MACROBENTHIC COMMUNITY STRUCTURE AT THE ENTRANCE TO THE CHESAPEAKE BAY

A Thesis

Presented to

The Faculty of the School of Marine Science

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In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

Roberto Javier Llansó

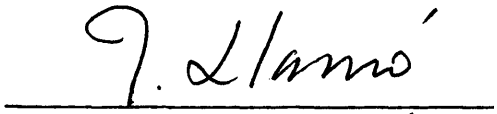
1985

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts



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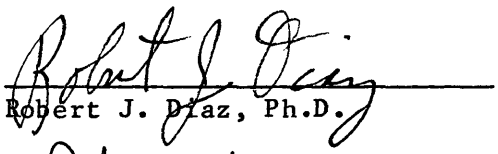
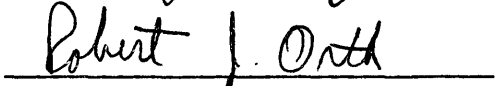


Robert J. Díaz, Ph.D.



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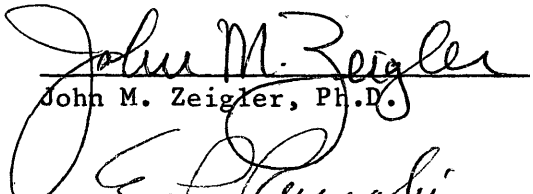

John M. Zeigler, Ph.D.

Evon P. Ruzecki, Ph.D.

Daniel M. Dauer, Ph.D.
Old Dominion University

To my parents, Luis and Esperanza.

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ABSTRACT

The macrobenthos at the entrance to the Chesapeake Bay was sampled in October 1982 to determine community structure, spatial distribution patterns and to relate these to sediment type, water depth and tidal circulation patterns.

Seventy-one 0.1 m^2 Smith-McIntyre grab samples were taken over an extensive area from Cape Charles to Cape Henry and off Virginia Beach using a stratified random sampling design. Over 20,000 individuals were collected, comprising 158 species distributed among 14 phyla. Annelid polychaetes accounted for 46% of the species list followed by crustaceans (25%) and molluscs (19%). The capitellid polychaetes Amastigos caperatus and Mediomastus ambiseta were among the most abundant macroinvertebrates collected, with average densities of 599 and 489 individuals per m^2, respectively.

Analysis of abundance data (numerical classification and ordination) and multiple discriminant analysis revealed three major assemblages of species related to sediment type: a clean, high energy, fine sand assemblage numerically dominated by the haustoriid amphipod Protohaustorius wigleyi and the polychaete Nephtys bucera; a less dynamic, fine and very fine sand assemblage characterized by the paraonid polychaete Aricidea wassi, the amphipod Synchelidium americanum and the gastropod Epitonium multistriatum; and a depositional, very fine sand and silt-clay assemblage dominated by capitellid and spionid polychaetes, and the bivalve Tellina agilis.

These assemblages of species were not distinctly separated in space. They were more in accordance with the concept of peaks of species abundance in a near-continuum responding to environmental gradients.

Distribution of species across the bay entrance seemed to reflect the tidal circulation patterns in the study area. The northern part of the entrance, physically characterized by flood and ebb-directed sediment transport, was colonized by species of the high energy, fine and very fine sand assemblages. The southern part is under the influence of surface ebb currents which transport fine sediment and organic particles from the bay. Most macroinvertebrates collected in this area were species of silt-clay substrates. Higher species richness in the southern part of the Chesapeake Bay entrance relative to the northern part may be explained by the greater spatial heterogeneity provided by shell fragments and animal tubes and by the less rigorous conditions of a depositional environment.

MACROBENTHIC COMMUNITY STRUCTURE AT THE ENTRANCE TO THE CHESAPEAKE BAY

INTRODUCTION

The importance of sediment properties, such as particle size, sorting and total organic carbon, on structuring marine and estuarine sublittoral macrobenthic communities is widely documented (e.g., Sanders, 1958; Cassie and Michael, 1968; Kinner et al., 1974; Warwick and Davies, 1977; Kiørboe, 1979). Basically, two major trophic groups are present in macrobenthic associations: deposit feeders and suspension feeders. In many benthic surveys, these two groups have been shown to be spatially separated depending on sediment type (Sanders, 1958; Bloom et al., 1972; Jaramillo et al., 1984). In the trophic group amensalism hypothesis, Rhoads and Young (1970) suggested that suspension feeders are excluded from areas where deposit feeders actively burrow and resuspend the sediment. This exclusion, as suggested by Rhoads and Young, is because of the clogging of suspension feeders' filtering structures by resuspended sediment and the burial and settlement inhibition of larvae by the instability of sediments.

While this trophic relationship may hold in muddy substrates, other factors such as current and wave induced sediment instability probably become more important in structuring macrobenthic communities in physically disturbed, shallow marine environments. Moreover, sediment type (i.e. grain size) is directly related to the energy regime of the

overlying water. Marine benthic environments physically dominated by tidal currents and waves have well sorted sands indicating a high degree of sediment mobility. Mobility of the sediments prevents sedentary and tube-building macrobenthic species from inhabiting these areas, while fast burrowing species, well adapted to shifting sands, are more likely to successfully live and reproduce (Holland and Dean, 1977; Withers and Thorp, 1978, Bierbaum, 1979; Vanosmael et al., 1982).

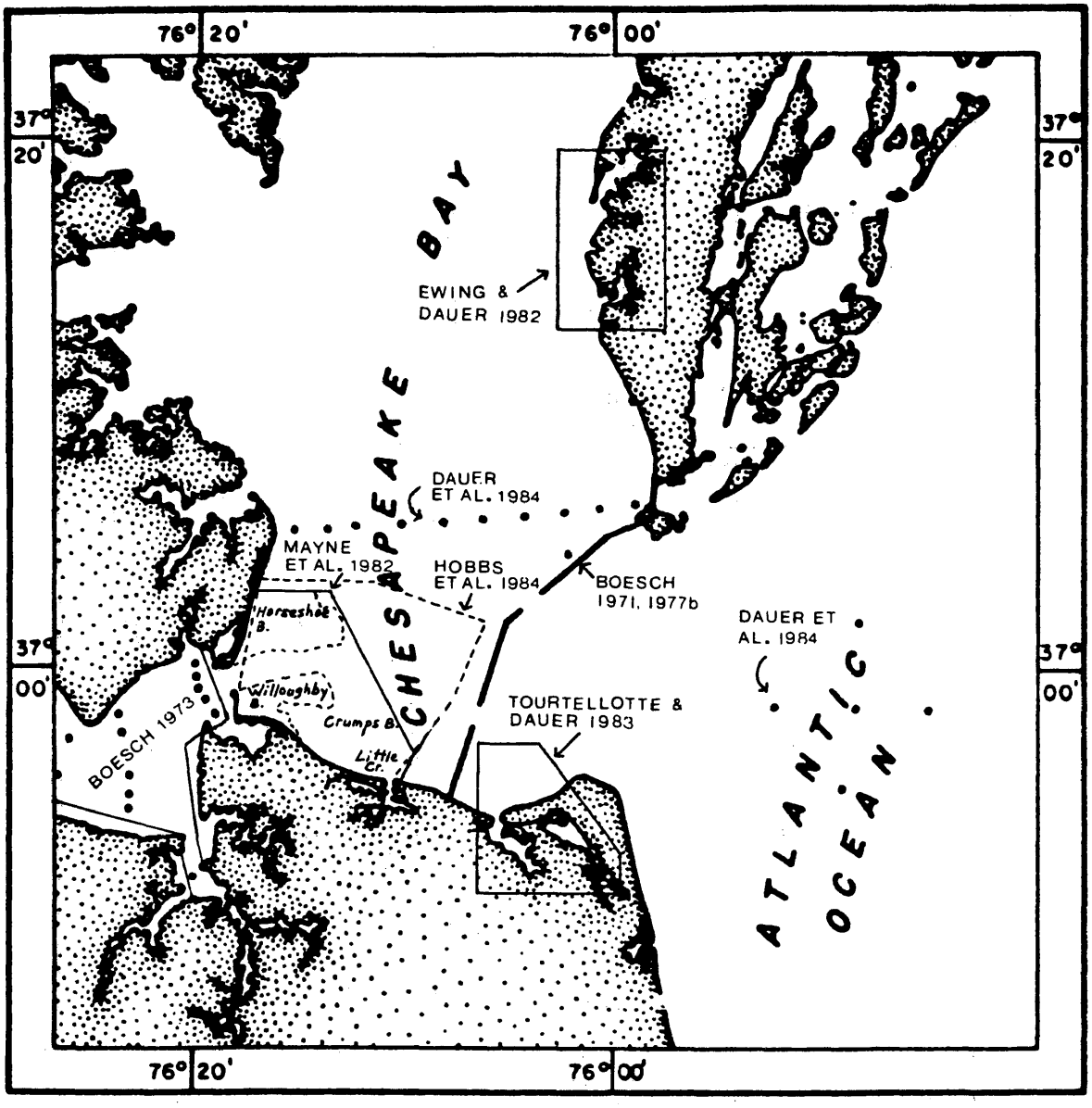
Lower energy, tidal current influenced but depositional environments, have sediments composed of finer sands with some silt and clay. These sediments, in contrast with the high energy, sandy bottoms of larger mean diameter grain-size, sustain benthic assemblages with greatest species diversity (Young and Rhoads, 1971; Boesch, 1973; Kinner et al., 1974). The higher diversity of this environment is a response to the wider range of sediment particle size and the organic content of the sediments. Sediments with higher permeability than muddy bottoms allow diffusion of water, bringing oxygen and food to the infauna. Higher species richness is likewise manifested where microhabitats provided by shell fragments and tubes of annelid polychaetes serve as a refuge or substrate for epifauna (Boesch, 1973). In summary, wave and tidal currents determine the nature of the bottom substrate and sediment stability; in addition, non-tidal currents infuence the food supply for the benthic organisms and may also affect seawater physical and chemical characteristics (e.g., salinity) that, in turn, may influence macrobenthic community structure.

Inlets are among those high energy environments where substrate instability is expected to be an important factor regulating species composition. The entrance to a large estuary, such as the Chesapeake Bay, exhibits complex circulation patterns, where shallow, dynamic sediments alternate with deeper, physically stable sediments. While tidal and wave exposure may control the macrobenthos in the former, sediment composition may become more important in deeper water. In view of the biological importance of these interactions, the macrobenthos of the Chesapeake Bay Entrance is the object of this study.

To date, studies of macrobenthic organisms in the Chesapeake Bay system have been mainly conducted in the tributaries of the bay, particularly the York and the James rivers. A few reports in the lower bay have focused on the potential effects of sand extraction operations (Mayne et al., 1982; Hobbs et al., 1984), and of activities related to the construction of the Second Hampton Roads Bridge Tunnel (Boesch and Rackley, 1974) on benthic communities. Although quantitative investigations of the benthic fauna in the lower Chesapeake Bay have been carried out (Stone, 1963; Boesch, 1972; Tourtellotte and Dauer, 1983; Dauer et al., 1982, 1984; Ewing and Dauer, 1982), benthic communities at the mouth of the Chesapeake Bay have not been extensively studied.

Five sampling stations for the EPA study on the biological processes affecting sediment dynamics (Nilsen et al., 1982) and one station studied by Boesch (1971, 1977b) to describe the distribution of the benthos in an estuary, were located near the entrance to the bay

Figure 1. Location of previous studies of macrobenthos on the lower Chesapeake Bay near the bay entrance.


76° 20'
76° 00'
37° 20'
37° 00'
CHESAPEAKE BAY
EWING & DAUER 1982
DAUER ET AL. 1984
MAYNE ET AL. 1982
HOBBS ET AL. 1984
BOESCH 1971, 1977b
DAUER ET AL. 1984
TOURTELLOTTE & DAUER 1983
BOESCH 1973
Horseshoe B.
Willoughby B.
Crumps B.
Little C.
ATLANTIC OCEAN

(figure 1). Close to the bay mouth are Crumps Bank and Horseshoe Bank, two areas among those sampled in the region proposed for sand minning operations (Hobbs et al., 1984), and one bay-wide transect and some inner continental shelf stations have been sampled to describe the distribution and abundance of the macrobenthos (Dauer et al., 1984). However, these studies were not specificly designed to characterize the benthos at the bay mouth.

Studies of subtidal benthos have been conducted in wide entrances and inlets of similar sedimentology along the east coast of the United States (Brett, 1963; Kinner et al., 1974; Dorges, 1977; Maurer et al., 1978; Ewing and Dauer, 1982). These studies are summarized below.

Inlets were among the environments studied by Brett (1963) in Bogue Sound, North Carolina. Both Beaufort and Bogue Inlet were the environments of highest energy. Sediments were characterized as fine, well sorted sands with low silt and clay content. Infauna was basically composed of gastropods and pelecypods, deposit feeders (37%) being the dominant feeding type. Almost as important were filter feeders (30%) and predators (29%). Many of the mollusc species were restricted to the inlet environment, while a relatively large number of other species showed a marked oceanic influence.

Kinner et al. (1974) described the macrobenthic communities at the mouth of the Delaware Bay. Grab samples taken over a wide range of sediment types, revealed two major animal-sediment associations: a sand with low silt-clay association and a high silt-clay association. The

later was confined to near shore sediments at Cape Henlopen. Sands were characterized by the amphipods Protohaustorius wigleyi and Rhepoxynius epistomus, and muds were characterized by two deposit feeders, the bivalve Nucula proxima and the polychaete Heteromastus filiformis. The bivalve Tellina agilis and the amphipod Ampelisca verrilli were transitional between sand and mud. Faunal density was low and species diversity was found to be greater in sandy sediments with low percentage (0-25%) of silt and clay. The species that characterized the communities in this study were also reported by Maurer et al. (1978). In their Delaware bay-wide survey, transects at the mouth of the bay revealed two benthic assemblages. These assemblages were respectively restricted to mobile medium and fine sands at the middle of the mouth, and to siltier fine sands near the capes.

The shoals at the entrance to Doboy Sound of Sapelo Island, Georgia, were studied by Dorges (1977). The area exhibited macrobenthic species typical of a high energy environment. Haustoriid amphipods and the clam Donax variabilis were the most abundant species. There was a difference in species abundance between high exposed and less exposed areas of a shoal, with increased number of individuals on the lee side.

Ewing and Dauer (1982) sampled the benthos of Old Plantation Creek, Kings Creek, Cherrystone Inlet and adjacent bay areas to define macrobenthic structure and distribution in the lower Chesapeake Bay. The nearshore shoal sites contained dynamic sandy sediments with low species richness and a community of species adapted for burrowing in shifting sands, similar to the communities of the studies summarized

above. The bivalve Gemma gemma was the most abundant species on shoals. Species richness and evenness increased in the offshore sites. These sites were inhabited by species common to deeper sands such as the polychaete Spiophanes bombyx, the molluscs Acteocina canaliculata and Tellina agilis and the amphipods Ampelisca verrilli and Rhepoxynius epistomus.

The aim of the present study is to gain a better understanding of how coastal oceanic conditions interact with a large estuarine system to influence macrobenthic community structure at the Chesapeake Bay entrance.

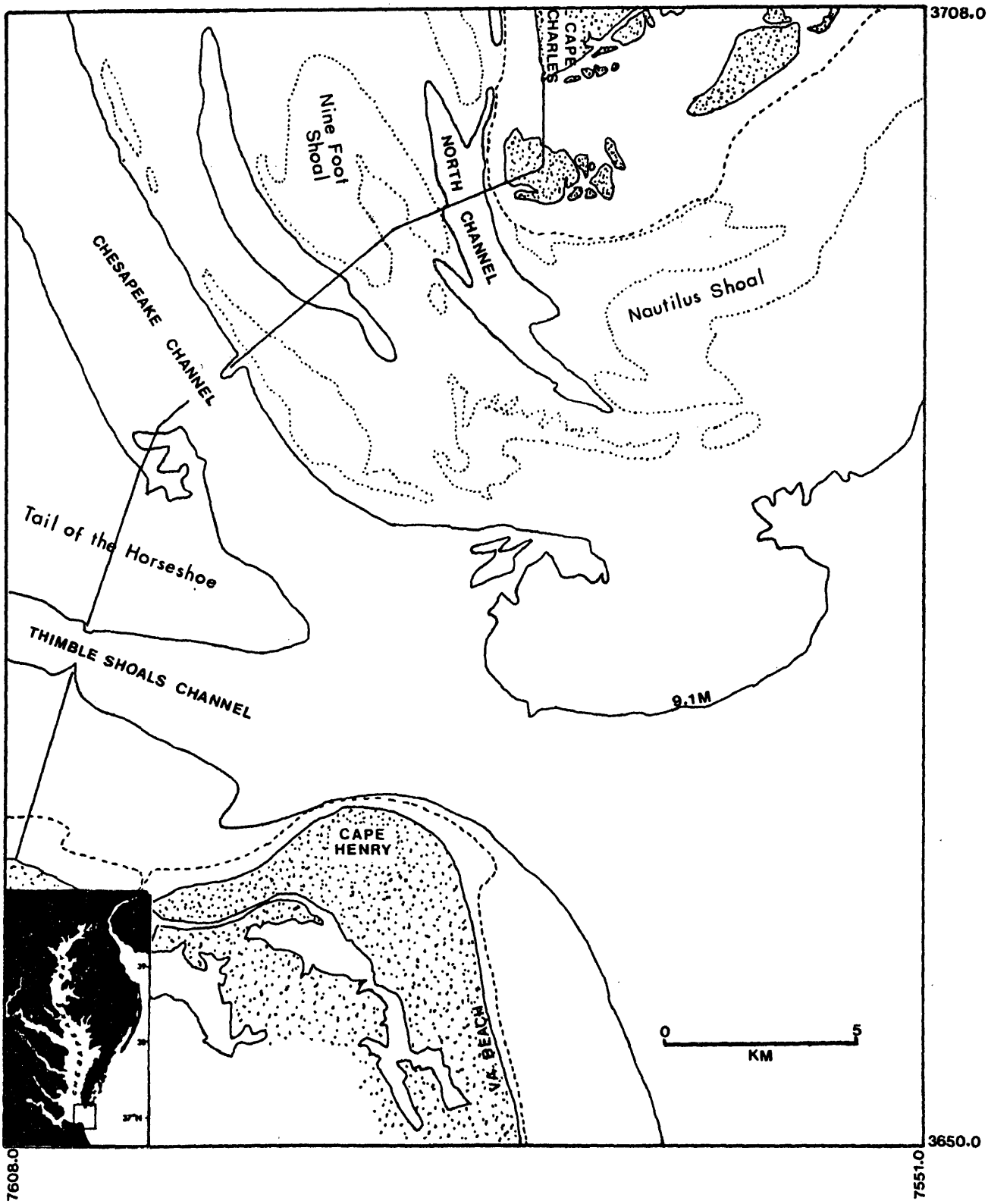
Objectives are:

1. To determine community structure of the macrobenthos.
2. To determine the spatial distribution patterns of macrobenthos.
3. To test the hypothesis that communities in the study area are similar with regard to water depth and sediment type.
4. To relate community patterns to physical environmental factors: sediment type, water depth and tidal circulation patterns.

Study Area

The study area is located between Cape Charles and Cape Henry at the entrance to Chesapeake Bay. It extends southward off Virginia Beach

Figure 2. Chesapeake Bay entrance. Study area.


3708.0
CAPE CHARLES
Nine Foot Shoal
NORTH CHANNEL
CHESAPEAKE CHANNEL
Nautilus Shoal
Tail of the Horseshoe
THIMBLE SHOALS CHANNEL
9.1M
CAPE HENRY
VA. BEACH
0
5
KM
3650.0
7608.0
7551.0

and westward into Thimble Shoal Channel, Chesapeake Channel and adjacent shoals. The exact location of the area with latitude and longitude coordinates is shown in figure 2.

Chesapeake Bay is the largest estuary in the United States; it has a drainage area of 120,000 km^2 and an annual average fresh water run-off rate of 1,600 $m^3 sec^{-1}$. The entrance to the bay is wide, measuring 17 km between Cape Charles and Cape Henry. Wave action is of moderate energy and tidal currents are strong in the area. At the surface, maximun ebb has been measured to be 132 cm/sec and maximun flood, 105 cm/sec. At the bottom, maximun ebb is 79 cm/sec and maximun flood, 66 cm/sec (Ludwick, 1973).

The main morphological features at the entrance are sand banks and shoals alternating with deep tidal channels (figure 2). Sand shoals and sediment transport processes, particularly in the northern part of the bay entrance, have been extensively studied by Ludwick (1973, 1974, 1975, 1981) and Granat and Ludwick (1980). These shoals form ebb and flood deltas almost linked in a zig-zag fashion. With an average depth of 2.5 m, they are often sites of active deposition, acting as a trap for sands that are eroded in neighboring areas and transported by near bottom flow.

In addition to the shoals, sand waves are also present. Sand waves and small current-generated ripples are found on the northern and southern margins of the North Channel, and on top of shoals at its seaward extremity. Sand waves range from 1.5 to 3 m in height and from

6 to 24.4 m in length between successive crests (Ludwick, 1970a, 1970b, 1972). Ludwick found that most of the sand waves studied are asymmetrical in profile, suggesting that they migrate in the direction of the predominant current in the area. Depending on whether the steep side is facing seaward or landward, sediment transport will be either ebb or flood directed, respectively. It has also been shown that grain size is bimodal in sand waves, with the coarser fraction either on crests or on troughs, depending on whether they are migrating or non-migrating waves (Ludwick and Wells, 1974).

Average water depth at the entrance to Chesapeake Bay is 11.3 m. The northern part is shallower with an average depth of 6.5 m and a maximum depth of 17.1 m at the North Channel. Towards the southern part, Chesapeake Channel and Thimble Shoal Channel have maximum depths of 16.8 m and 28 m respectively. The complex circulation patterns in the study area and adjacent inner continental shelf have been studied by Joseph, Hassmann and Norcross (1960), Norcross and Stanley (1967), Bumpus (1973), Ludwick (1973, 1974, 1975), Granat and Ludwick (1980) and Boicourt (1981).

The circulation at the entrance of the Chesapeake Bay is basically that of a typical partially mixed coastal plain estuary, consisting of a two-layer flow, with an upper layer of low-salinity water flowing seaward and a lower layer of higher salinity water flowing into the bay. This two-layered estuarine circulation is modified by local winds over the bay, prevailing winds over the Continental Shelf, and the season of the year. Marked stratification occurs during the spring months

coinciding with a peak in river discharge, while stratification is at a minimum in the winter.

It has been generally reported that coastal waters flow into the Chesapeake Bay around Cape Charles, while low salinity discharge water flows at the surface, passing around Cape Henry and flowing southward as a longshore jet (Joseph, Hassmann and Norcross, 1960). Ludwick (1970b) showed that, when data on the speed, direction and duration of near-bottom tidal currents is complimented with studies of sand wave migration and bottom topography, tidal circulation at the mouth of the bay results in a more complex pattern. According to Ludwick (1970b), and as it is shown in figure 3, predominant inflow at the bottom is along North Channel and around Cape Henry into Thimble Shoal Channel and Chesapeake Channel. Similarly, data from current meters and temperature-salinity recorders moored at several locations and depths across the bay entrance and offshore, revealed a main inflow of water along the deep channel near Cape Henry (Boicourt, 1981). Some inflow of water is also evident along the North Channel, although the study by Boicourt (1981) did not provide enough data for confirmation. The main and strong outflow at the surface of less dense water from the bay extends around Cape Henry and southward along Virginia and North Carolina coasts. This water appeared as a wide muddy plume leaving the bay, as observed during the flight of a VIMS research aircraft in March 1980, and as a narrower jet of turbid water alongshore in June and October 1980 flights (Thomas, 1981).

Figure 3. Net nontidal flow pattern at the bottom in the entrance to Chesapeake Bay. Arrows indicate ebb or flood flow predominance. After Ludwick (1970b).

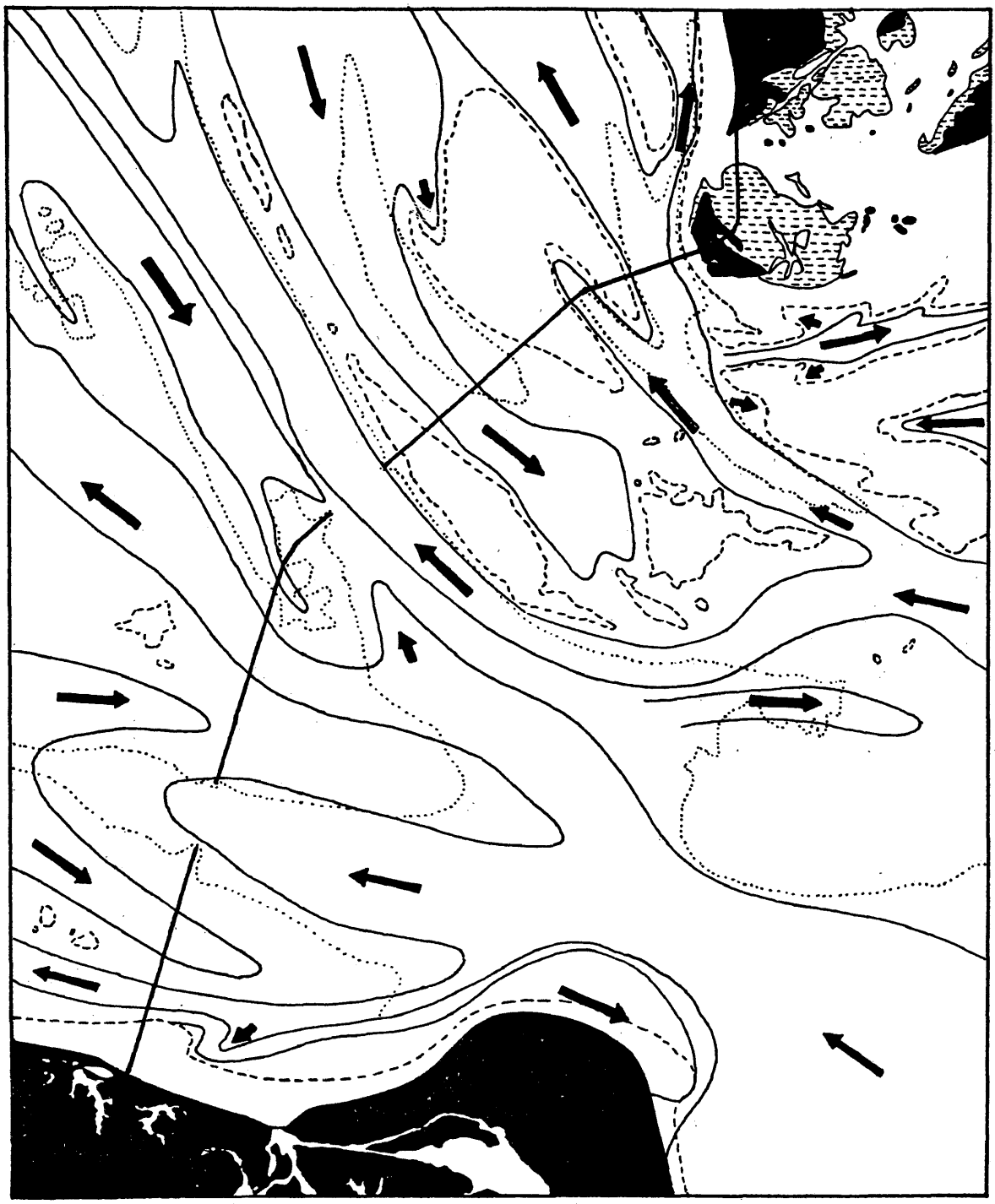
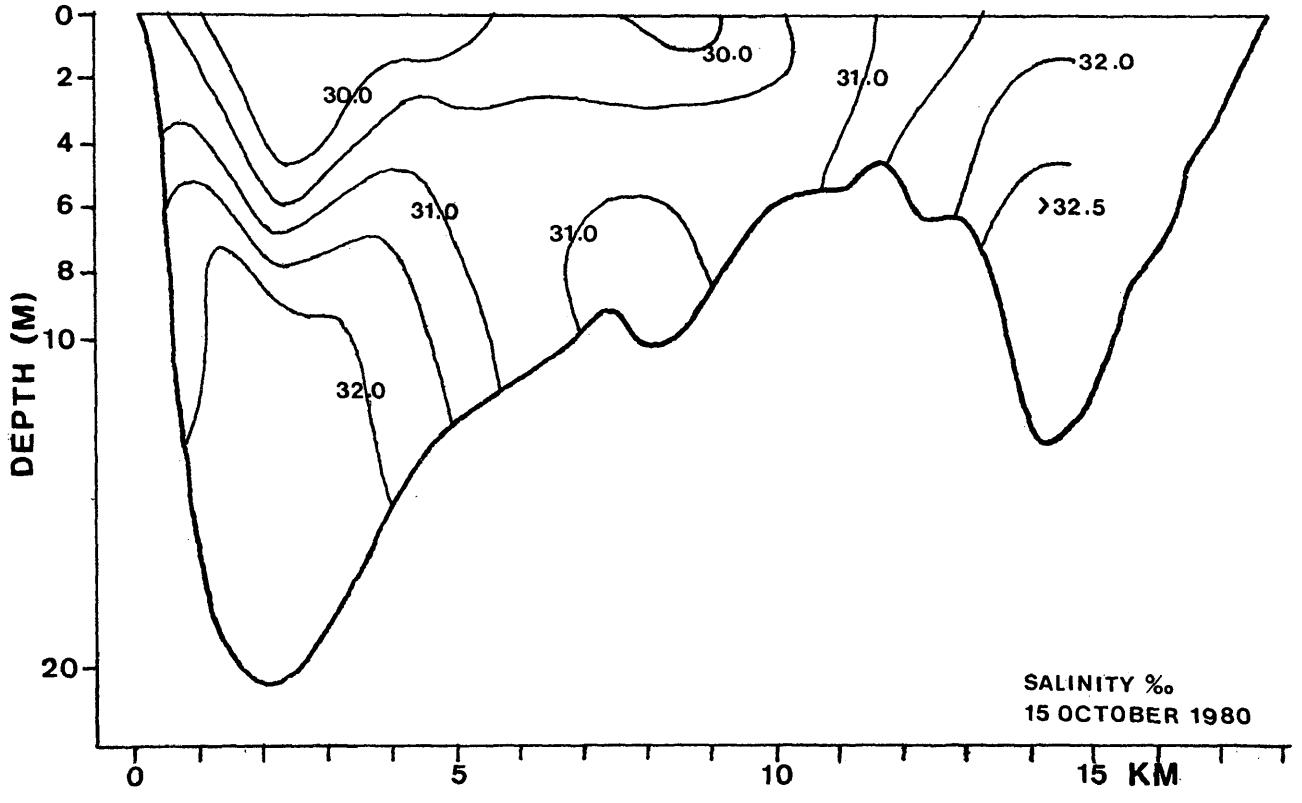


Figure 4. Salinity structure during flood across the bay entrance on October 15, 1980. Cape Henry is on the left. After Ruzecki (1981).


0
2
4
6
8
10
20
DEPTH (M)
30.0
30.0
31.0
31.0
31.0
32.0
32.0
>32.5
SALINITY ‰
15 OCTOBER 1980
0
5
10
15 KM

Salinity structure at the mouth of the bay is also dependent on wind and season. Figure 4 shows the salinity distribution across the entrance for October 15, 1980 as measured by Ruzecki (1981). Salinity distribution for July 1980 (Boicourt, 1981) is expected to be lower, showing a range of 29‰ to 31‰ at the bottom and 29‰ to 24‰ at the surface, from the northern to the southern part of the entrance.

The sediment of the bay mouth is characterized by uniform, well sorted fine and very fine sands, overlaying an unit of silty clay to sandy silt sediment deposited during the Holocene trangression (Meisburger, 1972). Patches of coarse sand are present in the northern part, and patches of silt and clay are present near the shore in the southern part, extending into the Bay along Thimble Shoal Channel and Chesapeake Channel.

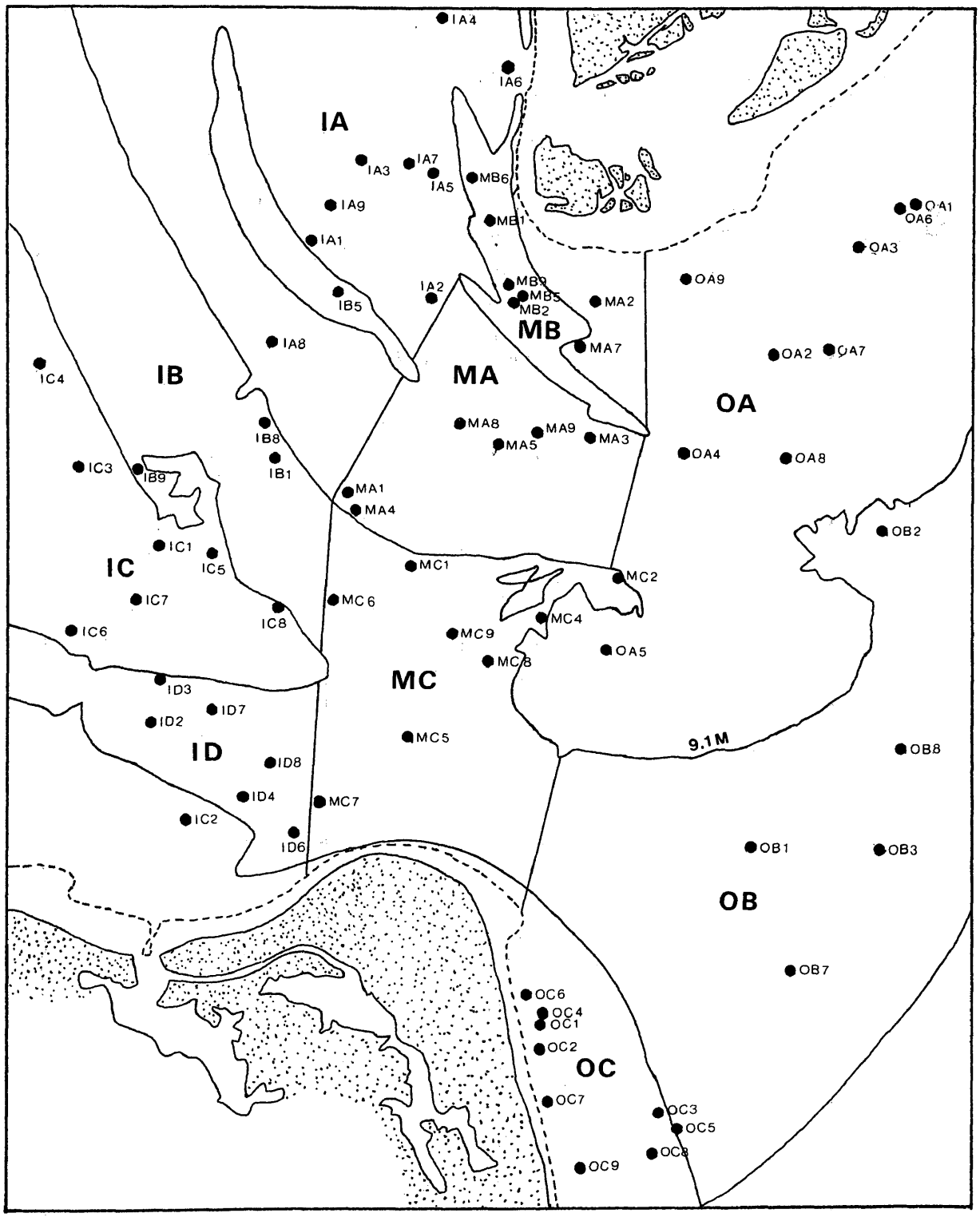
METHODS

Experimental Design

The entrance to the Chesapeake Bay is characterized by 4 natural tidal channels separated by shoals. Using this natural physical structure, the entrance can be divided into 10 strata (or subareas) encompassing 3 major areas (figure 5): Inner, with 4 strata (IA, IB, IC, ID); Middle, with 3 strata (MA, MB, MC); and Outer, with 3 strata (OA, OB, OC). Strata were arranged according to water depth. Shallow (< 9.1 m) and deep (> 9.1 m) strata are alternating in each area. This habitat deliniation lends itself to a stratified random sampling design. Stratified random sampling is best when the area to be sampled has a large-scale environmental pattern. Then, the area can be broken up into relatively homogeneous bottom subareas or strata followed by random allocation of sampling sites (Green, 1979).

Based on a preliminary consultation of detailed sediment charts produced by the VIMS Department of Geology, each stratum was assumed to be homogeneous with respect to sediment type and water depth. The emphasis of this study resides in comparing the three areas (Inner, Middle and Outer) and their strata to one another to detect possible differences in macrobenthic structure and species abundance which may be

Figure 5. Location of sampling strata with indication of random sampling stations and codes. Depth contour delineating strata is 9.1 m


IA4
IA6
IA
IA3
IA7
IA5
MB6
IA9
MB1
IA1
IA2
MB3
MB5
MB2
MA2
IB5
MB
IA8
MA7
IC4
IB
MA
OA
MA8
MA9
IB8
MA5
MA3
IC3
IB9
IB1
OA4
OA8
MA1
MA4
IC1
IC5
IC
MC1
MC2
IC7
MC6
IC8
MC4
IC6
MC9
OA5
MC8
MC
ID3
ID7
ID2
MC5
9.1M
ID
ID8
ID4
MC7
IC2
ID6
OB1
OB3
OB
OB7
OC6
OC4
OC1
OC2
OC
OC7
OC3
OC5
OC8
OC9
OA1
OA6
OA3
OA9
OA2
OA7
OB2
OB8

related to sediment parameters and tidal circulation patterns. Only sediments with less than 20% mud content were considered. In an otherwise sandy environment, avoiding muddy patches would allow us to describe the macrobenthos in terms of differences in sand grain size and sediment dynamics in the study area.

Nine sampling sites for each stratum were determined by selecting at random pairs of numbers from a random number table. A grid paper was superimposed for each stratum over a chart of the bay mouth, and each pair of random numbers defined a sampling site or station in the grid. Because of the design, the 9 samples in the stratum may be considered as true replicates. Samples from 71 stations (figure 5) were processed. Some of the remaining samples were lost and others contained silt-clay in excess of 20%.

Sampling and Laboratory Procedure

Macrobenthos was sampled during three days in October 1982. Sampling consisted of one 0.1 m^2 Smith-McIntyre grab per station. From each sample, a small sediment core (3.5 cm diameter) was removed for analysis of particle size distribution and organic carbon content. In addition, for each sample, sediment temperature and water depth were recorded.

The Smith-McIntyre grabs were emptied into buckets and their contents sifted on board through a 0.5 mm mesh Nitex screen. The

organisms trapped on the screen were transfered to labeled jars with seawater and anesthetized in isotonic $MgCl_2$ for about 30 minutes. Subsequently, the organisms were preserved in 10% buffered formalin with Rose Bengal as a vital stain.

In the laboratory, samples were washed in fresh water and the organisms sorted into major taxa using a binocular dissecting microscope. Samples with excessive amounts of sand were placed in an enamel pan and elutriated through a 0.5 mm mesh screen to separate the "light" fraction. The rest of the sample, or "heavy" fraction, was carefully examined with the naked eye for stained organisms. After sorting, the organisms were stored in 70% ethanol for subsequent identification.

Sediment Analyses

Sediment cores from the grabs remained frozen until total organic carbon was determined. From each sediment core, a sample was used for particle size analyses following the procedures described in Folk (1980). Sand was separated from mud by wet sieving. The mud fraction was then analyzed for percentage silt-clay by pipette, a method based on the settling velocity for particles smaller than 63 microns (Folk, 1980).

The sand fraction was analyzed using a Rapid Sediment Analyzer (RSA) located at VIMS Department of Geology. The RSA is a settling tube

system that measures falling velocities of sand-size (>63 microns) particles (Gibbs, 1974). An analog recording strip chart recorded the results in form of a cumulative curve of the weight as a function of time. Graphs were then digitized and sent to the computer for numerical analysis. The computer program developed uses an equation that relates sphere size to settling velocity (Gibbs et al., 1971). The grain size parameters calculated were: silt-clay, very fine sand, fine sand, medium sand and coarse sand percentages, according to Wentworth's (1922) grade scale. Because of the small amount of silt-clay present in most of the samples, the size distribution of this fraction was not measured. Therefore, it was not possible to calculate the graphic measures (i.e., mean, standard deviation and sorting) of Folk (1980). However, a measure of the sorting for the sand fraction was provided by the statistical standard deviation.

Percent total organic carbon (TOC) of several subsamples was measured with a LECO analyzer. The method consists of the combustion of organic carbon and the subsequent measurement of the volume displaced by the CO_2 produced. Previous to the analysis, the sediment subsamples were oven dried and weighed. Inorganic carbon was removed by digestion with 10% HCl for three hours.

Data Analyses

Data were reduced by elimination of low frequency species and of taxa above the species level with little or no biological meaning. For numerical classification and nodal analyses, species present in no more than 3 samples were deleted. For ordination, species present in no more than 5 samples were deleted.

Data reduction is a common procedure in ecological surveys that generate large amounts of information. It is left to the criteria of the investigator to decide which species should be eliminated from the analyses, but generally, rare species (i.e., species occurring in less than some arbitrary frequency) are deleted. Rare species, provided they are not habitat restricted, do not offer any particular pattern (Boesch, 1977a).

Data were analyzed using multivariate analyses (numerical classification and ordination) to show community distribution by grouping similar stations and species. Multiple discriminant analysis was used to correlate the station group separation with sediment type and water depth.

Previous to the analyses, data were transformed using $\log(x+1)$ (Sokal and Rohlf, 1981). Transformations were necessary to lessen the sensitivity of the similarity measure to large abundances.

Numerical classification assigns species and samples to groups according to their similarity. Results are graphically presented in the form of a dendogram where similar entities are grouped together. Seventy-one stations were analyzed using the computer program COMPAH (Boesch and Diaz, 1985). Two types of classifications were produced: normal (classification of stations) and inverse (classification of species). Normal classification grouped similar stations with species as attributes, while inverse classification grouped species according to their abundance.

The Bray-Curtis similarity coefficient (Clifford and Stephenson, 1975) was used in its dissimilarity form:

$$D_{jk} = \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}$$

where D_{jk} is the dissimilarity between samples j and k, x_{ij} is the abundance of species i in sample j and x_{ik}, the abundance of species i in sample k. This index, widely used in marine ecology (e.g., Nichols, 1970; Day et al., 1971; Gage, 1974), compares the percentage abundance of species present in two samples.

Flexible sorting (Lance and Williams, 1967) with the β coefficient set at -0.25 was the clustering method used. Combinatorial and hierarchical classificatory strategies, have been successful not only in terrestrial plant ecology but also in benthic ecology. Particularly, flexible sorting has been extensively used by the "Canberra School" of

ecologists (Stephenson et al., 1970; Stephenson and Williams, 1971; Stephenson et al., 1972; Williams and Stephenson, 1973). With the cluster intensity coefficient β set at -0.25, flexible sorting is a moderate space-dilating strategy that eliminates the excessive chaining of groups associated with space-contracting techniques. Also, space contracting techniques such as single linkage are prone to misclassifications (Stephenson et al., 1972). In addition, flexible sorting forms groups of rare species that, with other techniques, would be chained on to groups of abundant species. This seems meaningful since there is much lower resemblance between less common species than between abundant ones (Boesch, 1977a).

One step further toward the understanding of entity (samples and species) inter-relations based on their similarity, is to submit the data matrix to an ordination analysis. While classification assigns samples and species to groups, ordination arranges the entities in a multi-dimensional space. For ordinations to be useful, the greater percentage of the variance in the data matrix needs to be accounted for by the first three ordination axes. Ordination gives a clearer view of the separation of entities in space in terms of environmental gradients. Factors responsible for any environmental trend are not identified by the ordination; it is necessary to apply other multivariate approches (e.g., multiple discriminant analysis) to elucidate them.

Reciprocal Averaging (Hill, 1973) was applied to the data using the program ORDIFLEX (Gauch, 1977). Reciprocal Averaging is an ordination method that combines both weighted averages and eigenvector analyses.

In the iteration algorithm, weights are applied to the species of the data matrix, weighted averages are calculated and samples scores obtained from them. New species scores are calculated by using the samples scores as weights. The process is repeated until the scores stabilize and an optimal solution is reached (Hill, 1973). The advantage of this iterative method is that normal and inverse ordinations are obtained simultaneously. Thus, the ordinations can be compared to identify those species that are responsible for the arrangement of samples in the ordination space.

One of the major problems recognized in indirect ordination techniques is the assumption of linear change of variables along the environmental gradient (Gauch et al., 1977). As species distributions are curvilinear and non-monotonic, ordination techniques are affected by nonlinearity resulting in a distortion: the second axis is usually a quadratic distortion of the first axis. However, Reciprocal Averaging is less affected by nonlinearity than Principal Component Analysis, and it has been shown to be superior in analyzing community data sets (Gauch et al., 1977; Gauch, 1982).

Nodal Analyses (Williams and Lambert, 1961) were used to relate the groups derived from normal and inverse classifications. Nodal analyses are graphically displayed in two-way samples by species groups tables where the density pattern of the "cells" is expressed in terms of constancy, fidelity, species abundance and dominance.

Constancy is the average presence all members of a species group in a given sample group (Stephenson et al., 1970). It was computed as follows:

$$C_{ij} = \frac{a_{ij}}{(n_i n_j)}$$

where a_{ij} is the number of occurrences of the species of species group i in sample group j, and n_i and n_j are the numbers of entities in groups i and j. The index is 1 when all species occur in all samples in the group, and 0 when none of the species are present in the sample group.

Fidelity, the degree to which a species is restricted to a habitat, was computed as follows:

$$F_{ij} = \frac{a_{ij}}{n_j} \frac{\sum_j n_j}{\sum_j a_{ij}}$$

with the same terms as in the Constancy index. Fidelity expresses the frequency of species occurrence in a sample group compared to the overall frequency of occurrence in all sample groups. An index of less than 1 indicates that the frequency of the species group is less than its overall frequency, and an index greater than 1 indicates that the frequency of the group is greater than its overall frequency.

Abundance was computed for each species by dividing the mean abundance of the species in a sample group by its mean abundance overall, and averaging for the species group (Boesch, 1977a).

Multiple discriminant analysis (Rao, 1952; Cooley and Lohnes, 1962) was used to elucidate the abiotic factors most strongly related to station group separation, and hence, to the spatial distribution patterns of species abundances. The analysis was provided by the SPSS package (Nie et al., 1975). The variables (abiotic factors) used in the analysis were: water depth, percentages of silt-clay, medium, fine and very fine sand. Percentages were transformed to approximate normality using $\arcsin\sqrt{p}$ (Sokal and Rohlf, 1981), where p is a proportion.

Given a number of groups and a set of variables, discriminant analysis finds a linear combination of the variables (linear discriminant function) such that the difference between the groups is maximized. The set of variables are transformed by the linear discriminant function into a single discriminant score which maximizes the ratio of among group sum of squares to the within group sum of squares (Green and Vascotto, 1978).

The assumptions of the discriminant analysis are: 1) multivariate normal distribution of variables, and 2) homogeneity of variances and covariances within each group. Although most ecological data do not exhibit homogeneity of variance, the technique is robust and the assumptions are generally satisfied (Green, 1971). Furthermore, multiple discriminant analysis used to relate station groups to physical variables has been proved to be an useful tool in biological research (e.g., Cassie and Michael, 1968; Kiørboe, 1979; Flint and Rabalais, 1980; Shin, 1982; Vecchione and Grant, 1983).

The community structure statistics used were species richness and evenness. Species richness, S.R., (Margalef, 1958) was computed for each station as follows:

$$S.R. = \frac{s-1}{\ln N}$$

where s is the number of species and N, the total number of individuals. Evenness, J′, (Pielou, 1966) was computed for each station in the following way:

$$J' = \frac{H'}{\log_2 s}$$

where H′ is the diversity obtained from Shannon′s index of diversity (Shannon, 1948) and s is the number of species.

Test of Hypothesis

The hypothesis that communities in the area are similar was tested with nonparametric tests. Distribution-free statistical procedures were utilized since the assumptions of the One Way Analysis of Variance could not be met with the actual data. The assumption of homogeneity of variances was violated due to the presence of species with zero abundance in some stations and large abundances in others. Homogeneity of variances was tested for both transformed and untransformed data

using two tests: Bartlett's test and F-max test (ratio of the larger to the smaller variance).

To test whether the samples collected came from the same population, the Mann-Whitney U test was used when comparing two groups of samples, and the Krustal-Wallis test, when comparing more than two independent groups. These nonparametric statistical tests were provided by the SPSS package (Hull and Nie, 1981).

RESULTS

Sediments

Table 1 contains the station location, depth of water, percentages of silt-clay, coarse, medium, fine and very fine sand, and the statistical mean and standard deviation for the sand fraction in phi units. Sediment temperature ranged from 13.2° to 18° C. Samples were characterized by a low percentage of silt-clay (minimum 1.6%, maximum 16.0%). Higher silt-clay content was present in the stations of strata OC, off Virginia Beach, IB, Chesapeake Bay Channel, and ID, Thimble Shoal Channel.

Sands were mostly fine and very fine (sensu Wentworth, 1922). The stations of the northern part of the study area exhibited a high percentage of fine sands, while many of the stations located in the southern part were characterized by very fine sands, in particular stations of stratum OC. A few deep and shallow stations contained high percentage of medium sands. Although the sorting coefficient of Folk (1980) was not calculated, the standard deviation provided a relative measure of the sorting for the sand fraction at each of the stations. Sands were well sorted except in a few stations, where the cumulative

Table 1. Station location, water depth and sediment parameters for each station in the study area. An asterisk indicates stations with sediment bimodal distribution.

Station	North Latitude Dg Min	West Longitude Dg Min	Depth (m)	Silt-clay %	Coarse sand %	Medium sand %	Fine sand %	Very fin sand %	Mean (Phi)	St dev (Phi)	
OA1	37 05.37	75 51.96	6.4	2.6	0	7.2	55.3	35.0	2.85	.44	
OA2	37 03.20	75 54.47	5.5	2.9	0	1.2	88.9	8.0	2.68	.26	
OA3	37 04.74	75 52.95	4.6	2.0	15.0	13.9	60.0	6.3	2.12	.97	*
OA4	37 01.83	75 56.08	8.5	2.4	0	1.4	85.7	10.6	2.71	.28	
OA5	36 58.91	75 57.46	8.5	2.1	0	47.9	48.3	1.7	2.05	.40	
OA6	37 05.28	75 52.24	5.5	2.8	0	2.7	63.3	31.2	2.89	.33	
OA7	37 03.26	75 53.48	7.9	3.0	0	0.2	67.6	29.1	2.92	.23	
OA8	37 01.73	75 54.27	6.7	1.9	0	1.1	87.4	9.7	2.70	.27	
OA9	37 04.31	75 56.03	6.7	2.1	0	0.5	89.3	8.1	2.68	.24	
OB1	36 56.13	75 54.89	12.2	2.6	0	5.9	81.0	10.5	2.54	.38	
OB2	37 00.63	75 52.58	10.1	2.8	0.2	0.8	37.9	58.3	3.04	.26	
OB3	36 56.07	75 52.60	11.3	3.5	0	1.3	57.5	37.7	2.94	.28	
OB7	36 54.35	75 54.19	18.3	2.3	10.1	70.9	10.4	6.2	1.64	.63	*
OB8	36 57.52	75 52.22	11.3	3.6	0	1.0	53.0	42.4	2.99	.28	
OC1	36 53.63	75 58.56	6.7	5.8	0	2.0	48.6	43.6	2.97	.37	
OC2	36 53.23	75 58.61	8.2	4.5	0	2.7	57.0	35.9	2.93	.39	
OC3	36 52.35	75 56.53	8.2	10.0	0	1.3	31.7	57.1	3.08	.34	
OC4	36 53.74	75 58.54	6.7	6.6	0	3.0	48.2	42.1	2.94	.37	
OC5	36 52.11	75 56.14	9.8	13.7	0.2	0.8	20.9	63.1	3.20	.39	
OC6	36 54.01	75 58.88	5.5	13.5	0	0.6	24.5	61.1	3.15	.36	
OC7	36 52.50	75 58.44	7.6	4.5	0	2.5	57.9	35.2	2.91	.38	
OC8	36 51.75	75 56.60	8.2	8.0	0	1.7	35.4	54.9	3.05	.34	
OC9	36 51.53	75 57.87	7.9	3.2	0	0.8	43.5	52.5	3.03	.31	
MA1	37 01.19	76 02.01	5.2	1.8	0	5.6	86.9	5.7	2.57	.31	
MA2	37 03.94	75 57.68	7.9	5.2	5.2	41.0	43.9	4.7	2.01	.69	*
MA3	37 01.97	75 57.78	6.1	2.3	0	6.8	88.2	2.7	2.37	.29	
MA4	37 00.93	76 01.90	8.5	2.5	0	1.2	78.2	18.1	2.85	.25	
MA5	37 01.88	75 59.39	5.5	4.0	0	23.0	71.5	1.5	2.25	.36	

Table 1. (continued).

Station	North Latitude Dg Min	West Longitude Dg Min	Depth (m)	Silt--clay %	Coarse sand %	Medium sand %	Fine sand %	Very fin sand %	Mean (Phi)	St Dev (Phi)
MA7	37 03.28	75 57.98	7.9	16.0	0	3.5	57.0	23.5	2.79	.43
MA8	37 02.17	76 00.07	6.7	4.3	0	11.0	67.3	17.4	2.51	.48
MA9	37 02.05	75 58.70	5.5	1.6	0.9	19.7	76.8	1.0	2.22	.36
MB1	37 05.08	75 59.55	14.6	3.9	0	1.4	87.7	7.1	2.61	.29
MB2	37 04.00	75 59.02	-	5.0	0	0.7	72.6	21.7	2.84	.29
MB5	37 03.95	75 59.12	10.4	3.0	0	0.9	73.1	23.0	2.85	.26
MB6	37 05.69	75 59.88	11.3	6.7	0	1.1	70.4	21.9	2.85	.33
MB9	37 04.16	75 59.21	10.7	3.8	0.2	1.2	77.1	17.7	2.78	.32
MC1	37 00.14	76 00.93	12.2	3.8	0	0.4	58.0	37.9	2.98	.27
MC2	37 00.02	75 57.09	9.4	3.1	0.8	21.5	54.2	20.4	2.57	.59 *
MC4	36 59.39	75 58.59	9.8	2.5	0.6	37.1	53.3	6.6	2.21	.50
MC5	36 57.67	76 00.98	18.3	11.9	5.6	12.9	29.1	40.6	2.64	.80 *
MC6	36 59.65	76 02.27	11.0	3.1	0	1.6	62.0	33.3	2.90	.31
MC7	36 56.74	76 02.51	13.7	3.6	0	13.5	69.4	13.6	2.43	.47
MC8	36 58.75	75 59.54	11.3	3.0	2.3	80.9	13.8	0	1.75	.33
MC9	36 59.16	76 00.20	14.0	5.0	0	0	42.2	52.8	3.02	.26
IA1	37 04.79	76 02.72	4.3	3.0	0	1.6	75.7	19.7	2.78	.32
IA2	37 03.98	76 00.59	4.9	2.9	0	4.9	81.5	10.7	2.59	.35
IA3	37 05.95	76 01.82	3.7	2.0	0	3.9	78.0	16.2	2.73	.34
IA4	37 07.97	76 00.41	6.7	4.2	0	1.3	59.6	35.0	2.96	.27
IA5	37 05.76	76 00 58	5.5	5.2	0	1.4	73.0	20.4	2.82	.28
IA6	37 07.28	75 59.28	6.1	6.6	0	11.9	67.3	14.3	2.58	.46
IA7	37 05.91	76 00.99	3.0	2.8	0	2.3	77.8	17.2	2.74	.31
IA8	37 03.35	76 03.39	5.5	2.0	0	5.1	86.4	6.4	2.50	.33
IA9	37 05.30	76 02.37	4.9	3.7	0	1.1	72.2	23.0	2.83	.30
IB1	37 01.68	76 03.34	17.4	5.1	2.4	73.7	12.4	6.4	1.72	.60 *
IB5	37 04.08	76 02.25	9.1	6.7	0	1.5	27.6	64.2	3.13	.37
IB8	37 02.20	76 03.50	15.2	8.8	0	0.4	11.2	79.1	3.21	.29
IB9	37 01.51	76 05.72	9.8	2.0	0.6	60.6	34.7	2.1	1.90	.41
IC1	37 00.43	76 05.36	8.5	2.8	0	9.9	82.9	4.5	2.27	.31

Table 1. (concluded).

Station	North Latitude Dg Min	West Lngitude Dg Min	Depth (m)	Silt-clay %	Coarse sand %	Medium sand %	Fine sand %	Very fin sand %	Mean (Phi)	St Dev (Phi)
IC2	36 56.50	76 04.86	7.9	5.3	0	1.3	34.0	59.5	3.08	.33
IC3	37 01.55	76 06.81	7.9	2.0	0	31.9	66.1	0	2.09	.26
IC4	37 03.03	76 07.47	8.5	2.5	0.6	69.3	23.5	4.1	1.91	.38
IC5	73 00.30	76 04.39	8.8	2.2	0	34.1	61.4	2.3	2.10	.30
IC6	36 59.19	76 06.88	7.6	5.5	0	1.0	5.3	81.3	3.46	.39
IC7	36 59.64	76 05.76	7.3	2.8	0	0.4	78.2	18.5	2.72	.32
IC8	36 59.53	76 03.25	9.1	5.6	0	2.0	64.4	28.0	2.74	.47
ID2	36 57.89	76 05.48	11.9	8.8	0	5.4	40.5	42.0	2.93	.66 *
ID3	36 58.51	76 05.32	9.8	4.2	0	0.4	47.0	48.5	3.04	.27
ID4	36.56.84	76 03.85	10.7	12.4	0	0.7	19.4	67.5	3.16	.29
ID6	36 56.33	76 02.97	10.7	11.0	0	0.4	41.0	47.6	3.04	.30
ID7	36 58.06	76 04.42	13.4	2.4	9.1	51.9	26.1	10.5	1.88	.73 *
ID8	36 57.33	76 03.39	14.3	3.2	7.5	58.8	22.3	8.2	1.82	.67 *

percentage curve exhibited a bimodal distribution; these stations are marked with an asterisk in table 1.

Many samples contained detritus and, in some occasions, mucous tubes of anemones and polychaetes, tar and large pieces of shell. Other samples were clean and contained only small shell fragments. Samples with abundant detritus were confined to the stations of strata OC, MC, and ID with the exception of stations MC4 and MC8. Clean samples were characteristic of stations of strata OA, MA, MB and IA with the exception of stations IA4 and, to a lesser degree, IA6 and MB6. Stations of strata IC and OB had clean sediments with exception of IC2, IC4, IC6, OB7 and OB8 which contained detritus.

The presence of fine grained sediments and detritus in most of the stations located in the southern part of the bay entrance reflects the tidal circulation patterns in the area. Fine grain sediment and organic material are probably transported by ebb currents at the surface and deposited as the water leaves the bay around Cape Henry.

Percent total organic carbon (TOC) was measured from sediment samples of a few selected stations (table 2). Percent TOC at these stations was low (<0.26) as expected from an area where sediments are mostly sands with low percentage of silt-clay.

Table 2. Percent Total Organic Carbon content of selected stations.

Station	% TOC
OA1	0.068
OC8	0.262
MB2	0.039
ID3	0.107

Biological Results

The seventy-one stations sampled in the study area yielded a total of 20,492 individuals encompassing 158 species. All the taxa identified are listed in Appendix I. Although most of the taxa were identified to the species level, it was not possible to identify some of them beyond the generic level. Sixteen genera are present in Appendix I. In addition, individuals of the groups Hexacorallia, Rhynchocoela, Oligochaeta and Ostracoda, were not identified to the species level. The taxonomy for the sea anemones (Hexacorallia) in the Eastern United States is poorly understood, and the available taxonomic keys for nemerteans (Rhynchocoela) are designed to be used with live animals. Appendix II contains a reference list of all the taxonomic keys used in the present study.

Polychaetes were the most numerous of all the organisms collected, accounting for 46% (80) of the total number of species. Molluscs were represented by 33 species (19%) and crustaceans by 43 species (24.7%). Other groups constituted the remaining 10.3% of the species.

A list of the most abundant species is contained in table 3. Juveniles of the species marked with an asterisk were collected in relatively high numbers. The capitellid polychaetes Amastigos caperatus and Mediomastus ambiseta were the most abundant macrobenthic organisms with average densities of 599 and 489 individuals per m^2, respectively. Amastigos caperatus was present with high densities in many stations

Table 3. Twenty-five density dominants in the study area. Taxon code: A- Amphipod, B- Bivalve, G- Gastropod, P- Polychaete. Species with an asterisk consisted of many juveniles.

Species	Total Abundance
Amastigos caperatus (P)	4,738
Mediomastus ambiseta (P)	4,387
Tellina agilis (B)	1,162 *
Spiophanes bombyx (P)	1,069 *
Prionospio pygmaea (P)	768
Tharyx setigera (P)	752
Protohaustorius wigleyi (A)	710 *
Rhynchocoela	528
Glycera dibranchiata (P)	454 *
Oligochaeta	248
Rhepoxynius epistomus (A)	246
Ensis directus (B)	237
Microphthalmus sczelkowii (P)	227
Nephtys picta (P)	222
Acteocina canaliculata (G)	214
Polygordius sp. (P)	184
Aricidea wassi (P)	173
Magelona filiformis (P)	169
Corophium tuberculatum (A)	153
Synchelidium americanum (A)	138
Turbonilla interrupta (G)	137
Cylichnella bidentata (G)	134
Anthozoa	126
Nephtys bucera (P)	117
Listriella barnardi (A)	114

throughout the study area, while Mediomastus ambiseta was restricted to stations of the southern part of the bay entrance with the exception of station IA4. Particularly high densities of Mediomastus ambiseta were recorded for many stations of strata OC, MC and ID.

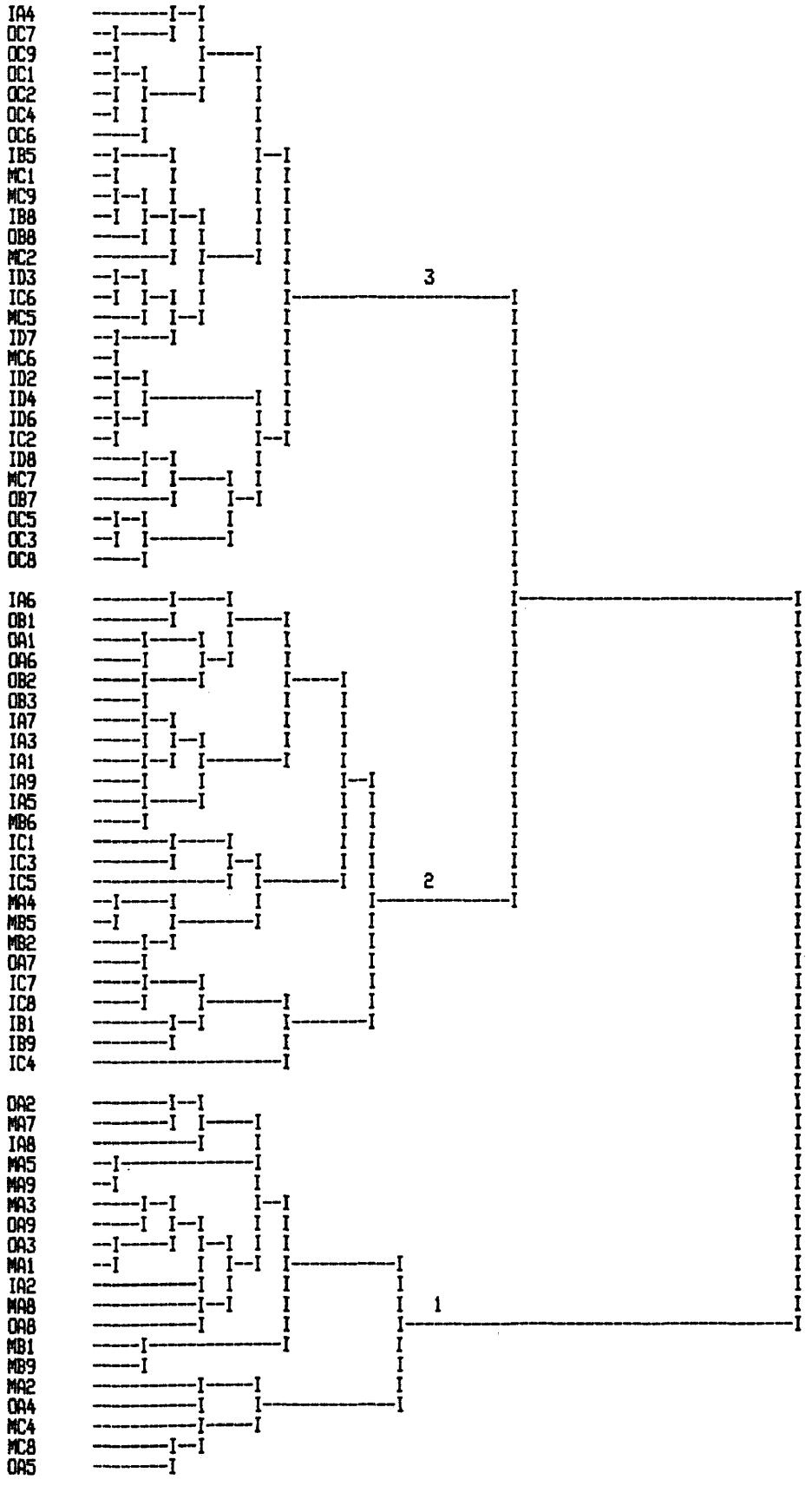
The tellinid bivalve Tellina agilis and the spionid polychaetes Spiophanes bombyx and Prionospio pygmaea were distributed throughout most of the study area. They reached maximum densities at the southern part of the bay entrance, in strata OC, MC and ID. Likewise, the cirratulid polychaete Tharyx setigera was specially abundant in the southern part. Relatively high densities of the haustoriid amphipod Protohaustorius wigleyi were present in many stations of the northern part of the bay entrance, particularly in the strata OA and MA. None or very few individuals of this species were collected in the southern part, strata OB, OC, MC, ID and IB. Other less abundant species showed similar trends in distribution between the northern part and the southern part of the entrance.

Classification and Ordination Analyses

Seventy-one stations and 92 (54.1%) of the original species and genera list were used in the Classification analysis. The higher taxa Anthozoa, Rhynchocoela, Oligochaeta, Ostracoda and Echiura were also included.

Results from the classification of stations are presented in figure

Figure 6. Numerical classification of collections of macrobenthos from stratified random stations at the Chesapeake Bay entrance.


IA4
OC7
OC9
OC1
OC2
OC4
OC6
IB5
MC1
MC9
IB8
OB8
MC2
ID3
IC6
MC5
ID7
MC6
ID2
ID4
ID6
IC2
ID8
MC7
OB7
OC5
OC3
OC8
IA6
OB1
OA1
OA6
OB2
OB3
IA7
IA3
IA1
IA9
IA5
MB6
IC1
IC3
IC5
MA4
MB5
MB2
OA7
IC7
IC8
IB1
IB9
IC4
OA2
MA7
IA8
MA5
MA9
MA3
OA9
OA3
MA1
IA2
MA8
OA8
MB1
MB9
MA2
OA4
MC4
MC8
OA5
3
2
1

6. Station IC4 was reallocated based on higher resemblance to stations OC4 and OC9 when the inter-entity resemblance matrix was visually inspected. Three major clusters were identified. These groups are labelled 1 to 3 in figure 6. The stations of each of the three groups were coded with different symbols in figure 7 for a better visualization of the group separation patterns. Three groups were considered because they showed a biological meaning in terms of their species distributions and abundances. When an attempt was made to look at more and smaller clusters of stations, no clear spatial patterns were revealed.

Group 1 was comprised of stations located in the northern part of the entrance with the exception of stations OA5, MC4 and MC8. Basically, this area contains shoals with dynamic sediments. Group 3 was comprised of stations from the southern part of the entrance plus stations IA4 and IB5. This area represents a depositional, less dynamic environment. Group 2 was more spatially dispersed, but with many stations located in the shallow strata IA and IC.

Results of the inverse classification are presented in figure 8. Thirteen clusters of species were recognized. Group 1 was constituted by species of fine to medium sands. Groups 2 and 3 contained species of finer sands; they included two abundant species: Protohaustorius wigleyi and Nephtys bucera. These three groups of species were collected in the most dynamic areas. Groups 4 and 5 contained very low abundant species, distributed in fine and very fine sands. Group 6 included epifauna and species inhabiting bottoms with large shell fragments, except Microphthalmus sczelkowii, an interstitial species. Group 7 contained

Figure 7. Geographical distribution of the three major station groups defined by numerical classification of macrobenthos.

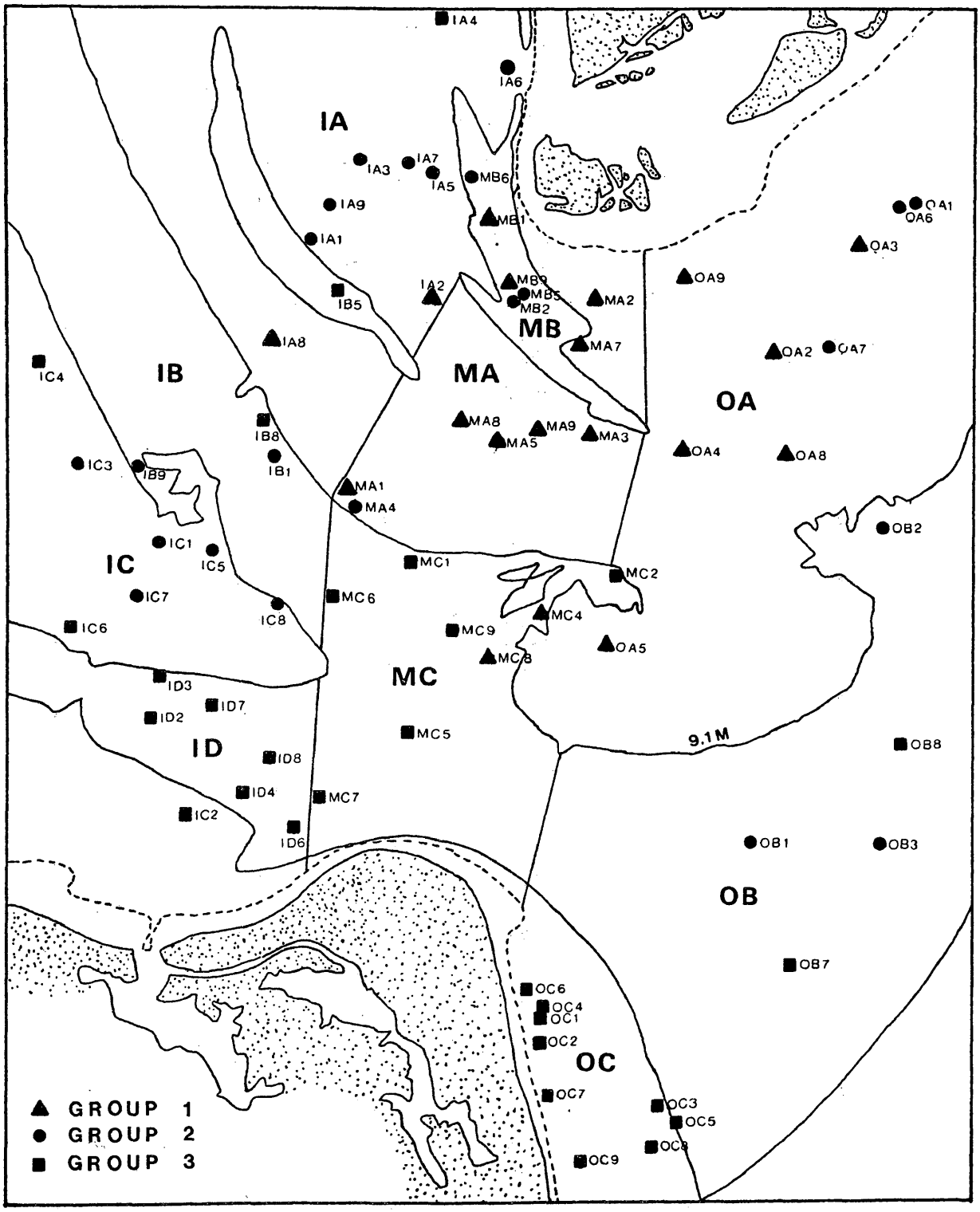
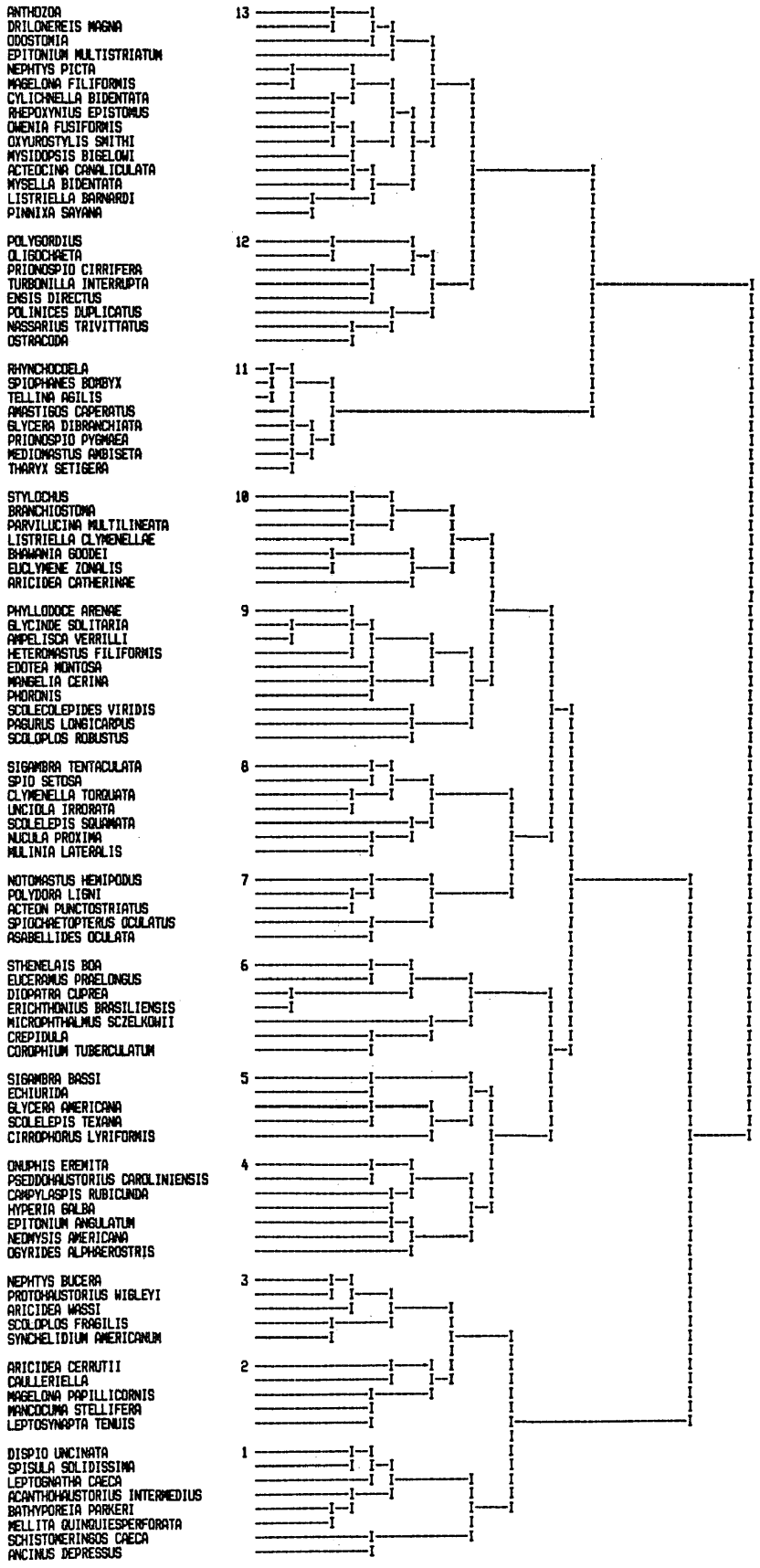

IA
IB
IC
ID
MA
MB
MC
OA
OB
OC
IA4
IA6
IA3
IA7
IA5
MB6
IA9
MB1
IA1
IA2
MB9
MB5
MB2
MA2
IB5
IA8
MA7
IC4
IB8
IB1
IC3
IB9
MA8
MA9
MA3
MA5
MA1
MA4
IC1
IC5
IC7
IC8
IC6
MC1
MC6
MC2
MC4
MC9
MC8
OA5
ID3
ID7
ID2
ID8
ID4
MC7
IC2
ID6
MC5
9.1M
OA1
OA6
OA3
OA9
OA2
OA7
OA4
OA8
OB2
OB8
OB1
OB3
OB7
OC6
OC4
OC1
OC2
OC7
OC3
OC5
OC8
OC9
GROUP 1
GROUP 2
GROUP 3

Figure 8. Numerical classification of species of macrobenthos from stations at the Chesapeake Bay entrance.


ANTHOZOA
DRILONEREIS MAGNA
ODOSTOMIA
EPITONIUM MULTISTRIATUM
NEPHTYS PICTA
MAGELONA FILIFORMIS
CYLICHNELLA BIDENTATA
RHEPOXYNIUS EPISTOMUS
OWENIA FUSIFORMIS
OXYUROSTYLIS SMITHI
MYSIDOPSIS BIGELOWI
ACTEOCINA CANALICULATA
MYSELLA BIDENTATA
LISTRIELLA BARNARDI
PINNIXA SAYANA
POLYGORDIUS
OLIGOCHAETA
PRIONOSPIO CIRRIFERA
TURBONILLA INTERRUPTA
ENSIS DIRECTUS
POLINICES DUPLICATUS
NASSARIUS TRIVITTATUS
OSTRACODA
RHYNCHOCOELA
SPIOPHANES BOMBYX
TELLINA AGILIS
AMASTIGOS CAPERATUS
GLYCERA DIBRANCHIATA
PRIONOSPIO PYGMAEA
MEDIOMASTUS AMBISETA
THARYX SETIGERA
STYLOCHUS
BRANCHIOSTOMA
PARVILUCINA MULTILINEATA
LISTRIELLA CLYMENELLAE
BHAWANIA GOODEI
EUCLYMENE ZONALIS
ARICIDEA CATHERINAE
PHYLLODOCE ARENAE
GLYCINDE SOLITARIA
AMPELISCA VERRILLI
HETEROMASTUS FILIFORMIS
EDOTEA MONTOSA
MANGELIA CERINA
PHORONIS
SCOLECOLEPIDES VIRIDIS
PAGURUS LONGICARPUS
SCOLOPLOS ROBUSTUS
SIGAMBRA TENTACULATA
SPIO SETOSA
CLYMENELLA TORQUATA
UNCIOLA IRRORATA
SCOLELEPIS SQUAMATA
NUCULA PROXIMA
MULINIA LATERALIS
NOTOMASTUS HEMIPODUS
POLYDORA LIGNI
ACTEON PUNCTOSTRIATUS
SPIOCHAETOPTERUS OCULATUS
ASABELLIDES OCULATA
STHENELAIS BOA
EUCERAMUS PRAELONGUS
DIOPATRA CUPREA
ERICHTHONIUS BRASILIENSIS
MICROPHTHALMUS SCZELKOWII
CREPIDULA
CROPHIUM TUBERCULATUM
SIGAMBRA BASSI
ECHIURIDA
GLYCERA AMERICANA
SCOLELEPIS TEXANA
CIRROPHORUS LYRIFORMIS
ONUPHIS EREMITA
PSEUDOHAUSTORIUS CAROLINIENSIS
CAMPYLASPIS RUBICUNDA
HYPERIA GALBA
EPITONIUM ANGULATUM
NEOMYSIS AMERICANA
OGYRIDES ALPHAEROSTRIS
NEPHTYS BUCERA
PROTOHAUSTORIUS WIGLEYI
ARICIDEA WASSI
SCOLOPLOS FRAGILIS
SYNCHELIDIUM AMERICANUM
ARICIDEA CERRUTII
CAULLERIELLA
MAGELONA PAPILLICORNIS
MANCOCUMA STELLIFERA
LEPTOSYNAPTA TENUIS
DISPIO UNCINATA
SPISULA SOLIDISSIMA
LEPTOGNATHA CAECA
ACANTHOHAUSTORIUS INTERMEDIUS
BATHYPOREIA PARKERI
MELLITA QUINQUIESPERFORATA
SCHISTOMERINGOS CAECA
ANCINUS DEPRESSUS
13
12
11
10
9
8
7
6
5
4
3
2
1

low abundant species of very fine sands. Group 8 was constituted of species mainly restricted to sediments of higher silt-clay content. Groups 9 and 10 also contained species mostly of very fine sands and some silt-clay. Group 11 included the dominant species; some of them (Rhynchocoela, Spiophanes bombyx, Tellina agilis and Amastigos caperatus) were collected throughout the bay entrance. Group 12 was constituted by subdominant species, most of them eurytopic. Group 13 included species of variable distribution between moderately mobile sediments and stable, more depositional areas.

Ordination analysis provided a clearer view of the station group separation and the species responsible for such separation. Seventy-one stations and 74 (43.5%) of the original species and genera list were included in the analysis. Results are presented in figures 9 and 10. The first axis accounted for 17.9% of the total variance of the ordination points, and the second axis accounted for 7.8%. The first three axes accounted for 31.8% of the total variance. This value is smaller than the range 40-90% of the total variance in many community studies, although the ecological interpretation of the results is more important than the percentage of variance accounted for (Gauch, 1982).

In general, peripheral points to the arch (figure 10) indicated species of narrow distributions, restricted to a particular habitat, and points interior to the arch were species with broad distributions. This is a property of reciprocal averaging associated to the arch distortion of the second axis.

Figure 9. Ordination of station groups of macrobenthos. Axes are scaled in proportion to the eigenvalues.

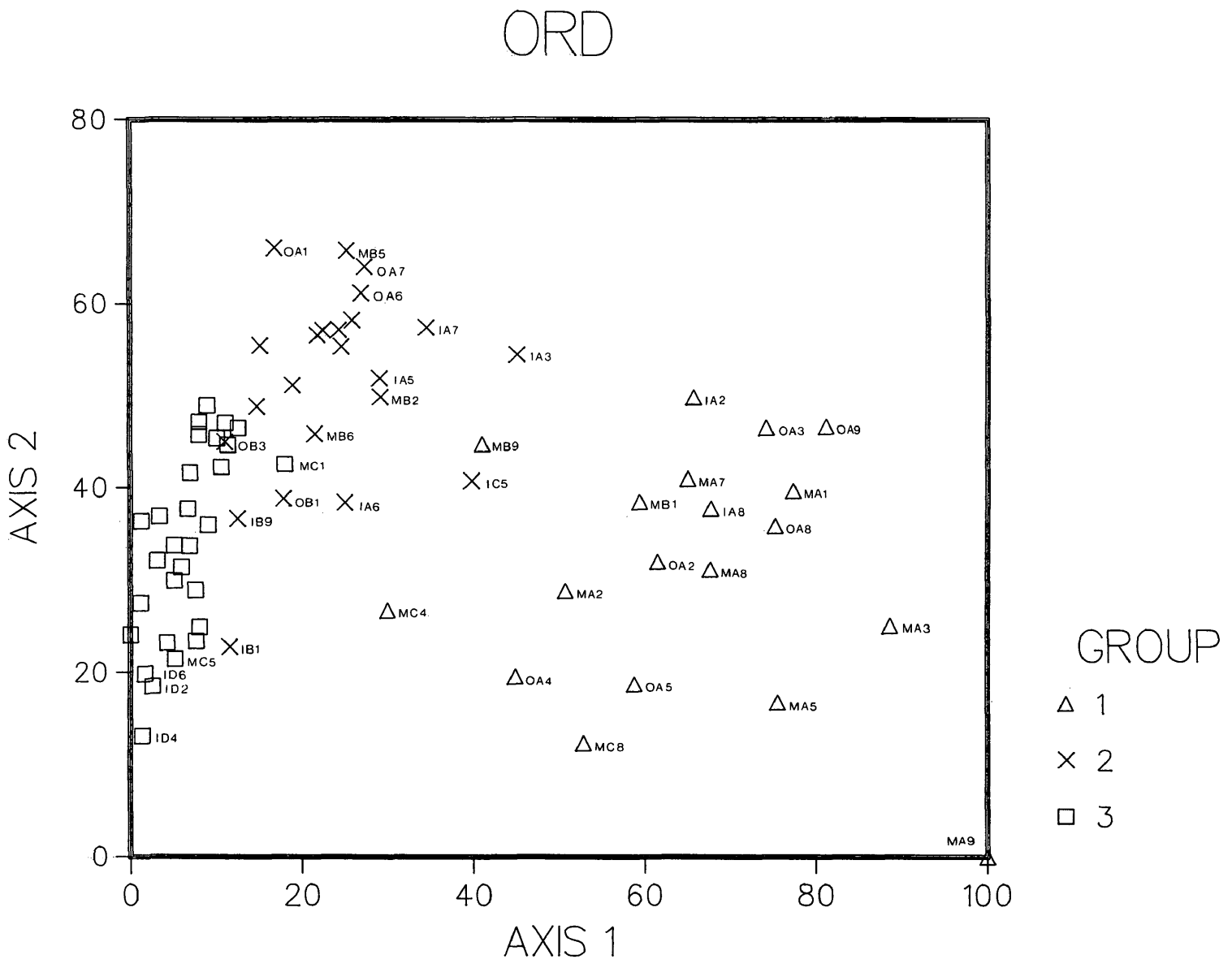
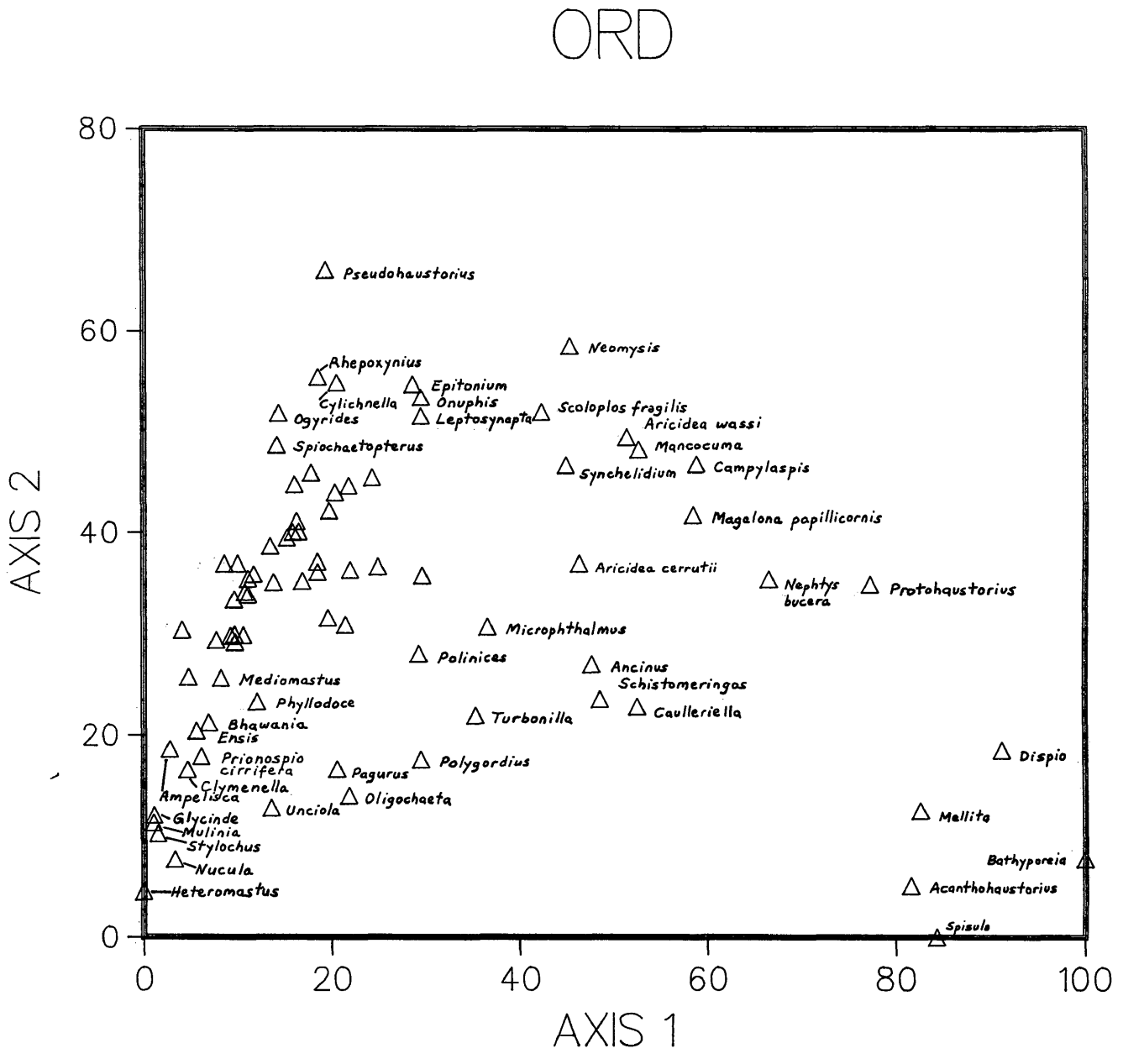

ORD
AXIS 2
AXIS 1
0
20
40
60
80
100
OA1
MB5
OA7
OA6
IA7
IA3
IA5
MB2
IA2
OA3
OA9
MB6
OB3
MB9
MC1
IC5
MA7
MA1
OB1
IA6
MB1
IA8
IB9
OA8
OA2
MA8
MA2
MC4
MA3
IB1
MC5
ID6
ID2
OA4
OA5
MA5
ID4
MC8
MA9
GROUP
1
2
3

Figure 10. Ordination of species of macrobenthos. Axes are scaled in proportion to the eigenvalues.


ORD
AXIS 2
AXIS 1
0
20
40
60
80
100
Pseudohaustorius
Neomysis
Rhepoxynius
Epitonium
Cylichnella
Onuphis
Scoloplos fragilis
Ogyrides
Leptosynapta
Aricidea wassi
Mancocuma
Spiochaetopterus
Synchelidium
Campylaspis
Magelona papillicornis
Aricidea cerrutii
Nephtys bucera
Protohaustorius
Microphthalmus
Polinices
Ancinus
Schistomeringos
Mediomastus
Phyllodoce
Caulleriella
Turbonilla
Bhawania
Ensis
Dispio
Prionospio cirrifera
Polygordius
Pagurus
Clymenella
Ampelisca
Oligochaeta
Unciola
Mellita
Glycinde
Mulinia
Stylochus
Bathyporeia
Nucula
Acanthohaustorius
Heteromastus
Spisula

Group 1 stations were very distinct in the ordination space. Species almost restricted to these stations were the spionid polychaete Dispio uncinata, juveniles of the mactrid bivalve Spisula solidissima, the haustoriid amphipods Acanthohaustorius intermedius and Bathyporeia parkeri, and the echinoid Mellita quinquiesperforata. The polychaete Nephtys bucera and the haustoriid amphipod Protohaustorius wigleyi reached maximun densities in the stations of Group 1. Species equally present in both Groups 1 and 2 were the polychaete Magelona papillicornis and the cumaceans Campylaspis rubicunda and Mancocuma stellifera.

Two species were characteristic of Group 2, reaching maximum densities in these stations: the paraonid polychaete Aricidea wassi and the amphipod Synchelidium americanum. The gastropod Epitonium multistriatum was less abundant but also characteristic of Group 2 stations. Two other relatively abundant species were well distributed in Groups 2 and 3; these were the opisthobranch gastropod Cylichnella bidentata and the amphipod Rhepoxynius epistomus.

Group 3 stations included many characteristic species (i.e., restricted or reaching maximum densities in this group). Species present in low densities but restricted to Group 3 were situated on the left end of the ordination space comprised by the first two axes. These species are the polychaetes Glycinde solitaria, Heteromastus filiformis, Bhawania goodei and Euclymene zonalis; the bivalves Mulinia lateralis and Nucula proxima; the amphipod Ampelisca verrilli; the polycladid turbellarian Stylochus sp. and the phoronid Phoronis sp. The six top

most abundant species (Table 3) reached maximun densities in the stations of Group 3.

Stations IB1 and OB3 may be reallocated to Group 3 stations based on their position in the ordination space. These seemed more appropriate since their faunal lists were similar to other stations of Group 3. These reallocations were used in Discriminant Analysis.

Nodal Analyses

Eight station groups and thirteen species groups were selected from the classification of macrobenthos as indicated in table 4. Cell constancy, fidelity and abundance matrices are shown in figures 11 to 13.

Species in Group A were highly constant in and faithful to Group I stations. They were also constant in and faithful to Group II stations, but they were rare elsewhere. As overall, these species were twice as abundant in Group I stations than in Group II, but, in general, densities were very low, only relatively higher in stations MA5 and MA9.

Species in Group B were moderately constant in Group I, II and V stations, showing fidelity to Group I stations and lower fidelity to Groups II and V stations.

Table 4. Species groups and stations groups selected from numerical classification of macrobenthos in the study area.

Species Group A	Species Group E
Ancinus depresus	*Cirrophorus lyriformis*
Schistomeringos caeca	*Scolelepis texana*
Mellita quinquiesperforata	*Glycera americana*
Bathyporeia parkeri	Echiurida
Acanthohaustorius intermedius	*Sigambra bassi*
Leptognatha caeca	
Spisula solidissima	
Dispio uncinata	
Species Group B	**Species Group F**
Leptosynapta tenuis	*Corophium tuberculatum*
Mancocuma stellifera	*Crepidula* sp.
Magelona papillicornis	*Microphthalmus sczelkowii*
Caulleriella sp.	*Erichthonius brasiliensis*
Aricidea cerrutii	*Diopatra cuprea*
	Euceramus praelongus
	Sthenelais boa
Species Group C	**Species Group G**
Synchelidium americanum	*Asabellides oculata*
Scoloplos fragilis	*Spiochaetopterus oculatus*
Aricidea wassi	*Acteon punctostriatus*
Protohaustorius wigleyi	*Polydora ligni*
Nephtys bucera	*Notomastus hemipodus*
Species Group D	**Species Group H**
Ogyrides alphaerostris	*Mulinia lateralis*
Neomysis americana	*Nucula proxima*
Epitonium angulatum	*Scolelepis squamata*
Hyperia galba	*Unciola irrorata*
Campylaspis rubicunda	*Clymenella torquata*
Pseudohaustorius caroliniensis	*Spio setosa*
Onuphis eremita	*Sigambra tentaculata*

Table 4. (continued).

Species Group I

Scoloplos robustus
Pagurus longicarpus
Scolecolepides viridis
Phoronis sp.
Mangelia cerina
Edotea montosa
Heteromastus filiformis
Ampelisca verrilli
Glycinde solitaria
Phyllodoce arenae

Species Group J

Aricidea catherinae
Euclymene zonalis
Bhawania goodei
Listriella clymenellae
Parvilucina multilineata
Branchiostoma sp.
Stylochus sp.

Species Group K

Tharyx setigera
Mediomastus ambiseta
Prionospio pygmaea
Glycera dibranchiata
Amastigos caperatus
Tellina agilis
Spiophanes bombyx
Rhynchocoela

Species Group L

Ostracoda
Nassarius trivittatus
Polinices duplicatus
Ensis directus
Turbonilla interrupta
Prionospio cirrifera
Oligochaeta
Polygordius sp.

Species Group M

Pinnixa sayana
Listriella barnardi
Mysella bidentata
Acteocina canaliculata
Mysidopsis bigelowi
Oxyurostylis smithi
Owenia fusiformis
Rhepoxynius epistomus
Cylichnella bidentata
Magelona filiformis
Nephtys picta
Epitonium multistriatum
Odostomia
Drilonereis magna
Anthozoa

Table 4. (concluded).

Station Group I	Station Group V
OA5	MB6 OB3
MC8	IA5 OB2
MC4	IA9 OA6
OA4	IA1 OA1
MA2	IA3 OB1
	IA7 IA6
Station Group II	**Station Group VI**
MB1 OA9	OC8 ID6
MB9 MA3	OC3 ID4
OA8 MA9	OC5 ID2
MA8 MA5	OB7
IA2 IA8	MC7
MA1 MA7	ID8
OA3 OA2	IC2
Station Group III	**Station Group VII**
IB9	MC6 OB8
IB1	ID7 IB8
IC8	MC5 MC9
IC7	IC6 MC1
	ID3 IB5
	MC2
Station Group IV	**Station Group VIII**
OA7 IC5	OC6 OC9
MB2 IC3	OC4 OC7
MB5 IC1	OC2 IC4
MA4	OC1 IA4

Species members of Group C were highly constant in Groups II, IV and V stations and they were moderately constant in Groups I, III and VIII stations. These species were more faithful to Groups I, II, IV and V stations than elsewhere. As overall, and as indicated in fig. 13, this group of species showed low abundance in the stations of Groups II and V. Most of the contributions came from the haustoriid amphipod Protohaustorius wigleyi, with high densities in Group II stations. The polychaete Nephtys bucera and the amphipod Synchelidium americanum were much less abundant but frequent in the stations of Groups II, IV and V.

Species in Groups D through G exhibited low constancy and abundance. Members of Group D were relatively faithful to Group V stations, and members of Groups F and G, to Group VI stations. The species of these groups were absent or nearly absent from Group I and II stations, with the exception of the hesionid polychaete Microphthalmus sczelkowii, collected with high density in station MA2.

Species in Groups H and I were moderately constant in Group VI and Group VIII stations, respectively. They were moderately abundant and faithful to stations of Group VI and less frequent or rare elsewhere. Stations ID2, ID4 and ID6 contributed with the maximun number of individuals.

Species members of Group K were highly constant in Groups I, II and IV stations and very highly constant in the remaining groups. Group K was constituted by eurytopic species, frequent everywhere, with low fidelity to any group of stations. Rhynchocoela and the capitellid

Figure 11. Nodal constancy for station-species group coincidence. Site and species groups are indicated in table 4.

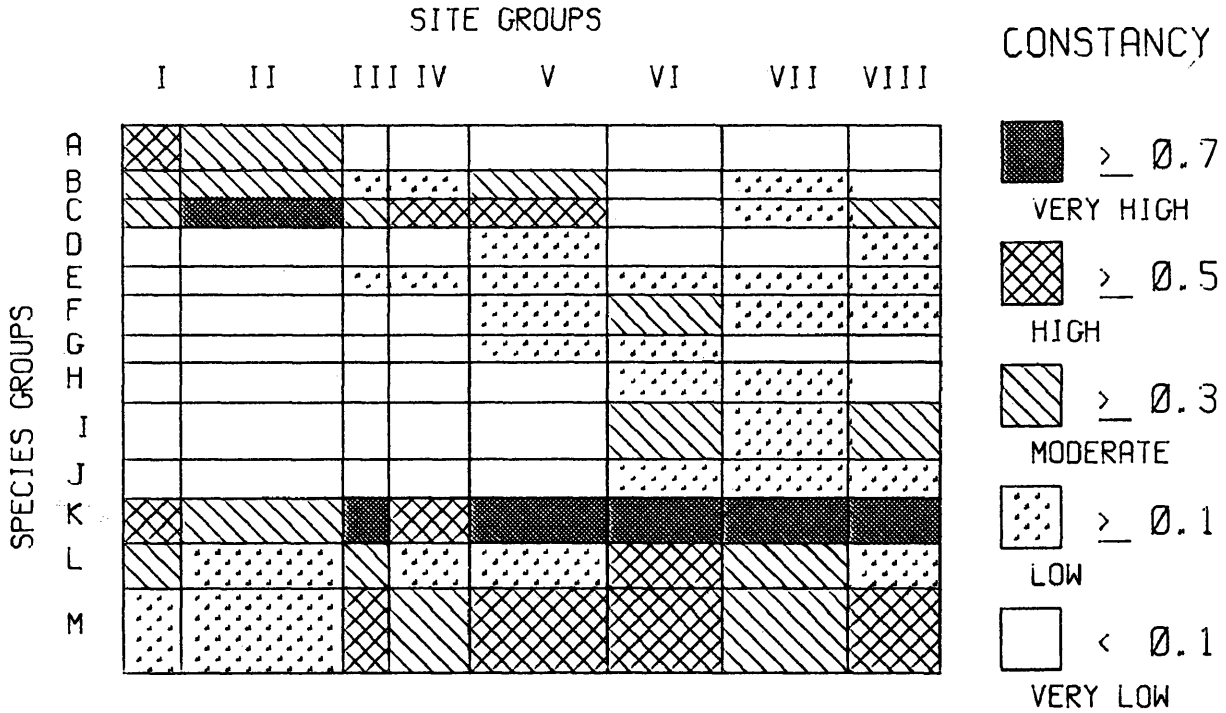

SITE GROUPS
I
II
III
IV
V
VI
VII
VIII
SPECIES GROUPS
A
B
C
D
E
F
G
H
I
J
K
L
M
CONSTANCY
≥ 0.7
VERY HIGH
≥ 0.5
HIGH
≥ 0.3
MODERATE
≥ 0.1
LOW
< 0.1
VERY LOW

Figure 12. Nodal fidelity of macrobenthos. Site and species groups are indicated in table 4.

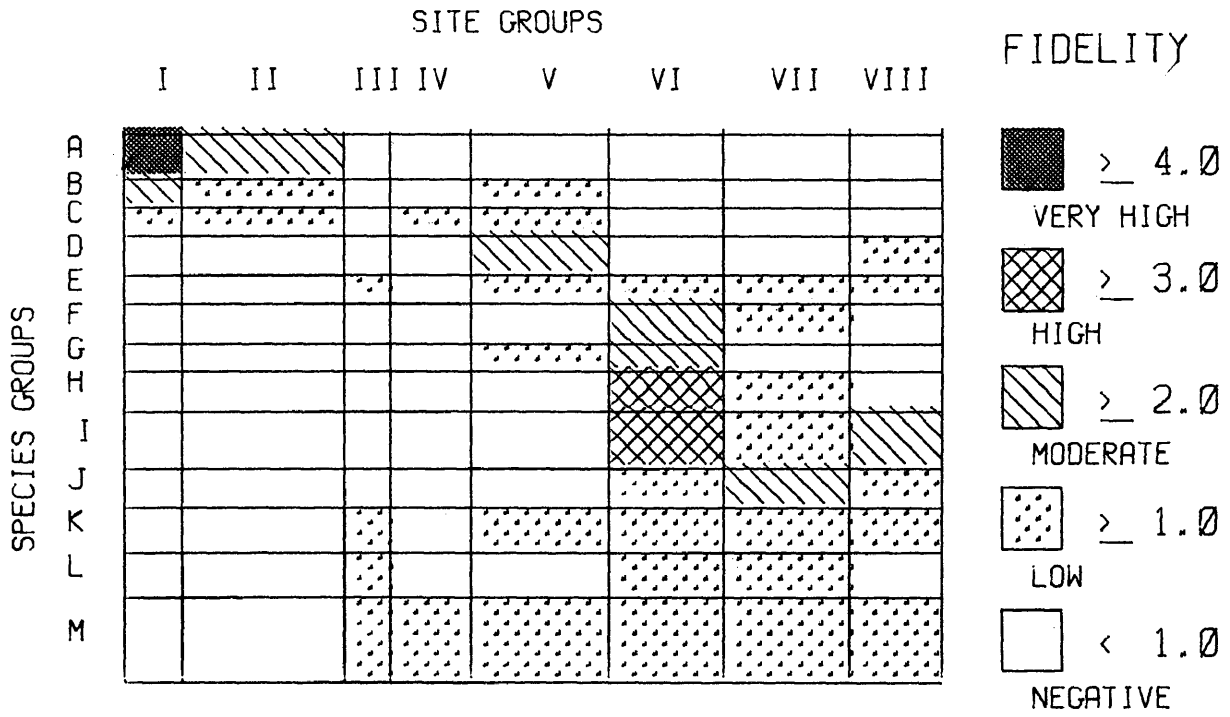
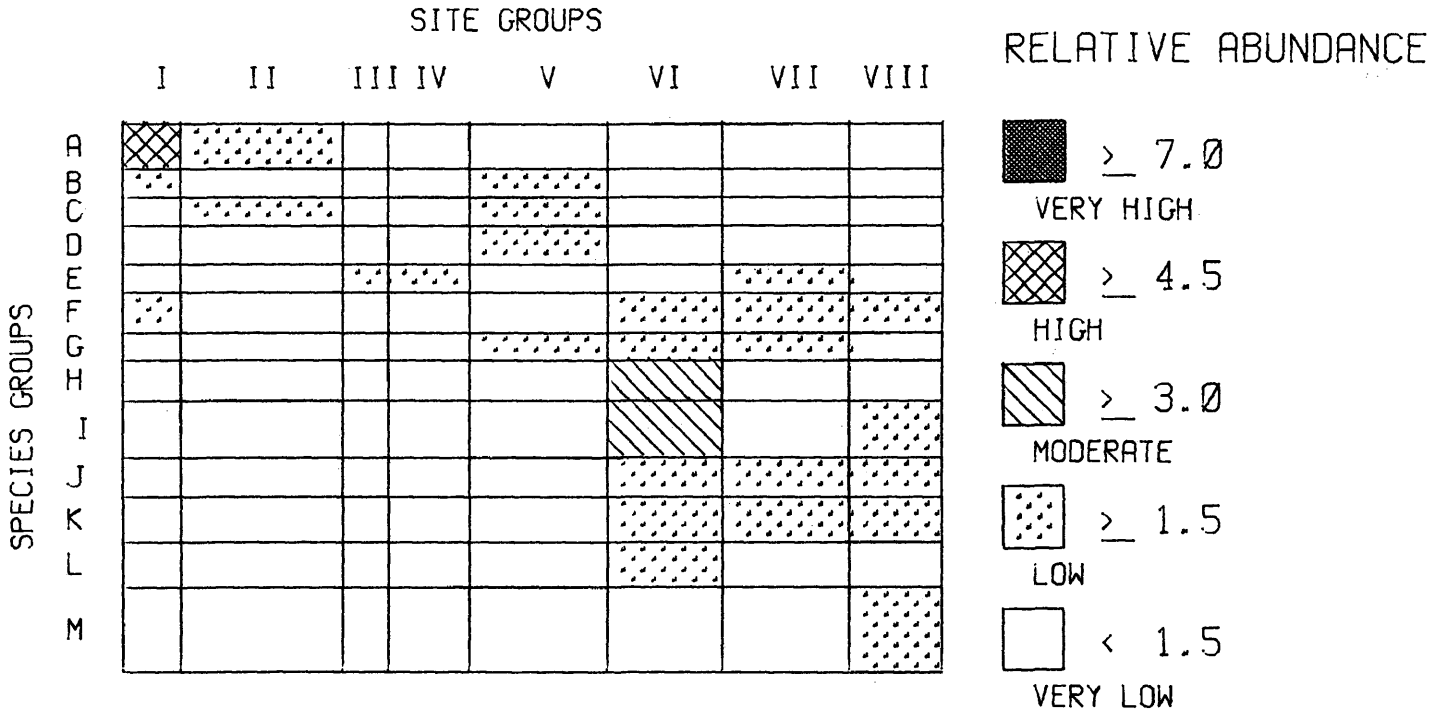

SITE GROUPS
I
II
III
IV
V
VI
VII
VIII
SPECIES GROUPS
A
B
C
D
E
F
G
H
I
J
K
L
M
FIDELITY
≥ 4.0
VERY HIGH
≥ 3.0
HIGH
≥ 2.0
MODERATE
≥ 1.0
LOW
< 1.0
NEGATIVE

Figure 13. Nodal relative abundance for macrobenthos. Site and species groups are indicated in table 4.


SITE GROUPS
I
II
III
IV
V
VI
VII
VIII
SPECIES GROUPS
A
B
C
D
E
F
G
H
I
J
K
L
M
RELATIVE ABUNDANCE
≥ 7.0
VERY HIGH
≥ 4.5
HIGH
≥ 3.0
MODERATE
≥ 1.5
LOW
< 1.5
VERY LOW

polychaete Amastigos caperatus were the most abundant taxa in Groups I and II stations. Densities increased in Groups III to V stations because of the contributions of the bivalve Tellina agilis and the spionid polychaetes Spiophanes bombyx and Prionospio pygmaea.

Species in Group L were also constantly distributed in the stations of Groups I, III and V to VII. They exhibited low fidelity and low abundance, reaching maximun densities in Group VI stations, in particular stations ID2, ID4 and ID6. The major contributors to stations of Groups I and III were oligochaetes and the archiannelid polychaete Polygordius sp.

Group M species were constant in and faithful to Groups III and VIII stations, although, as overall, fidelity was low. Abundance was very low, only higher in Group VIII stations. The amphipod Rhepoxynius epistomus, the polychaete Nephtys picta and the opistobranch gastropod Acteocina canaliculata were the most abundant among the members of Group M.

Discriminant Analysis

Multiple discriminant analysis was used to determine which environmental factors might account for the observed among-groups differences in species distribution and abundance responsible for the station group separation. The abiotic factors used in the analysis were: depth of water, percent silt-clay, percent medium, fine and very

fine sand. After reallocation of misclassifications, the abiotic values for each station (table 1) were assigned to one of the three groups resulting from numerical classification (figure 6).

The first discriminant function accounted for 96.7% of the among-group variance, and the second discriminant function accounted for the remaining 3.3%. The chi-squared test of significance for the first function was highly significant (X^2 = 82.15, 10 d.f.). Table 5 contains the standardized canonical coefficients for each discriminant function, and table 6 contains the pooled within-groups correlations between the discriminating variables and the discriminant functions. These correlations were used to plot the vectors indicating the orientation of the environmental factors more strongly related to the station group separation. Figure 14 shows the relative orientation of the three groups of stations in the discriminant space.

Discriminant function I was related to fine and very fine sands in the sediments. Stations in Groups 1 and 2 were associated with increasing percent fine sand, and stations in Group 3 were associated with increasing percent very fine sand. Ninety-six point eight per cent of the stations of Group 3 were correctly classified in the predicted group. There was overlap between Groups 1 and 2, with 78.9% (15 out of 19) and 66.7% (14 out of 21) of the stations classified in the predicted group, respectively.

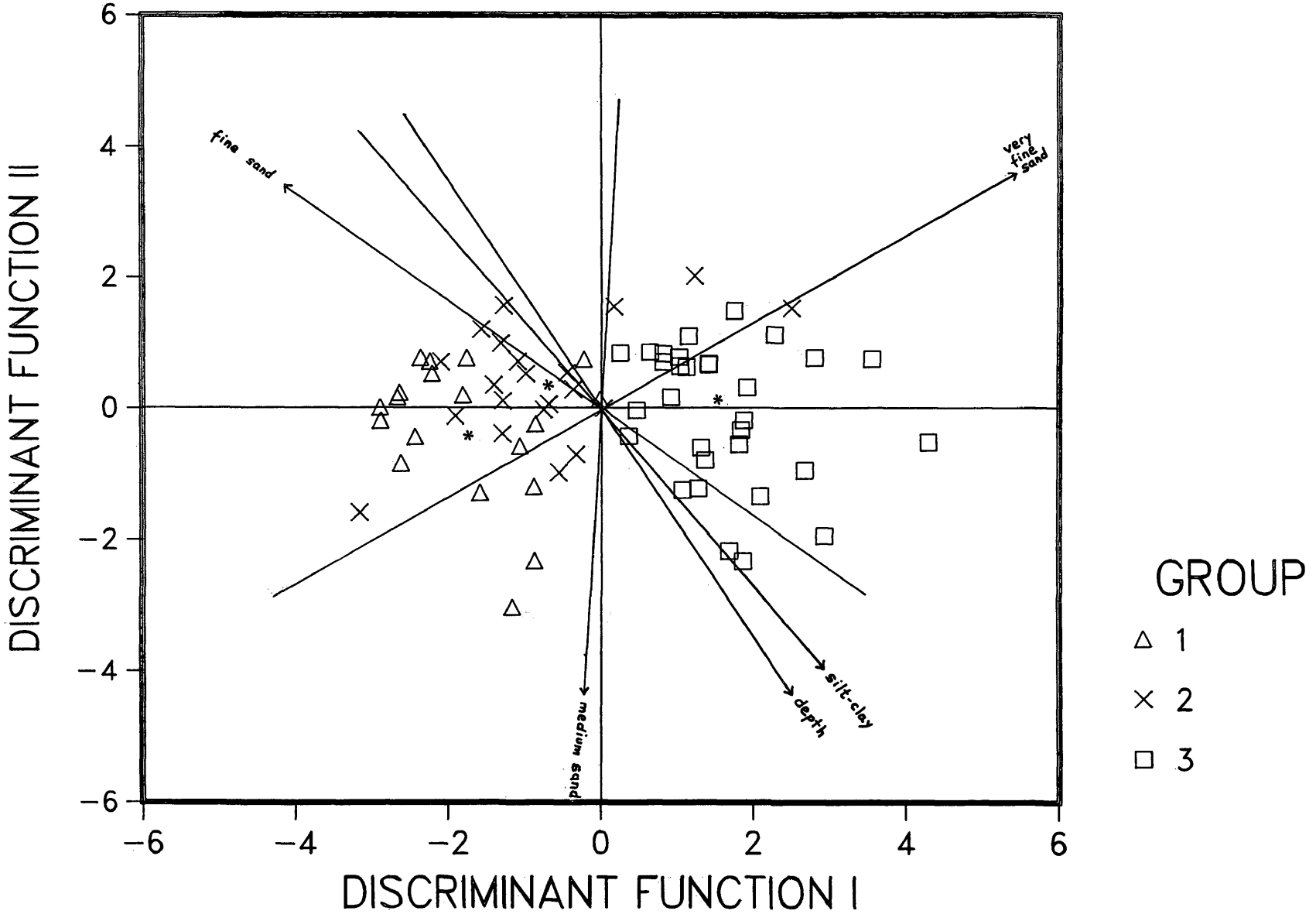
Table 5. Standardized discriminant function coefficients for each parameter utilized in the discriminant analysis.

PARAMETERS	DISCRIMINANT FUNCTION I	DISCRIMINANT FUNCTION II
Depth	0.41200	-0.36696
Silt-Clay	-0.07099	-0.57984
Medium Sand	2.00080	1.81802
Fine Sand	0.69692	1.36433
Very Fine Sand	2.34404	2.08183

Table 6. Pooled within groups correlations between the discriminating variables and the discriminant functions. The magnitude of the correlation is indicated.

PARAMETERS	DISCRIMINANT FUNCTION I	DISCRIMINANT FUNCTION II
Fine Sand	-0.61138	0.51251
Very Fine Sand	0.59872	0.39915
Depth	0.34832	-0.60120
Medium Sand	-0.04837	-0.53604
Silt-Clay	0.33896	-0.38581

Figure 14. Orientation of station groups in discriminant space. Vectors indicate the relative orientation of the environmental variables. Group centroids are indicated by asterisks.


DISCRIMINANT FUNCTION II
DISCRIMINANT FUNCTION I
6
4
2
0
−2
−4
−6
−6
−4
−2
0
2
4
6
fine sand
very fine sand
medium sand
silt-clay
depth
GROUP
1
2
3

Species Richness and Evenness

Mean species richness and evenness for each strata and some distinct stations is presented in table 7. The indicated values for species richness are conservative since higher taxa like Hexacorallia, Rhynchocoela and Oligochaeta were not included. In general, richness was higher in the stations of the southern part than in the stations of the northern part of the entrance. Evenness showed within habitat variations which were indicative of the numerical dominance of a few species.

Strata IA and IC exhibited relatively high species richness and moderately high evenness (Table 7). The mean evenness of stratum IC was higher (0.83) when excluding stations IC2, IC4 and IC6, which had a low evenness value. Stations IC2 and IC6 were dominated by the capitellid polychaetes Mediomastus ambiseta and Amastigos caperatus, and station IC4 was dominated by the polychaetes Tharyx setigera and Spiophanes bombyx. These three stations were grouped separately from the other stations of the stratum in numerical classification (figure 6).

Strata MA, MB and OA had the lowest richness in the study area and moderately high evenness. Station MA2 was an exception, exhibiting low evenness (0.37). This is because of the dominance of two polychaetes that reached high densities in this station: Amastigos caperatus and the hesionid Microphthalmus sczelkowii. The later, an active, interstitial species, was abundant only at this station (2,120 indiv./m^2), which was

Table 7. Margalef's species richness and Pielou's evenness for each stratum and some distinct stations. Values are means except for individual stations.

STRATA	STATIONS	SR	J'
IA		5.21	0.69
	IB1	4.64	0.78
	IB5	3.01	0.38
	IB8	3.01	0.63
	IB9	5.28	0.87
IC		4.96	0.74
ID		5.63	0.56
MA		3.48	0.66
MB		3.97	0.77
MC		5.09	0.65
	MC1	3.85	0.40
	MC9	3.77	0.52
OA		4.08	0.62
	OA2,4,8,9	2.67	0.45
	OA1,3,5,6,7	5.22	0.74
OB		5.66	0.77
OC		5.01	0.64
	OC1,7,8,9		0.79
	OC2,3,4,5,6		0.52

characterized by poorly sorted sands. Stratum OA encompassed two groups of stations in terms of species richness and evenness (Table 7).

Stations of strata OB, OC and MC exhibited, as an average, high richness and moderately high evenness, but some stations were dominated by a few species and had lower evenness values. Stations of stratum ID had highest richness and relatively low evenness.

Test of Hypothesis

Results from the classification analysis showed variability between strata abundance and distribution of species by forming some clusters of stations belonging to different strata. Therefore, it was considered meaningless to test the hypothesis (i.e., that communities in the study area are similar with regard to water depth and sediment type) among strata. Instead, the hypothesis of community similarity was tested among the groups of stations defined in numerical classification.

Pooled abundances of every species for each of the three groups were computed. The most representative species (i.e., abundant and characteristic species of any group) were used in the hypothesis testing. Species that exhibited high differences in abundance among groups, indicating a clear preference for a particular habitat, were not included in the test (for example: Mediomastus ambiseta, Ampelisca verrilli, Corophium tuberculatum, Acanthohaustorius intermedius, Bathyporeia parkeri and Protohaustorius wigleyi). For the remaining species, a Krustal-Wallis test was used to test whether the three groups

were from the same population. For species of similar abundance between Groups 2 and 3 stations, a Mann-Whitney U test was used.

Table 8 contains species abundances per m^2 in each group and the results of the tests. Species marked with an asterisk were significantly different ($\alpha = 0.05$) among groups. Most species showed significant differences. Considering these results and those of numerical classification, ordination and discriminant analysis, the hypothesis was rejected. The study area showed differences in community composition and abundance.

Table 8. Average species abundance per m^2 for each of the three groups defined in numerical classification. X^2 - Chi-square associated with the Krustal-Wallis test between the three groups, corrected for ties. Z - Standard normal deviate corrected for ties associated with the Mann-Whitney U test between groups 2 and 3. For the species tested, an asterisk indicates significant difference ($p < 0.05$); NS = not significant.

SPECIES	GROUP ONE	GROUP TWO	GROUP THREE	X^2	Z	
Anthozoa	0.5	23.2	24.7		-1.11	NS
Stylochus sp.	0	0	6.0			
Rynchocoela	46.8	65.0	98.7			
Polygordius sp.	40.5	10.0	28.3	0.87		NS
Sthenelais boa	0	0.9	2.7			
Bhawania goodei	0	0	6.3			
Phyllodoce arenae	1.6	1.8	10.0	12.10		*
Microphthalmus sczelkowii	112.1	1.8	3.3			
Sigambra tentaculata	0	0.5	2.3			
Sigambra bassi	0.5	1.8	1.7			
Nephtys bucera	43.2	13.2	2.0	35.40	-3.71	*,*
Nephtys picta	8.4	53.2	29.7	24.98	-2.36	*,*
Glycera americana	0	3.6	3.3			
Glycera dibranchiata	8.9	29.1	124.3	38.33		*
Glycinde solitaria	0	0	13.3			
Heteromastus filiformis	0	0	8.7			
Notomastus hemipodus	0.5	1.8	2.7			
Mediomastus ambiseta	3.7	14.1	1449.7			
Amastigos caperatus	330.0	356.8	1108.7	13.46		*
Clymenella torquata	0	0	2.3			
Euclymene zonalis	0	0.5	8.0			
Aricidea wassi	21.1	55.9	3.3	16.53		*
Aricidea cerrutii	3.7	2.7	3.3	4.69		NS
Aricidea catherinae	0.5	1.4	2.0			
Cirrophorus lyriformis	0	6.4	0			
Poydora ligni	0	2.3	1.7			
Prionospio cirrifera	1.6	0.5	14.0			
Prionospio pygmaea	2.6	60.5	210.0	33.70	-3.59	*,*
Scolecolepides viridis	0	0	2.7			
Scolelepis squamata	0	1.4	1.7			
Scolelepis texana	0	5.5	5.0			
Spio setosa	0	0	1.7			

Table 8. (continued).

SPECIES	GROUP ONE	GROUP TWO	GROUP THREE	X^2	Z	
Spiophanes bombyx	27.4	125.0	247.3	32.13	-2.87	*,*
Dispio uncinata	14.7	0.9	0			
Spiochaetopterus oculatus	0	1.8	0.7			
Diopatra cuprea	0	0	2.7			
Onuphis eremita	1.6	7.7	0.7			
Drilonereis magna	0	6.8	17.3		-1.62	NS
Schistomeringos caeca	4.2	5.0	0.3	4.21		NS
Magelona papillicornis	10.5	8.2	0.3	12.37		*
Magelona filiformis	5.3	25.0	34.7	17.32		*
Scoloplos fragilis	7.4	11.8	2.7	9.30		*
Scoloplos robustus	0	0.9	0.7			
Tharyx setigera	2.1	15.0	238.3		-5.49	*
Caulleriella sp.	29.5	12.3	7.3	11.64		*
Owenia fusiformis	1.1	15.9	17.3		-1.67	NS
Asabellides oculata	0	0	1.7			
Oligochaeta	28.9	9.1	57.7	3.34		NS
Epitonium multistriatum	2.6	31.4	3.7		-2.01	*
Epitonium angulatum	0.5	0.9	0.7			
Crepidula sp. (juveniles)	3.2	3.6	23.7	1.82		NS
Polinices duplicatus	5.8	4.5	7.3	0.86		NS
Nassarius trivittatus	0	3.6	9.0		-1.78	NS
Mangelia cerina	0	0	1.3			
Acteon punctostriatus	0	6.8	5.3			
Cylichnella bidentata	1.6	39.1	15.0	10.75	-1.42	*,NS
Acteocina canaliculata	1.1	31.8	47.3	18.07	-0.19	*,NS
Odostomia sp.	0	4.5	8.3			
Turbonilla interrupta	18.4	4.5	30.7	6.24		*
Nucula proxima	0	0	3.3			
Parvilucina multilineata	0	1.8	1.7			
Mysella bidentata	1.1	7.3	19.3	8.26		*
Tellina agilis	27.4	151.8	258.7	40.46		*
Ensis directus	0	27.3	59.0		-1.92	NS
Spisula solidissima	9.5	0.5	0			
Mulinia lateralis	0	0	6.7			
Ostracoda	0	3.2	6.3			
Neomysis americana	1.1	2.3	0.7			
Mysidopsis bigelowi	2.1	6.8	12.0	4.96		NS
Mancocuma stellifera	5.3	5.9	1.0	5.07		NS

Table 8. (concluded).

SPECIES	GROUP ONE	GROUP TWO	GROUP THREE	X^2	Z	
Oxyurostilis smithi	3.2	10.9	6.7	7.13		*
Campylaspis rubicunda	1.6	1.4	0			
Leptognatha caeca	5.8	0	0			
Edotea montosa	0	2.7	7.0			
Ancinus depresus	2.1	0.5	0.3			
Ampelisca verrilli	0	0	26.3			
Corophium tuberculatum	1.1	0.5	50.0			
Erichthonius brasiliensis	0	0	6.3			
Unciola irrorata	0.5	0.5	3.0			
Acanthohaustorius intermedius	32.6	0.5	3.0			
Bathyporeia parkeri	20.0	0	0			
Protohaustorius wigleyi	343.2	25.5	0.7			
Pseudohaustorius caroliniensis	0	7.3	1.7			
Listriella barnardi	0	9.5	31.0		-2.61	*
Listriella clymenellae	0	0	3.7			
Synchelidium americanum	22.1	32.7	8.0	13.10		*
Rhepoxynius epistomus	0	58.2	39.3		-2.73	*
Hyperia galba	2.1	2.3	0.3			
Ogyrides alphaerostris	0	2.3	4.3			
Euceramus praelongus	0	0	2.3			
Pagurus longicarpus	1.6	3.2	4.0			
Pinnixa sayana	0	6.4	23.3		-2.70	*
Echiurida	0	0	2.7			
Phoronis sp.	0	0	5.0			
Mellita quinquiesperforata	17.9	1.8	0.3			
Leptosynapta tenuis	1.1	5.0	2.0			
Branchiostoma sp.	0	0.9	2.0			

DISCUSSION

Physical Environment

Results of the present study suggest that species were related primarily to sediment composition although the dynamic properties of the sediments were also important. This is not surprising because, as stated earlier, sediment type has been shown to structure macrobenthic communities in many studies. What is interesting is that small changes in the grain size, especially in the relative percentages of medium, fine and very fine sands (sensu Wentworth, 1922), brought about changes in species composition and abundance.

Selection of an optimum substrate by some macrobenthic organisms may be a response to their feeding needs. Some species select sediment particles for feeding according to the grain size (Whitlatch, 1974; Clements and Stancyk, 1984), particle specific gravity and surface texture (Self and Jumars, 1978), and the nutritional value of the organic coating (Fenchel et al., 1975; Whitlatch, 1981; Taghon, 1982). Sediment selection may be related to the optimal grain size chosen for tube building (Busch and Loveland, 1975; Whitlatch and Weinberg, 1982). Sediment grain size also plays an important role in that some species avoid fine particles that will clog respiratory and filtering structures

(Webb and Hill, 1958). Ultimately, sediment grain size is a "super parameter" (Jansson, 1967) reflecting the degree of movement of the overlying water and controlling physical properties such as porosity and permeability (Crisp and Williams, 1971). Infaunal abundance and distribution have been related to both porosity and permeability (Rhoads, 1974) of the sediments.

Discriminant analysis of physical parameters (table 1) indicated that the stations of Group 3, as defined by numerical classification, were related to increasing percentage of very fine sands. The presence of some species was correlated with very fine sands and small amounts of silt and clay, which suggests that this sedimentary environment may be the most suitable habitat. Stations of Groups 1 and 2 were related to increasing percentage of fine sands. The importance of fine sands in habitat partitioning has also been reported in other studies (Bierbaum, 1979; Schaffner and Boesch, 1982). Groups 1 and 2 were not very well separated in the discriminant space (figure 14). Group 1, however, was very distinct in the ordination space (figure 9). The reason for this resides in the dynamic nature of the sediments of most Group 1 stations. Sediment mobility is a factor more difficult to measure, but important in excluding sedentary species or species not well adapted to an environment of shifting sands. This environmental factor was not included *per se* in the discriminant analysis. Thus, there was more overlap between the stations of Groups 1 and 2 than between these and Group 3 stations.

Both, percent silt-clay and water depth were less important

variables in discriminating between groups. The silt and clay content of the sediments sampled was low, but those stations exhibiting a higher proportion of finer sediment particles were restricted to Group 3, except station MA7.

Three major benthic habitats could be recognized in the study area. The first habitat, found in the northern part of the entrance to the Chesapeake Bay, was characterized by well-sorted, dynamic fine sands probably exposed to the action of waves and tidal currents. Another habitat was characterized by somewhat less dynamic, fine and very fine grained, sands. Several groups of stations including those of Nine Foot Shoal and The Tail of the Horseshoe, are of this habitat type. The third habitat was characterized, in general, by a higher proportion of very fine sands with varying low amounts (less than 14%) of silt-clay, reflecting a depositional environment. The later was constituted by stations mostly located in the deep channel of the southern part of the bay entrance and along Virginia Beach (figure 7).

These habitats seem to reflect the tidal circulation patterns in the study area. The northern part of the bay entrance, particularly the areas designated in this study as Outer A, Middle A and Middle B, is dynamic, characterized by flood and ebb-directed sediment transport (Ludwick, 1973). The southern part, particularly Thimble Shoal Channel, around Cape Henry and along Virginia Beach, is under the influence of surface ebb currents transporting fine sediment and organic particles from the bay. There was not a relationship between the biological data and the main current of water along the channel near Cape Henry, as

measured by Boicourt (1981). This is a mid-water "jet", and probably does not affect the benthos. In this area, only stations MC8 and, to a lesser degree, MC4 contained some species characteristic of mobile substrates (Bathyporeia parkeri, Acanthohaustorius intermedius, Spisula solidissima, Mellita quinquiesperforata and Schistomeringos caeca).

Spatial Distribution and Community Structure

Most of the macrobenthic species at the entrance to the Chesapeake Bay were not restricted to a particular habitat but showed a high degree of overlapping in their distributions. This was more in accordance with the concept of communities distributed as a near-continuum responding to environmental gradients (Mills, 1969) than with the tight concept of communities as units of characterizing species (Thorson, 1957). Nevertheless, three assemblages of species could be recognized, although it must be emphasized that their limits were not strict. These assemblages (or communities, using the classical term) were associated with the described habitats: high energy fine sands, less dynamic fine and very fine sands, and depositional, very fine sands and silt-clay.

The dominant species of the high energy, clean, fine sand assemblage (Group 1 stations, figure 7) were the haustoriid amphipod Protohaustorius wigleyi and the capitellid polychaete Amastigos caperatus. The later was an eurytopic species and was significantly more abundant in the very fine sand and silt-clay assemblage. The polychaete Nephtys bucera was significantly more abundant in the

high energy, fine sand assemblage. Characteristic species of this assemblage were the haustoriid amphipods Acanthohaustorius intermedius and Bathyporeia parkeri, the bivalve Spisula solidissima, the spionid polychaete Dispio uncinata and the echinoderm Mellita quinquiesperforata. All these species were related to fine and medium sands with low amounts (less than 11%) of very fine sands.

Haustoriid amphipods have been reported in many studies as dominants in mobile, clean, sandy substrates of shoals, sand bars and sand beaches (Howard and Dorjes, 1972; Kinner et al., 1974; Maurer et al., 1976; Dorjes, 1977; Maurer and Aprill, 1979; Maurer et al., 1979a; Tourtellotte and Dauer, 1983; Weston, 1983). These amphipods have pereopods adapted for burrowing in unstable sandy substrates (Bousfield, 1973). Protohaustorius wigleyi was associated with well-sorted, fine sands in this study, except station OA3 which was poorly sorted. Maurer et al. (1978) found P. wigleyi to be the dominant species in the fine to medium sands of shoals at the mouth of the Delaware Bay. Haustoriids were also distributed in fine sands at Barnstable Harbor, but decreased rapidly in number as the sediment became coarser (Sameoto, 1969). It is possible that these amphipods require sediment particles of the grain size range appropriate for their feeding habits and mechanisms. The subtidal genera, such as Protohaustorius, feed on microorganisms and organic particles (Bousfield, 1970). The restriction to clean sands may be explained by the greater permeability of this sediment type, which brings oxygen to the infauna.

The surf clam, Spisula solidissima, commonly inhabits substrates exposed to turbulent waters (Ropes, 1980). It has also been reported in other benthic studies as characteristic species of mobile, sandy environments (Brett, 1963). In the present study, the S. solidissima collected were juveniles and occured in very low densities, but they were restricted to the high energy, fine sand assemblage. The high fidelity of Dispio uncinata to the fine sand habitat may be explained by the dual feeding behaviour observed in some spionid polychaetes as they respond to water velocity, switching from deposit to suspension feeding (Taghon et al., 1980; Dauer et al., 1981). D. uncinata probably is well adapted to a suspension feeding mode, more efficient in collecting suspended matter from the water currents. On the other hand, the restriction of the species to this habitat may be unrelated to the feeding behaviour, but related to the greater permeability of the substrate. These are only speculations since, unlike other spionid polychaetes (Dauer et al. 1981; Dauer 1983, 1985), the ecology of Dispio uncinata has not been studied.

Mellita quinquiesperforata, a species of oceanic influence, was also characteristic of the high energy, fine sand habitat. Ghiold (1979) found that 3 ϕ was the optimum grain size for M. quinquiesperforata for burrowing. Ghiold's detailed microstructural and functional study of the test spines of sand dollars, showed different types of spines highly specialized for food particle selection and burrowing. When live Mellita were placed in different sand fractions (0-4 ϕ), very fine sand and silt particles were entrapped by mucus at the base of the spines, rendering the spines inmobile. He suggested

that the lack of movement from the spines probably leads to non-burial of the animal, and the accumulation of fine sediment prevents passage of dissolved oxygen and food particles, eventually causing its death. In coarse sands, Mellita was unable to burrow due to the difficulty for test margin spines in moving coarse particles. Recent studies revealed that this echinoid selectively feeds on microeucaryotes and bacteria, which obtains from a very small fraction of the total sediment in which it feeds (Findlay and White, 1983).

Dominant species of the less dynamic, fine and very fine sand habitat (Group 2 stations, figure 7) were the capitellid polychaete Amastigos caperatus and the bivalve Tellina agilis. The spionid polychaete Spiophanes bombyx also reached high densities in this habitat. These species were, again, eurytopic throughout the study area though significantly more abundant in the very fine sand and silt-clay habitat. An assemblage was recognized in terms of characteristic species. These species were the paraonid polychaete Aricidea wassi, the amphipod Synchelidium americanum and the gastropod Epitonium multistriatum. A. wassi has been commonly collected in the continental shelf macrobenthos (Boesch, 1979; Weston, 1983; Dauer et al., 1984), but, unlike other species of the family Paraonidae, it has not been reported in estuaries. A. wassi is a polyhaline species and probably, as generally recognized for the family, a motile, burrowing subsurface deposit feeder (Fauchald and Jumars, 1979). Synchelidium americanum was distributed preferentially in the northern part of the bay entrance. Bousfield (1973) cites the species as a burrower of fine sands in

semiprotected subtidal beaches. In the present study, S. americanum was collected more often in less dynamic, fine sands.

Of the four other species (Scoloplos fragilis, Cyrrophorus lyriformis, Onuphis eremita and Pseudohaustorius caroliniensis) characteristic of the less dynamic, fine and very fine sand assemblage, the orbiniid polychaete Scoloplos fragilis had a wider distribution in clean, sandy sediments. This is surprising, since orbiniids are common in muddy areas (Fauchald and Jumars, 1979). S. fragilis, a burrowing deposit feeder, was one of the few species collected exclusively in muddy areas in Hampton Roads (Boesch, 1973; figure 1). Ewing and Dauer (1982) also found S. fragilis inhabiting fine silt-clay sediments. Although not abundant, this species preferred clean, fine and very fine sands at the bay entrance.

The top six most abundant species (table 3) were dominants of the depositional, very fine sand assemblage (Group 3 stations, figure 7). This assemblage contained numerous species known of very fine sands and silt-clay substrates; many of them were sessile and motile surface deposit feeders.

Capitellid polychaetes are common opportunistic organisms often abundant in stressed environments (Grassle and Grassle, 1974). Mediomastus ambiseta is a nonselective, subsurface deposit feeder. It has been reported in the lower Chesapeake Bay in high densities at muddy-sand sediments (Ewing and Dauer, 1982; Tourtellote and Dauer, 1983). Amastigos caperatus is a newly described species (Ewing and

Dauer, 1981), only reported recently as dominant of the continental shelf macrobenthos (Dauer et al., 1984). In the present study, A. caperatus was found to be more of a generalist, present in all types of habitats. Conversely, M. ambiseta was highly faithful to the very fine sand and silt-clay habitat.

Spiophanes bombyx, one of the two spionid polychaetes (the other is Prionospio pygmaea) abundant in the very fine sand and silt-clay assemblage, has been found to characterize sand assemblages throughout the lower Chesapeake Bay (Boesch, 1973, 1977b; Ewing and Dauer, 1982; Mayne et al., 1982) and adjacent offshore area (Dauer et al., 1984). In the Chesapeake Bay entrance, S. bombyx was present in the three habitats. This is probably because of its ability to feed on suspended as well as on deposited particles. Likewise, this dual feeding mechanism may explain why the bivalve Tellina agilis was also distributed throughout a wide sediment range. Maurer (1967) and Trevallion (1971) have found different species of Tellina occasionaly suspension feeding from the water column.

Several epifaunal species were often found at stations where entire and large pieces of shell and large tubes of annelid polychaetes were present (particularly stations OC3, OC5, OC8, MC5 and ID2). Shelly bottoms provide microhabitats that serve as a refuge for numerous epifaunal and infaunal macroinvertebrates. Dauer, Tourtellote and Ewing (1982) used different densities of artificial clumps of oysters and glass tubes to investigate the effects of spatial refuges upon the benthic community in the lower Chesapeake Bay. They found a significant

increase in number and density of macrofaunal species in the treatment area. This effect was largely due to refuge from predation and to increased habitat heterogeneity. The effect of tubes of polychaetes in creating microhabitats for epifaunal species has also been documented in other studies (Woodin, 1978; Maurer et al., 1979b; Haines and Maurer, 1980). In Delaware Bay, Haines and Maurer (1980) found the polichaetes Sabellaria vulgaris, Polydora ligni and Polycirrus eximius, and the amphipods Unciola serrata and Corophium simile associated with calcareous tubes of the serpulid polychaete Hydroides dianthus. Tube aggregations provided environmental stability and crevices and burrows which served as refuges for some of their associated species. In the present study, the amphipods Corophium tuberculatum, Erichthonius brasiliensis and Unciola serrata, were almost exclusively associated with tubes of the polychaete Diopatra cuprea. These amphipods construct tubes of detritus under the shell fragments and other materials used by the polychaete in its tube building.

Other species collected in the very fine sand and silt-clay assemblage are known to be commensals in polychaete tubes. The amphipod Listriella barnardi is referred to as a commensal species in tubes of Amphitrite ornata and other marine polychaetes; Listriella clymenellae is commensal in tubes of Clymenella torquata (Bousfield, 1973). The decapod Pinnixa sayana has been found free in the water column, in mud and in tubes of Arenicola cristata (Williams, 1965). In the present study, only L. clymenellae was associated with the presence of the maldanid polychaete Euclymene zonalis in the samples. No apparent

association was found between L. barnardi, P. cf sayana and tubicolous polychaetes.

The presence of the phoxocephalid amphipod Rhepoxynius epistomus, a common sand dweller, has been reported in well-sorted, dynamic sands (Maurer et al., 1976; Weston, 1983). R. epistomus was found in fine and very fine sands at the bay entrance, but it was absent from the most dynamic areas.

The higher species richness in the southern part of the entrance relative to the northern part, is partially an indication of greater spatial heterogeneity provided by shells, pebbles, plant material, and tubes of polychaetes, anemones and phoronids. In addition, a more depositional environment, far from the rigorous conditions of shifting sands, allows more species to coexist. More feeding guilds were represented in this environment, with an increased number of deposit feeders. In general, species richness showed spatial variability among and within strata (table 7), suggesting that small scale changes in habitat complexity may have a profound impact in community structure. Most variability in evenness between stations was due to the dominance of a few species of wide distribution. This is in agreement with Boesch's (1973) findings for Hampton Roads macrobenthos, in that numerically dominant species were ubiquitous with respect to sediment type.

No salinity data was recorded in the present study, but some possible generalizations can be made. Changes in salinity represent an

increasing stress up the estuary, but towards the mouth of the bay, sediment type probably becomes more important in structuring macrobenthic communities. This is born out by the results of the present study and those by Boesch (1973), Ewing and Dauer (1982) and Tourtellotte and Dauer (1983). Euryhaline marine species are common and abundant in the lower portions of estuaries. These species tend to decrease in importance along the estuarine coenocline, and are substituted by euryhaline opportunists in lower salinity zones (Boesch, 1977b).

Comparisons With Other Macrobenthic Studies

Boesch (1973) conducted a survey of macrobenthos in the Hampton Roads area and the adjacent Elizabeth River (figure 1). Classification of sites and species for February, May and August 1969 resulted in four associations: mud, muddy-sand, sand and Elizabeth River stations.

Three of the species collected in his sand association were relatively common of the bay mouth macrobenthos: Tellina agilis, Glycera dibranchiata and Spiophanes bombyx. The amphipod Ampelisca verrilli was abundant in Boesch's sand association and, like the other three species, it had increased abundance and constancy at August sites. This increase was attributed to mid-summer recruitment, probably from populations at the bay mouth. In the present study, A. verrilli was not particularly abundant. Relative abundance of some species may show seasonal patterns at the Chesapeake Bay entrance. The objective of the

present study, however, is a spatial comparison of communities throughout the entrance, with no attempt to look at seasonal patterns. Most of Boesch's species were either not collected at the bay mouth or were represented by few individuals. Dominant species of the Hampton Roads sand substrate (Heteromastus filiformis, Polydora ligni, Unciola irrorata, Ensis directus and Acteocina canaliculata) exhibited very low abundances at the bay mouth, with the exception of A. canaliculata. Species of Boesch's muddy sand substrate (Spiochaetopterus oculatus, Paraprionospio pinnata and Phoronis architecta) were rare at the bay mouth. This is largely a problem of scale; Boesch's study encompassed more sediment types, with a greater percentage and influence of the silt-clay fraction. Many of the macrobenthic species of Hampton Roads area are common of muddy and muddy-sand sediments throughout the lower Chesapeake Bay. Instead, macrobenthic communities at the bay entrance were represented by many characteristic species of clean, dynamic sands and of oceanic influence. Boesch's study area is also exposed to greater temperature and salinity ranges, and it is influenced by dredging activities, and municipal and industrial pollution.

Species richness (SR) values for Boesch's sand stations were higher than those of the present study. This may be due to the higher percentage of silt-clay in Boesch's sand stations, and/or to station replication. Richness values in Boesch's study were calculated from three replicates. In the present study, richness was calculated for every station, not for within stratum replicates.

Mayne et al. (1982) sampled the macrobenthos of Crumps and Willoughby Banks on May 1980 and November 1981, Little Creek on October 1980, and Horseshoe Bank on April 1981 (figure 1) to asses the impact that sand extraction operations may have on macrobenthic communities. Both Willoughby Bank and Horseshoe Bank were areas of similar sedimentology to Chesapeake Bay entrance. Willoughby Bank contained medium sands with silt-clay not exceeding in 2%. Horseshoe Bank was characterized by fine to very fine sands with less than 7% silt-clay, except for one station. The areas were classified as of high and moderate wave exposure, respectively.

Numerically dominant species at Horseshoe Bank were Spiophanes bombyx, Phoronis psammophila, Tellina agilis, Craniella sp., Trichophoxus (= Rhepoxynius) epistomus, Ophelia bicornis, Gemma gemma, Acteocina canaliculata and Acanthohaustorius intermedius. With the exception of Craniella sp., O. bicornis and G. gemma, these species were collected at the bay entrance; some of them were abundant (table 3).

The venerid bivalve Gemma gemma was the dominant and most ubiquitous species at the crest of Willoughby Bank. This small bivalve is commonly associated to shoals exposed to wave action, where it has been reported to reach high densities (Sanders et. al., 1962; Ewing and Dauer, 1982). G. gemma, however, was not collected at the bay entrance. This absence may be partialy related to predation of some amphipods on juveniles bivalves (Orth, 1977). G. gemma is ovoviviparous; females brood the young releasing them throughout the summer. The spat, with no pelagic stage, settle near the parent at the sediment-water interface

(Sellmer, 1967). Amphipods may ingest the juveniles as they are swept by the currents created by the amphipod feeding appendages. This effect has been observed in the amphipod Ampelisca macrocephala held in laboratory conditions; Mytilus larvae, copepods and Artemia salina were ingested by the amphipod (Kanneworff, 1965). Segerstråle (1957) found that populations of the tellinid bivalve Macoma inconspicua in the Baltic sea were not present where the amphipod Pontoporeia affinis was abundant. He suggested that Macoma may ingest the larvae as they sink to the bottom. Areas of shifting sands at the Chesapeake Bay entrance contained high densities of the haustoriid amphipod Protohaustorius wigleyi, which may be related with the absence of Gemma gemma. Predation by polychaetes, nemerteans, holothurians and decapods (Sanders et al., 1962), intraspecific competition between juveniles and adults, and salinity (Weinberg, 1985) are also potential factors controlling G. gemma population densities.

Species richness (SR) and evenness (J') were calculated from nine 0.04 m^2 grabs per station, sieved through a 1 mm mesh screen, at Horseshoe Bank, and from one 0.1 m^2 grab per station at Willoughby Bar. Richness and evenness values (Range, SR: 1.97-4.40; J': 0.49-0.73) were lower than those at the bay mouth, but comparably similar to the values of most dynamic areas (table 7). In their study, low evenness was also indication of the dominance of a few species.

Dauer et. al. (1984) sampled the lower Chesapeake Bay on two bay-wide transects one time, and the inner continental shelf at four sites five times per year, from 1979 through 1981 (figure 1). Sampling

consisted of five 0.04 m^2 grabs per station, sieved through a 0.5 mm mesh screen. The two top ranked dominant species of their clean sand sites were not abundant (Mulinia lateralis) or not collected (Streblospio benedicti) at the bay mouth. Other abundant species in Dauer et. al. clean sites were also relatively abundant (Tellina agilis, Spiophanes bombyx, Glycera dibranchiata) or dominants (Mediomastus ambiseta, Amastigos caperatus) at the bay mouth. M. ambiseta was ranked second dominant in their silt-sand sites.

Mean species richness (SR: 4.32) and evenness (J′: 0.55) for their clean sand sites were comparably similar to the values of the most dynamic areas at the bay entrance. Their values for the silty-sand sites (SR: 5.61; J′: 0.65) were also similar to the values of the southern portion of the entrance (table 7).

Dauer et. al. density dominants for the inner shelf stations were: Spiophanes bombyx, Polygordius sp., Nephtys picta, Tellina agilis, Ampelisca verrilli, Aricidea wassi, Apropionospio (=Prionospio) pygmaea, Magelona sp., Spio setosa and Aricidea catherinae. All these species were present at the Chesapeake Bay entrance and some of them were collected in high densities (table 3). Mean richness (SR: 6.22) for all inner shelf sites was higher than any of the values in the present study. Their mean evenness (J′: 0.69) at these sites, was somewhat lower than the evenness at the bay entrance (table 7). The higher richness in their inner shelf stations was related to the collection of epifaunal species on shells and to the presence of a rich interstitial fauna among the coarsest sands.

The macrobenthos of Cherrystone Inlet, Old Plantation Creek and adjacent bay areas (figure 1) was sampled by Ewing and Dauer (1982). The top rank dominants of their offshore sand sites were Spiophanes bombyx, Tellina agilis and Acteocina canaliculata. These species were common in the present study. Their nearshore shoal sites exhibited high densities of the bivalve Gemma gemma. Paraonis fulgens, Spiophanes bombyx and Tellina agilis were also dominants at these sites.

Mean species richness (SR: 4.92) at the offshore sites, based on four 0.05 m^2 grabs per station sieved through a 0.5 mm mesh screen, were similar to the values of stations of moderately dynamic sands at the bay mouth (strata IA and IC in table 7); evenness (J′: 0.61) at the offshore sites was lower. For their nearshore shoal sites, mean richness and evenness (SR: 3.08; J′: 0.38) were lower than the values of the most dynamic areas at Chesapeake Bay entrance (strata MA and OA in table 7). This difference may be explained by the overwhelming densities of the bivalve Gemma gemma (6,400 indv./m^2) in Ewing and Dauer's study.

Kinner et al. (1974) sampled quarterly from December 1971 through June 1972 an area located near the mouth of Delaware Bay. Sampling consisted of 277 0.1 m^2 grabs sieved through a 1.0 mm mesh screen. The three most abundant species were the bivalves Tellina agilis, Gemma gemma and Nucula proxima. T. agilis and the amphipod Ampelisca verrilli were transitional between sand and mud, although greatest densities of T. agilis were recorded in sediments with 0-25% silt-clay. G. gemma and the amphipods Protohaustorius wigleyi and Trichophoxus (= Rhepoxynius)

epistomus exhibited high densities in their sand bottom assemblage (0-10% silt-clay). N. proxima and the polychaete Heteromastus filiformis were dominants of their soft bottom assemblage (50% silt-clay). These results are similar to those of the present study in that P. wigleyi and R. epistomus were also abundant in clean, fine sands at the Chesapeake Bay entrance, and T. agilis had a broader distribution in all type of sediments sampled (< 20% silt-clay). Similarly, N. proxima and A. verrilli were collected in the depositional assemblage at the Chesapeake Bay entrance. Dominants in the present study, however, were capitellid polychaetes, while molluscs were dominant in Kinner et al. study. This may be related to the sreen size (1.0 mm) used in their study, which would not retain small polychaetes such as capitellids.

Similarly to the findings of the present study, diversity at the mouth of Delaware Bay was greater in low silt-clay sediments, and a few macrobenthic species were dominants.

Remarkably similar to the high energy, fine sand assemblage of the present study was the clean fine sand assemblage defined by Maurer et al. (1979b) near Delaware Bay mouth. Characteristic species of Maurer et al. assemblage were the haustoriid amphipods Parahaustorius longimerus, Protohaustorius wigleyi, Acanthohaustorius millsi and Bathyporeia parkeri, and the polychaetes Nephtys bucera and Dispio uncinata. With the exception of P. longimerus and A. millsi (the later substituted by A. intermedius in the present study), these species were also found in fine sands at Chesapeake Bay entrance.

CONCLUSIONS

1. Macrobenthos at Chesapeake Bay entrance was correlated with fine and very fine sands. Sediment dynamics caused by tidal currents or wave action seemed to be as important in determining the type of infauna.

2. Three major assemblages of species related to sediment type were recognized: a clean, high energy, fine sand assemblage; a less dynamic, fine and very fine sand assemblage; a depositional, very fine sand assemblage with varying low amounts of silt-clay.

3. The macroinvertebrates of Chesapeake Bay entrance showed spatial distribution patterns across the entrance. This distribution is considered to be reflective of the tidal circulation patterns of the study area.

4. Species richness was lower in dynamic areas than in depositional ones. Evenness variability was related to the numerical dominance of a few species.

5. Some of the density dominant species were eurytopic with respect to sediment type and significantly more abundant in the depositional assemblage.

6. Deposit feeders constituted the largest trophic group of macroinvertebrates. Most of the species of clean, high energy sands were deposit feeders or carnivores. The presence of deposit feeders in this environment may be related to the dual feeding behavior suggested in the literature for some species.

7. Future benthic research at Chesapeake Bay entrance should be conducted towards determining the seasonal aspects of macrobenthos.

APPENDIX I. List of macrobenthic invertebrates collected at the Chesapeake Bay entrance.

PHYLUM PORIFERA
  PORIFERA

PHYLUM CNIDARIA
  HYDROZOA
  CLAVA
  HYDRACTINIA ECHINATA
  HALECIUM GRACILE
  CAMPANULARIIDAE
  OBELIA
  LOVENELLA GRACILIS
  SERTULARIIDAE
  SERTULARIA
  SERTULARIA ARGENTEA
  SCHIZOTRICHA TENELLA
  CAMPANULINA
  ANTHOZOA HEXACORALLIA
  ASTRANGIA DANAE

PHYLUM PLATYHELMINTHES
  TURBELLARIA POLYCLADIDA
  STYLOCHUS
  STYLOCHUS ELLIPTICUS

PHYLUM NEMERTINA
  RHYNCHOCOELA
  TETRASTEMMA
  TETRASTEMMA VERMICULUS

PHYLUM ANNELIDA
  POLYCHAETA
  POLYGORDIUS
  POLYNOIDAE
  HARMOTHOE
  HARMOTHOE EXTENUATA
  STHENELAIS
  STHENELAIS BOA
  STHENELAIS LIMICOLA
  SIGALION ARENICOLA
  BHAWANIA GOODEI
  PHYLLODOCIDAE
  ETEONE LACTEA
  ETEONE HETEROPODA
  PHYLLODOCE
  PHYLLODOCE ARENAE
  PHYLLODOCE GROENLANDICA
  EULALIA SANGUINEA
  HESIONIDAE
  GYPTIS VITTATA
  GYPTIS BREVIPALPA
  PODARKE OBSCURA
  MICROPHTHALMUS
  MICROPHTHALMUS SCZELKOWII

PILARGIDAE
CABIRA
SIGAMBRA
SIGAMBRA TENTACULATA
SIGAMBRA BASSI
SYLLIDAE
BRANIA WELLFLEETENSIS
NEREIS
NEREIS FALSA
NEPHTYIDAE
AGLAOPHAMUS VERRILLI
NEPHTYS
NEPHTYS BUCERA
NEPHTYS PICTA
GLYCERA
GLYCERA AMERICANA
GLYCERA DIBRANCHIATA
HEMIPODUS ROSEUS
GLYCINDE
GLYCINDE SOLITARIA
TRAVISIA CARNEA
CAPITELLIDAE
CAPITELLA CAPITATA
HETEROMASTUS FILIFORMIS
NOTOMASTUS LATERICEUS
NOTOMASTUS HEMIPODUS
MEDIOMASTUS AMBISETA
AMASTIGOS CAPERATUS
MALDANIDAE
CLYMENELLA TORQUATA
EUCLYMENE ZONALIS
ASYCHIS CAROLINAE
PARAONIDAE
ARICIDEA
ARICIDEA WASSI
ARICIDEA CERRUTII
ARICIDEA CATHERINAE
PARAONIS FULGENS
AEDICIRA
CIRROPHORUS LYRIFORMIS
SPIONIDAE
POLYDORA
POLYDORA LIGNI
POLYDORA SOCIALIS
POLYDORA SP. A
PRIONOSPIO
PRIONOSPIO CIRRIFERA
PRIONOSPIO PYGMAEA
PARAPRIONOSPIO PINNATA
SCOLECOLEPIDES VIRIDIS
SCOLELEPIS
SCOLELEPIS SQUAMATA
SCOLELEPIS cf TEXANA

SPIO SETOSA
SPIOPHANES BOMBYX
DISPIO UNCINATA
SPIOCHAETOPTERUS
SPIOCHAETOPTERUS OCULATUS
SABELLARIA VULGARIS
ONUPHIDAE
DIOPATRA CUPREA
ONUPHIS EREMITA
DRILONEREIS
DRILONEREIS MAGNA
DRILONEREIS SP. A
DORVILLEIDAE
SCHISTOMERINGOS CAECA
AMPHINOMIDAE
MAGELONA
MAGELONA PAPILLICORNIS
MAGELONA FILIFORMIS
ORBINIIDAE
ORBINIA
ORBINIA ORNATA
ORBINIA RISERI
SCOLOPLOS
SCOLOPLOS FRAGILIS
SCOLOPLOS ROBUSTUS
HAPLOSCOLOPLOS cf ACUTUS
CIRRATULIDAE
THARYX SETIGERA
CAULLERIELLA
CHAETOZONE
OWENIIDAE
OWENIA FUSIFORMIS
CISTENA GOULDII
AMPHARETIDAE
ASABELLIDES OCULATA
TEREBELLIDAE
LOIMIA MEDUSA
PISTA PALMATA
POLYCIRRUS EXIMIUS
AMAEANA TRILOBATA
FLABELLIGERIDAE
PHERUSA cf AFFINIS
SABELLIDAE
OLIGOCHAETA

PHYLUM MOLLUSCA
GASTROPODA
TEINOSTOMA
EPITONIUM
EPITONIUM MULTISTRIATUM
EPITONIUM RUPICOLUM
EPITONIUM ANGULATUM
CREPIDULA

CREPIDULA FORNICATA
POLINICES
POLINICES DUPLICATUS
MITRELLA LUNATA
ANACHIS
NASSARIUS TRIVITTATUS
MANGELIA CERINA
MELANELLA INTERMEDIA
ACTEONIDAE
ACTEON PUNCTOSTRIATUS
CYLICHNELLA BIDENTATA
ACTEOCINA CANALICULATA
PYRAMIDELLIDAE
ODOSTOMIA
ODOSTOMIA SP. 1
SAYELLA
SAYELLA FUSCA
TURBONILLA
TURBONILLA INTERRUPTA
TURBONILLA STRICTA
PELECYPODA
NUCULA PROXIMA
YOLDIA LIMATULA
ANADARA TRANSVERSA
ANADARA OVALIS
PARVILUCINA MULTILINEATA
MYSELLA BIDENTATA
MERCENARIA MERCENARIA
PITAR MORRHUANA
TELLINA AGILIS
DONAX VARIABILIS
SOLENIDAE
ENSIS DIRECTUS
SPISULA SOLIDISSIMA
MULINIA LATERALIS

PHYLUM ARTHROPODA
PYCNOGONIDA
CALLIPALLENE BREVIROSTRIS
OSTRACODA
CIRRIPEDIA
BALANUS
MYSIDACEA
NEOMYSIS AMERICANA
MYSIDOPSIS BIGELOWI
GASTROSACCUS DISSIMILIS
CUMACEA
MANCOCUMA STELLIFERA
LEUCON AMERICANUS
OXYUROSTYLIS SMITHI
CAMPYLASPIS cf RUBICUNDA
TANAIDACEA
LEPTOGNATHA CAECA

ISOPODA
EDOTEA MONTOSA
ANTHURIDAE
ANCINUS DEPRESSUS
AMPHIPODA
AMPELISCA
AMPELISCA ABDITA
AMPELISCA VERRILLI
BATEA CATHARINENSIS
COROPHIIDAE
COROPHIUM
COROPHIUM ACHERUSICUM
COROPHIUM TUBERCULATUM
COROPHIUM VOLUTATOR
ERICHTHONIUS BRASILIENSIS
UNCIOLA
UNCIOLA IRRORATA
UNCIOLA SERRATA
HAUSTORIIDAE
ACANTHOHAUSTORIUS INTERMEDIUS
BATHYPOREIA
BATHYPOREIA PARKERI
PROTOHAUSTORIUS
PROTOHAUSTORIUS WIGLEYI
PSEUDOHAUSTORIUS CAROLINIENSIS
LISTRIELLA BARNARDI
LISTRIELLA CLYMENELLAE
OEDICEROTIDAE
SYNCHELIDIUM AMERICANUM
PARAPHOXUS SPINOSUS
PHEPOXYNIUS EPISTOMUS
STENOTHOE MINUTA
HYPERIIDAE
HYPERIA GALBA
CAPRELLIDAE
DECAPODA
OGYRIDES ALPHAEROSTRIS (=LIMICOLA)
CRANGON SEPTEMSPINOSA
CALLIANASSA ATLANTICA
EUCERAMUS PRAELONGUS
PAGURIDAE
PAGURUS
PAGURUS LONGICARPUS
OVALIPES OCELLATUS
XANTHIDAE
NEOPANOPE TEXANA SAYI
DISSODACTYLUS MELLITAE
PINNIXA
PINNIXA CHAETOPTERANA
PINNIXA SAYANA
MAJIDAE

PHYLUM SIPUNCULA
  SIPUNCULA

PHYLUM ECHIURA
  ECHIURA
  THALLASEMA

PHYLUM PHORONIDA
  PHORONIS

PHYLUM ECTOPROCTA
  ECTOPROCTA

PHYLUM ECHINODERMATA
  ASTEROIDEA
  ECHINOIDEA
  MELLITA QUINQUIESPERFORATA
  OPHIUROIDEA
  MICROPHOLIS ATRA
  HOLOTHUROIDEA
  LEPTOSYNAPTA TENUIS

PHYLUM HEMICHORDATA
  ENTEROPNEUSTA
  SACCOGLOSSUS KOWALEWSKII

PHYLUM CHORDATA
SUBPHYLUM CEPHALOCHORDATA
  BRANCHIOSTOMA

SUBPHYLUM VERTEBRATA
  CONGRIDAE

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