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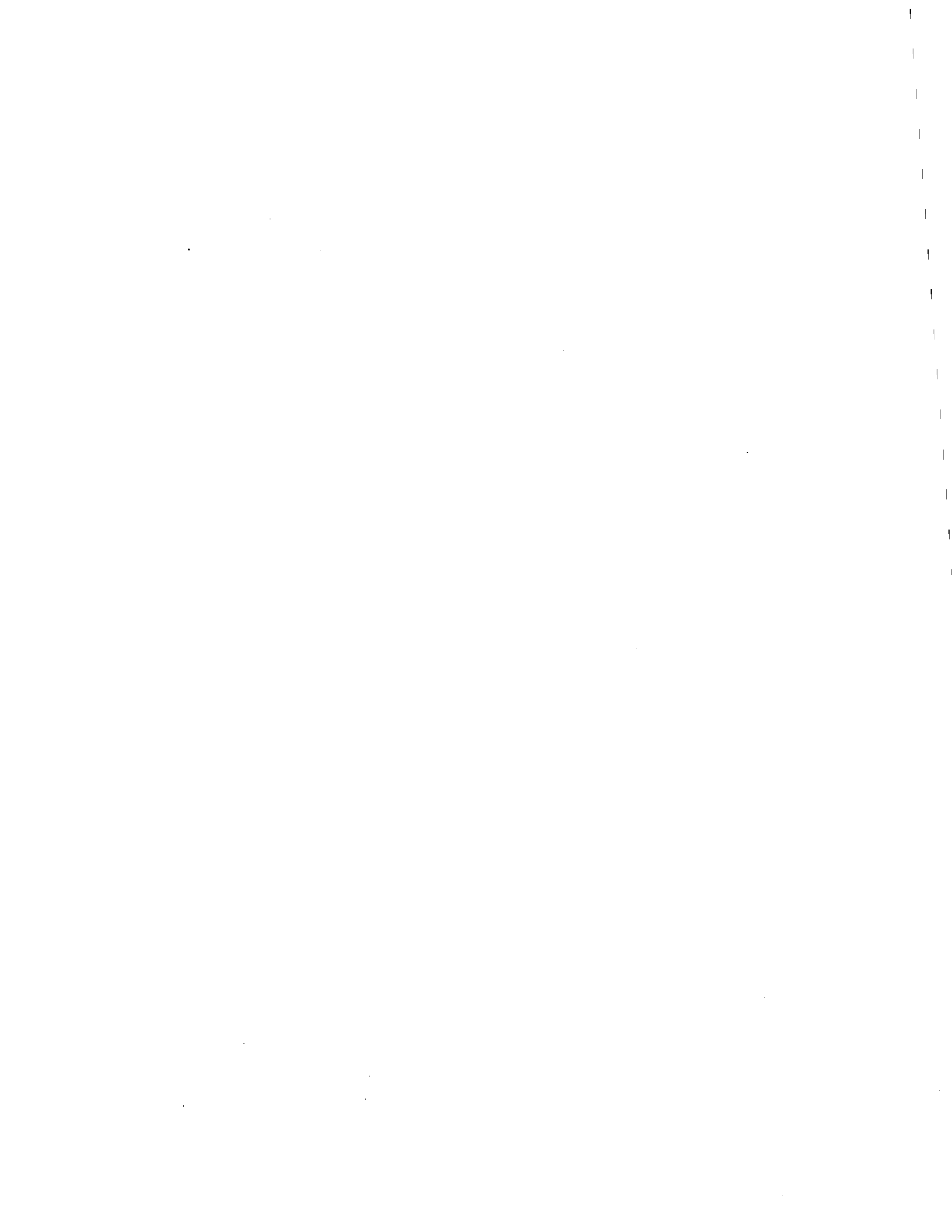
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BENTHIC POLYCHAETA

OF THE MIDDLE ATLANTIC BIGHT:

FEEDING AND DISTRIBUTION

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia
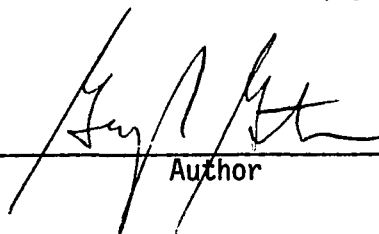
In Partial Fulfillment

Of the Requirements for the Degree of

Doctor of Philosophy

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by

Gary R. Gaston

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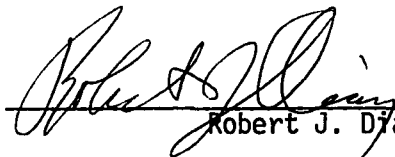
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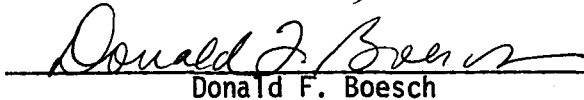
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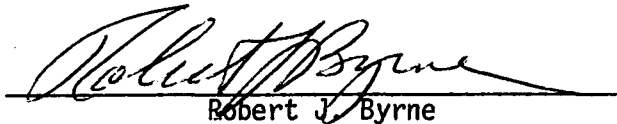
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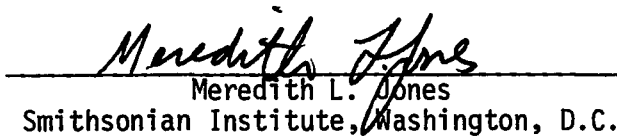
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ABSTRACT

Patterns in the distribution of feeding-biology categories of polychaetous annelids were used to characterize benthic habitats of the Middle Atlantic Bight. Feeding biology classifications were based on recent publications regarding polychaete feeding and on gut-contents analyses of polychaetes collected in the study area. Proportion of carnivorous polychaetes was greatest in coarser sediments, and decreased significantly with depth across the continental shelf. Surface deposit feeders numerically dominated most habitats. Abundance of surface deposit feeders decreased across the continental shelf and sharply increased at the shelf break, paralleling the pattern of water-column production. Proportion of subsurface deposit feeders was greatest in fine-sediment habitats, and increased significantly with depth and percent organic carbon across the continental shelf. Sessile polychaetes generally inhabited physically stable habitats of the study area. Proportion of sessile polychaetes was positively correlated with percent silt and clay and percent organic carbon. Feeding-morphology categories were generally less closely related to habitat differences than were feeding or motility categories. These results suggest that the diverse assemblages of polychaetes that inhabit topographic depressions of the Middle Atlantic Bight may be dependent on stability of sediment parameters. Furthermore, distribution and abundance of surface deposit feeders may depend on food resources from water-column production, and distribution of sessile polychaetes may be limited by physical disturbance.

BENTHIC POLYCHAETA OF THE MIDDLE ATLANTIC BIGHT:

FEEDING AND DISTRIBUTION

INTRODUCTION

It has been known for many years that there is a relationship between changes in benthic habitats and changes in benthic communities. As sediments grade between habitats, shifts often occur in the relative abundance and composition of the benthic taxa which inhabit them. Recently, interest has centered around shifts in dominance of feeding groups between habitats (e.g. Rhoads 1974, Jumars and Fauchald 1977, Woodin 1978, Fauchald and Jumars 1979, Whitlatch 1981, Maurer and Leathem 1981). These studies provide insight into energy flow through the community and a better understanding of the contribution of benthic communities to the ecosystem.

Maurer and Leathem (1981) investigated distribution of polychaete feeding guilds from Georges Bank, off New England. They applied the polychaete feeding biology categories established by Jumars and Fauchald (1977) to a data set, and examined relationships between combined feeding biology classes ("guilds") and environmental variables. They found significant relationships between certain guilds and depth, fine-grained sediment, and sediment nutrition.

One of the shortcomings of use of the Jumars and Fauchald (1977) classification scheme has been the general lack of data on polychaete feeding. Fauchald and Jumars (1979) reviewed the literature on polychaete feeding. They concluded that many of those data were based on casual observations and speculation, and that before benthic communities could truly be understood more extensive data on feeding were

needed. They hypothesized feeding modes for all polychaete families, but cautioned that a number of families lacked supportive data.

The purpose of the present investigation was to examine the relationship between Middle Atlantic Bight polychaete feeding biology and environmental variables. The relationship was examined by assigning each polychaete species a feeding biology classification, and then comparing the proportions of each class with physical and biological parameters of the area. The categories used were those of Jumars and Fauchald (1977). Included were three parameters of feeding biology: polychaete feeding; feeding motility; and feeding morphology. Before the polychaetes were classified all species which lacked conclusive data on feeding were dissected for gut content analyses. Included were some of the most species-rich and abundant families of polychaetes (e.g. Onuphidae, Nereidae, Goniadidae, Lumbrineridae). Many of these analyses led to changes in classifications from those hypothesized by Fauchald and Jumars (1979), and used by Maurer and Leathem (1981).

In this study it was expected that changes would occur in the proportional contribution of each polychaete feeding component with changes in available food resources. The first hypothesis was that the proportion of the three polychaete detritivore components (suspension feeders, surface deposit feeders, and subsurface deposit feeders) varied between habitats. To test this hypothesis the relative proportion of each component was compared between habitats of the continental shelf and slope described in terms of environmental parameters (e.g. sediment grain size, organic carbon).

A second hypothesis posed was that the distribution of sessile polychaetes was related to water depth and covariates of depth (e.g. sediment grain size). Jumars and Fauchald (1977) have shown a positive correlation between water depth and proportion of sessile polychaetes off Southern California. They postulated that the correlation was actually due to increased sediment stability with depth. To test this, data collected in outer-shelf ridge fields of the Middle Atlantic Bight were included in the present investigation. Thus, proportion of sessile polychaetes was compared among habitats of comparable depth, but variable sediment stability. It was expected that sessile polychaetes would be associated with finer-sediment habitats.

A third hypothesis concerned the relationship of carnivorous polychaetes to sediment characteristics. Boesch (1979a) reported a trend toward dominance of carnivorous species in coarser sediments of the Middle Atlantic Bight. The a priori hypothesis of this study, therefore, was that proportion of carnivorous polychaetes was related to proportion of coarse sediments. To test this hypothesis, distribution of carnivorous polychaetes was compared with sediment grain size and other sediment parameters.

The proportions of several polychaete morphology classes were examined by habitat. It was expected that soft proboscis polychaetes would be in greatest abundance in finer sediments and areas of high organic carbon, since the majority were expected to deposit feed. Jawed polychaetes were expected to dominate coarse sediment habitats as Maurer and Leathem (1981) demonstrated. The hypothesis tested, there-

fore, was that proportions of the polychaete morphological components were associated with sediment parameters.

Background: Biological Environment

Collections of Middle Atlantic Bight macrobenthos have continued for many years, although few of the resulting data were published in the formal literature. Sampling throughout the area was conducted during the Woods Hole Oceanographic Institution -- U.S. Geological Survey Continental Margins Program (Emery and Schlee 1963, Wigley et al. 1976, Wigley and Theroux 1981). These collections led to the first extensive survey of abundance and biomass of macrobenthos in the study area (Wigley and Theroux 1976). Studies by Pratt (1973) included a classification scheme of 3 depth-related faunal zones. These zones were based on presumed sedimentary regimes in the Middle Atlantic Bight. Recent investigations of the Middle Atlantic Bight conducted by the Virginia Institute of Marine Science under contract with the Bureau of Land Management (Boesch et al. 1977, Boesch 1979a) were the most extensive biological and chemical studies to date of the area, and provided the data base for this investigation. The BLM data showed complex patterns related to depth-induced changes and habitat complexity.

The importance of interaction between surface deposit feeders, tube dwellers, and burrowers has been well established (Rhoads and Young 1970, Woodin 1974, 1976, 1978, Rhoads 1974, Brenchley 1979, Tsuchiya and Kurihara 1980). Only recently have investigators begun to

interrelate distribution of benthic species with medium and small scale geological features. Biernbaum (1979) investigated the influence of sedimentary factors on medium scale distribution of Amphipoda. Eckman (1979) investigated small scale distribution patterns associated with sedimentary patterns in Puget Sound. Yingst and Rhoads (1980) and Aller (1978, 1980) studied small scale interactions of species relative to tube dwelling and burrowing, and the enhancement of bacterial growth and concentration of microbes that resulted from such interactions (Yingst and Aller 1982).

Background: Physical Environment

The geological and physical oceanography of the Middle Atlantic Bight continental shelf has been extensively investigated in recent years (e.g. Emery and Uchupi 1972, Milliman 1973, Swift 1976, Freeland and Swift 1978, Butman and Noble 1979, Butman et al. 1979, Welch and Ruzecki 1979, Fischer 1980). The Middle Atlantic Bight is approximately 100 km long, and encompasses a shelf about 100-150 km wide. Until the last decade most of what was known of circulation in the area was inferred from drift bottle and seabed drifter studies. Today these data are supplemented by continuous monitoring data from data buoys, daily satellite imagery, and over flights that help establish monthly surface temperature contour maps. The circulation may be generally characterized as having a mean flow of 5-10 cm s^{-1} to the southwest, paralleling the shoreline (Beardsley et al. 1976). Deep ocean currents periodically provide additional forcing near the shelf break

(Schmitz 1974), and estuarine waters lead to a density-driven cross-shelf flow (Gordon et al. 1976).

The geological processes of the Middle Atlantic Bight have received intense attention over the past decade. The Middle Atlantic shelf is a broad platform (120-160 km wide) extending from Cape Cod to Cape Hatteras. The zone of shelf break is incised by numerous submarine canyons (Figure 1). The sediments of the Middle Atlantic Bight are generally sands or gravelly sands which accumulated during Holocene transgression, and today compose a surficial sheet of sand 0-30 m thick (Swift et al. 1972). These relict sands rest on a nearly flat surface of early Holocent or Pleistocene lagoonal and nearshore deposits (Freeland and Swift 1975, 1978, Stubblefield et al. 1975, Knebel and Spiker 1977). The relict sands of the Middle Atlantic Bight have been variously modified (Figure 2) into terraces and scarps which are remnants of sea-level still stands (Freeland and Swift 1978), shoal retreat massifs resulting from withdrawal of nearshore or estuarine depositional center (Swift et al. 1972), antecedent stream systems and ridge and swale topography. Though ridge and swale topography is small in scale by comparison to canyons or estuarine systems in the Middle Atlantic Bight, these topographic features are widely distributed and locally very important in distribution of macrobenthos (Boesch 1979a). Ridges of these systems are generally spaced about 2 km apart, are 2 to 10 m high, and about 9 to 56 km long (Freeland and Swift 1978).

In general, the Middle Atlantic shelf sediments contain over 90% sand. This composition is the result of rapid Holocene transgression

Figure 1. Bathymetry of the New York Bight (Uchupi 1970).

75°   74°   73°   72°   71°

41°

LONG   ISLAND   SOUND

Montauk Point

Block Island

LONG   ISLAND

New York

Sandy Hook

40°

Atlantic City

Cape May

39°

75°   74°   73°   72°   71°

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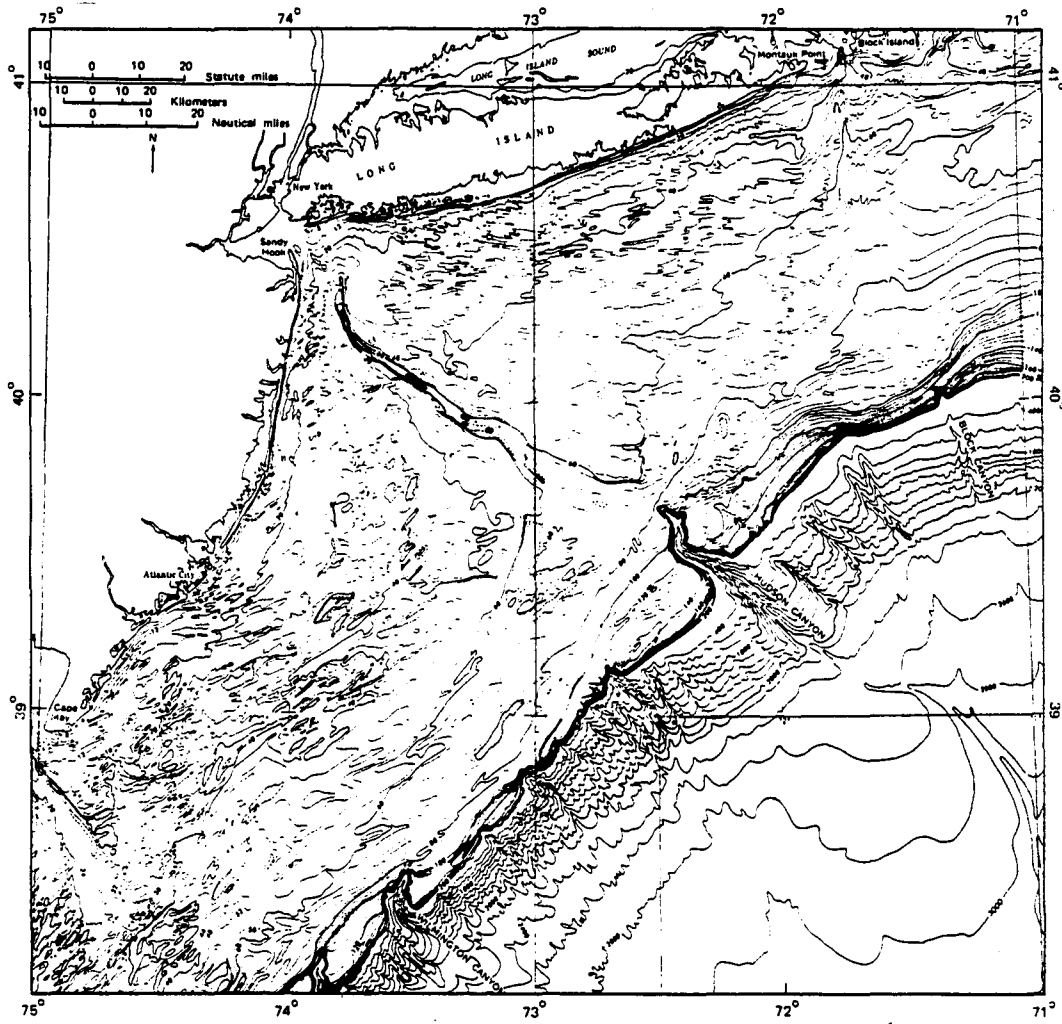
Figure 2. Topographic features of the Middle Atlantic Bight
           (Swift et al. 1972).
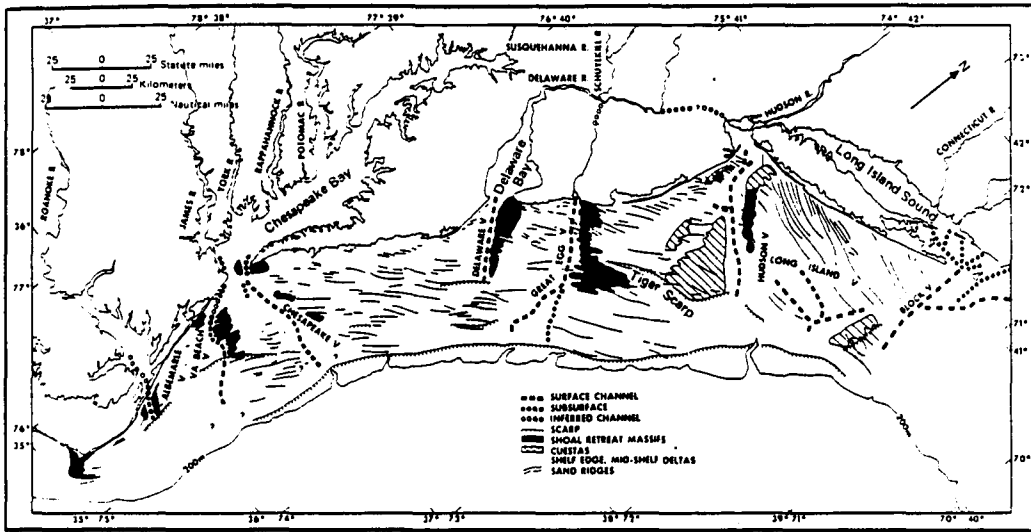
and limited input of modern detrital sediment (Freeland and Swift 1978). The most notable exceptions to this generalization are the fine sediments of the upper Hudson Canyon and topographic depressions associated with the aforementioned features, especially ridge and swale topography and antecedent stream systems (e.g. Hudson Shelf Valley). Even these are periodically scoured by storm-generated currents.

There is a steep gradient of sediments on the upper continental slope from shelf sands to clayey-silts. The shelf break is generally at about 140 m depth, but varies from 80 to 160 m (Freeland and Swift 1978). Off New Jersey the break is at about 120 m where silt-clay is 5% to 10%. Sediments at 400 m (e.g. station H1, Figure 3) contain approximately 30% silt-clay. At 600 m silt-clay content exceeds 90% (Boesch 1979b).

The locations of sampling sites selected for the BLM Middle Atlantic Study and used in this investigation are noteworthy. Stations were generally positioned to sample a range of habitats, with special emphasis on outer shelf petroleum and natural gas lease tract areas. Stations north and south of these areas were positioned to avoid obvious major topographic features, and should not be interpreted as indicative of areas of less topographic complexity.

Little was known of the feeding biology of Middle Atlantic poly-chaetes prior to the analyses of this investigation. Similarly, knowledge of the surficial geology of the middle and outer shelf was lacking until recent years. The extensive biological and chemical data collected under the auspices of the Bureau of Land Management (1975-

Figure 3. Sampling sites occupied for macrobenthic sampling
during the BLM Middle Atlantic Benchmark Program.
General topography and approximate depth are
provided.
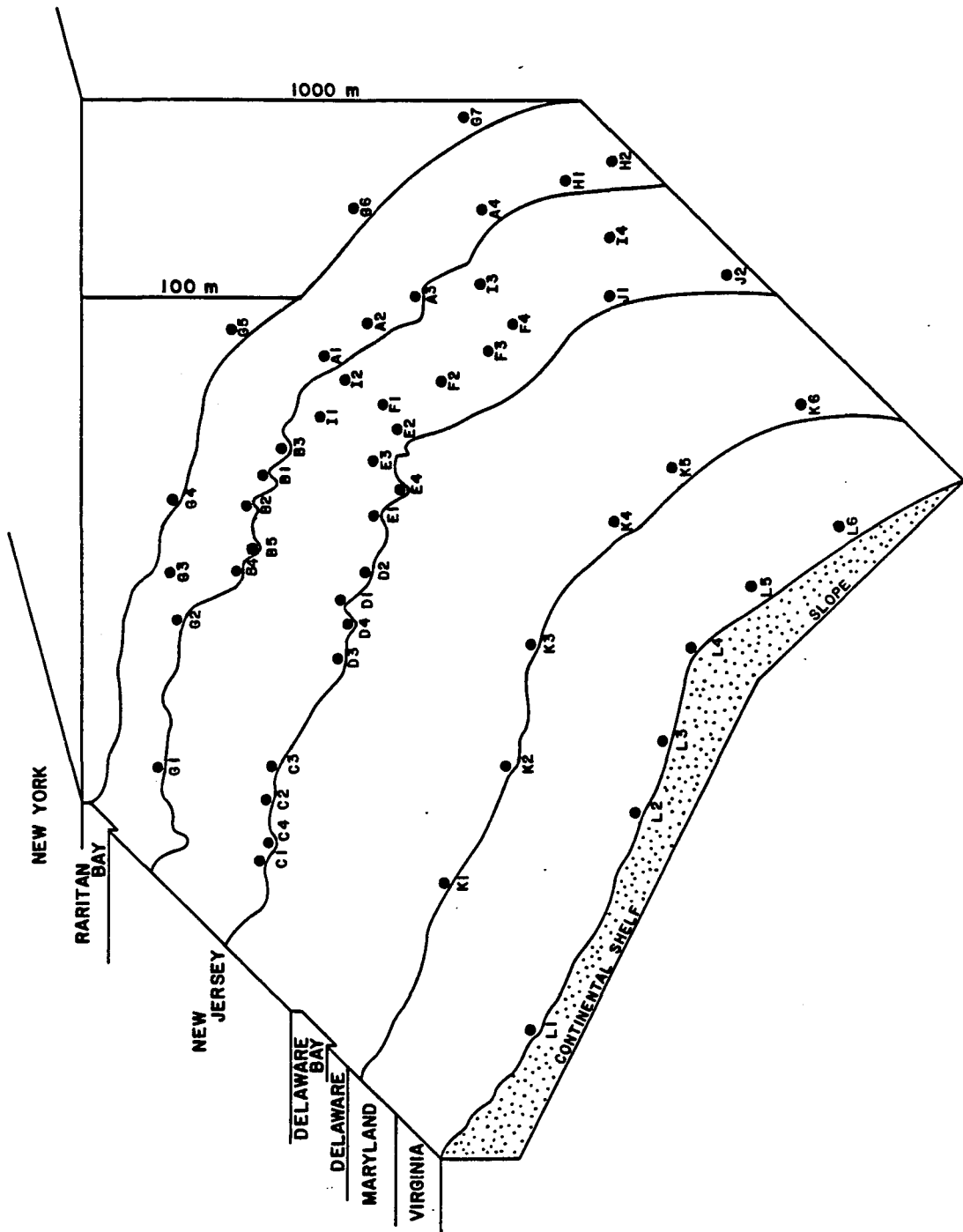
1977) in the Middle Atlantic Bight provided the data necessary to assess patterns in the feeding biology of polychaetes across the Middle Atlantic Bight, and to test the hypotheses posed on distribution of feeding biology parameters.

MATERIALS AND METHODS

All species of polychaetous annelids collected in the Middle Atlantic Bight during the BLM program were included in these analyses. Available literature concerning the three feeding biology parameters (polychaete feeding, motility, morphology), summarized for all major polychaete families by Fauchald and Jumars (1979), were used in this investigation except where characterizations from the present study contradict existing characterizations. In cases where contradictions occur, both characterizations are discussed, but the present characterizations are subsequently used. Data concerning species distribution were taken from the data base of the BLM Middle Atlantic Benchmark Program.

During the two year BLM Middle Atlantic Bight study, a total of 52 stations were repetitively sampled (Figure 3 and Table 1). Table 2 lists these stations, and indicates the number of replicates collected and time of collection. All samples of macrobenthos were collected with a 0.1 m^2 stainless steel Smith-McIntyre grab sampler equipped with a Benthos Edgerton 35 mm camera and flash.

Once onboard ship each sample was emptied into a 5-gallon galvanized bucket and washed with sea water. Light-bodied organisms were thus floated out of the sample and collected on a 0.5 mm mesh Nitex screen below the bucket. The screen was removed when rinsing was completed, placed in a labelled cloth bag, anesthetized in isotonic $MgCl_2$, and killed and fixed with 10% buffered formalin with Rose

Table 1. General sediment characteristics at each station. Grand means (mean of seasonal means) of important parameters are given together with the range of seasonal means in parentheses. From Boesch (1979b).

Station	Depth (m)	Topographic Location	Sediment Description	Median Diameter (Ø)	Sorting Coefficient (Ø)	Percentage Silt & Clay	Organic Carbon (mg/g)
A1	90.4(89-92)	outer shelf	med.-fine sand	1.88(1.4-2.1)	1.05(0.6-2.4)	10.43(6.9-17.9)	2.91(2.0-3.6)
A2	129.3(127-133)	shelf break	silty med.-fine sand	2.24(2.0-2.5)	2.99(2.5-3.4)	25.60(22.5-30.6)	4.31(3.9-4.7)
A3	138.8(135-149)	shelf break	med.-fine sand	1.91(1.8-2.0)	1.99(1.6-2.5)	19.22(15.2-29.9)	3.61(3.2-4.2)
A4	196.3(188-203)	shelf break	med.-fine sand	2.24(2.2-2.4)	1.64(1.4-2.2)	15.37(13.8-17.6)	3.35(2.9-3.7)
B1	63.8(63-65)	flank	medium sand	1.69(1.5-1.9)	0.43(0.4-0.5)	2.48(1.3-4.5)	1.01(0.5-1.2)
B2	60.8(58-62)	ridge	medium sand	1.27(1.1-1.5)	0.74(0.6-1.0)	0.57(0.2-1.4)	0.49(0.3-0.8)
B3	72.4(71-74)	swale	med.-fine sand	2.21(2.0-2.4)	0.65(0.5-0.7)	6.50(5.1-8.2)	2.34(1.9-3.0)
B4	41.0(40-42)	terrace	med.-coarse sand	1.05(0.9-1.3)	0.78(0.5-1.1)	0.12(0.0-0.2)	0.40(0.1-0.8)
B5	65.7(65-66)	flank-swale	medium sand	1.67(1.4-1.9)	0.61(0.4-0.7)	4.02(3.1-5.9)	1.40(1.1-1.9)
C1	15.8(14-17)	ridge	med.-coarse sand	1.18(0.6-2.1)	0.75(0.4-0.9)	0.12(0.1-0.2)	0.36(0.2-1.3)
C2	25.0(21-26)	flank	med.-coarse sand	1.23(1.0-1.5)	0.65(0.4-0.8)	0.32(0.1-0.8)	0.43(0.2-0.6)
C3	24.3(24-25)	flank	med.-coarse sand	0.83(0.9-1.1)	0.90(0.8-1.0)	0.13(0.1-0.2)	0.27(0.1-0.3)
C4	34.2(33-37)	swale	med.-fine sand	2.46(1.6-3.0)	1.20(0.5-2.7)	13.25(0.5-39.3)	2.76(0.8-3.9)
D1	31.7(29-40)	ridge	med.-fine sand	1.99(1.7-2.4)	0.43(0.4-0.5)	0.41(0.0-2.3)	0.46(0.1-1.4)
D2	32.6(32-33)	flank	medium sand	1.41(1.1-1.7)	0.49(0.4-0.6)	0.13(0.1-0.2)	0.42(0.2-0.8)
D3	36.0(34-39)	flank	medium sand	1.57(1.5-1.7)	0.50(0.4-0.6)	0.52(0.1-1.6)	0.29(0.2-0.4)
D4	49.3(48-51)	swale	med.-fine sand	2.25(1.7-2.7)	0.69(0.4-0.9)	5.34(1.7-7.8)	1.54(0.7-2.2)
E1	65.1(61-68)	ridge	medium sand	1.61(1.3-2.0)	0.53(0.4-0.7)	0.54(0.2-2.1)	0.54(0.3-0.9)
E2	72.0(64-76)	flank-swale	med.-fine sand	1.95(1.8-2.2)	0.76(0.5-1.0)	4.94(0.3-10.4)	1.30(0.6-2.3)
E3	63.3(56-66)	flank	medium sand	1.22(1.1-1.3)	0.60(0.5-0.7)	0.60(0.3-1.9)	0.50(0.3-0.9)
E4	78.0(75-80)	swale	shelly-med.-co. sand	1.29(0.5-2.1)	1.07(0.8-1.4)	4.69(3.0-5.9)	1.98(0.8-3.4)

Table 1. continued

Station	Depth (m)	Topographic Location	Sediment Description	Median Diameter (Ø)	Sorting Coefficient (Ø)	Percentage Silt & Clay	Organic Carbon (mg/g)
F1	83.8(79-86)	outer shelf	med.-fine sand	1.92(1.5-2.2)	0.50(0.4-0.7)	1.51(0.6-2.5)	0.81(0.6-1.3)
F2	111.0(103-116)	shelf break	fine sand	2.32(2.2-2.6)	0.41(0.3-0.5)	5.34(4.0-6.6)	1.71(0.8-2.4)
F3	154.0(150-162)	shelf break	med.-fine sand	2.18(2.1-2.4)	0.81(0.8-0.9)	7.34(5.1-9.1)	2.16(0.9-2.6)
F4	185.1(179-206)	shelf break	med.-fine sand	2.33(2.2-2.7)	0.87(0.8-1.0)	9.72(6.8-14.3)	2.75(1.4-3.9)
G1	25.5(24-27)	inner shelf	gravelly coarse sand	0.28(0.2-0.3)	1.09	0.40(0.2-0.6)	0.37(0.3-0.4)
G2	36.4(36-37)	central shelf	medium sand	1.25(0.7-1.8)	0.56(0.5-0.6)	1.80(0.3-5.8)	0.56(0.2-1.1)
G3	72.8(71-74)	shelf valley	shelly med.-fine sand	1.77(1.5-2.1)	1.29(0.8-2.0)	9.52(8.1-12.4)	3.04(2.1-4.1)
G4	55.6(55-56)	outer shelf	med.-coarse sand	1.21(1.0-1.4)	0.71(0.7-0.8)	0.71(0.5-1.1)	0.59(0.3-0.7)
G5	89.3(85-92)	outer shelf	medium sand	1.68(1.5-1.8)	0.82(0.8-0.9)	10.46(8.9-12.2)	2.53(1.4-4.4)
G6	171.5(167-178)	shelf break	med.-fine sand	2.17(2.1-2.2)	1.95(1.7-2.4)	18.10(15.7-21.4)	3.17(2.6-3.9)
G7	330.0(310-350)	upper slope	silty med.-fine sand	3.14(2.9-3.4)	1.78(1.5-2.0)	25.30(21.0-29.6)	2.69
H1	388.8(350-400)	upper slope	silty med.-fine sand	2.77(2.5-3.2)	2.75(2.2-3.0)	28.20(24.4-32.6)	3.71(2.0-4.7)
H2	742.3(720-750)	mid-slope	clayey-silt	7.16(7.1-7.2)	2.05(1.9-2.2)	87.13(84.6-91.3)	6.12(4.9-7.3)
I1	77.8(77-80)	outer shelf	mixed sand	1.51(1.1-2.4)	0.83(0.7-0.9)	4.16(2.3-6.2)	1.70(1.3-2.0)
I2	93.8(93-95)	canyon head	med.-coarse sand	0.76(0.5-1.0)	1.42(1.3-1.5)	4.76(4.2-6.6)	2.39(2.1-2.7)
I3	175.6(170-181)	canyon head	med.-fine sand	2.12(1.8-2.4)	1.11(0.9-1.3)	11.36(8.6-16.3)	3.16(2.2-3.9)
I4	469.8(445-514)	upper slope	sand-silt-clay	4.69(3.8-6.3)	2.91(2.4-3.2)	56.13(46.9-67.9)	6.47(4.9-8.2)
J1	384.4(350-470)	upper slope	silty-fine sand	3.34(3.2-3.4)	2.13(1.7-2.4)	26.67(23.6-30.6)	3.93(2.9-4.6)
J2	736.5(680-760)	mid-slope	clayey-silt	7.37	1.61	94.04(92.3-95.9)	9.63(8.7-10.6)

Table 1. concluded

Station	Depth (m)	Topographic Location	Sediment Description	Median Diameter (∅)	Sorting Coefficient (∅)	Percentage Silt & Clay	Organic Carbon (mg/g)
K1	29.0	inner shelf	med.-coarse sand	1.13(1.1-1.2)	0.71(0.6-0.8)	0.20	1.16(0.6-1.7)
K2	41.3(40-42)	central shelf	medium sand	1.53(1.4-1.6)	0.65(0.6-0.7)	0.65(0.6-0.7)	0.74(0.4-1.5)
K3	53.0	outer shelf	med.-coarse sand	1.17(1.1-1.2)	0.62	0.13(0.1-0.2)	0.28
K4	103.3(102-105)	shelf break	fine sand	2.57(2.3-2.7)	0.58(0.3-0.7)	10.41(8.8-12.7)	3.61(2.9-4.2)
K5	149.5(140-152)	shelf break	med.-fine sand	1.85(1.7-1.9)	1.13(1.0-1.4)	8.08(7.2-8.9)	2.51(1.7-3.3)
K6	361.1(339-370)	upper shelf	fine sand	3.16(2.9-3.3)	2.11(2.0-2.2)	20.78(17.9-24.3)	3.26(2.0-4.0)
L1	25.0(24-26)	inner shelf	fine sand	2.77(2.6-3.0)	0.65(0.5-0.8)	0.83(0.7-0.9)	0.65(0.6-0.7)
L2	43.8(41-48)	central shelf	fine sand	3.10(2.8-3.3)	0.46(0.4-0.6)	1.18(0.7-1.8)	1.33(0.9-1.9)
L3	62.0(58-66)	outer shelf	med.-fine sand	1.87(1.8-1.9)	0.47(0.4-0.5)	0.74(0.3-1.2)	0.47(0.4-0.6)
L4	93.9(90-97)	outer shelf	med.-coarse sand	1.38(1.2-1.6)	0.89(0.8-1.0)	0.86(0.5-1.2)	0.87(0.6-1.3)
L5	177.5(140-200)	shelf break	mixed sand	1.56(1.4-1.7)	1.58(1.4-1.9)	10.19(8.7-13.3)	3.41(2.2-4.3)
L6	353.1(325-380)	upper slope	sand-silt-clay	3.54(3.0-4.4)	3.04(2.8-3.2)	40.71(30.4-53.3)	4.48(2.3-6.0)

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Table 2. Sampling schedule and replication of grab samples taken for macrobenthos.

Station	1975 Fall	1976 Winter	1976 Spring	1976 Summer	1976 Fall	1977 Winter	1977 Spring	1977 Summer
Number of Replicates			**Year 1**				**YEAR 2**	
A1-4, B1-4, C2, C4, D1, D4 E1-4, F1-4	6	6	6	6	6	6	6	6
C1, C3, D2, D3	6	6	6	6				
B5 (Recolon. Study)					6	6	6	6
G2-6, I1-3, K2, K4-6 L2, L4-6		6		6		4		4
H1-2, I4, J1-2		6		6		6		6
G1, K1, K3, L1, L3		6		6				
G7		1		6				

Bengal as a stain. The sediments and heavy organisms which remained in the bucket (heavy fractions) were washed on a 0.5 mm mesh screen sieve, treated as above, and returned to the laboratory with the light fraction. Macrobenthic organisms were removed from the sediment in the laboratory, where all specimens were sorted to major taxa, preserved in ethanol, identified to the lowest practicable level, usually to the species level, and counted.

A special habitat delineation study was conducted during the fall 1976 sampling period. The study was designed to delineate mesoscale patterns of distribution of benthic organisms and demersal fishes in areas B and E, two areas of complex topography. The term "mesoscale" was defined for the habitat delineation study by Boesch (1979a) as encompassing horizontal distances of 10^2 to 10^3 m, a scale which includes major topographic features of the shelf, but not the small transient features such as sand ripples, current lineations, and sand waves. The areas were first stratified, based on existing data. Area B was divided into six habitat strata, and Area E into five (e.g. terraces, ridges, ridge flanks, swales). Single grab samples were then randomly collected within each stratum. Samples were processed by the same methods described above; no attempt was made to replicate the samples.

Polychaete specimens to be dissected for gut-content analyses in this study were stored in 70% ethanol until dissections began. Length and width for all specimens were measured. The widest portion of the anterior body, usually around setiger 5, was measured. Measurements

were made to the nearest 0.1 millimeter with an ocular micrometer, and where necessary, a hand-held 5.0 mm scale micrometer and 150 mm plastic ruler. All specimens were dissected using a stereomicroscope. Exact methods varied somewhat among species, but all specimens of a given species were handled in the same manner. The large specimens (e.g. Nephtyidae, Phyllodocidae, Glyceridae) were first opened with iris scissors to expose the digestive tract. The entire tract was then removed and placed in a dissecting dish with 70% ethanol. The entire length of the gut was opened with a 0.5 mm or 1.0 mm microknife to expose any ingested material. A record was made of the location of any ingested material in the gut (i.e. pharynx, esophagus, intestine). The material was finally mounted in glycerin and viewed with a compound microscope.

Medium-sized specimens (5.0 to 50 mm) were generally dissected in glycerin on a depression slide. Most specimens were opened with micro-scissors or a microknife and the gut material transferred to glycerin on a second slide. Again, a record was made of where the ingested material was located. In some of the elongate species (e.g. Eunicidae, Onuphidae) the ingested material was located by backlighting specimens over a darkfield stereomicroscope stage, and the setigers of the worm containing the ingested material removed, mounted in glycerin, and the material teased from the gut with a probe. The material was then viewed with a compound microscope. Small species (less than 5.0 mm) were too samll to dissect with a microknife. These species (e.g. Syllidae, Sphaerodoridae) were mounted whole on a slide in glycerin,

examined with a steromicroscope, the intestinal wall pierced with a probe where ingested material was located, and the ingested material squeezed out into the glycerin with a probe.

All material viewed with a compound microscope was classified according to origin. Permanent slides were made of most species. The gut content classification included enumerating and measuring the ingested materials and putting them in one of the following classes: 1) prey or prey parts (e.g. setae, spines); 2) live diatoms; 3) dead diatoms or pieces or frustules; 4) foraminifera; 5) dinoflagellates; 6) coarse quartz or feldspar sand; 7) fine sand; 8) sand masses agglutinated with mucus; 9) detritus (percentage of gut filled); 10) fecal pellets; and 11) other (e.g. calcareous sand, plant material).

Examination of gut material under the compound microscope led to inconclusive results for certain species: Marphysa bellii; Eunice vittata; Onuphis pallidula; Ceratocephale loveni; Schistomeringos caeca. Gut material from selected specimens of these species was viewed with a scanning electron microscope (SEM). The Virginia Institute of Marine Science AMRAY 1000 SEM was used. Gut material was removed from each specimen and placed in a capsule with 12 micron Nucleopore filter ends. Each capsule was immersed for 10 minutes in consecutive treatments of 70%; 80%; 90%; 95%; and 100% ethanol, and then 5 minutes in acetone. The material was dried in a critical-point dryer for 5 minutes, allowed to sit for one hour, then dried for another 5 minutes. Specimens were then mounted on aluminum stubs with DAG paint, and coated with a 200 angstrom-thick coating of gold pal-

ladium in the vacuum evaporator. The same classes of ingested material as above were utilized in analyses of this material.

Each species was classified according to feeding biology (e.g. carnivore, herbivore, detritivore). The classification scheme of Jumars and Fauchald (1977) was used. Each species was characterized by three parameters: feeding mode; motility; and functional morphology. Feeding mode includes five components: 1) surface deposit-feeder; 2) subsurface deposit-feeder; 3) suspension-feeder; 4) carnivore; and 5) herbivore. Motility includes three components: 1) motile; 2) discretely motile; and 3) sessile. "Discretely motile" means that the organism is capable of moving from place to place, but must be sessile to feed. Functional feeding morphology includes: 1) jawed; 2) tentaculate; 3) pumping; 4) soft proboscis. Each polychaete species was classified, and the classification scheme was used to characterize the areas of study.

Some investigators have expressed a concern that specimens anaesthetized with magnesium chloride might regurgitate their gut contents (Fauchald, personal communication). Specimens of Nereis lamellosa, N. succinea, Cossura soyeri, Cirratulus cf. filiformis, Polydora ligni, and Glycinde solitaria were collected near Cameron, Louisiana and maintained in the laboratory to determine influence of magnesium chloride. The specimens were placed in Syracuse watch glasses for observation with a stereomicroscope. Using a dark field background and backlighting it was possible to determine the location of food in the gut. The specimens were then transferred to watch glasses containing iso-

tonic magnesium chloride or to watch glasses with seawater where they could be observed for reaction to the solutions. None of the species reacted violently to the solution. None of them regurgitated any material. After 30 minutes only single specimens of P. ligni and C. cf. filiformis evacuated any significant part of their gut contents, which included only the posterior-most contents, passed as an apparent normal defecation.

Numerical classification (cluster analyses) was performed using the Virginia Institute of Marine Science program COMPAH (Combinatorial Polythetic Agglomerative Hierarchical Program). Log transformation (log X+1) and the Bray-Curtis similarity measure (Bray and Curtis 1957) were employed in the clustering. This similarity measure can be expressed as:

$$S_{jk} = 1 - \frac{\sum\limits_{i=1}^{n} |X_{ji} - X_{ki}|}{\sum\limits_{i=1}^{n} (X_{ji} + X_{ki})}$$

where, in normal clustering, S_{jk} equals the similarity between stations j and k, and X_{ji} and X_{ki} equal the abundance of species i and station j and k respectively. Flexible sorting (Lance and Williams 1967), with beta established at -0.25 was employed.

Statistical analyses in this investigation included determination of correlation coefficients for polychaete feeding biology components

and sediment parameters. The methods used were those of the Pearson

product-moment correlation coefficient (Sokal and Rohlf 1981).

RESULTS

The results are given in three major sections: 1) polychaete feeding modes and gut contents analyses; 2) broad scale distribution patterns of polychaete feeding classes in the Middle Atlantic Bight; 3) medium scale distribution patterns of polychaete feeding classes in Areas B and E. The first section reviews findings of the laboratory and gives literature summaries of polychaete feeding modes. General data on distributions and abundances of polychaetes collected during the BLM Middle Atlantic Bight program are also addressed in this section. These data are summarized in Table 3. Sections two and three are characterizations of habitats based on the feeding classifications of section one. A summary of laboratory analyses are included in Appendix A.

Feeding Classification

The following data result from feeding mode and gut content investigations of polychaetes collected in the Middle Atlantic Bight. Each family is discussed separately, and the study is organized alphabetically by family. Numbers of specimens dissected and a summary of gut contents identified are provided in Appendix A. Families of polychaetes for which extensive literature and substantial credible data on feeding are available (e.g. Chaetopteridae, Serpulidae, Magelonidae) have been omitted from this summary. More extensive literature sum-

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Table 3. Feeding biology classes, distribution, and relative abundance of all species collected. Classifications: surface deposit feeder (S); subsurface deposit feeder (B); suspension feeder (F); carnivore (C); herbivore (H); motile (M); discretely motile (D); sessile (L); tentaculate (T); jawed (J); pumping (P); soft proboscis (X). [absent (0); rare (*); moderately abundant (2); abundant (3); patchy distribution (*)].

	CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Ampharetidae:							
Amage tumida	SLT	0	0	1	1-2	1	0
Ampharete arctica	SLT	1	2	2	1-2	1	0
Amphicteis gunneri	SLT	0	0	1	1	1	0
Amphicteis vesta	SLT	0	0	1	0	0	0
Anobothrus gracilis	SLT	0	2*	0	0	0	0
Asabellides oculata	SLT	3*	1	1	1	0	0
Auchenoplax crinita	SLT	0	0	0	1	2-3	1
Lysippe labiata	SLT	0	0	0	1	0	0
Melinna cristata	SLT	0	0	1-2	1	0	0
Sabellides octocirrata	SLT	0	0	0	0	1	0
Samytha sexcirrata	SLT	0	0	1	1	1	0
Amphictenidae:							
Cistena gouldii	BMX	1	0	0	0	0	0
Cistena hyperborea	BMX	0	0	0	1	0	0
Amphinomidae:							
Paramphinome jeffreysii	CMX	0	0	1	1	3	1-2

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Aphroditidae:						
Aphrodita hastata — CMJ	0	1	1	1	0	0
Laetmonice filicornis — CMJ	0	0	1	0	0	0
Apistobranchidae:						
Apistobranchus tullbergi — SDT	0	0	1	0	0	0
Arabellidae:						
Arabella iricolor — CMJ	1	0	0	0	0	0
Arabella mutans — CMJ	0	1	1	1	0	0
Drilonereis caulleryi — CMJ	0	0	1	1	1	0
Drilonereis longa — CMJ	1	2	2-3	2	1	1
Drilonereis magna — CMJ	1	1-2	1-2	1	1	0
Notocirrus spinifer — CMJ	1	1	0	1	0	0
Capitellidae:						
Branchiocapitella sp. — BMX	0	0	1	1	0	0
Capitella capitata — BMX	0	0	1	0	0	0
Heteromastus cf. filiformis — BMX	0	0	0	0	0	1
Leiocapitella glabra — BMX	0	0	0	1-2	1	0
Mediomastus californiensis — BMX	0	1	1	0	0	0
Mediomastus sp. A — BMX	0	0	0	0	1	0
Notomastus latericeus — BMX	1*	1	3	3	3	1
Notomastus teres — BMX	1	0	0	0	0	0
Notomastus sp. A — BMX	0	0	0	0	0	1

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Chaetopteridae:						
Spiochaetopterus oculatus — FLP	1	1	1	1	0	0
Chrysopetalidae:						
Paleanotus heterosetae — CMX	1	0	0	0	0	0
Cirratulidae:						
Caulleriella sp. — SMT	2*	1-2	3	2	0	0
Chaetozone sp. — SMT	1	1	1	0	1	0
Dodecaceria sp. A — SLT	0	0	0	1	1	0
Tharyx sp. — SMT	1	2-3	3	3	2	2
Cirratulidae sp. A — SMT	0	0	0	0	1	0
Cossuridae:						
Cossura longocirrata — BMX	0	0	1	2-3	2	1
Dorvilleidae:						
Protodorvillea minuta — CMJ	0	0	1	1	1	1
Protodorvillea gaspeensis — CMJ	1	1	1	0	0	0
Protodorvillea kefersteini — CMJ	1	1-2	1-2	1*	1*	0
Schistomeringos caeca — SMJ	1	1	0	1	1	0
Schistomeringos sp. A — SMJ	0	0	0	1	1	0
Eunicidae:						
Eunice antennata — BDJ	0	0	1	1-2	0	0
Eunice norvegica — BDJ	0	0	0	1	0	0

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Eunice pennata — BDJ	0	0	0	1	0	0
Eunice vittata — BDJ	0	0	1	1-2	0	0
Lysidice ninetta — BDJ	0	1	0	0	0	0
Marphysa bellii — BDJ	1	1	1-2	1	1	0
Marphysa sanguinea — BDJ	0	0	1	1	1	0
Nematonereis unicornis — BDJ	0	0	1	0	0	0
Euphrosinidae:						
Euphrosine armadillo — CMX	0	0	1	1	0	0
Fauveliopsidae:						
Fauveliopsis sp. A — SLX	0	0	0	1	1-2	1
Flabelligeridae:						
Brada granosa — SDT	0	0	0	1	1	0
Brada villosa — SDT	0	1	1	1	1-2	1
Pherusa affinis — SDT	1	2-3	1-2	1	0	0
Therochaeta collarifera — SDT	0	0	0	1	1	0
Flabelligeridae sp. A — SDT	0	0	0	1	0	0
Glyceridae:						
Glycera capitata — CDJ	0	2*	1	1	1	1
Glycera dibranchiata — CDJ	1-2	2-3	1-2	1	0	0
Glycera papillosa — CDJ	0	0	0	1	1	1
Glycera robusta — CDJ	0	1-2	1	1	0	0
Glycera sp. A — CDJ	0	1	0	0	0	0

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Glycera sp. B — CDJ	0	0	1	0	0	0
Hemipodus roseus — CDJ	2	2*	1	0	0	0
Goniadidae:						
Goniada brunnea — CDJ	0	1	2-3	1	1	1
Goniada maculata — CDJ	0	0	1	1	1	0
Goniada norvegica — CDJ	0	0	1	0	0	0
Goniada teres — CDJ	0	0	0	1-2	0	0
Goniadella gracilis — CMJ	3	3*	3*	1	0	0
Hesionidae:						
Gyptis sp. A — CMJ	0	0	1	1-2	1	0
Podarke cf. obscura — CMJ	0	0	1	0	0	0
Hesionidae sp. A — CMJ	0	0	0	0	1	0
Lacydoniidae:						
Paralacydonia paradoxa — CMX	0	1	1	1-2	1	0
Lumbrineridae:						
Lumbrinerides acuta — CMJ	3*	3*	3*	1	0	0
Lumbrineris albidentata — CMJ	0	0	1-2	1-2	1	1
Lumbrineris fragilis — BMJ,CMJ	1-2	2	1-2	1	1	1
Lumbrineris impatiens — BMJ	1	3*	3	3*	2	1-2
Lumbrineris latreilli — BMJ	0	1	3*	3	3	1
Lumbrineris cf. tenuis — BMJ	0	0	1-2	1	2-3	2
Ninoe brevipes — BMJ	0	0	0	1	1	0
Ninoe nigripes — BMJ	1	1-2	1	1	1	0

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
SDT						
Magelonidae:						
Magelona sp.						
Maldanidae:						
Asychis biceps — BLX	0	0	0	0	1-2	1
Asychis carolinae — BLX	0	2*	2*	3*	0	0
Axiothella sp. A — BLX	0	1	0	0	0	0
Clymenella torquata — BLX	0	3*	2*	1	0	0
Clymenella sp. A — BLX	1	0	1	1-2	1	0
Clymenura sp. A — BLX	1	3*	3*	1	1	0
Euclymene zonalis — BLX	0	3*	3*	2	1	0
Maldane sp. A — BLX	0	0	0	0	0	0
Praxillella sp. A — BLX	0	1	1	1	1	0
Praxillella gracilis — BLX	0	0	0	0	1	0
Praxillura longissima — SLX	0	0	1	1	1	1
Rhodine loveni — BLX	0	1	1-2*	1	1	0
Nephtyidae:						
Aglaophamus circinata — CMJ	1	2-3	3	2	1	0
Nephtys bucera — CMJ	1-2	2	1	1	0	0
Nephtys caeca — CMJ	0	1	0	0	0	0
Nephtys incisa — CMJ	0	1-2	1	1	1	0
Nephtys picta — CMJ	3*	1	0	0	0	0
Nephtys squamosa — CMJ	0	0	1	1-2	0	0
Nephtys sp. A — CMJ	1	0	0	0	0	0

Table 3. continued

	CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Nereididae:							
Ceratophale loveni	SDJ	0	0	0	1	1	1
Neanthes succinea	SDJ	1	2	1	0	0	0
Nereis grayi	SDJ	1	1-2	3*	1-2	1	0
Nereis zonata	SDJ	0	1-2	1	1	1	0
Onuphidae:							
Diopatra cuprea	HDJ	1	1	0	0	0	0
Diopatra sp. A	HDJ	1	0	0	0	0	0
Hyalinoecia artifex	CMJ	0	0	0	0	2*	1
Nothria conchylega	SMJ	0	0	2*	3*	0	0
Onuphis atlanticum	SDJ	0	1	1	3*	2*	1
Onuphis eremita	SDJ	1	0	0	0	0	0
Onuphis nebulosa	SDJ	0	0	0	1	0	0
Onuphis opalina	SDJ	0	0	0	0	1	0
Onuphis pallidula	SDJ	0	0	3*	3	1	0
Onuphis declivorum	SDJ	0	0	0	0	1	0
Rhamphobrachium sp. A	SDJ	0	0	0	1	0	0
Opheliidae:							
Ophelina denticulata	BMX	1	1-2	1	0	0	0
Ophelina acuminata	BMX	0	1	1-3	1-3	1	1
Ophelina sp. A	BMX	0	0	0	0	0	1
Travisia forbesii	BMX	1	0	0	0	0	0
Travisia parva	BMX	1	0	0	0	0	0
Travisia sp. A	BMX	0	0	0	0	0	1
Opheliidae sp. A	BMX	0	0	0	0	0	1

Table 3. continued

	CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Orbiniidae:							
Orbinia ornata	BMX	0	0	0	1	0	0
Orbinia swani	BMX	1	1	1	1	1	1
Orbinia michaelseni	BMX	0	0	1	1	1	1
Scoloplos acmeceps	BMX	0	1	1-3	1-2	0	0
Scoloplos armiger	BMX	1	1	0	0	0	0
Leitoscoloplos fragilis	BMX	1	1	1	0	0	0
Leitoscoloplos robustus	BMX	1	1-2	0	0	0	0
Leitoscoloplos sp. A	BMX	0	0	0	0	1-2	0
Oweniidae:							
Myriochele heeri	FDT	0	0	1	1	1	1
Myriowenia sp. A	SDT	0	0	1	1	1	1
Owenia fusiformis	FDT,SDT	1	1	0	0	0	0
Paraonidae:							
Aedicira sp. A	SMX	0	1	0	0	0	0
Aricidea catherinae	SMX	1-2	2	2	2-3	1	0
Aricidea cerrutii	SMX	1	3	1	1	1	1
Aricidea quadrilobata	SMX	0	0	0	1	1	1
Aricidea simplex	SMX	0	1	3*	3*	1	1
Aricidea suecica	SMX	0	0	1	1	1	0
Aricidea wassi	SMX	1-2	3	1-3	1	0	0
Cirrophorus lyriformis	SMX	0	1	1-2	1-2	1	1
Levinsenia gracilis	SMX	1	1	1-2	1-2	2-3	1
Paradoneis lyra	SMX	1	1	1	3	1-2	0
Paraonis fulgens	SMX	0	1	1-2	0	0	0

Table 3. continued

	CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Paraonis pygoenigmatica	SMX	0	1	1	0	0	0
Paraonis sp. A	SMX	0	0	1	0	0	0
Paraonis sp. B	SMX	0	0	1	1	0	0
Phyllodocidae:							
Anaitides arenae	CMX	1	1	1	0	0	0
Anaitides longipes	CMX	0	0	1	0	0	0
Anaitides mucosa	CMX	1	1-2	1-2	1	1	0
Anaitides sp. A	CMX	0	0	0	0	0	0
Eteone heteropoda	CMX	1	0	0	0	0	0
Eteone lactea	CMX	0	0	1	1	0	0
Eteone sp. A	CMX	0	1	1	0	0	0
Eteone sp. B	CMX	1-2	1	1-2	1	1	0
Eulalia bilineata	CMX	0	2*	1-2	1	1	0
Eulalia viridis	CMX	0	0	1	0	0	0
Eulalia sp. A	CMX	0	0	1	0	0	0
Eumida sanguinea	CMX	0	0	1	0	0	0
Eumida fusigera	CMX	0	0	0	0	0	0
Hesionura sp. A	CMX	0	0	1	1	1	1
Lugia sp. A	CMX	0	1	1	1	0	0
Notophyllum foliosum	CMX	0	0	1	1	0	0
Paranaitis kosteriensis	CMX	0	1	0	0	0	0
Paranaitis speciosa	CMX	0	1	0	0	0	0
Pilargiidae:							
Ancistrosyllis groenlandica	CMJ	0	0	0	1	1	1
Synelmis albini	CMJ	0	0	0	1	1	1

Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Pisionidae:						
Pisione remota — BMX	1-2	0	0	0	0	0
Poecilochaetidae:						
Poecilochaetus sp. A — SDT	0	0	0	1	1	0
Polygordiidae:						
Polygordius sp. A — SMX	3*	3*	3*	1	1	1
Polynoidae:						
Alentiana aurantiaca — CMJ	0	0	0	0	1	0
Austrolaenilla mollis — CMJ	0	0	1	0	0	0
Harmothoe extenuata — CMJ	1-2	1-3	1-2	1	1	0
Harmothoe imbricata — CMJ	0	0	0	1	0	0
Harmothoe sp. A — CMJ	1	0	0	0	0	0
Questidae:						
Questa sp. A — BMX	0	1	0	0	0	0
Sabellariidae:						
Sabellaria vulgaris — FLT	0	1	0	0	0	0
Sabellidae:						
Chone infudibuliformis — FLT	1	3*	2-3	1-2	1	0
Euchone elegans — FLT	0	1-2	3*	1-2	1	0
Euchone incolor — FLT	0	3*	3*	1-2	1	0
Fabricia sabella — FLT,SDT	0	0	1	1	0	0

Table 3. continued

	CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Jasmineira filiformis	FLT	0	0	0	1	1	0
Megalomma bioculatum	FLT	0	0	0	1	0	0
Myxicola infundibulum	FLT	0	0	1	0	0	0
Potamilla reniformis	FLT	0	0	0	1	1	0
Scalibregmidae:							
Scalibregma inflatum	BMX	1	1-3	3*	1	1	0
Serpulidae:							
Filograna implexa	FLT	0	0	0	1	0	0
Hydroides protulicola	FLT	0	1	1-2	1	0	0
Hydroides sp. A	FLT	0	0	1	0	0	0
Serpulidae sp. A	FLT	0	0	0	1	0	0
Sigalionidae:							
Neoleanira tetragona	CMJ	0	0	0	0	1	1
Pholoe minuta	CMJ	0	1-2	1-2	1	1	1
Sigalion arenicola	CMJ	1-2	1	1	0	0	0
Sthenelais limicola	CMJ	1	1-3	1-2	1-2	0	0
Sphaerodoridae:							
Sphaerodoridium claparedii	SMX	0	0	1	1	0	0
Sphaerodoropsis corrugata	SMX	0	0	0	1	1	0
Sphaerodoropsis minuta	SMX	0	0	1	1	1	0
Sphaerodoridae sp. A	SMX	0	0	0	1	0	0

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Table 3. continued

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Spionidae:						
Laonice cirrata	SDT,FDT	0	1	1-3	1-2	1	0
Malacoceros sp. A	SDT,FDT	0	0	1	1-2	1	0
Polydora caulleryi	SDT,FDT	0	1	1	3*	1	0
Polydora concharum	SDT,FDT	1	1	1-2	1-2	0	0
Polydora socialis	SDT,FDT	0	1	1-2	1	1	0
Prionospio cirrobranchiata	SDT,FDT	0	1	1	1	0	0
Prionospio cristata	SDT,FDT	0	0	0	1	0	0
Prionospio dayi	SDT,FDT	0	1	1-2	1-2	1-2	0
Prionospio steenstrupi	SDT,FDT	0	1-3	1-3	1-3	0	0
Prionospio sp. A	SDT,FDT	1	1-2	0	0	0	0
Scolelepis squamata	SDT,FDT	1	1-2	0	0	0	0
Spio cf. setosa	SDT,FDT	1	1-2	1	1	0	0
Spio pettiboneae	SDT,FDT	0	1	0	1	1	1
Spiophanes bombyx	SDT,FDT	3*	3*	2-3	1	1	0
Spiophanes wigleyi	SDT,FDT	1	1	2-3	2-3	1-2	0
Spiophanes sp. A	SDT,FDT	1	0	0	0	0	0
Sternaspidae:						
Sternaspis scutata	BMX	0	0	0	0	1	0
Syllidae:						
Autolytus alexandri	CMJ	0	0	1	1-2	0	0
Brania wellfleetensis	HMJ,CMJ	0	0	0	1	0	0
Eusyllis lamelligera	CMJ	0	0	1	1	0	0
Eusyllis sp. A	CMJ	0	0	1	0	1	1
Exogone dispar	HMJ,CMJ	0	0	1	1	0	0
Exogone hebes	HMJ,CMJ	1	1-3	2-3	1	0	0

Table 3. concluded

CLASSIFICATION	INNER SHELF	MIDDLE SHELF	OUTER SHELF	SHELF BREAK	UPPER SLOPE	MIDDLE SLOPE
Exogone naidina — HMJ,CMJ	0	0	1-2	1	0	0
Exogone verugera — HMJ,CMJ	1	1-2	2-3	1-3	1	0
Exogone sp. A — HMJ,CMJ	0	0	0	0	1	0
Odontosyllis longiseta — CMJ	0	0	0	1	0	0
Parapionosyllis longicirrata — CMJ	1-2	2	1	1	1	0
Pionosyllis sp. A — CMJ	0	0	0	0	0	0
Proceraea sp. A — CMJ	0	0	1	0	0	0
Sphaerosyllis erinaceus — HMJ,CMJ	1	1	1-2	1-2	1	0
Streptosyllis arenae — CMJ	1	1	1-2	1	1	0
Streptosyllis varians — CMJ	0	1	1	0	0	0
Streptosyllis websteri — CMJ	0	1	0	0	0	0
Syllides convoluta — CMJ	0	1	0	0	0	0
Typosyllis hyalina — CMJ	0	0	1	0	0	0
Typosyllis tegulum — CMJ,SMJ	1	1	1-2	1-2	0	0
Terebellidae:						
Artacama sp. A — SDT	0	0	1	0	1	0
Lysilla alba — SDT	1	1	1	1	0	0
Nicolea venustula — SDT	0	1	1-2	1	0	0
Polycirrus eximius — SDT	0	1-2	1-2	1-2	1	0
Polycirrus phosphoreus — SDT	0	0	1	0	0	0
Streblosoma phosphoreus — SLT	0	1	1-2	1	1	0
Terebella cf. rubra — SLT	0	0	1	0	0	0
Trichobranchidae:						
Terebellides stroemi — SLT	0	0	1-2	1-3	1-2	1

maries, including all major families of Polychaeta, are available in Fauchald and Jumars (1979).

Ampharetidae

Ampharetids are generally considered to be surface deposit feeders that occupy mucus-lined tubes oblique to the surface of the substratum (Yonge 1928, Dales 1963, Day 1967, Fauchald and Jumars 1979). Food is collected by ciliated buccal tentacles. Gut content analyses by Fauvel (1897) and Hessle (1925) indicate that ampharetids primarily ingest detritus. Additionally, Fauchald and Jumars (1979) hypothesized that ampharetids are selective deposit feeders, utilizing deposited material near their tube openings.

A total of 11 species of ampharetids was collected in the Middle Atlantic Bight during the present investigation:

Amage tumida Ehlers, 1887

Ampharete arctica Malmgren, 1886

Amphicteis gunneri (Sars, 1835)

Amphicteis vesta Hartman, 1865

Anobothrus gracilis (Malmgren, 1866)

Asabellides oculata (Webster, 1879)

Auchenoplax crinita Ehlers, 1887

Lysippe labiata Malmgren, 1886

Melinna cristata (Sars, 1851)

Sabellides octocirrata (Sars, 1835)

Samytha sexcirrata (Sars, 1856)

Of these, Ampharete arctica, Melinna cristata, Auchenoplax crinita, and Anobothrus gracilis occurred in moderate abundance in the Middle Atlantic Bight. All other species were rare in occurrence. Each of the more abundant species was dissected for gut content analyses, and each was filled with detritus. Ampharete arctica and Asabellides gracilis both form loosely-packed fecal pellets. The pellets included mostly unidentifiable detritus and numerous small centric diatoms and diatom pieces. Guts of Auchenoplax crinata were filled with detritus including silt and clay particles, some fragments of diatoms, and a few coarse sand grains. M. cristata, like A. crinata, does not form fecal pellets. It apparently ingests sediment. Guts were filled with particles of sediment from medium quartz sand (0.4 mm diameter) to silt and clay. This ingested material included numerous small centric diatoms (usually 10 to 50 μm diameter) and diatom fragments, pieces of dinoflagellates, and an abundance of unidentifiable detritus. Nothing observed in the material ingested by these species indicated any feeding mode other than surface deposit feeding.

Amphinomidae

Amphinomids are usually considered to be mobile carnivores that feed on Anthozoa (Ebbs 1966), sponges and hydroids (Dales 1963), or any of numerous other sessile invertebrates including other species of polychaetes (Day 1967). They lack jaws, but have muscular cushion-like lips possibly used for sucking. Many amphinomids (e.g. Hermodice, Eurythoe) are active browsers in tropical reefs where they seek out

prey. Others (e.g. Paramphinome, Pseudeurythoe) are associated with fine sediments where they may occur at the sediment surface, or in burrows at depth. There is some recent evidence that Eurythoe (Kudenov 1974) and, possibly, Chloeia (Fauchald and Jumars 1979) feed more on carrion than live prey.

Paramphinome jeffreysii (McIntosh 1868) was the only amphinomid collected during this study. It occurred at many outer shelf and shelf-break stations, and in abundance on the continental slope (e.g. stations H1, H2, J1, J2, K6, L6). Gut contents analyses revealed that all specimens dissected had completely empty guts. These data, though inconclusive, are generally considered indicative of a predatory life history wherein animal prey are relatively infrequently consumed and rapidly digested. For this investigation P. jeffreysii is considered a carnivore.

Aphroditidae

Early investigations of feeding by aphroditid species concluded that they are slow, mobile carnivores armed with chitinized jaws and a muscular proboscis. Blegvad (1914) found that Aphrodita aculeata feeds on nemerteans and sabellid and terebellid polychaetes. Hunt (1925), who examined numerous specimens of A. aculeata from four separate areas near Plymouth, England, reported numerous polychaete species as prey including many terebellids and specimens of amphictenids, lumbrinerids, polynoids, and nereids. They also contained crustaceans and a nemertean. Recently, Mettam (1980) recounted an observation by Gunnar

Thorson of A. aculeata feeding on a large Nereis virens, which contradicts earlier assumptions that aphroditids should be slow-moving and capable of feeding only on sessile or discretely motile prey. Laboratory experiments by Mettam corroborate Thorson's observations. Mettam found that both Nereis diversicolor and Nephtys hombergi were taken when various potential prey were offered.

Both Aphrodita hastata Moore, 1905 and Laetmonice filicornis Kinberg, 1855 were collected during the present study. Both species occurred throughout the study area, however, neither species was collected in abundance. L. filicornis was more common in collections made by a small biology trawl than A. hastata, possibly due to a difference in burrowing habits of the two species at the sediment-water interface. The guts of most specimens examined were empty. Three specimens of A. hastata, however, contained remains of polychaetes. Each of these three specimens also had ingested medium quartz sand grains (15 to 30 μm diameter) with the prey. One specimen contained nereid setae and a well digested mass of tissue. The other two specimens each contained remains of a single Glycera dibranchiata. Based on these and historical data, both A. hastata and L. filicornis are considered carnivores.

Arabellidae

Arabellids are elongate, cylindrical eunicidans usually with well developed jaws. Some species are parasitic in other polychaetes, especilly in eunicids, syllids, onuphids, and terebellids (Pettibone

1963). The parasitic species usually have a reduced jaw apparatus. Most species, however, are free-living active burrowers. Most authors agree that the free-living burrowers are carnivorous as adults (Pettibone 1957, 1963, Southward 1957, Day 1967), though many may be parasitic as juveniles (Pettibone 1957, Emerson 1974). Sanders et al. (1962) however, found evidence that specimens of Drilonereis longa collected in Barnstable Harbor, Massachusetts ingested sand. This led Fauchald and Jumars (1979) to categorize the family Arabellidae as both carnivores and surface deposit feeders.

Six species of arabellids were collected in the Middle Atlantic Bight during the present study:

Arabella iricolor (Montagu, 1804)

Arabella mutans (Chamberlin, 1919)

Drilonereis longa Webster, 1879

Drilonereis magna Webster and Benedict, 1887

Drilonereis caulleryi Pettibone, 1957

Notocirrus spiniferus (Moore, 1906)

D. longa and D. magna occurred throughout the study area, though only D. longa occurred in abundance. Gut contents analyses of numerous specimens of these species and of Arabella mutans indicated a carnivorous life style. Only empty guts were found in dissected specimens of A. mutans, but one specimen of D. magna contained unidentifiable remains of a crustacean, and D. longa specimens were either empty or contained tightly bound mucus and sand masses. These masses included no prey or prey components, but may be indicative of carnivory, since

similar masses were regularly found in clearly predatory species (e.g.
Goniadidae, some Lumbrineridae). Sand masses may represent sediment
which remains in the gut of prey following digestion or an unsuccessful
feeding attempt which may account for observations made by Sanders et
al. (1962) of sand in the gut of D. longa.

Capitellidae

Capitellids are simple in morphology, generally rounded in cross-
section, lacking appendages on the prostomium. All feed on detritus by
everting a papillose, sac-like pharynx (Fauchald and Jumars 1979).

A total of 9 species was collected during this investigation:

Branchiocapitella sp.

Capitella capitata (Fabricius, 1780)

Heteromastus cf. filiformis (Claparede, 1864)

Leiocapitella glabra Hartman, 1965

Mediomastus californiensis Hartman, 1944

Mediomastus sp. A

Notomastus latericeus Sars, 1850

Notomastus teres Hartman, 1965

Notomastus sp. A

Notomastus latericeus was the most abundant capitellid collected
in the Middle Atlantic Bight. It occurred throughout much of the study
area, often as one of the ten most abundant macroinvertebrates at a
collection site (e.g. stations A1, A2, B3, E2, E4). Species of

Mediomastus were most abundant where finer sediments occurred (e.g. stations H1, H2, I4, J2).

All of the above species are motile deposit feeders that ingest material as they move through the sediment. Capitella capitata, Heteromastus filiformis, Notomastus latericeus, and probably the other species listed above, also all build tubes (Fauchald and Jumars 1979). Nothing in the present investigation indicated any behavior other than deposit feeding. Species that were dissected (N. latericeus and M. californiensis) were filled with detritus and fine sediments, and lacked large diatoms present in deposit feeders of some other families (e.g. Eunicidae).

Dorvilleidae

Dorvilleids are motile polychaetes with well-developed jaws, prostomial appendages, and parapodia. The investigators disagree on the food and feeding mode of these worms. Day (1967) listed Dorvillea (now Schistomeringos, in part) as carnivorous, though earlier investigations (Hempelmann 1931, Yonge 1954) reported that guts of Schistomeringos rudolphi included algae and detritus. Schistomeringos neglecta and Protodorvillea kefersteini are known to be carnivores (Pearson 1971, Rasmussen 1973, Wolff 1973). Fauchald and Jumars (1979) concluded that dorvilleids are all facultative carnivores, but can survive on plant material.

Five species of dorvilleids were collected during this investigation:

Protodorvillea minuta Hartman, 1965

Protodorvillea gaspeensis Pettibone, 1961

Protodorvillea kefersteini (McIntosh, 1869)

Schistomeringos caeca (Webster and Benedict, 1884)

Schistomeringos sp. A

Both P. kefersteini and S. caeca occurred in low abundance across the shelf. Schistomeringos sp. A and P. minuta were limited to outer shelf and slope habitats (e.g. stations J1, K6, L5, L6). P. gaspeensis was never collected in abundance. It occurred rarely in inner, middle, and outer shelf habitats.

Guts were empty in specimens of all the above species except Schistomeringos caeca. Specimens of this species were filled with amorphous detritus, fine sediments, foram tests, and a few diatoms. The forams and diatoms appeared to be only empty tests and frustules rather than live organisms. S. caeca is here considered a detritivore. All other species are considered carnivores.

Eunicidae

Eunicids have well-developed maxillae and mandibles, parapodia, and prostomial appendages. The jaw apparatus is eversible and muscular. They occupy diverse habitats, and depending on the species, may be tubicolous, free-living, or change to a tubicolous life style after being free-living as juveniles (Day 1967, Fauchald and Jumars 1979).

Investigations of Eunice aphroditois (Hempelmann 1931, Evans 1971) and E. tubifex (Day 1967) indicate a carnivorous life style. Other Eunice are known to feed on carrion (Mortensen 1922). Palola viridis ingests red algae and sponges (Hauenschild et al. 1969). Other tropical species (e.g. P. paloloides, E. schemacephala) may ingest coral sediment or corallinaceous algae (Ebbs 1966, Day 1967, Fauchald 1970). Literature on other genera and species is either conflicting or lacking.

Eight species of eunicids were collected in this study:

Eunice antennata (Savigny, 1820)

Eunice norvegica (Linnaeus, 1767)

Eunice pennata (Muller, 1776)

Eunice vittata (delle Chiaje, 1828)

Lysidice ninetta Audouin and Milne-Edwards, 1833

Marphysa bellii (Audouin and Milne-Edwards, 1833)

Marphysa sanguinea (Montagu, 1815)

Nematonereis unicornis (Grube, 1840)

M. bellii occurred in low to moderate abundance across the shelf. It was most abundant in outer shelf habitats (e.g. stations E3, E4, F1). Only single specimens of E. norvegica, N. unicornis, and L. ninetta were collected; these species have not been included in the gut content analyses. No complete specimens of M. sanguinea were collected; therefore, it too was eliminated from dissection analyses, but, as have all species collected, has been included in the distribution analyses. E. antennata and E. pennata occurred only rarely in the study area, but

have been included in analyses. Both were limited to outer shelf and shelf break habitats. E. vittata occurred rarely on the outer shelf and was moderately abundant at the shelf break.

Only two complete specimens of Eunice antennata and E. pennata were available for dissection. Both species included unidentifiable detritus, a few large sand grains (250 to 500 μm), but no large diatoms or other plant material. One specimen of E. pennata contained a fecal pellet, perhaps ingested with other particulate material. Both species are classified as deposit feeders.

Twenty-one specimens of Eunice vittata were dissected. Fecal pellets were removed from two of the specimens for examination under SEM. Analyses under light microscopy revealed that the fecal pellets contained mostly detritus, occasionally some diatoms or other plant material, and some fine sand (100 to 125 μm). Very few whole diatoms were observed. The fecal pellets selected for observation under SEM included one composed primarily of detritus, and two that contained numerous diatoms. The "typical" pellet (Figure 4) included mostly fine amorphous material, a few sand grains (50 to 60 μm), and a few small diatoms (10 to 50 μm) that were probably ingested incidentally. The other two pellets were almost exclusively composed of centric diatoms (Figures 5 and 6). One of the two "atypical" pellets included a 100 μm piece of plant material (Figure 7) and many small (less than 10 μm) coccoliths (Figure 8). The centric diatoms in the two pellets ranged in size from less than 10 μm to one equalling 175 μm. No pennate diatoms at all were observed. Despite the presence of diatoms and

Figure 4. Scanning electron micrograph of gut contents of <u>Eunice</u>
           <u>vittata</u>. Diatom is at center and cocolith is at upper
           right.

10 μm

Figure 5. Scanning electron micrograph of fecal pellet of <u>Eunice</u> <u>vittata</u>. Centric diatoms are at lower right and near the center.

100 µm

Figure 6. Scanning electron micrograph of centric diatom
(Coscinodiscus sp.) in gut of Eunice vittata.

10 μm

51
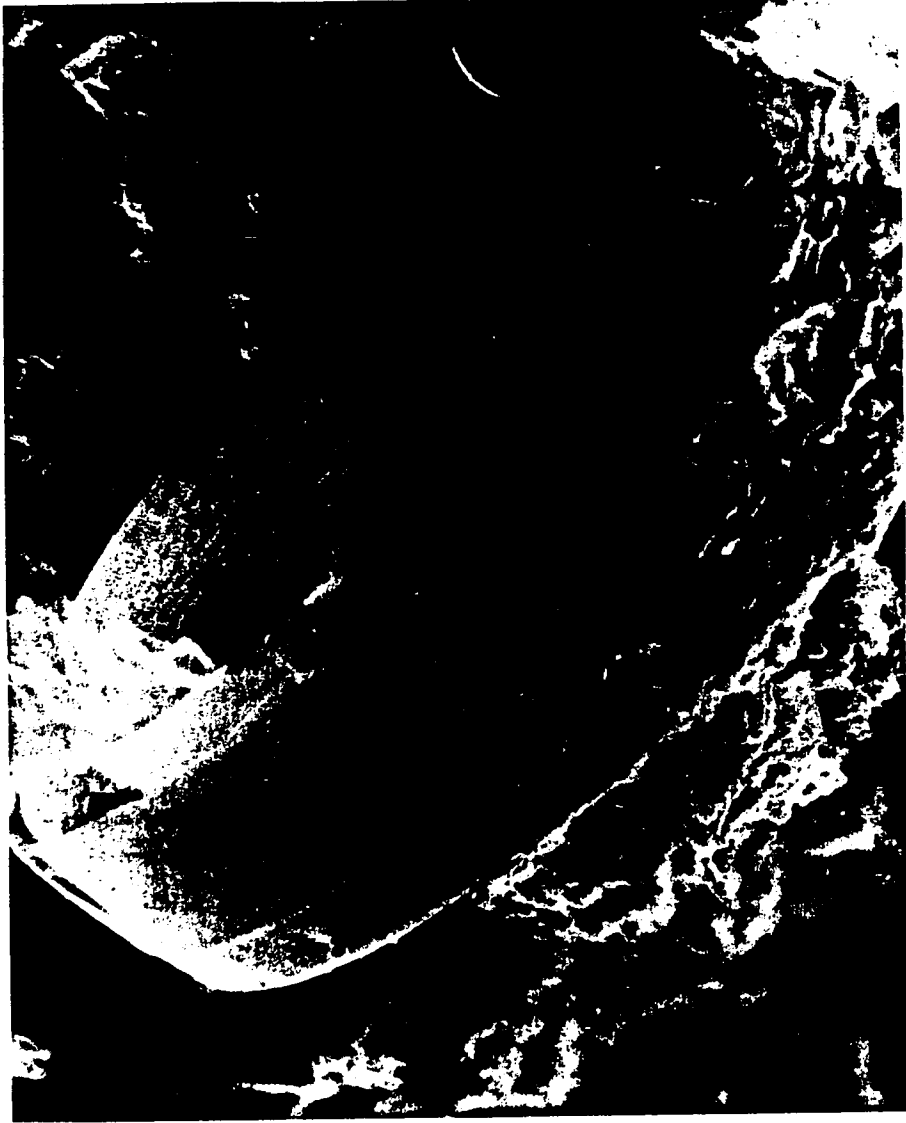
Figure 7. Scanning electron micrograph of gut contents of <u>Eunice</u>
<u>vittata</u>. Plant material extends from lower left to
upper right.

10 μm

Figure 8. Scanning electron micrograph of gut contents of Eunice
          vittata. Centric diatoms are at lower right and upper
          left. Two coccoliths are at left center.

10 µm

plant material, E. vittata is here considered a deposit feeder. The diatoms ingested were probably recently settled planktonic species, since most E. vittata occur at depths too great to support diatom growth.

Thirteen specimens of Marphysa bellii were dissected for observation with a light microscope, and of these 3 were viewed under SEM. Of those examined under light microscope, most had formed fecal pellets of detritus and a few diatoms. Included in the detritus were various items such as small peices of chitin and a few setae. Because of the small size of these items, it is postulated that they were ingested with the detritus. None of the specimens contained large sand grains. The SEM was used to view numerous fecal pellets. They revealed that the great majority of material in the fecal pellets was amorphous detritus. Each pellet included many broken pieces of diatoms (Figure 9), a few small centric diatoms (5 to 10 μm), and a few coccoliths. One contained two setae (10 and 15 μm in diameter), and much detritus tightly bound by mucus (Figure 10 and 11). The vast majority of all the pellets consisted of amorphous detritus bound by mucus, indicative of deposit-feeding habits.

Fauveliopsidae

Fauveliopsidae is a newly-described family (see Hartman 1971) of deep-water polychaetes closely allied to flabelligerids. They may be characterized as having only a few (10 to 50) biramous segments, a reduced prostomium, a ventral muscular pad on the proboscis, and only a

Figure 9. Scanning electron micrograph of gut contents of
Marphysa bellii. Diatom fragments are at bottom and
upper left.

10 µm

55
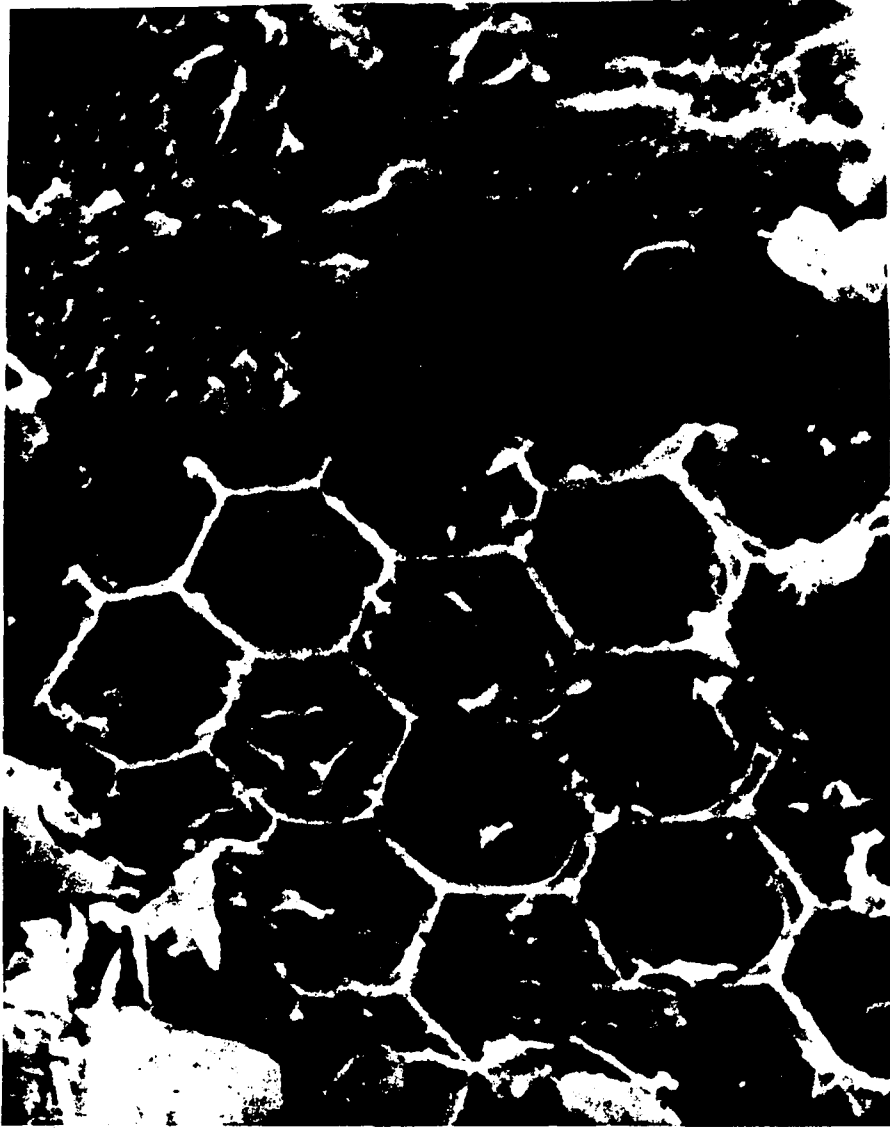
Figure 10. Scanning electron micrograph of gut contents of
Marphysa bellii. Polychaete seta is at upper left.
Feldspar particles are at lower right and upper center.

10 µm

Figure 11.　Scanning electron micrograph of gut contents of
　　　　　　 Marphysa *bellii*.　Polychaete seta is at upper left.
　　　　　　 Two coccoliths are at lower right.

10 μm

few smooth acicular setae (Fauveliopsis and Bruunilla) or no setae (Flota). Little is known of their feeding habits. Fauchald and Jumars (1979) postulated that they are subsurface deposit feeders.

Only a single species, Fauveliopsis sp. A, was collected in this investigation. All specimens were found scattered at shelf-break and in slope depths, and all occcupied small shells of the gastropod, Mitrella amphissella. The guts were filled with very fine sediment. Since all specimens examined occupied tubes constructed within the aperture of Mitrella, and since all specimens were extremely small in comparison to the gastropod shells, Fauveliopsis is here characterized as a sessile, surface deposit feeder.

Glyceridae

Glycerids are free living, elongate polychaetes with four jaws on an eversible, muscular pharynx. They are capable of rapid burrowing, and often inhabit physically dynamic habitats such as open beach zones.

Most investigators categorize all members of the family as carnivores (Blegvad 1914, Hunt 1925, Yonge 1928, Hempelmann 1931, Southward 1957, Day 1967, Evans 1971, Pearson 1971, Ronan 1977). Some species, however, are reportedly detritivores: Glycera dibranchiata (Klawe and Dickie 1957, Sanders et al. 1962); G. capitata and G. gigantea (Hartmann-Schroder 1971); G. unicornis (Stolte 1932). Fauchald and Jumars (1979) concluded that the carnivorous habit is the

primary feeding mode, but that some species have become detritivores.
Furthermore, bathyal and abyssal species may use both modes.

In this investigation seven species of glycerids were collected:

Glycera capitata Oersted, 1843

Glycera dibranchiata Ehlers, 1868

Glycera papillosa Grube, 1857

Glycera robusta Ehlers, 1868

Glycera sp. A

Glycera sp. B

Hemipodus roseus Quatrefages, 1865

G. dibranchiata was the only glycerid collected across the shelf. It
was most abundant at middle shelf depths and absent in slope habitats.
It was one of few large polychaetes (i.e. longer than 50 mm) which
occurred at all depths on the shelf. Both G. robusta and G. capitata
were similarly widely distributed, but in less abundance. H. roseus
was limited in distribution to inner and middle shelf habitats (e.g.
station C1, C2, C3, G1, K1). The other species, G. papillosa, Glycera
sp. A, Glycera sp. B, were never collected in abundance.

Only the four most abundant species (G. dibranchiata, G. robusta,
G. capitata, and H. roseus) were dissected for gut contents. In light
of the characterization of Glycera dibranchiata as one of few glycerid
detritivores (Klawe and Dickie 1957, Sanders et al. 1962) and its
abundance in the study area, especially careful dissections of this
species were made. Klawe and Dickie (1957) reported that G.
dibranchiata regurgitated fecal pellets rather than pass them through

the anus; therefore, care was also taken in dissecting the foregut and midgut areas where the fecal pellets reportedly occur. In most specimens the gut was completely devoid of any material whatsoever. Several specimens contained one or two large quartz sand grains that may have been incidentally ingested during predatory feeding. One 118 mm specimen contained an amphipod crustacean, some polynoid polychaete setae, and several large quartz sand grains in the midgut. All specimens of the other three species dissected, G. capitata. G. robusta, and Hemipodus roseus, had empty guts except for a few large sand grains in a specimen of H. roseus. All four species of glycerids analyzed from the study area are considered carnivores.

Goniadidae

Goniadids are elongate polychaetes with a muscular, eversible pharynx encircled by a series of finly-toothed jaws. Such morphology has been considered indicative of a carnivorous life style by many authors, (e.g. Southward 1957, Wolff 1973) though only scant data on feeding by goniadids are available. Fauchald and Jumars (1979) note that only three species, Glycinde armigera, G. nordmanni, and Goniada maculata, have been investigated in feeding studies. All were considered carnivores, but based on weak evidence. For instance, Blegvad (1914) dissected only nine specimens, all with empty guts, before concluding that Goniada maculata was a carnivore. Fauchald and Jumars (1979) agreed that all goniadids probably are carnivores, but indicated a need for additional data on both feeding and locomotory habits.

Five species of goniadids were collected in this investigation:

Goniada _brunnea_ Treadwell, 1906

Goniada _maculata_ Oersted, 1843

Goniada _norvegica_ Oersted, 1845

Goniada _teres_ Treadwell, 1931

Goniadella _gracilis_ (Verrill, 1873)

Goniadella _gracilis_ was the most abundant goniadid, and occurred predominantly in unstable sands across the shelf. Its distribution is described in detail later. _Goniada_ _maculata_, _G_. _norvegica_, and _G_. _brunnea_ also had widespread distribution, but were less abundant. _Goniada_ _teres_ was limited to outer shelf and slope habitats (e.g. stations K4, L4, L5).

All five species were dissected for gut contents, though most of the effort was spent on the more abundant species. The diminutive size of _Goniadella_ _gracilis_ (usually less than 10 mm in length) made dissections extremely tedious; however, more than 100 specimens were examined. In all, 96 of these were completely empty. Three specimens contained minute amounts of fine detritus, presumably incidentally ingested during predatory feeding or remaining from prey gut content. Three specimens contained spines and setae of other polychaetes, possibly syllid setae, sand masses tightly bound in mucus and large quartz sand grains. Twelve specimens contained only sand. Numerous carnivores (e.g. Aphroditidae, Glyceridae) ingest large sand grains, and their presence in an otherwise empty gut may indicate predatory feeding.

The guts of all <u>Goniada</u> <u>brunnea</u>, <u>G</u>. <u>norvegica</u>, <u>G</u>. <u>maculata</u>, and <u>G</u>. <u>teres</u> were completely empty, with the exception of one specimen of <u>G</u>. <u>brunnea</u> which contained a tiny amount of unidentifiable organic material in the posterior gut. It was not possible to determine whether the material was a digested organism or ingested detritus. There was no fine sand mixed in with the organic material as is sometimes the case in detritivores, but on the other hand there were no chitinized or calcified parts, which could provide conclusive evidence of animal prey, either. All species of goniadids collected in this investigation are, nevertheless, considered carnivores. Furthermore, due to the physically unstable nature of the sediments occupied by <u>Goniadella</u> <u>gracilis</u>, it is hypothesized that this particular species does not form burrows, but moves freely through the sediments in search of prey. Smaller and juvenile specimens may feed on interstitial organisms, especially in habitats of medium to coarse sand where little silt and clay are present.

Hesionidae

Hesionids have a well-developed prostomium with eyes and elongate sensory appendages. The pharnyx is eversible, but often without jaws. Parapodia are strong, well developed for rapid locomotion, and are usually equipped with long dorsal cirri. Fauchald and Jumars (1979) noted a lack of literature on most species; however, they postulated that non-interstitial species are carnivorous. Studies by Westheide (1967) and Wolff (1973) established that interstitial species feed on

diatoms, bacteria (by ingesting detritus), and possibly copepods and forams. Recent investigations by Shaffer (1979) and Oug (1980) provide data in support of Fauchald and Jumars' hypothesis. Shaffer found that Podarke pugettensis preys on a variety of small invertebrates, including members of at least nine families of polychaetes. The most abundant prey items, however, were harpacticoid copepods. Oug found that Ophiodromus flexuosus and Nereimyra punctata were also predaceous, feeding mostly on small crustaceans and polychaetes. Limited amounts of bottom material (i.e. algae, diatoms, detritus) was found in their fecal pellets as well, but this probably was passively ingested during predatory feeding. Oug determined that O. flexousus is a motile predator on the sediment surface. N. punctata constructs a burrow system from which it ambushes prey; however, evidence indicates that N. punctata may also leave the burrows to seek prey on the sediment surface. Quantitative information on feeding in any other species of non-interstitial hesionids is completely lacking.

Three species of hesionids were collected in this investigation:

Gyptis sp. A

Hesionidae sp. A

Podarke cf. obscura Verrill, 1873

None of these species was ever collected in abundance. Gyptis sp. A and Podarke cf. obscura usually occurred in outer shelf and shelf break habitats (e.g. stations A1, A2, A3). Hesionidae sp. A was collected only on the slope (i.e. stations J1, J2, H1), and never in abundance.

No complete specimens of any of these species were collected during the BLM Middle Atlantic Bight Study. Incomplete specimens (i.e. those lacking a posterior gut) of _Gyptis_ sp. A were examined for gut content; all were empty. Based on the morphology and the results of Shaffer's (1979) and Oug's (1980) studies, these three hesionids ae considered carnivores.

Lumbrineridae

Lumbrinerids are elongate, cylindrical polychaetes with well-developed jaws, but usually with no eyes or obvious sensory prostomial appendages. The jaw apparatus consists of a pair of mandibles, four pairs of maxillae, and a pair of maxillary carriers. The first pair of maxillae are modified into pincer-like jaws which may be armed with poison glands (Fauchald, personal communication). All species are active burrowers that may inhabit temporary burrows (Fauchald and Jumars 1979).

Lumbrinerids are generally considered to be carnivores, though there is little direct evidence to support such an assumption. Blegvad (1914) reported several polychaetes, nemerteans, bivalves, ophiuroids, and crustaceans among prey of _Lumbrineris fragilis_. In 1975, Zibrowius et al. described the commensal life style of _L. flabellicola_, a lumbrinerid that feeds on material captured by cnidarians of the genera _Caryophyllia_ and _Flabellum_. Feeding in other lumbrinerids has not been described.

Though many authors report carnivory among all lumbrinerids (e.g.
Blegvad 1914, Hunt 1925, Yonge 1928, Day 1967, Pearson 1971, Wolff
1973), studies on Lumbrineris impatiens indicate herbivorous feeding
(Hemplemann 1931, Yonge 1954, Hartmann-Schroder 1971, Fauchald and
Jumars 1979). Additionally, Sanders et al. (1962) characterized Ninoe
nigripes as a selective deposit feeder. Four species studied by Banse
and Hobson (1968), L. bicirrata, L. californiensis, L. cruzensis, and
L. luti, all contained limited amounts of detritus and sand, indicating
deposit feeding.

Eight species of lumbrinerids were collected during this investi-
gation:

Lumbrinerides acuta (Verrill, 1879)

Lumbrineris albidentata (Ehlers, 1908)

Lumbrineris fragilis (Muller, 1776)

Lumbrineris impatiens (Claparede, 1868)

Lumbrineris latreilli (Audouin and Milne-Edwards, 1833)

Lumbrineris cf. tenuis (Verrill, 1873)

Ninoe brevipes (McIntosh, 1903)

Ninoe nigripes Verrill, 1873

Several of these species, including Lumbrineris fragilis, L.
latreilli, L. impatiens, Ninoe nigripes, and Lumbrinerides acuta
occurred in abundance across the shelf. L. latreilli and L. acuta were
among the most abundant of macroinvertebrate species collected in the
Middle Atlantic Bight BLM study (Boesch 1979a). L. albidentata was
limited to outer shelf, shelf break, and slope habitats (e.g. stations

F1, F2, H1, H2). L. cf. tenuis, and N. brevipes were rare to moderately abundant, and occurred only in deep water habitats (e.g. stations K6, H2, J1, J2). All species except L. cf. tenuis and N. brevipes were included in gut content studies.

Lumbrinerides acuta was most abundant in unstable sand habitats (e.g. stations B4, E3, G1). The majority of specimens collected were small (5 to 15 mm in length), and are probably interstitial burrowers. Gut contents analysis failed to reveal a specific diet, though predation is the likely feeding-mode. Of over 100 specimens dissected, none contained an identifiable prey item. Most specimens (over 90%) were completely empty. Two specimens contained a minute amount of fine detritus. Two other specimens contained only 1 or 2 large quartz sand grains. Several contained tightly-bound fine sand grains that appeared to have been ingested and later bound with mucus in the gut. These sand grains first were thought to be forams with agglutinated sand tests; however, closer observation ruled this out. It is possible that this species preys on soft-bodied organisms such as archiannelids or nematodes that are easily digested and have no chitinized parts detectable by dissection. The detritus found in the guts of the specimens mentioned above may have originated in prey organisms. It is hypothesized that L. acuta is a predator.

Lumbrineris albidentata is a relatively large lumbrinerid (often more than 50 mm long). It is probably carnivorous. The guts were empty in most specimens, and only a few large sand grains were in those not empty.

Gut analysis of <u>Lumbrineris fragilis</u> shorter than 20 mm in length revealed detritus, fine sand, amorphous organic material, empty foraminiferan tests, pieces of diatom frustules, but no live diatoms or other living material except commensal ciliates often found in the guts of the polychaetes. Specimens longer than 20 mm had gut contents indicating carnivorous habits. The majority of dissected larger specimens were completely empty. Although no whole prey organisms were found, spines and setae of polychaetes were present in several specimens. Others contained only a few large sand grains. It is hypothesized, therefore, that juvenile specimens are facultative detritivores and large specimens exclusively carnivores.

<u>Lumbrineris impatiens</u>, like juvenile specimens of <u>L</u>. <u>fragilis</u>, is a deposit feeder. Fauchald and Jumars (1979) and others indicated that this species should be a herbivore, however, specimens collected in the Middle Atlantic Bight never contained plant material or any live diatoms. Gut contents primarily consisted of amorphous organic material and fine sand. A few pieces of diatom frustules were also found in one specimen. As discussed above (see Eunicidae), most specimens of <u>L</u>. <u>impatiens</u> occur at depths too great to support diatom growth. Diatoms present in the guts of these species probably settled from the water column, and therefore, would be considered detrital in origin.

The gut content of <u>Lumbrineris latreilli</u> gut contents analyses indicate a deposit-feeding habit. None of the specimens examined had guts entirely filled with detritus; however, all specimens contained some. Included in the items ingested were particles of fine sand (100

to 130 μm), pieces of diatoms, and 1 to 2 medium sand grains (250 to 280 μm). A specimen collected at the shelf break (station A4) contained several empty tests of the foraminiferan genus, Globigerina, which constitute much of the sand size particles in sediments of this location.

Guts of the specimens of Ninoe nigripes were filled with detritus; as suggested by Sanders et al. (1962), this species must be a detritivore. Both juvenile (less than 25 mm in length) and adult specimens contained large amounts of detritus, much fine sand and silt, and the amorphous material characteristic of detritus-feeding forms. Among the material which was apparently ingested incidentally with the detritus was a dinoflagellate, both large and small entire centric and pennate diatoms, and several black mineral grains. The small diatoms (less than 0.5 mm) were apparently live when ingested. The large diatoms, mostly centric, were primarily broken frustules; however, one centric diatom, found in a 55 mm Ninoe, was apparently live when ingested (i.e. the striae were filled with mucus and/or protoplasm).

Maldanidae

The feeding of maldanids is well documented in the literature (e.g. Mangum 1964, Rhoads 1967, 1974, Kudenov 1977, 1978). There is ample evidence to indicate that most species investigated feed while orientated prostomium-down in their tubes. In so doing, they are characterized as subsurface deposit feeders in the literature.

However, one species, Praxillura longissima, is here considered a surface deposit feeder. P. longissma is most abundant in outer shelf and slope habitats (e.g. stations H1, H2, I4). It apparently feeds prostomium-up on material surrounding its tube. The evidence in support of this hypothesis is based on bottom photographs (Boesch, personal communication) and observations on preserved specimens. Anterior ends of Praxillura were collected in the Smith-McIntyre grabs and Anchor dredges, indicating that the sampler failed to penetrate the entire length of the species' tube. No posterior ends were collected. Additionally, the morphology of Praxillura seems adaptive to surface feeding. Praxillura possesses an enormous mouth, different in shape from that of most shallow-water maldanids. Such a structure could be used to ingest surface material within reach of the tube opening. Its tube is thin-walled, but firm and flexible, with sand agglutinated to a mucus lining. The guts were filled with coarse sand and little detritus. Most large particles ingested were 300 to 1000 μm diameter quartz sand.

All other species collected in this investigation are assumed to be subsurface deposit feeders. Those species include:

Asychis carolinae Day, 1973

Asychis biceps (Sars, 1861)

Axiothella sp. A

Clymenella torquata (Leidy, 1855)

Clymenella sp. A

Clymenura sp. A

Euclymene zonalis (Verrill, 1874)

Maldane sp. A

Praxillella sp. A

Praxillella gracilis (Sars, 1861)

Rhodine loveni Malmgren, 1865

Clymenella torquata and E. zonalis and Clymenura sp. A were the three most abundant maldanids collected. All occurred across the shelf, but most densely populated quiescent areas of finer sediments (e.g. stations A2, D4, F4). Asychis carolinae also was abundant, but limited to middle shelf to shelf break habitats (e.g. stations F2, G5, I3, K5). The distributions of these species are discussed later in this study. None of the other species occurred in appreciable numbers.

Nephtyidae

Nephtyids are active, burrowing polychaetes which feed with a large eversible pharynx equipped with a single pair of jaws. Most investigators (e.g. Blegvad 1914, Hunt 1925, Yonge 1928, Southward 1957, Day 1967, Ronan 1977, Rao and Sarma 1978) are in agreement that nephtyids are carnivorous. Their prey probably reflect the composition of the invertebrate fauna they encounter, including molluscs, crustaceans, and other annelids. There is evidence that populations of Nephtys incisa which inhabit Long Island Sound and Buzzard's Bay may be deposit-feeders (Sanders 1956, 1960). Fauchald and Jumars (1979) hypothesize that N. incisa populations in these areas, though similar in

morphology to <u>N</u>. <u>incisa</u> in Europe, are actually divergent groups. The two populations may actually represent separate species, though Fauchald and Jumars did not indicate that such was suspected.

Seven species were collected during this investigation:

<u>Aglaophamus</u> <u>circinata</u> (Verrill, 1874)

<u>Nephtys</u> <u>bucera</u> Ehlers, 1868

<u>Nephtys</u> <u>caeca</u> (Fabridius, 1780)

<u>Nephtys</u> <u>incisa</u> Malmgren, 1865

<u>Nephtys</u> <u>picta</u> Ehlers, 1868

<u>Nephtys</u> <u>squamosa</u> Ehlers, 1887

<u>Nephtys</u> sp. A

Both <u>A</u>. <u>circinata</u> and <u>N</u>. <u>bucera</u> occurred in abundance across the shelf. The most abundant nephtyids, however, were the indistinguishable juveniles of the two species. Because juvenile nephtyids were among the most numerically dominant polychaetes collected at many sites, they were included as a separate group in the gut content analysis. <u>N</u>. <u>incisa</u> and <u>N</u>. <u>picta</u> were the only other taxa dissected. All other species were considered motile carnivores.

Fifty specimens of <u>Aglaophamus</u> <u>circinata</u> were examined for gut content. Only six contained any ingested material at all. The material included large quartz sand grains (400 to 500 μm diameter), tightly-bound mucus masses of sand similar to that found in <u>Lumbrinerides</u> <u>acuta</u>, and remains of lumbrinerid and spionid polychaetes. These results indicate carnivorous habits.

Dissections of _Nephtys_ _bucera_ led to the same conclusion. Specimens contained polychaete setae and peracaridan crustaceans. Only one specimen contained the large sand grains (200 to 500 μm diameter) seen in _Aglaophamus_ _circinata_.

Juvenile nephtyids (mostly 2.5 to 5.0 mm in length) were mostly empty. Of forty specimens dissected, only four contained ingested material. One contained a few large sand grains and a minute amount of detritus. Three specimens had ingested unidentifiable prey organisms. All three contained detritus and an abundance of capillary setae, indicating carnivorous feeding.

All specimens of _Nephtys_ _incisa_ and _N. picta_ were empty. They were included with the other nephtyids as carnivores.

Nereidae

Nereids are probably the best investigated of all polychaetes. They are often used as the "typical" polychaete, probably because they have numerous sensory appendages on the prostomium, four eyes, well-developed parapodia, and are readily accessible to biological supply companies. Their muscular pharynx is eversible, and is equipped with a pair of jaws usually supplemented by auxilliary paragnaths.

A great deal of information is available of feeding in nereids, probably because of their use in laboratory experiments. A complete list of literature on nereid feeding is provided by Fauchald and Jumars (1979). The most comprehensive of the studies was conducted along the German Coast by Goerke (1966, 1971). Using both field and laboratory

data, Goerke concluded that Nereis pelagica, N. virens, and N. diversicolor are omnivores. N. succinea and N. longissima were determined to be "mainly deposit and detritus feeders," and N. fucata (a commensal with pagurids) to be primarily carnivorous. In general, the literature presented by Fauchald and Jumars characterized the majority of nereids as free-living omnivores that may occupy temporary tubes of sand and mud.

Since Fauchald and Jumars (1979) completed their investigation, additional information has been published. Tsuchiya and Kurihara (1979) investigated detritus feeding in Neanthes japonica, and provided data on both the components of detritus and on the importance of each component to the nutrition of the species. Jorgensen (1979, 1980) measured the uptake of amino acids in Nereis virens to provide insight into its role in nutrition of invertebrates. Woodin (1977) described "gardening" by N. vexillosa and Platynereis bicanaliculata, a method by which these species attach drift algae to their tubes for later consumption. In a North Carolina estuary, Cammen et al. (1978) measured microbial carbon assimilation in Nereis succinea, concluding that nutritional requirements of the species exceeded the energy provided by the digestion of microbes. Cammen's information of the previously untested hypothesis that all nutrition of detritivores comes solely from microbes, suggests that alternate feeding methods or direct uptake or dissolved organic matter may be more important than previously believed.

Four species of nereids were collected during this investigation:

Ceratocephale loveni Malmgren, 1867

Neanthes succinea (Frey and Leuckart, 1847)

Nereis grayi Pettibone, 1956

Nereis zonata Malmgren, 1867

Only N. grayi occurred in abundance across the shelf. N. zonata was most abundant in mid-shelf depths, and C. loveni was limited in distribution to shelf break and slope habitats. N. succinea, typically an estuarine species, occurred mostly in inner and middle shelf habitats. Members of all species except N. succinea were dissected for gut contents.

Nereis grayi is a deposit feeder. Guts of dissected specimens contained an abundance of detritus including forams, both whole and broken diatoms, fine and medium quartz sand grains (80 to 300 μm), ingested fecal pellets, and numerous small unidentifiable items.

Nereis zonata also ingested detritus, and, therefore, is characterized as a deposit feeder. It should be noted, however, that none of the specimens examined contained filled guts as did those of N. grayi. Gut contents included small amounts of detritus, both medium and small quartz and feldspar sand grains (100 to 300 μm), dinoflagellate tests, foram tests, and several unidentifiable items. One specimen included a minute piece of a terrestial plant.

Ceratocephale loveni also is a deposit feeder. Guts of this species were filled with detritus and fine sand. Identifiable items included diatom test (broken and entire), forams, and small pieces of

echinoderm tests. All of these items were probably incidentally in-
gested with the fine sand.

Gut contents of two specimens of C. loveni were also examined
under SEM. Most of the ingested material was sediment. There was
little indication that this species is particularly selective in
sediment ingested, as the particles ranged from coarse silt (65 µm) to
medium clay (1 to 2 µm). No sand particles were observed; however,
sand contributes only about 6% of the sediment at slope depths (e.g.
station J2) where these two specimens were collected (Boesch 1979b).

Onuphidae

Onuphids are elongate polychaetes with numerous sensory appendages
on the prostomium. All species are tubicolous, though two of the
species collected in this investigation (Nothria conchylega and
Hyalinoecia artifex) move about freely dragging their tubes along.

Feeding of onuphids has been intensively investigated, though no
clear pattern has emerged for the family. They have been characterized
as carnivorous by Schafer (1962) and Hartmann-Schroder (1971). Numer-
ous species, including Diopatra ornata, D. neapolitana, D. cuprea, D.
monroi, and Epidiopatra gilchristi are, at least in part, herbivorous
(Hempelmann 1931, Yonge 1954, Day 1967, Mangum and Cox 1971, Myers
1972). Hyalinoecia spp. has been attracted to carrion (Dayton and
Hessler 1972). Fauchald and Jumars (1979) hypothesized that onuphids
are omnivorous scavengers, and specialize as the availability of food
varies in different depths and habitats. Furthermore, deep-water

species of <u>Nothria</u>, which are thought to be sessile, may be truly omnivorous due to the scarcity and inconstancy of food supply in the deep sea.

Eleven species of onuphids were collected during this investigation:

<u>Diopatra</u> <u>cuprea</u> (Bosc, 1802)

<u>Diopatra</u> sp. A

<u>Hyalinoecia</u> <u>artifex</u> Verrill, 1880

<u>Nothria</u> <u>conchylega</u> (Sars, 1835)

<u>Onuphis</u> <u>atlanticum</u> (Hartman, 1965)

<u>Onuphis</u> <u>eremita</u> Audouin and Milne-Edwards, 1833

<u>Onuphis</u> <u>nebulosa</u> Moore, 1911

<u>Onuphis</u> <u>opalina</u> (Verrill, 1873)

<u>Onuphis</u> <u>pallidula</u> (Hartman, 1965)

<u>Onuphis</u> <u>declivorum</u> Fauchald, 1982

<u>Rhamphobrachium</u> sp. A

The two most abundant onuphids were <u>N</u>. <u>conchylega</u> and <u>O</u>. <u>pallidula</u>. Both numerically dominated the macroinvertebrate fauna of certain outer shelf and shelf break habitats, but were uncommon in mid-shelf and slope habitats. <u>Onuphis</u> <u>atlanticum</u> was most abundant in shelf break and slope habitats (e.g. stations A4, H1, J1). Only two other species occurred in abundance: <u>H</u>. <u>artifex</u>, limited to slope depths; and <u>D</u>. <u>cuprea</u>, an inner shelf and estuarine species. Only <u>N</u>. <u>conchylega</u>, <u>O</u>. <u>atlanticum</u>, <u>O</u>. <u>pallidula</u>, and <u>H</u>. <u>artifex</u> were included in the analysis. No complete specimens of the other species were available.

For Onuphis pallidula, dissections revealed that most specimens ingested small amounts of detritus. Guts were never completely filled. In addition to unidentifiable detritus, guts of most specimens contained numerous diatoms. Several specimens contained what appeared to be tube fragments as well as the diatoms. Three tubes of O. pallidula were examined with stereo and compound microscopes to determine whether similar diatoms collected in the tubes. Few diatoms were observed in the tubes. The ingested diatoms were apparently planktonic in origin, and ingested with other detrital material.

Onuphis pallidula fecal pellets were also examined under SEM. The pellets were tightly bound with mucus, and covered with bacteria (Figure 12). A few diatoms (Figure 13), only one of them pennate (20 μm in length), were observed. Most diatoms were either dead when ingested or diatom fragments. There were also abundant fine silt and clay particles (2 to 10 μm in diameter). O. pallidula ingests sediment, though there is no indication of the origin of the material (i.e. tube, sediment surface, subsurface).

Onuphis atlanticum similarly ingested numerous diatoms, but, unlike O. pallidula, also contained an abundance of fine sand and detritus which was formed into fecal pellets. In addition, whole and broken forams were observed.

Ingested material in specimens of Nothria conchylega, like O. atlanticum, was formed into fecal pellets in the posterior gut. One specimen contained numerous diatoms; however, guts of most specimens were filled with unidentifiable detritus and only a few diatoms and

Figure 12. Scanning electron micrograph of bacteria among the gut
contents of <u>Onuphis</u> <u>pallidula</u>.

├───┤
1 μm

78

Figure 13. Scanning electron micrograph of gut contents of <u>Onuphis</u> <u>pallidula</u>. Diatom at center is <u>Nitzchia</u>.

10 μm

forams. N. conchylega, Onuphis pallidula and O. atlanticum are here considered selective deposit feeders.

Hyalinoecia artifex is a large onuphid that inhabits a quill-like tube that is carried around with the worm. Bottom photographs taken during the Middle Atlantic Bight (BLM) investigation (Boesch 1979a) showed that H. artifex is a very motile species, capable of dominating the sediment surface habitat. Gut contents analysis confirmed that it may do just that. Guts contained numerous peracaridan crustaceans and echinoid spines. The peracaridans were apparently ingested while with their tubes, indicating voracious predatory feeding. Though they may actually be omnivorous scavengers over their distribution range, specimens dissected in this investigation are predatory. Almost every specimen dissected contained some item, usually peracaridans.

Paraonidae

Paraonids are small, elongate polychaetes with an eversible, unarmed pharynx. All species are generally considered to be deposit feeders (e.g. Day 1967, Pearson 1971, Rasmussen 1973). Noteworthy exceptions to this generalization include reports of selective feeding on pennate diatoms by Paraonis fulgens in Europe (Roder 1971, Risk and Tunnicliffe 1978), and observations by Fauchald and Jumars (1979) on selective ingestion of foraminifera by paraonids in the deep sea.

Fourteen species of paraonids were collected during this investigation:

Aedicira sp. A

Aricidea catherinae Laubier, 1967

Aricidea cerrutii Laubier, 1966

Aricidea quadrilobata Webster and Benedict, 1887

Aricidea simplex (Day, 1963)

Aricidea suecica Eliason, 1920

Aricidea wassi Pettibone, 1965

Cirrophorus branchiatus Ehlers, 1908

Tauberia gracilis (Tauber, 1879)

Paradoneis lyra (Southern, 1914)

Paraonis fulgens (Levinsen, 1883)

Paraonis pygoenigmatica Jones, 1968

Paraonis sp. A

Paraonis sp. B

A. catherinae, *A. cerrutii*, *C. lyriformis*, *P. lyra*, and *L. gracilis* were all abundant across the shelf. *A. catherinae* and *P. lyra* were most abundant, however, in shelf-break habitats (e.g. stations A4, F3, F4), where *A. simplex* was similarly among the most numerically dominant species. *A. wassi* was most abundant in inner and middle shelf habitats (e.g. stations D1, D2, G2, L1, L3), but occurred to the shelf break. None of the other species occurred in abundance. Only a few specimens of *P. fulgens* were collected, all on the inner shelf.

Specimens of the seven species discussed above (excluding *P. fulgens*) were dissected for gut content. All contained only detritus, fine sand (70 to 150 um), much silt and clay, and a few small diatoms, characteristic of material ingested by deposit feeders. None contained

an abundance of diatoms such as those reportedly ingested by <u>Paraonis</u> <u>fulgens</u>. All of these species of paraonids, therefore, are classified as surface deposit feeders.

Phyllodocidae

Phyllodocids are free-living polychaetes with well-developed anterior sensory structures including eyes, antennae, and tentacular cirri in most species. The pharynx is muscular and eversible, but without jaws. Most species are hunting carnivores (e.g. Newell 1970, Evans 1971, Pearson 1971, Wolff 1973, Emson 1977). A report by Sanders et al. (1962) that <u>Eteone heteropoda</u> ingests sediment was later compli- cated by observations of carnivory and cannibalism in the same species (Simon 1965, Evans 1971). A similar species, <u>E. longa</u> is reportedly carnivorous (Retiere 1967). Fauchald and Jumars (1979) hypothesized that all phyllodocids are hunting predators, and attributed the obser- vations by Sanders et al. (1962) to be evidence of an alternate feeding method used by populations of <u>Eteone heteropoda</u> in Long Island Sound.

Eighteen species of phyllodocids were collected during this inves- tigation:

<u>Anaitides</u> <u>arenae</u> (Webster, 1880)

<u>Anaitides</u> <u>longipes</u> (Kinberg, 1866)

<u>Anaitides</u> <u>mucosa</u> (Oersted, 1843)

<u>Anaitides</u> sp. A

<u>Eteone</u> <u>heteropoda</u> Hartman, 1951

<u>Eteone</u> <u>lactea</u> Claparede, 1868

Eteone sp. A

Eteone sp. B

Eulalia bilineata (Johnston, 1840)

Eulalia viridis (Linnaeus, 1767)

Eulalia sp. A

Eumida sanguinea (Oersted, 1843)

Eumida fusigera (Malmgren, 1865)

Hesionura sp. A

Lugia sp. A

Notophyllum foliosum (Sars, 1835)

Paranaitis kosteriensis (Malmgren, 1867)

Paranaitis speciosa (Webster, 1880)

Only A. mucosa and E. bilineata were widely distributed. They were present across the shelf, but most abundant in the middle and outer shelf. All other species occurred only rarely or in low abundance. Only A. mucosa and Eteone sp. A were dissected for gut contents analyses during this study. All specimens dissected were completely empty. All phyllodocids are here considered hunting carnivores.

Sphaerodoridae

Sphaerodorids are one of the least investigated families of polychaetes. Most species are minute, possibly interstitial where they occur in sandy habitats, and armed with a muscular, eversible pharynx. Though no quantitative studies of their feeding habits have been conducted, Fauchald and Jumars (1979) hypothesize that all species are

free-living deposit-feeders which browse the sediment surface. Schafer (1962) earlier postulated the same for Sphaerodoridium claparedii.

Though sphaerodorids occurred only rarely in the study area, they have been included in this investigation due to the scarcity of information about their habits. Only four species were collected:

Sphaerodoridium claparedii (Greeff, 1866)

Sphaerodoropsis corrugata (Hartman, 1965)

Sphaerodoropsis minuta (Webster and Benedict, 1887)

Sphaerodoridae sp. A

S. claparedii was the only species examined for gut content. Dissections were conducted by piercing the gut of whole mount specimens, allowing the ingested material to spill into the mounting medium. Since the body wall is transparent in such small species, gut material is readily apparent when present. Only 4 of 24 specimens available contained any material whatsoever. Each contained only small amounts of detritus, never enough to fill the gut. Ingested material included a small centroid diatom, fine quartz sand (60 to 80 μm), silt and clay, and some amorphous organic matter. The information is inconclusive, and neither confirms nor refutes Fauchald's and Jumars' (1979) hypothesis of surface detritus feeding. For the purposes of this study, all species are considered detritivores.

Spionidae

Feeding by spionids has been extensively investigated. Fauchald and Jumars (1979) provide an excellent summary of the available liter-

ature. They postulate, based on the literature and personal observa-
tions, that spionids are discretely motile surface deposit feeders that
are capable of highly discriminatory selection of particles. They
suggest that suspension feeding, as observed in species of Polydora
(Linke 1939, Korriga 1951, Dorsett 1961), may supplement surface
deposit feeding. Recent investigations by Taghon et al. (1980) confirm
the hypothesis, and indicate that suspension feeding by Pseudopolydora
kempi japonica, Boccardia proboscidea, and Pygospio elegans occurs in
response to increased water velocity, maximizing suspension feeding
during the greatest flux of suspended materials. Similar observations
have been made on United States east coast spionids by Dauer et al.
(1981). Levin (1980) observed that Pseudopolydora paucibranchiata and
Streblospio benedicti both periodically suspension feed. Additionally,
she noted that Pseudopolydora aggressively defends it territory for
acquisition of food and tube-building materials, a behavior previously
observed only in nereid polychaetes (Roe 1975).

For the purposes of this investigation, spionids are classified
both as surface deposit feeders and suspension feeders. Half of the
specimens of each species are entered in the analyses below as suspen-
sion feeders and half as surface deposit feeders.

Syllidae

The morphology of syllids varies considerably between genera.
Most species are considered non-tubicolous (Fauchald and Jumars 1979);
they feed with the aid of a muscular, eversible pharynx connected to a

cylindrical organ presumably used for sucking, called the proventriculus. Most species also possess a sharp tooth or series of teeth on the pharynx.

There is considerable variation in the feeding of syllids, as described in Fauchald and Jumars (1979): Autolytinae feed primarily on hydroids (Okada 1928, Hamond 1969, Hughes 1975); species of Sphaerosyllis eat diatoms and detritus (Jones 1961, Hughes 1975, Schafer 1962); Exogone gemmifera feeds on fish larvae (Rasmussen 1973); Streptosyllis websteri eats diatoms (Hartmann-Schroder 1971, Wolff 1973). In addition, Fauchald and Jumars postulate that all Exogoninae are highly selective deposit feeders that may periodically function as carnivores or carrion-feeders.

Twenty species of syllids were collected during this investigation:

Autolytus alexandri Malmgren, 1867

Brania wellfleetensis Pettibone, 1956

Eusyllis lamelligera Marion and Bobretsky, 1875

Eusyllis sp. A

Exogone dispar (Webster, 1879)

Exogone hebes (Webster and Benedict, 1884)

Exogone naidina Oersted, 1845

Exogone verugera (Claparede, 1868)

Exogone sp. A

Odontosyllis longiseta Day, 1973

Parapionosyllis longicirrata (Webster and Benedict, 1884)

Pionosyllis sp. A

Proceraea sp. A

Sphaerosyllis erinaceus Claparede, 1863

Streptosyllis arenae Webster and Benedict, 1884

Streptosyllis varians Webster and Benedict, 1887

Streptosyllis websteri Southern, 1914

Syllides convoluta Webster and Benedict, 1884

Typosyllis hyalina (Grube, 1863)

Typosyllis tegulum Hartman and Fauchald, 1971

Exogone hebes occurred across the shelf. E. verugera was also abundant across the shelf, but was not as common in shallow habitats (e.g. stations C1, C2, D3). Parapionosyllis longicirrata, Streptosyllis arenae and Sphaerosyllis erinaceus were moderately abundant from the inner shelf to the shelf break (e.g. stations B4, E1, E3, F4). Typosyllis tegulum was widely distributed on the shelf, but was most abundant on the outer shelf and shelf break habitats (e.g. stations E2, E4, F1). None of the other species were collected in abundance.

Exogone verugera, E. hebes, Sphaerosyllis erinaceus, and Typosyllis tegulum were dissected for gut contents analyses. E. verugera contained hundreds of fine quartz grains (approximately 3-12 um in diameter), and very small amounts of amorphous detritus in the middle and posterior gut. No diatoms, forams, or pieces of debris observed in guts of species that ingest sediment (e.g. Ninoe nigripes) were seen in any of the 36 specimens examined. Twenty-three of the specimens were completely empty. E. hebes apparently feeds on the same

material as E. verugera, though only three of 57 specimens dissected contained any material whatsoever in their guts. Gut analyses revealed the identical contents observed in E. verugera: hundreds of fine quartz grains and small amounts of fine detritus. No diatoms or forams were seen. It should be noted that in both species the ingested material only filled small portions of the gut. No specimens had filled guts, and none contained material in the anterior gut.

The hypothesis by Fauchald and Jumars (1979) that Exogone spp. are selective deposit feeders is not at all supported by these data. Rather, this information may indicate feeding on hydroids, Anthozoa, or other animal prey, assuming the fine sediment was previously ingested by the prey organisms.

Sphaerosyllis erinaceus also contained only small amounts of very fine detritus, but differed from Exogone spp. in lacking the abundance of fine sediments seen in the species discussed above. The fine detritus was limited to the posterior gut, and represented only small amounts of material (i.e. the gut was nearly empty). Most specimens (19 of 23) were completely empty. These observations do not lead to any conclusions. Perhaps, S. erinaceus sucks the contents from prey organisms, leaving little material in the gut to be observed following digestion.

Specimens of Typosyllis tegulum contained various materials in their guts. One specimen had ingested a mass of sand and detritus containing coarse and fine sand, forams, and remains of two dinoflagellates. Another contained some detritus and a piece of chitin,

possibly indicating predatory feeding. Other specimens contained only fine detritus and fine sand. Many (8 of 13) were completely empty. These data do not support the postulate by Fauchald and Jumars (1979) that all Syllinae are carnivores on colonial invertebrates. Rather, T. tegulum appears to be a facultative carnivore, capable of both carnivory and selective deposit feeding. Its occurrence on the outer shelf and slope, where colonial hydroids are uncommon, may have forced it to function as an omnivore, as these data suggest.

Broad Scale Patterns

The spatial patterns here defined as "broad scale" referred to distribution on a scale of tens of thousands of meters. Habitat zones of the Middle Atlantic Bight were divided into 5 habitat groups for analyses of broad scale patterns in polychaete feeding biology: inner shelf; middle shelf; outer shelf; shelf break; and slope. The zone divisions were based primarily on relative depth, and to a lesser degree, on general sediment characteristics.

Boesch (1979a) had shown that macrofaunal assemblages in habitats within these zones could be distinguished by numerical classification (cluster analysis). Before analyses of polychaete feeding biology began for this study cluster analysis was conducted on polychaete abundance and distribution data. This was expected to demonstrate that many of the same habitats distinguished by Boesch could be distinguished using polychaete data alone, and would give credence to feeding biology paterns should the same habitats be distinguished by the

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feeding biology classification scheme. All polychaete species were included in the cluster analysis, as were all BLM stations and all 8 quarterly cruises (Table 2). The resultant cluster is shown in Figure 14. Site groups are indicated in Table 4. The cluster analysis indicates the distinction of middle slope polychaetes from all other assemblages. This is probably due to the low abundance of polychaetes on the middle slope. Also clearly distinguished are the shelf break-upper slope, dynamic inner and middle shelf, and intermediate depth assemblages. Most importantly, the assemblages of specific habitats are distinct within the cluster. This illustrates the importance of mesoscale features in the Middle Atlantic Bight, and demonstrates the necessity for an understanding of both broad scale and medium scale faunal patterns.

Each of the 5 broad scale zones is discussed below in terms of polychaete feeding biology, then in terms of species distributions. Polychaete species which primarily accounted for relative proportion variations in feeding biology are included in the discussions by broad scale zone.

A number of hypotheses were posed in this study. The first was that abundance of carnivorous polychaetes decreased with depth, percent silt-clay, and organic carbon content, and increased with course sand. Maurer and Leathem (1981) found that density of motile, jawed carnivorous polychaetes from Georges Bank increased significantly with sand and decreased with carbon during certain seasons. Boesch (1979a) observed a trend toward carnivory in coarse sediments

Figure 14. Numerical classification of Middle Atlantic
Bight stations. Classification hierarchies are
indicated at left. Sampling sites of each site
group are in Table 4 (Bray-Curtis similarity,
flexible sorting, beta = -0.25).

SIMILARITY

| 0.50 | 0.40 | 0.30 | 0.20 |

Dynamic Inner Shelf
  (Fine Sand)   1

Dynamic Inner Shelf   2

Dynamic Middle Shelf   3

Inner Shelf   4

Dynamic Middle Shelf
  (Fine Sand)   5

Dynamic Middle-Outer Shelf   6

Inner Shelf Swales
  (Pre-Hypoxia)   7

Middle-Outer Shelf Shallow
  Swales   8

Outer Shelf Flanks -
  Deep Swales   9

Shelf Break
  (85 - 95 m)   10

Shelf Break (90 - 110 m)   11

Shelf Break (130 - 140 m)   12

Upper Slope (310 - 400 m)   13

Middle Slope (450 - 750 m)   14

Table 4. Site groups selected from numerical classification of polychaetes collected at stations across the shelf and slope. Sites are identified by station and cruise.

Site Group 1
L1-2,4

Site Group 2
C1-1,2,3,4
C2-1,2,3,4
C3-1,2,3,4
D2-2,3
G1-2,4
G2-4
K1-2,4

Site Group 3
D1-1,3,5,7,8
D2-1,4
D3-1,2,3,4

Site Group 4
C2-5,6,7,8
C4-5,6,7,8
G2-6,8

Site Group 5
D1-2,4
L2-2,4,6,8

Site Group 6
B2-5,7,8
B4-1,5,6,7,8
E1-1,4,5,6,7,8
E3-1,5,6,7,8
G4-6,8
K2-4,6,8
L3-2,4

Site Group 7
C4-1,2,3,4

Site Group 8
B1-1,2,3,4,5,6,7,8
B5-5,6,7,8
D4-1,2,3,4,5,6,7,8

Site Group 9
B3-1,2,3,4,5,6,7,8
E2-1,2,3,4,5,6,7,8
E4-1,2,3,4,5,6,7,8
G3-2,4,6,8
I1-2,4,6,8

Site Group 10
F1-1,2,3,4,5,6,7,8
I2-2,4,6,8
L4-2,4,6,8

Site Group 11
A1-1,2,3,4,5,6,7,8
A3-1,2,3,4,5,6,7,8
A4-1,2,3,4,5,6,7,8
F2-1,2,3,4,5,6,7,8
F3-1,2,3,4,5,6,7,8
F4-1,2,3,4,5,6,7,8
G5-2,4,6,8
I3-2,4,6,8
K4-2,4,6,8
K5-2,4,6,8
L5-2,4,6,8

Site Group 12
A2-1,2,3,4,5,6,7,8
G6-2,4,6,8

Site Group 13
G7-2,4
H1-2,4,6,8
I4-2
J1-2,4,6,8
K6-2,4,6,8
L6-2,4,6,8

Site Group 14
H2-2,4,6,8
I4-4,6,8
J2-2,4,6,8

of the Middle Atlantic Bight, so a relationship between sediments and carnivorous species was expected in this study.

Other hypotheses tested in this investigation pertained to the proportions of the three components of detritivores (suspension feeders, surface deposit feeders, and subsurface deposit feeders), and their relationship with sediment characteristics and other parameters variable from habitat to habitat. Boesch (1979a) reported that surface deposit feeders numerically dominated portions of the Middle Atlantic Bight, and attributed this to a response of the benthic community to influx of organics from water column production. Though Boesch primarily limited his analyses to dominant macrofaunal species and this study was limited to the Polychaeta, the same trends were expected. Relatively lower proportions of suspension feeders were expected to inhabit the middle slope, because suspended organics would predictably be less available there. Similarly, less tube-dwelling suspension feeders would be expected in physically unstable habitats such as the inner shelf where sediments would be periodically scoured.

Finally, hypotheses concerning polychaete motility were tested. Jumars and Fauchald (1977) found significantly greater proportions of of sessile polychaetes with depth across the continental shelf, then a trend toward motility at bathyal and abyssal depths. They believed the relationship was due to sediment stability and flux of organic matter. Maurer and Leathem (1981) did not find a similar correlation, perhaps because their samples were limited to 600 m depth and their continental shelf samples were taken in areas of complex topography. They did

conclude that sessile polychaetes generally inhabited more stable sediments, and motile species were more abundant in coarser grained sediment. In this study the investigator tested whether the distributions of motile, discretely motile, and sessile polychaetes were associated with depth and sediment variables.

Feeding Biology

The proportions of feeding biology components are presented in Figure 15. Carnivorous and herbivorous species were omitted from the upper portion of the figure so that the three detritivore components were better compared. Herbivorous polychaetes were uncommon in the study area, and never contributed over 2% of the polychaetes. All other components of the classification are included.

There was a significant negative correlation between the proportion of surface deposit feeders and increasing depth across the shelf ($r = -0.944$, $\alpha \leq 0.05$), an increase at the shelf break, and a slight decrease down the slope. Proportion of subsurface deposit feeders increased significantly with depth across the shelf ($r = 0.982$, $\alpha \leq 0.01$), decreased at the break then increased again down the slope. Suspension feeders were in greatest relative abundance at intermediate shelf depths, and were very poorly represented on the inner shelf and middle slope.

Motile polychaetes numerically dominated all depth zones (Figure 15). The proportion of sessile polychaetes was positively correlated with both organic carbon ($r = 0.999$, $\alpha \leq 0.05$) and percent silt and clay ($r = 0.998$, $\alpha \leq 0.05$) in non-swale habitats on the shelf. The

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Figure 15. Percentage of polychaete feeding, motility and
            morphology by major habitat. Carnivores and herbivores
            are excluded. [subsurface deposit feeders (B); surface
            deposit feeders (S); suspension feeders (F); discretely
            motile (D); motile (M); sessile (L); jawed (J); soft
            proboscis (X); tentaculate (T); pumping (P)].
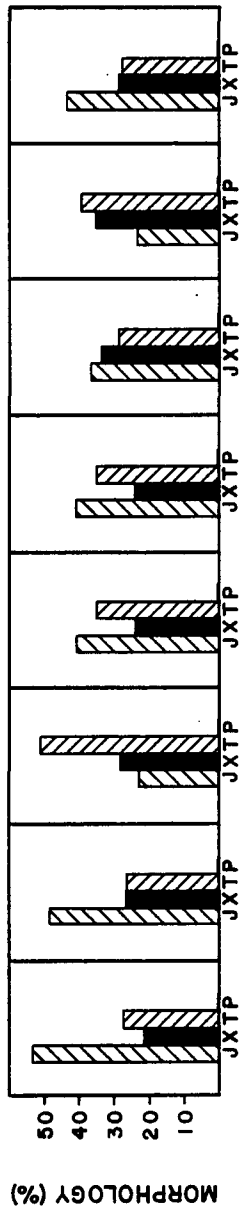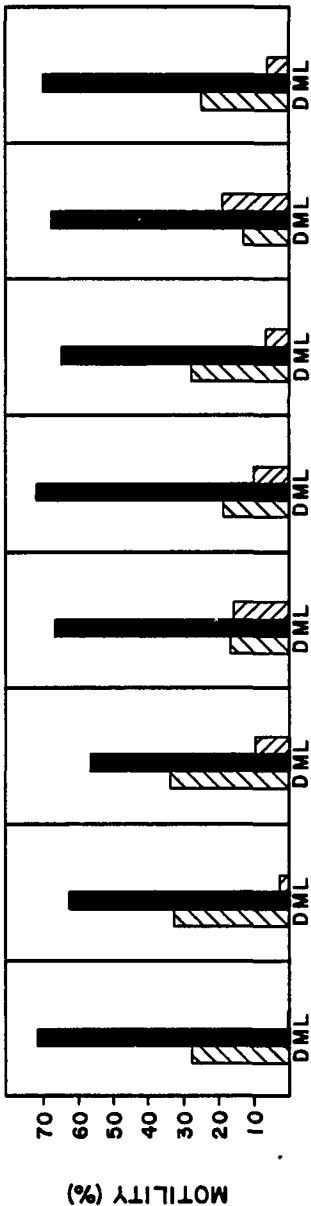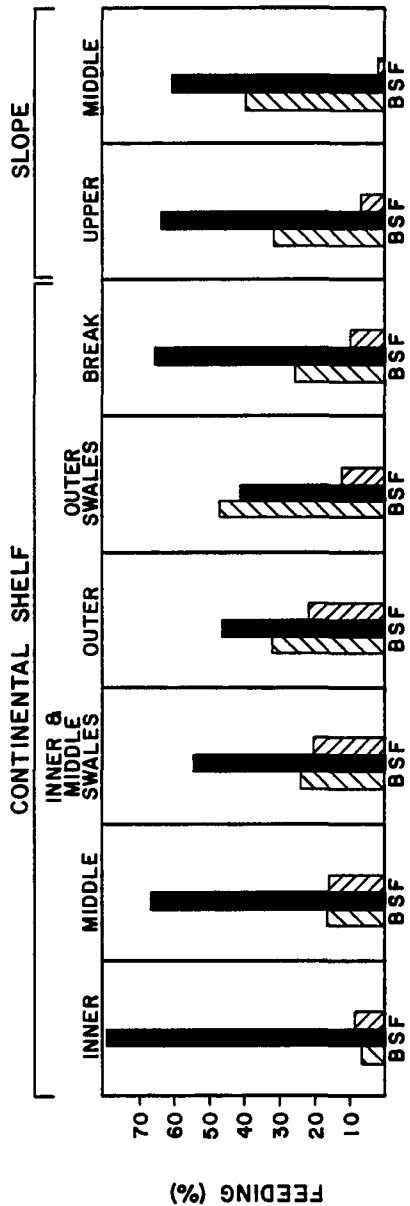
relative proportion of sessile polychaetes was greatest at the upper slope (19%), and was lowest on the inner shelf (less than 1%). The proportion of discretely motile polychaetes was greatest on the inner (28%) and middle shelf (33%) and at the shelf break (28%).

The polychaete morphological components are presented for comparison at the bottom of Figure 15. Jawed polychaetes were in greatest proportion at non-swale habitats of the inner (53%) and middle shelf (48%), and were in considerably less proportion (23%) at inner and middle shelf swales (topographic lows). Tentaculate polychaetes were abundant in all zones, but in greatest proportion in the inner and middle shelf swales (51%). Only a single species, Spiochaetopterus oculatus, was included in the class "pumping". This species was not abundant in the Middle Atlantic Bight. It contributed less than 1% of the polychaetes in the zones here examined, and was excluded from subsequent analyses.

Carnivorous polychaetes were in greatest proportion in the inner (53%) and middle shelf zones (40%) and in least proportion at the shelf break (7%). There was a negative correlation ($r = -0.970$, $\alpha \leq 0.05$) between percentage of carnivorous polychaetes and increasing depth across the shelf. Carnivorous polychaetes were also negatively correlated ($r = -0.757$, $\alpha \leq 0.05$) with organic carbon from the inner shelf to the slope.

As will be demonstrated below, it became apparent that longshore variability in abundance of carnivorous polychaetes in the study area was too great to demonstrate significant associations of polychaetes

with sediment variables of combined depth zone transects. For this reason, the transects of stations G1-G7, K1-K6, and L1-L6 (Figure 3) were analyzed separately. Carnivorous polychaete relative abundance to other feeding components was negatively correlated with organic carbon ($r = -0.788$, $\alpha \leq 0.05$), percent silt and clay ($r = -0.791$, $\alpha \leq 0.05$), and median diameter of sediments ($r = -0.828$, $\alpha \leq 0.05$) from the inner shelf to the slope in transect G. There was a strong negative correlation ($r = -0.920$, $\alpha \leq 0.01$) between carnivorous polychaetes and organic carbon along transect K. None of the above parameters were significatly correlated with proportion of carnivorous polychaetes in transect L. These variations between transects probably resulted, at least in part, from the differences between sediments of the northern and southern Middle Atlantic Bight inner and middle shelf. Generally the northern areas graded from coarse to fine sediments with depth, whereas the inner and middle shelf surficial sand off Virginia was primarily fine or very fine sand. On the outer shelf the sediments of transect L were anomalously coarser than were inner shelf sediments. The polychaetes which dominated the sediments of the different areas also varied dramatically, as will be demonstrated below.

Figures 16 through 18 are ternary diagrams which provide a spatial distribution model of each station by feeding, motility, and morphology classifications. Carnivorous and herbivorous species have been excluded from Figure 16. As evidenced by Figure 16, non-swale inner shelf habitats were dominated by surface deposit feeders, providing over 95% of the individuals at some stations (e.g. stations C2, C3).

Figure 16. Tenary diagram of broad scale sampling sites identified
by habitat. Sites are distributed by percentage of the
three components of deposit feeding polychaetes:
surface, subsurface and suspension. Mean values of
sites in each habitat are plotted as centroids in small
diagram at right.

100% SUSPENSION FEEDERS

PERCENT SUSPENSION FEEDERS →

100 % SUBSURFACE DEPOSIT FEEDERS

← PERCENT SURFACE DEPOSIT FEEDERS

PERCENT SUBSURFACE DEPOSIT FEEDERS →

100% SURFACE DEPOSIT FEEDERS

90 80 70 60 50 40 30 20 10

10 20 30 40 50 60 70 80 90

90 80 70 60 50 40 30 20 10

- INNER SHELF
▲ MIDDLE SHELF
■ INNER-MIDDLE SWALES
△ OUTER SHELF
□ OUTER SHELF SWALES
○ SHELF BREAK
⊕ SLOPE

OL4
▲L2
△L3
FINE SAND
OK2
OUTER SHELF
SHELF BREAK
SLOPE
MIDDLE SHELF
INNER SHELF

Figure 17. Tenary diagram of broad scale sampling sites
            identified by habitat. Sites are distributed by
            percentage of the three components of polychaete
            motility: motile, discretely motile and
            sessile. Mean values of sites in each habitat
            are plotted as centroids in small diagram at
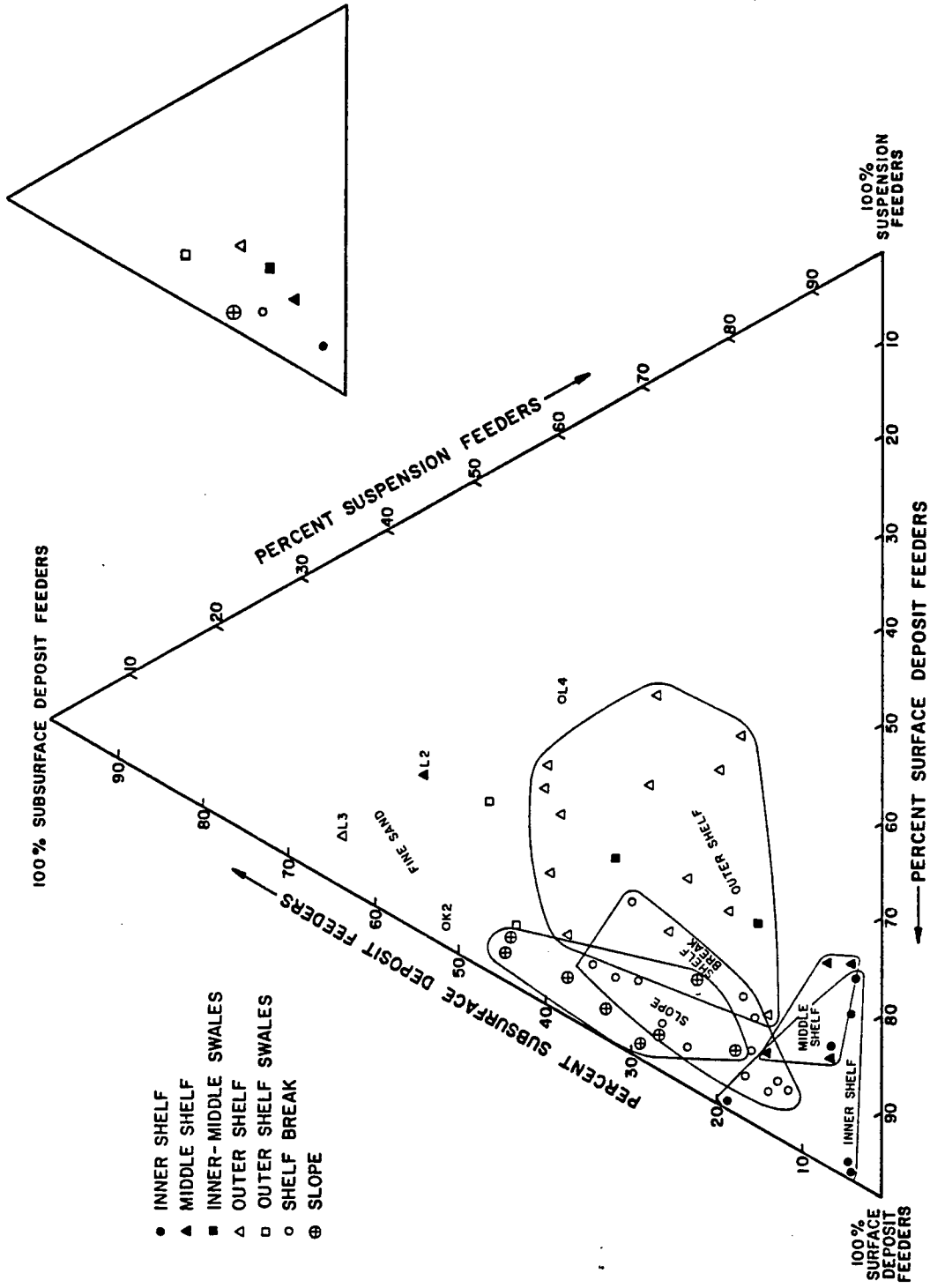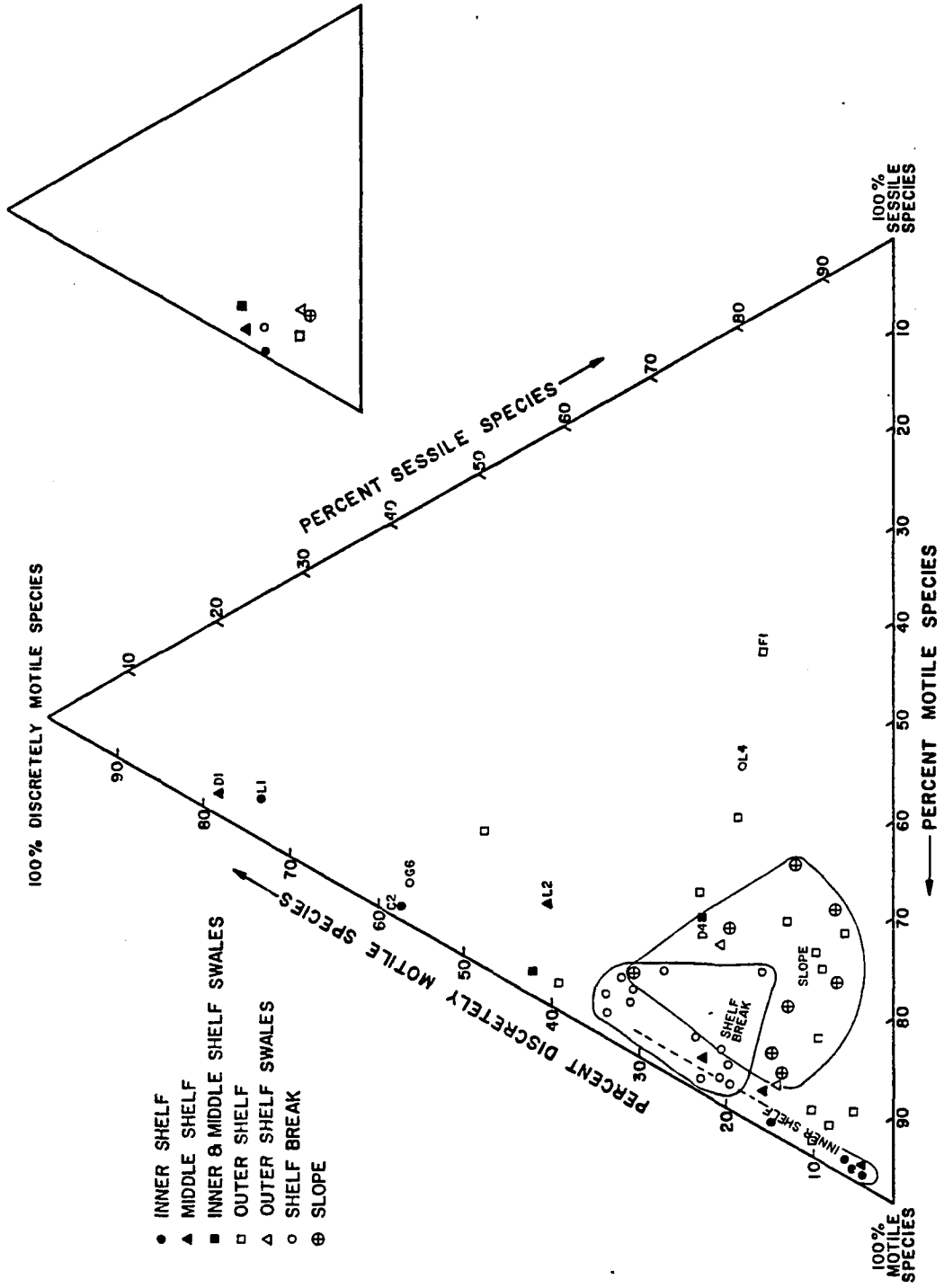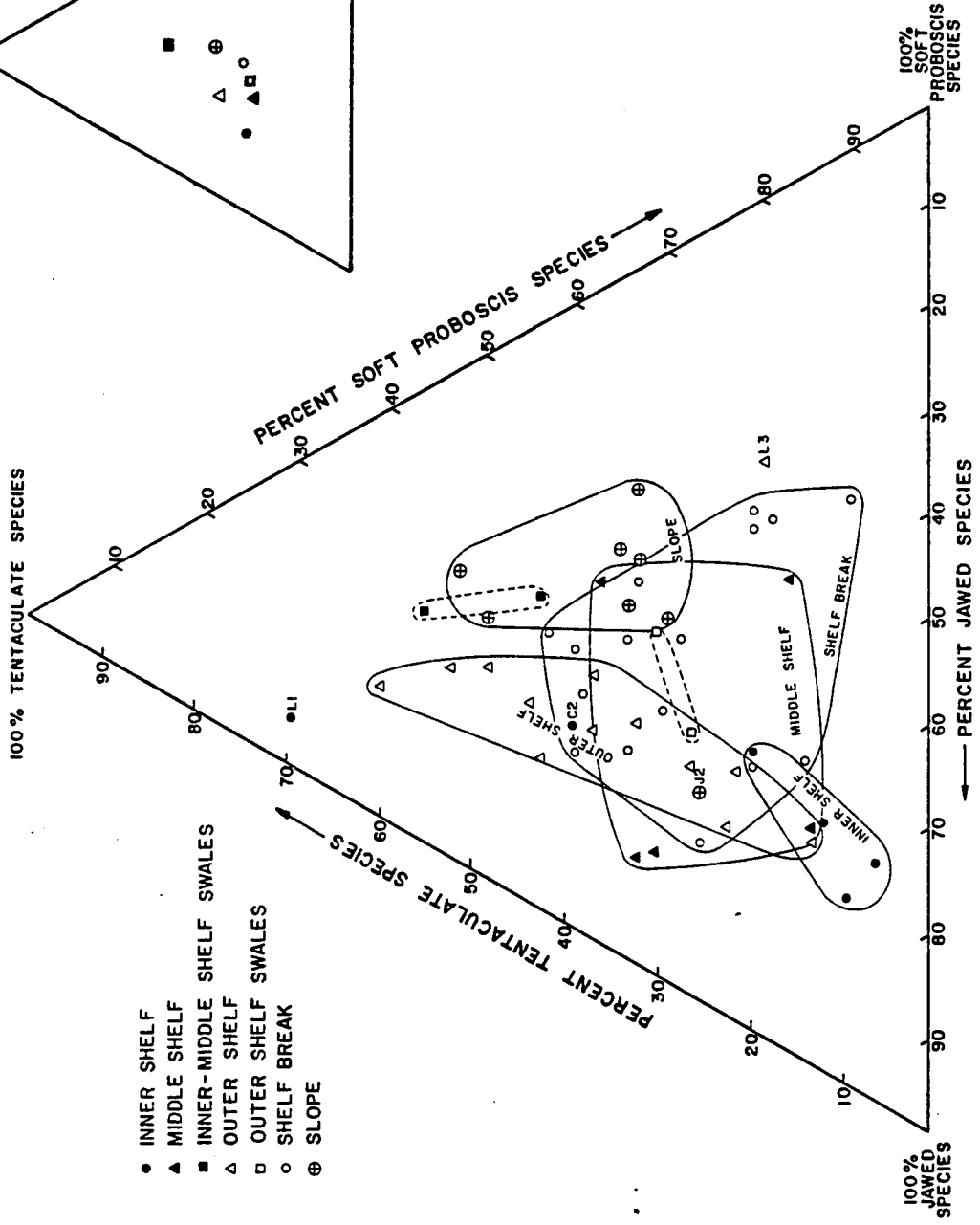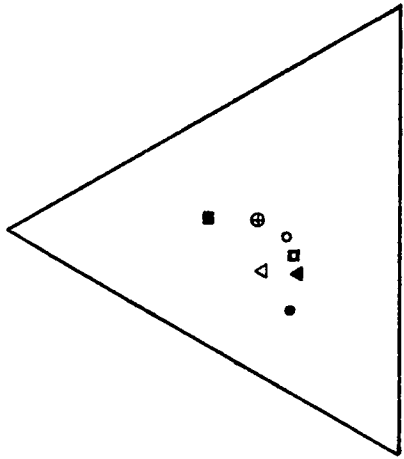   right.

Figure 18.   Tenary diagram of broad scale sampling sites
identified by habitat. Sites are distributed
by percentage of the three primary components
of polychaete morphology: jawed, tentaculate
and soft proboscis. Mean values of sites in
each habitat are plotted as centroids in small
diagram at right.

Middle shelf sites, with the notable exception of station L2, were dominated by surface deposit feeders. Station L2 was abundant in subsurface deposit feeders, primarily lumbrinerids. There was a distinction between inner and middle shelf swale habitats and other inner and middle shelf stations. The swales had a greater proportion of subsurface deposit feeders, and in that regard more closely resembled outer shelf stations. Shelf break stations generally contained a lower proportion of subsurface deposit feeders. There was an increase in proportion of suspension feeders from inner to outer shelf habitats. Shelf break stations generally contained a lower proportion of suspension feeders than non-swale outer shelf stations. Slope stations were distinguished in generally having a greater proportion of subsurface deposit feeders than the inner and middle shelf, and fewer suspension feeders than the outer shelf.

Figure 17 is the ternary diagram for motility. Most of the stations were numerically dominated by motile species. Inner shelf stations generally contained the greatest proportion of motile polychaetes. The only inner shelf stations with less than 80% motile polychaetes were station L1, a habitat of physically dynamic fine or very fine sand, and station C2 located on a ridge flank with medium-coarse sand. Both were abundant in discretely motile species, primarily magelonids and spionids (e.g. Prionospio dayi and Spiophanes bombyx). Most middle shelf sites contained less than 2% sessile species, and were widely dispersed along the discretely motile-motile axis. Outer shelf sites generally contained a greater proportion of sessile

polychaetes than the inner or middle shelf. Station F1, a medium-fine sand habitat on the shelf break, had a greater proportion of sessile polychaetes (50%) than any other site. This resulted from the extensive populations of <u>Chone infundibuliformis</u> supported there. Most shelf break stations contained 20 to 35 percent discretely motile species. Exceptions were station L4, abundant in the sessile species <u>C</u>. <u>infundibuliformis</u>, and station G6, occupied by 58% discretely motile polychaetes (e.g. onuphids and eunicids). Many slope stations were generally similar to outer shelf stations in proportion of the motility components, though as will be demonstrated below, the two zones did not share similar polychaete assemblages.

The feeding morphology ternary diagram (Figure 18) indicates the greater proportion of jawed polychaetes at most inner shelf stations. The exceptions were stations C2 and L1, both relatively abundant in tentaculate polychaetes (e.g. magelonids and spionids). None of the depth zones were clearly separated by morphological characteristics, though there was a trend toward more tentaculate species on the outer shelf than at shallower zones. Station L3 was distinguished from other outer shelf sites due to abundance of soft proboscis polychaetes, especially orbiniids and paraonids. Slope stations generally had fewer jawed polychaetes than most other habitats. The exceptions were the inner and middle shelf swales which had similar proportions of each morphological component that inhabited the slope, but a different polychaete fauna.

Polychaete Species Distributions

Figures 19 through 28 indicate the distribution of feeding biology classes (e.g. surface deposit feeding, subsurface deposit feeding, suspension feeding) by collection site in broad scale areas of the Middle Atlantic Bight. The figures are discussed by depth zone below. This allows comparison of habitats within each zone, and included species assemblage comparisons.

Boesch (1979a) found the New Jersey inner shelf inhabited primarily by small macrofauna and large motile megafauna including decapods and sea stars. This pattern among the benthos was severely disrupted by hypoxic and anoxic conditions of July and August of 1976. Many of the megafaunal species were temporarily eliminated from the New Jersey inner shelf, and the macrofauna subsequently became dominated by tube-dwelling opportunistic species (e.g. Spiophanes bombyx, Asabellides oculata) and cerianthid anemones (Steimle and Radosh 1979). The causes and effects of the 1976 oxygen depletion were well documented in a summary by Swanson and Sindermann (1979), and therefore were not extensively detailed in this study. It should be noted, however, that the affected area extended from the inner shelf off Delaware Bay to the inner shelf off Long Island, and to the New Jersey middle shelf. Numerous of the polychaete species included in this investigation were impacted. Interstitial-feeding species such as Lumbrinerides acuta were almost completely eliminated at station C2, whereas populations of another interstitial-feeding polychaete, Goniadella gracilis, persisted through conditions of low oxygen. Post-hypoxia population irruptions

Figure 19. Abundance (m^{-2}) of surface deposit feeding
at polychaetes at sampling sites in the Middle
Atlantic Bight.

1000 m

100 m

NEW YORK

RARITAN BAY

NEW JERSEY

DELAWARE BAY

DELAWARE

MARYLAND

VIRGINIA

CONTINENTAL SHELF

SLOPE

G7 H2 H1 G6 A4 I4 J2 G5 A3 I3 J1 A2 F4 K6 A1 F3 I2 F2 K5 I1 B3 F1 E3 B1 E2 K4 B4 B2 E4 E1 L6 B5 G4 G3 D2 L5 D1 D4 D3 L4 G2 K3 L3 G1 L2 C1 C4 C2 C3 K2 K1 L1

1000 INDIVIDUALS m^{-2}
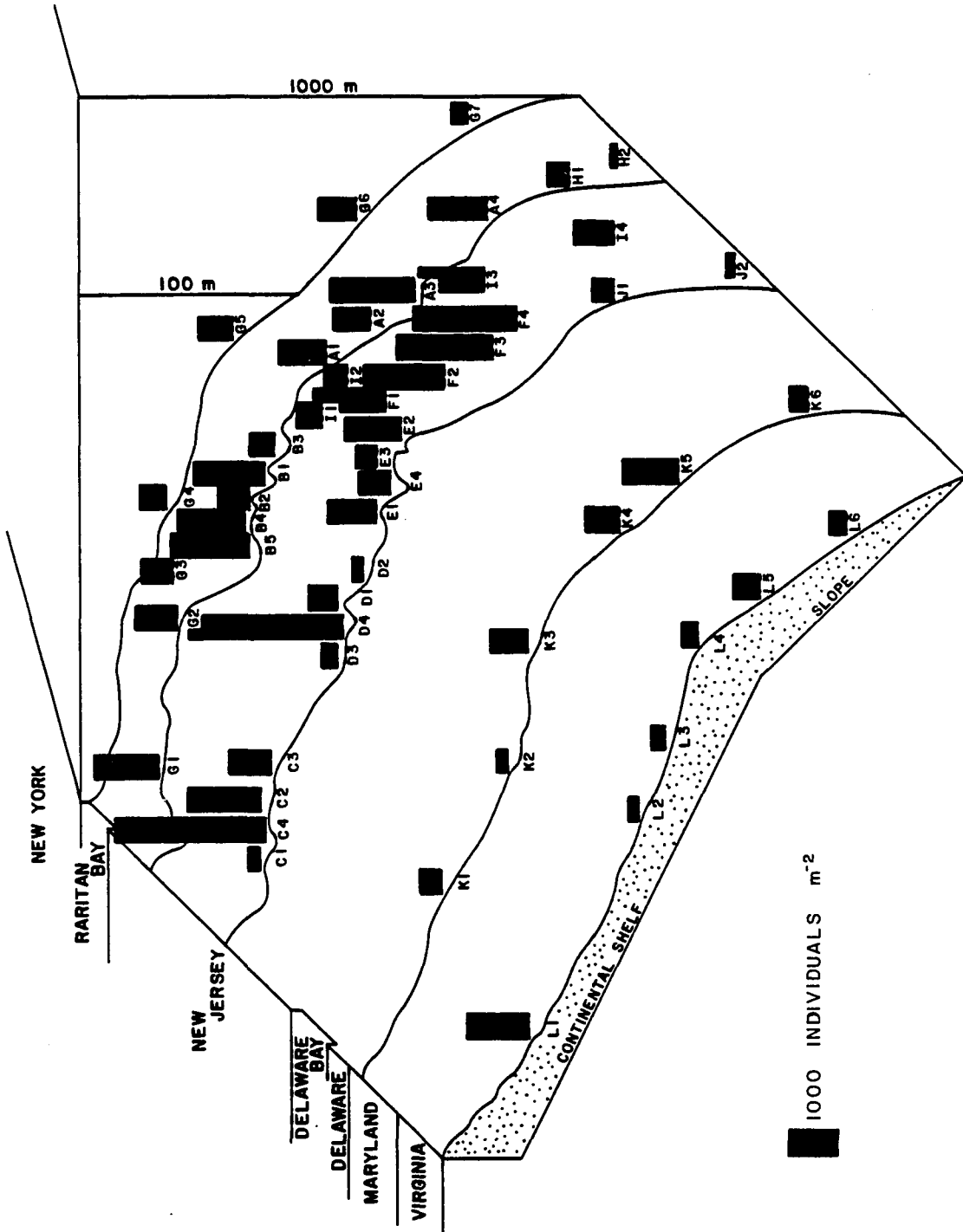
Figure 20. Abundance (m^{-2}) of carnivorous polychaetes at sampling sites in the Middle Atlantic.

1000 INDIVIDUALS m^{-2}
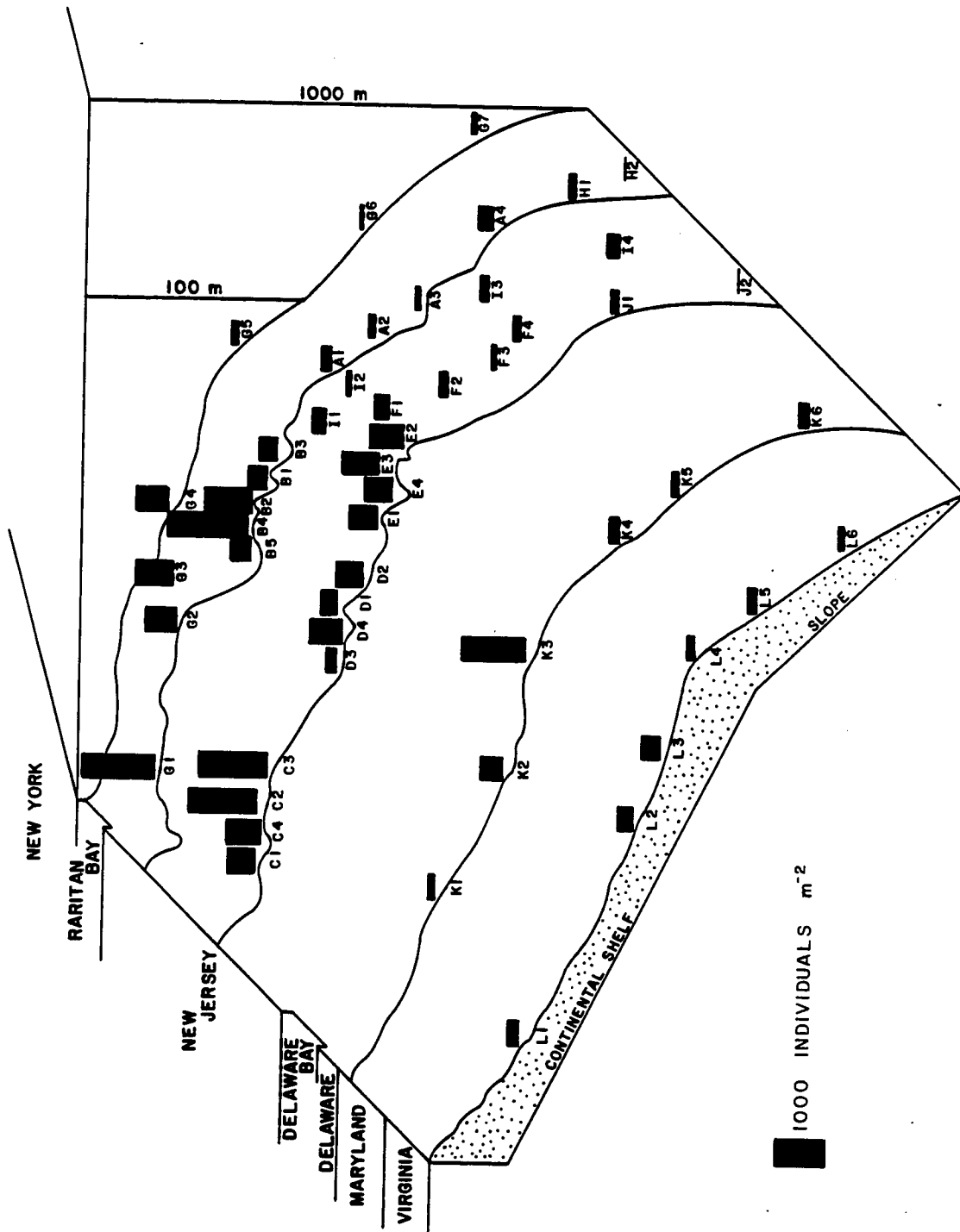
Figure 21. Abundance (m^{-2}) of jawed polychaetes at
sampling sites in the Middle Atlantic Bight.

1000 INDIVIDUALS m^{-2}
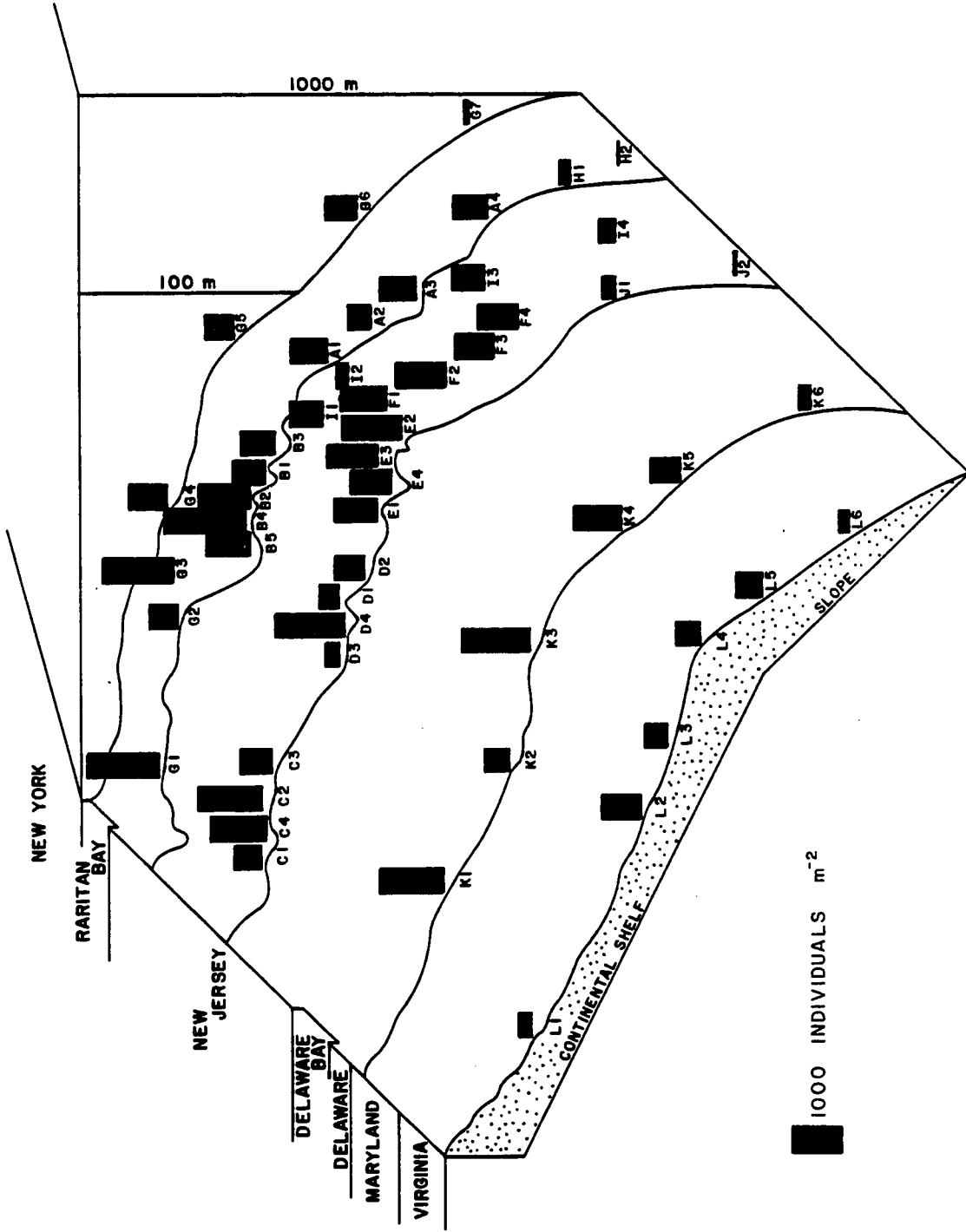
Figure 22. Abundance (m^{-2}) of subsurface deposit
feeding polychaetes at sampling sites in the
Middle Atlantic Bight.

1000 m

100 m

NEW YORK

RARITAN BAY

NEW JERSEY

DELAWARE BAY

DELAWARE

MARYLAND

VIRGINIA

CONTINENTAL SHELF

SLOPE

G7
H2
H1
A4
I4
J2
G6
A3
I3
J1
G5
A2
F4
A1
F3
I2
F2
F1
I1
B3
E2
B1
E3
B4 B2
E4
B5
E1
D2
G4
D1
G3
D4
G2
D3
C3
G1
C2
C4
C1
K6
K5
K4
L6
K3
L5
L4
K2
L3
K1
L2
L1

1000 INDIVIDUALS m^{-2}

Figure 23. Abundance (m^{-2}) of suspension feeding
polychaetes at sampling sites in the Middle
Atlantic Bight.

Figure 24. Abundance (m^{-2}) of motile polychaetes at
sampling sites in the Middle Atlantic Bight.

1000 INDIVIDUALS m⁻²

Figure 25. Abundance (m^{-2}) of sessile polychaetes at
sampling sites in the Middle Atlantic Bight.

110

Figure 26. Abundance (m^{-2}) of soft proboscis
polychaetes at sampling sites in the Middle
Atlantic Bight.

NEW YORK

RARITAN BAY

NEW JERSEY

DELAWARE BAY

DELAWARE

MARYLAND

VIRGINIA

1000 m

100 m

CONTINENTAL SHELF

SLOPE

1000 INDIVIDUALS m^{-2}
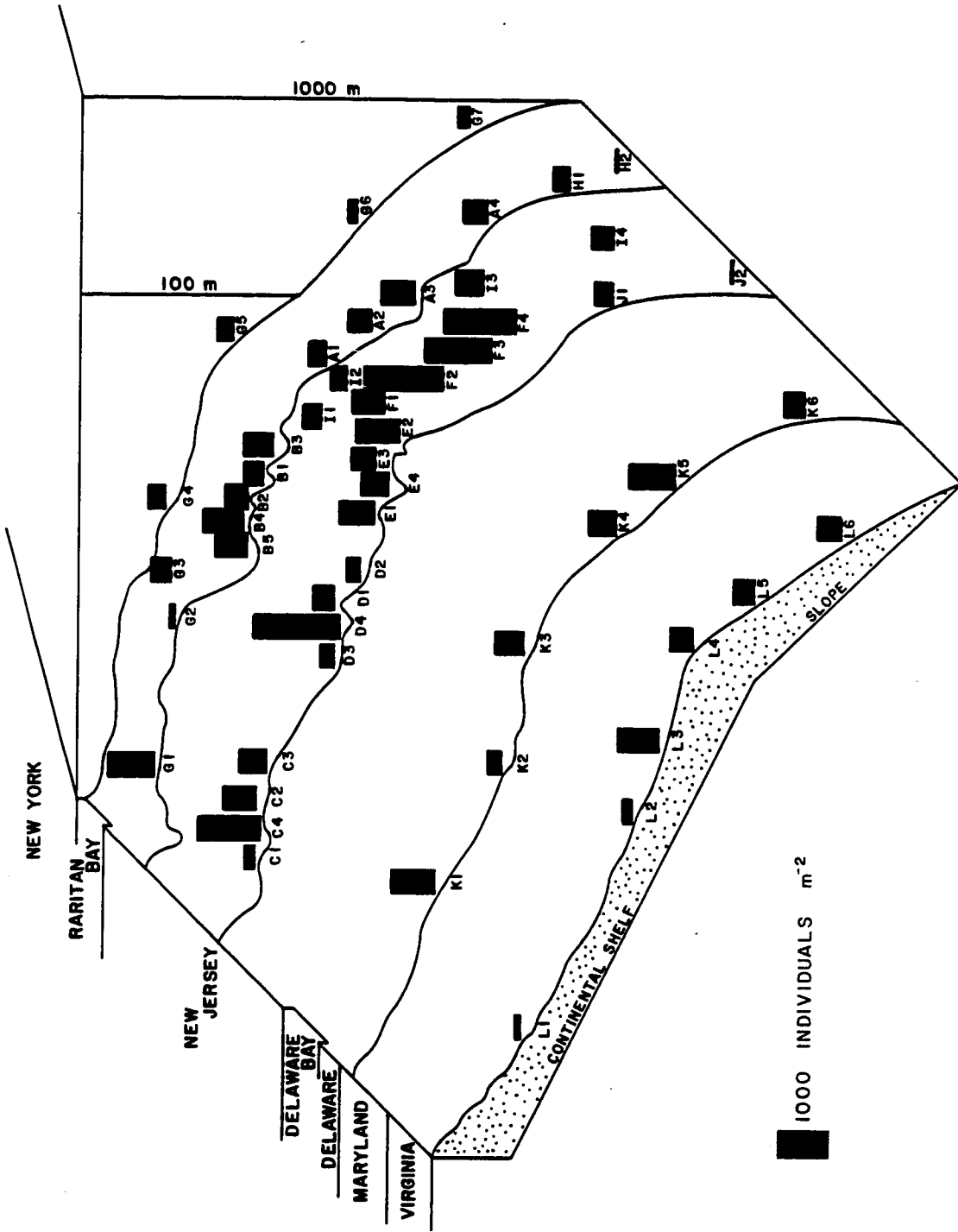
Figure 27. Abundance (m^{-2}) of tentaculate polychaetes at sampling sites in the Middle Atlantic Bight.

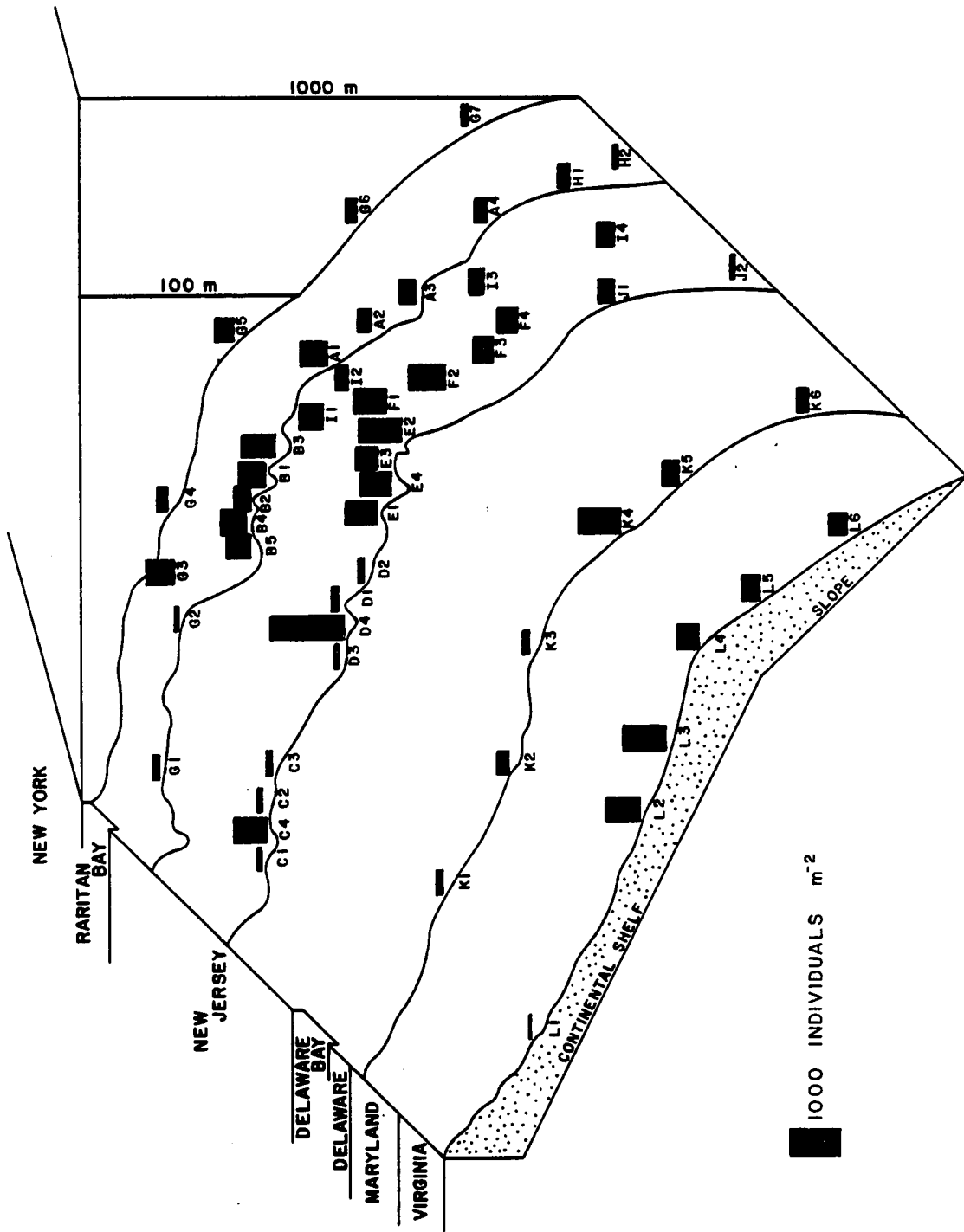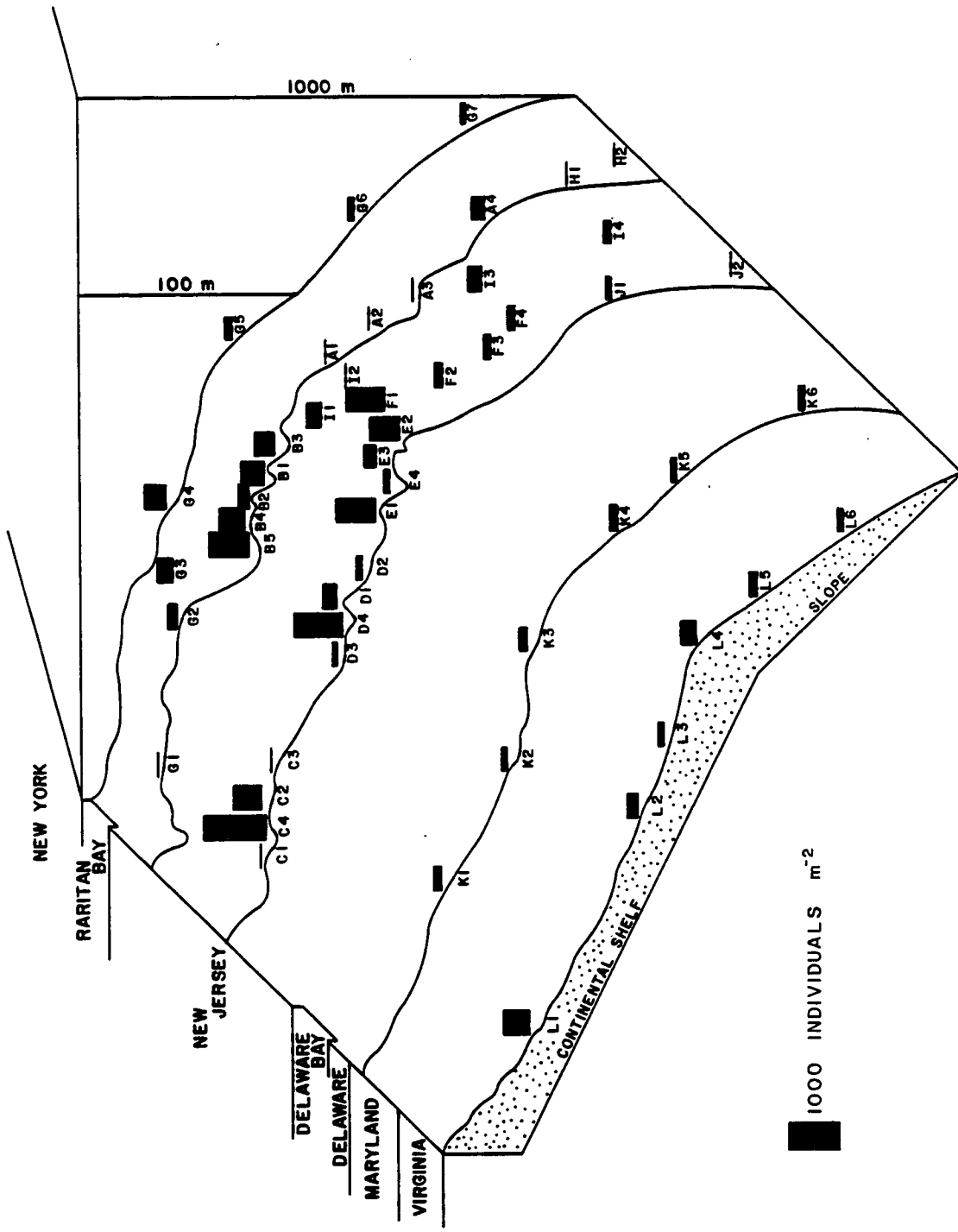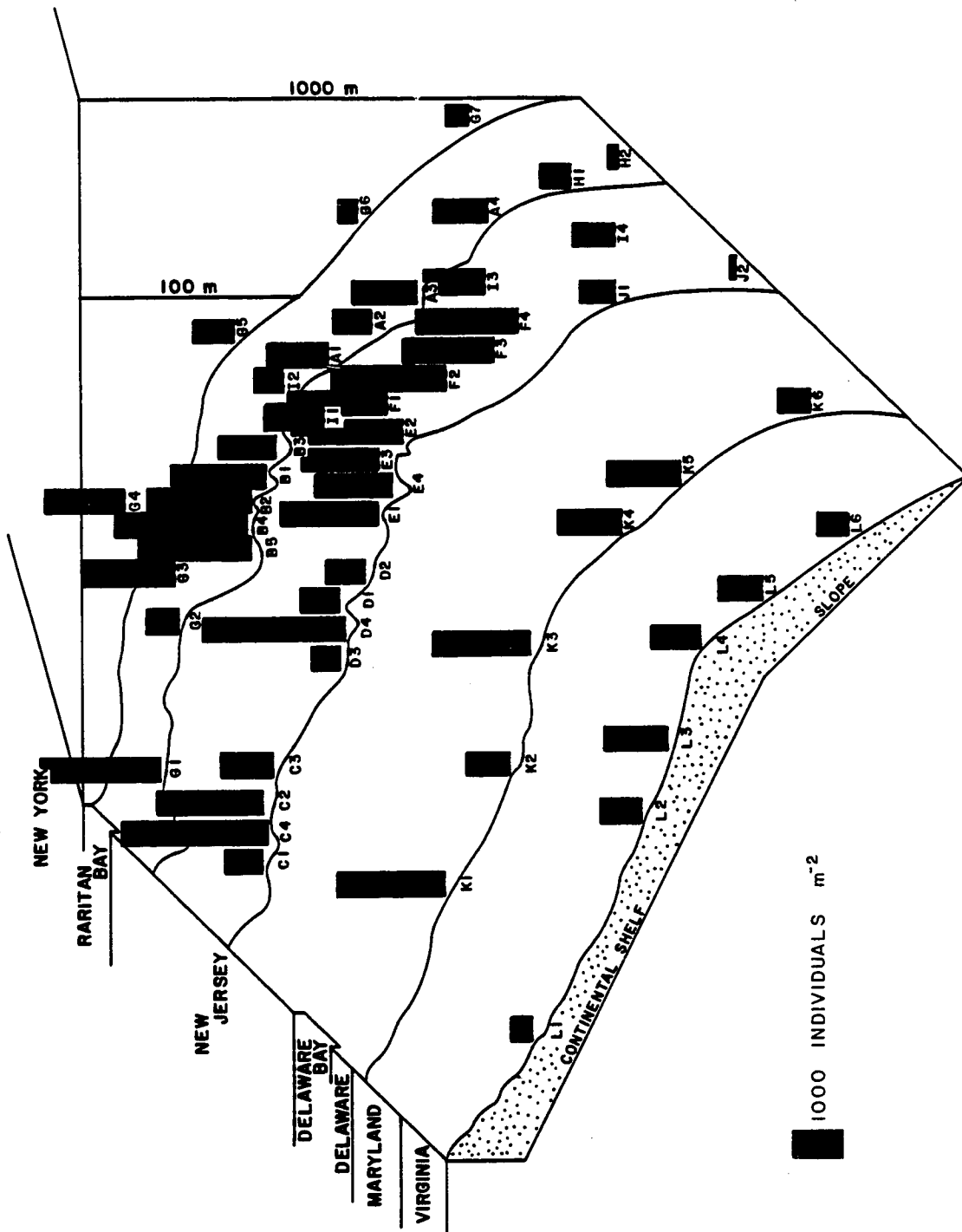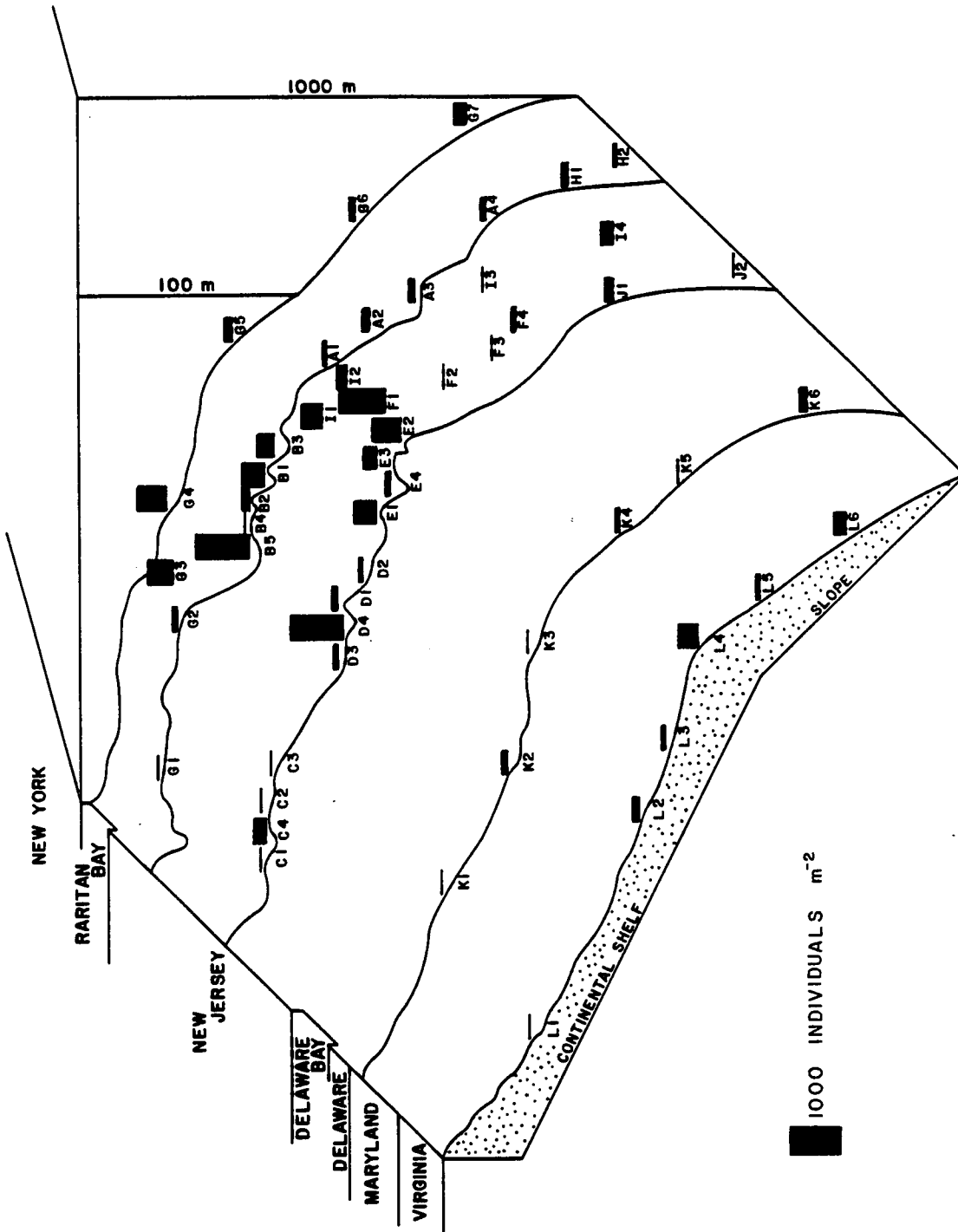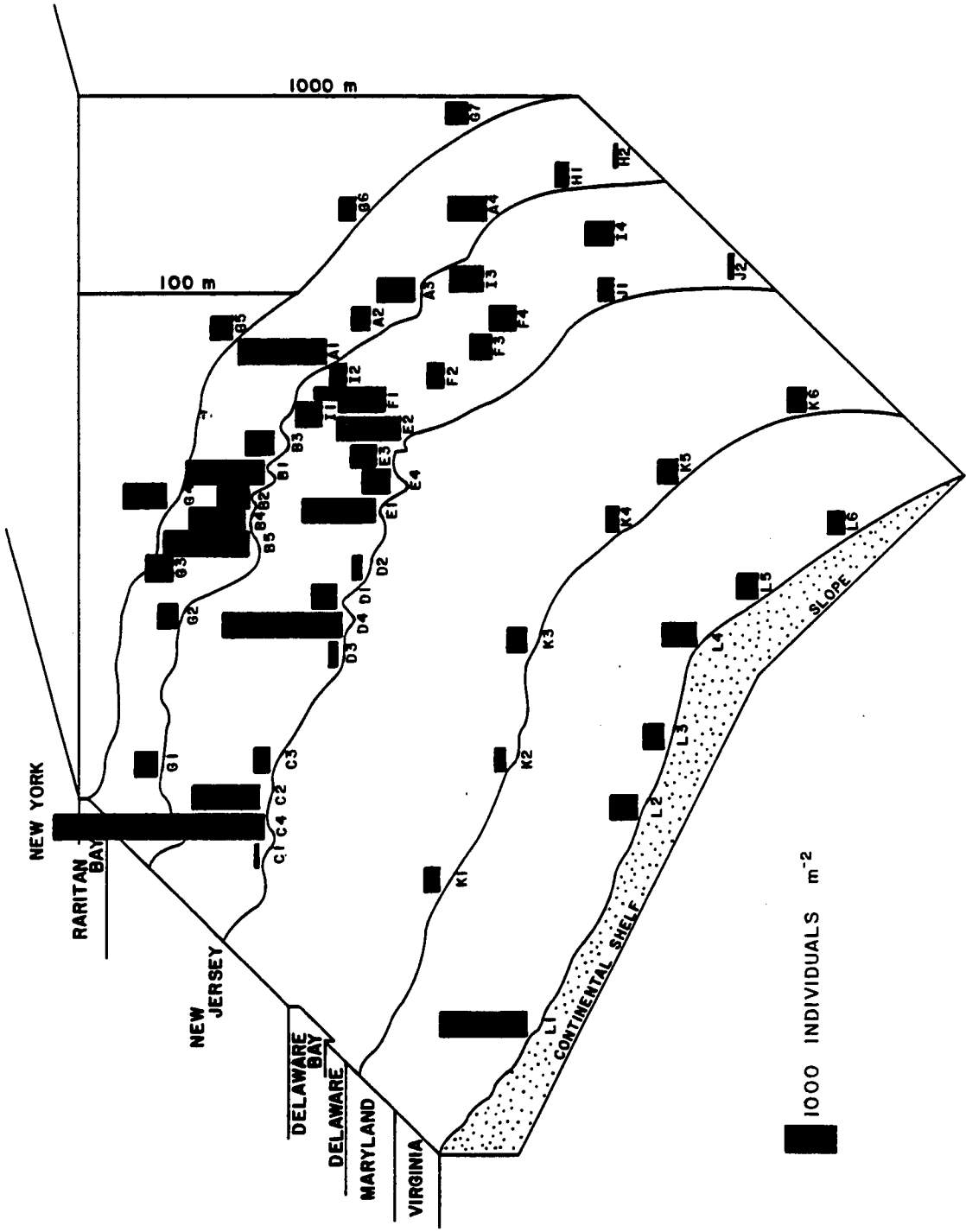Figure 28. Abundance (m^{-2}) of discretely motile polychaetes at sampling sites in the Middle Atlantic Bight.
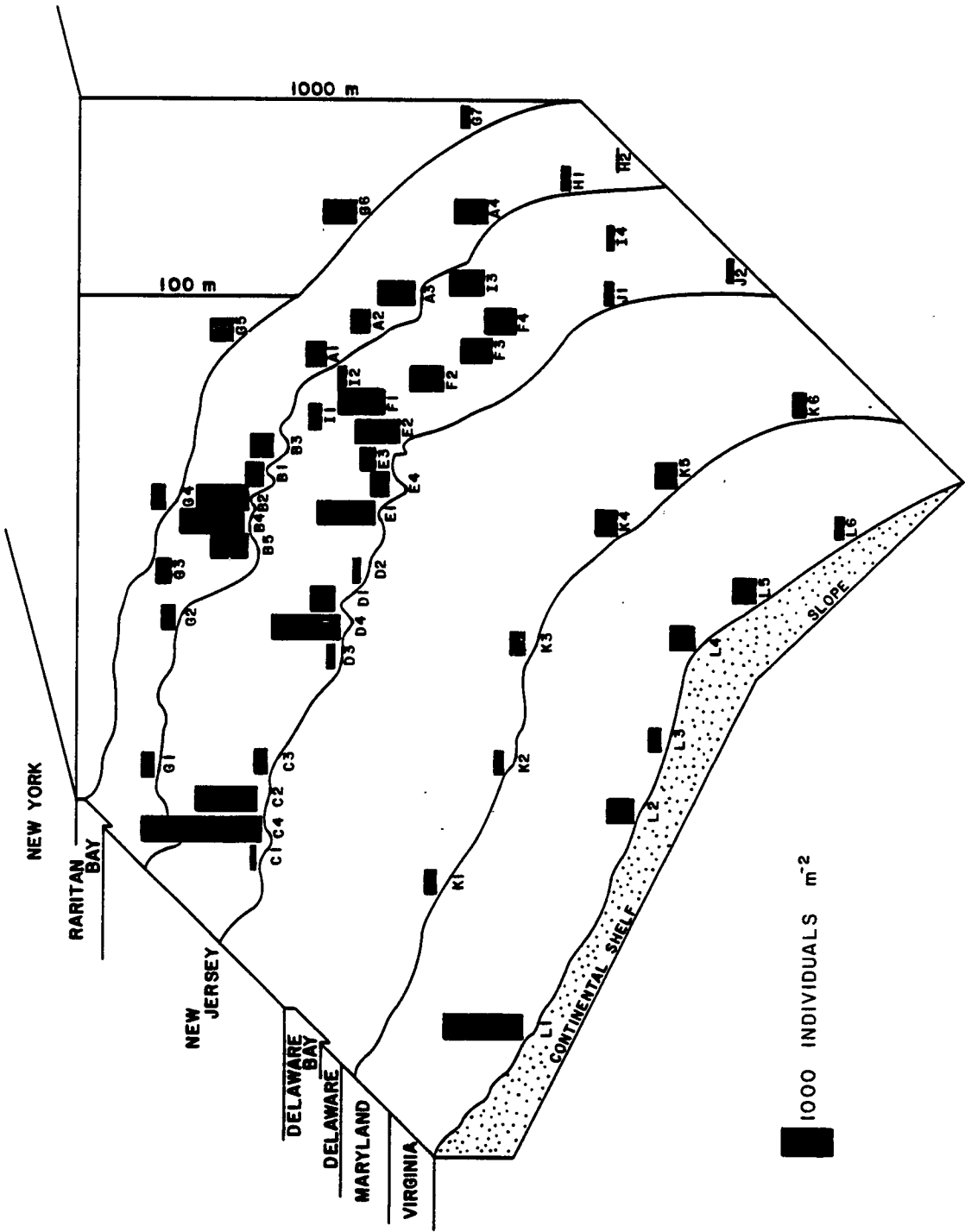
by opportunistic species such as <u>Spiophanes</u> <u>bombyx</u> drastically altered the ratios of feeding classifications present before hypoxia at certain inner shelf stations.

Except in areas affected by hypoxia, the Middle Atlantic Bight inner shelf polychaete fauna may be generally characterized as being dominated by active burrowers, some predaceous (e.g. <u>Goniadella</u> <u>gracilis</u>, <u>Lumbrinerides</u> <u>acuta</u>) in dynamic habitats, and surface or sub-surface deposit feeders (e.g. <u>Aricidea</u> <u>catherinae</u>, <u>Euclymene</u> <u>zonalis</u>, <u>Lumbrineris</u> <u>impatiens</u>) in more quiescent depressions such as swales. In fine sand habitats off Virginia (station L1) where interstices between sand grains were smaller than those of the coarse sands off New Jersey, the polychaete fauna consisted primarily of burrowing species of magelonids and nephtyids and periodically species of spionids.

A total of seven inner shelf stations was sampled. These included four in ridge fields (stations C1-C4), and three on relatively level bottom (stations G1, K1, L1). The general sediment characteristics for each station are summarized in Table 1.

The feeding classification ratios of polychaetes on the inner shelf are presented in Figure 15. The inner shelf was distinguished in having lower percentages of subsurface deposit feeders and filter feeders, and higher percentages of surface deposit feeders, than the remainder of the shelf. The most abundant surface deposit feeding species on the inner shelf were <u>Asabellides</u> <u>oculata</u>, <u>Polygordius</u> sp. A, and <u>Spiophanes</u> <u>bombyx</u> (Table 3). Of these, only <u>Polygordius</u> typically

inhabits high energy habitats on the shelf. S. bombyx and A. oculata are opportunistic species most abundant in shelf depressions.

Figure 19 indicates the relative abundances of surface deposit feeders across the shelf. With the exception of stations C1 and C4, most inner shelf sites provided habitat for about 1000 surface deposit feeding polychaetes m^{-2}. Station C1 was relatively depauperate of annelids (Figure 29), while the swale habitat of station C4 was occupied by approximately 3500 surface deposit feeders.

The distributions and abundance of carnivores on the shelf is provided in Figure 20. On the inner shelf, carnivores were most abundant at stations G1 (1400 individuals m^{-2}), C2 and C3 (both approximately 1250 individuals m^{-2}), and least abundant at station K1 (50 individuals m^{-2}). Station G1 was the only inner shelf station with gravelly-coarse sand (Table 1). The others were medium-coarse sand habitats. The most abundant carnivores at these sites were Goniadella gracilis, Lumbrinerides acuta, and Nephtys picta. All typically inhabit dynamic sand habitats.

The inner shelf sites were occupied by higher percentages of jawed polychaetes than any other portion of the shelf or slope (Figure 3). Tentaculate and soft proboscis species included only 27% and 21% (respectively) of the specimens. Goniadella gracilis, Lumbrinerides acuta, and Nephtys picta contribute most of the jawed specimens. On the inner shelf these were most common at stations C2, K1, and G1 (Figure 21). All were commonly collected in physically dynamic habitats. On the inner shelf these were generally coarse sand or gravelly

Figure 29.   Total annelids (m^{-2}) at sampling sites in
             the Middle Atlantic Bight.

1000 m

100 m

NEW YORK

RARITAN BAY

NEW JERSEY

DELAWARE BAY

DELAWARE

MARYLAND

VIRGINIA

CONTINENTAL SHELF

SLOPE

5000 INDIVIDUALS m^{-2}

G7
H2
H1
B6
A4
I4
J2
G5
A3
I3
A2
F4
A1
F3
I2
F2
I1
F1
B3
E2
B1
E3
E4
B4 B2
E1
B5
G4
D2
G3
D4 D1
G2
D3
C1 C4 C2 C3
G1
K6
K5
K4
L6
K3
L5
L4
K2
L3
L2
K1
L1
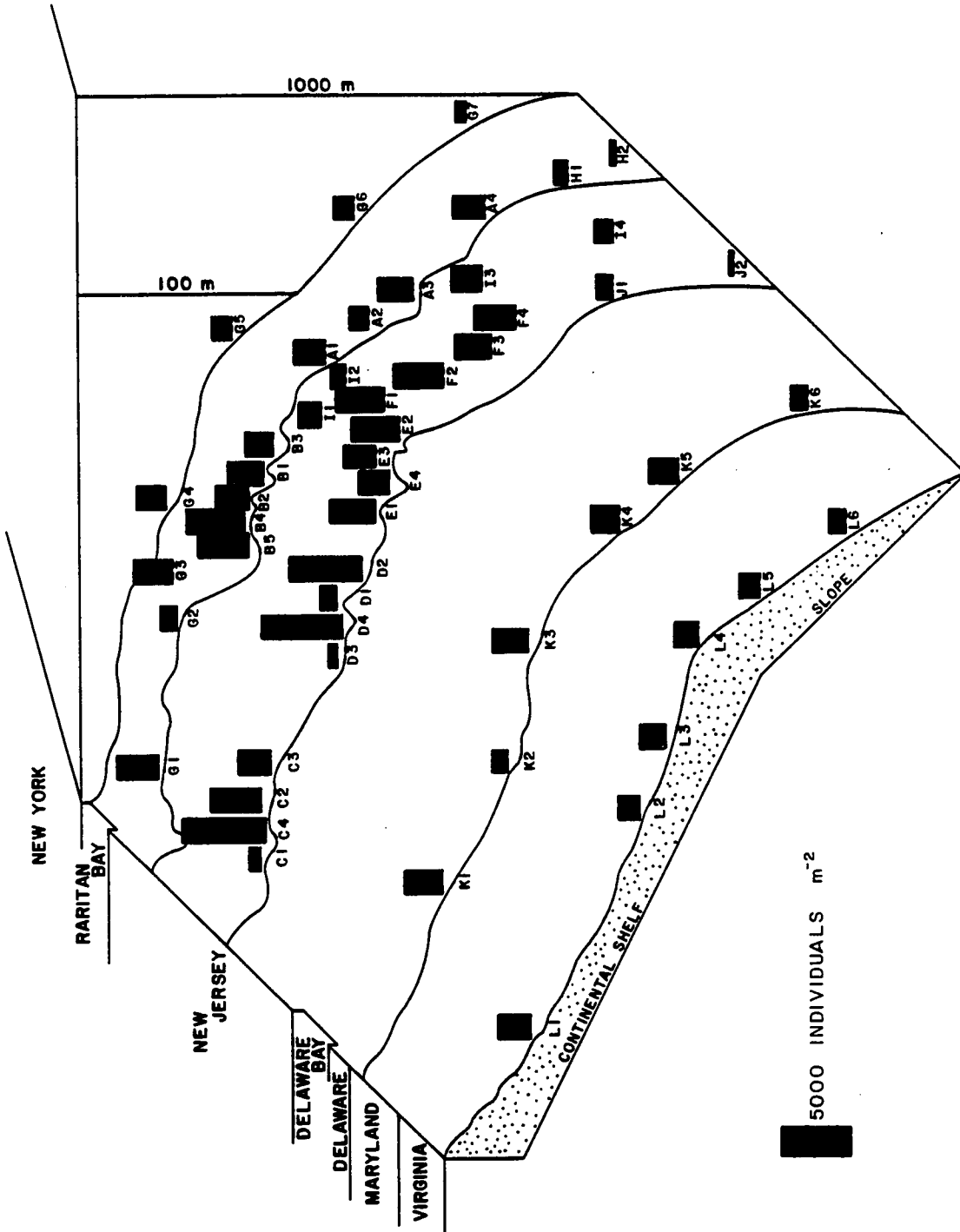
sand habitats (e.g. stations G1, K1). In this shelf zone, jawed species contributed up to 1500 individuals m^{-2} (Figure 21), 72% of the polychaetes (station G1). In the fine sand of station L1, on the other hand, jawed species represented only 23% of the individuals (219 individuals m^{-2}).

Many of the inner shelf macrofaunal dominant species also were dominants on the middle shelf. This was expected since there were no distinct breaks between the zones. The fauna actually constitutes a coenocline, or community continuum, across the shelf of the Middle Atlantic Bight (Boesch 1979a). For instance, Spiophanes bombyx and Goniadella gracilis were abundant in both inner and middle zones of the shelf.

The middle shelf sampling included stations D1 through D4, G2 and L2. Area D includes a ridge field, and each of the stations within the area is located at discrete habitats in the field (Table 1). Stations G2 and L2 are medium sand and fine sand habitats (respectively) on relatively level bottom.

Although many of the species of inner and middle shelf habitats were similar, the ratios of feeding, motility, and morphology of the poly- chaete fauna differed (Figure 15). There were more suspension feeders on the middle shelf (16%) than the inner shelf (9%), but fewer surface deposit feeders (67%:84%). Additionally, there were more subsurface deposit feeders (17%:12%).

Species abundant on the middle shelf that were not abundant on the inner shelf included Tharyx sp., Pherusa affinis, Glycera dibranchiata,

Lumbrineris impatiens, Clymenella torquata, Euclymene zonalis, Aglaophamus circinata, Aricidea wassi, Aricidea cerrutii, Euchone incolor, Scalibregma inflatum, and Exogone hebes (Table 3). All had wide distribution on the shelf, but were less common in dynamic inner shelf habitats.

The feeding classifications on the middle shelf were numerically dominated by surface deposit feeders (Figure 19). At all non-swale sites the abundances of surface deposit feeders were below 600 individuals m^{-2}. At station D4, however, these polychaetes contributed over 2600 individuals m^{-2}, comparable to the swale habitat (station C4) on the inner shelf. The most abundant surface deposit feeders in these swales were Polygordius sp. A, Tharyx sp., Spiophanes bombyx, and Ampharete arctica. Except in swale habitats, subsurface deposit feeders were uncommon in the middle shelf (Figure 22). Station D4 was inhabited by over 1400 individuals m^{-2}, but other middle shelf sites generally had less than 100. An exception was the fine sand habitat of station L2 which supported numerous subsurface deposit feeding species, most notably Lumbrineris impatiens. The increase in overall abundance of suspension feeders over values of the inner shelf resulted primarily from the abundance of the spionids Spiophanes bombyx and Prionospio steenstrupi and the sabellid Euchone incolor at swale station D4. Suspension feeders contributed less than 200 individuals m^{-2} at other middle shelf stations (Figure 23). Carnivores were generally less abundant at middle shelf sites than on the inner shelf (Figure 20).

The motility classifications of polychaetes of the middle shelf, like the inner shelf, were dominated by motile species (Figure 15). Motile species contributed 63% of the individuals, compared to 72% on the inner shelf. Although sessile species were represented in only 3% of the total polychaetes, this value exceeded that of the inner shelf (0.3%). The proportions of discretely motile species on the inner and middle shelf were similar (28%:33%, respectively). The most abundant motile species on the middle shelf were Goniadella gracilis, Lumbrinerides acuta, Lumbrineris impatiens, Aglaophanus circinata, Aricidea cerrutii, Aricidea wassi, Scalibregma inflatum, Sthenelais limicola and Exogone hebes (Table 3). Though well-represented at all stations, motile species were most abundant at station D4 (Figure 24), also the habitat most inhabited by sessile species (Figure 25). Of the above species, those motile species most common in the D4 swale were L. impatiens, A. cerrutii and A. wassi.

Like the inner shelf, most middle shelf species (48%) were jawed (Figure 15), rather than tentaculate (26%) or soft proboscis (26%). On the middle shelf, jawed species (e.g. Lumbrinerides acuta, Goniadella gracilis, Lumbrineris impatiens) occurred in excess of 500 individuals m^{-2} at most stations (Figure 21), and over 1300 m^{-2} at station D4.

The outer shelf included 15 sampling sites. Both ridge field areas B and E are on the outer shelf, and will be discussed at length with respect to medium scale distribution patterns later in this investigation. Also included on the outer shelf was station G3, located in

the Hudson Shelf Valley, and numerous additional stations of various sediment types in areas of relatively level topography.

The classification ratios for feeding, motility, and morphology of outer shelf polychaetes are separated into two groups in Figure 15: outer shelf swales and other outer shelf stations. At the non-swale stations the polychaete fauna was dominated by surface deposit feeders (46%), though more polychaetes on the outer shelf were subsurface feeders (32%) and suspension feeders (22%) than at shallower depths. Of the subsurface deposit feeders which occurred in greater numbers on the outer shelf than at shallower depths, the most abundant were Notomastus latericeus, Lumbrineris latreilli, Euclymene zonalis, Ophelina acuminata, Scoloplos acemceps and Scalibregma inflatum (Table 3). The outer shelf also supported more suspension feeders, due primarily to the abundance and diversity of small sabellids and spionids at that depth zone (Table 3). These exceeded 800 individuals m^{-2} at some stations (Figure 23).

Carnivores (Figure 20) were more abundant on the outer shelf than in any other zone of the Middle Atlantic Bight. In the habitat of station B4 (medium-coarse sand) they exceeded 1500 individuals m^{-2}. At that site, the most abundant carnivores were Lumbrinerides acuta and Goniadella gracilis, both active burrowers.

Most polychaetes on the outer shelf (67%) were motile (Figure 15). These include the arabellids, capitellids, cirratulids, lumbrinerids, orbiniids, paraonids, and syllids mentioned above. Though abundant at

all outer shelf stations (Figure 24), motile species were most numerous at terrace station B4 (2600 individuals m^{-2}).

Morphology of outer shelf polychaetes was diverse (Figure 15), even considering the variety of habitats. In all 41% were jawed, 24% were soft proboscis species, and 35% were tentaculate. There was a relatively even distribution of jawed species on the outer shelf (Figure 21), with most habitats supporting 800 to 1200 individuals m^{-2}. The same was true of the distribution of soft proboscis species (Figure 26), though their abundance was generally only 400 to 800 individuals m^{-2}. Tentaculate species varied greatly with habitat, however, with the greatest numbers occupying finer sediment habitats (Figure 27). An exception was the medium-fine sand habitat of station L3, which supported less than 300 tentaculate polychaetes m^{-2}.

Outer shelf swales provided habitat for more subsurface deposit feeders (47%) than surface deposit feeders (41%), as shown in Figure 15. This resulted from a diverse group of burrowing polychaete species in swale habitats, most notably capitellids and lumbrinerids. These also accounted for the abundance of motile species in swales. Less than 7% of the total polychaete fauna in swales were sessile, mostly ampharetids and sabellids.

The shelf break is the zone of transition between continental shelf and slope habitats, covering roughly between 100 and 200 m depths in the Middle Atlantic Bight. Like the outer shelf, it is an area of diverse topographic features and various sediment types. Unlike the other shelf fauna, the shelf break fauna was not abundant in wide

depth zones, but generally occurred only in outer shelf topographic depressions and along the shelf break. Boesch (1979a) attributed this primarily to influence of the thermal regime in the area, since the sediment characteristics of the shelf break cannot solely account for the abrupt change in faunal dominants.

Fifteen shelf break stations were occupied. Most stations were in habitats of medium-fine sand (Table 1), though some were in areas of slightly finer sediments (e.g. stations K4 and F2) or coarser sediments (e.g. stations I2, L4 and L5). The general sediment characteristics of the shelf break closely resembled those of outer shelf swales (e.g. station B3).

At the shelf break there was an abrupt change from the gradual pattern of less surface deposit feeders with depth, as occurred across the shelf (Figure 15). Unlike the outer shelf, which supported only 46% surface deposit feeders, and outer shelf swales with 41%, the shelf break polychaetes were 66% surface deposit feeders. A pattern of greater domination by subsurface deposit feeders with depth occurred across the shelf, but at the shelf break this pattern discontinued. Only 25% of shelf break polychaetes were subsurface deposit feeders, and only 9% were suspension feeders. The abundance of surface deposit feeders resulted from the occurrence of numerous species at the shelf break which were absent or uncommon on the shelf. The most noteworthy were Onuphis pallidula, O. atlanticum, Aricidea simplex, Paradoneis lyra and Polydora caulleryi.

The ratios of polychaete motility at the shelf break provide little indication of the distinct nature of this faunal zone. Most notable were the differences between the shelf break and outer shelf swales, two areas generally comparable in sediment type. The shelf break supported a greater percentage of discretely motile polychaetes (28%:19%), and less motile (65%:72%) and sessile (7%:10%) individuals. The abundance of discretely motile polychaetes on the shelf break is evidenced in Figure 28. Stations A2, A3, A4, F2, F3, F4, and I3 all supported 600-800 individuals m^{-2}, while outer shelf swales (B3, E4) had only about 300. The two areas had many common species. It was their abundance at the shelf break that accounted for the discrepancy. The abundances of these species were not evenly distributed among the shelf break stations (Figure 19), though all supported over 500 surface deposit feeders m^{-2}. Their greatest abundances occurred at stations F2, F3, and F4, which all have approximately 2000 m^{-2}. The similarity between these stations is somewhat misleading, however. Among the surface deposit feeding dominants at each site were Spiophanes wigleyi and Onuphis pallidula (station F2), Aricidea simplex (station F3), and Tharyx sp. (station F4). Suspension feeders were not abundant at any of the shelf break stations (Figure 23), though they occurred at all. The most widely distributed suspension feeders were the spionids, especially species of Polydora and Prionospio. Carnivores (Figure 20) were generally not as abundant on the shelf break as on the shelf.

The jawed, tentaculate, and soft proboscis polychaetes were represented in roughly equal numbers (37%:34%:29%, respectively) at the shelf break. The primary difference between polychaete fauna at the shelf break and shallower depths in terms of morphology was the diversity of jawed species (e.g. eunicids, lumbrinerids, and onuphids) at the shelf break, the diversity and abundance of soft proboscis species (e.g. paraonids and cossurids) there, and the reduced abundances of shelf break tentaculate species (e.g. sabellids and spionids). The abundance of soft proboscis species at the shelf break exceeded that of most of the shelf (Figure 26), with greatest numbers at stations F2, F3, and F4. All of these stations were rich in soft proboscis species (e.g. Notomastus latericeus, Aricidea simplex, A. catherinae, Paradoneis lyra). There were generally less tentaculate species at shelf break stations than the shelf (Figure E), due to the absence of abundant sabellids and spionids, which were numerous in ridge fields (e.g. areas B, C, E) on the shelf.

The Middle Atlantic Bight continental slope contains finer sediments than any zone on the shelf. Sediments at all stations had silt and clay in excess of 25%, and those on the middle slope (i.e. stations H2, J2) had over 85% (Table 1). Sampling included 6 stations on the upper slope (300 to 500 m depth) and two on the middle slope (650 to 750 m). Like the shelf break, the slope was distinct from other depth zones. Numerous polychaetes were restricted to slope depths in the Middle Atlantic Bight, including Paramphinome jeffreysii and Ceratocephale loveni as more or less abundant species, and numerous

rare polychaetes (e.g. _Sternaspis_ _scutata_, _Fauveliopsis_ sp. A, _Praxillella_ _gracilis_). The middle slope, stations H2 and J2, supported the lowest abundance of polychaetes (Figure 29), and lowest polychaete biomass (Figure 30) of all sites sampled. Sediments at both sites were clayey-silt.

On the slope, the polychaete fauna had a higher percentage of subsurface deposit feeders than at the shelf break, 31% on the upper slope and 39% on the middle slope (Figure 15). In that respect, the fauna more closely resembled outer shelf communities. The surface deposit feeding species were equally-well represented on the shelf break (66%), upper slope (63%), and middle slope (60%). Suspension feeders on the slope, however, contributed little to the polychaete fauna, 6% (upper slope) and 1% (middle slope). The most abundant surface deposit feeders on the slope were ampharetids and paraonids (Table 3). These contributed 400 to 600 individuals m^{-2} at most upper slope sites (Figure 19). The increase in percentage of subsurface deposit feeders resulted from presence of abundant lumbrinerids at some sites, and perhaps more importantly, absence of the abundant onuphids, paraonids, and spionids which occurred at shallower depths. Figure 22 shows the fairly even distribution of subsurface deposit feeders among the upper and among the middle slope sites. Carnivores were generally uncommon on the slope (Figure 20), where most sites supported less than 200 individuals m^{-2}. The only carnivores in abundance were _Paramphinome_ _jeffreysii_ and _Hyalinoecia_ _artifex_.

Figure 30. Wet weight mean biomass (g m^{-2}) of annelids
at sampling sites in the Middle Atlantic Bight.

NEW YORK

RARITAN BAY

NEW JERSEY

DELAWARE BAY

DELAWARE

MARYLAND

VIRGINIA

1000 m

100 m

SLOPE

CONTINENTAL SHELF

10 g m⁻²

G7

H1

H2

G6

A4

I4

G5

A2

A3

I3

J1

J2

A1

F4

I2

F3

I1

F1

F2

E2

B3

E3

K6

B1

E4

B4 B2

E1

K5

B5

K4

G4

L6

G3

D2

G2

D1

K3

L5

D4

D3

K2

L4

G1

L3

C3

C2

K1

L2

C1 C4

L1
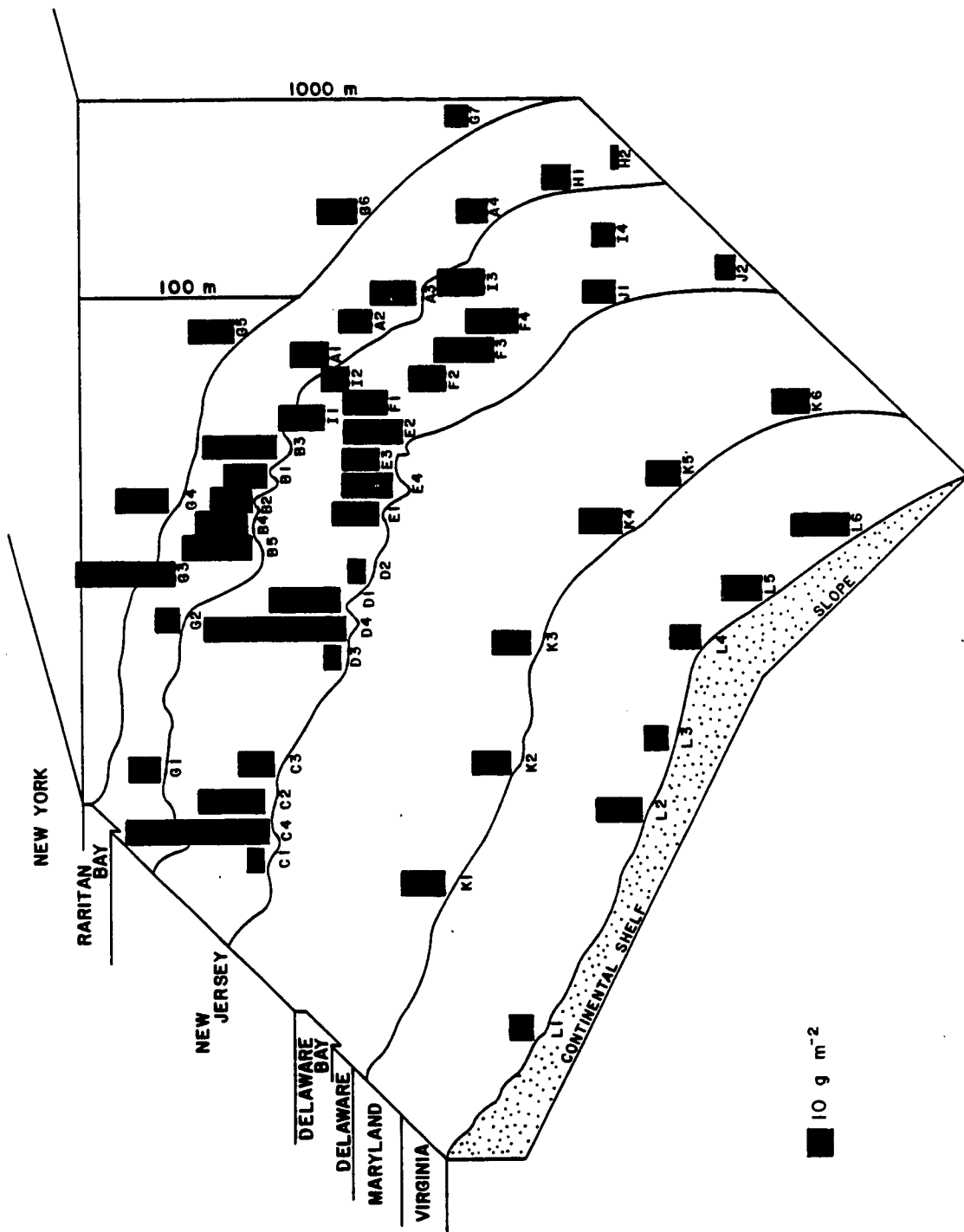
Like all other depth zones on the shelf, the slope was dominated by motile polychaetes, 68% on the upper and 70% on the middle slope (Figure 15). The abundances of P. jeffreysii and H. artifex were the primary reason for this pattern, which is ironic in that H. artifex is a tube-dwelling species. The dominant morphology of lower slope polychaetes was anomalous in that jawed species constituted a larger percentage (44%) than any other morphological classification. Generally, on the shelf quiescent habitats had fewer jawed polychaetes than physically dynamic ones (Figure 15). The reason for more jawed polychaetes there was the moderate abundance of lumbrinerids in these otherwise low-density habitats.

Medium Scale Patterns

The spatial distribution patterns referred to here as "medium scale" or "mesoscale" are defined as those patterns that can be discerned on a scale of hundreds to thousands of meters. Whereas broad scale patterns encompass cross-shelf and latitudinal faunal patterns, mesoscale patterns include response to local sediment and topographic features which may result in major community changes over rather short distances. Two areas of the Middle Atlantic Bight were selected for this investigation: Areas B and E (Figure 3). These areas were intensively sampled to ascertain mesoscale feeding biology and faunal patterns. Sampling procedures included stratified random sampling within a priori selected strata (Boesch 1979a). In this investigation, the results of the stratified random study were combined with quarterly

sampling data to provide the data base for mesoscale faunal investigations.

The dominant topographic features in Areas B and E were those associated with ridge and swale topography. An understanding of these features is essential in ecological investigations of the areas. These features are discussed below. Specific sediment characteristics are discussed later by study area.

Ridge and swale topography consists of fields of linear sand ridges separated by topographic lows (swales). These features, their genesis and associated processes were discussed in detail by Duane et al. (1972) and Swift et al. (1972). The ridges of areas B and E (off New Jersey) trend roughly northeast to southwest about 30° oblique to the shoreline (Knebel and Folger 1976).

There are two populations of ridges in the Middle Atlantic Bight, with a smaller ridge system superimposed on a larger system (Swift 1976). Off New Jersey the ridges of the inner shelf have a mean spacing of 1.4 km and 4.7 m relief. On the central shelf these structures are 2.5 km apart and 6 m high, while those of the outer shelf are spaced 6.1 km and 6-10 m high (McKinney et al. 1974). Ridges of the inner shelf are believed to be less than 11,000 years old and those of deeper water somewhat older (Swift et al. 1973).

The ridges exhibit a characteristic sediment textural pattern related to their genesis and maintenance. Grain-size profiles across ridges are asymmetrical. Sands are coarsest in the landward flank, constant across the ridge crest, and finer again on the seaward flank

(Stanley and Swift 1976, Swift et al. 1977). Finer grained sediments (fine sands with small amounts of silt and clay) are deposited in the swales under fair weather conditions, because these less dynamic areas serve as a sediment sink. On the other hand, periodic scouring of the swales by storm-induced currents may erode the fine sediments and cut into underlying cohesive lagoonal silty clay. Thus, although muddy fine sands are typically found in swales, erosional windows containing poorly sorted sediments (including clay lumps, shell and coarse sand and gravel lag) may also be encountered (Figure 31).

Before investigations by Boesch (1979a) little attention had been focused on the ecology of the Middle Atlantic Bight benthos mesoscale faunal patterns. Boesch identified assemblages of macrobenthos for each habitat type. He found coarser sediments of dynamic areas (e.g. ridge crests) were populated by interstitial organisms and deposit feeders utilizing recently sedimented surface floc. Finer, more stable sediments of topographic depressions (e.g. swales) had sediments with small interstices which precluded interstitial feeding. These depressions were populated by a variety of deposit feeders, mostly poly- chaetes, which took advantage of the abundant sedimented organic matter.

Boesch's conclusions were based primarly on distribution of domi- nant species of macrobenthos. Since the present study included all polychaete species, and many that were reclassified following gut con- tent analyses, the conclusions of Boesch were reexamined. Several hypotheses were here posed concerning mesoscale distribution patterns.

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Figure 31. Evolution of ridge and swale topography
            (Stubblefield and Swift 1976).

A Retreating shoreline left surficial sand sheet on early Holocene clay; internal stratification of ridges indicates growth by lateral and crestal aggradation.

PRIMARY
RIDGE   PRIMARY   TROUGH   PRIMARY   RIDGE

HOLOCENE SILTY CLAY
PLEISTOCENE SAND
PLEISTOCENE SILTY CLAY
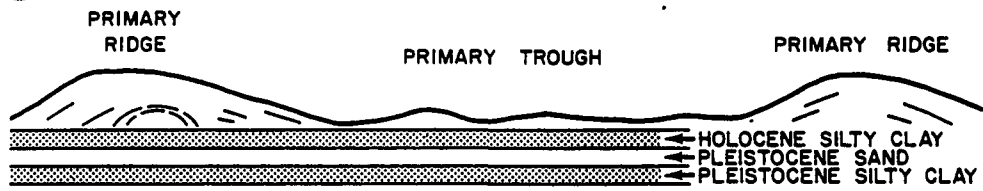
B Continued scour in troughs results in incision of secondary troughs into upper silty clay layer; secondary ridges may appear as levee-like forms associated with secondary troughs.

PRIMARY
RIDGE

IMMATURE
SECONDARY
TROUGH

SECONDARY
TOPOGRAPHY   PRIMARY   RIDGE
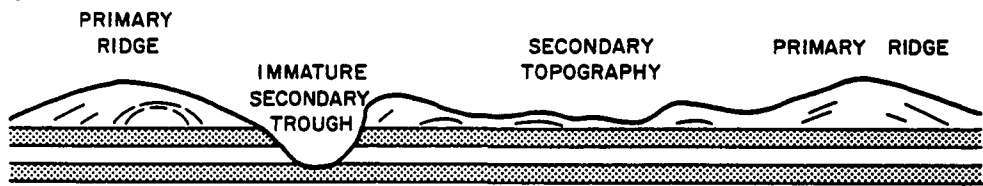
C Downward erosion in secondary troughs inhibited by lower silty clay; secondary trough widens by erosion of Pleistocene sand and undermining of upper silty clay.

PRIMARY
RIDGE

MATURE
TROUGH

MATURE
SECONDARY
TOPOGRAPHY   PRIMARY
RIDGE

First, it was hypothesized that the proportions of the three detritivore components (suspension, surface deposit, and subsurface deposit feeders) were related to sediment variables. Using all macrobenthic taxa, Boesch (1979a) had demonstrated trends toward dominance of subsurface deposit feeders in topographic depressions (swales) and dominance of surface deposit feeders in middle range sediments. It was expected, therefore, that subsurface deposit feeders would be associated with finer sediments and greater organic carbon content. Surface deposit feeders were expected to be in greater proportion in coarser sediment habitats such as ridges and ridge flanks.

It was also hypothesized that the distribution of carnivorous polychaetes was related to sediment variables. Boesch (1979a) observed a trend toward dominance of carnivorous macrobenthic species in coarse sediments. Maurer and Leathem (1981) found the density of motile, jawed carnivorous polychaetes associated with coarse-grained sediment. It was expected, therefore, that the coarse sediment habitats of Areas B and E would have a greater proportion of carnivorous polychaetes than finer sediment habitats.

Another hypothesis tested was that polychaete motility was related to sediment variables. The previous investigations of polychaete distribution using the Jumars and Fauchald (1977) classification primarily concerned broad scale patterns in polychaete motility. However, since Jumars and Fauchald (1977) and Maurer and Leathem (1981) all concluded that sessile polychaetes generally inhabited more stable sediments, it was here proposed that similar patterns could be demonstrated in Areas

B and E. It was expected that motile polychaetes would be in greatest proportion in coarser sediment habitats and sessile species would be in greatest proportion in finer sediment habitats.

It was hypothesized that the distribution of polychaete morphological classes was associated with sediment variables. Since Maurer and Leathem (1981) had shown that the feeding guilds which included most jawed polychaetes (CMJ and HMJ) were positively correlated with coarser sediments, it was expected that jawed polychaetes in Areas B and E would similarly be associated with coarser sediments. Additionally, it was expected that soft proboscis polychaetes would be in greater proportion in topographic depressions and other areas high in organic carbon content, since many of the deposit feeders which Boesch (1979a) found dominant in topographic depressions were soft proboscis polychaetes.

Area B Feeding Biology

Area B includes both deep ridge and swale topography (60 to 75 m depth), and a portion of a terrace (40 to 42 m depth) shoreward of a sealevel still stand. The individual habitats of the area are shown in Figure 32. In general, the terrace and ridge crests are medium-coarse sand habitats. Fine-skewed medium sand is found on the escarpment base below the terrace. Sediments grade into muddy fine sand in a large swale east of the scarp and in the deeper swale to the southeast. Sediment parameters and depth of each habitat sampled in Area B are provided in Table 5.

Figure 32. Distribution of major habitats in Area B.
Quarterly and stratified random sampling sites
are identified by points (redrawn from Boesch
1979).

TERRACE   RIDGE   MED-SAND   MED-FN.   ERODED   SHALLOW   DEEP
                    FLANK   SAND   FLANK   SWALE   SWALE
                               FLANK
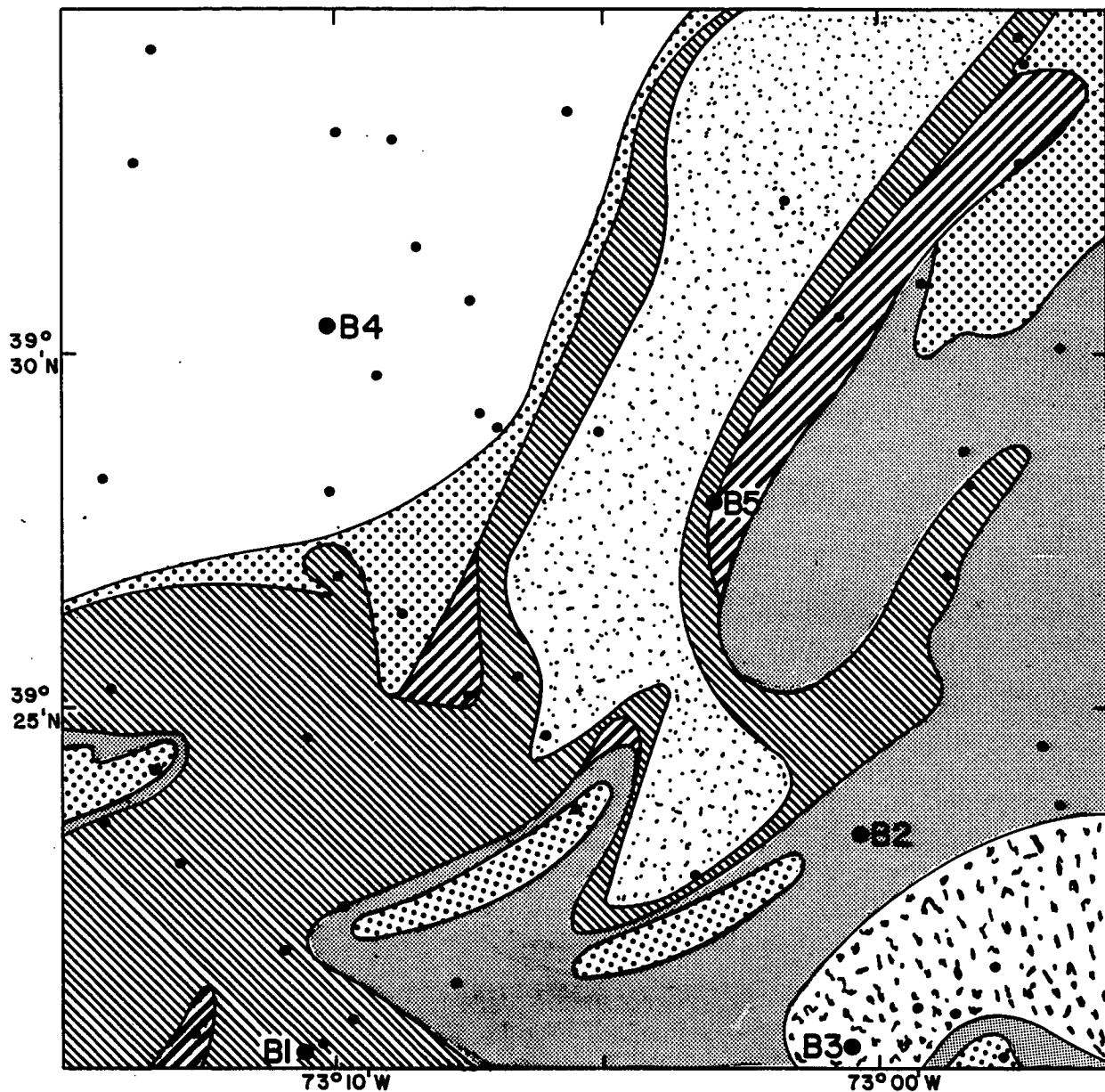
Table 5. Mean values of sediment parameters and depth of Area B stratified random habitats. Depth range and standard error are indicated in parentheses.

Habitat	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter	Sorting Coefficient
Terrace	45 (41-52)	4.9 (1.01)	31.8 (2.45)	58.3 (2.55)	4.9 (0.58)	0.2 (0.06)	0.35 (0.04)	1.15	0.68
Ridge	62 (58-66)	11.4 (6.67)	30.1 (2.12)	51.2 (7.88)	6.9 (1.19)	0.4 (0.15)	0.85 (0.13)	1.08	0.75
Shallow Flank	64 (62-66)	2.1 (0.66)	15.1 (2.30)	71.0 (2.72)	11.3 (0.58)	0.3 (0.05)	0.94 (0.20)	1.50	0.50
Deep Flank	65 (62-68)	3.8 (0.88)	10.0 (2.20)	54.5 (3.13)	28.1 (3.84)	3.6 (0.49)	1.03 (0.10)	1.72	0.59
Shallow Swale	66	3.2 (0.72)	4.9 (1.61)	39.9 (3.43)	45.5 (1.29)	3.8 (1.30)	1.00 (0.28)	2.01	0.55
Deep Swale	74 (74-75)	3.4 (1.66)	3.7 (0.71)	26.4 (3.95)	60.9 (3.10)	5.7 (1.04)	1.91 (0.09)	2.23	0.55

As with the broad scale analyses, numerical classification was conducted on the abundance and distribution data of polychaetes collected in Area B. This was expected to show that many of the habitats within Area B could be distinguished using polychaetes alone, and would give credence to polychaete feeding biology patterns associated with the same habitats. Boesch (1979a) had previously shown that these habitats were distinguished by use of all macrobenthic taxa. Only polychaete species were here included in the cluster analysis. These included both quarterly and stratified random collections at stations within Area B. Since replicate samples were taken in the quarterly sampling, but not in the stratified random study, all collections were standardized to individuals per square meter. As with all numerical classification in this investigation, the methods included log transformed data, Bray-Curtis similarity, and flexible sorting with beta established at -0.25. The resultant cluster of Area B stations is shown in Figure 33 and Table 6. This analysis showed the similarity between ridge and terrace habitats. Both are areas of physically dynamic medium and medium-coarse sand which supported an abundance of polychaetes. Deep swale stations also formed a tight cluster. Intermediate habitats were less easily distinguished since they shared a similar fauna, and the communities changed gradually between them. Deep and shallow flank stations were not well distinguished in the analysis, and therefore are simply grouped under "flank" in Figure 33. Though all shallow swale stations were grouped together, they were very similar to flanks in the analysis.

Figure 33. Numerical classification of Area B stations
(Bray-Curtis similarity, flexible sorting, beta
= -0.25).

SIMILARITY

TERRACE

RIDGE

FLANK

SHALLOW
SWALE

DEEP
SWALE
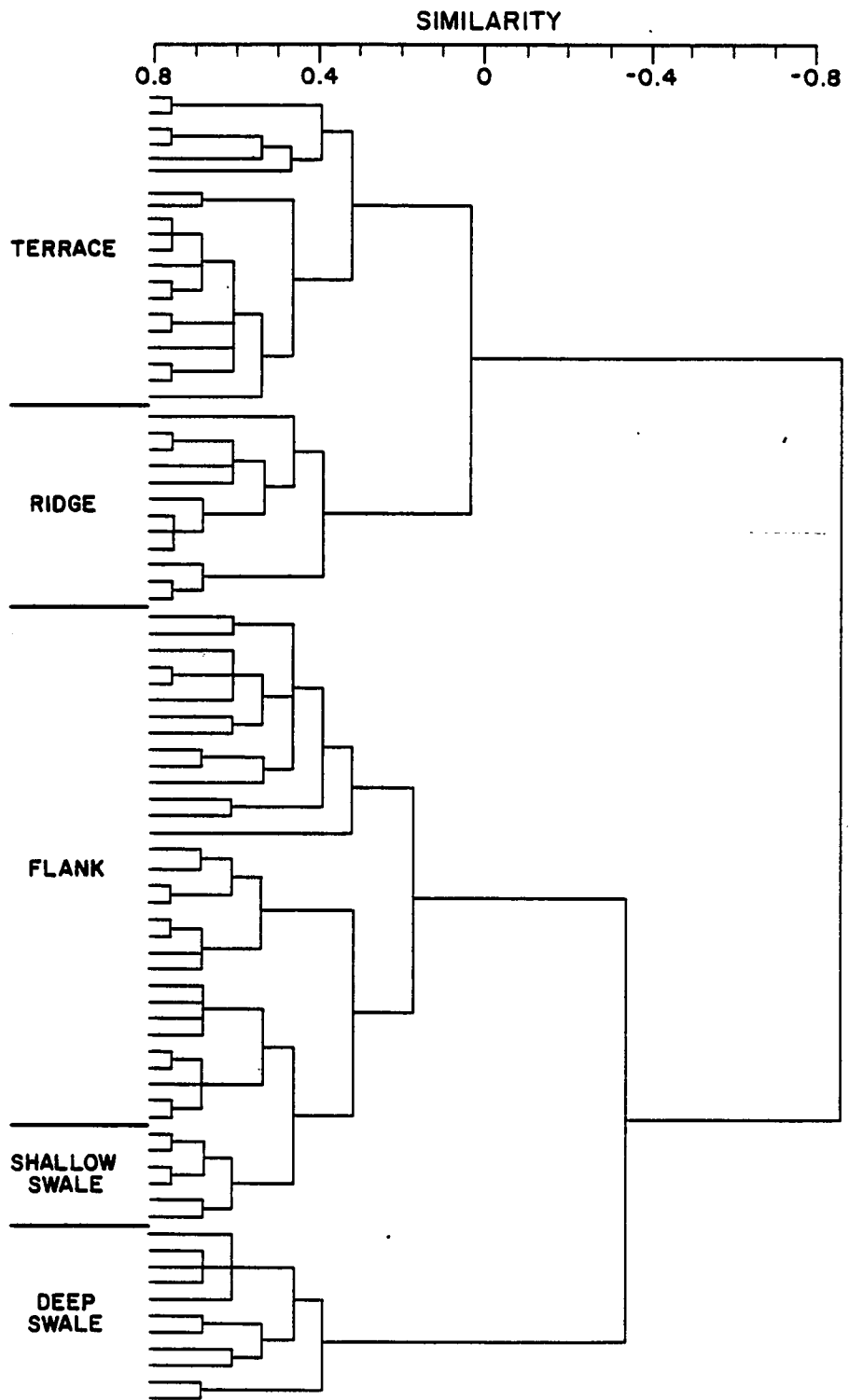
Table 6. Station groups by habitat selected from numerical classification of polychaetes collected in Area B. Hyphenated sites are quarterly cruise stations. Others are stratified random stations described by Boesch (1979a, 1979b).

Terrace	Ridge	Flank	Shallow Swale	Deep Swale
B4-1	B2-1	B1-1	B5-6	B3-1
B4-2	B2-2	B1-2	B5-7	B3-2
B4-3	B2-3	B1-3	B5-9	B3-3
B4-4	B2-4	B1-4	BR3	B3-4
B4-5	B2-5	B1-5	BS1	B3-5
B4-6	B2-6	B1-6	BS3	B3-6
B4-7	B2-7	B1-7	BS6	B3-7
B4-8	B2-8	B1-8		B3-8
BF1	BF3	B5-5		BD6
BF2	BR2	BD1		BS8
BPO	BR4	BD2		BS9
BP1	BR5	BD3		
BP2		BD4		
BP3		BD5		
BP4		BF4		
BP5		BF5		
BP6		BF6		
BP7		BM1		
BP8		BM2		
BP9		BM3		
		BM4		
		BM5		
		BM6		
		BR6		
		BR7		
		BR8		
		BR9		
		BSO		
		BS4		
		BS5		
		BS7		

The proportions of the feeding biology components are presented in Table 7 by habitat. Percentage values in the table are average percentages of collections rather than percentage of the total individuals collected, and include both stratified random and quarterly cruises in Area B.

Proportions of the three detritivore components were hypothesized to be associated with sediment variables, and therefore vary between habitats. Table 7 indicates an increase in proportion of subsurface deposit feeders (B) from the terrace (20%) to the deep swale (52%) which was positively correlated ($r = 0.850$, $\alpha \leq 0.05$) with organic carbon content of the sediments. Greater proportions of surface deposit feeders (S) were found in coarser sediment habitats such as terrace and ridges than were found in finer sediment habitats such as swales. The proportion of surface deposit feeders was negatively correlated with organic carbon ($r = -0.858$, $\alpha \leq 0.05$) and percent fine sand ($r = -0.853$, $\alpha \leq 0.05$) from terraces to deep swales.

Carnivorous polychaetes (C) were predicted to be in greatest proportion in coarse sediment habitats. Carnivores generally decreased in proportion from dynamic to more stable habitats, and were positively correlated ($r = 0.926$, $\alpha \leq 0.01$) with coarse sand in Area B habitats. Proportion of carnivores was greatest in ridges (45%) and least in deep flanks (12%).

Motile polychaetes (M) numerically dominated all habitats in Area B (Table 7). Proportion of motile species was greatest in ridges (82%). There was a trend of increased relative abundance of sessile

Table 7. Percentage of each feeding, motility and morphological classification by habitat in Area B. Percentage values are average percentages of collections in each habitat. Classifications: surface deposit feeder (S); subsurface deposit feeder (B); suspension feeder (F); carnivore (C); motile (M); discretely motile (D); sessile (L); tentaculate (T); jawed (J).

CLASSIFICATIONS

	B	S	F	C	D	M	L	J	X	T
Terrace										
Percentage	9	33	19	39	37	58	5	38	20	42
Percentage BSF	20	54	26							
Ridge										
Percentage	14	31	10	45	7	82	11	43	23	34
Percentage BSF	26	56	18							
Shallow Flank										
Percentage	16	42	18	24	13	76	11	30	20	50
Percentage BSF	22	54	24							
Deep Flank										
Percentage	13	50	25	12	19	60	21	21	15	64
Percentage BSF	15	57	28							
Shallow Swale										
Percentage	22	42	21	15	31	59	10	32	17	51
Percentage BSF	26	47	27							
Deep Swale										
Percentage	41	24	16	19	18	67	15	33	37	32
Percentage BSF	52	31	17							

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polychaetes (L) from physically dynamic habitats to more stable habitats. Sessile polychaetes were in least proportion in terraces (5%) and greatest proportion in deep flanks (21%). Discretely motile polychaetes (D) were in greatest proportion in the terrace (37%) and in shallow swales (31%). There was an increase in relative abundance of discretely motile polychaetes from ridges (7%) to shallow swales (31%) which positively correlated with percent fine sand (r = 0.986, $\alpha \le$ 0.05).

The proportions of each morphological component are also presented for comparison in Table 7. Jawed polychaetes (J) were in greatest proportion in the most physically dynamic habitats, the terrace (38%) and ridges (43%), but were also well represented in the deep swales (33%). Soft proboscis polychaetes (X) were in greatest relative abundance in deep swales (37%). Tentaculate polychaetes (T) contributed the greatest proportion of polychaetes in intermediate habitats: shallow flanks (50%); deep flanks (64%); and shallow swales (51%).

Figures 34 through 36 are ternary diagrams of polychaete feeding, motility, and morphology. As with broad scale pattern analyses, carnivorous and herbivorous polychaetes were excluded from the feeding diagram (Figure 34) to allow for comparison of the detritivore components. The dominant detritivores in Area B were surface deposit feeders (Figure 34). Terrace stations were widely distributed due primarily to the patchy distribution of the spionid, Spiophanes bombyx. S. bombyx is an opportunistic species that is widely distributed in Area B and common on the terrace. Ridges generally had fewer suspensions feeders than

Figure 34. Ternary diagram of Area B sampling sites
identified by habitat. Sites are distributed by
percentage of the three components of deposit
feeding polychaetes: surface, subsurface and
suspension. Mean values of sites in each
habitat are plotted as centroids in small
diagram at right.

PERCENT SUSPENSION FEEDERS →

100% SUSPENSION FEEDERS

100% SUBSURFACE DEPOSIT FEEDERS

← PERCENT SURFACE DEPOSIT FEEDERS

PERCENT SUBSURFACE DEPOSIT FEEDERS

TERRACE WITHOUT SILT-CLAY

TERRACE WITH 0.1-0.7 % SILT-CLAY

100% SURFACE DEPOSIT FEEDERS

○ TERRACE WITHOUT SILT-CLAY
⊙ TERRACE WITH 0.1-0.7 % SILT-CLAY
⊕ RIDGES
□ SHALLOW FLANKS
■ DEEP FLANKS
△ SHALLOW SWALES
▲ DEEP SWALES

DEEP SWALES

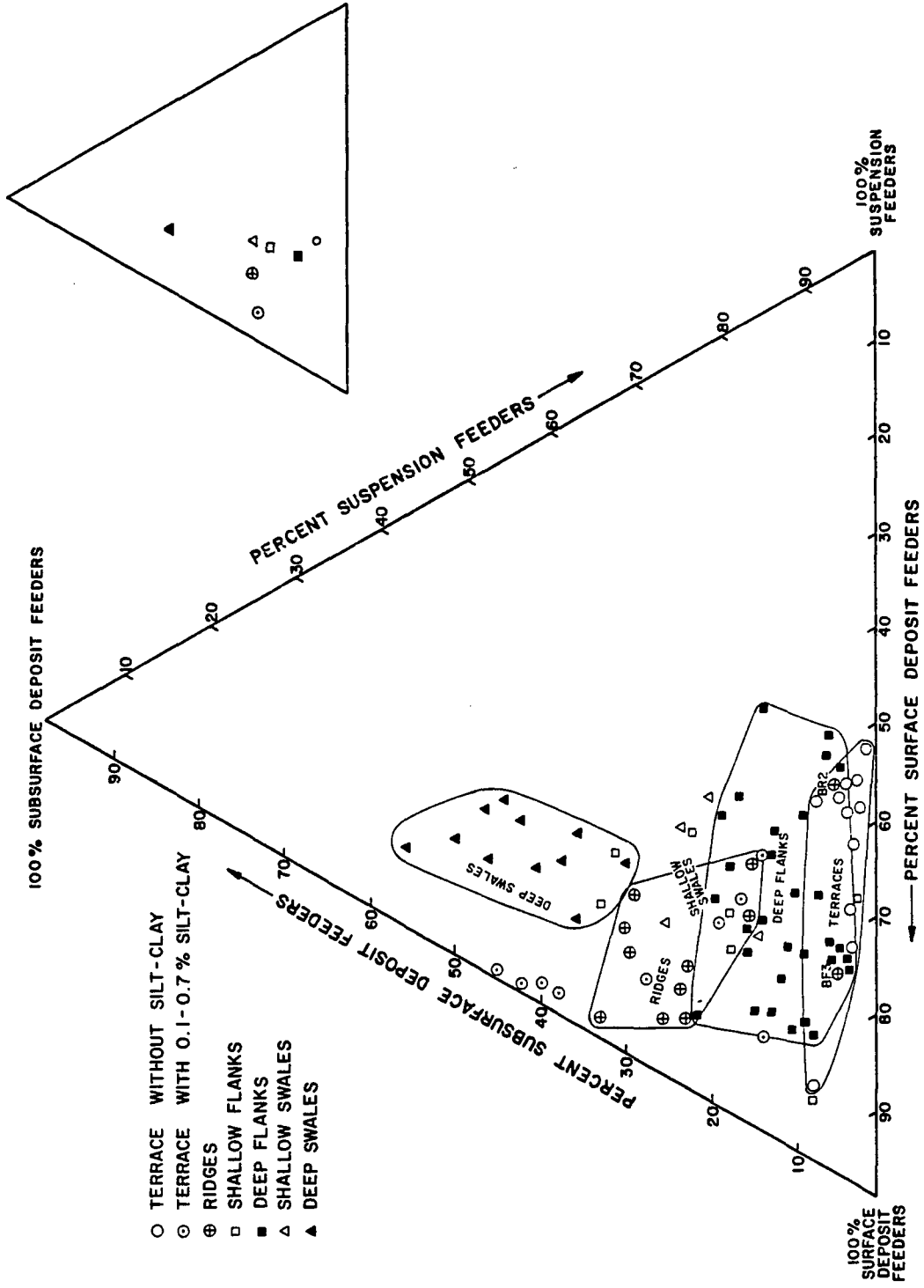SHALLOW SWALES

DEEP FLANKS

RIDGES

TERRACES

BR2

BF3

Figure 35. Ternary diagram of Area B sampling sites
identified by habitat. Sites are distributed by
percentage of the three components of polychaete
motility: motile, discretely motile and
sessile. Mean values of sites in each habitat
are plotted as centroids in small diagram at
right.

PERCENT SESSILE SPECIES

100% SESSILE SPECIES

PERCENT MOTILE SPECIES

100% DISCRETELY MOTILE SPECIES

PERCENT DISCRETELY MOTILE SPECIES

100% MOTILE SPECIES

TERRACES WITH SILT-CLAY

SWALES

FLANKS

RIDGES

O TERRACE
⊙ TERRACE WITH 0.1 - 0.7 % SILT-CLAY
● RIDGES
△ SHALLOW FLANKS
▲ DEEP FLANKS
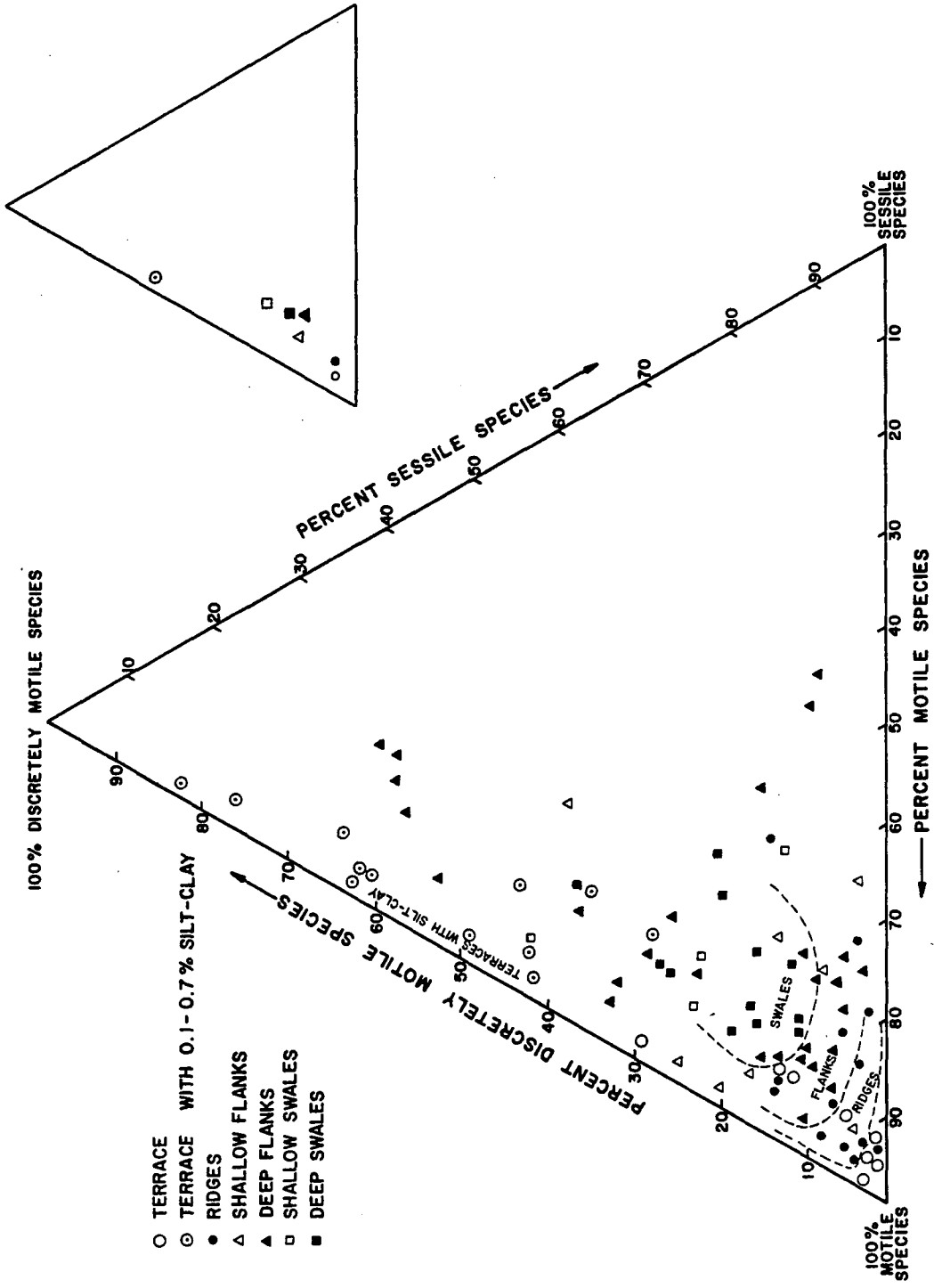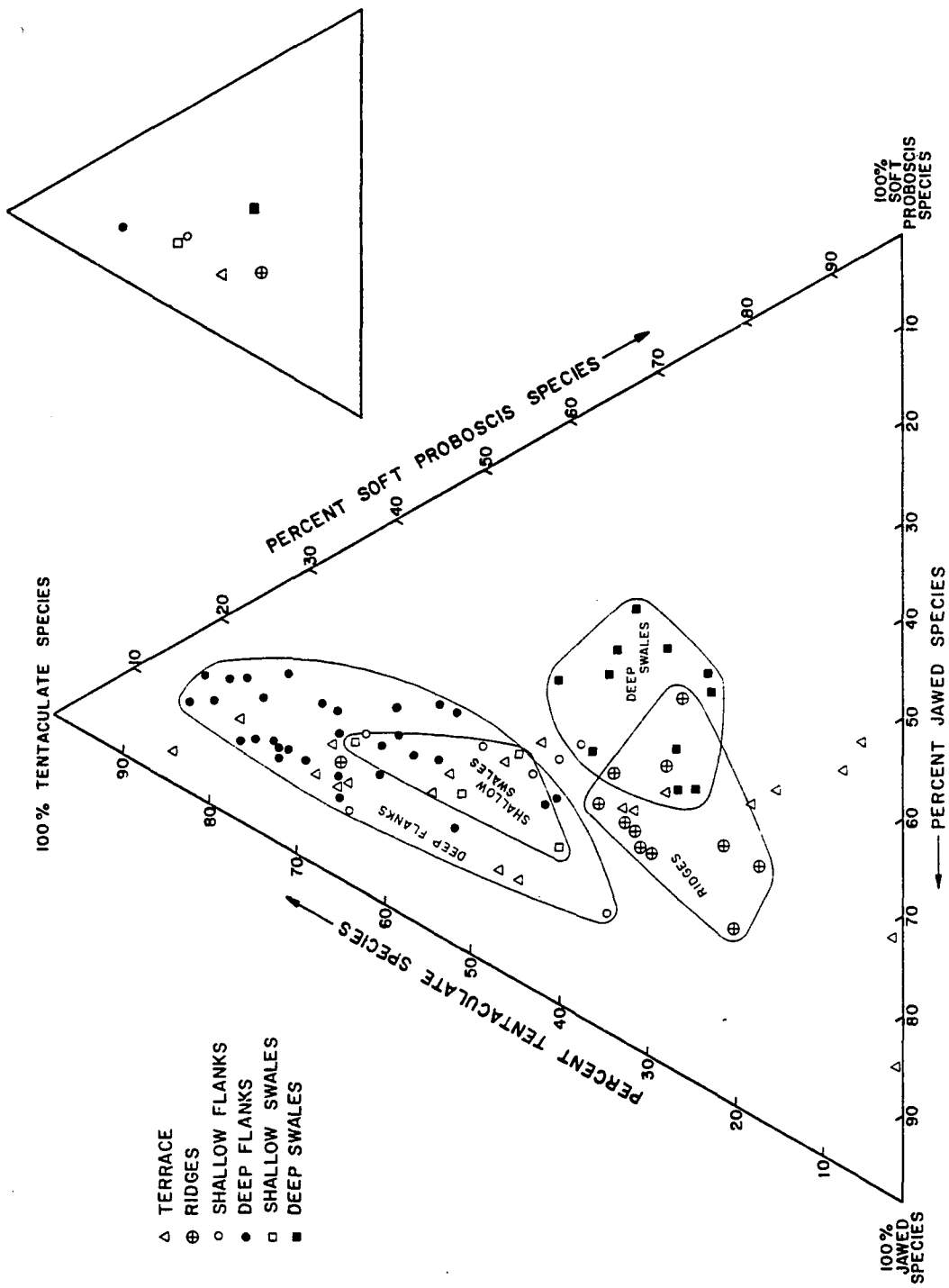□ SHALLOW SWALES
■ DEEP SWALES

Figure 36. Ternary diagram of Area B sampling sites
identified by habitat. Sites are distributed by
percentage of the three primary components of
polychaete morphology: jawed, tentaculate and
soft proboscis. Mean values of sites in each
habitat are plotted as centroids in small
diagram at right.

terrace stations without silt and clay, and greater proportion of subsurface deposit feeders. Deep swales had a consistent pattern of 10% to 20% suspension feeders and nearly equal numbers of subsurface and surface deposit feeders.

Figure 35 shows Area B with respect to polychaete motility. Although the stations were not in well-distinguished groups, there was a trend of decreasing proportion of motile species with depth (i.e. from terrace to swales), excluding terraces with silt and clay.

The ternary diagram for polychaete morphology is Figure 36. The terrace stations were widely distributed due to the patchy distribution of Spiophanes bombyx; however, other habitats were generally distributed in clusters which distinguished the habitats. Deep swales had approximately equal numbers of each morphological component. Ridges were similar in having nearly equal proportions of the three components, but trended toward domination by jawed polychaetes. Flank stations generally supported more tentaculate polychaetes and nearly equal numbers of jawed and soft proboscis polychaetes.

Area B Species Distributions

The physically dynamic medium-coarse sand habitats of Area B, such as the terrace and ridges, had an abundance of interstitial burrowers (e.g. Goniadella gracilis, Lumbrinerides acuta), and included diverse deposit-feeding forms (e.g. Spiophanes bombyx, Euclymene zonalis, Tharyx spp., Aricidea spp.). In the swales were higher proportions of fine sands (46% and 62%, respectively), 4-6% silt and clay, and greater

concentrations of organic carbon (ca. 2 mg/g in the deep swale). These habitats supported dense populations of lumbrinerids (e.g. Lumbrineris impatiens) and capitellids (e.g. Notomastus latericeus). Each habitat in the area resembled comparable ridge field habitats in shallower zones of the shelf, but reflected the effects of greater water depth (i.e. finer sediments). For example, ridges on the inner shelf were also inhabited by abundant populations of the interstitial-feeding species, but differed in lacking abundant deposit feeders.

The most abundant surface deposit feeder on the terrace was Spiophanes bombyx. This species was joined by species of cirratulids (e.g. Caulleriella spp. and Tharyx spp.) as the dominants in ridges, flanks, and shallow swales. The paucity of surface deposit feeders in deep swales resulted from the virtual absence of S. bombyx and low abundance of cirratulids. Subsurface deposit feeders were poorly represented in the more dynamic habitats (e.g. terrace, 8%; ridges, 14%), but abundant in swales (shallow swales, 24%; deep swales, 49%). The most abundant subsurface deposit feeders were Notomastus latericeus, Lumbrineris impatiens, and Scalibregma inflatum. Suspension feeders represented only 16 to 33% of the deposit feeders in Area B. It was the abundance of small sabellids (Euchone incolor and E. elegans) that accounted for the relatively high percentages in intermediate depth habitats (e.g. shallow flanks to shallow swales). Carnivorous polychaetes were much more abundant in physically dynamic habitats than in deep flanks or swales. This resulted primarily from abundances of Lumbrinerides acuta and Goniadella gracilis.
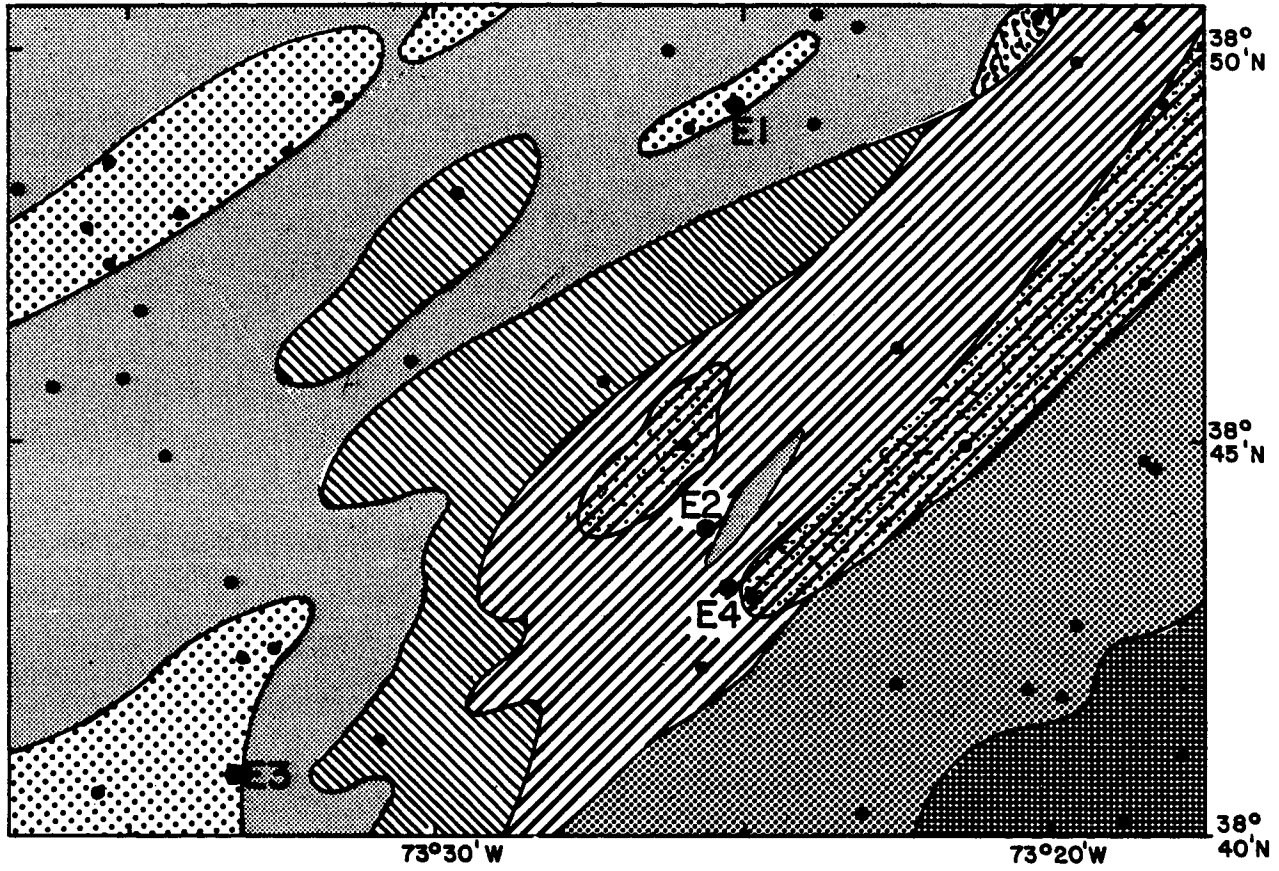
Most polychaetes in Area B were motile. The anomalous ratios of discretely motile:motile polychaetes on the terrace were due solely to the high abundance of S. bombyx. It contributed 90% of all polychaetes collected there. In dynamic sands of ridges and shallow flanks, where S. bombyx was less abundant, motile species dominated (87% and 77%, respectively). Sessile species were rare on the terraces (only 3%), and provided less than 25% of the fauna at any site. The most numerous sessile species were the small sabellids.

Feeding morphological characteristics of polychaetes in Area B provided few data with which to distinguish habitats. Generally, the least dynamic habitats had approximately equal percentages of jawed, tentaculate, and soft proboscis species. Except for the terrace stations abundant in S. bombyx, the dynamic habitats were dominated by jawed species. Intermediate areas (flanks and shallow swales) were more abundant in tentaculate polychaetes such as cirratulids and sabellids. Deep swales had a greater proportion of soft proboscis polychaetes (e.g. capitellids and scalibregmids).

Area E Feeding Biology

Area E includes deep ridge and swale topography (60 to 80 m depth) and a portion of shelf break habitat as defined in the broad scale analysis. The habitats and sampling sites are shown in Figure 37. Like Area B, Area E was sampled both quarterly and during the stratified random study. Sediment parameter data are provided in Table 8. Sediments in the area graded from coarse-skewed medium sand on ridge

Figure 37. Distribution of major habitats in Area E.
Quarterly and stratified random sampling sites
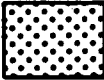are identified by points (redrawn from Boesch
1979a).
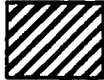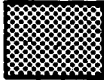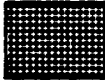
RIDGE MEGARIPPLES MED-FN. SAND FLANK SHALLOW SWALE DEEP SWALE ERODED SWALE UPPER SHELF BREAK MID SHELF SHELF BREAK

Table 8. Mean values of sediment parameters and depth of Area E stratified random habitats. Depth range and standard error are indicated in parentheses.

Habitat	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter	Sorting Coefficient
Ridge	60 (52-74)	6.1 (1.26)	27.4 (2.98)	57.2 (3.35)	8.8 (1.40)	0.3 (0.12)	0.44 (0.05)	1.25	0.77
Shallow Flank	60 (57-62)	2.3 (0.77)	3.6 (2.15)	31.1 (11.06)	62.6 (13.71)	0.4 (0.06)	0.52 (0.06)	2.09	0.38
Deep Flank	68 (66-71)	3.4 (1.04)	6.8 (3.05)	66.2 (8.10)	22.8 (6.82)	0.8 (0.24)	0.71 (0.13)	1.72	0.43
Swale	73 (69-77)	2.4 (1.04)	3.3 (1.20)	42.4 (11.20)	50.1 (10.90)	1.8 (0.59)	0.78 (0.11)	2.02	0.41
Eroded Swale	77 (76-78)	8.8 (2.07)	10.8 (2.94)	37.5 (5.26)	35.1 (8.98)	7.7 (1.94)	1.67 (0.40)	1.84	1.09
Shelf Break	80 (74-89)	2.4 (0.68)	9.3 (2.64)	59.3 (8.56)	27.6 (9.59)	1.2 (0.57)	0.74 (0.11)	1.73	0.45

crests to fine-skewed medium and fine sand in swales. Eroded swales had more heterogeneous sediments than shallow swales, including shell rubble and shell hash. The upper shelf break had clean, well-sorted medium sand. Below 80 m sediments graded to muddy, fine sands.

Results of numerical classification which was conducted on the abundance and distribution data of polychaetes collected in Area E are presented in Figure 38 and Table 9. Methods were the same as those used for Area B. The results were expected to be similar to the cluster analysis conducted on Area B data in that habitats would be distinguished. There were three major habitat groups in the Area E cluster: ridge; flank; and swale-shelf break. Within the latter cluster, the eroded swale stations and swale stations were distinguished from shelf break stations. As in the Area B cluster, flank stations were not clearly separated into shallow and deep habitats.

The proportions of the feeding biology components of Area E are presented in Table 10 by habitat. As with Area B data, carnivores were separated in the table from detritivores. Percentage values were computed as average percentages of collections, and included both stratified random and quarterly cruises in Area E.

Unlike detritivore classifications for similar habitats in Area B, Area E habitats (Table 10) were not dominated by surface deposit feeders (S). There was a general trend of increasing dominance by subsurface deposit feeders (B) from ridge to eroded swales (i.e. with depth). At the break, however, subsurface deposit feeders represented only 21% of the fauna. Conversely, surface deposit feeders and suspen-

Figure 38. Numerical classification of Area E stations
(Bray-Curtis similarity, flexible sorting, beta
= -0.25).

SIMILARITY
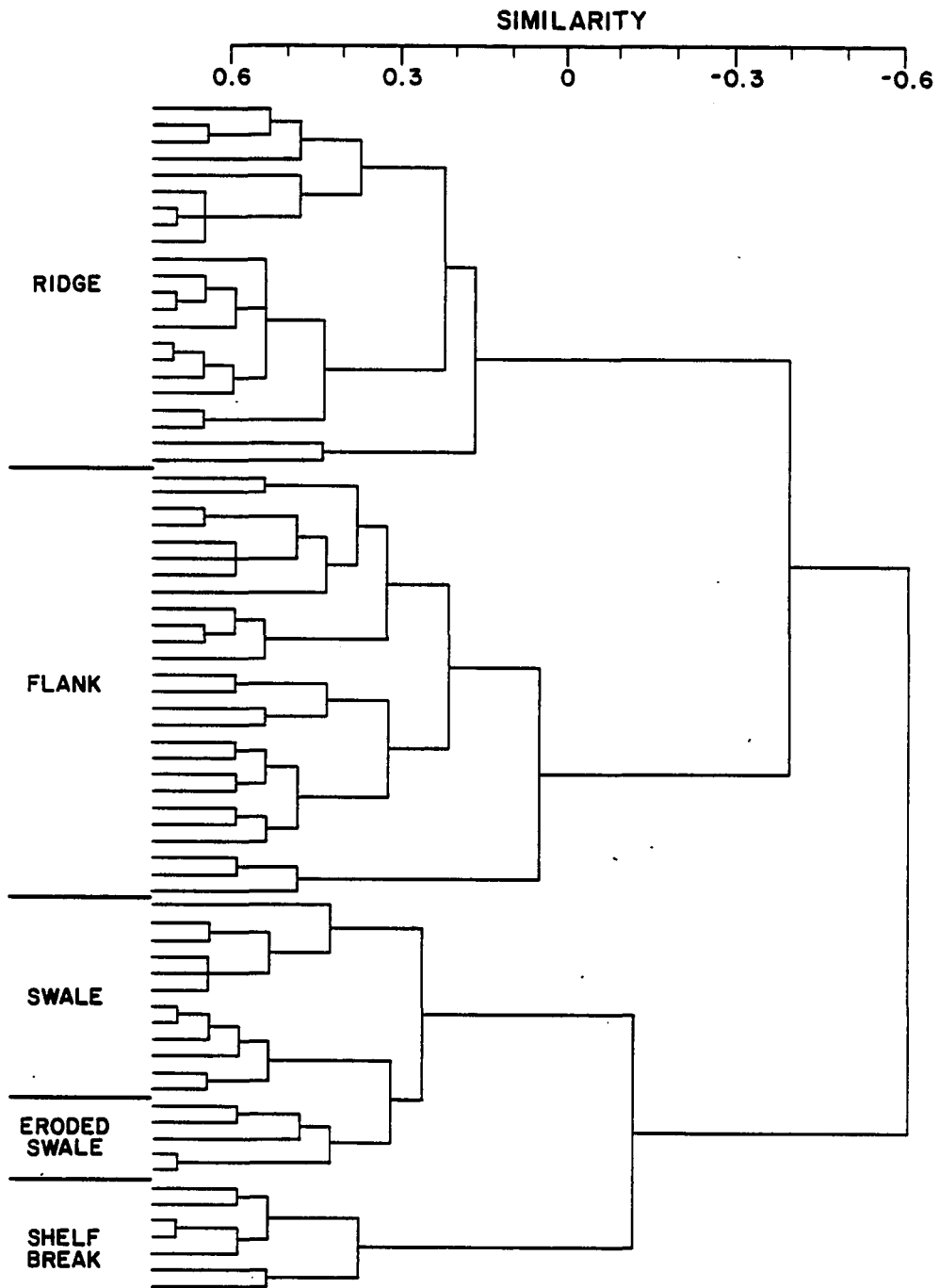
Table 9. Station groups by habitat selected from numerical
classification of polychaetes collected in Area E.
Hyphenated sites are quarterly cruise stations.
Others are stratified random stations described by
Boesch (1979a, 1979b).

Ridge	Flank	Swale	Eroded Swale	Shelf Break
E1-1	E2-1	E2-5	E4-5	EL1
E1-2	E2-2	E2-6	ED8	EL2
E1-3	E2-3	E2-7	ES3	EL3
E1-4	E2-4	E2-8	ES5	EL4
E1-5	E3-1	E4-1	ES6	EL5
E1-6	E3-2	E4-2		EL6
E1-7	E3-5	E4-3		ES7
E1-8	ED0	E4-4		
E3-3	ED1	E4-6		
E3-4	ED2	E4-7		
E3-6	ED3	E4-8		
E3-7	ED4	ES4		
E3-8	ED5			
ED7	ED6			
EF7	ED9			
EF8	EF1			
ER1	EF2			
ER2	EF3			
ER3	EF4			
ER4	EF5			
ER5	EF6			
ER6	ER7			
	ER8			
	ES1			
	ES2			

Table 10. Percentage of each feeding, motility and morphological classification by habitat in Area E. Percentage values are average percentages of collections in each habitat. Classifications: surface deposit feeder (S); subsurface deposit feeder (B); suspension feeder (F); carnivore (C); motile (M); discretely motile (D); sessile (L); tentaculate (T); jawed (J).

CLASSIFICATIONS

	B	S	F	C	D	M	L	J	X	T
Ridge										
Percentage	19	27	24	30	22	57	21	37	23	40
Percentage BSF	32	39	29							
Shallow Flank										
Percentage	17	27	20	36	21	65	12	41	22	37
Percentage BSF	31	44	25							
Deep Flank										
Percentage	32	30	21	17	22	64	14	33	26	41
Percentage BSF	39	38	23							
Swale										
Percentage	28	29	22	21	21	65	14	34	26	40
Percentage BSF	39	39	22							
Eroded Swale										
Percentage	43	33	9	15	26	70	5	33	38	29
Percentage BSF	52	38	10							
Shelf Break										
Percentage	22	15	56	7	18	37	45	24	17	59
Percentage BSF	26	17	57							

sion feeders (F) generally decreased with depth except at the shelf break where suspension feeders dominated (64%).

Carnivores (C) were expected to be in greatest proportion in coarse sediment habitats. They dominated the polychaete fauna of ridge (30%) and shallow flank (36%) stations, and were least abundant at the shelf break (7%).

Except in shelf-break habitats, Area E was dominated by motile polychaetes (M). Motile species represented 70% of the polychaete fauna in eroded swales where they were in greatest proportion, and only 37% at the shelf break. Discretely motile polychaetes (D) were relatively evenly distributed between habitats. Sessile polychaetes generally decreased in proportion from ridges (21%) to eroded swales (5%), and numerically dominated the shelf break (45%).

Jawed (J) and tentaculate (T) polychaetes dominated most habitats in Area E (Table 10). Jawed species were in greatest proportion in coarse sediment habitats such as ridges and shallow flanks, and in least proportion at the shelf break. Shallow and deep flanks were distinct in having 41% and 33% jawed species, respectively. Tentaculate species represented 37% to 41% of the polychaetes in ridges, flanks, and swales, but only 29% in eroded swales. The shelf break was dominated by tentaculate polychaetes (59%). Soft proboscis polychaetes (X) were in greatest proportion in eroded swales (38%), and least proportion at the shelf break (17%).

Ternary diagrams of polychaete feeding biology in Area E are presented in Figures 39 through 41. Distribution with respect to detriti-

Figure 39. Ternary diagram of Area E sampling sites
identified by habitat. Sites are distributed by
percentage of the three components of deposit
feeding polychaetes: surface, subsurface and
suspension. Mean values of sites in each
habitat are plotted as centroids in small
diagram at right.

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Figure 40. Ternary diagram of Area E sampling sites
            identified by habitat. Sites are distributed by
            percentage of the three components of polychaete
            motility: motile, discretely motile and
            sessile. Mean values of sites in each habitat
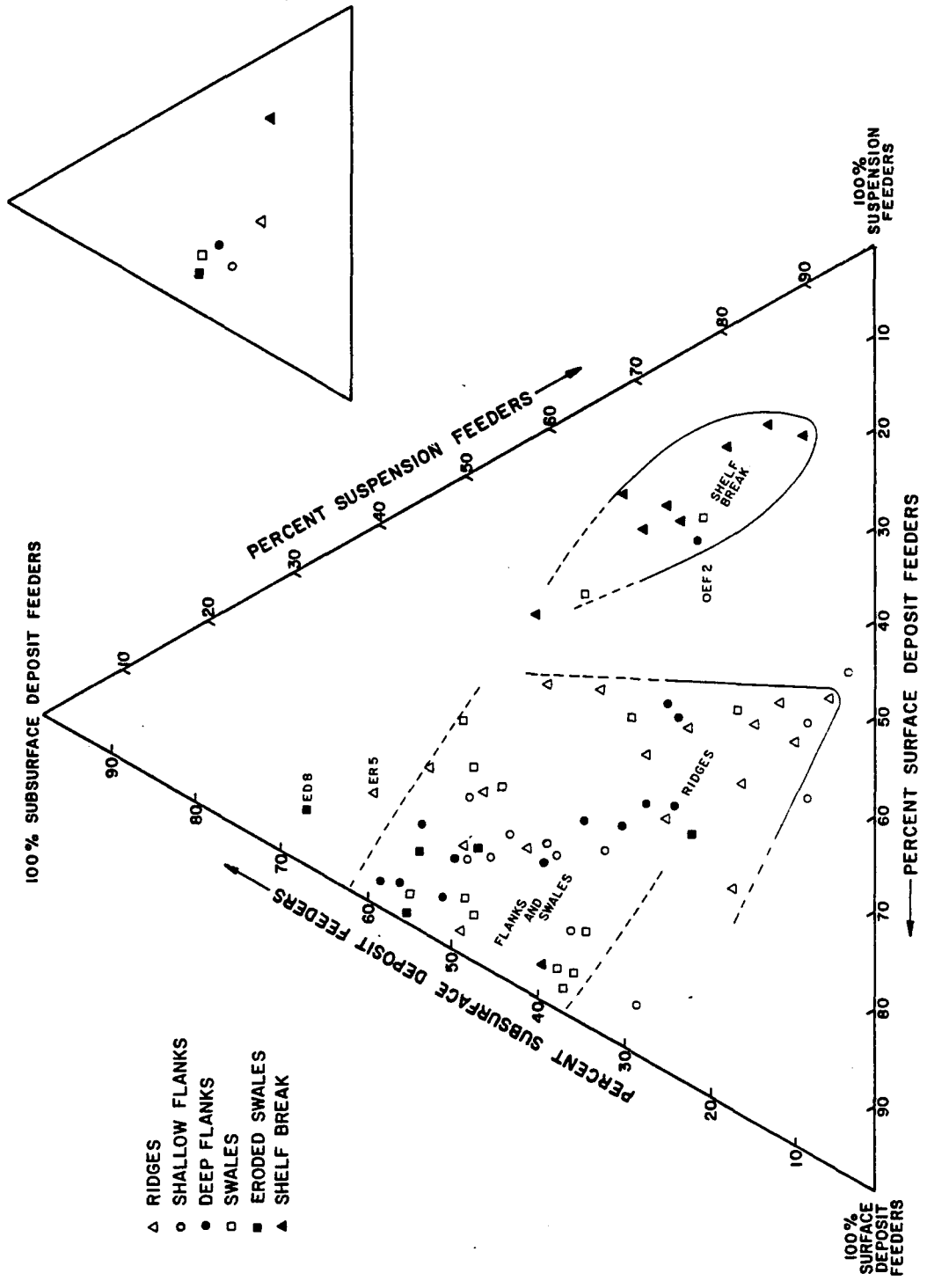   are plotted as centroids in small diagram at
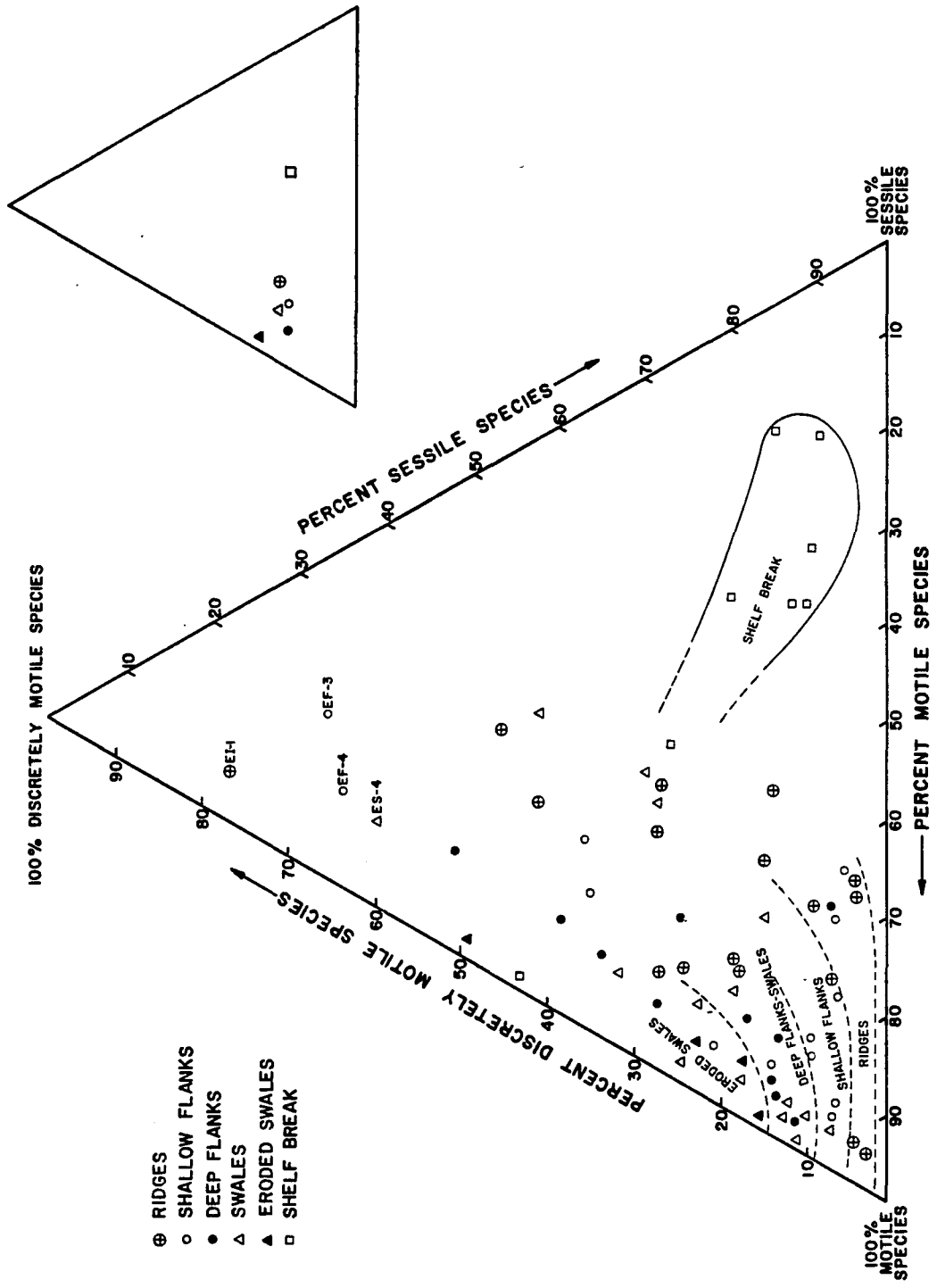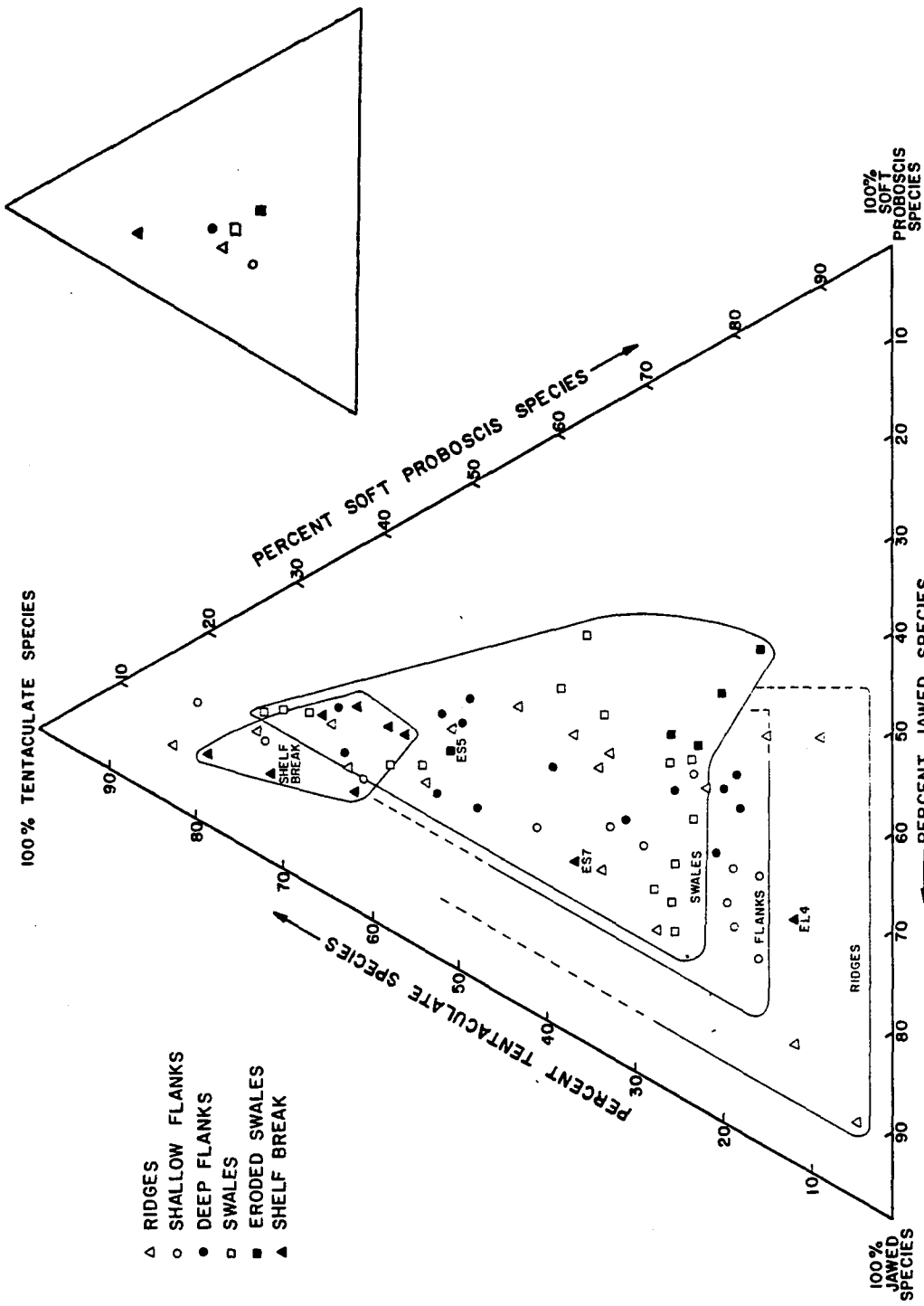   right.

Figure 41. Ternary diagram of Area E sampling sites
identified by habitat. Sites are distributed by
percentage of the three primary components of
polychaete morphology: jawed, tentaculate and
soft proboscis. Mean values of sites in each
habitat are plotted as centroids in small
diagram at right.

vore feeding components (Figure 39) illustrated the distinction of shelf break habitats from all others. Most shelf break stations were dominated by suspension feeders, and were inhabited by fewer subsurface than surface deposit feeders. The shelf break stations, and the two swale and deep flank stations within the shelf break distribution area of Figure 39, were dominated by sabellids. Eroded swale stations were generally dominated by subsurface deposit feeders, mostly lumbrinerids and capitellids. Flanks and swales generally had equal numbers of surface and subsurface deposit feeders, and few suspension feeders.

Figure 40 illustrates the distribution of stations with respect to motility. Except for the shelf break sites which had many sessile polychaetes, no clear patterns of motility distinguished the habitats. There was, however, a general trend of fewer sessile polychaetes from ridges to eroded swales.

The primary morphological components are presented for comparison in Figure 41. Shelf break stations had more tentaculate polychaetes than most other stations due to abundance of sabellids at the shelf break. Most other habitats had roughly equal numbers of the three components. There was a general trend of more soft proboscis polychaetes from ridges to eroded swales, and more jawed polychaetes at certain ridge stations.

Area E Species Distributions

Generally, the habitats of Area E supported assemblages closely similar to comparable habitats of Area B. The upper shelf break and

eroded swales, habitats not included in Area B, were dominated by <u>Chone</u> <u>infundibuliformis</u> and <u>Notomastus latericeus</u>, respectively. In deeper areas of the shelf break, <u>Chone</u> was not so abundant, and other poly- chaetes contributed heavily to the fauna: <u>Onuphis pallidula</u>; <u>Lumbrineris laterilli</u>; <u>Notomastus latericeus</u>; <u>Aricidea simplex</u>. Ridges were occupied by few subsurface deposit feeders, and an abundance of suspension feeders (e.g. <u>Euchone incolor</u>, <u>Caulleriella</u> spp., and <u>Spiophanes bombyx</u>). The ridge stations of Area E resembled those of Area B in having comparable proportions of surface and subsurface deposit feeders, but differed in having numerous suspension feeders. Flank stations were abundant in <u>Lumbrineris impatiens</u>, <u>Scalibregma inflatum</u> (motile, subsurface deposit feeders) and <u>Tharyx</u> spp. (motile, surface deposit feeders). Swales generally included these species, but were occupied by additional species of motile, soft proboscis subsur- face deposit feeders (e.g. <u>Notomastus latericeus</u> and <u>Scoloplos acmeceps</u>). Many of these species also occurred on the shelf break, but the abundance of <u>Chone</u> at the shelf break overshadowed them. Other habitats (i.e. flanks, swales) supported additional, though small, populations of sessile species: <u>Euchone incolor</u>, <u>Euchone elegans</u>, <u>Euclymene zonalis</u>. The abundance of discretely motile species in ridges resulted from populations of <u>Spiophanes bombyx</u> present at some sites.

As in Area B, morphological characters provide few data with which to distinguish habitats in Area E. The dominance of tentaculate species at the shelf break was due to <u>Chone</u> alone. In Area E ridges,

habitats that were scarce in tentaculate species in Area B, several species accounted for the difference: <u>Spiophanes</u> <u>bombyx</u>, <u>Euchone</u> <u>incolor</u>, <u>Caulleriella</u> spp. All were present in ridges of Area B, though their abundances were relatively low. In Area E, they contributed over 60% of the polychaete fauna on ridges.

DISCUSSION

This study was the first application of the Jumars and Fauchald (1977) polychaete feeding biology categories in which analyses were made of gut content of species collected in the area of study. Feeding classifications used in previous investigations have relied either on existing literature (Maurer and Leathem 1981) or on existing literature supplemented with casual observations (Jumars and Fauchald 1977). The gut content analyses of this investigation led to more accurate feeding classification of the polychaetes than was previously possible, and provided a more credible data base with which to test hypotheses.

Based on investigations by Jumars and Fauchald (1977), Boesch (1979a) and Maurer and Leathem (1981), I hypothesized that the feeding biology of polychaetes in the Middle Atlantic Bight was related to sediment variables, and that patterns existed in the distribution of feeding biology parameters which would distinguish habitats. Specifically, it was hypothesized that carnivorous polychaetes were in greatest proportion in coarser sediments. Cross-shelf analyses indicated that carnivores were in greatest proportion in coarser sediments of the Middle Atlantic Bight inner shelf, and that the proportion of carnivores to other feeding classes decreased significantly with depth. Carnivores were positively correlated with coarse sand in the outer shelf ridge field habitats of Area B. These results confirmed observations by Boesch (1979a) that there is a trend toward carnivory in coarser sands of the Middle Atlantic Bight. Boesch's (1979a) conclu-

sions were based primarily on distribution of numerically dominant species of macrobenthos. He predicted that two polychaete species, Lumbrinerides acuta and Goniadella gracilis, which he found dominant in much of the inner and middle shelf and in the coarse sediment habitats of the outer shelf, were interstitial-feeding carnivores. This study confirmed Boesch's predictions of carnivory in these two species.

The correlations of proportion of carnivorous polychaetes with depth and coarse sand probably had more to do with sediment character-istics than with depth. Most specimens of carnivorous polychaetes collected in the study area were small (e.g. dorvilleids, phyllodocids, juvenile nephtyids), and their feeding was probably dependent to a great extent on size of the interstices of the sediments. Coarser sediments have greater pore space between sand grains. This greater space enhances abundance of interstitial or burrowing prey organisms, enhances movement of the carnivores, and enhances oxygen penetration of the sediments (Fenchel 1970). In contrast, if all else were equal, most carnivorous polychaetes in finer sediment habitats of the Middle Atlantic Bight would probably feed at the sediment surface because of limited pore space in the sediments. However, inhabitants of finer-sediment habitats of the study area are probably influenced by numerous other physical and biological parameters. For instance, bottom photo-graphs indicated that many of the finer sediment habitats (e.g. topographic depressions) are covered with shell rubble, clay lumps, and other material that generally increased structural heterogeneity Boesch 1979a). This provides increased surface area and habitat suitable

for carnivores, including those species that feed on colonial invertebrates (e.g. syllids), hunting carnivores (e.g. phyllodocids), and other surface epifaunal, and burrowing species.

Another hypothesis posed in this investigation was that subsurface deposit feeders were in greater proportion in finer sediments. The cross-shelf analyses of this investigation indicated a positive correlation of the proportion of subsurface deposit feeders with depth and a negative correlation of the proportion of surface deposit feeders with depth. Proportion of subsurface deposit feeders was positively correlated with organic carbon, and proportion of surface deposit feeders was negatively correlated with organic carbon in ridge fields of the outer shelf (Area B). Surface deposit feeders numerically dominated most habitats, and when compared to other detritivores, were in greatest proportion in coarser sediment habitats. These are physically dynamic habitats that are periodically scoured by currents (Swift 1976), allowing little surface detritus accumulation. Boesch (1979a) proposed that deposit feeders in such coarse sediment habitats of the Middle Atlantic Bight are primarily dependent on recently sedimented plankton detritus. In light of the dominance of surface deposit feeders in coarse sediments this certainly appears to be true.

If abundance of surface deposit feeders in the Middle Atlantic Bight is dependent on recently sedimented food, then the greatest abundance of surface deposit feeders would be expected in areas of greatest plankton production. Phytoplankton biomass and productivity in the Middle Atlantic Bight generally decreases from the inner to the

outer shelf, then sharply increases at the shelf break (Walsh et al. 1978, Malone et al. 1979). The increase at the shelf break is believed by Malone et al. (1979) to be due to increased enrichment provided by a frontal system at the shelf break. Broad scale analysis in this study showed that abundance and proportion of surface deposit feeders in the Middle Atlantic Bight closely paralleled the pattern of phytoplankton production. Surface deposit feeders were most abundant and in greatest proportion on the inner shelf, decreased across the shelf, then increased at the shelf break.

There are two primary criteria which affect the distribution of subsurface deposit feeders: 1) the presence of ample subsurface food resources; and 2) the adequate exchange of solutes between the sediments and the overlying water column. As discussed above, most sedimented nutrients in coarse-sediment habitats of the study area probably are ingested at the sediment surface. Fine-sediment habitats, such as topographic depressions, are more likely to provide the subsurface food resources necessary to support subsurface deposit feeders. Generally, topographic depressions act as sediment sinks that accumulate sediment and subsequently bury detritus. Although scouring limits net accumulation, fine sediments periodically collect in swales (Swift 1976). It was not surprising, therefore, that the greatest proportion of subsurface deposit feeders in the Middle Atlantic Bight was found in finer sediment habitats (i.e. swales).

The abundance of subsurface deposit feeders in topographic depressions is also dependent on the second criterion: the adequate exchange

of solutes between sediments and overlying water. Without this exchange, metabolites accumulate in the sediment and oxygen penetration is limited (Fenchel 1970). Recent investigations have demonstrated that tube-dwelling macrobenthos (e.g. Aller and Yingst 1978, Brenchley 1979, Aller 1980, 1982) and surface and subsurface deposit feeders (e.g. Thayer 1979, Yingst and Rhoads 1980, Hammond 1981) may have an indirect influence on the distribution of subsurface species by altering the physical and geochemical characteristics of the sediments. Additionally, biogenic reworking of sediments by burrowers and tube irrigation by tube dwellers enhance the exchange of solutes between the water column and pore water (Rhoads et al. 1978, McCaffrey et al. 1980). Thus, presence of macrobenthic organisms may increase vertical penetration of oxygen to the sediments, increase rate of transfer of nutrients into sediments, and eliminate metabolites from sediments. This effectively increases standing stocks of bacteria (Yingst and Rhoads 1980) and other microorganisms which are recognized by most investigators (e.g. Kofoed 1975, Tenore et al. 1978) as the actual food source of deposit feeders. Therefore, except where biogenic activity in sediments is extreme or where tube dwellers are so close as to abut, the presence of populations of deposit feeders and tube dwellers improves habitat for subsurface deposit feeders. As demonstrated by Boesch (1979a), topographic depressions on the Middle Atlantic continental shelf are occupied by rich assemblages of benthic organisms. These all may contribute to the exchange of solutes between sediments and the water column which ultimately enhances the presence of subsurface deposit feeders.

I hypothesized that polychaete motility in the study area was associated with sediment variables, and specifically that sessile species were associated with finer sediments. Broad scale analyses indicated that proportion of sessile polychaetes was positively correlated with percent silt and clay and percent organic carbon. Jumars and Fauchald (1977) proposed that sediment stability and flux of organic matter were the covariables most responsible for similar correlations of proportion of sessile polychaetes with depth. They provided an extensive discussion of the relationship between polychaetes and their environment, including influence of sediment mobility, foraging radius of species, and variations in nutritional influx. Though the bathymetric range of the Middle Atlantic Bight study area limited adequate testing of many of Jumars and Fauchald's (1977) hypotheses concerning the association of sessile species with foraging radius and sediment stability, the positive correlation of sessile polychaetes of the study area with organic carbon and silt and clay supports their contention that sessile polychaetes generally inhabit continental shelf habitats which are physically stable. Furthermore, the dominance of motile polychaetes at all cross-shelf depth zones (Figure 15) in the Middle Atlantic Bight is probably indicative of the generally unstable nature of most habitats. Discretely motile polychaetes dominate some fine-sediment habitats of the inner and middle shelf off Virginia. Generally, however, surficial sediments of the study area are coarser sand-sized particles. Rapid transgression following the last glacial period left the continental

shelf of the Middle Atlantic Bight covered by an unconsolidated sur-
ficial sand sheet (Freeland and Swift 1978). Many investigators (e.g.
Duane et al. 1972, Swift et al. 1972, Swift 1976) have characterized
the bottom currents of the shelf as both erosional and constructional
in nature, because the surficial sand that composes the topographic
features is believed to be regularly redistributed. This sediment
movement is probably greatest on the inner shelf, but may occasionally
occur at all shelf depths. Using in situ instrumentation, Butman et
al. (1979) demonstrated that intermittent movement of bottom sediment
occurred on the Middle Atlantic Bight outer continental shelf (60 to 87
m depth) in response to numerous forcing mechanisms (e.g. currents,
internal waves). It is not surprising, therefore, that motile species
dominated all depth zones. It is likely that domination by motile
species also exists in other continental shelf areas covered by physi-
cally dynamic sediments, such as the South Atlantic Bight (Florida to
North Carolina).

This investigation also concerned the association of the classes
of polychaete feeding morphology with sediment variables. Since most
soft proboscis polychaetes in the Middle Atlantic Bight are deposit
feeders, it was expected that soft proboscis polychaetes would be in
greatest proportion in habitats of greatest accumulation of detritus
(i.e. swales). The outer-shelf ridge and swale habitats of Area B and
E were proposed as study areas to test this hypothesis. Soft proboscis
species did not numerically dominate any of the habitats of these
areas; however, soft proboscis polychaetes were in greatest pro-

portion in deep swales of Area B and eroded swales of Area E. These were the ridge and swale habitats of greatest silt and clay content and greatest organic carbon content (Tables 5 and 8). Other feeding morphology components were also associated with particular habitats. Tentaculate polychaetes were most abundant in inner and middle shelf swales. In Areas B and E jawed polychaetes were generally associated with coarse sediment habitats (e.g. ridges, terrace) and tentaculate polychaetes were associated with intermediate habitats (e.g. ridge flanks, shallow swales). The trend toward dominance of coarse sediments by jawed polychaetes was expected, since most jawed species in Areas B and E were motile carnivores. The functional advantage of jawed motile carnivores in coarse-grained sediments was discussed by Fauchald and Jumars (1979). They proposed that jawed species are better adapted to ingesting variable prey sizes than nonjawed species. Furthermore, motility is adaptive for carnivory when food is scarce, but not limiting.

Based on the information collected in this study a number of predictions concerning polychaete feeding biology can be posed as general hypotheses for future testing. Subsurface deposit feeders would likely be be most important where greatest sedimentation occurs in conjunction with high water-column production. The best areas to test this might be delta regions of large river systems, such as the Mississippi or Amazon Rivers. Secondly, as stated by Jumars and Fauchald (1977), suspension feeders would likely be in greatest proportion where adequate suspended material would exist, and where intensity and frequency

of physical disturbance would not be limiting. Such conditions would likely occur in broad estuaries such as the Chesapeake Bay and Long Island Sound. Finally, carnivorous polychaetes would likely be in greatest proportion in physically dynamic coarse sediment habitats such as beaches and tidal inlets. Greatest abundance of carnivores would be expected in those physically dynamic habitats that would support the greatest abundance of prey organisms.

Polychaetes are an integral part of macrobenthic communities. Although our knowledge of their relationships with other taxa is poor, this investigation provides insight into their feeding biology as a group and provides a base of knowledge from which to expand our research.

SUMMARY

1. Analyses of gut content in specimens of 64 polychaete species from
    20 families led to new feeding classifications for many Middle
    Atlantic Bight polychaetes.

2. The greatest proportion and greatest abundance of carnivorous poly-
    chaetes in the study area occurred in coarse unstable sediments.
    Cross-shelf analyses indicated that the proportion of carnivores
    decreased significantly with depth. Carnivores were positively
    correlated with percent coarse sand in a topographically complex
    area of the outer shelf.

3. Of the three detritivore components, subsurface deposit feeders
    were in greatest proportion in finer sediments. Proportion of sub-
    surface deposit feeders increased significantly with depth and per-
    cent organic carbon across the continental shelf. Surface deposit
    feeders numerically dominated most habitats in the study area, and
    were in greatest proportion in coarse sediment habitats. Abundance
    of surface deposit feeders decreased from the inner to the outer
    shelf and increased sharply at the shelf break, perhaps in response
    to a similar pattern in water-column production. Suspension
    feeders were in least abundance on the inner shelf and middle
    slope, probably due to instability of inner shelf sediment and
    scarcity of suspended food resources on the middle slope.

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4. Soft proboscis polychaetes were most abundant and in greatest pro-
    portion in topographic depressions, probably in response to detri-
    tus accumulation. Jawed and tentaculate polychaetes were abundant
    throughout the Middle Atlantic Bight. Jawed polychaetes on the
    outer shelf were in greatest proportion in physically dynamic habi-
    tats. Tentaculate polychaetes were most abundant in topographic
    depressions (swales) of the inner and middle shelf, and ridge
    flanks of Areas B and E.

5. Sessile polychaetes generally inhabited the more physically stable
    habitats of the continental shelf. Cross-shelf analyses indicated
    that the proportion of sessile polychaetes was positively corre-
    lated with percent silt and clay and percent organic carbon. Mo-
    tile polychaetes numerically dominated most habitats, perhaps indi-
    cative of the physically dynamic processes and generally unstable
    nature of the study area.

6. Topographic depressions of the Middle Atlantic Bight were distin-
    guished from surrounding habitats in the proportional importance of
    feeding behaviors among the polychaetes and the composition and
    abundance of the polychaete species. This is probably because
    topographic depressions act as particle sinks that accumulate food
    resources in otherwise nutrient-poor areas, and accumulate lag
    deposits which increase structural heterogeneity. The abundance

of polychaetes in topographic depressions of the inner and middle shelf of the study area was substantially greater than that of surrounding habitats. The difference in abundance was not as evident in outer shelf topographic depressions.

Appendix A. Gut content analyses by species and classification.

	TOTAL SPECIMENS	EMPTY GUTS	DETRITUS	SAND ONLY	DIATOMS	OTHER
Ampharetidae:						
Ampharete arctica	3	0	3	0	3	
Anobothrus gracilis	14	0	14	0	12	
Auchenoplax crinita	5	0	5	0	3	
Melinna cristata	1	0	1	0	1	dinoflagellates (1)
Amphinomidae:						
Paramphinome jeffreysii	26	26	0	0	0	
Aphroditidae:						
Aphrodita hastata	25	18	0	4	0	nerids(1),G. dibranchiata(2)
Laetmonice filicornis	2	2	0	0	0	
Arabellidae:						
Arabella mutans	5	5	0	0	0	
Drilonereis longa	19	13	0	0	0	sand masses (6)
Drilonereis magna	11	11	0	0	0	crustacean (1)
Capitellidae:						
Mediomastus californiensis	15	0	15	0	0	diatom fragments (15)
Notomastus latericeus	15	0	15	0	0	small diatoms and diatom fragments (15)
Dorvilleidae:						
Protodorvillea minuta	29	28	0	1	0	
Protodorvillea gaspeensis	5	5	0	0	0	
Protodorvillea kefersteini	12	11	0	0	0	chitin (1)
Schistomeringos caeca	17	0	17	0	1	forams (1)
Schistomeringos sp. A	1	1	0	0	0	

Appendix A. continued

	TOTAL SPECIMENS	EMPTY GUTS	DETRITUS	SAND ONLY	DIATOMS	OTHER
Eunicidae:						
Eunice antennata	2	0	2	0	1	fecal pellet(1)
Eunice pennata	4	0	4	0	0	plant material(1)
Eunice vittata	21	0	21	0	6	spines(1),chitin(1)
Marphysa bellii	13	0	13	0	5	
Fauveliopsidae:						
Fauveliopsis sp. A	8	0	8	0	0	
Glyceridae:						
Glycera capitata	15	15	0	0	0	amphipod(1),polychaete(1)
Glycera dibranchiata	29	22	0	5	0	
Glycera robusta	6	6	0	0	0	
Hemipodus roseus	5	4	0	1	0	
Goniadidae:						
Goniada brunnea	18	17	0	0	0	prey?(1)
Goniada maculata	4	4	0	0	0	
Goniada norvegica	2	2	0	0	0	
Goniada teres	2	2	0	0	0	
Goniadella gracilis	114	96	3	12	0	polychaete(3), sand masses(3)
Hesionidae:						
Gyptis sp. A	8*	8	0	0	0	
Lumbrineridae:						
Lumbrinerides acuta	103	92	2	2	0	sand masses(7)
Lumbrineris albidentata	8	6	0	2	0	

Appendix A. continued

	TOTAL SPECIMENS	EMPTY GUTS	DETRITUS	SAND ONLY	DIATOMS	OTHER
Lumbrineris fragilis	40 (15 juv)	20	15 (juv)	3	0	setae(2),forams(3)
Lumbrineris impatiens	62	12	50	0	0	
Lumbrineris latreilli	20	0	20	0	0	foram (1)
Ninoe nigripes	48	0	48	0	12	dinoflagellate(1)
Maldanidae:						
Praxillura longissima	3	0	3	0	0	
Nephtyidae:						
Aglaophamus circinata	50	44	0	2	0	sand masses(2),polychaetes(2)
Nephtys bucera	27	24	0	1	0	setae(2),peracarids(1)
Nephtys incisa	4	4	0	0	0	
Nephtys picta	5	5	0	0	0	
Nephtyidae (juv)	40	36	4	0	0	setae(3)
Nereididae:						
Ceratocephale loveni	20	0	20	0	9	spines(8),forams(5)
Nereis grayi	49	5	44	0	14	fecal pellets(4)
Nereis zonata	21	8	13	0	6	plant material(1)
Onuphidae:						
Hyalinoecia artifex	6	0	0	1	0	peracarids(5),spines(1)
Nothria conchylega	14	0	14	0	4	forams(3)
Onuphis atlanticum	6	0	6	0	4	
Onuphis pallidula	54	5	49	0	31	
Paraonidae:						
Aricidea catherinae	13	0	13	0	3	

Appendix A. continued

	TOTAL SPECIMENS	EMPTY GUTS	DETRITUS	SAND ONLY	DIATOMS	OTHER
Aricidea cerrutii	10	0	10	0	3	
Aricidea simplex	5	0	5	0	2	
Aricidea wassi	5	0	5	0	0	
Cirrophorus lyriformis	5	0	5	0	5	
Levensenia gracilis	5	0	5	0	0	
Paradoneis lyra	5	0	5	0	5	
Phyllodocidae:						
Anaitides mucosa	12	12	0	0	0	
Eteone sp. A	10	10	0	0	0	
Sphaerodoridae:						
Sphaerodoridium claparedii	24	20	4	0	1	
Syllidae:						
Exogone hebes	57	54	3	0	0	
Exogone verugera	36	23	13	0	0	
Sphaerosyllis erinaceus	23	19	4	0	0	chitin(1),sand masses(1)
Typosyllis tegulum	13	8	5	0	0	dinoflagellates (1)

* incomplete specimens

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