957). Attempts to model or predict strata formation in the estuary depend on characterizing important processes and understanding the relevant scales of heterogeneity. However for large, spatially complex estuaries like the Chesapeake Bay the extent to which biological and physical processes act and interact to establish the stratigraphic record is largely unknown (Schaffner et al., 1987).

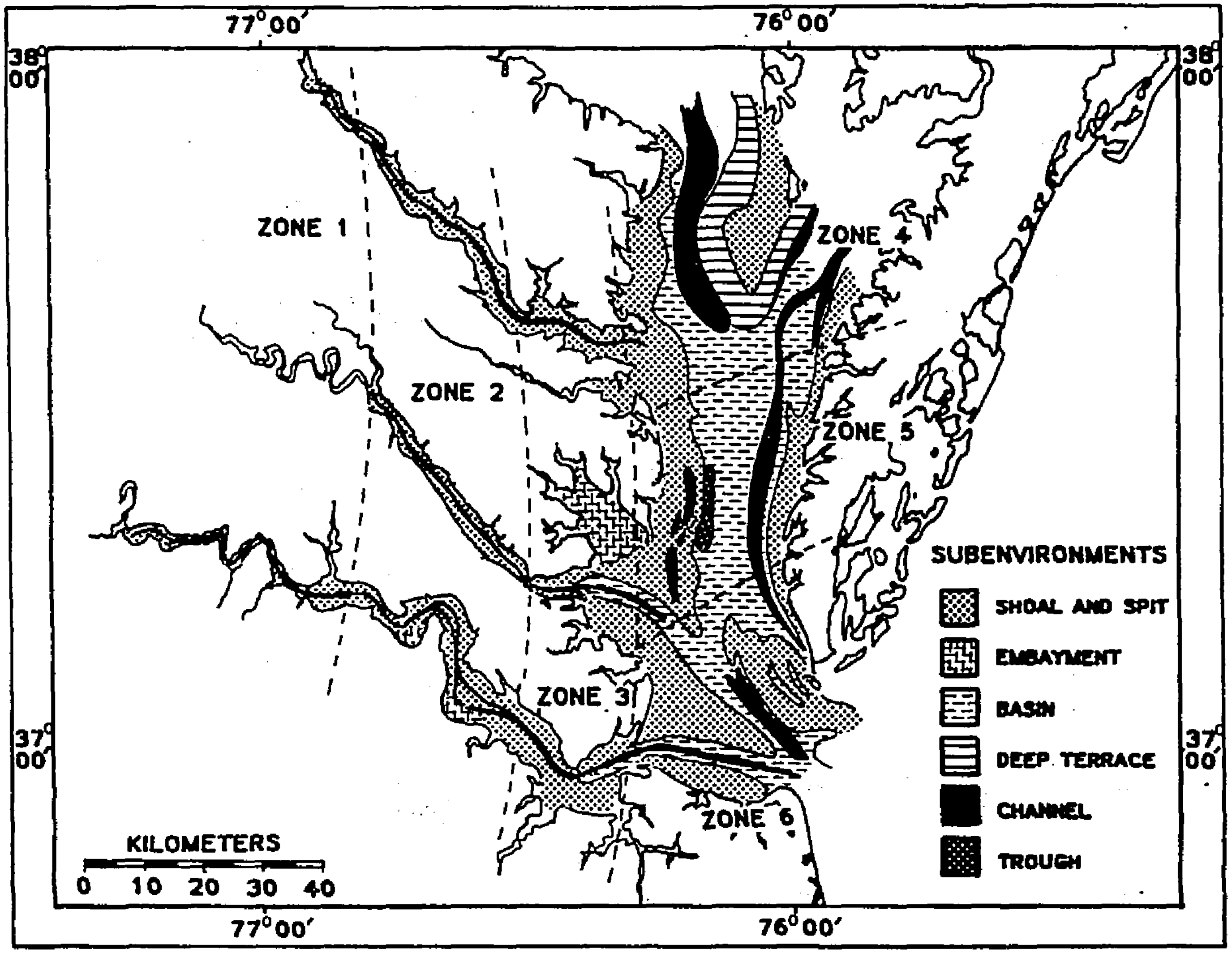
Major physical processes influencing strata formation in the estuary include those that control the intensity and periodicity of hydrodynamic forcing (Reinharz et al., 1982; Boon et al., 1987; Wright et al., 1987) and the source and rate of sediment supply (Nittrouer and Sternberg, 1981; Allen, 1982a,b; Nichols and Biggs, 1985; Schaffner et al., 1987). Organisms associated with the bottom continuously rework physically structured sediments through burrowing, feeding, tracking and tube-building activities (Rhoads and Young, 1971; Rhoads, 1974; Thayer, 1979; Jumars et al., 1981; Nowell et al. 1981). They homogenize bedding, produce new structures and alter sediment erodability and mass property characteristics (Jumars and Nowell, 1984; Luckenbach, 1986). The distribution, abundance and functional characteristics (feeding type - motility) of the benthic fauna have been used to estimate rates and mechanisms of biotic reworking for intertidal and shallow subtidal areas (Winston and

Anderson, 1971; Howard and Frey, 1975) and for continental shelves (Nittrouer and Sternberg, 1981; Rhoads et al., 1985).

Since 1978 I have documented the recent sediment record (0 to 30+ cm depth) from over 350 locations in the lower Chesapeake Bay and associated tributaries (Figure 1). The study sites ranged from muddy, tidal-freshwater environments to the sandy, high salinity bay mouth. I encountered a full spectrum of depositional environments, from areas where accumulation rates exceed 3 cm per year to areas where net erosion occurs. Sites ranged from areas where the fauna included many large and deep-living organisms to nearly depauperate areas. The sites span the full range of hydrodynamic regimes which result from the interaction of oceanic forcing, wind-generated wave disturbance, tidal energy and net non-tidal flow (Nichols, 1972; Wright et al., 1987).

This study discusses variation in the recent stratigraphic record of the Chesapeake Bay and the biological, physical and geological processes which produce this record. An a posteriori stratification scheme, based on physical, geological and biological attributes of the bay bottom, is used to allocate x-radiographs of sediment cores into distinct subenvironments (Wright et al., 1987) and salinity zones. I hope to gain insight into the relative importance of processes and to increase our understanding of mechanisms and rates of strata formation by identifying patterns in the variation within and among subenvironments.

Figure 1. Map of the Chesapeake Bay study area indicating subenvironments and estuarine zones.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SUBENVIRONMENTS
SHOAL AND SPIT
EMBAYMENT
BASIN
DEEP TERRACE
CHANNEL
TROUGH
KILOMETERS
0 10 20 30 40

METHODS

Most sediment cores for x-radiography were obtained using a spade box core and following procedures described by Reinharz et al. (1982) and Schaffner et al. (1987). Some cores were taken by inserting smaller tubes into the core box, others were diver collected. Radiography was accomplished using standard techniques (Howard and Frey, 1975; Reinharz et al., 1982). Cores were dissected following radiography to identify sediment structures and resident organisms. Rates of sediment accumulation for some cores were determined from radionuclide profiles using methods outlined in Schaffner et al. (1987). Grain size data was collected for all cores in accordance with procedures outlined in Folk (1974).

Data used to discern faunal trends was compiled from 15 studies (779 station collections) that spanned the full length of the bay and the James, York and Rappahannock rivers. The original data, provided by Dr. Robert Diaz, were collected by VIMS between 1969 and 1986. Criteria for inclusion of data included complementary sediment and salinity data. Some stations were previously assigned averaged salinity values using the Chesapeake Bay Institute salinity atlas (1963). Data were converted to square meter areal units and blocked by sediment type(<25%, 25-75%, >75% sand) and salinity (Zone 1 - 0-0.3ppt, Zone 2 - 0.3-5ppt, Zone 3 - 5-15ppt, Zone 4 - 15-20ppt, Zone 5 - 20-25ppt, Zone 6 - 25-30ppt) classes. Estimates of faunal wet weight biomass were made from box cores collected in conjunction with cores for x-radiography. Additional data compiled from Diaz et al. (1978), Reinharz and O'Connell (1981), Schaffner et al. (1987) and

Llanso (unpublished) supplements information for low salinity areas and the baymouth region. Values from Diaz et al., Reinharz and O'Connell and Schaffner et al. were converted from dry weights to wet weights using the conversion given by Waters (1977). This conversion is known to be appropriate for annelids in the lower Chesapeake Bay (D. Huggett, personal communication).

I identified 6 major subenvironments and 6 estuarine zones for the lower Chesapeake Bay-tributary system (Figure 1, Table 1). Some subenvironment/estuarine zone combinations represent large areas (eg. shoals in Zone 6) while other combinations do not exist (eg. basin subenvironment in Zone 1, tidal-freshwater). Some subenvironments were well sampled (eg. basin) for sediment stratigraphy and supporting data, while others were under-sampled considering the surface areas they encompass (eg. the deep terrace). However, the large number of samples overall provides sufficient information to discern some important trends.

TABLE 1. SUBENVIRONMENTS IN THE LOWER CHESAPEAKE BAY N EQUALS NUMBER OF CORES EXAMINED

SUBENVIRONMENT	DEPTH (M)	SEDIMENT COMPOSITION[A]	HYDRODYNAMIC REGIME[B]	N OF CORES
SHOAL AND SPIT	<9,[C] <5[D]	>75% SAND	WAVE AND TIDE DOMINATED	73
FRINGE EMBAYMENT	<9,[C] <5[D]	<75% SAND	INFREQUENT WAVE DISTURBANCE	14
BASIN	9–20	<90% SAND	TIDE DOMINATED	210
DEEP TERRACE	9–25	>75% SAND	?WIND–DRIFT CURRENT	10
CHANNEL	>10	VARIABLE	TIDAL, NON–TIDAL FLOW	53
TROUGH	>10	<25% SAND	QUIESCENT	6

[A] DATA FROM BYRNE ET AL. (1982)

[B] MODIFIED FROM WRIGHT ET AL. (1987), BYRNE ET AL. (1982) AND NICHOLS (1972)

[C] DEPTHS IN BAY

[D] DEPTHS IN TRIBUTARIES

RESULTS

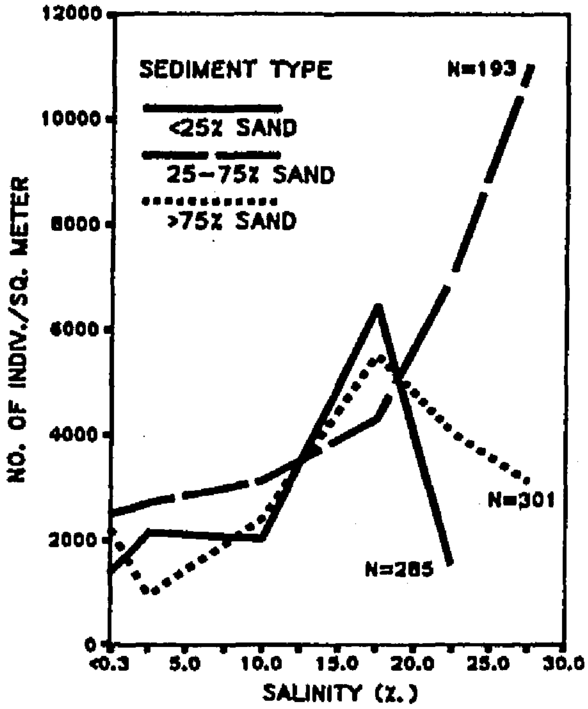
Benthic Fauna

Patterns in faunal characteristics that affect sediment stratigraphy (ie. abundance, biomass and functional grouping) have not previously been examined for the lower Chesapeake Bay-tributary system. The results of analyses for macrofaunal organisms ($\geq$ 0.5 mm) are presented in Figures 2 and 3. Faunal densities were variable for all salinity/sediment comparisons made, when averaging over both space (subenvironments) and time (seasons and years). Mean faunal densities generally ranged between 1,000 and 7,000 individuals per square meter (Figure 2a). Densities were highest in the sands and mixed sediments of the lower bay-baymouth region.

The mixed basin sediments of Zones 4-6 support the highest levels of biomass recorded for the system (Figure 2b). This can be attributed to dense populations of maldanid, chaetopterid and nephtyid polychaetes (Boesch, 1973, 1977; Dauer et al., 1984; Chapter 2). High molluscan biomass values in the upper and mid-estuary regions are due to two species of large, sedentary bivalves, <u>Rangia</u> <u>cuneata</u> in Zones 2 and 3 and <u>Macoma</u> <u>balthica</u> in Zones 3 and 4 (Schaffner et al., 1987).

Ternary diagrams summarizing annelid feeding and motility types for each salinity/sediment combination are presented in Figure 3. The annelids were chosen for these analyses because they comprise at least 75% of the fauna (by numbers) throughout the system, and because their

Figure 2.a. Relationship between faunal abundance and salinity for 3 sediment types in the Chesapeake Bay tributary system. Data were blocked by salinity zones as explained in the text. b. Faunal biomass for 3 sediment types and six salinity zones. No mud sediments (<25% sand) are present in zone 6.


SEDIMENT TYPE
<25% SAND
25-75% SAND
>75% SAND
N=193
N=301
N=285
NO. OF INDIV./SQ. METER
12000
10000
8000
6000
4000
2000
0
<0.3
5.0
10.0
15.0
20.0
25.0
30.0
SALINITY (%.)

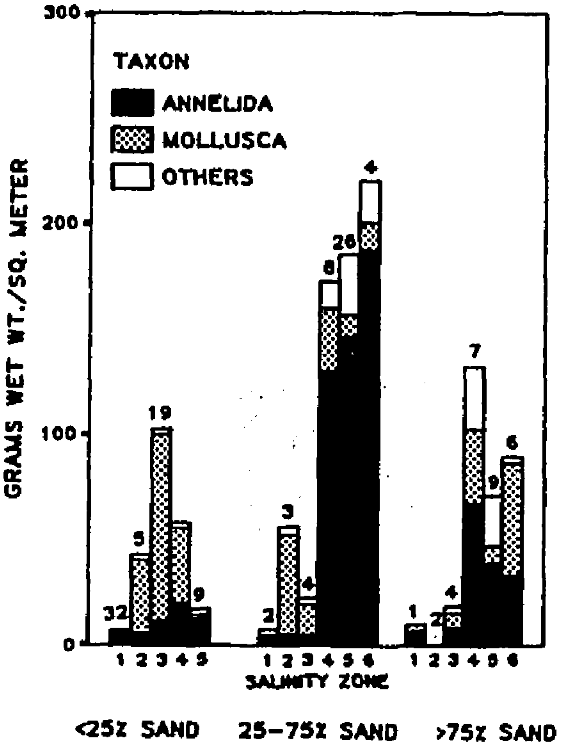
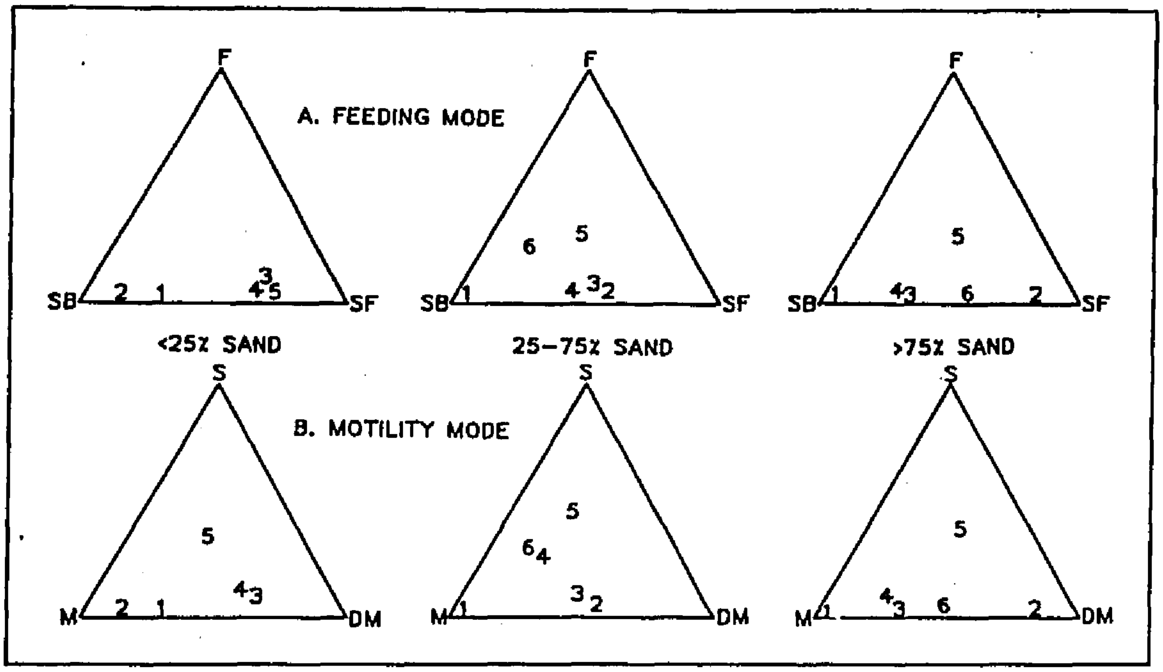

TAXON
ANNELIDA
MOLLUSCA
OTHERS
GRAMS WET WT./SQ. METER
300
200
100
0
32
5
19
9
2
3
4
8
26
4
1
2
4
7
9
6
1 2 3 4 5
1 2 3 4 5 6
1 2 3 4 5 6
SALINITY ZONE
<25% SAND
25-75% SAND
>75% SAND

Figure 3. Ternary diagrams describing the feeding and motility modes of annelid assemblages characteristic of each sediment type and salinity zone (indicated by numbered data points 1-6). Each corner indicates a maximum contribution of 100% for the designated mode. For feeding: F—filtering, SB—subsurface feeding, SF—surface feeding. For motility: S—sedentary, M—motile, DM—discretely motile.


A. FEEDING MODE
F
SB
SF
2
1
3
4
5
F
6
5
SB
1
4
3
2
SF
F
5
SB
1
4
3
6
2
SF
<25% SAND
25–75% SAND
>75% SAND
B. MOTILITY MODE
S
5
M
2
1
4
3
DM
S
5
6
4
M
1
3
2
DM
S
5
M
1
4
3
6
2
DM

functional group characteristics reflect both adaptations to their environments (Gaston, 1983) and the nature of their effects on sediment mixing (Nittrouer and Sternberg, 1981; Lee and Swartz, 1980). Motile organisms cause primarily diffusive sediment mixing (Piper and Marshall, 1969) while sedentary organisms often build tube and burrow structures. Organisms that feed in the water column may enhance deposition but have little affect on subsurface sediments while subsurface feeders may rework sediments to depths exceeding 30 cm (Lee and Swartz, 1980) Polychaetes were assigned to feeding and motility modes using the classification system of Fauchald and Jumars (1979). We classified all oligochaetes as motile, subsurface deposit feeders and excluded predatory forms from the feeding mode diagrams.

Throughout most of the estuary, the annelid fauna is dominated by motile and discretely motile forms. Motile forms are primarily the slowly mobile capitellid polychaetes and oligochaetes. Both taxa include "conveyor-belt" species (Rhoads, 1974) which feed at depth (subsurface) and defecate on the surface, thus having an important affect on sediment distribution. Discretely motile spionid polychaetes are the other dominant annelid taxon in the estuary. These worms feed at the sediment-water interface (Taghon et al., 1980; Dauer et al., 1981;) and are classified as surface feeders. Sedentary annelids are most commonly found in the higher salinity estuarine zones, particularly on mixed sediments. Sands at the bay mouth (Zone 6) are too mobile for sedentary forms (Wright et al., 1987), but they are common on the sandy substrates of Zone 5. Many of the sedentary forms feed in the water column using a filtering mechanism (eg. chaetopterids) and presumably enhance biodeposition.

Some sedentary forms are surface or subsurface deposit feeders (eg. terebellids and maldanids, respectively). All of these taxa build tubes or permanent burrow structures.

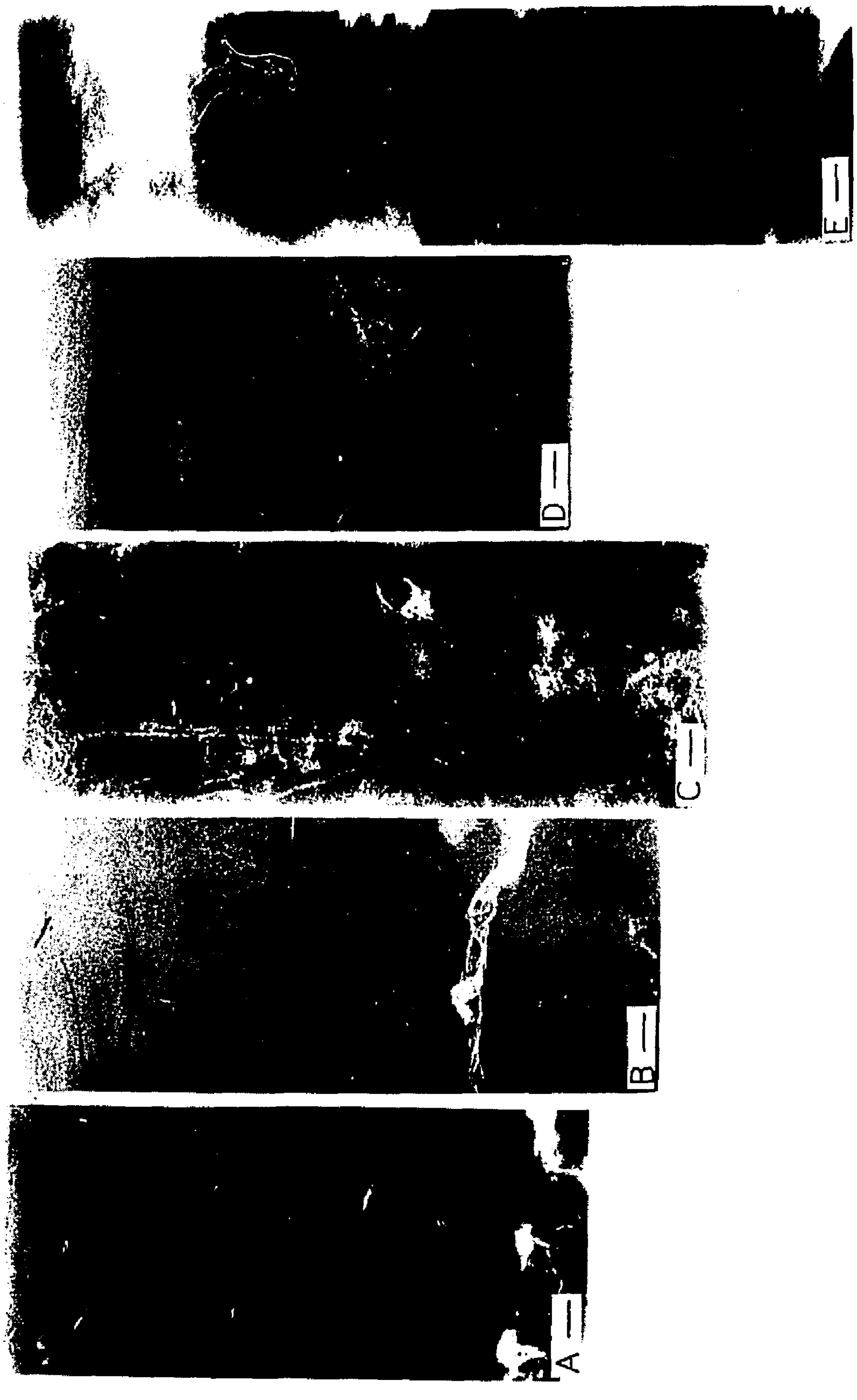
Sediment Structure

I used the subenvironment/estuarine zone schemes presented above to classify each radiograph from the locations sampled. I then interpreted radiographs from each combination with consideration of faunal motility, feeding, abundance and biomass, sources/rates of sediment supply as determined from the literature (Nichols, 1972; Byrne et al., 1982) and accumulation rates calculated from radionuclide profiles or based on previously published data (Cutshall et al., 1981; Byrne et al., 1982; Officer et al., 1984; Schaffner et al., 1987). The results, organized by subenvironment type, are presented below.

A. Shoals and Spits:

In the baymouth region shoals and spits are wave and tide dominated environments characterized by shifting sediments and motile organisms. Radiographs from these regions have ripple laminated surface sediments and shell lag deposits, but subsurface sediments can appear homogeneous due to biotic reworking (Figure 4a). Cores from slightly deeper shoal areas exhibit some near-surface tube and burrow structures (Figure 4b). As the energy regime becomes less intensive away from the baymouth, more sedentary species can maintain living

Figure 4. X-radiographs (positives) of cores from shoals and spits. Scale bars equal 1 cm. A. 3 m depth in the baymouth region (zone 1) B. 6 m depth, zone 5 C. 6 m depth, zone 4 D. 3 m depth, zone 3 (York River), 10 days after a severe storm E. 1 m depth, zone 1.


A
B
C
D
E

positions in shallow sands. Radiographs from shoals in Zones 3 and 4 exhibit evidence of biological mixing and permanent tube and burrow structures (Figure 4c). However, infrequent storms produce physically structured sediments which are not immediately reworked by resident fauna (Figure 4d). As faunal density and biomass decrease in Zones 1 and 2, so does the potential for biotic reworking, and sediments are physically laminated even in quiescent areas where muds are deposited (Figure 4e).

B. Fringe Embayment:

Fringe embayments are often sites of rapid sediment accumulation (>3 cm/yr; Nichols, 1972; Cutshall et al., 1981; Schaffner et al., 1987). However, sediments can appear completely homogenous due in part to the presence of the surface-feeding bivalve _Macoma_ _balthica_ (Figure 5a). This organism, which lives as much as 30 cm below the sediment surface, feeds at or near the sediment-water interface via long siphons. Sediments are apparently ingested and pelletized as they accumulate. Fringe embayment sediments may also contain abundant deposits of shells which are produced by nearby oyster reefs and bars (Figure 5b).

C. Basin:

Much of the lower bay is encompased in an expansive basin region. Land runoff brings fine silts and clays to this subenvironment from the northern and western tributaries while oceanic sources contribute coarser silts and sands through the bay mouth (Byrne et al., 1982). In the vicinity of the York River, basin depths average 10-13 m and sediments are silty-very fine sands. Further north, sediments grade to sandy-silts and clays at 13-16 m depths near the mouth of the Rappahannock River. Basin faunal densities and biomass can be very high (Figure 2 and Chapter 2). In combination with a moderate, tidally-controlled energy regime and relatively distant sediment sources, biotic reworking produces sediments with little evidence of physical structuring (Figure 6a-c). However, subtle shifts in grain size and biological characteristics along the north-south basin axis produce clear trends in sediment stratigraphy. The southern, sandier (65-75% sand) end of the gradient supports many "conveyor-belt" organisms which rework sediments to depths as great as 20 cm, while at the northern (25-35% sand) end tube-building surface feeders predominate. Sediments at the southern end appear nearly homogeneous below a tidally reworked surface (Figure 6a) while many tubes and backfilled burrows are evident in sediments from the northern end of the basin (Figure 6c). In the central basin (40-60% sand) the record is intermediate (Figure 6b). Although long-term bathymetric changes suggest that sediment accumulations rates in the basin may be as high as 1-3 cm/yr (Byrne et al., 1982), there is no apparent effect on the ability of the fauna to control sediment reworking processes. This is in sharp contrast to the lower salinity tributaries where accumulation rates in this range generally result in physically laminated sediments (see below, and Schaffner et al., 1987). Physical reworking can

Figure 5. X-radiographs (positives) of cores from fringe embayments. Scale bar equals 1 cm. A. 3 m depth, zone 2 (James River) B. 8 m depth, zone 3.

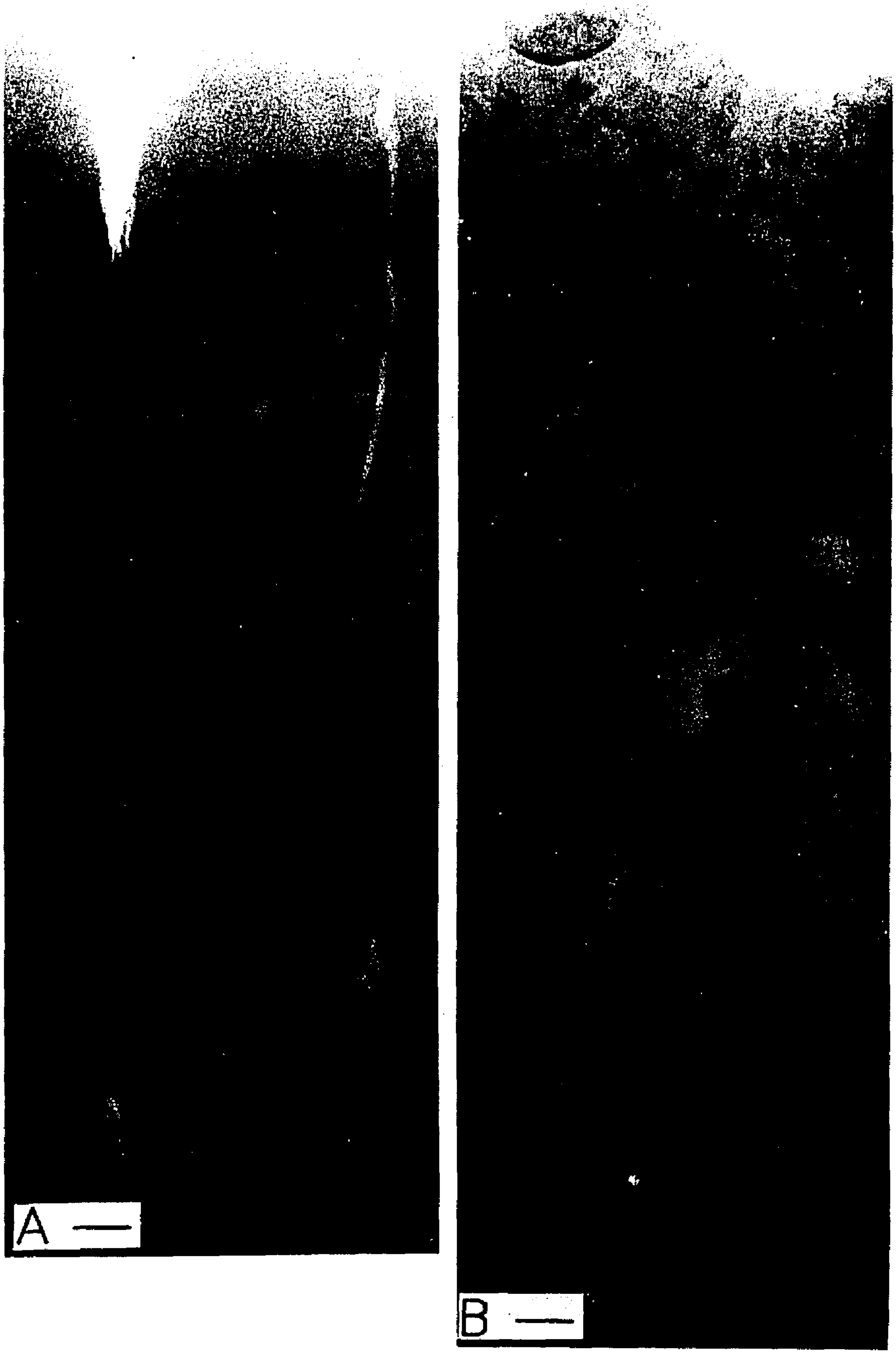
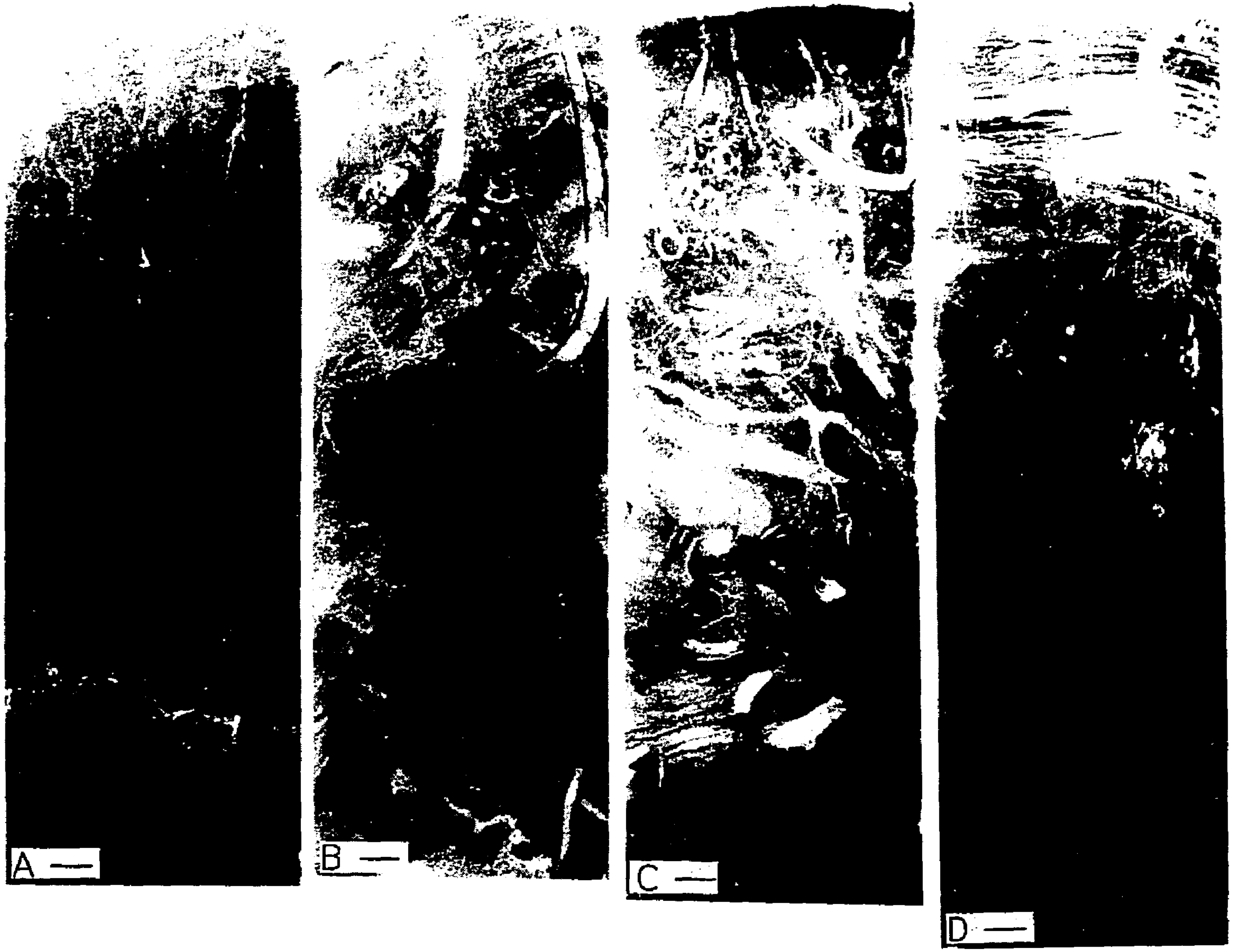

A
B

Figure 6. X-radiographs (positives) of cores from the basin. Scale bar equals 1 cm. A. 12 m depth, zone 6 B. 13 m depth, zone 5, summer C. 14 m depth, zone 4 D. 13 m depth, zone 5, spring.


A
B
C
D

produce laminated basin sediments (Figure 6d), but my observations suggest that this tidally-induced effect is a winter-early spring phenomenon reflecting minimal biotic reworking due to depressed temperatures.

D. Deep Terrace:

The deep terrace or sand shield subenvironment is probably a relict feature formed during an earlier lower stand of sea level (Byrne et al., 1982). Sediments are medium sands and a wind-drift induced current regime has been inferred from observed patterns of sediment migration at the southern and western fringes. Near-surface sediments from shallow terrace depths appear homogeneous with no apparent physical structures (Figure 7a). Relatively large animal tubes are observed in cores from deeper (15-17 m) terrace stations (Figure 7b,c) indicating infrequent sediment disturbance.

E-F. Channel and Trough:

Channels are generally found at depths exceeding 10 m, but are as shallow as 5 m in the upper tributaries. The bottoms of channels may be scoured, but the flanks are frequently depositional (Nichols, 1972; Byrne et al., 1982). Sediments in the scoured regions have not been well sampled for stratigraphy, but a core from this region (36 m) of the deep channel that parallels the eastern shore of the lower bay exhibits little evidence of physical struturing (Figure 8a). A shell

Figure 7. X-radiographs (positives) of cores from the deep terrace. Scale bar equals 1 cm. A. 10 m depth, zone 4 B. 20 m depth, zone 4 C. 23 m depth, zone 4.

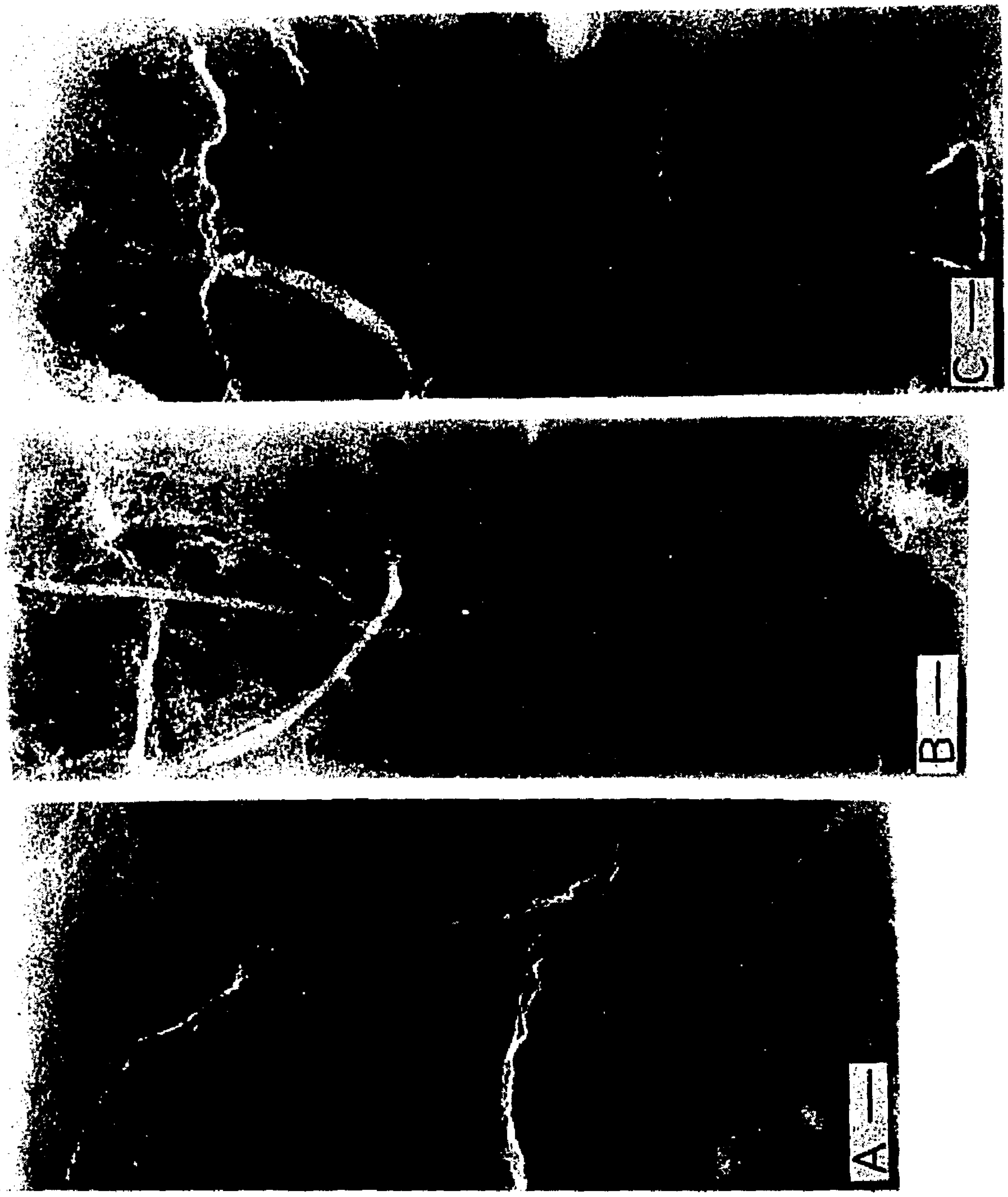

A
B
C

Figure 8. X-radiographs (positives) of cores from channels. Scale bar equals 1 cm. A. 36 m depth, zone 5 B. 20 m depth, zone 3 (Rappahannock River) C. 6 m depth, zone 2 (Rappahannock River) D. 8 m depth, zone 1 (James River).


A
B
C
D

lag deposit in the upper few centimeters of the core indicates that currents winnow fines away. On the flanks of this channel (20-30 m) sediment texture and the structures preserved resemble those observed at shallower basin depths (see Figure 6).

In Zones 1-4 channels are characterized by finer sediments than those observed in channels near the bay mouth. Sediment accumulation rates can be high enough (>3cm/yr) to mask the effects of biotic reworking on sediment stratigraphy. Periodic anoxia followed by reoxygenation of deeper channel areas leads to population irruptions of opportunistic species (Reinharz and O'Connell, 1981; Holland, 1985). Sediments appear laminated, some shell layers produced by the small bivalve Mulinia lateralis are frequently present and only small patches or bands of sediment appear mixed (Figure 8b). Near-surface sediments in troughs (channel-like bathymetric depressions which are not involved in any obvious circulation pathways) are similar in appearance to those observed in the depositional channel areas of comparable salinities.

The contribution of varying sediment sources and presumably different energy regimes can be seen in radiographs of cores from the narrower reaches of the tributaries (Zones 1 and 2). Erosion of sediment from upstream or adjacent shorelines and shoals introduces coarse sandy material to the channels at unknown intervals (Figure 8c). Patterns of faunal reworking and erosion sequences in the lower half of this core suggest some periodicity to the timing of events. Similar records have been observed in the James River where radionuclide profiles indicate that long-term accumulation rates are moderate (1-2cm/yr, Schaffner et al., 1987). I infer that accumulation rates in these areas must be very low during periods when biological structures are created in the sediments and that the physical transport and deposition processes that control lamination sequences do not greatly disturb the bed once biotic structures have been produced.

Further upstream in the channel region of Zone 1 I have observed a single type of sediment record from the James, York and Rappahannock rivers (Figure 8d). Although these areas are dominated by deep-living oligochaetes that can process significant quantities of sediment (McCall and Fisher, 1980), the characteristic rates of accumulation (>3cm/yr) result in physically laminated sediments. Radiographs show evidence of methanogenesis and the inclusion of much organic detritus.

DISCUSSION

Inferences about present and past environments based on the characteristics preserved in stratigraphy, are frequently made by geochemists, geologists, paleontologists and ecologists. However, these records represent the time-averaged integration of a complex of biological, geological and physical processes. Some understanding of the mechanisms and rates of important processes and the ways in which these processes interact is a prerequisite for interpreting the record.

Changes in the recent stratigraphic record of the Chesapeake Bay are gradual and continuous if similar subenvironments are compared along the estuarine gradient. Cross-estuary gradients in physical, geological and biological processes are generally sharp and produce concommitantly rapid changes in the types of biological and physical structures observed in the sediment record. In low salinity areas sediments are physically structured when sediment accumulation is rapid, but biotic reworking is occasionally important in areas of fluctuating deposition or erosion-deposition cycles. Biological mixing predominates in high salinity areas even when theses areas are characterized by moderate to rapid accumulation (1 to ≥ 3 cm/yr) or tidal currents. Yet, inferred high rates of biotic mixing cannot destroy physical structuring in areas characterized by intensive wind and oceanically-derived wave activity.

The subenvironment delineation scheme proved useful in identifying both within and between subenvironment variation in the recent estuarine stratigraphy. While observed stratigraphic patterns can be directly related to gradients in biological, physical and geological processes the relationships are somewhat obscured by comparisons of stratigraphy among rather than within subenvironments.

Previous investigations of near-surface stratigraphy in the mainstem of the Chesapeake Bay (Reinharz et al., 1982) and in the James River estuary (Schaffner et al., 1987) highlight the difficulties associated with adequate interpretation of near-surface records. Reinharz et al. found most sediments in the bay to be thoroughly bioturbated. The results of this study suggest that very different combinations of processes can result in "thoroughly" reworked sediments and that the rates of reworking will not remain constant. Schaffner et al. were unable to find relationships between faunal abundance, biomass and depth distribution patterns and the levels of biotic reworking observed in their cores which were collected from areas of various accumulation rates and salinities ranging from tidal-freshwater to nearly 18 ppt. In the context of the present study however, it becomes clear that the low salinity end of the system (most of their study area) is unlikely to be strongly affected by biological processes, particularly if sediment accumulation rates exceed 2-3 cm/yr. However, biotic reworking can homogenize sediments in fringe embayments even though rates of accumulation may exceed 3cm/yr. This suggests that the mode or timing of sediment input is another important variable. Continuously-supplied sediments may be more effectively reworked by resident organisms than are sediments which are transported and deposited in large pulses (Nichols et al., 1978).

Measurements of faunal abundance, biomass and functional groups and hydrodynamics made contemporaneously with observations of recent near-surface stratigraphy may or may not adequately reflect the suite of processes acting or the appropriate time scales for strata formation. Repeated observations of sediment structures over time and space, coupled with long-term estimates of biological, geological and physical processes will provide the strongest base for interpretation of the record.

CHAPTER 3.

DISTRIBUTION AND ABUNDANCE OF OVERWINTERING BLUE CRABS, *CALLINECTES SAPIDUS*, IN THE LOWER CHESAPEAKE BAY

ABSTRACT

A study was conducted to define winter distribution patterns of blue crabs, Callinectes sapidus, in the lower Chesapeake Bay and to relate these patterns to environmental variation. During February 1986 a stratified random survey was conducted to examine the distribution of blue crabs with respect to three major habitat types: 1) high energy, wave and tide dominated, spits and shoals, 2) moderate energy, tide dominated basins and 3) variable energy, tide dominated or quiescent channels (natural or cut). Each major habitat type was further stratified on the basis of location (to account for possible salinity effects) resulting in a total of 17 habitat/stratum combinations. Blue crabs exhibited significant differences in abundance among habitats. Crabs were most abundant in the basin habitat and least abundant in the shoal and spit habitat. Densities were the most variable in the channel habitat. A posteriori evaluations of abundance patterns in relation to sediment type and depth showed that crabs were significantly more abundant where sediments contained between 41 and 60% sand and at depths exceeding 9 m. The sampled population of blue crabs was dominated by mature females. There were no significant differences in crab sex ratios between habitats, but significant differences between two fixed sites sampled through the winter showed that there were proportionately more male crabs at the western site than there were at the eastern site. The observed patterns suggest that some spatial habitat partitioning occurs and that overwintering female crabs are found preferentially in areas characterized by moderate energy regimes and fine, but sandy sediments.

INTRODUCTION

Life history patterns of the blue crab, Callinectes sapidus, in the Chesapeake Bay have been documented since the early 1900's (Hay 1905; Churchill 1921). However, despite the commercial and recreational importance of this species particular aspects of its ecology remain poorly understood (see reviews by Millikin and Williams 1984; Van Den Avyle and Fowler 1984; and references contained therein). This is in part due to the blue crab's relatively complicated spawning and migratory patterns.

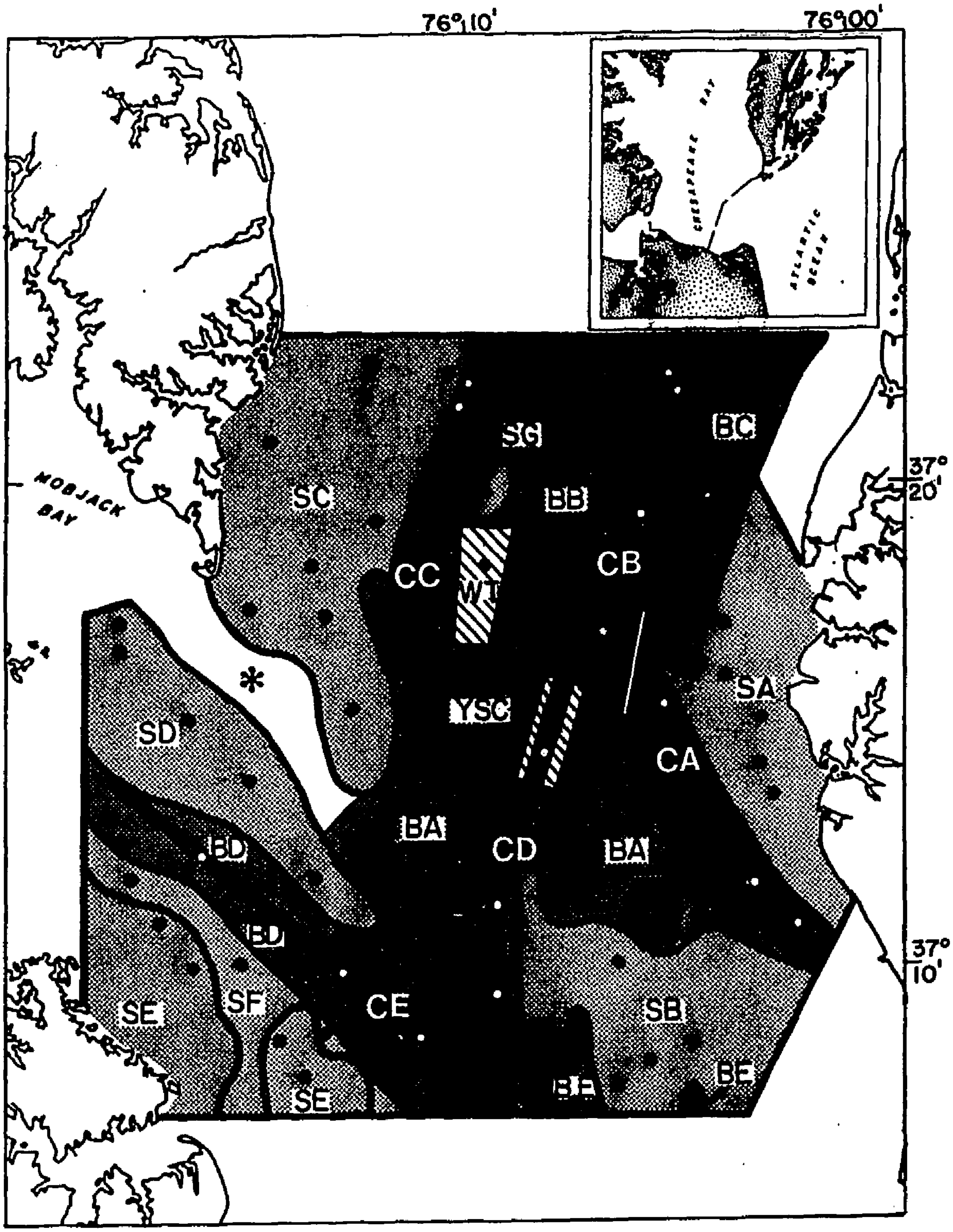
The life history of the blue crab in the Chesapeake Bay may be generalized as follows. Crabs hatch as zoeae near the mouth of the Bay, primarily during July and August (Provenzano et al. 1982; McConaugha et al. 1983). Megalopae are abundant in the neuston of offshore waters during late summer and early fall and some are be returned to the Bay by wind-driven flow (Johnson 1985). Juveniles appear to migrate towards lower salinity waters where maturation takes place in approximately 15 to 24 months (Van Engel 1958). Gravid females return to the mouth of the Bay to spawn. This migration appears to begin in late summer-early fall, slows down or ceases during the winter months and resumes again during the spring. Males tend to remain in lower salinity waters throughout their life cycle (Churchill 1921). Distribution and migration patterns for adult crab populations along the Atlantic and Gulf coasts have been elucidated primarily through the use of tagging studies and catch statistics (Porter 1956; Cargo 1958; Tagatz 1968; Judy and Dudley 1970; Jaworski 1972; Perry 1975; Oesterling 1976; Eldridge and Waltz 1977) and less commonly by direct sampling (Darnell 1959; Norse 1975; Heck and Orth 1980). In the Chesapeake Bay direct sampling is easily accomplished during the winter months when crabs are both sluggish due to low water temperatures and closely associated with the bottom (Churchill 1921, Van Engel 1962). Direct sampling of the overwintering blue crab population should provide information regarding both the extent of migration and spatial variability in winter distribution patterns. The major objectives of the study reported herein are to 1) identify patterns in the winter distribution of crabs in a portion of the lower Chesapeake Bay and 2) relate these patterns to variation in benthic habitats.

METHODS

Dredge sampling for blue crabs was conducted in a portion of the lower Chesapeake Bay during the winter of 1985-86 (Fig. 1). During February 10-14, 1986 a stratified random survey was conducted to collect information on crab abundance and sex ratio distribution in major habitat types of the lower bay overwintering grounds. A mid-winter sampling date was chosen so that variability introduced by crab movement due to potentially warm water temperatures earlier or later in the winter would be minimized. Recent evidence indicates that the lower Chesapeake Bay is characterized by a high spatial diversity in bottom types resulting from varying sediment sources, rates of accumulation and hydrodynamic regimes (Bryne et al., 1982; Boon et al., 1987; Wright et al., 1987). To account for physically induced variability I delineated three major habitats within the study area. These were: shallow shoals and spits (<9 m), basins (9-15 m) and channels, natural or cut (>11 m). Within habitats further separation was made on the basis of sediment type (from Byrne et al. 1982) and relative location (i.e. north or south, east or west), to partition variation related to salinity (Table 1). The resultant 17 strata and 94 stations are shown in Figure 1. Sampling effort was divided among strata on the basis of relative surface area. Sampling locations were occupied using LORAN navigation. Blue crabs were counted and sexed.

Repetitive sampling was conducted at two fixed sampling sites (Wolf Trap (WT) and the York Spit Channel (YSC) Study Regions) which were visited during December 10-12, 1985, January 29-31, 1986 and February 26-28, 1986. The Wolf Trap Study region was chosen because

Figure 1. Study region in the Lower Chesapeake Bay during winter 1985-86. Fixed sampling sites are hachured. Refer to Table 1 for information on habitats/strata delineated for the stratified random survey. *Area excluded due to high spatial variability in bottom type.



76°10'
76°00'
37° 20'
37° 10'
MOBJACK BAY
CHESAPEAKE BAY
ATLANTIC OCEAN
SG
BC
SC
BB
CB
CC
WT
SA
SD
YSC
CA
BA
CD
BA
BD
BD
SF
CE
SE
SB
SE
BE
BE
*

Table 1. Habitat stratification of the study area based on bathymetric location, sediment type and relative salinity and mean number of crabs/5 min. tow/1.2 m dredge collected during February 1986.

			Physical Characteristics			Crab Abundance	
Habitat/ Stratum	Location	No. of Stations	% Sand	Mean (mm) Grain Size	Depth	$\bar{X}$	(SD)
Shallow		36				1.8	(3.39)
SA	Old Plantation Flats, eastern bay	7	>95	0.250	<9 m	1.0	(2.65)
SB	north of Inner Middle Ground, eastern bay	7	>98	0.125	<9 m	6.9	(3.98)
SC	New Point Comfort and Wolf Trap Shoals, western bay	9	>90	0.190	<9 m	0.8	(1.99)
SD	York Spit, western bay	5	>95	0.270	<9 m	0.0	
SE	Poquoson Flats, western bay	4	>95	0.290	<9 m	0.0	
SF	Poquoson Flats, western bay	3	70-95	0.350	<9 m	1.0	(1.73)
SG	Wolf Trap Region, western bay	1	>90	0.145	<9 m	0.0	
Basin		43				9.1	(7.47)
BA	lower-transitional region between mouth of bay and main basin	21	50-90	0.092	9-15 m	9.6	(7.64)
BB	main basin region	13	<70	0.050	9-15 m	10.8	(7.09))
BC	eastern bay between Old Plantation Flats and natural channel	4	>80	0.200	9-17 m	10.5	(8.19)

Table 1 (continued)

Habitat/ Stratum	Location	No. of Stations	Physical Characteristics			Crab Abundance	
			% Sand	Mean (mm) Grain Size	Depth	$\bar{X}$	(SD)
BD	York River Entrance	3	<50	0.020	9-15 m	0.7	(1.15)
BE	northern limits of bay mouth	2	>80	0.095	9-15 m	2.0	(1.41)
Channel		15				5.7	(6.72)
CA	eastern bay - natural, deep, southern end	3	50-90	0.062	21-43 m	4.3	(4.04)
CB	eastern bay - natural, northern end	4	60-80	0.065	19-26 m	8.3	(3.86)
CC	western bay - natural	2	<50	0.021	12-15 m	1.5	(0.71)
CD	eastern bay - York Spit Channel	3			11-15 m	2.7	(2.08)
CE	western bay - York River Entrance Channel	3			11-15 m	9.7	(14.22)
	Grand Total	94					
	Grand Mean					5.7	(6.89)

it is an area being considered for dredge material disposal. The YSC site lies within an area that will be dredged to deepen the channel by the U.S. Army Corps of Engineers.

Sampling for the random survey was accomplished using a 1.22 m crab dredge (with 15 cm stretch mesh) towed from the stern of the vessel at a controlled speed of 4.8 km/hr. All tows were of 5 minute duration. Dredging at fixed stations was accomplished using two 2.13 m crab dredges with 15 cm stretch mesh towed simultaneously at a controlled speed of 4.8 km/hr aboard a commercial crab dredging vessel. Speed was determined as "speed over ground" from a Northstar LORAN C positioning unit and was continually checked by manual or automated position plotting. At the YSC site sampling was conducted both within the buoyed channel and on the nearby flank regions. Although the overall towing times varied at fixed sampling sites, a significant portion of the variance of crab abundance at each site is explained by regression on tow time (ANOVA for WT, F= 28.7 and df= 9; ANOVA for YSC, F= 52.2 and df= 21). All data reported here from the fixed sampling sites are standardized to 5 minutes tow duration and a 1.22 m dredge width so that samples from fixed and random surveys are comparable.

After insuring that assumptions had been met numerous statistical tests were used to evaluate the significance of distribution patterns. Differences in crab abundances between habitats were evaluated using an ANOVA design in which strata were nested within habitats. A one-way ANOVA and a Scheffe Multiple Range Test were used to evaluate patterns of crab abundances relative to categories of sediment type and water depth identified a posteriori. In these comparisons some channel stations were eliminated because of insufficient sediment data. For fixed sites, differences in abundance between sample dates were evaluated using a one-way ANOVA and a Scheffe Multiple Range Test. These analyses were done on a Prime 9955 computer using the SPSSX statistical package (SPSS Inc. 1983). Sex ratios were compared between habitats and between dates or sites for fixed sites using a chi square analysis for independently collected proportions (Fleiss, 1981).

RESULTS

Patterns in Crab Abundances

During the February 1984 random survey significant differences in crab densities were observed among habitats ($F=9.8$, $df=2$, $p \leq 0.002$) but not among strata within habitats ($F=1.5$, $df=14$, $p > 0.1$). On average, crabs were most abundant in the basin and least abundant in the shoal and spit habitat. Abundances in the channels were intermediate (Figure 2).

Crab abundances differed significantly with respect to depth and sediment type (Figure 3). When averaged over all depths sampled, crabs were significantly more abundant on bottoms where the sediments contained 41 to 60% sand than they were on other bottom types ($F= 27.8$, $df= 78$; Scheffe test $p \leq 0.05$)). Crab density also varied significantly with depth ($F= 45.3$, $df=94$)). However, comparisons within both the 9-12 meter and 12-15 meter depth zones indicate that crabs were always more abundant on sediments with intermediate sand concentrations (Table 2).

Collections from fixed stations were used to examine temporal patterns in blue crab abundance through the winter (Table 3). Densities at the Wolf Trap site did not vary significantly through the winter. In the channel, crab densities in February were significantly lower than they were in December and January. Outside the channel, both January and February crab abundances were significantly lower than those observed in December.

Figure 2. Geometric mean number of crabs and 95% C.I. collected per tow for all random samples broken down by major habitat. Numbers in parentheses are numbers of tows in each category.

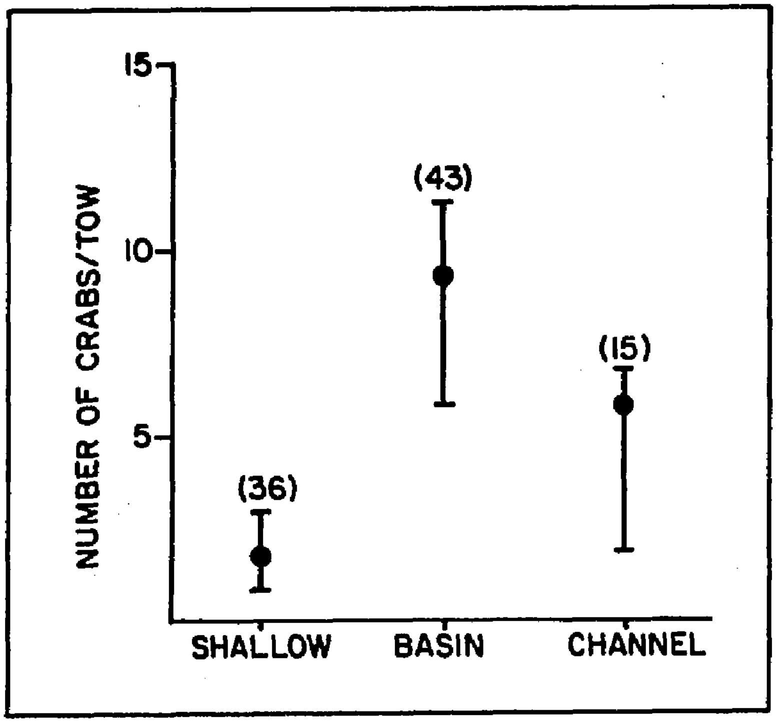

NUMBER OF CRABS/TOW
15
10
5
(36)
(43)
(15)
SHALLOW
BASIN
CHANNEL

Figure 3. Geometric mean number of crabs and 95% C.I. collected per tow for all random samples broken down by a) percent sand and b) depth classes. Numbers in parentheses are numbers of tows in each category.

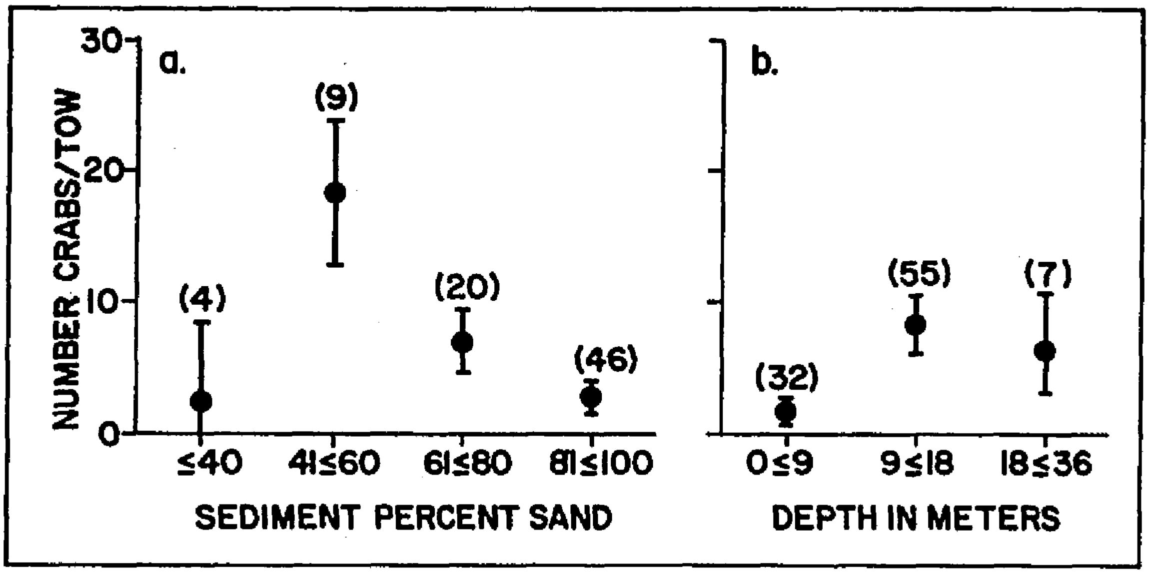

a.
b.
NUMBER CRABS/TOW
0
10
20
30
(4)
(9)
(20)
(46)
≤40
41≤60
61≤80
81≤100
SEDIMENT PERCENT SAND
(32)
(55)
(7)
0≤9
9≤18
18≤36
DEPTH IN METERS

Table 2. Results of one-way ANOVA and Scheffe Multiple Range Test comparing geometric mean crab abundances for random survey collections by depth of station. Some channel stations were excluded due to insufficient sediment data.

I. Depth Range: 9≤12 m

% Sand	Mean Crab Abundance (SD)	n	Scheffe ≤40%	41≤60%	61≤80%
≤40	2.5 (1.9)	4	--		
41-60	17.8 (4.2)	5	*	--	
61-80	5.1 (0.9)	13	n.s.	*	--
81-100	5.7 (1.6)	12	n.s.	*	n.s.

F ratio = 8.5 (p<0.001)
* groups significantly different at (α = 0.05)
n.s. not significant

II. Depth Range: 12≤15 m

% Sand	Mean Crab Abundance (SD)	n	Scheffe 41≤60%	61≤80%
≤40	no samples			
41-60	21.7 (3.2)	3	--	
61-80	12.7 (3.0)	4	n.s.	--
81-100	7.7 (2.3)	3	*	n.s.

F ratio = 5.3 (p<0.04)
* groups significantly different at (α = 0.05)
n.s. not significant

Table 3. Results of one-way ANOVA and Scheffe Multiple Range Test comparing geometric mean crab abundances for fixed site collections by date.

I. Wolf Trap

Month	Mean Crab Abundance (SD)	n	Scheffe		
			Dec	Jan	Feb
December	4.8 (8.2)	20	--		
January	8.5 (10.3)	22	n.s.	--	
February	9.0 (6.4)	20	n.s.	n.s	--

F ratio = 1.9, n.s. not significant

II. York Spit - In channel

Month	Mean Crab Abundance (SD)	n	Scheffe		
			Dec	Jan	Feb
December	16.7 (4.3)	12	--		
January	16.5 (6.3)	10	n.s.	--	
February	8.7 (8.7)	10	*	*	--

F ratio = 5.0 , n.s. not significant, * significant at $\alpha = 0.05$

III. York Spit - Out of channel

Month	Mean Crab Abundance (SD)	n	Scheffe		
			Dec	Jan	Feb
December	26.0 (9.0)	10	--		
January	14.0 (6.0)	10	*	--	
February	6.7 (3.1)	10	*	n.s	--

F ratio = 22.8, n.s. not significant, * significant at $\alpha = 0.05$

Patterns in sex ratio distributions

The population of overwintering blue crabs in the study area was strongly dominated by mature females (Table 5). The ratios of male to female crabs were similar in the major habitats. Sex ratios did not change through time at the fixed sampling sites. However, sex ratios based on counts averaged over collection dates for each of the fixed sampling sites (ie. WT and YSC) were significantly different. Males were relatively more abundant at WT than they were at YSC.

Table 4. Sex ratios of crabs collected during the winter of 1985-86 at random and fixed sites.

	mature females		immature females		males	
	n	%	n	%	n	%
Shoal and Spit	60	92.3	2	3.1	3	5.6
Basin	373	95.4	5	1.3	13	3.3
Channel	82	95.3	0		4	4.7
Wolf Trap						
December	279	93.6	0		19	6.4
January	352	90.0	6	1.5	33	8.5
February	197	90.8	1	0.5	19	8.7
York Spit - In						
December	739	96.5	0		27	3.5
January	737	97.2	0		21	2.8
February	409	94.7	0		23	5.3
York Spit - Out						
December	319	96.4	0		12	3.6
January	528	97.6	0		13	2.4
February	265	96.0	0		11	4.0

DISCUSSION

During the winter of 1985-86 blue crabs in the study region were most abundant in the basin habitat. Blue crabs were rare or absent in the high energy spit and shoal areas. These areas are characterized by highly mobile sandy sediments (Wright et al., 1987; Schaffner et al., 1987) and it seems likely that overwintering crabs in these shallow regions would have a poor chance of survival given the inferred high levels of bottom disturbance. At greater depths in the study area, a wider range of sediment types are found and the patterns of crab distribution suggest that some habitat partitioning occurs. Crabs were abundant on silty-very fine sands (40-80 % sand) at depths below 9 meters, but were less common when sediments were finer (ie. <40% sand) or coarser (ie. >80% sand.

Temporal patterns in crab abundance at the YSC suggest a general decline through the winter. In late January and early February of 1986, many boats were observed to be dredging crabs in this area of the bay and these activities may have reduced crab densities in the region of the channel.

When the Wolf Trap site on the west side of the study area and the York Spit Channel site on the east side of the study area were compared, male crabs were found in significantly higher proportion towards the west. Churchill (1921) suggested that male crabs have a tendency to remain at relatively lower salinities than do females. In the study area, this would mean that males should be relatively more abundant to the west and north where salinities tend to be lower (Stroup and Lynn, 1963).

The data presented indicate that overwintering blue crabs have distinct habitat preferences. Based on a knowledge of major habitat type and bottom characteristics it is possible to predict where overwintering blue crabs will be found in the lower bay and what their relative abundances will be. Indeed, the winter dredge fishery concentrates in areas of "basin" habitat and do not limit themselves strictly to the deepest channel areas (Schaffner pers. obs.). Assuming that crab distributions are predictable, it should then be possible to accurately estimate the abundance of the overwintering adult crab populations. However, reasonable estimates cannot be made until the absolute capture efficiency of the crab dredge is known. Additional studies should be made to address this problem and to determine year to year variability in winter distribution patterns. These types of estimates would allow an adequate assessment of stock size and aid in elucidating the population dynamics of Callinectes sapidus in the Chesapeake Bay system.

Chapter 4.

ECOLOGY OF A POLYHALINE ESTUARINE COMMUNITY DOMINATED BY THE POLYCHAETES *CHAETOPTERUS* AND *EUCLYMENE* IN THE LOWER CHESAPEAKE BAY

ABSTRACT

The benthic community at the Wolf Trap study site in the polyhaline basin habitat in the lower Chesapeake Bay was studied. Box core samples were used to identify resident species, and to discern patterns of faunal abundance and biomass, and species diversity. Box cores and diver collected samples and photographs were used to identify small-scale horizontal and vertical distribution patterns and spatial relationships among species. At least four major groups of organisms were among the dominants. These included: 1) relatively large, long-lived and deeply distributed euryhaline marine species, 2) small, short-lived and shallowly distributed euryhaline marine species, 3) organisms that depend on structures for habitat including epifauna, co-inhabitants and commensals, and 4) deeply-dwelling infaunal predators. The fauna at Wolf Trap includes species that are distributed among a wide range of functional groups, with no clear domination by one group. The 'typical' estuarine fauna, characterized by the numerical dominance of a few small and short-lived species, was not observed. Large tube and burrow-building polychaetes were especially abundant and their presence may influence the availability of habitat for other resident organisms.

INTRODUCTION

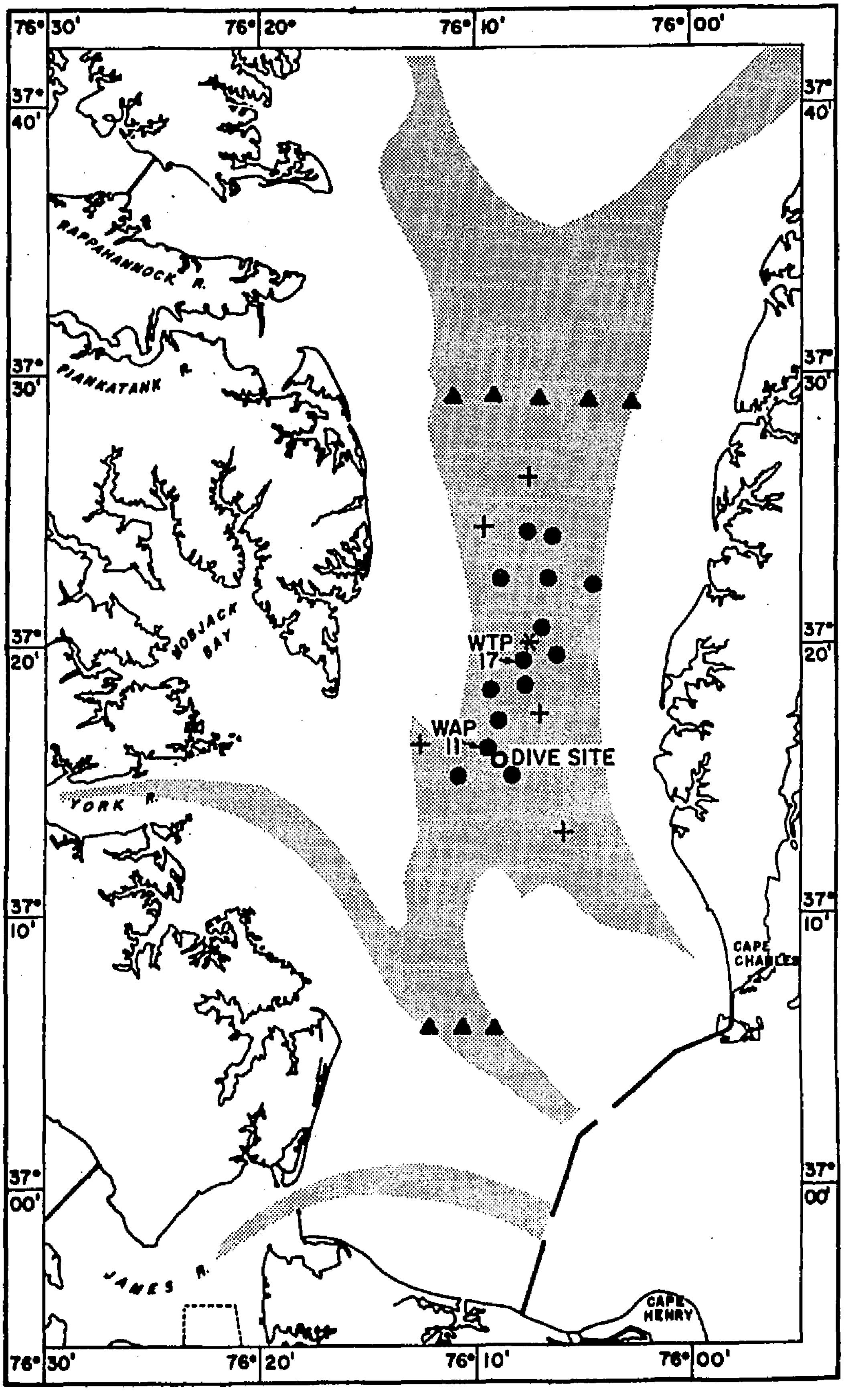
Benthic organisms play an important role in the functioning of estuarine systems. They are major prey items in the diet of fishes and crabs (Arntz and Brunswig, 1975; Arntz, 1978; Virnstein, 1977; Blundon and Kennedy, 1982; Moeller et al., 1985) forming an important energy link between primary producers and higher trophic levels. Infauna often control the movement of dissolved and particulate materials within the sediment bed and across the sediment-water interface (Myers 1977a, 1977b; Aller et al., 1983; Aller and Aller, 1986; Lee and Swartz, 1980; Schaffner et al., 1987). This sediment processing role may influence the fate of sediment-borne toxicants (Lee and Swartz, 1980) and nutrient regeneration rates (Aller, 1982). Thus, an understanding of processes governing the distribution and abundance of benthic organisms is often a prerequisite to a more general understanding of estuarine dynamics and functioning.

The formulation and testing of hypotheses regarding the mechanisms controlling benthic community structure depend on our ability to elucidate faunal response to variation associated with the complex estuarine gradient and to identify when the potential exists for species interactions. The relatively high levels of spatial and temporal variability characterizing the estuary can make it difficult to identify important patterns (Boesch, 1971; Boesch et al., 1976; Diaz, 1984; Holland, 1985; Holland et al., 1987).

As the largest estuary in the United States, the Chesapeake Bay system has been extensively studied. Spatial and temporal patterns for macrobenthos in the oligo- and mesohaline waters of the tributaries (Boesch et al., 1976a; Boesch, 1977; Diaz, 1977; Schaffner et al., 1987) and upper bay (Holland et al., 1977; Mountford et al., 1977; Holland et al., 1980; Hines and Comtois, 1985) have been particularly well documented. Community structure and faunal patterns in response to sediment variation have been investigated in the high salinity baymouth region (Boesch 1971, 1977; Dauer et al., 1984 and Llanso, 1985). Spatial and temporal patterns for macrobenthic communities at the polyhaline mouths of the James and York river tributaries have also been investigated (Boesch, 1973; Boesch et al. 1976a; Diaz, 1984). However, only a limited number of samples have been collected and evaluated for faunal characteristics in the expansive, polyhaline basin of the lower bay (Figure 1) despite the fact that this major benthic habitat type exhibits distinct physical characteristics and bottom sediments which delineate it from the tributary mouths (Chapter 2, this volume; Wright et al., 1987). The relative paucity of information on the benthos of the basin makes it difficult to develop a synthetic and representative overview of the Chesapeake Bay estuary and prevents adequate comparisons with other systems.

This paper presents results of a study of the benthic macrofauna at the Wolf Trap study site, an area located centrally within the basin of the lower Chesapeake Bay (Figure 1). The specific objectives of this study were to characterize faunal density and biomass, community composition and biomass, small-scale horizontal and vertical

Figure 1. The study area in the lower Chesapeake Bay. Shaded area shows approximate limits of basin habitat. ● denotes locations of fixed sampling sites, * denotes location of the "clustered box cores" collected in May and November 1984, + indicates locations of basin samples collected by Nilsen et al. (1982), ▲ indicates location of basin samples collected by Dauer et al. (1984).


76° 30'
76° 20°
76° 10'
76° 00'
37° 40'
37° 30'
37° 20'
37° 10'
37° 00'
RAPPAHANNOCK R.
PIANKATANK R.
MOBJACK BAY
YORK R.
JAMES R.
WTP
17
WAP
11
DIVE SITE
CAPE CHARLES
CAPE HENRY
76° 30'
76° 20'
76° 10'
78° 00'

distribution patterns and spatial relationships among species. These results are compared with those found by investigators studying the fauna in other parts of the bay and the adjacent shelf and in other estuarine areas worldwide. Previous generalizations regarding the factors controlling the distribution and abundance patterns of estuarine organisms, particularly with respect to the polyhaline zone, are reconsidered.

STUDY AREA

Detailed physical characteristics of the basin habitat are presented in Wright et al. (1987) Boon et al. (1987) and Chapter 2 (this volume). Sediments are silty, very fine sands or coarse silts with some very fine sands. Clay contents are generally less than 15%. Depths are generally between 10 and 14 meters, but range from 8 to 15 meters. Mean bottom salinities range between 20 and 27 ppt, with typical lateral differences of 2 to 3 ppt and 3 to 4 ppt differences from north to south (Stroup and Lynn, 1963). Average bottom temperatures range from a winter low of 4°C to a summer high of 25°C (Stroup and Lynn, 1963). However, recent evidence suggests that both salinity and temperature can fluctuate rapidly (hours or days) in this part of the bay due primarily to destratification events resulting from meteorologically driven exchange with the coastal ocean as well as wind and tidally induced mixing (Goodrich, 1985). Tidal currents dominate in the basin (Boon et al., 1987). Some tidal reworking of sediments does occur (Chapter 2, this volume), but resuspension appears to be relatively low (Boon et al., 1987).

METHODS

Quantitative benthic sampling was conducted during November 1983, February 1984, May 1984, August 1984 and November 1984 at 14 fixed locations (Figure 1). These samples were collected using a spade box corer (0.06 m^2, 15 cm deep). One core collected for each location/date combination was used for quantitative abundance estimates. A second core, partitioned into vertical sections (0-2, 2-5, 5-10 and 10-15 cm), was collected at each location for biomass estimates. During May and November 1984 additional cores for determination of vertical distribution patterns of dominant species were collected in the vicinity of sampling location WTP17 ('clustered box cores', Figure 1). Samples were sieved on 500 um mesh screen in the field and formalin fixed.

During May 1984 I examined the distribution and abundance patterns of small macrobenthos in a single box core from the study area that contained tubes of the polychaetes *aetopterus variopedatus*, *Loimia medusa*, and *Euclymene zonalis*. Intact sediment horizons from two depth intervals (0 to 2 cm and 2 to 4 cm) were further partitioned with a contiguous 5x8 array of 2.5 cm^2 cores ('core array samples'). Each core was formalin fixed and sieved on 250 um mesh screen. The residue from each core was examined for tubes or other structures.

Resolution of faunal distribution patterns at the sediment-water interface and in association with large resident tube-builders were made by direct observations, photographic recording and quantitative sampling between June 1984 and December 1986 at a site near WAP09

(Figure 1). During June 1984 patterns of faunal distribution directly around and near to the tubes of the polychaetes _Chaetopterus variopedatus_ and _Euclymene zonalis_ were determined by comparison of diver collected pairs of small cores (2.5 cm diameter taken to a depth of 5 cm). The first member of these 'paired' core samples was taken by inserting a core tube down into the sediment so that it included the tube of _Chaetopterus_ or _Euclymene_ (this is the 'with' core). Before the first core was removed, a second core was inserted into the sediment adjacent to the first but into an area that contained no tubes of either species (this is the 'near' core). Both cores were then capped, removed from the sediment and bound together as a pair with a rubber band. During June 1985, I partitioned tubes (these are called 'partitioned' samples) of _Chaetopterus_ by separating the section of tube projecting above the sediment surface ('above ground') from the portion extending from the surface to a depth of 5 cm ('below ground'). The portions above the surface were clipped with scissors and placed into whirlpac bags. Below surface samples were taken with 2.5 cm diameter core tubes. This subsectioning allowed me to determine if organisms associated with the tube were living on the part of the tube which projected above the sediment surface or below the sediment-water interface. On other dates in 1985 only 'above ground' portions of tubes were collected. These samples were used to generate a list of species associated with tube tops. Lastly, co-inhabitants of _Chaetopterus_ tubes were elucidated by sealing and collecting tubes in the field during October 1985 and July 1986. When these tubes were removed from the bed, adhering sediment was rinsed away so that only the tube and resident organisms were collected.

During February 1984 cores were collected and dissected shipboard to uncover the living positions of larger macrobenthos. These observations of subsurface features were supplemented with information from x-radiographs of sediment cores (see Chapter 2) and sediment profile photographs taken concurrently at each station (see Rhoads and Germano 1986 for a description of the camera and techniques used).

In the laboratory wet weight biomass estimates for major groups were obtained from formalin stored organisms sorted to water. Shell weights for molluscs were included. Cores for quantitative abundance estimates and other small samples were sorted to lowest possible taxon and enumerated.

Species richness (SR) and evenness (J') were calculted for each quantitative box core using the formulas given by Margalef (1958) and Pielou (1966).

A one-way ANOVA was used to compare total numbers of organisms among all 'paired' core samples. For individual species, the assumptions of ANOVA could not be met, and I employed the non-parametric Kruskal-Wallis test. These statistics were computed using SPSSX software (SPSS, Inc., 1983) on a Prime 9950 computer.

RESULTS

Faunal composition, abundance and biomass

At least 127 species of non-colonial macrobenthic invertebrates have been identified from the 25,978 individuals collected in quantitative box core samples. Polychaetes were the dominant taxon (47 species) generally accounting for more than 70% of the individuals. Bivalves, gastropods and crustaceans each comprised less than 10% of the total individuals. Of the 31 crustacean species, 11 were amphipods and 6 were cumaceans or isopods. Bivalves and gastropods accounted for 18 and 15 species, respectively. The remaining 16 or more non-colonial taxa included oligochaetes, turbellarian flatworms, anthozoans, phoronids, nemerteans, echinoderms, hemi- and urochordates and echiurids. At least 6 species of colonial hydrozoans, bryozoans and sponges were also collected.

Faunal densities ranged between 1,984 and 11,302 individuals per square meter. Mean densities were highest during the fall of 1983 and lowest during the summer of 1984 (Table 1). With the exception of the Phoronida, all major taxa were less abundant at the end of the study than they were when sampling first began in November 1983.

Biomass values for the total fauna ranged between 71 and 1,512 grams of wet weight per square meter. Values were lowest during February 1984 and highest in August and November 1984 (Table 2). Polychaetes contributed most of the biomass in all collections,

Table 1. Distribution of individuals among major taxonomic groups at the Wolf Trap study region. Values for each cruise are means from 2 cores (0.12 m^2) collected at each of the 14 fixed stations standardized to a square meter. Numbers in parentheses are standard deviations.

Major Taxon	Nov 1983	Feb 1984	May 1984	Aug 1984	Nov 1984	Total
Annelida						
Polychaeta	4636(2051)	3203(826)	3113(1218)	2168(834)	3100(714)	3244(1437)
Oligochaeta	14(33)	17(21)	25(31)	6(14)	12(17)	15(24)
Mollusca						
Bivalvia	223(116)	263(184)	533(374)	314(150)	43(39)	275(255)
Gastropoda	171(88)	127(60)	161(97)	38(31)	150(131)	129(98)
Crustacea						
Amphipoda	391(145)	307(205)	258(166)	203(131)	192(182)	270(179)
Other Crustacea	59(42)	46(54)	44(32)	9(16)	48(41)	41(41)
Echinodermata	42(31)	18(23)	17(16)	15(17)	14(18)	21(24)
Anthozoa	18(15)	17(18)	7(14)	8(11)	12(19)	13(16)
Rynchocoela	125(78)	83(45)	68(56)	96(83)	45(40)	84(67)
Turbellaria	48(39)	36(20)	52(57)	46(46)	38(37)	44(41)
Phoronida	7(11)	24(17)	30(42)	29(28)	25(19)	23(26)
Miscellaneous Groups						
Hydrozoa						a
Bryozoa						a
Hemichordata	17(24)	12(13)	19(32)	4(10)	7(13)	12(20)
Urochordata	1(2)	1(3)	0	1(4)	1(4)	1(3)
Echiurida	5(11)	0	0	0	0	1(5)
Grand Mean	5757(2274)	4155(1103)	4327(1663)	2939(880)	3687(821)	4173(1694)
n =	14	14	14	14	14	70

a - Colonial fauna not enumerated

Table 2. Distribution of wet weight biomass (grams) among major taxonomic groups at the Wolf Trap study regions. Values are based on 1 core (0.6 m^2) collected at each of the 14 fixed stations during each cruise. Values are standardized to a square meter. Numbers in parentheses are standard deviations.

Major Taxon	Nov 1983	Feb 1984	May 1984	Aug 1984	Nov 1984	Total
Annelida	216(121)	182(67)	213(117)	181(71)	231(251)	204(139)
Mollusca						
Bivalvia	7(6)	10(8)	23(13)	114(182)	52(161)	41(113)
Gastropoda	1(> 1)	1(1)	3(2)	1(1)	1(1)	1(1)
Crustacea	4(10)	3(3)	5(4)	1(2)	6(7)	4(6)
Echinodermata	2(4)	1(2)	4(8)[a]	4(5)	15(17)	5(10)
Anthozoa	27(45)	8(20)	1(1)	1(3)	4(11)	8(24)
Rynchocoela	2(3)	1(2)	2(7)	7(14)	2(6)	3(8)
Turbellaria	< 1(< 1)	< 1(< 1)	1(< 1)	< 1(< 1)	< 1(< 1)	< 1(< 1)
Phoronida	< 1(< 1)	1(1)	2(2)	1(1)	1(1)	1(1)
Others[b]	5(10)	3(6)	7(10)	6(7)	10(11)	6(9)
Grand Mean	266(130)	210(68)	261(125)	317(201)	323(277)	275(175)

[a] Computed using a value which excluded the weight of a single large holothurian *Sclerodactyla briareus* (actual weight 76 grams).

[b] Includes colonial taxa.

however, bivalves recruited into the area in the spring of 1984 made a large biomass contribution during August 1984. Sparsely distributed, but large organisms such as the echinoderms (primarily ophiuroids) and anthozoans (primarily ceriaenthids), were important biomass contributors. On average, these groups contributed 8 and 4% of the biomass respectively. Colonial forms were not included in estimates of faunal densities and were not biomassed individually. However, they were conspicuous components of the epibenthic fauna of the lower bay. In a seperate study conducted during the winter of 1986, I estimated the densities of hydoids, bryozoans and sponges to average about 5 to 6 grams of wet weight per square meter in the basin region (Schaffner, unpublished). In November 1983, 41% of the individuals and 65% of the total biomass were found 5 cm or more below the sediment-water interface (Figure 2). Similar patterns in the depth distributions of individuals were observed in the clustered box core collections from May and November 1984 (Figure 3).

Species richness

An average of 229 individuals per core was distributed among 32 species. The number of species, the calculated species richness (SR) measure and evenness (J') values are presented in Table 3.

Figure 2. The distribution of individuals and total wet weight biomass with depth in the sediment from cores collected during November 1983. Values are means based on 14 cores.

NOVEMBER 1983

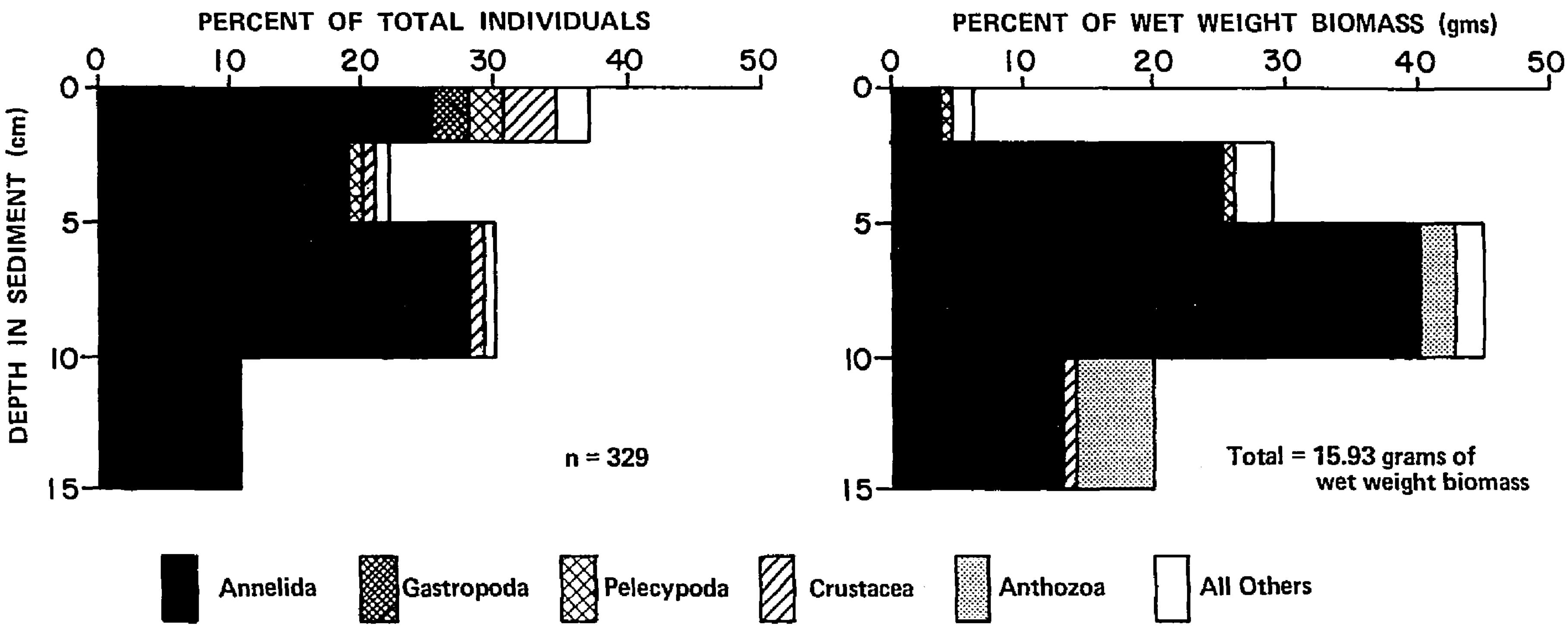


Figure 3. The distribution of individuals with depth in the sediment for "clustered box cores" collected during May and November 1984. Values are means based on 6 cores.

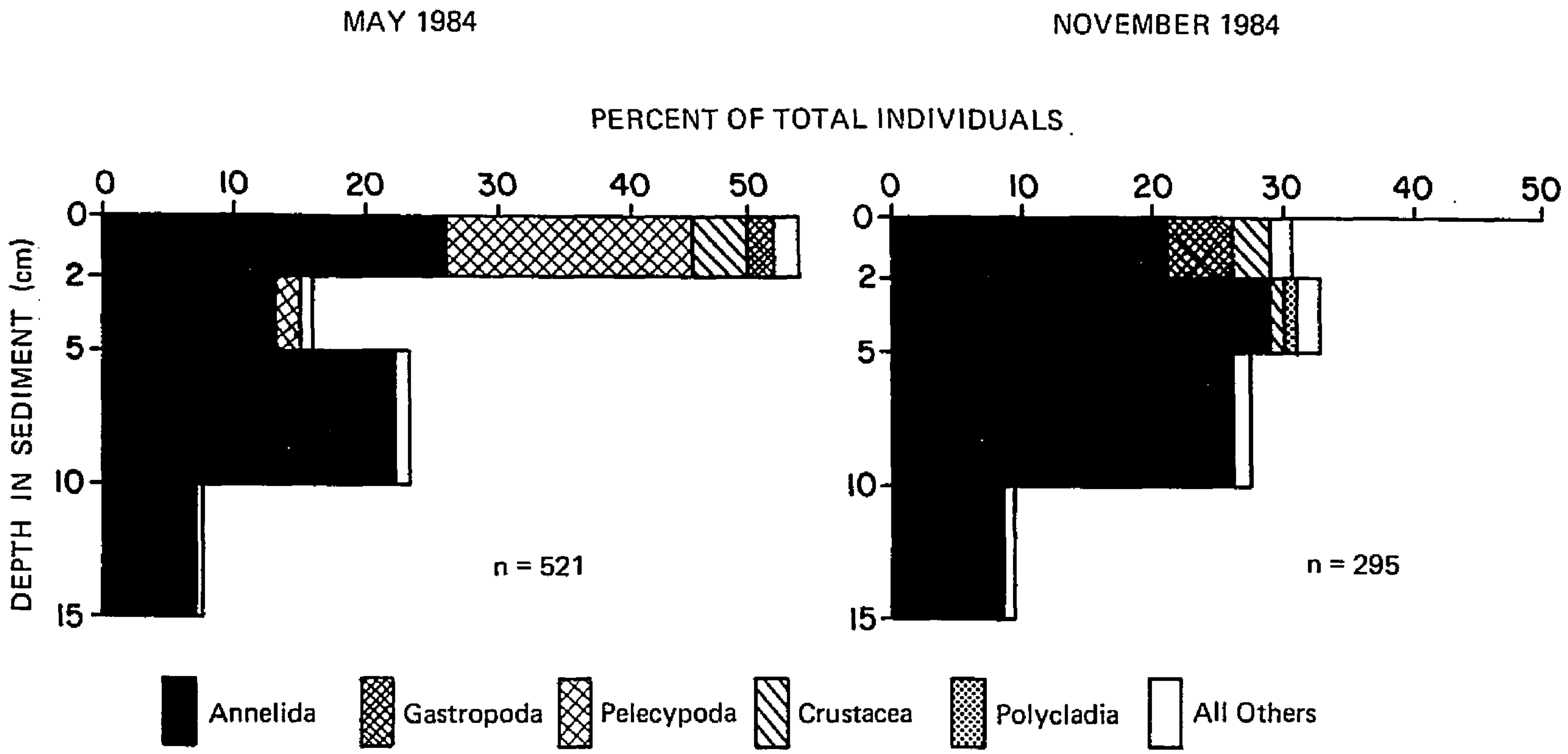

MAY 1984
NOVEMBER 1984
PERCENT OF TOTAL INDIVIDUALS
0
10
20
30
40
50
DEPTH IN SEDIMENT (cm)
0
2
5
10
15
n = 521
n = 295
Annelida
Gastropoda
Pelecypoda
Crustacea
Polycladia
All Others

Table 3. Summary of total macrobenthic density, areal species richness, evenness (J') and species richness (SR) for fixed stations at the Wolf Trap study area. Values are means (standard deviations) for each date based on 14 0.06 square meter cores. Total n = 70.

	no. of indiv.	no. of species	Evenness J'	Richness SR
November 1983	318 (124)	40 (5)	0.76 (0.02)	6.7 (0.9)
February 1984	211 (70)	31 (4)	0.75 (0.06)	5.6 (0.7)
May 1984	231 (97)	34 (6)	0.76 (0.06)	6.1 (0.9)
August 1984	172 (50)	25 (5)	0.76 (0.04)	4.9 (0.9)
November 1984	213 (48)	27 (5)	0.71 (0.05)	4.9 (0.8)
Total	229 (93)	32 (7)	0.75 (0.05)	5.7 (1.1)

Dominant species

Fifty taxa, most identified to the species level, accounted for 95% of the fauna during this study (Table 4). Nearly all major taxa were included, but the polychaetes were the most common (26 taxa) and included 7 of the top ten dominants. Information on feeding type, motility mode and living positions for each of the dominants based on observations made during this study and information from the literature (Bousfield, 1973; Fauchald and Jumars, 1979; Biernbaum, 1979; Williams, 1984) is summarized in Table 4.

Nearly half of the dominant organisms at Wolf Trap build tubes (Table 5). These range from the substantial, leathery u-shaped tubes of *Chaetopterus variopedatus*, and the thick, u-shaped mud tube of *Loimia medusa* to the fragile mucous tube of *Mediomastus ambiseta*. *Chaetopterus* and *Loimia* are sedentary, however *Mediomastus* is classified as motile because it moves slowly through the sediment as it feeds. The dominant feeding types are predator/omnivore, subsurface deposit and surface/interface. Nearly all of the predators/omnivores are freely burrowing organisms, although some (ie. the polychaete *Glycera americana*) were observed to build mucous-lined burrow networks in this and another study (Nilsen et al., 1982).. Epizooic organisms associated with *Chaetopterus* tube tops and co-inhabitants or commensals of large tube and burrow builders were also included among the dominants.

Table 4. Abundance, frequency of occurrence and ecological classification of the dominant fauna at the Wolf Trap study area. Feeding, motility and living position categories are defined in Table 5. For taxonomic groups: P = polychaete, B = bivalve, G = gastropod, A = amphipod, Ph = phoronid, Op = ophiuroid, H = hemichordate, U = urochordate, N = nemertean, An = enthozoan. Total n for statistics equals 70 cores.

Taxon	Mean Number/m^2	(SD)	Frequency	Feeding Type	Motility Mode	Living Position
Euclymene zonalis (P)	970	(447)	.98	SB	S	T
Paraprionospio pinnata (P)	533	(358)	.94	SF	DM	T
Bhawania heteroseta (P)	267	(285)	.96	P-O	M	FL
Nephtys spp. juveniles (P)	241	(253)	.74	P-O	M	FL
Sigambra tentaculata (P)	239	(203)	.98	P-O	M	FL
Notomastus latericeus (P)	179	(317)	.90	SB	M	B
Nephtys picta (P)	131	(117)	.96	P-O	M	FL
Macoma tenta (B)	110	(103)	.84	SF	DM	B
Gyptis brevipalpa (P)	97	(75)	.94	P-O	M	FL
Listriella barnardi (A)	90	(104)	.87	O-S	M	C
Ampelisca abdita (A)	78	(62)	.90	SF	DM	T
Loimia medusa (P)	68	(68)	.76	SF	S	T
Tubulanus pellucidus (N)	65	(62)	.84	P-O	M	FL
Chaetopterus variopedatus (P)	63	(91)	.57	F	S	T
Glycinde solitaria (P)	57	(57)	.87	P-O	M	FL
Pseudeurythoe ambigua (P)	54	(93)	.80	P-O	M	FL
Cirratulidae (primarily *Tharyx*) (P)	48	(66)	.66	SF	DM	FL
Acteocina canaliculata (P)	48	(46)	.84	O-S	M	FL
Glycera americana (P)	46	(43)	.77	P-O	M	B
Polydora ligni (P)	41	(86)	.47	SF	DM	T
Mytilus edulis (B)	39	(150)	.21	F	S	E-O
Macoma spp. juveniles (B)	37	(72)	.40	SF	DM	B
Mediomastus ambiseta (P)	36	(58)	.67	SB	M	T
Yoldia limatula (B)	35	(60)	.64	SF	M	FL
Polycladia	34	(37)	.73	P-O	M	FL

Table 4 (cont'd.)

Taxon	Mean Number/m^2	(SD)	Frequency	Feeding Type	Motility Mode	Living Position
Listriella clymenellae (A)	33	(40)	.67	O-S	M	C
Nassarius trivittatus (G)	29	(44)	.60	O-S	M	FL
Clymenella torquata (P)	24	(29)	.67	SB	S	T
Erichthonius brasiliensis (A)	23	(71)	.37	SF	DM	ET
Phoronis sp. (Ph)	23	(26)	.63	F	S	T
Cistena gouldii (P)	22	(85)	.51	SB	M	T
Turbonilla interrupta (G)	20	(29)	.50	P-O	M	FL
Malmgreniella (*lunulata*?) (P)	19	(24)	.54	P-O	M	C
Micropholis atra (Op)	19	(21)	.63	SB	S	B
Mulinia lateralis (B)	18	(63)	.20	F	S	FL
Owenia fusiformis (P)	15	(17)	.59	SF	S	T
Oligochaeta spp.	15	(25)	.44	SB	M	FL
Nereis succinea (P)	13	(21)	.47	O-S	DM	E-O
Corophium tuberculatum (A)	13	(32)	.33	SF	DM	E-T
Odostomia engonia (G)	13	(29)	.33	P-O	M	FL
Saccoglossus kowalewskii (H)	12	(20)	.43	SB	S	B
Ampelisca verrilli (A)	11	(21)	.33	SF	S	T
Cabira incerta (P)	10	(22)	.37	P-O	M	FL
Cylichna alba (G)	9	(14)	.40	O-S	M	FL
Asychis elongata (P)	9	(11)	.50	SB	S	T
Molgula manhattensis (U)	8	(25)	.17	F	S	E-O
Prionospio cirrifera (P)	8	(25)	.20	SF?	DM?	T?
Micrura sp. (N)	8	(14)	.35	P-O	M	FL
Gyptis vittata (P)	7	(20)	.23	P-O	M	FL
Ceriatheopsis americanus (An)	7	(13)	.37	F	S	T
Mean density - 50 dominants	3994	(1630)				
Grand mean density	4195	(1683)				
% of total by dominants	95%					

Table 5. Classification of dominant organisms with reference to categories of feeding type, motility mode and living position.

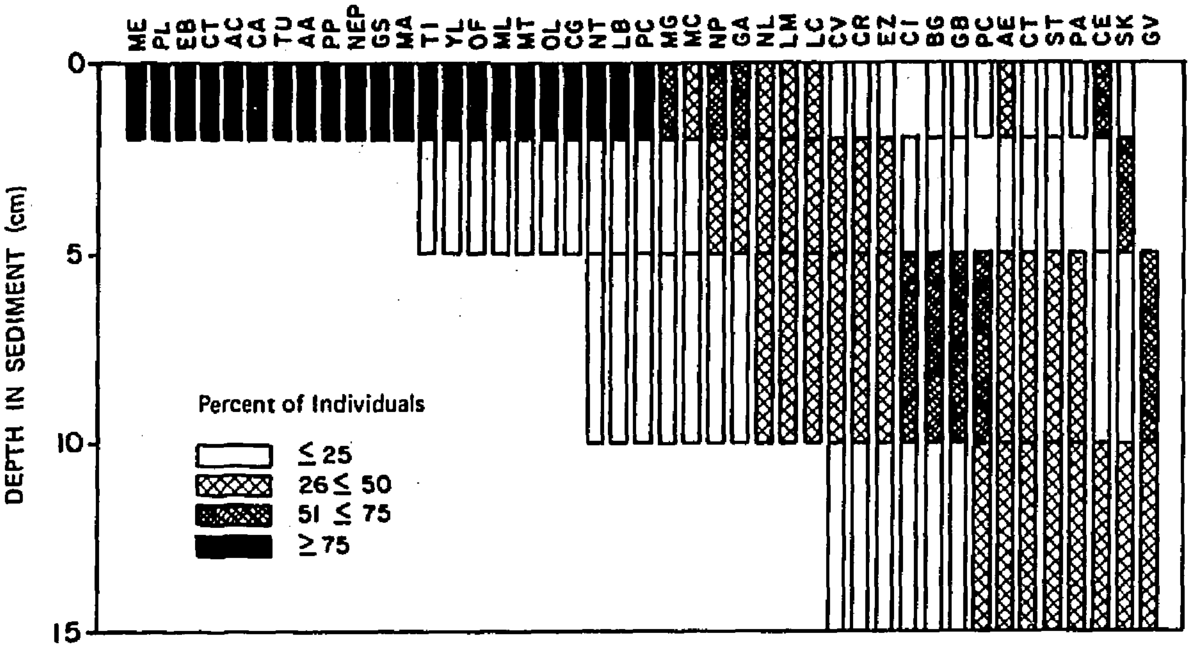
Feeding type:	
Predator-Omnivore (P-O)	33%
Subsurface Deposit (SB)	32%
Surface Deposit (SF)	26%
Omnivore-Scavenger (O-S)	5%
Filter or Suspension (F)	4%
Motility mode:	
Motile (M)	45%
Sedentary (S)	34%
Discretely Motile (DM)	21%
Living position:	
Tube (T)	47%
Free-living (FL)	36%
Burrow (B)	10%
Co-inhabitants/Commensals(C)	4%
Epizooic-tube builders (ET)	2%
Epizooic-other (EO)	1%

Patterns of vertical distribution for dominant species

The vertical distribution patterns of numerically dominant species are shown in Figures 4 and 5. During the spring, half of the species had their distributions concentrated near to or above the sediment surface (ie. captured in the 0-2 cm horizon). Organisms such as the polychaetes Nephtys picta, Glycera americana and Asychis elongata and anemone Ceriantheopsis americana which can burrow deeply as adults, were represented at shallow depths by small individuals, suggesting recent recruitment. Adults of these species were found to at least 10 cm depths in the same samples. Small individuals of the brittle star Micropholis atra and juveniles of its commensal, the polychaete Malmgreniella (lunulata?), also were abundant near the surface while adults of both species were found more deeply. The polychaetes Notomastus latericeus and Loimia medusa and amphipod Listriella clymenellae were distributed throughout the upper 10 cm of the sediment. Thirteen of the dominants had highest densities below the surface. These included the head-down deposit feeding maldanids Euclymene zonalis and Clymenella torquata, the predatory polychaetes Bhawania heteroseta, Gyptis brevipalpa, Gyptis vittata, Sigambra tentaculata, Cabira incerta, and Psuederythoe ambigua, the large sedentary polychaete Chaetopterus variopedatus, the small spionid polychaete Prionospio cirriferra and a small cirratulid polychaete cf. Tharyx.

During the fall, fewer organisms and species were concentrated in the shallow surface layer. Species limited to the 0-2 cm layer during

Figure 4. Depth distribution patterns for dominant species found during May 1984. The percentage distributions of individuals in each depth horizon are shown. Abbreviations are as follows with the number of specimens shown in parentheses: ME, *Mytilus* (511); PL, *Polydora* (125); EB, *Erichthonius* (11); CT, *Corophium* (19); AC, *Acteocina* (78); CA, *Cylichna* (21); TU, *Tubulanus* (41); AA, *Ampelisca abdita* (26); PP, *Paraprionospio* (159); NEP, Nepthyiidae juv. (196); GS, *Glycinde* (38); MA, *Mediomastus* (32); TI, *Turbonilla* (25); YL, *Yoldia* (75); OF, *Owenia* (19); ML, *Mulinia* (43); MT, *Macoma tenta* (31); OL, Oligochaeta (65); CG, *Cistena* (6); NT, *Nassarius* (27); LB, *Listriella barnardi* (69); PC, Polycladia (23); MG, *Malmgreniella* (27); MC, *Micropholis* (13); NP, *Nephtys picta* (37); GA, *Glycera* (31); NL, *Notomastus* (155); LM, *Loimia* (22); LC, *Listriella clymenellae* (27); CV, *Chaetopterus* (37); CR, Cirratulidae (21); EZ, *Euclymene* (771); CI, *Cabira* (4); BG, *Bhawania* (208); GB, *Gyptis brevipalpla* (78); PC, *Prionospio* (8); AE, *Asychis* (8); CT, *Clymenella* (25); ST, *Sigambra* (109); PA, *Pseudeurythoe* (24); CE, *Ceriantheopsis* (6); SK, *Saccoglossus* (14); GV, *Gyptis vittata* (9). Full species names are given in Table 4.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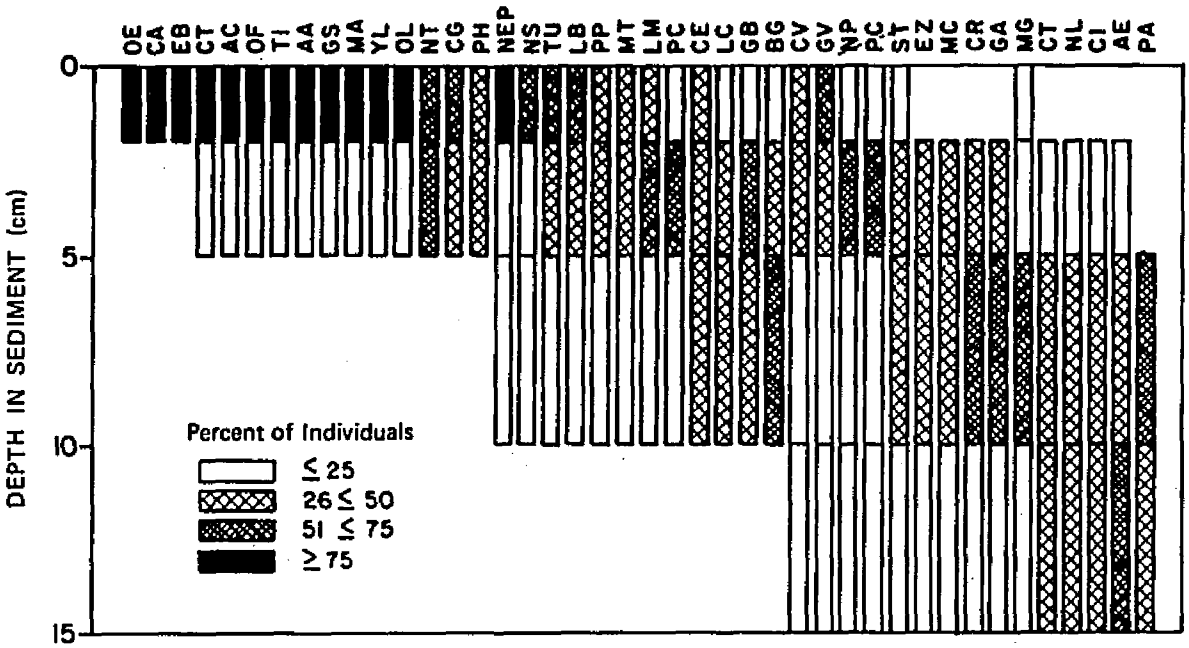
NL
LM
LC
CV
CR
EZ
CI
BG
GB
PC
AE
CT
ST
PA
CE
SK
GV
DEPTH IN SEDIMENT (cm)
0
5
10
15
Percent of Individuals
≤ 25
26 ≤ 50
51 ≤ 75
≥ 75

Figure 5. Depth distribution patterns for dominant species found during November 1984. The percentage distributions of individuals in each depth horizon are shown. Abbreviations are as follows with the number of specimens shown in parentheses: OE, *Odostomia* (101); CA, *Cylichna* (16); EB, *Erichthonius* (11); CT, *Corophium* (12); AC, *Acteocina* (40); OF, *Owenia* (12); TI, *Turbonilla* (11); AA, *Ampelisca abdita* (34); GS, *Glycinde* (67); MA, *Mediomastus* (49); YL, *Yoldia* (10); OL, Oligochaeta (18); NT, *Nassarius* (6); CG, *Cistena* (10); PH, *Phoronis* (22); NEP, Nephtyiidae juv. (16); NS, *Nereis* (31); TU, *Tubulanus* (24); LB, *Listriella barnardi* (30); PP, *Paraprionospio* (421); MT, *Macoma tenta* (17); LM, *Loimia* (66); PC, Polycladia (21); CE, *Ceriantheopsis* (12); LC, *Listriella clymenellae* (42); GB, *Gyptis brevipalpa* (21); BG, *Bhawania* (128); CV, *Chaetopterus* (22); GV, *Gyptis vittata* (13); NP, *Nephtys picta* (38); PC, *Prionospio* (22); ST, *Sigambra* (89); EZ, *Euclymene* (426); MC, *Micropholis* (16); CR, Cirratulidae (34); GA, *Glycera* (17); MG, *Malmgreniella* (20); CT, *Clymenella* (45); NL, *Notomastus* (28); CI, *Cabira* (10); AE, *Asychis* (6); PA, *Pseudeurythoe* (23). Full species names are given in Table 4.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PC
ST
EZ
MC
CR
GA
MG
CT
NL
CI
AE
PA
0
5
10
15
DEPTH IN SEDIMENT (cm)
Percent of Individuals
≤ 25
26 ≤ 50
51 ≤ 75
≥ 75

the spring that had deeper depth distributions in the fall included the polychaetes *Glycinde solitaria*, *Mediomastus ambiseta*, *Paraprionospio pinnata* and juvenile *Nephtys* spp., the bivalve *Yoldia limatula*, the gastropod *Acteocina canaliculata*, the amphipod *Ampelisca abdita* and nemertean *Tubulanus pellucidus*. Some species that appeared in the surface layers of cores as juveniles and deeper layers as adults during the spring were mainly represented by deeply distributed adults during the fall. Included in this group were the brittlestar *Micropholis atra*, and polychaetes *Malmgreniella* (*lunulata*), *Notomastus latericeus* and *Glycera americana*. A few species had greater percentages of their populations more shallowly distributed in the fall (eg. the polychaetes *Bhawania heteroseta*, *Gyptis brevipalpa*, *Gyptis brevipalpa*, *Sigambra tentaculata* and *Prionospio cirriferra*).

Small scale distribution patterns relative to tube structures

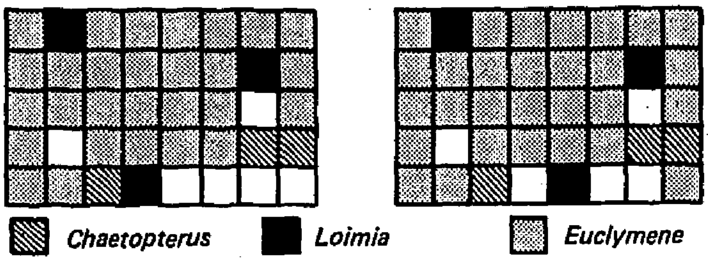
The patterns of total macrobenthos and 3 commonly encountered species within each horizon of 'core array' samples relative to the positions of tubes are shown in Figure 6. The highest densities of organisms in both horizons were found in cores containing either a *Chaetopterus* or *Loimia* tube. The organisms reaching high densities in these cores were the polychaete *Polydora ligni* and the amphipod *Corophium tuberculatum*. However, four other cores within each horizon also contained large tubes, but did not exhibit similarly high densities of organisms. Almost all cores contained pieces of *Euclymene* or *Clymenella* tubes so that it was difficult to resolve

Figure 6. Spatial patterns in the "core array horizons". Cores containing tubes of *Chaetopterus*, *Euclymene* and *Loimia* are indicated, along with the numbers of individuals for the total fauna, *Polydora ligni*, *Corophium tuberculatum* and *Mediomastus ambiseta*.

SEDIMENT HORIZON

0 - 2 cm　　　　2 - 4 cm

TUBES



0 - 2 cm

░	■	░	░	░	░	░	░
░	░	░	░	░	░	■	░
░	░	░	░	░	░		░
░		░	░	░	░	▨	▨
░	░	▨	■				

2 - 4 cm

░	■	░	░	░	░	░	░
░	░	░	░	░	░	■	░
░	░	░	░	░	░		░
░		░	░	░	░	▨	▨
░	░	▨		■			░

▨ *Chaetopterus*　■ *Loimia*　░ *Euclymene*

TOTAL FAUNA

0 - 2 cm

10	8	9	4	9	9	7	9
5	4	11	10	14	5	15	
2	6	7	14	8	10	11	6
2	1	3	15	8	8	12	12
9	2	35	53	12		3	8

2 - 4 cm

5	2	1	5		1	3	
2		2	3	1	3	1	3
	1		1		3	4	
2	1	4	7	3	3	2	1
1	2	7	9	1		2	2

Polydora ligni

0 - 2 cm

1		4		3	3	1	5
		2		5	2	8	
	1	2	13	3	1	2	
			9	2	2	7	9
6	2	27	23	3			

2 - 4 cm

	1						
			2		1		
					1		
			4	1			
			8				

Corophium tuberculatum

0 - 2 cm

		3	16				

2 - 4 cm

		3					

Mediomastus ambiseta

0 - 2 cm

2	1	3		1		1	1
2	2	4	6	3	1		
2	3	1			4	3	2
2		1		2	1	2	
		2	9	4			2

2 - 4 cm

4			1				
							1
1		1					
	1						

potential relationships between faunal densities and the presence of those tube builder. Some organisms encountered in the array did not exhibit patterns easily related to structures observed within the array (eg. *Mediomastus ambiseta*).

In the 'paired' core samples from June 1984 organisms were more abundant in cores with *Chaetopterus* tubes than they were in cores near to *Chaetopterus* tubes and with or near to *Euclymene* tubes (Table 6). Species exhibiting significantly different densities among cores are also listed in Table 6. Most species were more abundant or limited to the cores containing a *Chaetopterus* tube. Three of these species (ie. the polychaete *Polydora ligni*, amphipod *Corophium tuberculatum* and bivalve *Mytilus edulis*) were attached directly to exposed *Chaetopterus* tube tops.

Abundant species associated with 'above ground' tube tops in June 1985 included the amphipods *Corophium tuberculatum*, *Erichthonius brasiliensis* and *Parametopella cypris*, the polychaete *Polydora ligni* and urochordate *Molgula manhattensis* and colonial hydroids which were not enumerated (Tables 7 and 8). Abundant organisms found around tubes 'below ground' were the infaunal polychaetes *Mediomastus ambiseta*, *Streblospio benedicti* and juvenile *Euclymene zonalis* and the infaunal tubicolous amphipod *Ampelisca abdita*. Because the data from 1984 indicated that infaunal species would not be found at increased abundances near to *Chaetopterus* tubes I did not collect paired samples that excluded *Chaetopterus* tubes.

Chaetopterus tubes collected during the spring and fall of

Table 6. Mean densities of species exhibiting significant differences in samples with or near to _Chaetopterus_ tubes (WC vs. NC) and with or near to _Euclymene_ tubes (WE vs. NE). For species, levels of significance for H (K-W Test) are given. For total fauna, levels of significance for F ratio (ANOVA) are given.

N equals	WC 20	NC 20	WE 11	NE 11	level of sign.
Corophium tuberculatum	10.1	0.3	0.2	0.0	0.0001
Polydora ligni	4.3	0.1	0.3	0.2	0.0001
Metazoan #1	2.8	0.3	1.1	0.0	0.001
Nereis succinea	1.5	0.0	0.0	0.0	0.001
Mytilus edulis	0.7	0.0	0.0	0.0	0.003
Glycinde solitaria	0.0	0.3	0.0	0.0	0.02
Streblospio benedicti	0.9	1.5	1.7	2.5	0.05
Total Fauna	43.3	16.3	18.2	19.5	0.001

Table 7. Densities of selected species found on Chaetopterus tubes above the sediment-water interface or in cores (2.5 cm diameter) around tubes below the interface to a depth of 5 cm.

Species	Above Interface $\overline{x}$	(SD)	Below Interface $\overline{x}$	(SD)
Corophium tuberculatum	70.3	(57.6)	5.8	(7.1)
Erichthonius brasiliensis	40.0	(52.7)	0	
Parametopella cypris	5.4	(11.3)	1.1	(2.0)
Polydora ligni	10.0	(14.4)	1.0	(3.0)
Nereis succinea	2.8	(4.0)	1.8	(2.5)
Glycinde solitaria	0		0.7	(0.9)
Ampelisca abdita	0.3	(0.7)	2.2	(2.5)
Streblospio benedicti	0.2	(0.4)	2.5	(2.5)
Mediomastus ambiseta	0		54.9	(44.5)
N equals	9		9	

Table 8. Species found in association with the tube tops of *Chaetopterus* during 1985. +++ - abundant, ++ - common, + - rare

Taxon	4 April	11 April	7 May	17 June	1 Oct.
N equals	9	11	15	11	13
Annelida					
Polydora ligni	+++	+++	+++	+++	
Mediomastus ambiseta	++	++	++		
Harmothoe extenuata	++	++	++	++	
Nereis succinea	++	++	++	++	++
Maldanidae juv.	++	++	++	++	
Eteone heteropoda	++	++	++	++	
Sabellaria vulgaris	+				
Paranaitis speciosa		+			
Tubificoides sp.		+		+	
Proceraea sp.		+			
Autolytus sp.			+		
Ampharetidae juv.			+		
Bhawania heteroseta			+		
Streblospio benedicti			+	+	
Sabella micropthalma			+		
Eulalia sanguinea			+		
Chaetozone sp			+		
Sigambra tentaculata			+		
Nephtyiidae juv.					+
Crustacea					
Corophium tuberculatum	+++	+++	+++	+++	+
Caprella equilibra	++	++	++	++	
Erichthonius brasiliensis	+++	+++	+++	+++	+
Parametopella cypris	++	++	++	++	+
Melita sp.	+				
Stenothoe minuta		+			
Photis dentata		+			
Edotea montosa		+			
Neopanope sayi		+		+	
Caprella penantis			+		
Ampelisca cf. *abdita*			+	+	
Monoculodes edwardsi				+	

Table 8. (cont'd)

Taxon	4 April	11 April	7 May	17 June	1 Oct.
Pelecypoda					
Mytilus edulis	++	++	++	++	
Anadara transversa	+	+			
Tellinidae juv.		+			
Mulinia lateralis		+			
Lyonsia hyalina			+		
Gastropoda					
Odostomia engonia		+			
Nudibranch sp. 1			+		
Anachis lafresnayi				+	
Mitrella lunata					+
Anthozoa sp.			+		
Nemertea					
Tubulanus pellucidus	+	+			
Amphiporus bioculatus			+		
cf. *Zygonemertes*			+		
Nemertea sp. 1			+		
Polycladia			+		+
Hydrozoa					
Sertularia argentea	++	++	++	++	
Tubularidae	++	++	++		
Obelia bidentata		++			
Clytia paulensis		++	++		++
Bryozoa					
Bryozoa sp. 1	+				
Alcyonidium verrilli		+	+		
Urochordata					
Molgula manhattensis	++	++	++	++	++

1985 at the dive site near WAP09, yielded many species that were generally rare in quantitative box core samples. The list presented in Table 8 also demonstrates the high variability observed in species composition on tube tops over a relatively short time period.

Other species associated with tube-builders

Although numerous species live associated with the tube top of Chaetopterus, few actually reside inside the tube. The most abundant co-inhabitants were two small decapods, Polyonyx gibbesii and Pinnixa chaetopterana (Table 9). Adults of the polychaetes Nereis succinea and Bhawania heteroseta were found living within the complex outer layers of large Chaetopterus tubes collected during October 1985 and July 1986. These layers are composed of old material that remains after the worm has expanded its tube. There are more layers on tubes that look the 'oldest' (ie. heavy walls and stained with iron oxides, personal observation).

No commensals or co-inhabitants were found within the limited number (n=17) of Loimia medusa tubes examined from box core collections. The scale worm Harmothoe aculeata was found associated with the anemone Ceriantheopsis americanus during core dissections but it is not certain that the worms were actually inside the tubes.

Table 9. Organisms found associated with the subsurface portion of tubes of *Chaetopterus*.

Species	October 1985 $\overline{X}$ (SD)	July 1986 $\overline{X}$ (SD)
Inside tube		
Polyonyx gibbesi	1.1 (0.8)	1.0 (0.7)
Pinnixa chaetopterana	0.1 (0.2)	0.1 (0.3)
Listriella barnardi	0.2 (0.7)	0
Outside layers		
Nereis succinea	1.9 (2.3)	0.6 (0.6)
Bhawania heteroseta	0.7 (0.7)	0.8 (1.2)
N equals	19	19

DISCUSSION

At least four major groups of organisms were among the dominants that characterized the Wolf Trap community. These were: 1) large, relatively long-lived and deeply-distributed burrow or tube dwellers, 2) small, short-lived and shallowly distributed species, 3) organisms that depend on structure for habitat, including epifauna, co-inhabitants and commensals and 4) deeply-dwelling freely burrowing infaunal predators.

The most obvious members of the Wolf Trap fauna were large, deeply-dwelling polychaetes that were also very abundant (ie. Euclymene zonalis, Notomastus latericeus, Chaetopterus variopedatus and Loimia medusa). At this estuarine site, abundances of these species exceeded those typically reported for the adjacent continental shelf and other shallow coastal areas (Boesch, 1979; Reid et al., 1979; Reid, 1979; Larsen et al., 1983; Knott et al., 1983; Van Dolah et al., 1979, 1983, 1984; Wildish et al., 1983; Shaw et al., 1982; Dauer et al., 1984). Only Euclymene zonalis (as Clymenella zonalis, Boesch, 1971) was included among the dominants listed for other studies in the lower Chesapeake Bay. Dauer et al. (1984) found a related species, Clymenella torquata, among the dominants at their silty-sand sites. It is difficult to ascertain what roles large, but less numerous species play in benthic communities in the bay because previous studies have typically listed only the ten numerical dominants. In some previous studies, it is also possible that these large and deep-living organisms were not adequately sampled by the gear employed (ie. shallowly penetrating grabs).

Included among the dominants for this study were numerous short-lived, shallowly distributed species (eg. Paraprionospio pinnata, Ampelisca abdita, Glycinde solitaria and Mediomastus ambiseta). In the Chesapeake Bay these species are known to be widely distributed and abundant throughout the mesohaline zone on a wide range of bottom types (Boesch, 1971, 1973; Diaz, 1977; Mountford et al., 1977; Ewing and Dauer, 1982; Hawthorne and Dauer, 1983; Tourtellotte and Dauer, 1983). Based primarily on his observations in the polyhaline tributary mouths and the Hampton Roads area, Boesch (1976; 1977) noted that these 'euryhaline opportunists' were abundant in the polyhaline zone following disturbance or in areas characterized by pollution. He suggested that they should generally be limited from the polyhaline estuarine zone by biotic interactions with long-lived 'equilibrium' species, but this generalization is not supported by faunal distribution and abundance patterns in the polyhaline basin of the main-stem.

Epifaunal species are an important component of the basin fauna. Three of the ten dominants listed for the polyhaline, silty-sand assemblage identified by Dauer et al. (1984), the urochordate Molgula manhattensis, the bivalve Mytilus edulis, and amphipod Corophium tuberculatum, are epifaunal species that were also abundant during this study. Based on collections, direct observations and photographs of the bottom (eg. Figures 7 and 8), I estimate that 90% or more of all attachment sites for epifauna requiring solid substrate at Wolf Trap were provided by Chaetopterus tubes. Other attachment sites included the tubes of the relatively rare polychates Diopatra cuprea

Figure 7. Photographs of the sediment surface taken at the Wolf Trap dive site during the winter and spring. The field of view in each photograph is approximately 15 X 23 cm. Dates of photos as follows: a. December 1986, b. April 1986, c. April 1985, d. May 1985.

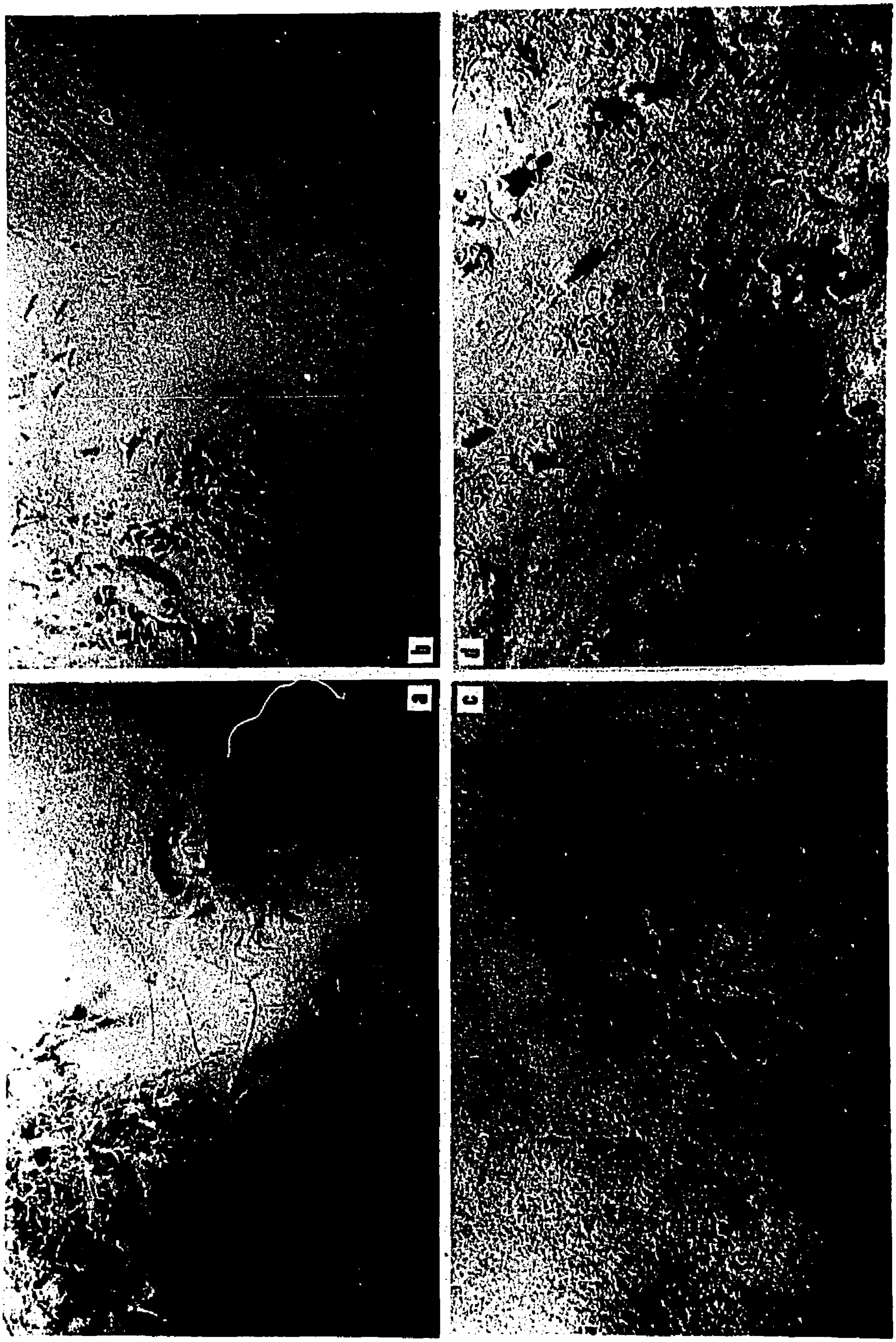
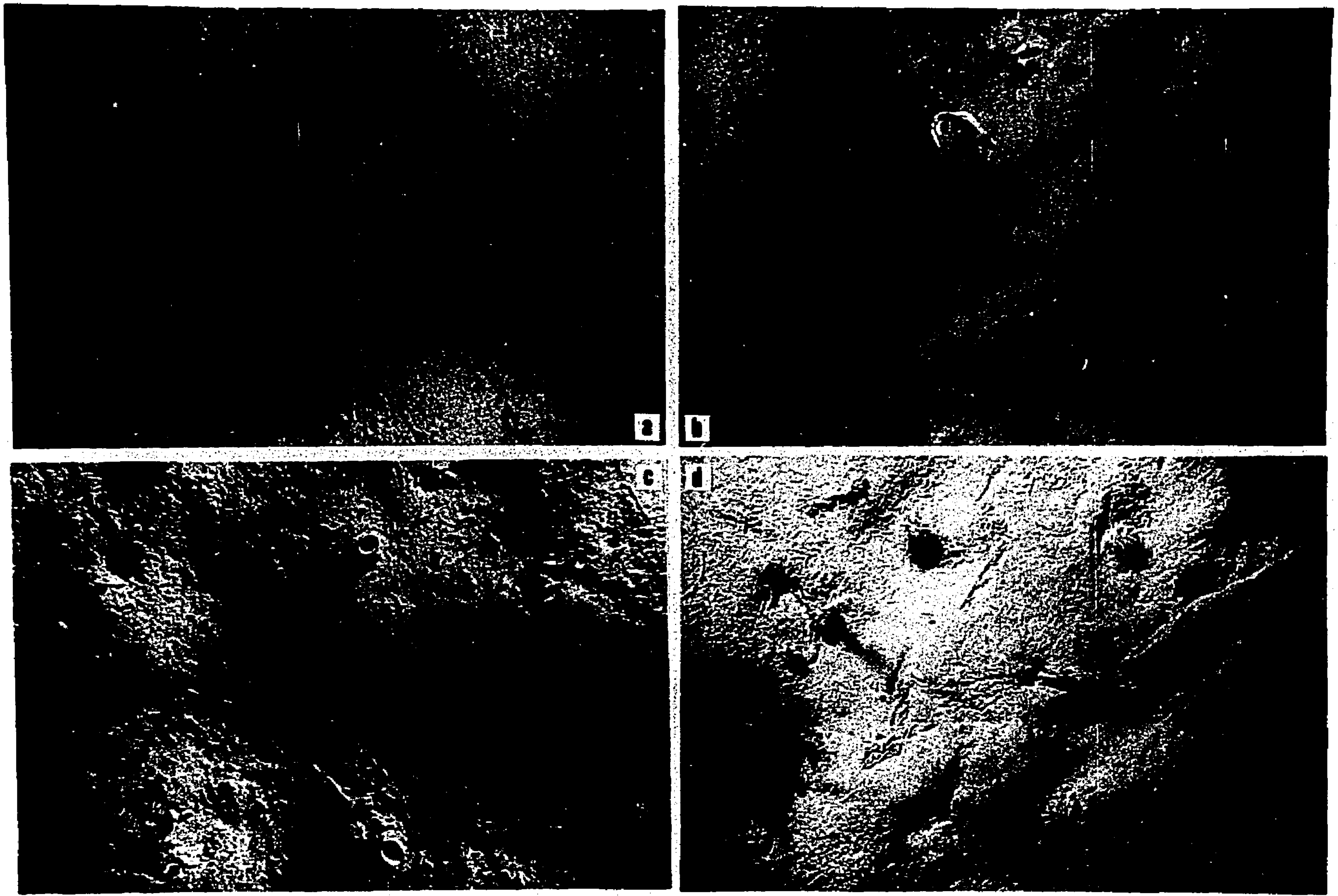

a
b
c
d

Figure 8. Photographs of the sediment surface taken at the Wolf Trap dive site during the summer and fall. The field of view in each photograph is approximately 15 X 23 cm. Dates of photos as follows: a. July 1984, b. November 1985, c. June 1985, d. November 1985.


a
b
c
d

(see Mangum et al., 1968 and Brenchley, 1975) and occasional shells. Organisms that were nearly limited to tube tops at Wolf Trap would likely disappear if Chaetopterus was not present. However, it is clear from direct observations that a complex of biological, geological and physical factors influence the availability and predictability of tube top habitat. For example, the relative height of tubes above the sediment surface can change. Both biotic mound formation and burrow excavation and some tidally induced deformation of the sediment surface have been observed at the study site. These processes alter local bed relief by millimeters to a few centimeters. This can result in a situation where some tube tops are nearly flush with the sediment surface while others project as much as 3-4 centimeters above the interface. Habitat complexity on the tube top is further increased or modified by attached hydroids, bryozoans and the urochordate Molgula manhattensis. In total, these factors greatly increase habitat heterogeneity for epifaunal species and make it difficult to predict patterns of distribution and abundance.

Species that are known to co-inhabit tubes and burrows of larger organisms were among the dominants for the Wolf Trap fauna. Both the scale worm Malmgreniella (lunulata?) its host, the brittlestar Micropholis atra were abundant. At least 3 other species of scale worms were collected during the study, but only Harmothoe aculeata was found clearly associated with a potential host, the anemone Ceriantheopsis americanus. Two species present at Wolf Trap, the amphipod Listriella clymenellae and bivalve Aligena (=Montacuta) elevata live associated with the tube-building maldanid Clymenella torquata (Bousfield, 1973; Gage 1968), and the decapods Polyonyx *gibbesi* and *Pinnixa chaetopterana* are co-inhabitants of *Chaetopterus* tubes. It is not clear which organism(s) serves as the host for the amphipod *Listriella barnardi*. Generally this species is thought to co-inhabit tubes of terebellids and other marine polychaetes (Bousfield, 1973), but Biernbaum (1979) indicates that the species may be epifaunal. Other small decapod crustaceans (*Pinnixa cylindrica*, *P. retinens*, *P. sayana* and *Neopanope sayi*) are associated with burrow openings and the base of tubes of larger structurers (Wass, 1955; McDermott, 1963; and observations during this study). The consistently deep sediment depth distributions and relatively small sizes of two polychaetes commonly encountered during this study, the spionid *Prionospio cirrifera* and a cirratulid cf.*Tharyx* suggest that these species are co-inhabitants of deeper burrow structures produced by larger infauna. Indeed, Josefson (1981) found *P. cirrifera* co-inhabiting burrows of the Norwegian lobster *Nephrops*. He recorded *P. cirrifera* to sediment depths as great as 28 cm in the Skageraak. No similar recorded observations have been found for cirratulids which are typically thought to be shallow-living surface deposit feeders (Fauchald and Jumars, 1979).

Some large, deeply-dwelling predatory polychaetes (ie. *Nephtys*, *Glycera* and *Pseudeurythoe*) are common in the bay, although the actual species that dominate may change from study to study. Of the small, deeply-distributed predators that were abundant during this study, ie. the polychaetes *Bhawania heteroseta*, *Sigambra tentaculata* and *Gyptis brevipalpa*, only *Sigambra* is commonly collected in other parts of the bay (personal observation). In this study, the chrysopetalid *Bhawania heteroseta*, was found closely associated with the outsides of

Chaetopterus tubes. This same species (as Paleonotus heteroseta) was found living within the cemented tube aggregations of the maldanid polychaete Petaloproctus (Wilson 1979). Related species are common on wood panels in the deep sea (Ruth Turner pers. comm.), in crevices and with coral-boring sipunculids on coral reefs and amongst dense tube mats of the polychaete Phyllochaetopterus socialis (Gibbs 1969, 1971). Gyptis brevipalpa has been reported from the burrows of the polychaete Glycera robusta and the holothurian Leptosynapta tenuis and Gyptis vittata, a related species also collected at Wolf Trap, has been reported from the burrow of Notomastus lobatus (Gardiner, 1976). Although none of these host species are present at Wolf Trap, closely related species such as Glycera americana and Notomastus latericeus are commonly found. It is clear from the literature that tube and burrow structures and feeding voids act as localized sites of enhanced microfaunal and meiofaunal activity (Reise, 1981; Aller and Aller, 1986). Thus, it seems plausible that deeply distributed predator-omnivores might be positively associated with the subsurface biogenic features that are abundant at the study site (eg. Figures 9 and 10). Attempts to quantitatively sample sub-surface structures with which these species might be associated were largely unsuccessful for two reasons. First, some structures (eg. maldanid tubes) were so abundant at the study area that it was difficult to locate sub-surface areas within the observed depth ranges of these species that excluded structures. Secondly, some structures, including the extensive feeding voids of Euclymene (Figure 9) and some burrow networks, were difficult to define in a manner that would facilitate quantitative

Figure 9. A sediment profile photograph of a maldanid feeding void. Area of photograph is approximately 12 X 20 cm.

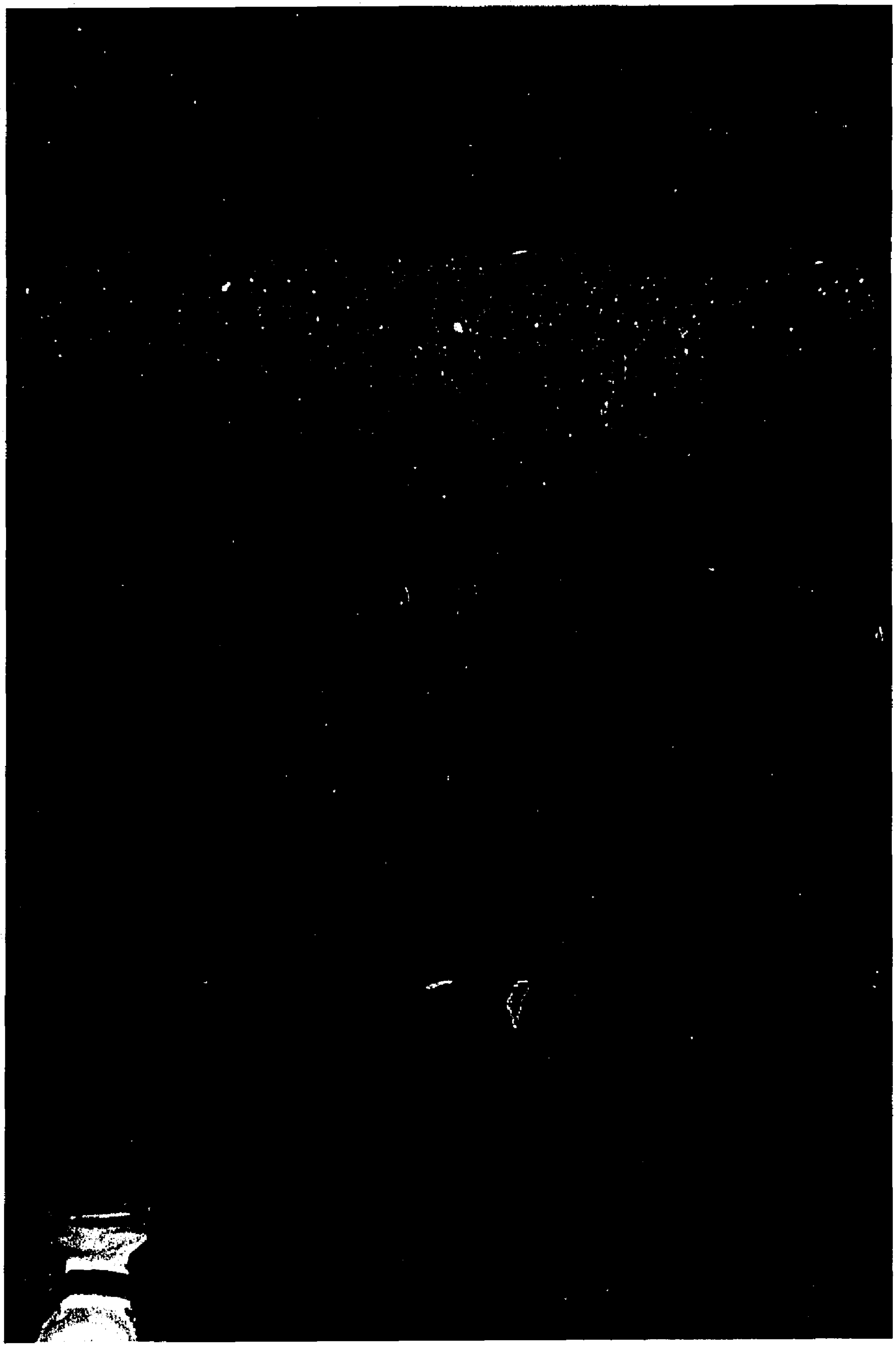
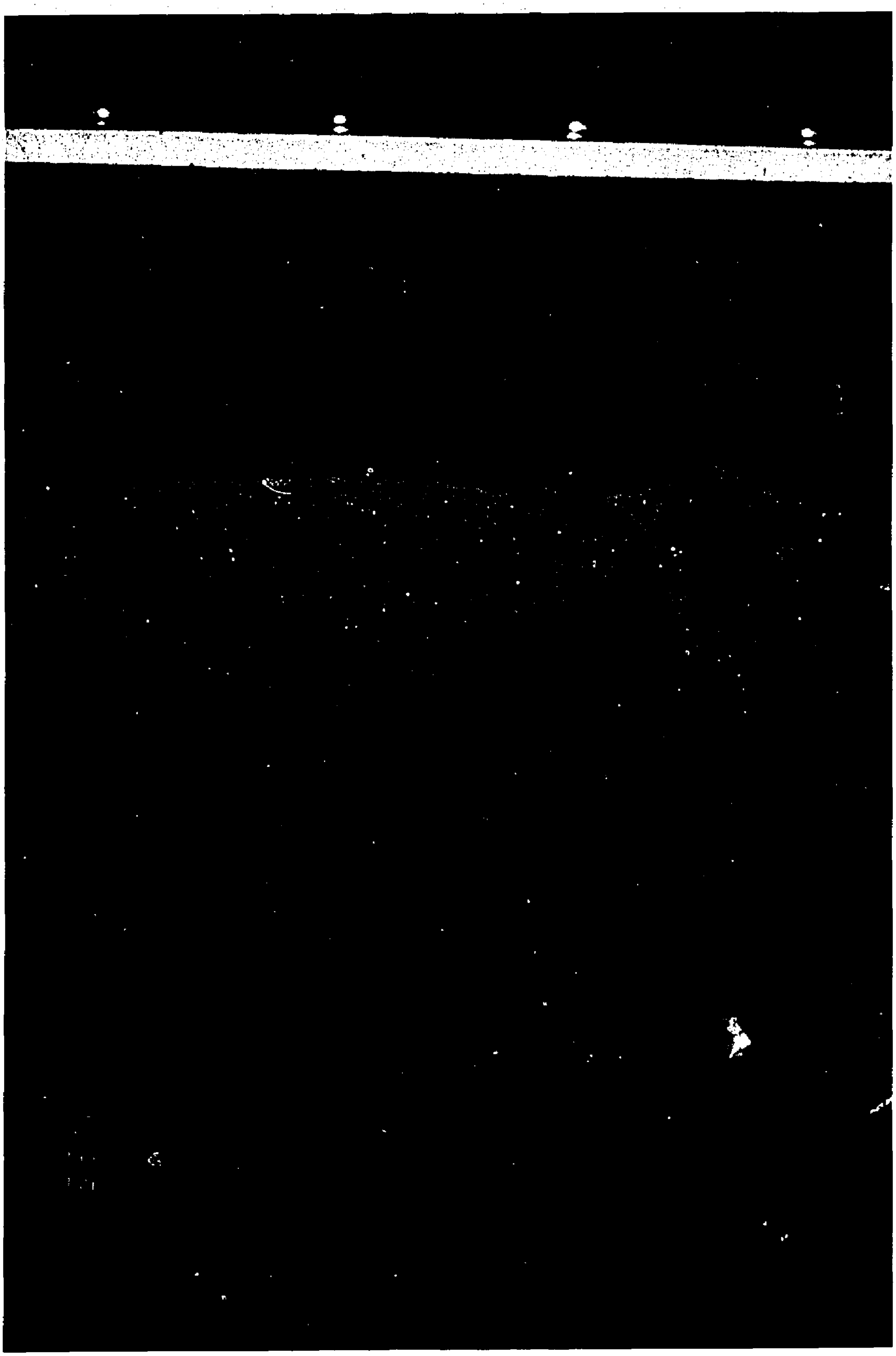


Figure 10. A sediment profile photograph showing a bisected *Chaetopterus* tube. Area of photograph is approximately 12 X 20 cm.



sampling. I suggest that future attempts to experimentally define these relationships might prove more fruitful.

Of the 43 dominants from the Wolf Trap study site that were fully identified to the species level, many have also been recorded from lower salinity areas. During a study conducted concurrently with this one, 42 (98%) of the species were found at the northern end of the basin habitat in the meso-polyhaline transitional region of the bay main-stem (Diaz, unpublished). However, extensive sampling on a range of sediment types in the meso-polyhaline lower York River between 1961 and the present produced only 37 (86%) of these dominants (Hinde, 1981; Diaz et al., 1987; Virginia Institute of Marine Science, unpublished archives) and fewer (22 or 51%) were recorded during extensive sampling of sandy to muddy bottoms in the primarily mesohaline upper bay between 1980 and 1986 (Holland et al., 1986). Most of the dominant species at Wolf Trap during this study (42, 98%) have also been recorded south of Wolf Trap in the vicinity of the baymouth (Boesch, 1971; Llanso, 1985; and Diaz, unpublished). Although many of the species found at the study area are distributed through a range of salinities, patterns of abundance for some of the larger or more deeply distributed species suggest that within the Chesapeake Bay the central basin area is an optimal habitat. Densities of some of the dominants (eg. Chaetopterus, Euclymene, Bhawania, Notomastus) were an order of magnitude higher at the Wolf Trap site than they were at the northern basin site located off the Rappahannock River. Similarly, densities of many of these dominants were higher at the Wolf Trap site than they were in samples collected near the baymouth by Boesch (1971), Dauer et al. (1984) and Llanso (1985).

Large standing stocks of annelid biomass were documented during this study. The greatest biomass contributions were made by the polychaetes *Chaetopterus* and *Euclymene* each of which accounted for 30-50% of the annelid biomass during this study (Huggett, 1987). Typically, lower salinity areas with high standing stocks have abundant filter or interface feeding bivalve populations. This is true in the upper bay-tributary system (Reinharz and O'Connell, 1981; Holland et al., 1986) and in the tributaries of the lower bay (Schaffner et al., 1987) where *Rangia cuneata* and *Macoma balthica* or *Macoma mitchelli* dominate the biomass. The large standing stocks in shallow European waters are apparently also dominated by molluscan biomass, while annelids and echinoderms may dominate the biomass in deeper, higher salinity areas (Blegvad, 1930; Muus, 1973; Ankar and Elmgren, 1976; Ankar, 1977). In the Skagerrak, where the polychaetes *Rhodine loveni*, *Heteromastus filiformis* and *Chaetopterus variopedatus* were among the dominants they accounted for 21% (48.5 grams of wet weight) of the total faunal biomass or 58% of the non-*Brissopsis* (echinoderm) biomass (Josefson 1981). Standing stocks in the coastal areas of the Gulf of Mexico (<10 m, with 25-75% sand sediments) are dominated by annelids and echinoderms, but the range in the spring and fall average values of 19-76 grams of annelid wet weight biomass per square meter are lower than those observed during this study (Shaw et al., 1982).

Since much of the annelid biomass at the study site was contributed by large deeply-dwelling organisms, it was not readily available to predators. However, maldanids with regenerating tails were observed in the collections and tail cropping, like clam siphon nipping (De Vlas, 1985), is a potential mechanism for the transfer of energy from the benthos to higher trophic levels. Clearly, Chaetopterus provides habitat space to many types of organisms both above and below the sediment surface. Many of the small worms, crustaceans and bivalves living attached to the tops of Chaetopterus tubes are also potential food items for higher trophic levels. These large organisms likely influence the overall productivity of the basin habitat in other ways as well. The prolific biodeposits resulting from the filter-feeding of Chaetopterus may provide an important energy pathway linking the water column and the benthos. Euclymene zonalis is a sediment reworker which presumably plays a major role in governing the pathways of particulates and solutes through the sediment bed. Oxygenated areas around the extensive feeding voids of this species are likely to be important areas for bacterial growth and the development of meiofaunal populations.

Detailed evaluations of spatial patterns in multispecies assemblages provide clues regarding the physical and biological processes that govern species interactions. For the basin fauna, an assemblage characterized by relatively complex small scale spatial patterns, this type of detailed evaluation has identified numerous potentially important patterns and suggested some directions for future research.

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