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Middle Atlantic Outer Continental Shelf Environmental Studies Volume II-B: Chemical and Biological Benchmark Studies

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MIDDLE ATLANTIC
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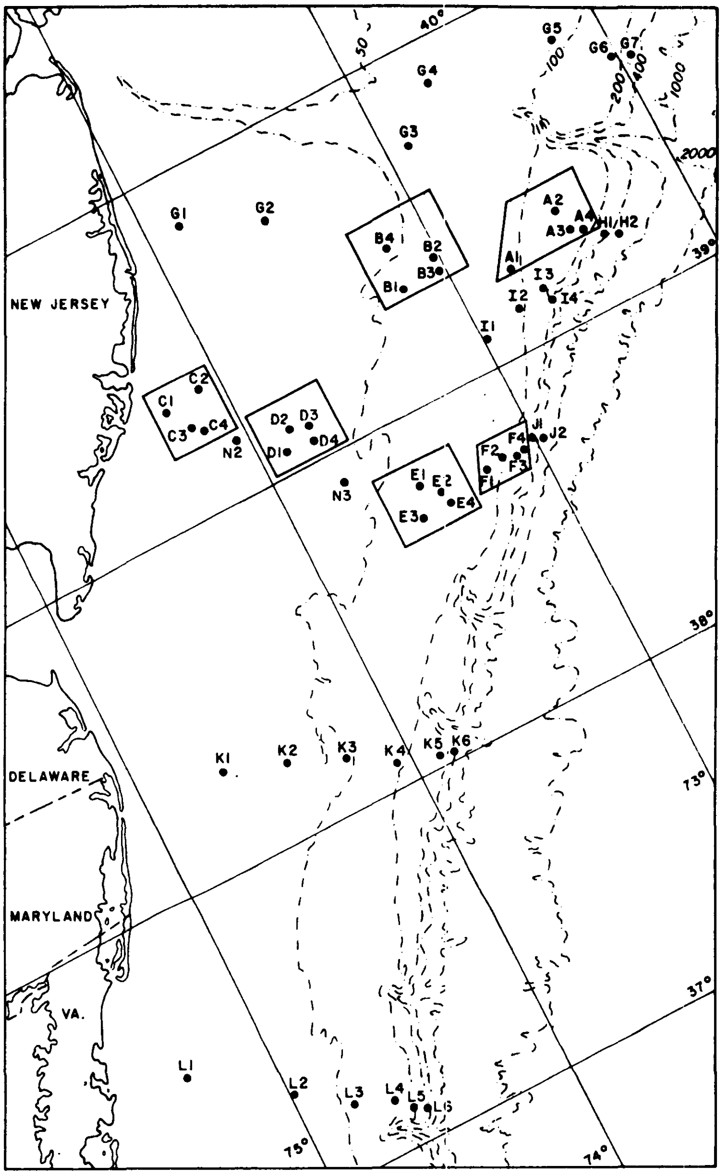
ENVIRONMENTAL STUDIES

VOLUME II-B. CHEMICAL AND BIOLOGICAL BENCHMARK STUDIES



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With the

Bureau of Land Management
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This volume contains element reports for sediments and benthic ecology (macrobenthos, meiobenthos, and foraminifera). The sediment chapter includes a discussion of patterns of sediment texture and the relationship between percent silt/clay and organic carbon. The macrobenthos and meiobenthos chapters include faunal composition, patterns of distribution, sampling variability, community characterization and factors controlling community structure. The foraminifera chapter presents information on species diversity, live/dead test ratios and species distribution.

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MIDDLE ATLANTIC OUTER CONTINENTAL SHELF ENVIRONMENTAL STUDIES

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The use of trade names or identification of specific products or equipment by manufacturer does not constitute endorsement or recommendation for use.

PREFACE

The final report on contract AA550-CT6-62 between the Bureau of Land Management and the Virginia Institute of Marine Science consists of the following:

Volume I. Executive Summary.

This volume contains the Executive Summaries of the work conducted by VIMS under contract AA550-CT6-62 and the U. S. Geological Survey under Memorandum of Understanding AA550-MU7-31.

Volume IIA, IIB, IIC and IID. Chemical and Biological Benchmark Studies.

This volume contains the individual program element reports for the work completed by VIMS during the first year of the Chemical-Biological Benchmark Studies in the Middle Atlantic outer continental shelf region. Microfiche appendices containing field, laboratory, and data processing forms are included at the end of Volume IID.

Volume III. Geologic Studies.

This volume contains the individual program element reports for the work completed by USGS during the first year of the Geologic Studies in the Middle Atlantic outer continental shelf region. Microfiche appendices and a map supplement are included.

In addition to the printed and microfiched material, the final report also includes a complete, documented set of the environmental data generated by VIMS which has been deposited with the Environmental Data Service, National Oceanic and Atmospheric Administration, U. S. Department of Commerce, Washington, D. C. 20235. Data documentation has also been provided to BLM.

Copies of computer programs developed by VIMS during this study have been deposited with BLM as has a microfiched set of the raw data. Anyone desiring access to the computer programs, data documentation, or raw data can contact:

Environmental Studies Field Coordinator
Bureau of Land Management
Atlantic Outer Continental Shelf Office
6 World Trade Center, Suite 600D
New York, New York 10048

Eugene M. Burreson
Program Manager

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This report is the result of the cooperative efforts of many people, especially the authors of the chapters of this volume who were also the principal investigators of the various program elements. Scientists, graduate assistants, and technicians throughout the Virginia Institute of Marine Science are also deserving of our acknowledgements.

Special appreciation goes to our patient clerical personnel, Cheryl Ripley, Ruth Edwards, Patti Alderman, and Annette Stubbs for typing, proofreading, and assistance in coordination of this volume.

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E. M. Burreson
D. F. Boesch
B. L. Laird

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[1] Appendices are provided on microfiche at the end of Volume IID.

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CHAPTER 5

Bottom Sediments and Sedimentary Framework

D. F. Boesch

Special Report in Applied Marine Science
and Ocean Engineering No. 193

CHAPTER 5

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CHAPTER 5

BOTTOM SEDIMENTS AND SEDIMENTARY FRAMEWORK

D. F. Boesch

INTRODUCTION

The great emphasis placed on the seabed in these Middle Atlantic OCS Environmental Studies is a reflection of the sedimentary nature of anticipated contaminants resulting from oil and gas development and the sedentary nature of the benthic biota. There appears to be a greater potential to detect low level contamination of bottom sediments and organisms and resulting effects on the seabed than in the more transient pelagic realm.

A commonality of all the seabed-related studies is their reliance on a good understanding of the physical nature of the bottom sediments of the continental shelf and slope. Furthermore, the processes, both past and present, affecting the composition of bottom sediments must be considered in interpretation of chemical and biological data.

This section reports data on the grain size and organic carbon and nitrogen concentrations of sediments at all stations sampled for benthos, hydrocarbons, and trace metals over the two years of study. It is supportive of the biological and chemical studies rather than constituting a report of sedimentology *per se*. However, the results are interpreted in reference to the sedimentary framework of the Middle Atlantic shelf and slope to provide the biological and chemical studies a dynamic perspective of shelf sediments.

This report extends and synthesizes the preliminary report based on the first year data (Boesch 1977). Particular questions to be addressed in this report include:

1) The relationship of sediment grain size to depth, topography, and depositional history.

2) The relationship of organic carbon and nitrogen levels to sediment grain size distribution and inferred sedimentary conditions.

3) The spatial and temporal variability of the grain size, carbon and nitrogen parameters at repetitively sampled stations and the effect this variability may have on biological and chemical variables.

SEDIMENTARY FRAMEWORK

The Middle Atlantic continental shelf has been the subject of extensive geological studies making it one of the best known in the world. Several comprehensive reviews emphasizing the Middle Atlantic shelf and slope are available (Emery and Uchupi 1972; Milliman 1973; Swift et al. 1972a; Swift 1976; Southard and Stanley 1976). No attempt will be made here to review all available information, but this serves as an abbreviated perspective to assist interpretation of sediment data presented.

Physiography

The Middle Atlantic continental shelf is a broad, gently sloping platform varying in width from 160 km south of Cape Cod to 140 km off New Jersey and 25 km off Cape Hatteras (see bathymetry in Uchupi 1970). The shelf break, that zone where the declivity of the depth gradient changes abruptly, begins at between 100 and 150 m depth along the central Middle Atlantic shelf (Emery and Uchupi 1972; Wear et al. 1974). The continental slope, characterized by steep gradients (4-5°), ranges from the shelf break to the continental rise at about 2000 m. The continental slope and edge of the shelf are incised by numerous submarine canyons. In the study area, the major canyons are, from the north, Hudson, Wilmington, Baltimore, Washington, and Norfolk (Wear et al. 1974). The shelf surface is not flat and featureless but is crossed by depressions and covered by an obviously complex topography evidenced by convoluted isobaths. These topographic patterns are largely the result of processes which occurred during the low sea level stand during the last glacial period, roughly 14,000 years B.P., and the subsequent post-glacial retreat of the shoreline with the rise of sea level (Swift et al. 1972a).

Old river valleys filled mainly by estuarine deposits underlie the principal cross-shelf depressions in the study area, the Hudson, Great Egg, Delaware, and Chesapeake shelf valleys (Figure 5-1). Topographic highs composed of linear shoal fields occur to the north of each shelf valley. These shoal retreat massifs mark the retreat paths of littoral drift depositional centers that occur on the north sides of the mouths of estuaries (Swift et al. 1972a). The shelf valleys often terminate in flat areas on the outer shelf thought to represent former deltas, however, the subsurface structure can be traced to the major submarine canyons at the shelf edge (Twichell et al. 1977). Terraces running parallel to the isobaths can often be traced over large sections of the Middle Atlantic shelf (Milliman 1973). These are evidently erosional features reflecting former shorelines during major sea level stillstands.

Superimposed on these relict large scale features is a whole spectrum of topographic features of smaller scales, which may be more the result of contemporary processes. Of major importance and wide

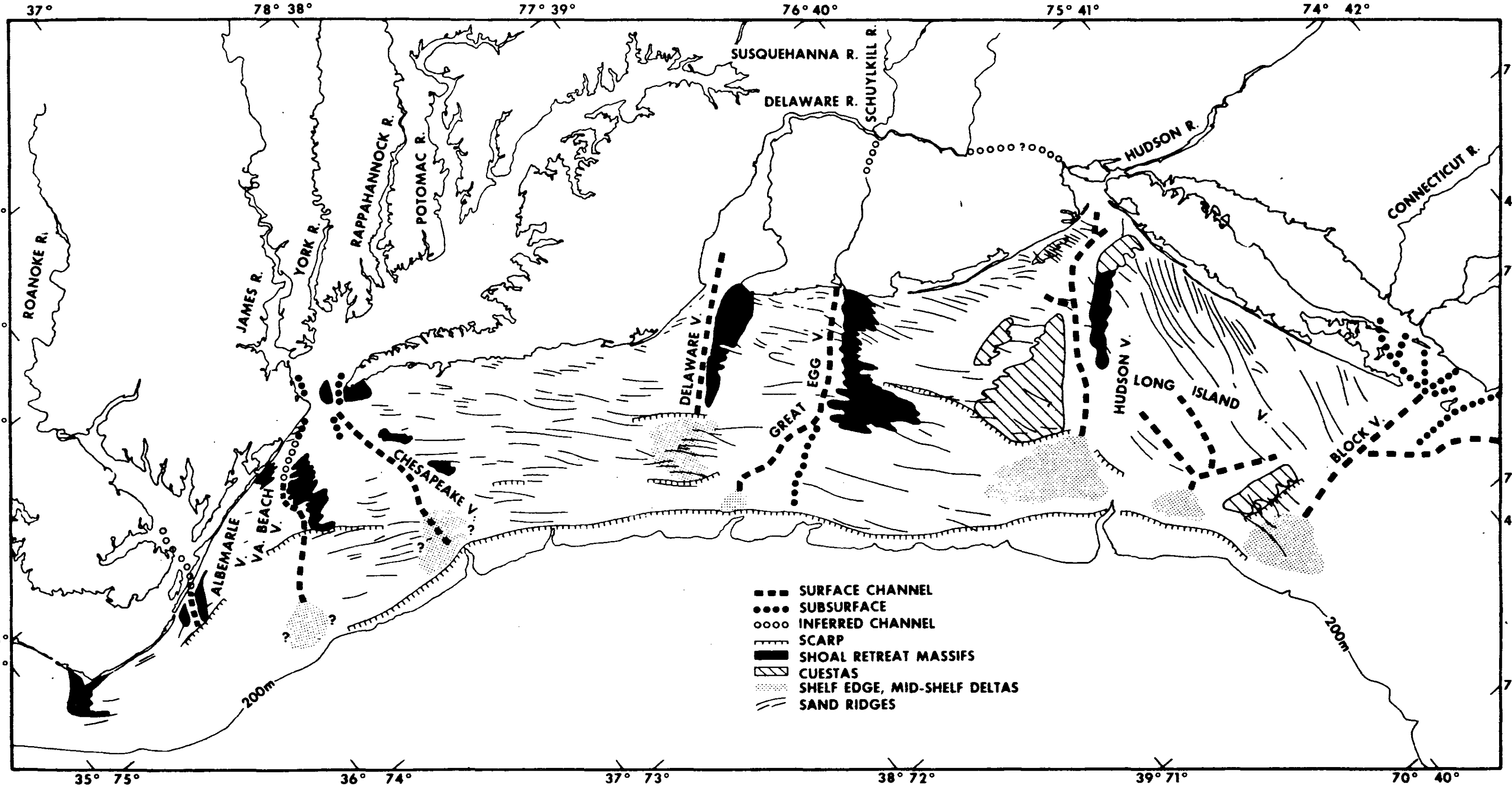


Figure 5-1. Major morphologic elements of the Middle Atlantic Bight (from Swift 1975).

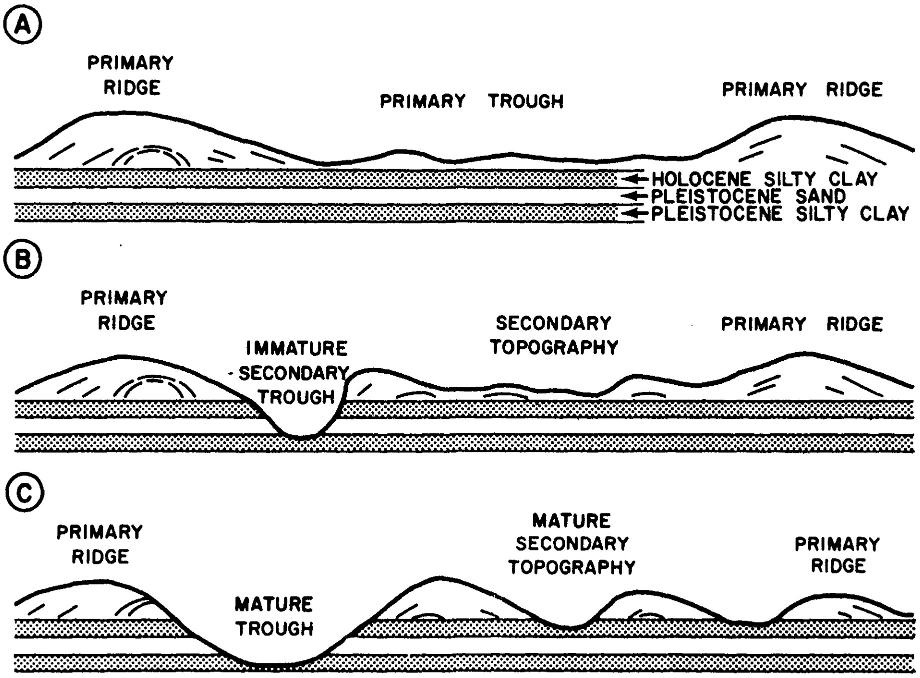
distribution is the so-called ridge and swale topography (Duane et al. 1972; Swift et al. 1972a). The linear sand ridges trend roughly northeast to southwest, or slightly oblique to the shoreline. Swift et al. (1972a) examined the size and spacing of ridges and swales on the New Jersey shelf and showed on this innermost shelf that the mean ridge spacing (crest to crest) was 1.4 km and mean relief was 4.7 m, whereas on the central shelf these mean dimensions were 2.5 km and 6 m. Outer shelf ridge spacing averaged 6.1 km and relief 6.0 m. Furthermore, McKinney et al. (1974) recognized two morphological orders of ridge and swale topography on the central New Jersey shelf. A first-order system had ridges 14 m high and 2-6 km apart trending north-northeast, and a second-order system with ridges 2-5 m high and 0.5-1.5 km apart trending northeast. The origin and development of the ridge and swale topography have been the subject of much debate, but most current investigators believe the ridges had their genesis at the shoreface, were stranded by transgression but were modified by hydrodynamic processes on the shelf (Figure 5-2). A major conclusion drawn from the first year of the Middle Atlantic Benchmark Program was that the ridge and swale topography found over approximately 75% of the width of the continental shelf of the study area is of major importance in the distribution of sediments, their chemical constituents and benthic organisms (VIMS and USGS 1977).

Smaller scale topography features are also found and they too may be of geochemical and biological importance. Sand waves are known to occur in some regions of the Middle Atlantic continental shelf. Knebel and Folger (1976) describe asymmetrical sand waves having a spacing of 100-650 m and a relief of 2-9 m near the head of Wilmington Canyon. Current lineations of 1.5 m amplitude and less than 100 m spacing have been found associated with ridge and swale topography on the central New Jersey shelf (McKinney et al. 1974). Finally, wave and current ripple patterns of a few cm scale are very characteristic of the central and inner continental shelf and may periodically develop in response to storms out to the shelf break.

These topographic patterns introduce considerable heterogeneity in grain size, chemical, and biological parameters. Sampling and interpretation must take full cognizance of the complexity of the shelf surface.

Sediments

Most of the Middle Atlantic continental shelf is covered by a sheet of sand 0-30 m thick overlying older, finer sediments. They are palimpsest sediments (Swift et al. 1972a), meaning they are relict in the sense that they have been eroded from a local, pre-Recent substrate and modern in the sense that they have been redeposited under the present hydraulic regime. Thus, broad scale patterns of distribution of sediments tend to be related to source of material and



DEVELOPMENT OF RIDGE TOPOGRAPHY

Figure 5-2. Schema for ridge and swale evolution based on observations on the central New Jersey shelf (Stubblefield and Swift 1976). Primary ridges are formed by the detachment of shoreface connected ridges during Holocene transgression. Scouring during storms forms a secondary trough and locally penetrates underlying deposits. Secondary trough erodes laterally and secondary ridges develop from sand eroded upcurrent.

historical processes, whereas smaller scale patterns seem to be more related to contemporary processes.

Because of fairly rapid Holocene transgression and limited input of modern detrital sediments from rivers, shelf sediments contain remarkably little silts and clays. Most sediments can be classified as sand (greater than 75% sand) or gravelly sand to water depths at least as deep as 200 m. The only major exception is the large area of fine sediments on the outer shelf off southern New England, just to the northeast of the present study area.

On the upper continental slope, shelf sands grade quickly into clayey-silts. In the central study area sediments at 400 m contain roughly 30% silt-clay, whereas deeper than 600 m most sediments are over 90% silts and clays.

Broad scale patterns of grain size distribution within the study area are well known (Milliman 1973; Johnson 1977). Medium sands predominate over most of the continental shelf. Large patches of coarser sediment (coarse sand or gravel predominating) are found on the inner shelf off central New Jersey and off the mouth of Delaware Bay. Fine and very fine sands predominate on the inner shelf off southern New Jersey and on the inner half of the shelf off the southern Delmarva Peninsula. As mentioned above, silts and clays are rare over the entire continental shelf in this region and do not become predominant until the upper continental slope (Southard and Stanley 1976).

Presentations of broad scale patterns of such grain size parameters as general size classes (Milliman 1972) or central tendency measures such as median grain size (Johnson 1977) tend to convey a misleading sense of homogeneity. More detailed studies of grain size distribution (e.g. Stubblefield et al. 1975; Southard and Stanley 1976) often show more complicated patterns of potential biological and geochemical importance. Stubblefield et al. (1975) found that in a region of the central New Jersey continental shelf (containing cluster area D of the present study) fine sand and moderate sorting occur on the flanks, medium to fine sand and moderate sorting occur on the crests, and sediments in the swales were either coarse, poorly sorted sands, or fine, well-sorted sands. Southard and Stanley (1976) similarly showed complex distribution of sediment texture at the shelf break between Wilmington and Norfolk Canyons (Figure 5-3). A narrow band of gravel concentration is continuous on the outer shelf shoreward of the break and mosaics of texture types characterize the heads of the major submarine canyons. On an even smaller scale, Knebel (1975) examined the significance of sediment textural variables on within-sample, within-station and between-station bases and found significant within-station variance for several grain size parameters.

Despite the apparent small and meso-scale variation in sediment texture, the sediments show remarkable temporal persistence.

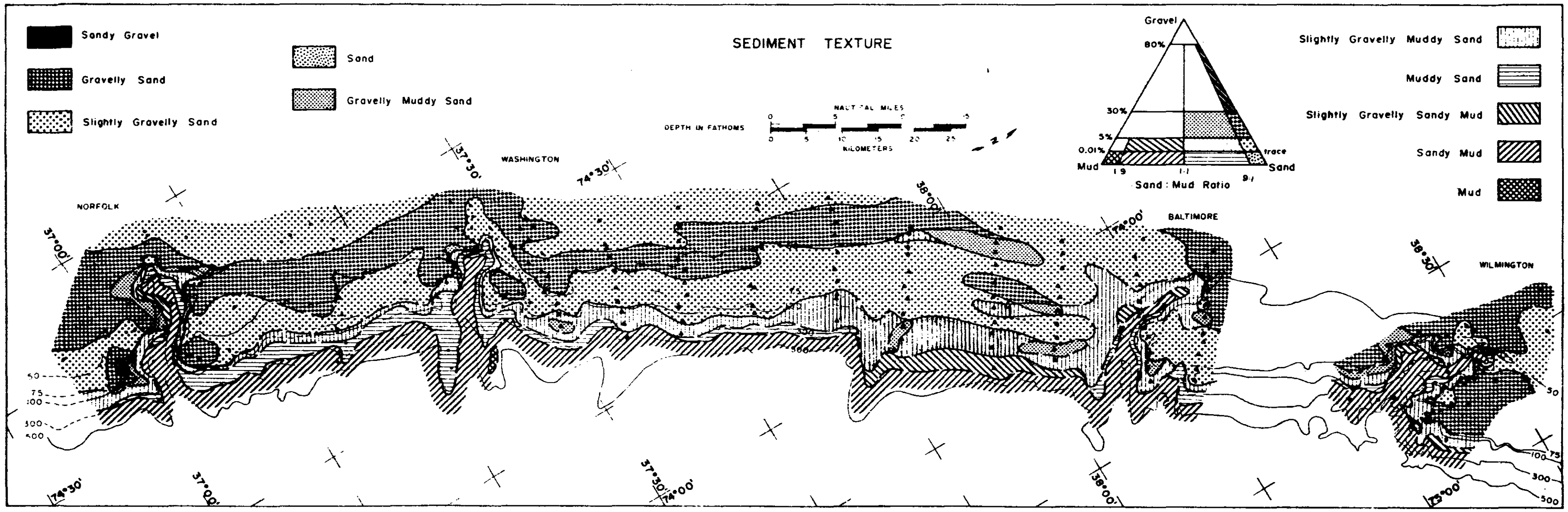


Figure 5-3. Distribution of surface sediments on the outer continental margin between Wilmington and Norfolk canyons (from Southard and Stanley 1976).

Stubblefield et al. (1977) repeatedly surveyed two transects in the New York Bight Apex over a year and half by grab sampling of textural parameters and side scan sonar examination. These results indicated no systematic seasonal variation and the variation observed was attributed to small positioning errors. They concluded that the bottom is "in a state of textural equilibrium with the hydraulic climate."

In terms of minerology, Middle Atlantic shelf sands are predominantly quartz (subarkosic) with biogenic carbonate locally important, particularly at the shelf break (Milliman 1972). Carbonates of the shelf break consist mainly of planktonic foraminifera and the light density of their tests posed some problems in the analysis of grain size of shelf break and slope sediments (see Methods). Local concentrations of glauconite, an authigenic mineral, are also found in the study area south of the Hudson Shelf Valley and at the shelf break.

Sedimentary Processes

Of the various processes affecting granulometric patterns, two are of particular relevance to the interpretation of biological and geochemical benchmark studies. The first concerns the origin and distribution of fines (silt and clay) with which trace metals, hydrocarbons, and biologically important materials (e.g. organic carbon) are often associated (Emery and Uchupi 1972; Farrington and Trip 1977). The second concerns the transport of sediment with respect to bathymetry, both in relation to depth and local topography.

As mentioned above, Middle Atlantic continental shelf sediments are notable for their lack of fines (< 63 μm) out to slope depths. Since the fine component is of particular biological and chemical importance, it is relevant to consider why fine sediments are not better represented and the origin of the fine sediments present. Although the Middle Atlantic Bight receives the drainage of several large river systems (in particular, the Connecticut, Hudson, Delaware, Susquehanna, Potomac, and James rivers) and these rivers carry large quantities of suspended sediment (Meade 1969), the major rivers empty into large estuaries rather than into the ocean directly. The basins and wetlands of these estuaries act as traps for fluvial sediments. Furthermore, bottom waters at the estuary mouths, which have greater suspended sediment loads than surface waters, have a net non-tidal flow into the estuary. Surprisingly, this means that large estuaries such as the Chesapeake and Delaware Bays have a net import of sediment from the ocean (Schubel and Carter 1976). Nonetheless, some fluvial sediment does escape the estuary for potential deposition on the continental shelf. However, Schubel and Okubo (1972) demonstrate that sediments originating from the Chesapeake Bay mainly bypass the shelf to be deposited on the continental slope or rise.

Milliman and Bothner (1977) report that seston in the Middle Atlantic Bight is principally biogenic, composed largely of phytoplankton. Since much of this material is degradable or is larger sized skeletal material, the standing seston must not contribute significantly to accumulation of fines in bottom sediments. A thin surface floc of fine sediments over "clean" sands has been often directly observed or seen in bottom photographs (Folger 1977). This material is probably considerably organic and appears to be easily resuspended. Although this mobile floc does not contribute significantly to the surface sediments (Bothner 1977), it may be of considerable biological importance.

Another locally important source of fine sediments on the Middle Atlantic continental shelf is the erosion of relict (Pleistocene or Holocene) fine deposits underlying the surficial sand sheet. These possible lagoonal deposits are locally eroded particularly in swales (McKinney et al. 1974). The stiff material is fragmented into lumps and the fines are further disaggregated by physical and biological forces. The importance of the contribution of this source to the fine component of surrounding sediments is unknown. However, clay lumps can evidently be transported over considerable distances as evidenced by their inclusion in barrier island washover deposits (Meza and Paola 1977).

The disturbance of bottom sediments by physical or biological forces is important in redistributing sediments, thus affecting granulometric distributions. Furthermore, sediment movement is of direct ecological importance, because benthic organisms must be able to cope with shifting sediments in which they live.

It is apparent from sediment distribution patterns and observations made during these studies that bottom sediment movement is widespread and frequent over much of the Middle Atlantic continental shelf. Bottom currents which potentially cause sediment movement have several causes, outlined in Table 5-1. The sediment textural and morphologic patterns on the Middle Atlantic shelf are largely storm dominated (Swift 1976). Wave induced oscillations are important in setting sediment in motion on the inner half of the shelf, and tidal currents may be locally important. Predominant currents during fair-weather conditions are driven by the geostrophic response of the stratified shelf water column to freshwater runoff and to winds (Beardsley et al. 1976). Neither these currents nor tidal currents are strong enough to result in significant sediment transport on the outer continental shelf. Rather, strong currents are generated during winter storms, when air-water coupling is more efficient and northeast winds induce a setup of shelf water against the coast (Swift 1976). Sediment movement observation and direct current measurements in VIMS Areas B and E (60-90 m) by the USGS (Butman et al. 1977) confirm that on the outer shelf, wave oscillations, geostrophic flow, internal waves, and fair-weather winds do not cause significant sediment transport at these depths. However, winter storms cause

Table 5-1. Bottom currents potentially causing sediment movement (after Southard and Stanley 1976).

CAUSE	TIME SCALE
Surface waves	Seconds
Barotrophic motions	Diurnal or semidiurnal
Wind-driven	Storm events or seasonal
Differences in atmospheric pressure	Storm events
Thermohaline circulation	Meso-megascale
Internal waves	Hours

bottom currents of over 35 cm sec^{-1}, well above the sediment resuspension threshold of 25-30 cm sec^{-1}, causing considerable resuspension of and movement of bed forms. Summer storms resulting from extratropical depressions are irregular but not uncommon occurrences in the area. Because they pass through the area rather quickly and without prolonged winds from one direction and because of the strong density stratification existing during the summer, these storms apparently have much less effect on bottom sediments of the outer shelf.

At the shelf break, conditions are apparently more quiescent and bottom sediment transport is less frequent. However, ripples were occasionally observed in bottom photographs of the sea bed down to 200 m. Sediments appear to be more dynamic in the vicinity of submarine canyons (Southard and Stanley 1976; Knebel and Folger 1976) possibly in response to increased velocity of tidal currents or internal waves.

Important local differences exist in bottom sediment transport with respect to ridge and swale topography. These are responsible for sediment textural patterns of profound biological and geochemical importance. Stubblefield et al. (1975) developed a model of sediment transport inferred from surface sediment distribution and near-surface structure in the vicinity of VIMS area D. They hypothesized up-flank rheologic and suspensive transport of medium and fine sand during intense storms and subsequent down-flank winnowing of fine sand during less intense meteorological events. This results in a pattern of slightly coarser sand on the ridges than on the flanks and finer sands in the swales except in erosional pockets which contain a lag of coarse sand and shell.

METHODS

Sampling

Sediment samples for grain size, organic carbon, and nitrogen analyses were collected at 52 grab stations (Figure 5-4) according to the schedule in Table 5-2. At each station 10-12 replicate 0.1 m^2 Smith-McIntyre grab hauls were made except at some deep stations where, because of long haul time, fewer hauls were made. From each of these successful hauls a 3.5 cm inside diameter clear acrylic core was inserted, removed and capped on both ends for grain size analysis. Length of the core sample varied with depth of penetration of the grab, but generally the cores contained the top 10 cm of sediment. During the first year of sampling cores from the grabs taken for trace metal or hydrocarbon samples, usually the first six, were sent to the USGS, Woods Hole, where a single grain size analysis was performed on composited aliquants from the cores. Grain size analyses were performed on all six sediment samples from the grabs taken for faunal analysis, usually grabs 7-12, and two of the individual samples taken

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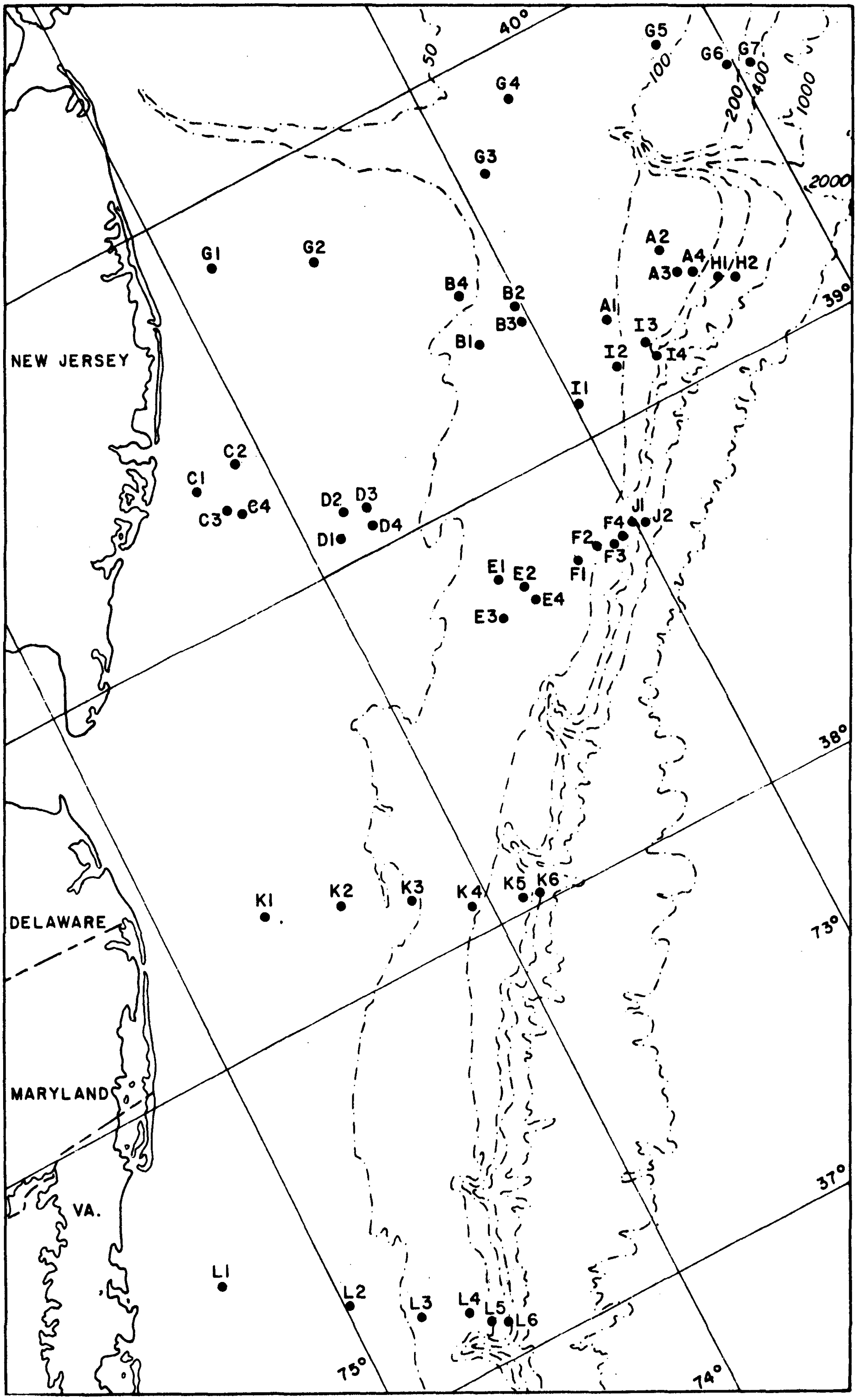


Figure 5-4. Study area showing location of stations from which sediments were analyzed for grain size, organic carbon and nitrogen.

Table 5-2. Number of replicate grab samples analyzed for grain size distribution (GS), organic carbon (C) and nitrogen (N) at each repetitively sampled station during each seasonal sampling period.

Station	Analysis	Fall 1975	Winter 1976	Spring 1976	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
A1	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
A2	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
A3	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
A4	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
B1	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
B2	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
B3	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
B4	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
B5	GS					12	6	12	12
	C					12	6	12	12
	N					0	6	6	6
C1	GS	8	8	8	8	1	1	1	1
	C	6	6	6	6	1	1	1	1
	N	6	0	0	0	0	1	0	1
C2	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
C3	GS	8	8	8	8				
	C	6	6	6	6				
	N	6	0	0	0				
C4	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6

Table 5-2. (Continued)

Station	Analysis	Fall 1975	Winter 1976	Spring 1976	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
D1	GS	8	8	8	8	12	12	12	12
	C	6	6	5	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
D2	GS	8	8	8	8				
	C	6	6	6	5				
	N	6	0	0	0				
D3	GS	8	8	8	8				
	C	6	5	6	6				
	N	5	0	0	0				
D4	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
E1	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
E2	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
E3	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
E4	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	6	0	0	0	6	6	6	6
F1	GS	8	8	8	8	12	12	12	12
	C	6	5	6	6	12	12	12	12
	N	0	0	0	0	6	6	6	6
F2	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	0	0	0	0	6	6	6	6
F3	GS	8	8	8	8	12	12	12	12
	C	6	6	6	6	12	12	12	12
	N	0	0	0	0	6	6	6	6
F4	GS	8	8	8	8	12	12	12	12
	C	6	6	5	6	12	12	12	12
	N	0	0	0	0	6	6	6	6
G1	GS		8		8				
	C		6		5				
	N		0		0				
G2	GS		8		8		12		10
	C		6		6		12		10
	N		0		0		6		4

Table 5-2. (Continued)

Station	Analysis	Fall 1975	Winter 1976	Spring 1976	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
G3	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
G4	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
G5	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
G6	GS		8		8		10		10
	C		6		5		10		10
	N		0		0		4		4
G7	GS		1		12				
	C		0		6				
	N		0		0				
H1	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
H2	GS		6		6		6		12
	C		6		2		6		12
	N		0		0		0		6
I1	GS		8		8		12		10
	C		6		6		12		10
	N		0		0		6		4
I2	GS		8		8		12		10
	C		6		6		12		10
	N		0		0		6		4
I3	GS		8		10		12		10
	C		6		6		12		10
	N		0		0		6		4
I4	GS		7		8		10		10
	C		6		6		10		10
	N		0		0		4		4
J1	GS		8		8		12		10
	C		6		5		12		10
	N		0		0		6		4
J2	GS		6		6		6		12
	C		6		6		6		12
	N		0		0		0		6
K1	GS		8		8				
	C		6		6				
	N		0		0				

Table 5-2. (Concluded)

Station	Analysis	Fall 1975	Winter 1976	Spring 1976	Summer 1976	Fall 1976	Winter 1977	Spring 1977	Summer 1977
K2	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
K3	GS		8		8				
	C		6		6				
	N		0		0				
K4	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
K5	GS		5		8		10		10
	C		3		6		10		10
	N		0		0		4		4
K6	GS		6		8		10		10
	C		6		6		10		10
	N		0		0		4		4
L1	GS		8		8				
	C		6		6				
	N		0		0				
L2	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
L3	GS		8		8				
	C		6		5				
	N		0		0				
L4	GS		8		8		10		10
	C		6		6		10		10
	N		0		0		4		4
L5	GS		8		9		10		10
	C		6		6		10		10
	N		0		0		4		4
L6	GS		6		8		10		10
	C		6		5		10		10
	N		0		0		4		4

for chemical analysis, usually samples from grabs 1 and 2. During the second year grain size analyses were performed on individual samples from each grab sample collected.

Organic carbon and nitrogen samples were collected in a similar fashion but in smaller diameter core tubes (2.2 cm inside diameter). One core sample each was taken only from the six grabs collected for analyses of macrobenthos during the first year. During the second year carbon samples were also taken from chemistry grabs. Samples were quickly frozen and remained so until analysis.

Laboratory Methods

Since the sediments encountered varied in composition from predominantly sand and gravel to predominantly silt and clay, no single size analysis technique could cover the size range for all samples. Consequently, a combined analysis was performed using sieve separation, pipette analysis, rapid sand analyzer, and Coulter electronic particle counter. The analysis followed the flow chart shown in Table 5-3 and was discussed in detail in the report on the first years' results (Boesch 1977).

During analysis of the first year's samples the rapid sand analyzer (RSA) used employed a differential hydrostatic pressure sensor. This sensor was delicate and was very sensitive to motion and environmental conditions. Prior to analysis of second year samples the RSA was outfitted with a gravimetric sensor consisting of a Cahn Model DTL eletromagnetic balance from which was suspended a weighing pan at the bottom of the column. The voltage output from the balance was recorded on a strip chart recorder and the signal represented the accumulated (coarse to fine) mass distribution of the sediment sample. With both gravimetric and pressure sensors the RSA was calibrated using sieve fractionated sand from the study area.

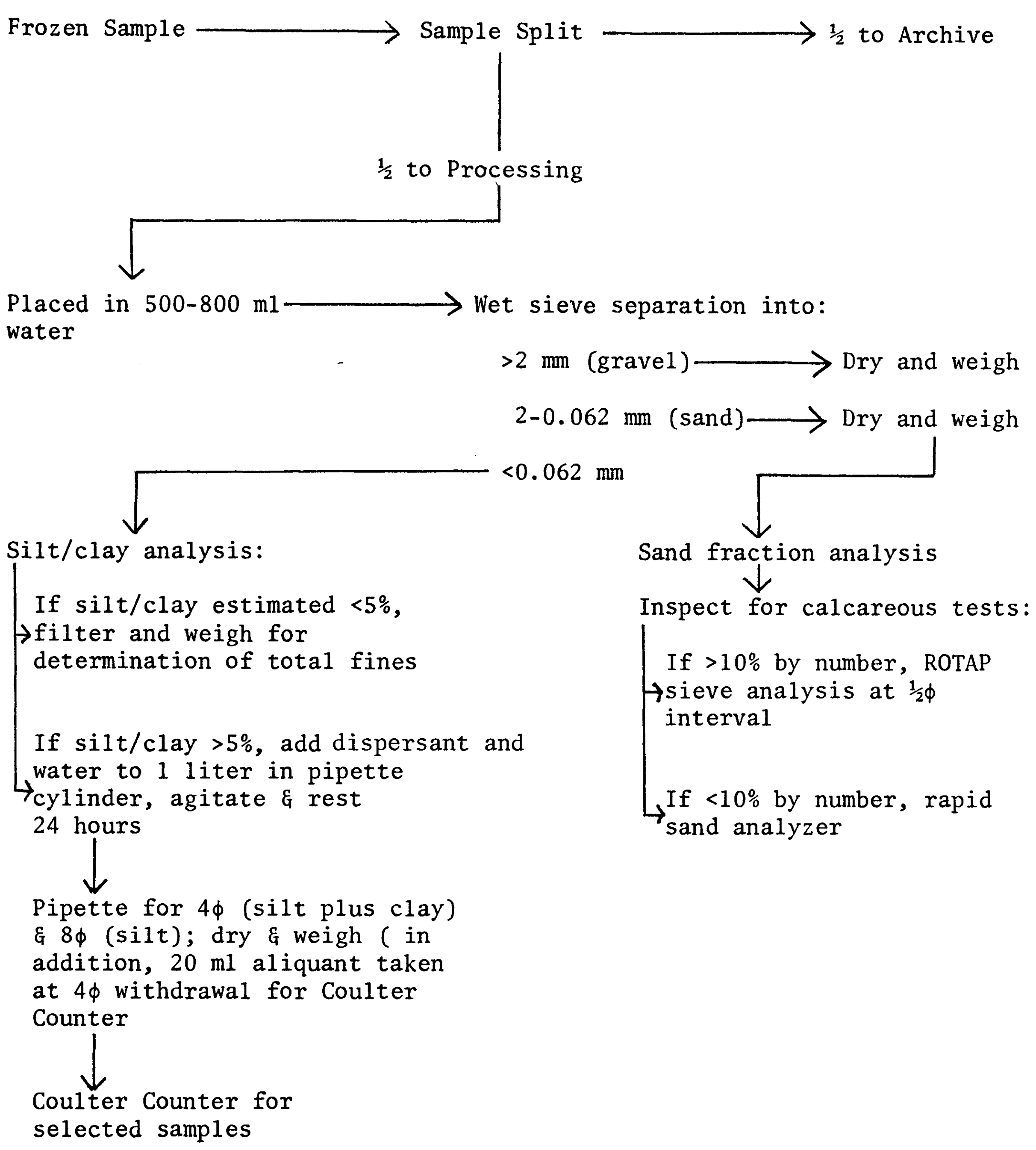
Calculation of Size Parameters

The results of various subanalyses were recombined to construct the cumulative frequency curve for a sample. The following statistics were computed from the distribution:

a) the gravel, sand, silt, and clay fraction percentages

b) the median, mean, standard deviation, skewness, and kurtosis using the graphic measures of Folk (1968):

Table 5-3. Flow chart for sediment analysis.



$$\phi \text{ Graphic Median; } Md_\phi = \phi_{50}$$

$$\phi \text{ Graphic Mean; } M_\phi = \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3}$$

$$\phi \text{ Graphic Standard Deviation; } \sigma_{G\phi} = \frac{\phi_{84} - \phi_{16}}{2}$$

$$\phi \text{ Graphic Skewness; } Sk_{G\phi} = \frac{\phi_{16} + \phi_{84} - 2(\phi_{50})}{(\phi_{84} - \phi_{16})}$$

$$\phi \text{ Graphic Kurtosis; } K_{G\phi} = \frac{\phi_{95} - \phi_5}{2.44\ (\phi_{75} - \phi_{25})}$$

c) the percent weight in each successive whole ϕ interval

During the first year this data reduction and computations were done by hand with the help of a programmable calculator. During the second year, the original data generated were card coded and calculations executed by computer using a specially developed program.

Total Organic Carbon

Sediment samples were oven dried at 100°C, sieved through a 1 mm sieve to remove shell and pebbles, powdered on an analytical mill, and weighed to 0.01 g. The sample was then placed in an ampule; 5 ml of 12% phosphoric acid was added. The ampule was purged of inorganic carbon constituents for 4 to 6 min and then sealed in a special apparatus to prevent CO_2 contamination from the sealing flame. Sealed ampules were heated at 125°C for four hours in an autoclave to oxidize the organic carbon to carbon dioxide. The carbon dioxide of each ampule was flushed with a nitrogen stream and measured by an infrared analyzer (Model 524, Oceanography International Carbon Analyzer). Instrument output was recorded on a Hewlett-Packard (Model 724A) potentiometric strip chart recorder equipped with an integrator. Standard carbon dioxide conversion graphs are made by plotting the integrated area versus carbon for standardized sodium carbonate solution. Triplicate determinations were averaged and reported and mg/g dry weight of sediment.

Total Nitrogen

For the samples collected during the first year either the persulfate digestion method of D'Elia et al. (1977) or a gas-chromatographic method (Boesch 1977) was employed. Both techniques suffered analytical problems and limited sensitivity at the low concentrations characteristic of shelf sands.

For the second year samples a modified Kjeldahl procedure was employed (Strickland and Parsons 1972). Nitrogenous compounds were reduced to ammonia which was detected spectrophotometrically.

RESULTS

Sediments at Repetitive Stations

General Characteristics

Sediment texture and organic carbon content is generally described together with the depth and topographic location of each repetitively sampled station in Table 5-4. Sediments on the continental shelf are mainly medium and coarse sand and grade to finer and muddier sands at the shelf break. Continental slope sediments become 90% or more silt and clay below 700 m.

Sediment texture on the continental shelf reflects the source of sediments and the contemporary hydraulic regime at the station. Sediment texture is strongly related to the mesoscale topography, particularly the linear ridge and swale topography, of the shelf. This relationship is more thoroughly described later in the presentation of results of stratified-random sampling conducted in a habitat delineation study in areas B and E (see Chapter 6).

Sediments at stations on the inner and central shelf in the study area are mainly well-sorted (sorting coefficient (< 0.5 ϕ) to moderately well-sorted (sorting coefficient 0.5-0.7 ϕ) sands with very little silt and clay except in topographic depressions (e.g. C4, D4). These sands vary considerably in size, and although medium sand usually predominates, coarse sand is abundant off central and northern New Jersey (B4, C stations, G1 and G2) and fine sands predominate off the southern Delmarva Peninsula (L1, L2). Outer continental shelf sediments also largely consist of medium sands, frequently with a sizeable coarser component. Silt and clay content is also generally low but may be slightly higher than inshore and locally greater in depressions (B3, E4). Sediments on the outer shelf in the vicinity of the Hudson Canyon (A1, G5) have a larger silt-clay component of about 10%. At the shelf break (100-200 m) sediments become considerably finer, both in terms of sand-sized particles and in terms of increased silt and clay (5-10% except around Hudson Canyon were 15-30% silt and clay was found). Thus, the shelf break sediments are generally less well sorted than those on the shelf. On the continental slope sediments quickly grade to muddy-fine sands (20-40% silt and clay) at 300-350 m and thence to clayey-silt (> 90% silt and clay) at 700 m.

Organic carbon content of sediments is most closely correlated with the proportion of silt and clay in the sediment. The increase in organic carbon with an increase in silt and clay is depicted in Figure

Table 5-4. General sediment characteristics at each station repetitively sampled during the two years of study. Nomenclature of sediment texture is adapted from Shepard (1954). Grand means (mean of seasonal means) of important parameters are given together with the range of seasonal means in parentheses.

Station	Depth(m)	Topographic Location	Sediment Description	Median Diameter (ϕ)	Sorting Coefficient (ϕ)	Percent Silt & Clay	Organic Carbon (mg/g)
A1	90.4(89-92)	outer shelf	med.-fn. 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.-fn. sand	2.24(2.0-2.5)	2.99(2.5-3.4)	25.6(22.5-30.6)	4.31(3.9-4.7)
A3	138.8(136-149)	shelf break	med.-fn. 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.-fn. 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.-fn.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.-co. sand	1.05(0.9-1.3)	0.78(0.5-1.1)	0.12(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.-co. 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.-co. 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.-co. 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	34.3(33-37)	swale	med.-fn. 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.-fn. sand	1.99(1.7-2.4)	0.43(0.4-0.5)	0.41(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.-fn. 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.-fn. 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)	4.68(3.0-5.9)	1.98(0.8-3.4)
F1	83.8(79-86)	outer shelf	med.-fn. 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.-fn. 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.-fn. 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 co. sand	0.28(0.2-0.3)	1.09	0.4(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)	1.8(0.3-5.8)	0.56(0.2-1.1)

Table 5-4. (concluded)

Station	Depth(m)	Topographic Location	Sediment Description	Median Diameter (ϕ)	Sorting Coefficient (ϕ)	Percent Silt & Clay	Organic Carbon (mg/g)
G3	72.8(71-74)	shelf valley	shelly med.-fn. 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.-co. 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.-fn. 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.-fn. 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.-fn. sand	2.77(2.5-3.2)	2.75(2.2-3.0)	28.2(24.5-32.6)	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.-co. 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.-fn. 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	4.96(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)
K1	29.0	inner shelf	med.-co. 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)	0.40(0.3-0.5)	0.74(0.4-1.5)
K3	53.0	outer shelf	med.-co. 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.-fn. 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 slope	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(26-24)	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.-fn. 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.-co. sand	1.38(1.2-1.6)	0.89(0.8-1.0)	0.86(0.5-1.2)	0.87(0.5-1.3)
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)

5-5 showing grand mean values of the two parameters for each station. The correlation is highly significant ($r = 0.71$, $p < 0.01$) but the relationship appears non-linear. Low organic carbon levels of 1 mg/g dry weight or less are found in clean shelf sands. Sediments in swales and other topographic depression contain higher concentrations of organic carbon (to 3 mg/g) concomittant with their elevated silt and clay content. Sediments at the shelf break become consistently muddy and typically have 2-4 mg/g organic carbon. Continental slope sediments contain more than 3 mg/g organic carbon to as high as 10 mg/g (i.e. 1%) at Station J2.

Variability over Time

The variation in the key sediment parameters (median diameter, percent gravel, coarse, medium, and fine sand, silt and clay and organic carbon content) witnessed among sampling periods is here discussed for each station as depicted in a series of figures (Figures 5-6 to 5-32). These changes are considered in the context of the spatial variability found in each sampling period by comparing 95% confidence limits of the means of the parameters. The probable causes of the observed variability in sediment parameters are interpreted with respect to spatial heterogeneity, the precision of station location and seasonal sediment processes.

A1 (Figure 5-6). Sediments in the vicinity of the station are relatively patchy and thus showed appreciable variability from sampling period to sampling period. Sediments were poorly sorted medium to medium-fine sand. Winter 1976 samples yielded coarser sediments (median diameter $< 1.5\ \phi$) and fall 1976 and spring 1977 samples were predominantly five sands (median diameter $> 2\ \phi$). Mean silt and clay content ranged from 7 to 18% but did not parallel changes in the sand size distribution. Mean silt and clay content was less than 10% except in winter and spring 1977. Organic carbon levels ranged between 1.9 and 2.9 mg/g and were roughly concordant with the silt and clay content.

A2 (Figure 5-6). This station had the muddiest sediments except for the mid-slope stations. It is located on the broad, presumably depositional, fan south of Hudson Canyon. The sand fraction of sediments was very poorly sorted medium and fine sand. The median diameter and particle size distribution of sediments sampled were rather persistent over eight sampling periods. Silt and clay content was also constant; seasonal means ranged from 23 to 31%.

A3 (Figure 5-7). Sediment parameters were very constant with no apparant temporal trends. Sediments at this station were fine-skewed medium sand with a silt and clay content of 16-21%.

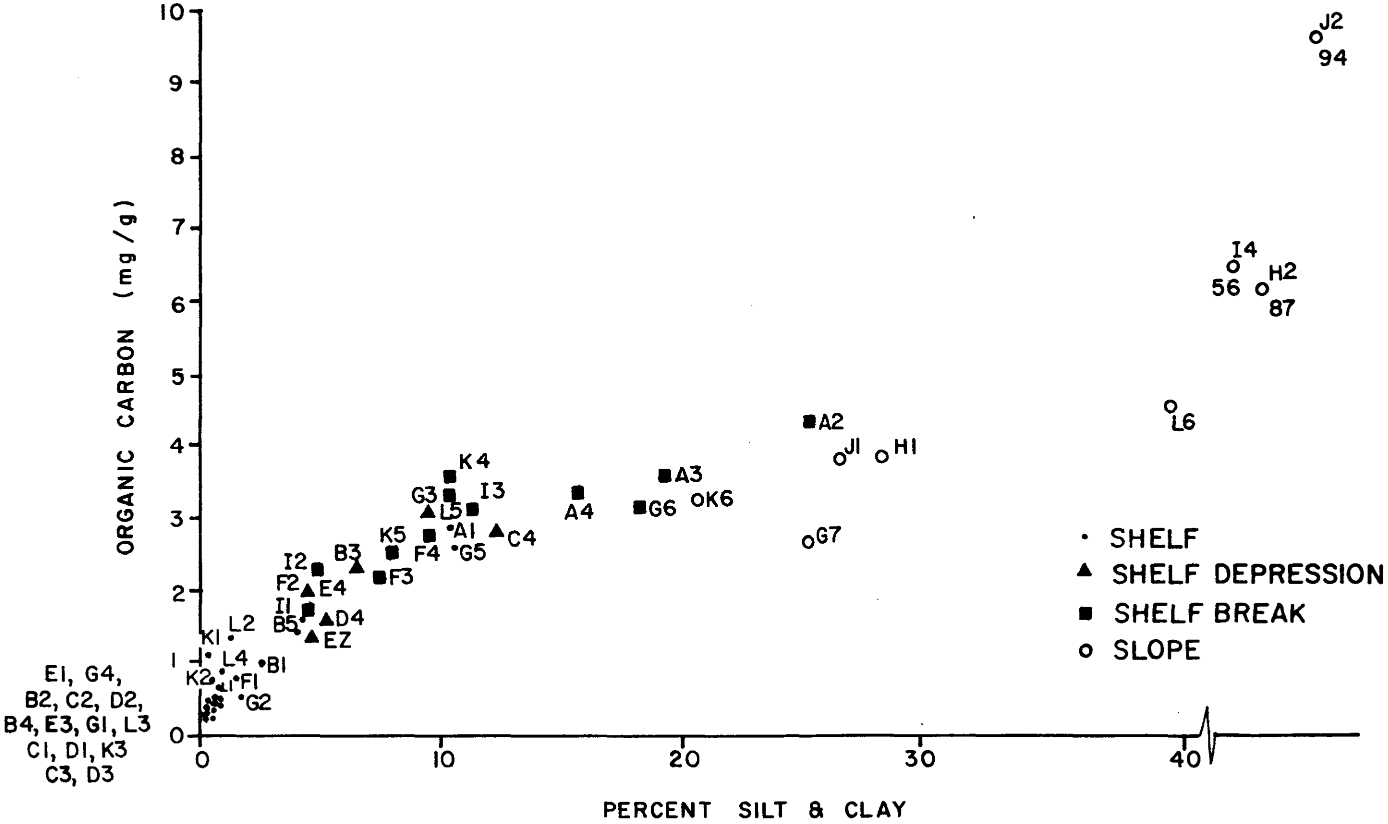


Figure 5-5. Relationship of the grand means of sediment organic carbon content and percent silt and clay at the 52 repetitively sampled stations.

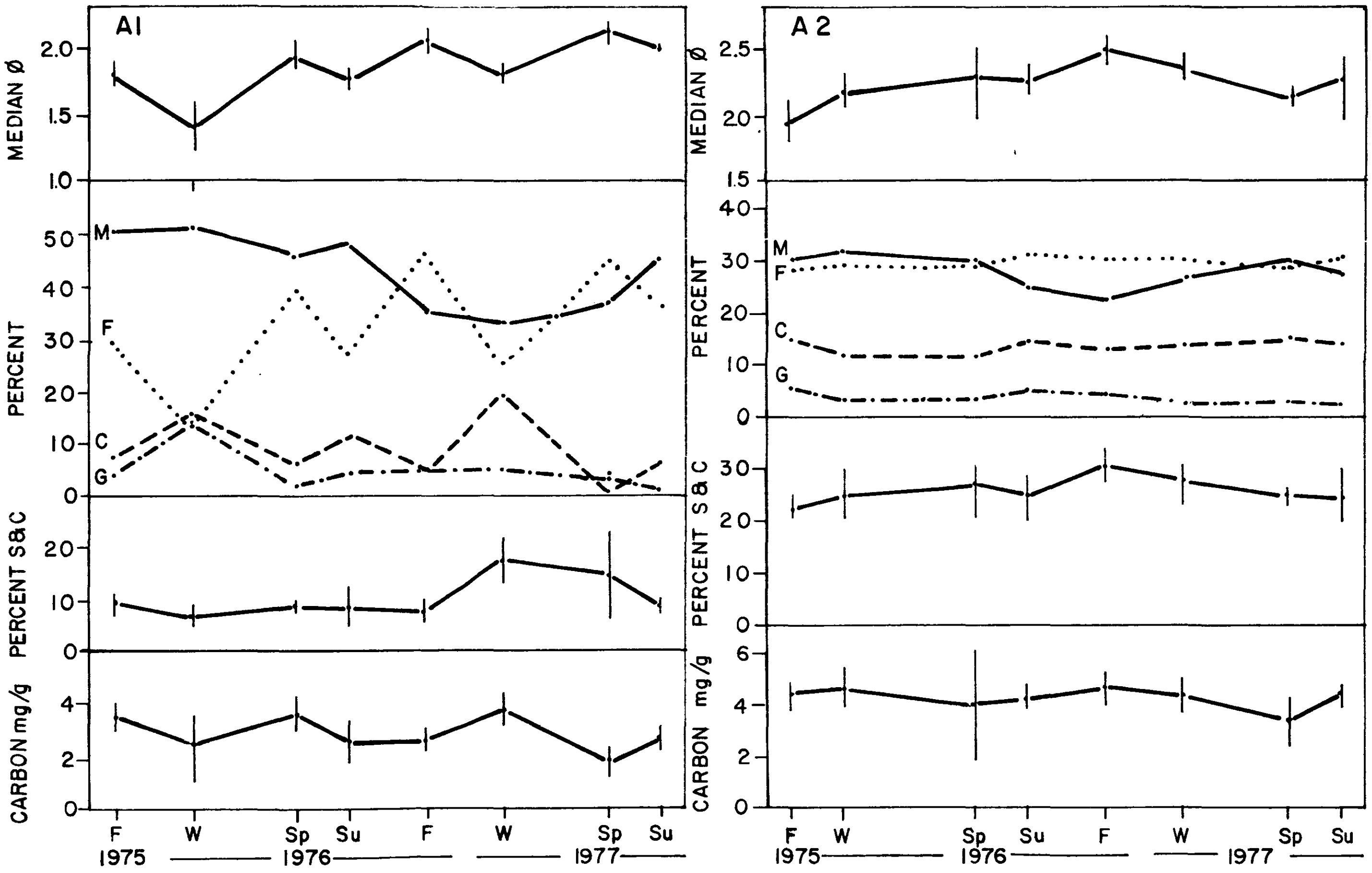


Figure 5-6. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean $(\bar{x} \pm S_{\bar{x}}\, t_{0.05})$.

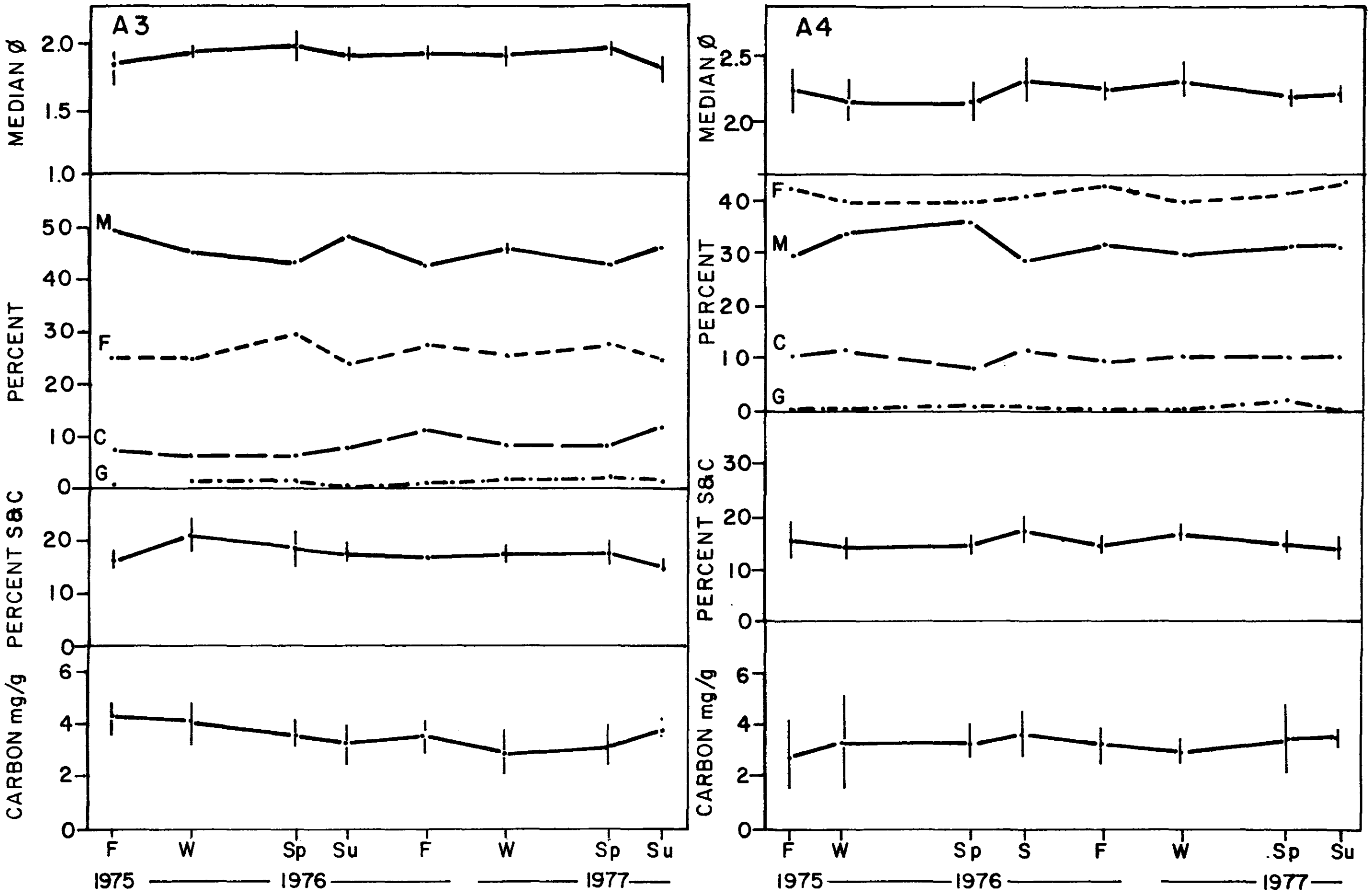


Figure 5-7. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

A4 (Figure 5-7). Sediments consisted of somewhat finer sands than at A3 but silt and clay and organic carbon levels were comparable and similarly persistent.

B1 (Figure 5-8). Sediments at this "flank"station were well sorted medium sands and showed a steady increase in the fine sand component from fall 1976 through spring 1977. The silt-clay percentage was small (1.5 to 4%), spatially and temporally variable, and higher in fall 1976, winter and summer 1977.

B2 (Figure 5-8). This station was located atop a ridge and had coarse-skewed medium sands. Shifts in the median diameter between sampling periods reflect shifts between the medium and coarse sand fractions. Slightly finer sediments were collected in fall 1976 and spring 1977. Silt and clay content was low, always less than 1% except in winter 1976 when the mean value was 1.5%. A slight increase in organic carbon paralleled this silt-clay increase in winter 1976.

B3 (Figure 5-9). Fine sand was predominant at this swale station except during fall 1975 when fine and medium sands were codominant. A slight progressive increase in fine sand was evident over the two years of sampling. Mean silt and clay content ranged from 5-8% and showed a slight tendancy to increase with the increase in the fine sand component. Mean organic carbon levels (2-3 mg/g) showed no significant differences among seasons.

B4 (Figure 5-9). This station is located on a terrace atop Tiger Scarp and thus is characterized by clean medium-coarse sands. Sediment samples from summer 1976 - summer 1977 contained more medium sand and less coarse sand than in the first three sampling periods. Silt and clay and organic carbon concentrations were consistently very low.

B5 (Figure 5-10). This station, the site of the recolonization experiments (Chapter 6) was sampled only during the second year of sampling. The station was located at the transition from eroded flank sediments to fine sands of a large swale-like depression (see following habitat delineation results. As a consequence, even though the station was very precisely relocated because of the *in situ* experiments, sediment parameters varied considerably among the sampling periods. Sediments sampled during winter and spring 1977 were medium and fine sands while those collected during fall 1976 and summer 1977 consisted more of medium sand. Silt and clay content was relatively high (3-6%) for shelf sediments, probably due to the disaggregation of eroded Holocene clay lumps present in the sediment.

C1 (Figure 5-11). Replicate samples were taken at this station only during the first sampling year, single sediment samples were taken and analyzed during the second year in conjunction with continued bacteriological sampling at this site. The station is

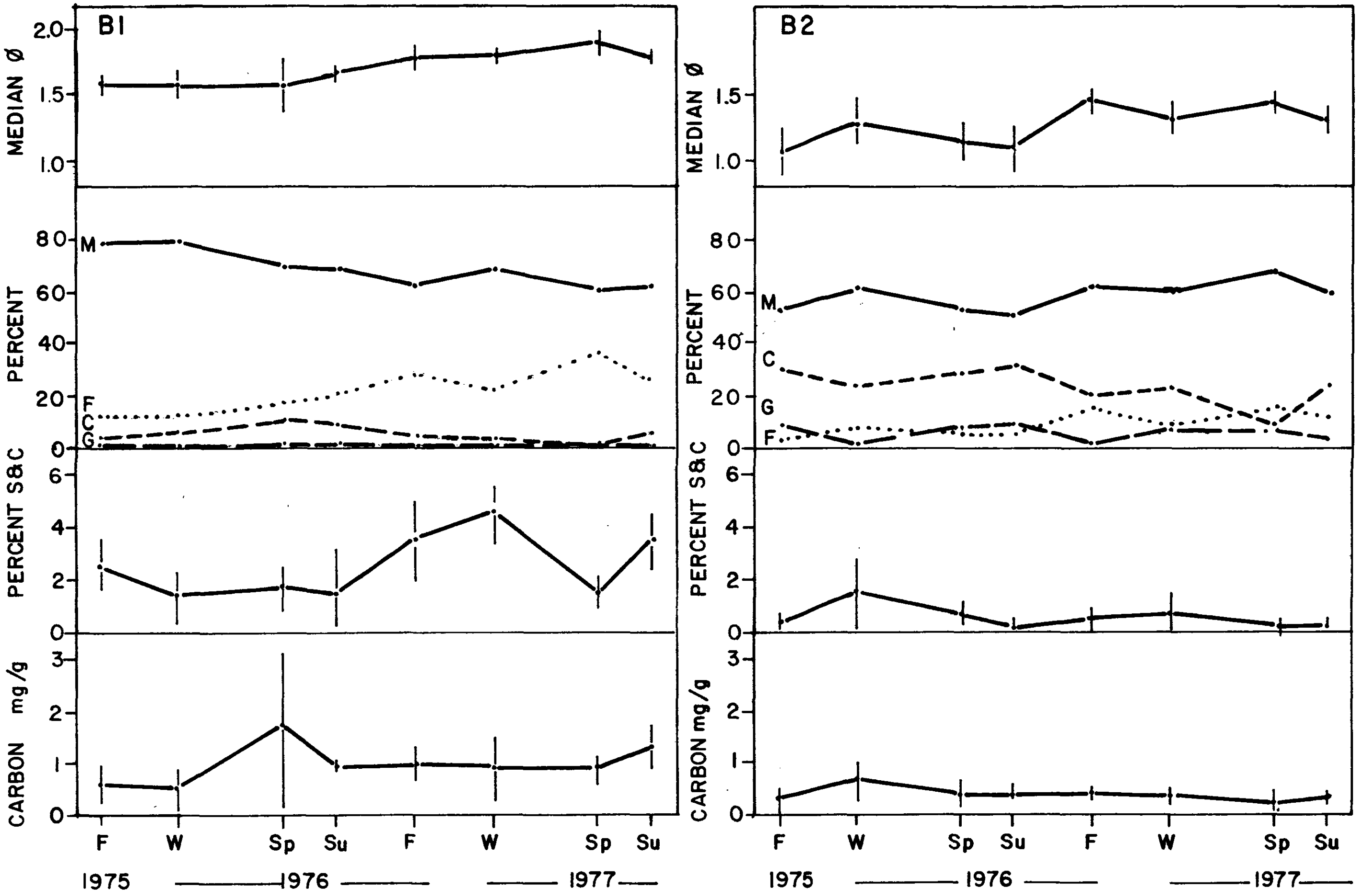


Figure 5-8. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

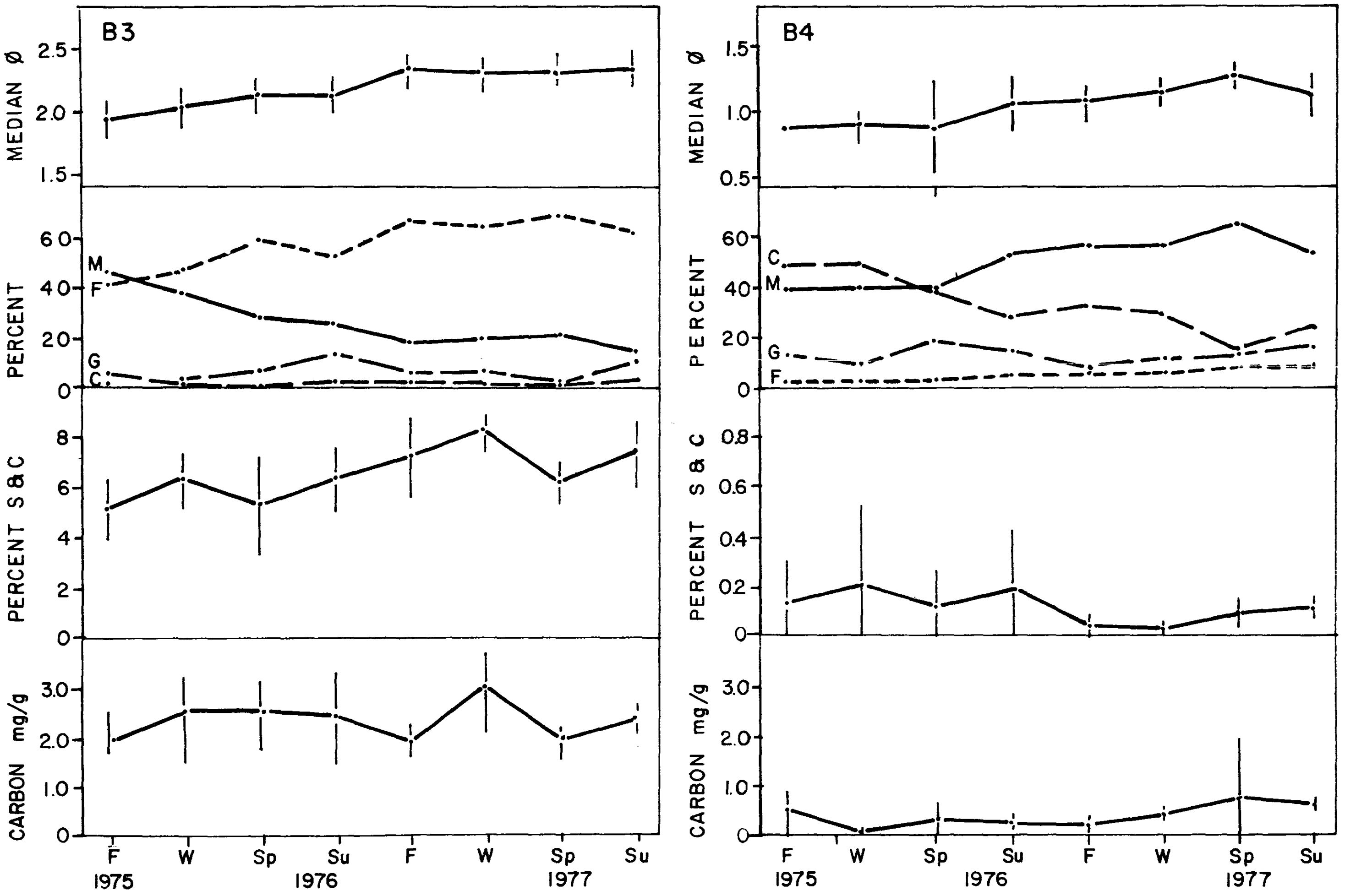


Figure 5-9. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

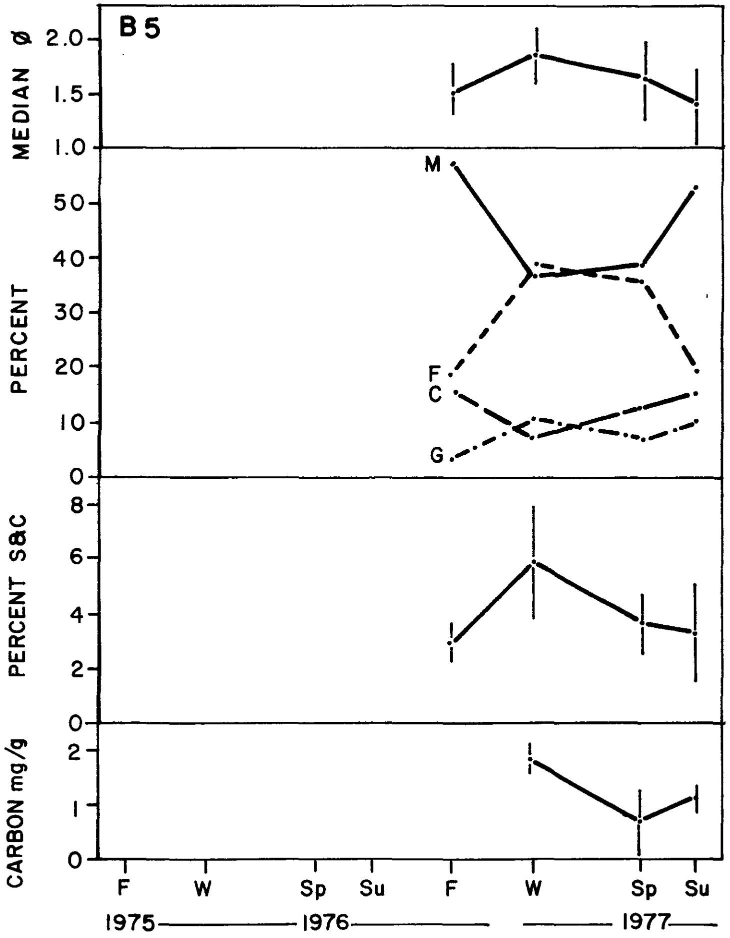


Figure 5-10. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean $(\bar{x} \pm S_{\bar{x}} t_{0.05})$.

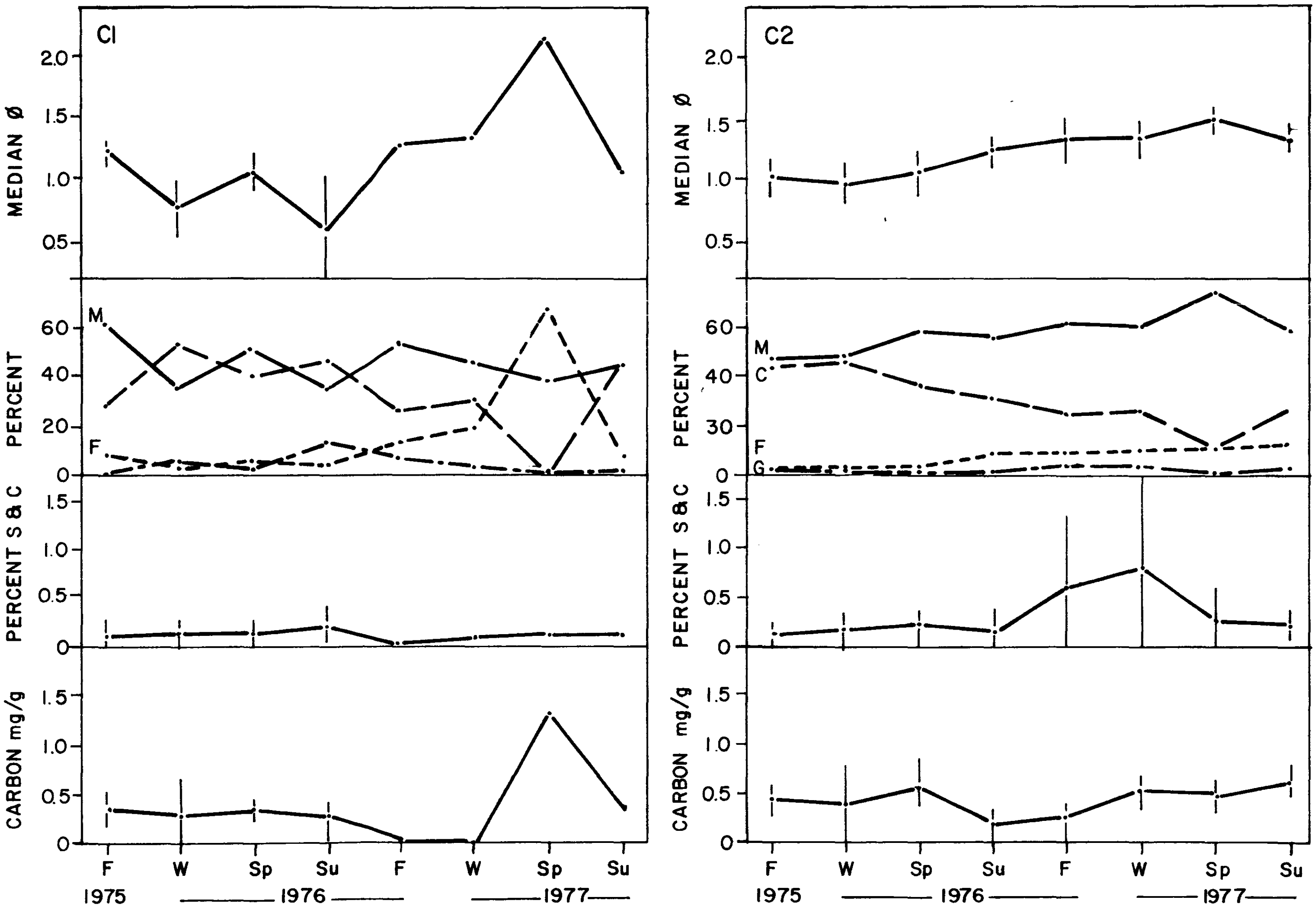


Figure 5-11. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

located on an inner shelf ridge and sediments were medium-coarse sand except in the spring 1977 samples, when fine sands became predominant. This change probably represents imprecise station relocation rather than any actual change in the sediments at that site. Silt-clay and organic carbon levels were consistently low except in spring 1977 where organic carbon was higher in the finer sands.

C2 (Figure 5-11). Sediments on the exposed flank at this site were medium and coarse-skewed medium sand. After winter 1976 there was a progressive shift from coarse to medium sand and a concomitant increase in the phi median grain size. Silt-clay and organic carbon levels were low. The proportion of silt-clay increased slightly in fall 1976 and winter 1977, although it was highly variable among the replicate samples (large confidence limits). This increase probably resulted from the biodeposition and biogenic binding of fine sediments by dense populations of tube dwelling benthos which proliferated subsequent to hypoxia in summer 1976 (Chapter 6).

C3 (Figure 5-12). Sediments at this station were coarse and medium sands with very low silt-clay and organic carbon content. No significant variation in key sediment parameters were observed over the four periods this station was sampled.

C4 (Figure 5-12). Sediments at this inner shelf swale station were the most variable of any station. Essentially two types of sediment were found: highly variable, muddy, poorly sorted sand (fall 1975 and summer 1976) and fine sand with less, but still appreciable, silt and clay. The former condition probably represents erosional windows within the swale wherein coarser sediment lag is mixed with relict silt and clay eroded and partially disaggregated from the underlying Holocene deposits. The sediments in which fine sands predominated probably represent areas of deposition of sediments winnowed from the surrounding seabed or transported from land erosion. As such, the silt and clay in these sediments may have a more contemporary deposition. This may be reflected in the relationship of organic carbon concentration to percent silt and clay. Organic carbon content tracks silt and clay closely but the peaks during fall 1975 and summer 1976 are somewhat attenuated in comparison. This implies that organic carbon is less concentrated in the relict than the recent fine sediments.

D1 (Figure 5-13). This station was located on a central shelf ridge where sediments were clean medium and fine sands. Sediments collected in fall 1975 and spring 1976 were coarser than otherwise found. The predominance of fine sand and the elevated silt-clay and organic carbon concentrations in sediments from winter 1976 stem from failure to relocate this station accurately. These samples were actually collected from a swale rather than a ridge.

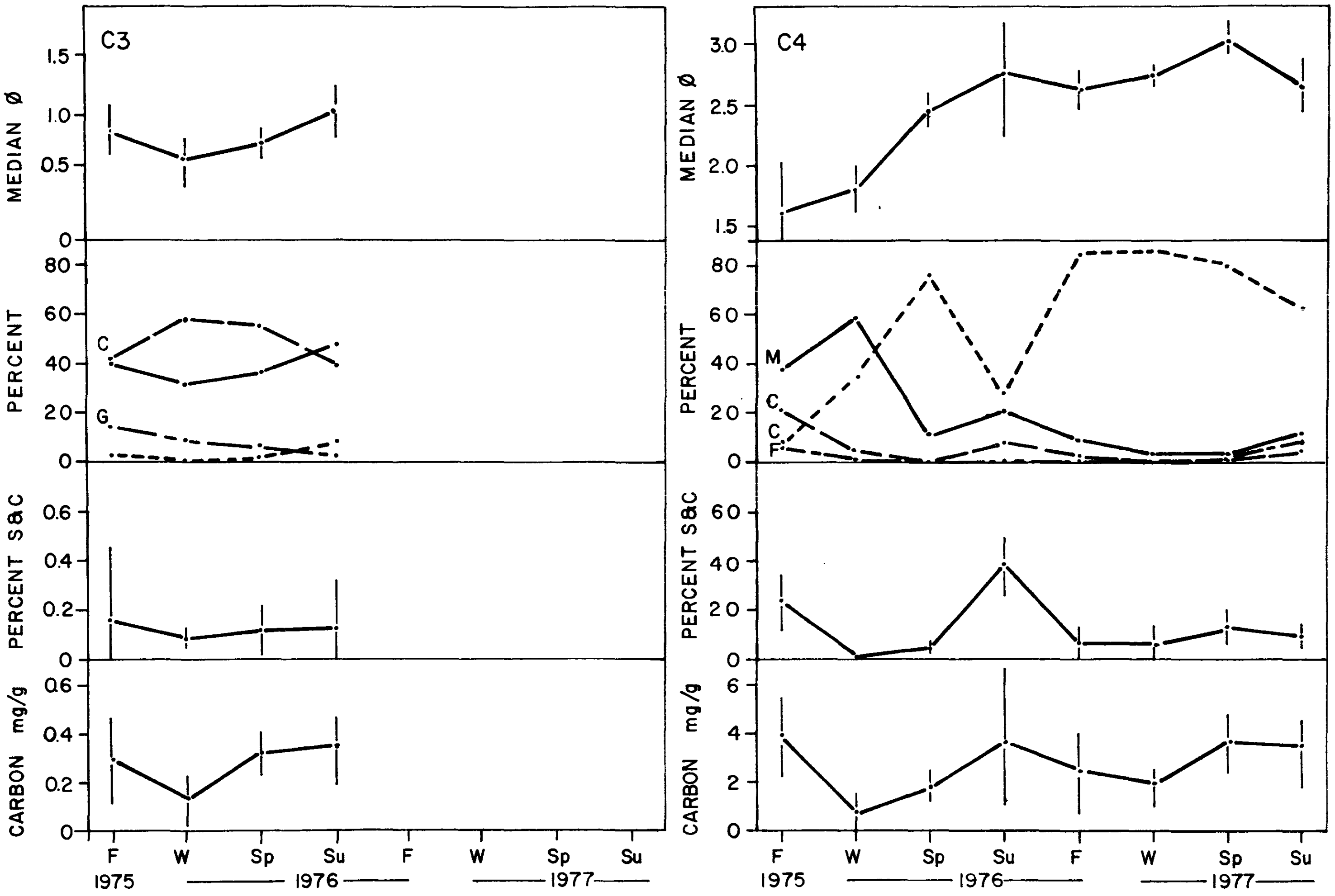


Figure 5-12. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}} t_{0.05}$).

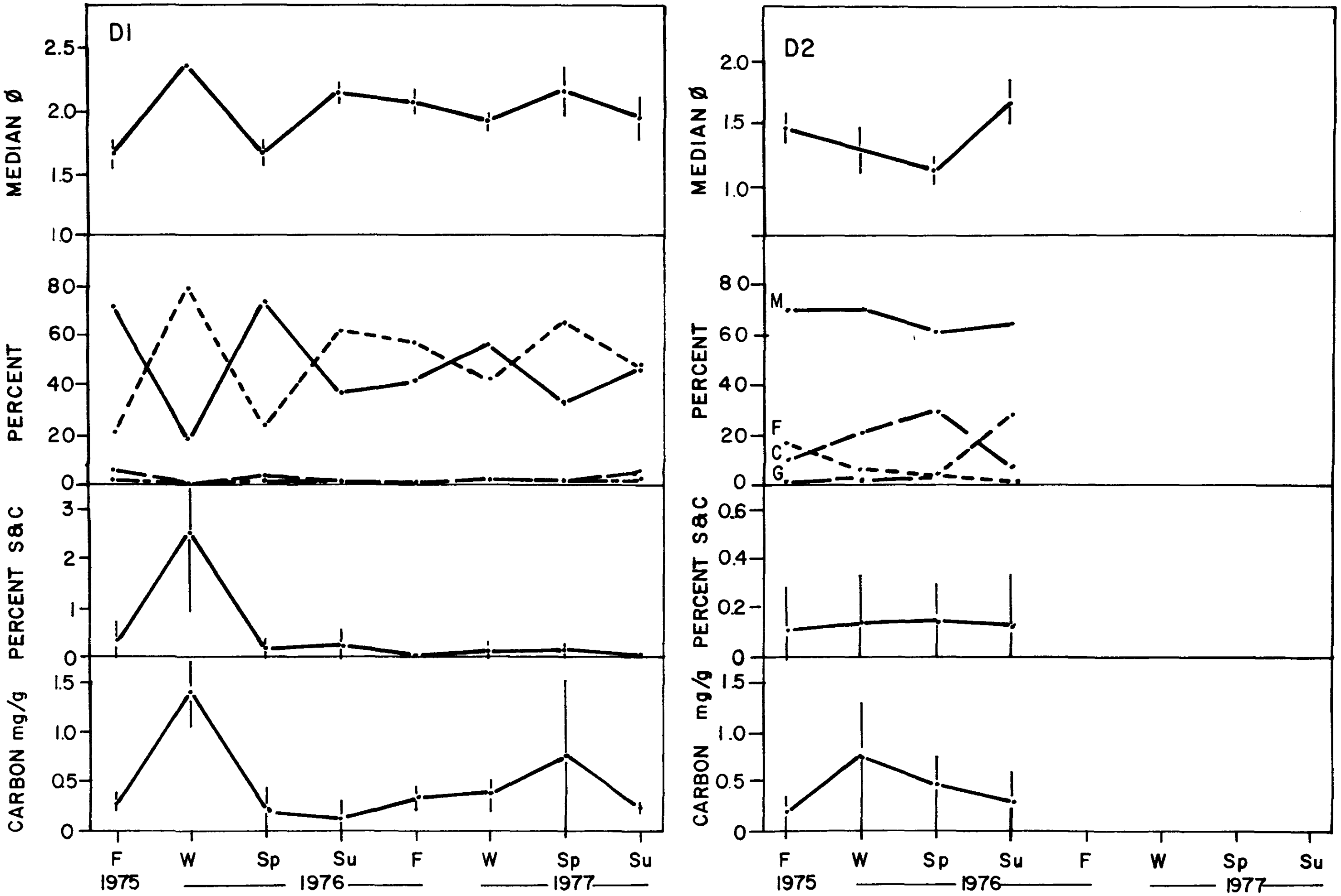


Figure 5-13. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

D2 (Figure 5-13). Sediments at this flank station were medium sands with very little silt-clay and organic carbon. Sediments collected during spring 1976 were significantly coarser than those collected in fall 1975 and summer 1976.

D3 (Figure 5-14). Sediments at this flank station were finer than those at D2. Sediment parameters were consistent among sampling periods during the first year when this station was sampled.

D4 (Figure 5-14). Samples collected at this swale station were fine and medium-skewed fine sands, except during spring and fall 1976 when more poorly sorted sands were found. The coarser sediments, high variability in sediment parameters and relatively low organic carbon to silt and clay ratio during these two sampling period are indicative of the inclusion of samples from within erosional windows in the swale.

E1 (Figure 5-15). Sediments from this ridge station were usually medium sands with very little silt and clay. Samples from summer 1976 and spring 1977 were apparently collected off feature and consist of much more fine sand and, in summer 1976, somewhat more silt and clay.

E2 (Figure 5-15). This station was located deep on the flank of one of the outermost ridges found on the shelf. Considerable sediment change over a short distance is found in the vicinity of E2. Imprecise location of the station resulted in the collection of sediments consisting of finer sand with more silt and clay during summer 1976 and winter, spring and summer 1977, when the station was position down-flank in a swale, and sediments consisting more of medium sand during the other sampling periods.

E3 (Figure 5-16). Sediments collected at this ridge station were consistently coarse-skewed medium sands. Higher silt and clay and organic carbon levels were found in a few replicate samples during winter 1976.

E4 (Figure 5-16). The swale in which this station was located is presumably erosional and covered with a shell lag. The usual sediment conditions sampled are represented in fall 1975, winter, spring and summer 1976 and winter 1977 when coarse sand and gravel fractions were large. Samples collected in fall 1976 and spring 1977 came from a different sedimentary regime characterized by a predominance of fine sand (median diameter > 2 ϕ).

F1 (Figure 5-17). This station was situated at the edge of the shelf where sediments grade rapidly from medium to fine sand with increasing depth. Consequently there was substantial variability in the sand size fractions and median diameter found among the sampling periods. Fine sands predominated in summer and fall 1976 and spring 1977. Despite this variability there was little variability in the low concentration of silt-clay and organic carbon found.

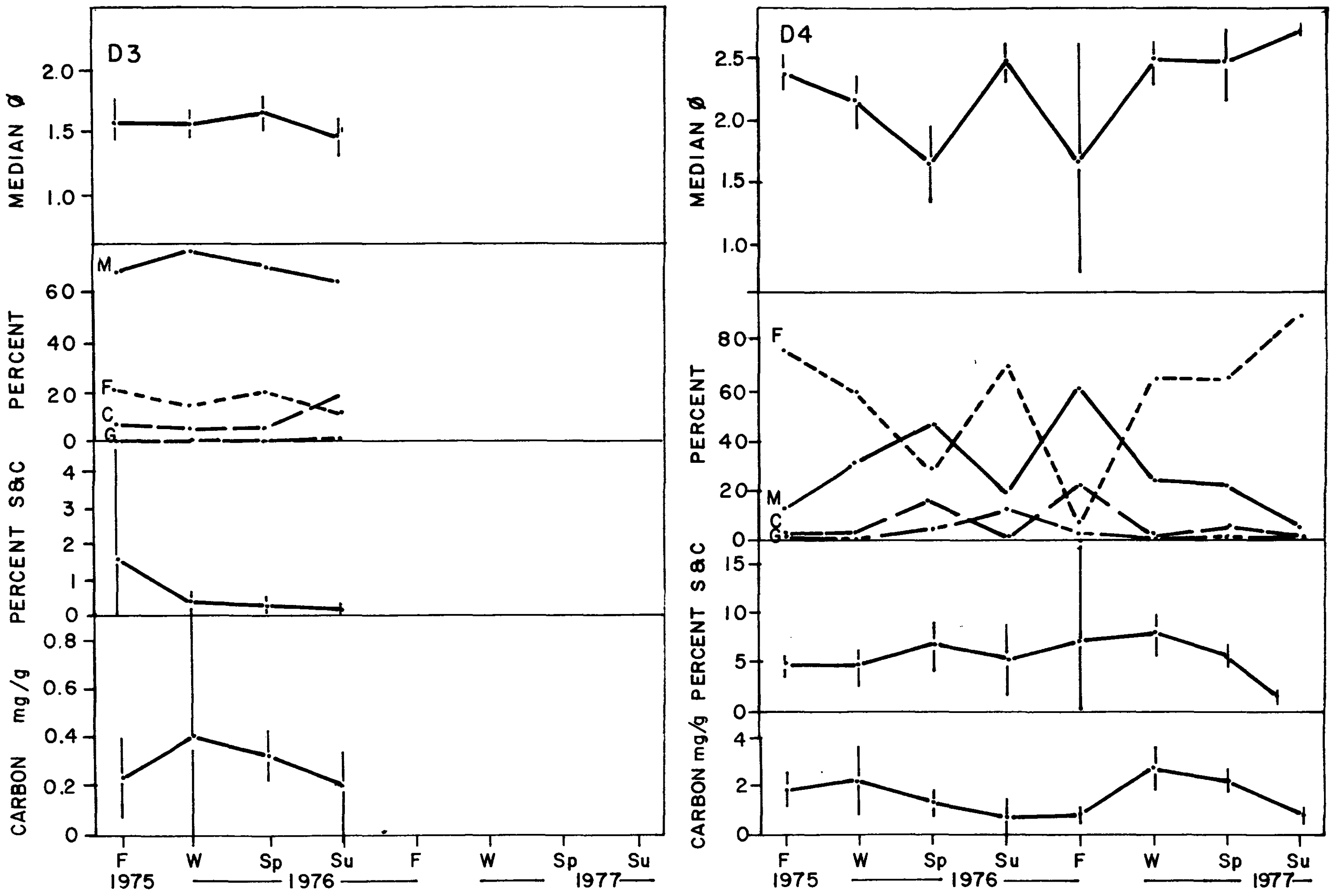


Figure 5-14. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

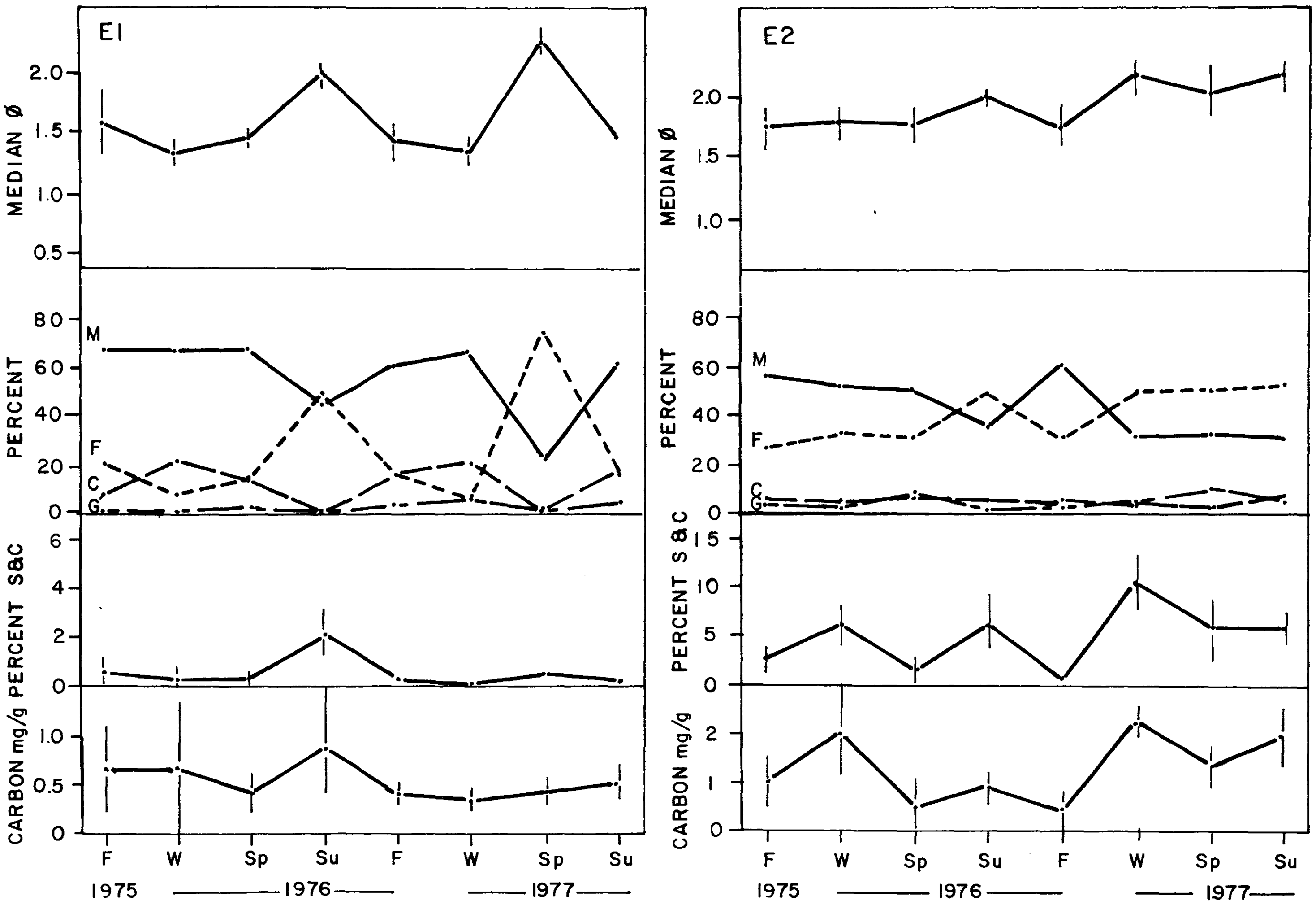


Figure 5-15. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}} t_{0.05}$).

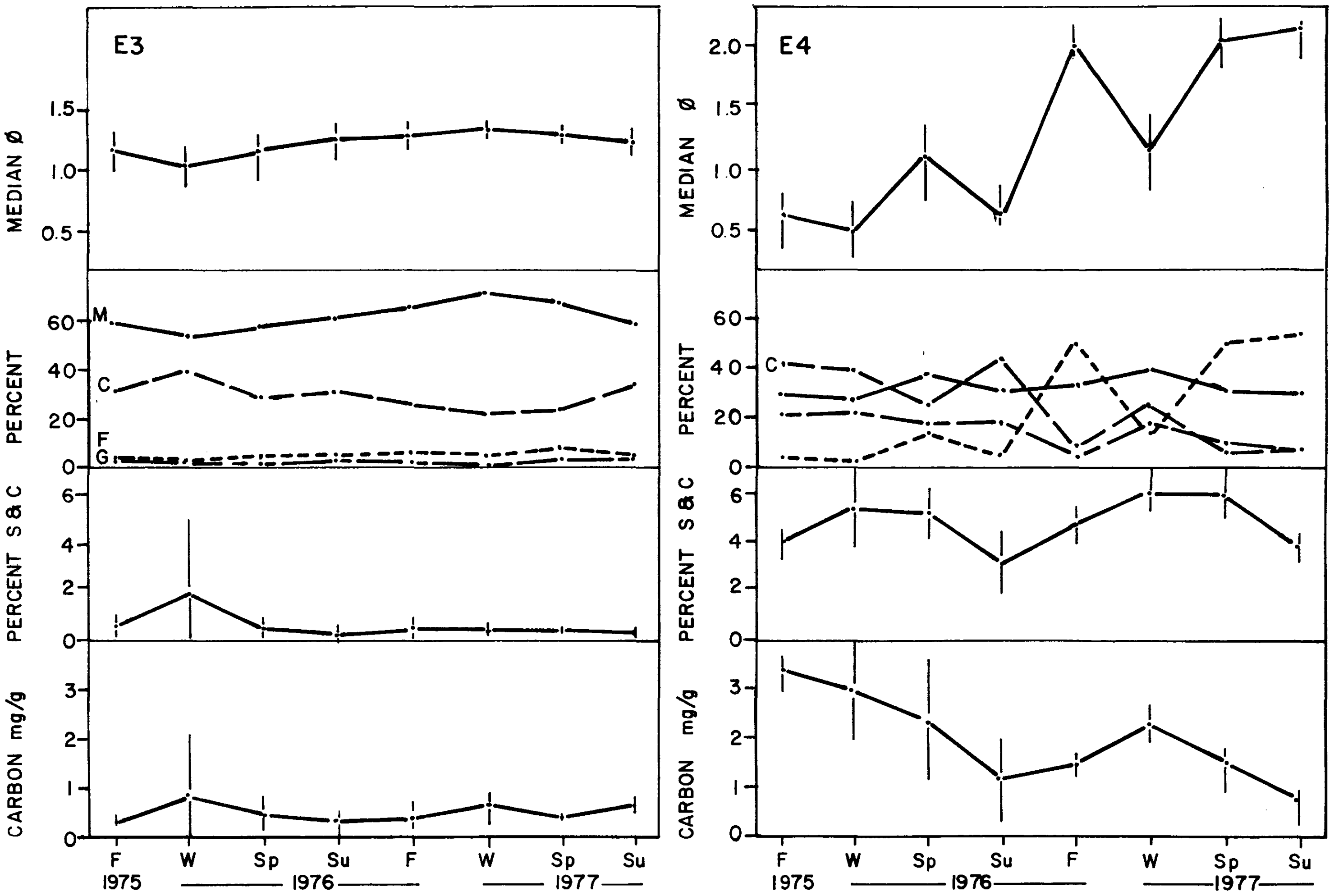


Figure 5-16. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

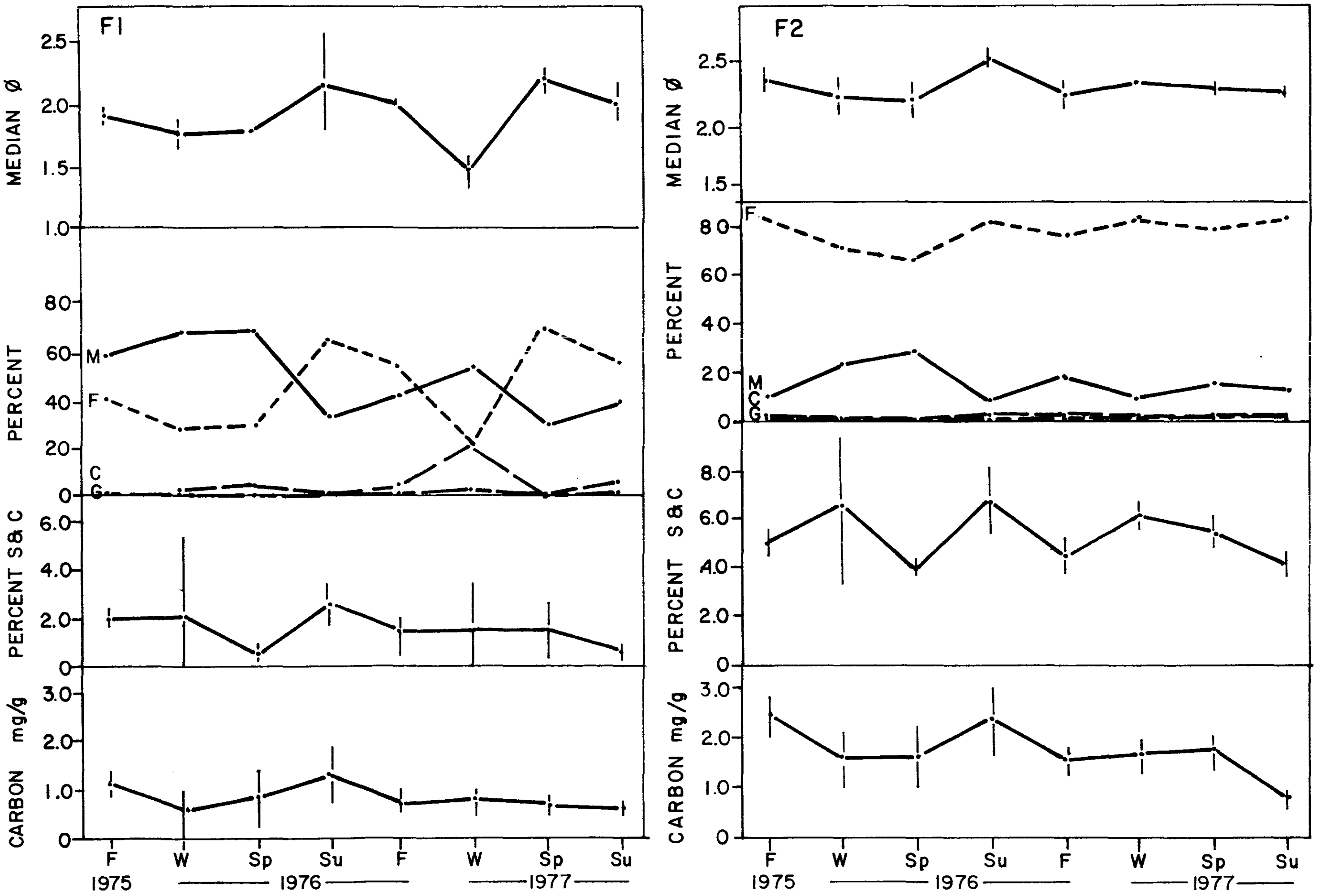


Figure 5-17. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

F2 (Figure 5-17). Deeper in the shelf break zone at F2 sediments were finer and more homogeneous. Thus grain size parameters were more constant. Active sorting by shelf edge currents probably account for this homogeneity.

F3 (Figure 5-18). Sediments collected were very persistent but were coarser than at F2. Medium sands were codominant with fine sands. More silt and clay (6-9% average) was contained in sediments collected at F3 than F2.

F4 (Figure 5-18). Sediments collected here were somewhat more variable among the sampling periods than at F2 and F3. Sands were finer in summer 1976 and winter 1977 samples and silt and clay was higher (12-13% average) than in other sampling periods (7-10%). Organic carbon levels followed silt and clay patterns, except that the lower levels were found in fall 1976 than could be explained by the silt-clay content.

G Stations (Figures 5-19 to 5-23). Only major temporal variations will be discussed for the semiannually sampled stations.

At G2 an abrupt change in sediment texture was seen in winter 1977 when very poorly sorted sediments including clay lumps were collected. An erosional window was sampled in some replicates. This result resulted in the higher, but very variable, silt and clay and organic carbon value for these samples. This silt and clay was probably mostly relict.

Station G3 was located in the Hudson Shelf Valley and sediments at that site were very mixed and spatially heterogeneous (Figure 5-20). The increase in silt and clay in the winter 1977 samples was not significant because of wide confidence limits. Samples collected in summer 1977 had considerably more fine sand than in previous samples.

H, I and J stations (Figures 5-23 to 5-26). Sediments collected at continental slope stations generally showed little variability among collection periods. However, sediments at the head of Tom's Canyon (I1 and I2) were quite variable. Sands were relatively coarse and were mixed with variable amounts of silt and clay. Interreplicate variability (i.e. spatial heterogeneity) was high. Samples collected at I1 in summer 1977 showed a substantial shift to finer sands and a highly significant increase in median phi diameter (Figure 5-24). The 1977 sediment samples at I4 had more silt and clay and organic carbon than did the 1976 samples.

K stations (Figures 5-27 to 5-29). Sediments collected at K1 were coarse skewed medium sands, while those at K2 consistently were finer, symmetrical medium sands. Significantly higher organic carbon concentrations were inexplicably found in sediments collected at K2

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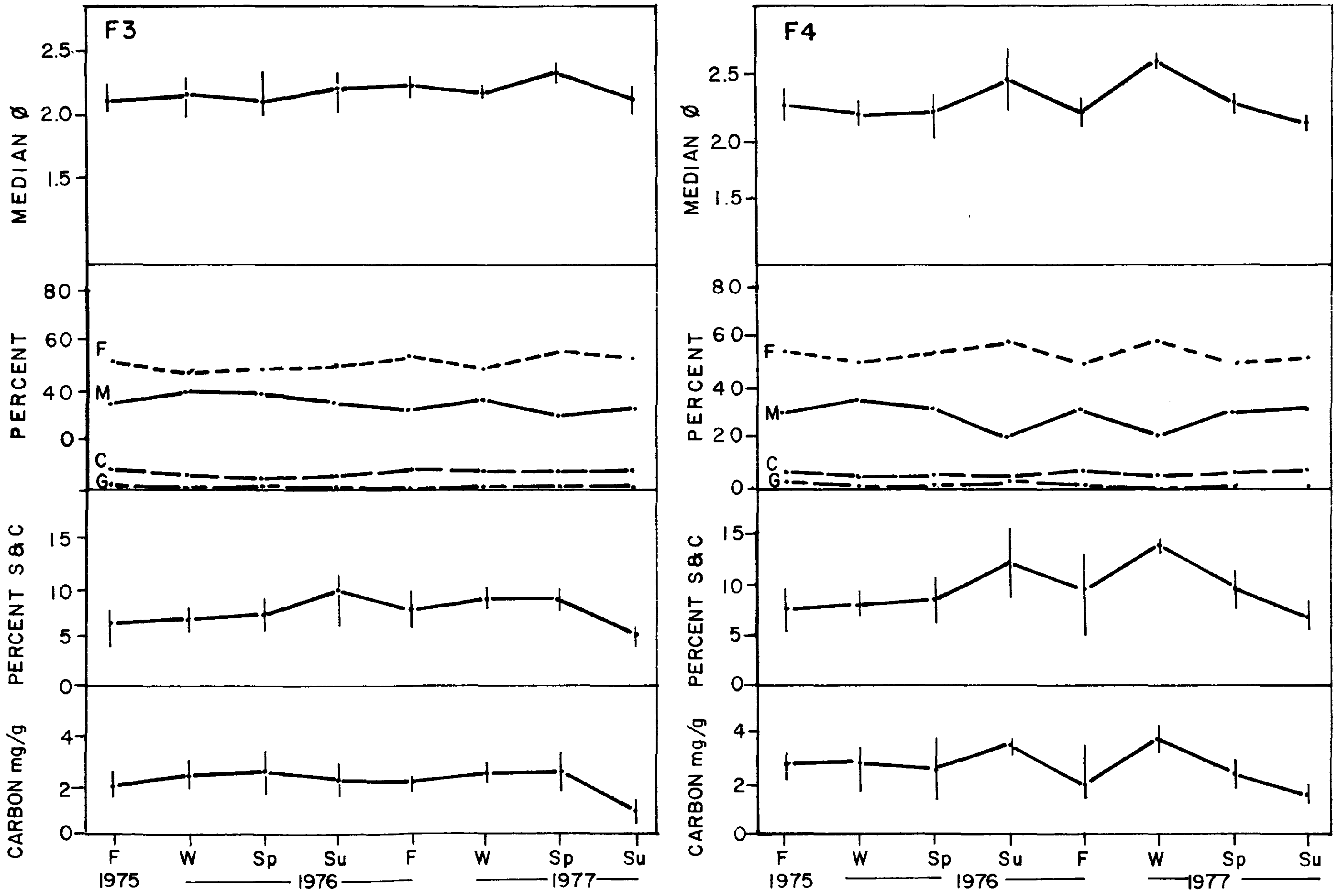

Figure 5-18. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

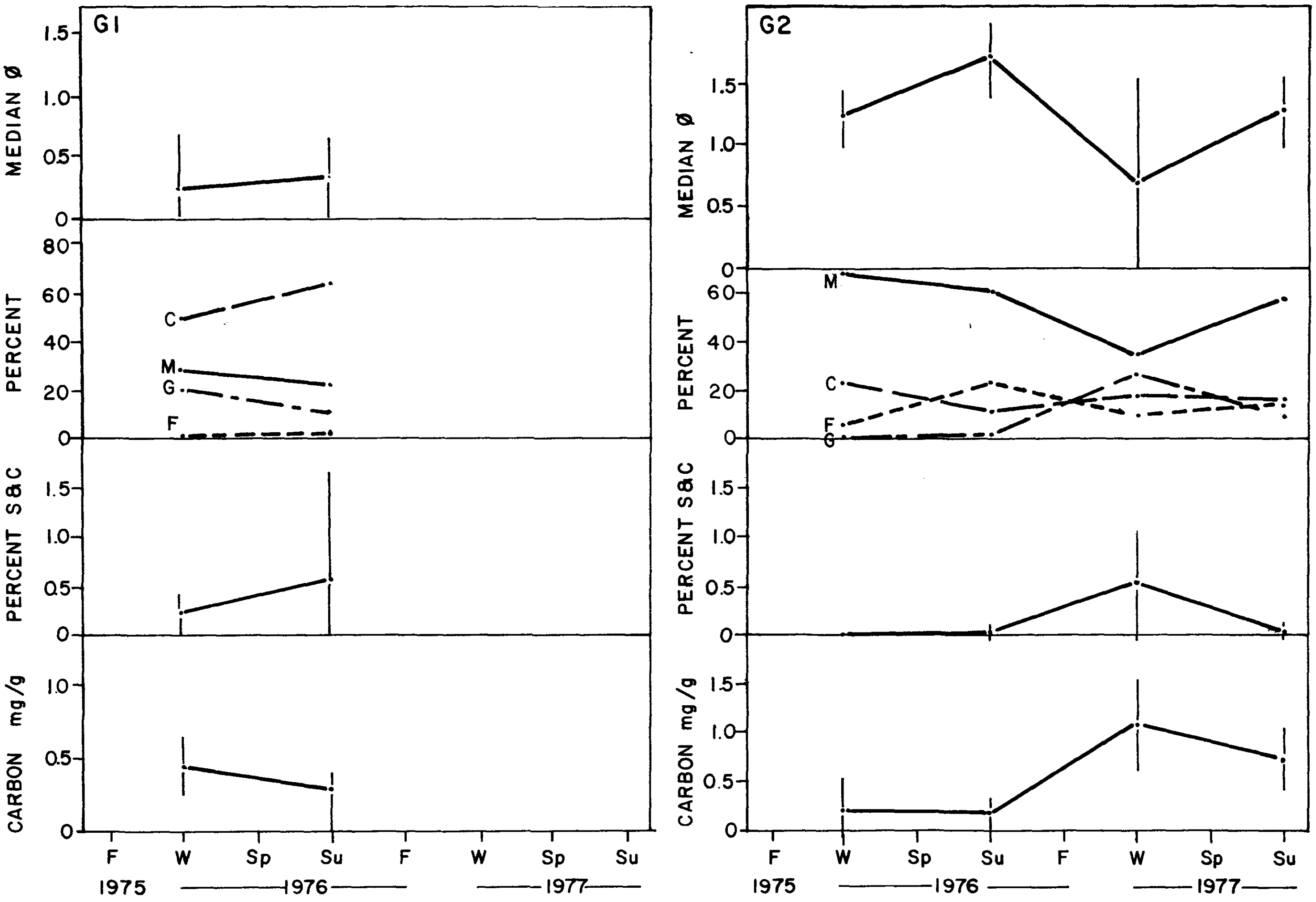

Figure 5-19. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

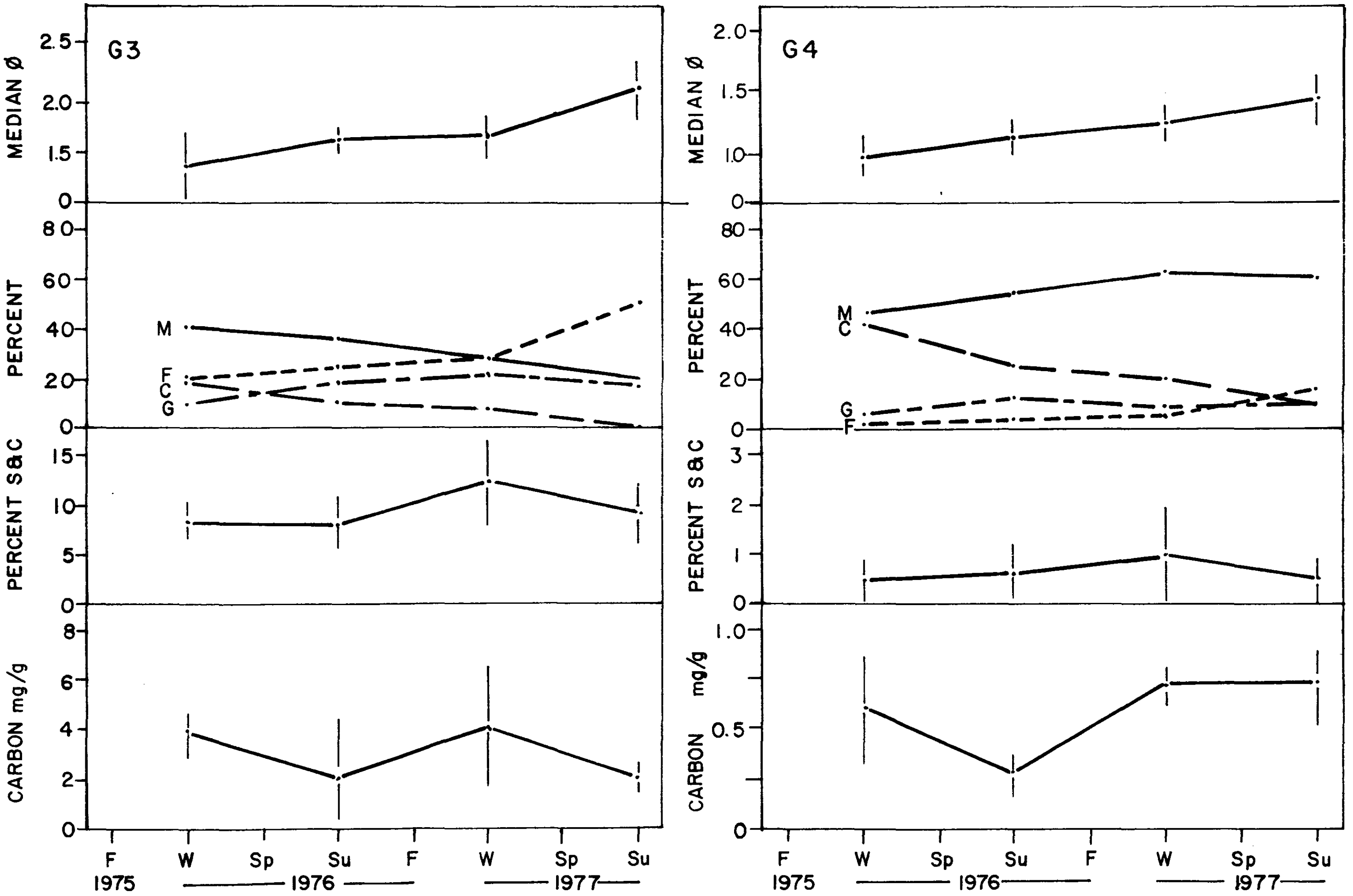

Figure 5-20. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

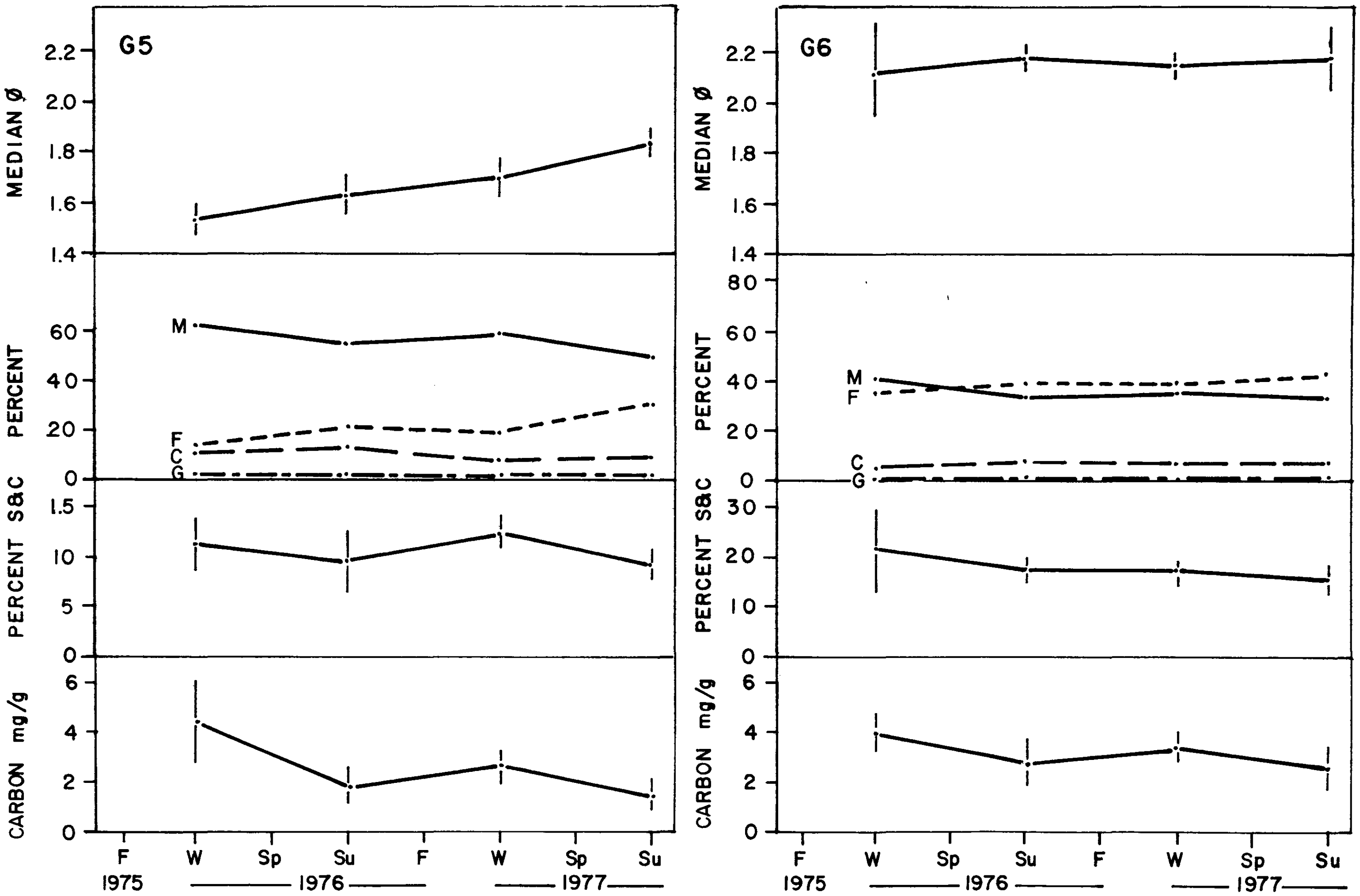

Figure 5-21. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

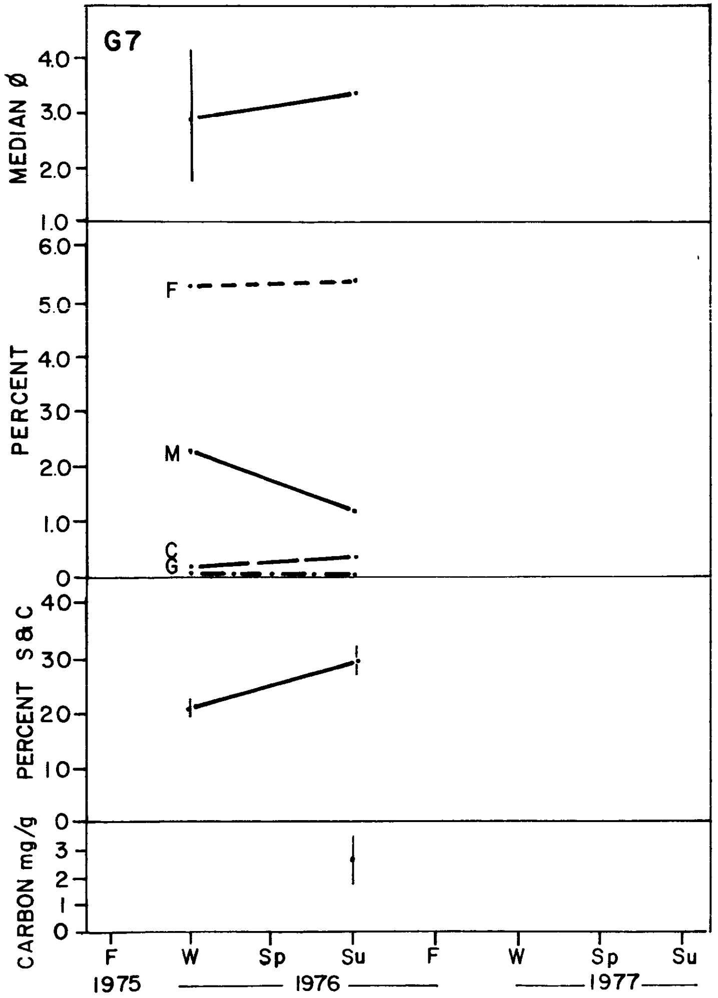

Figure 5-22. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

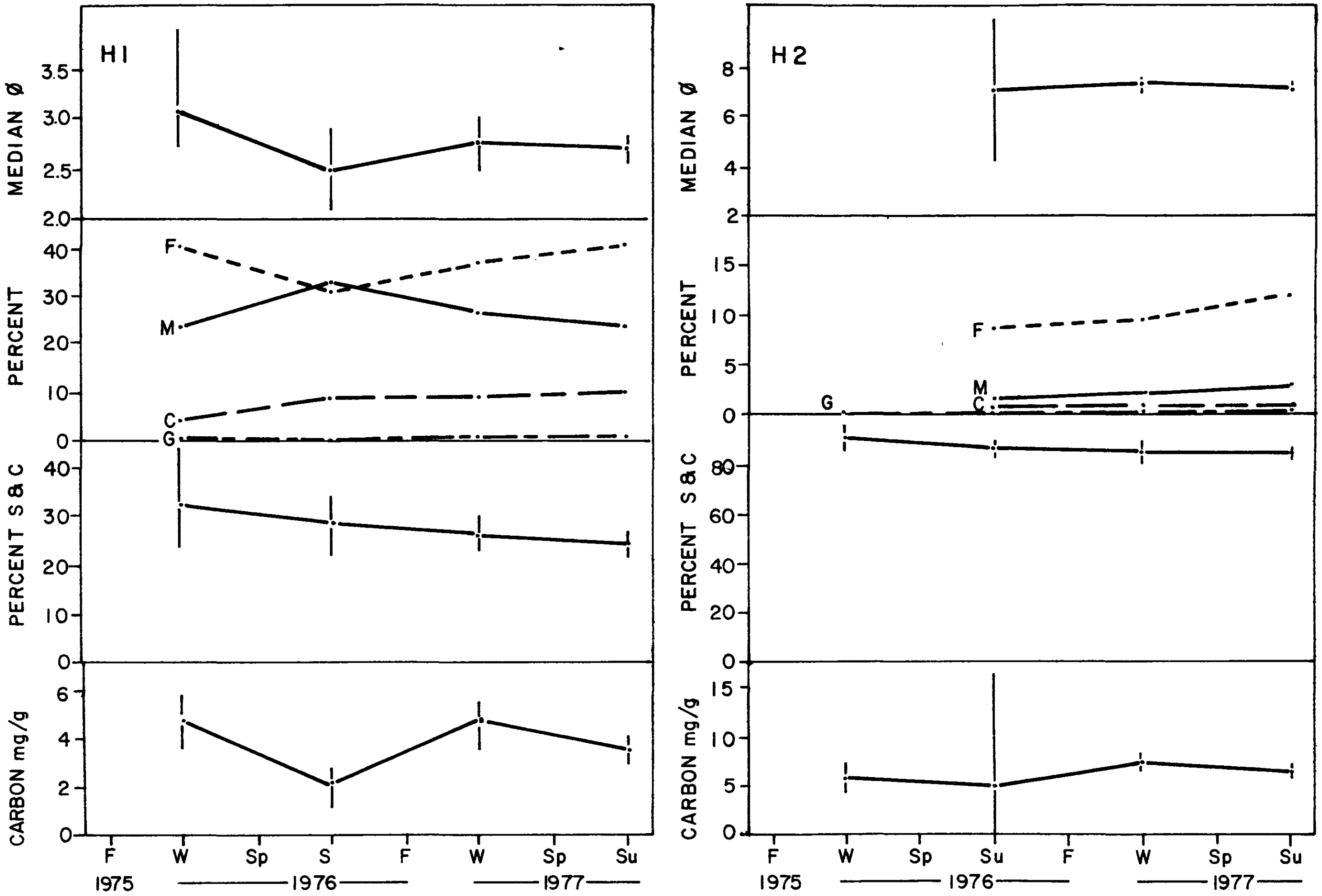

Figure 5-23. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

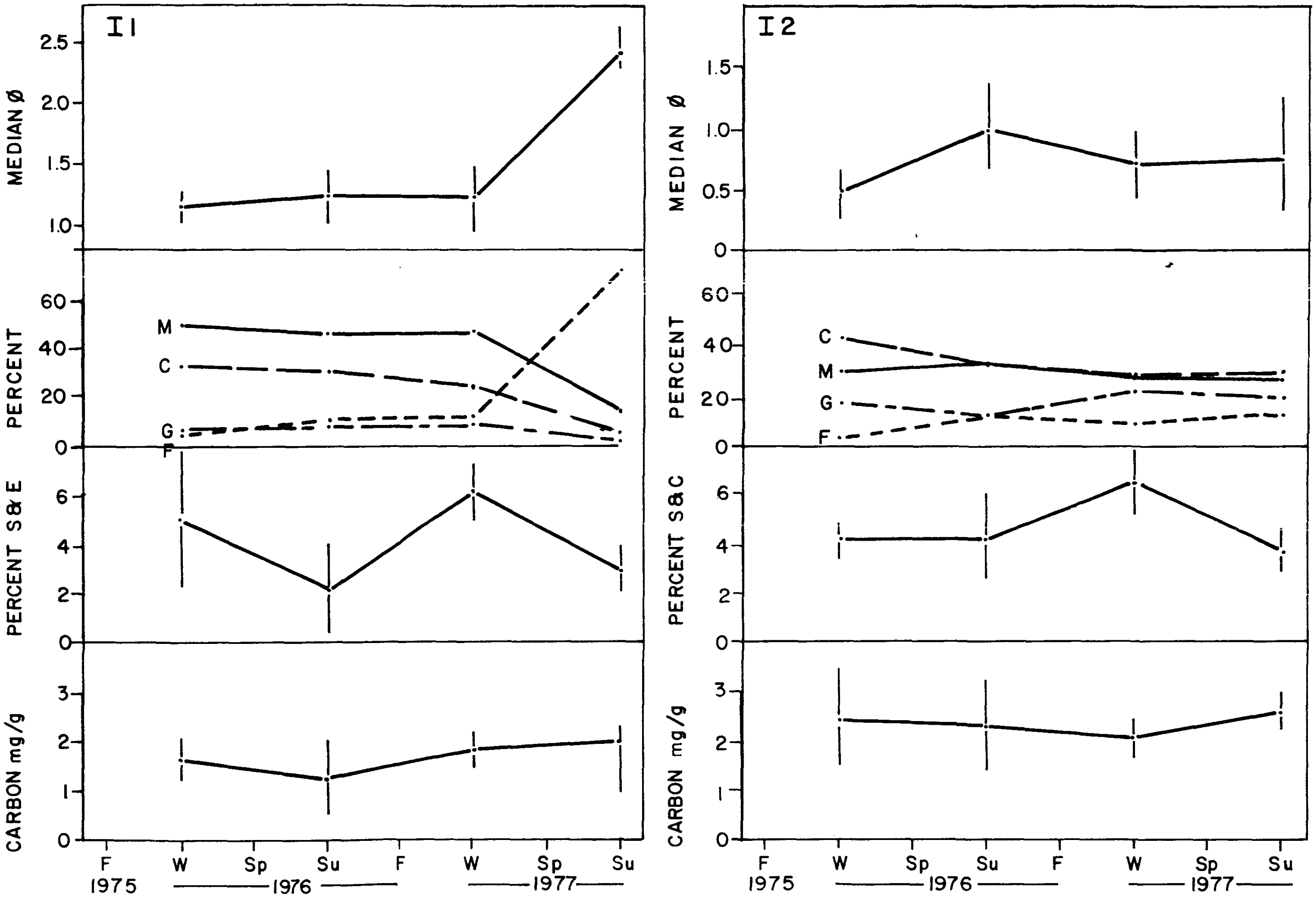

Figure 5-24. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

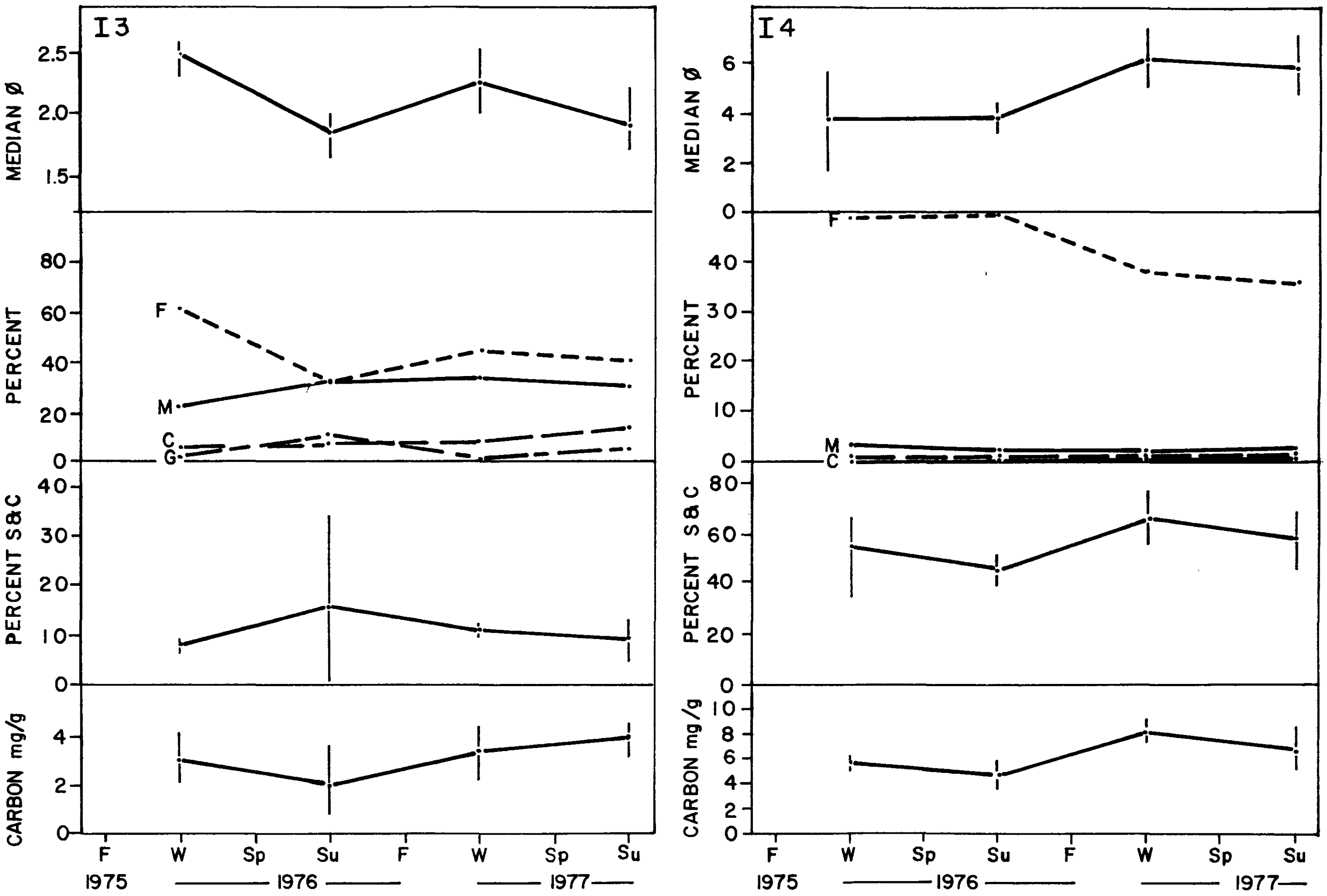

Figure 5-25. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

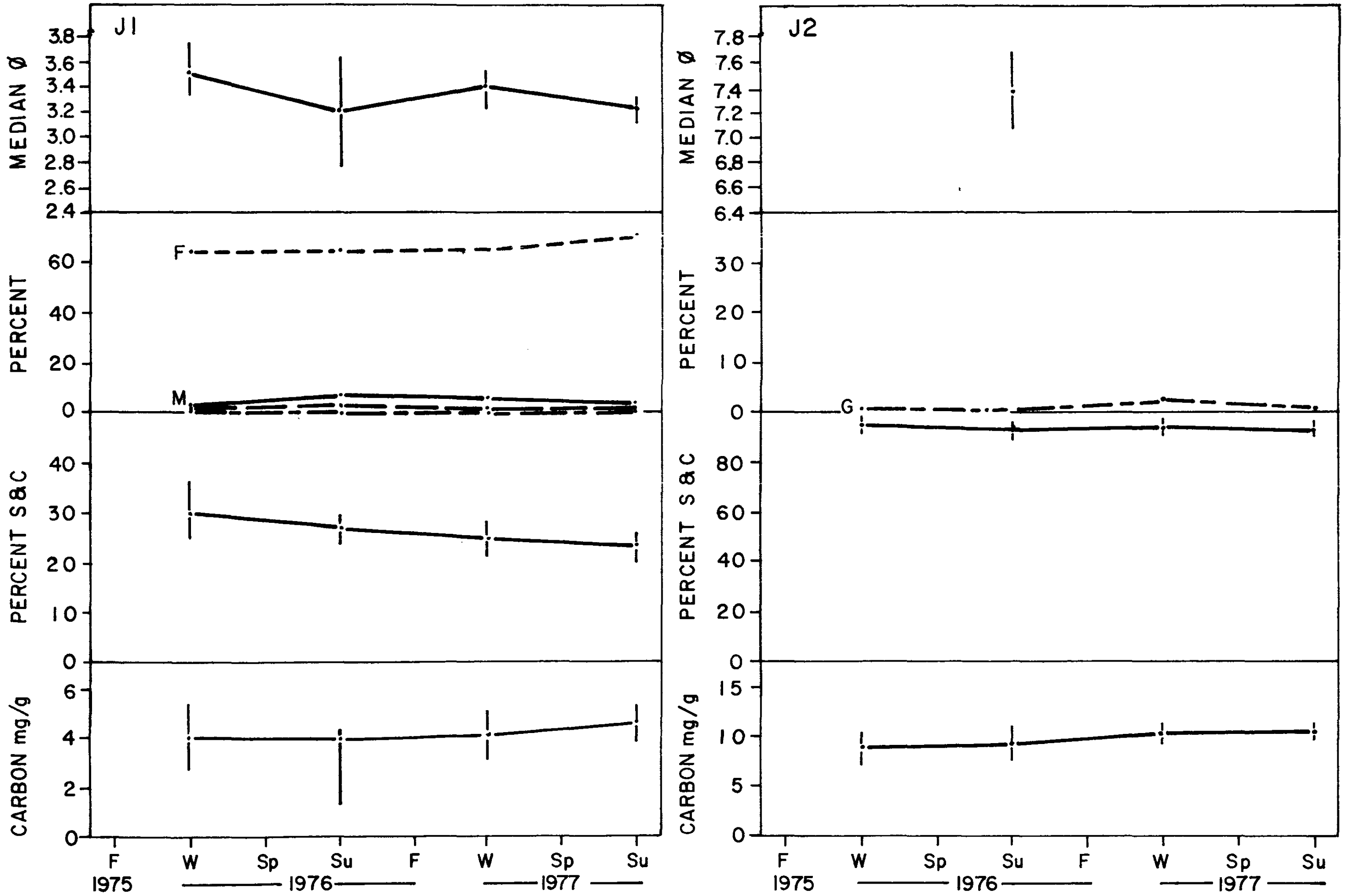

Figure 5-26. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

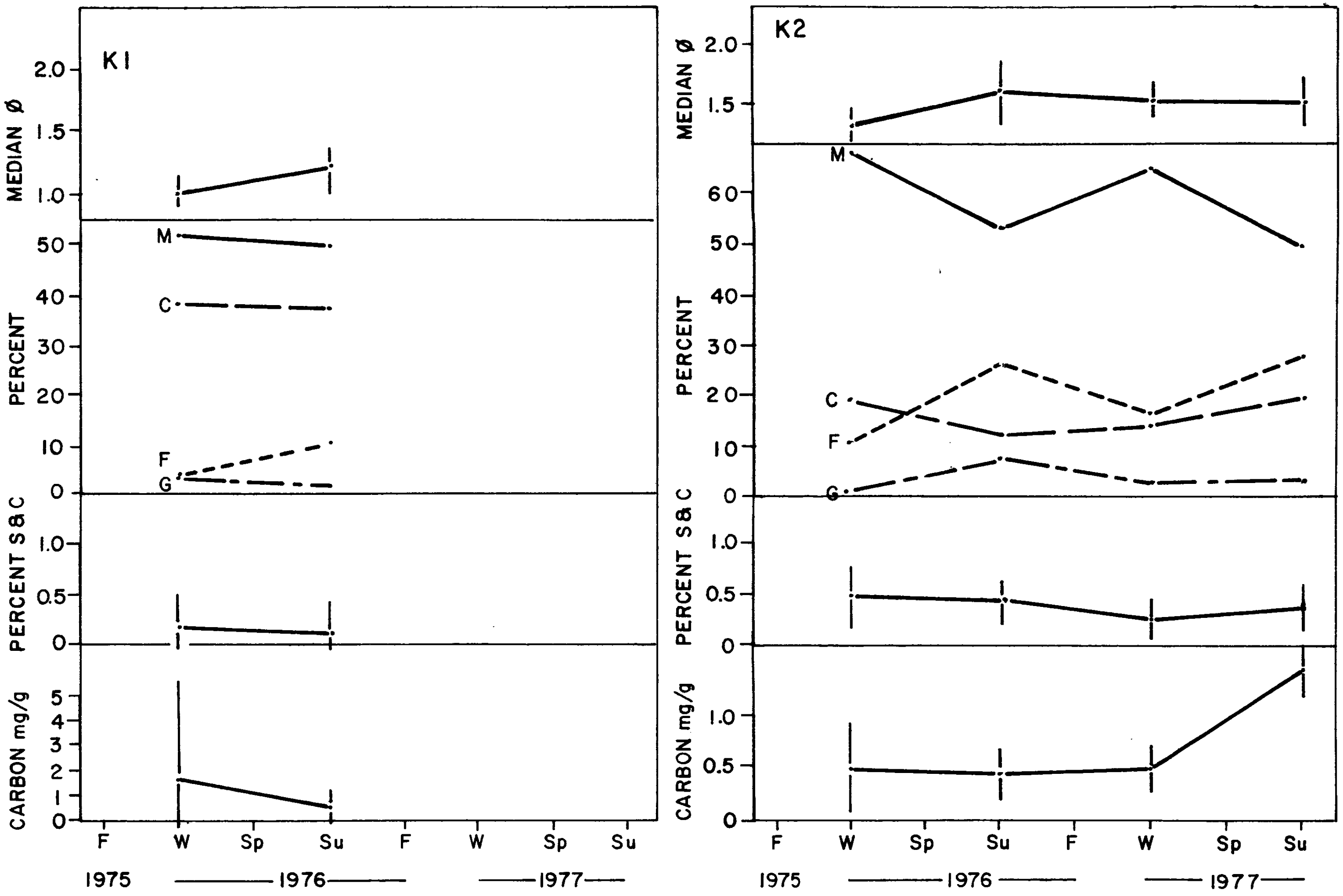

Figure 5-27. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

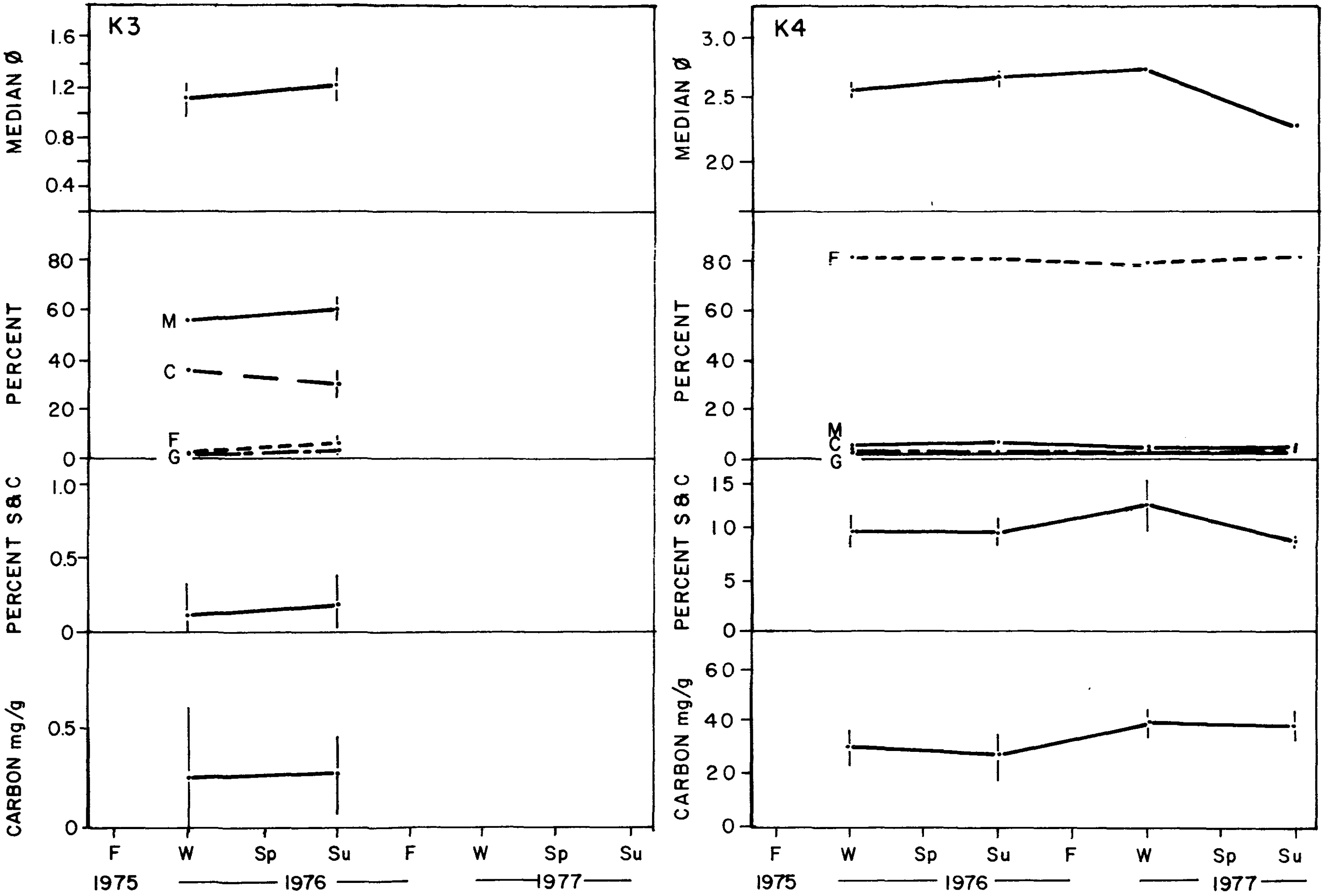

Figure 5-28. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

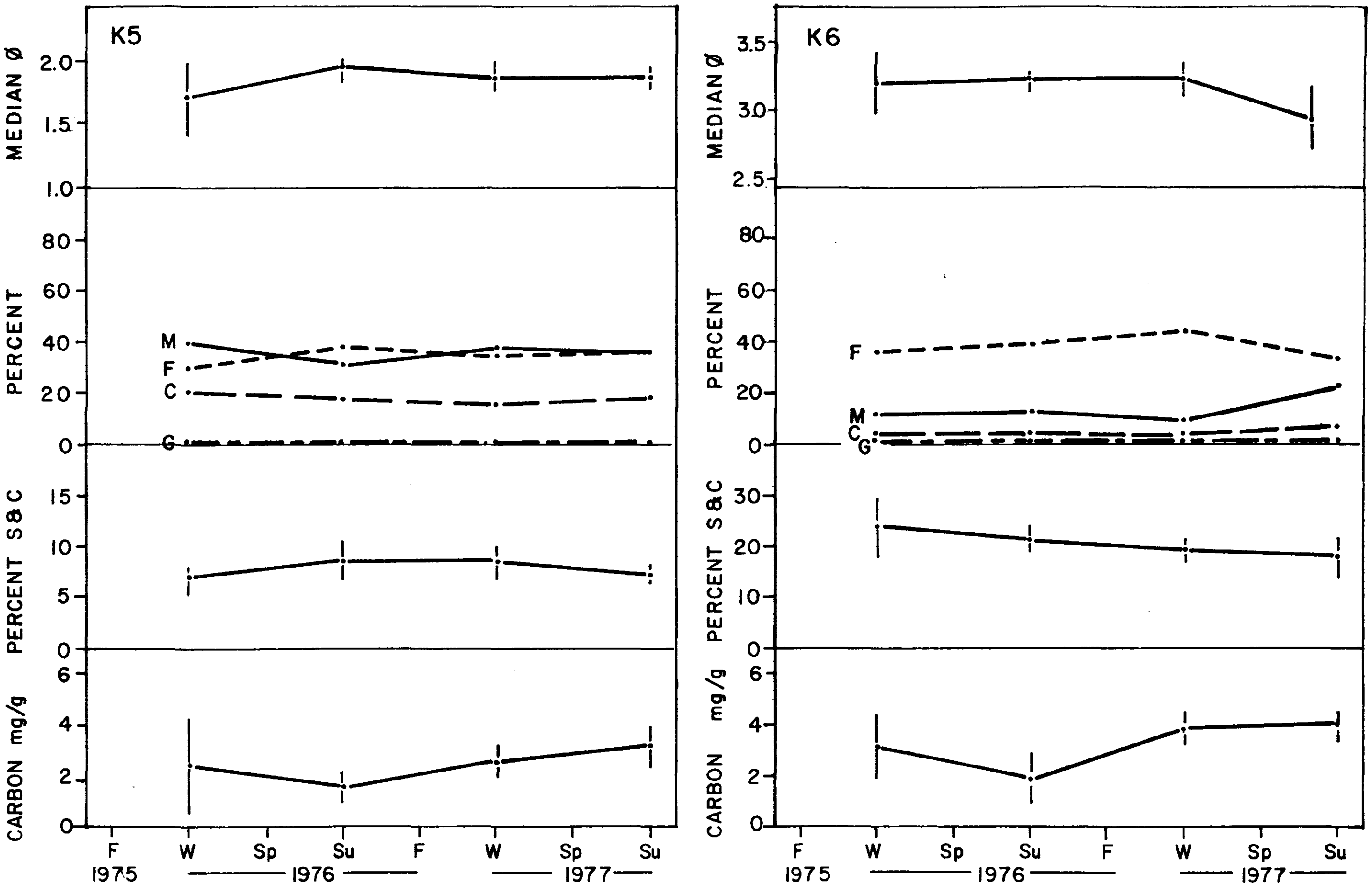

Figure 5-29. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

during summer 1977. Key parameters of sediments collected at the remaining K stations were highly persistent during two years of sampling.

L stations (Figure 5-30 to 5-32). Sediment parameters at stations on the L transect were likewise highly constant and few significant differences were observed between seasons.

Significance of Temporal Variability. The significance in variation of sediment parameters varied among stations and among sediment parameters. One way analyses of variance (ANOVA) were conducted on all computed grain size, carbon and nitrogen parameters to determine whether the variance among cruises was significantly greater than the variance among replicates within seasons. The incidence of highly significant ($p < 0.01$) F ratios was very large (Table 5-5). This is not surprising given the known spatial heterogeneity of shelf sediments (Knebel 1975) and the imperfect precision of stations relocation (Chapter 2).

In general, sand size distribution and statistics derived from the distribution were most variable, while silt and clay and organic carbon levels were less variable temporally, except in shelf swales. Sediment distribution in swales is apparently highly patchy, thus the variability of sediments sampled at swale stations was generally greatest. Most of the significant temporal variability in key sediment parameters could be explained in terms of apparent patchiness or imprecise station location (Table 5-5; Figures 5-6 to 5-32).

It is important to note that there is very little evidence of systematic variation in sediment parameters which would be indicative of wide spread, seasonal changes in sediments or systematic analytical variation. For several stations (B1, B2, B3, and C2) sands inexplicably tended to be finer during the second sampling year than the first. The lack of a similar trend at a majority of the stations, however, makes it improbable thus was a result of analytical differences between years. At a number of stations, there appeared to be a trend of higher organic carbon levels during the winter and/or spring and lower levels in summer, but this was not concordant over all stations.

Organic Carbon and Nitrogen

As demonstrated above, total organic carbon concentrations are highly correlated with percent silt and clay in continental shelf and slope sediments. This relationship is not linear over the full range of sediments sampled. The rate of increase of organic carbon with increasing silt and clay declines, such that most continental slope sediments composed of 50%, or more silt and clay contain less than 6 mg/g organic carbon, except J2 which had consistently higher levels near 10 mg/g. This is in part due to the fact that, although the sediments are finer they are further removed from sources of

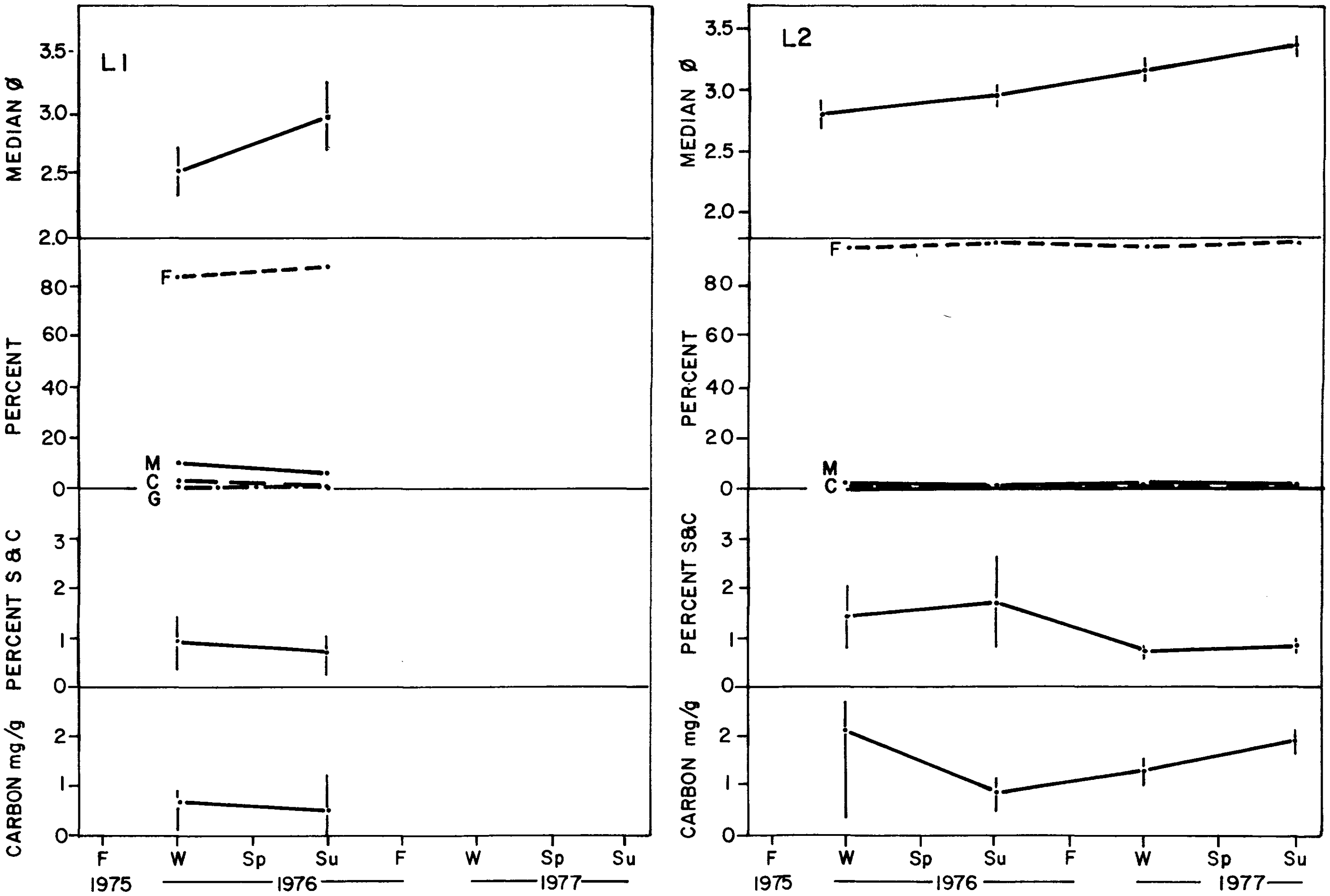

Figure 5-30. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

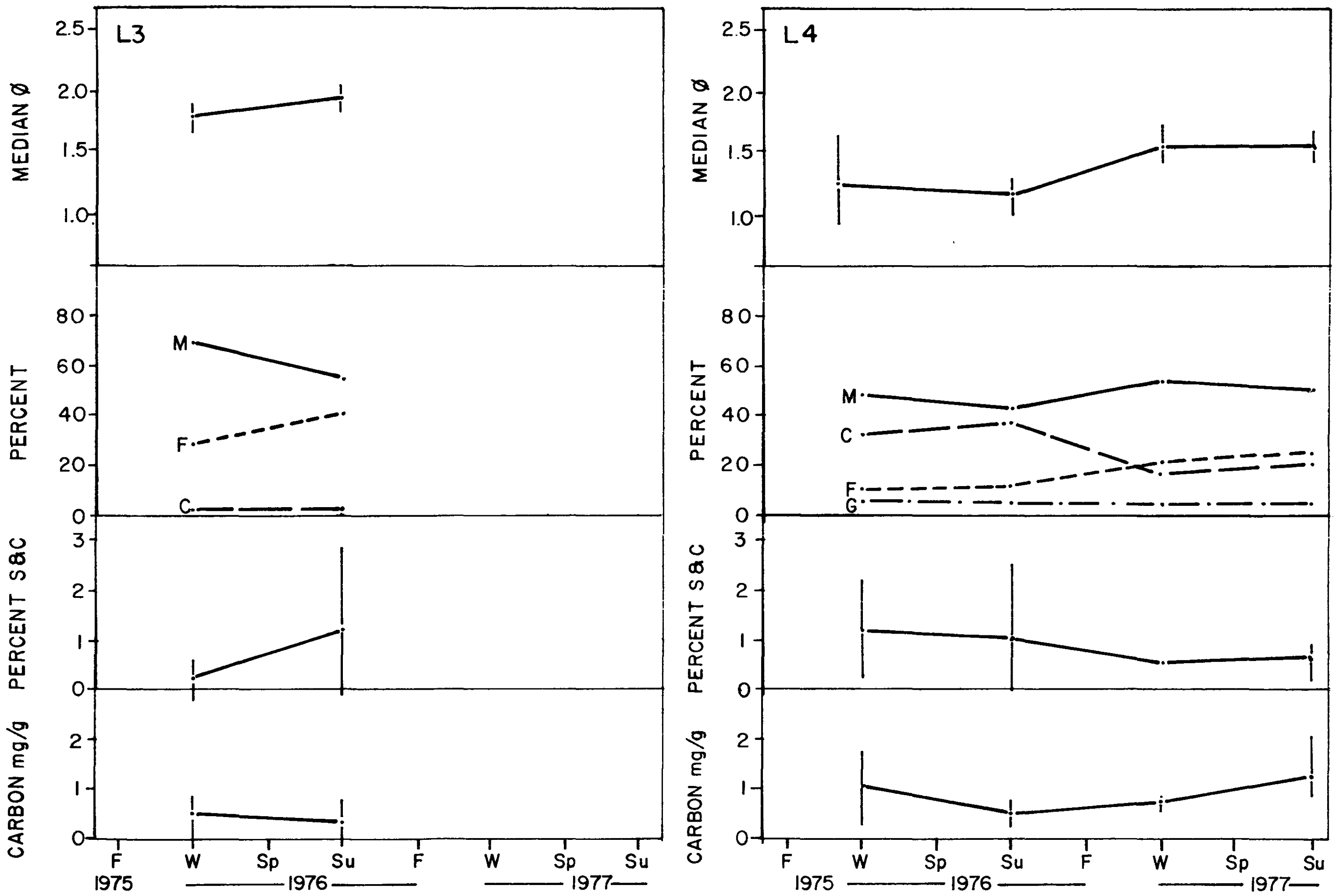

Figure 5-31. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\ t_{0.05}$).

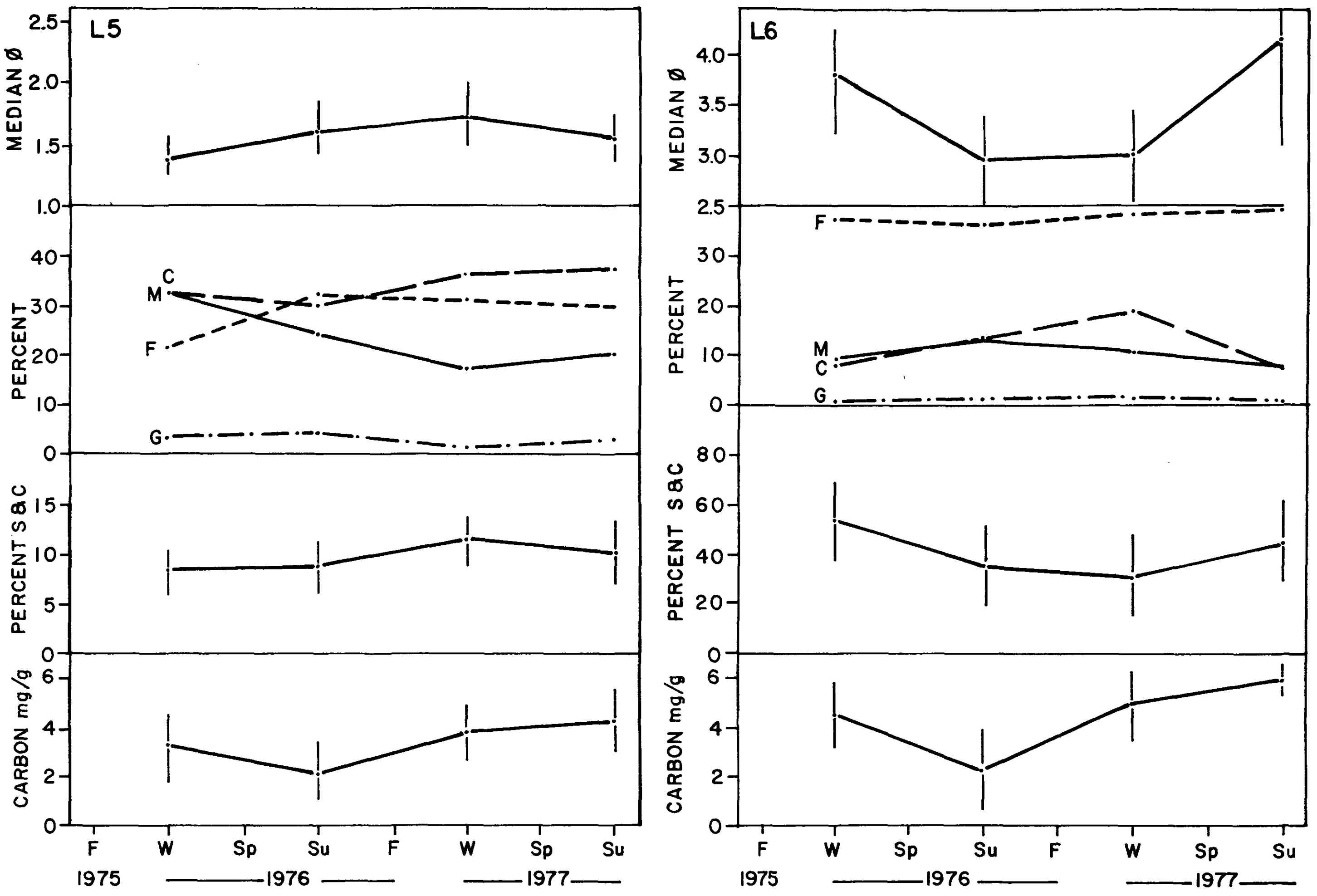

Figure 5-32. Variation in important sediment parameters at repetitively sampled stations. Lines connect means of all replicate sediment samples, vertical lines represent 95% confidence limits on the mean ($\bar{x} \pm S_{\bar{x}}\, t_{0.05}$).

Table 5-5. Significance of variability in sediment parameters among sampling periods at cluster stations sampled during 8 seasons. Significance of F-ratio comparing among-season to among-replicate variance in a one-way analysis of variance: *, $p<0.01$; **, $p<0.001$.

Station	Median Diameter (ϕ)	Percent Silt & Clay	Percent Fine Sand	Organic Carbon	Probable Cause(s) of Variation
A1	**		**	*	Region of heterogeneous sediments
A2	*				Sand fraction, fall 1975 cf. fall 1976
A3					
A4					
B1	**		**		Sand finer in second year
B2	*		*		Sand grading on ridge
B3	**		**		Sand finer in second year
B4					
C2	**		*		Less coarse sand in second year
C4	**	**	**		Extreme sediment patchiness in swale
D1	**	**	**		Station positioning, first year
D4			**	**	Sediment patchiness in swale
E1	**	**	**		Station positioning, summer '76, spring '77
E2	**	**	**	**	Rapid sediment grading on deep flank
E3					
E4	**	*	**	**	Sediment patchiness in swale
F1	**		**		Shifts from medium to fine sand
F2	**			**	Slightly finer sediments, summer '76, high carbon, fall '75, low carbon, summer '77
F3				*	Low carbon, summer 1977
F4	**	*		**	Higher silt and clay, winter 1977

productivity, thus the increase in organic carbon is not proportional to that of silt and clay.

Despite the high overall correlation between silt and clay and organic carbon, correlations between these parameters within the replicates at any one station were generally poor. Significant ($p < 0.05$) correlations were found at less than 10% of the stations. Two non-exclusive explanations for this are suggested. First, the variability in sedimentary parameters, including silt-clay percentage and carbon concentration, within a single grab sample, may be as great as that among replicate grab samples. Thus, since two separate cores were taken for granulometric and carbon analyses their comparability is compromised. Secondly, the relationship between silt and clay and organic carbon may be to some degree indirect. That is, areas of silt-clay deposition may also be sites for organic carbon deposition rather than any direct causal relationship between the two parameters. Biological processes may be more important in determining the localized distribution of organic carbon. Thus, although the overall correlation between the two parameters may be good, their local distribution is controlled by processes other than sedimentation. In reality, both explanations probably pertain.

Organic nitrogen may be a better measure of the biological activity and food quality of sediments than total organic carbon. Unfortunately, methodological problems in the analysis of nitrogen in the first year's samples hinder the intrepretation of these data. Variability was extremely high and reagent availability forced a change in the method employed from a gas chromatographic method to persulfate determination. Results from the analysis of second year samples using Kjeldahl determination were much more consistent and interpretable and these are discussed here.

Kjeldahl nitrogen was significantly correlated with organic carbon in sediments (Figure 5-33) ($r = 0.71$, $p < 0.001$). However, as with the organic carbon-silt clay relationship, the carbon:nitrogen relationship was not linear. The carbon:nitrogen ratio (C/N), often used as an index of the quality of organic material as a food source, was high in sandy sediments with little silt and clay and organic carbon and low in muddier, carbon rich sediments. Mean C/N typically ranged from 7 to 9 in coarser sands, such as at stations B2, B4, C2, and E3, and from 12 to 15 in muddy, finer sands of the shelf break region. High C/N characterized the sediments of swales and other shelf depressions (15-25) and the continental slope (13-20). It should be pointed out, however, that C/N ratios were extremely variable, due to high variability in nitrogen values. The patterns of C/N indicate that even though there is little organic material in clean, coarse shelf sediments it is relatively labile, perhaps consisting largely of living organisms (microbes and meiofauna). On the other hand, the sediments of depositional evnironments, relatively rich in organic carbon, contain proportionally more refractory, non-living organic carbon.

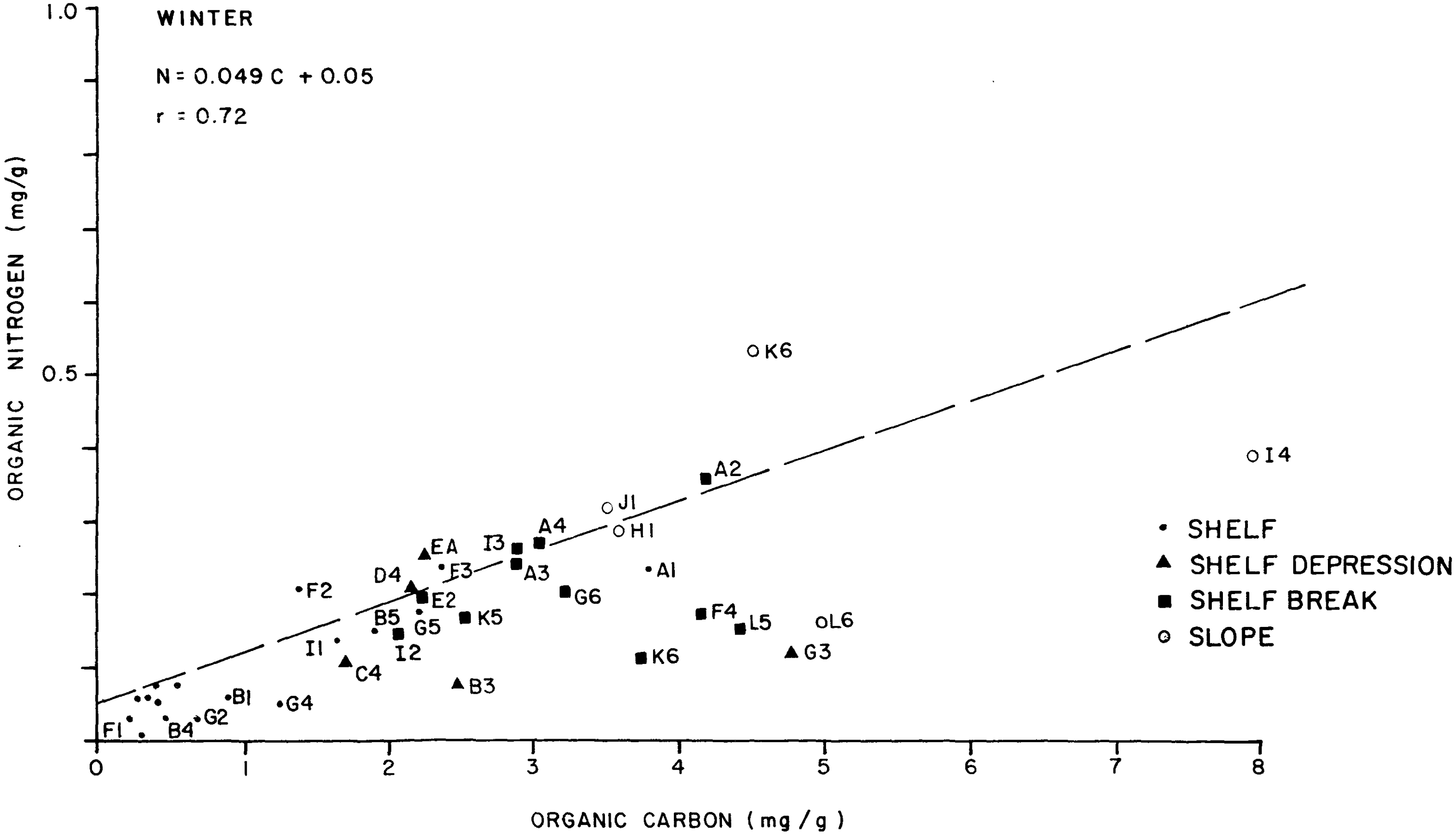

Figure 5-33. Relationship of sediment Kjeldahl nitrogen content with total organic carbon at stations sampled in winter 1977 (means of replicate samples).

Mesoscale Sediment Patterns

The habitat delineation study, described in detail in Chapter 6, involved stratified-random sampling in Areas B and E for the purposes of delineating the major habitats of benthos with respect to meso-scale topography. Sediment parameters of the stratified-random samples are summarized in Tables 5-6 and 5-7. Sediment distribution maps for both Areas B and E are given in Figures 5-34 and 5-35, based on these samples, supplemented in Area B by a previous USGS sediment survey of the area. Sediment facies were delimited consistent with the topography as much as possible.

Based on the sediment parameters and the distribution of macrobenthos and megabenthos, the two areas were restratified and five major habitats were delineated as described in Chapter 6. Key sediment parameters for each of the these redefined habitat-strata and several subdivision thereof are compared in Figures 5-36 and 5-37.

In Area B, habitat 1, represents a shallow terrace (< 52 m) atop Tiger Scarp where sediments consist of medium and coarse sand. Ridges below the scarp (habitat 2A) also have clean, medium-coarse sands. Some flanks are covered with predominantly medium sands (habitat 2B) and other flanks have finer sands and a small amount of silt and clay (habitat 3A) or have coarser but very mixed and somewhat muddy sediments representing eroded flanks (habitat 3B). The large swale sitting between Tiger Scarp and a ridge to the east has sediments consisting of 40-50% fine sand (habitat 4). The deeper (> 70 m) swale to the southeast (habitat 5) is covered with even finer and muddier sediments which contain much higher levels of organic carbon than elsewhere found in Area B.

In Area E, habitat 1A represents ridge crests covered with coarse-skewed medium sands. Similar sediments were found in a deeper bottom (habitat 1B) which is apparently subject to eroding currents as evidenced by megaripples in a bottom photograph. Medium sand flanks (habitat 2) have sediment properties similar to habitat 2B in Area B. Swales may be divided into shallow (habitat 3A), deep (habitat 3B) and eroded (habitat 4). Eroded swales have very mixed sediments with more coarse sand and shell than the other swales. The shelf break habitat is faunally distinctive, but consists of a shallower zone with clean medium sand sediments (habitat 5A) grading below 80 m to sediments which are slightly muddier, fine sands (habitat 5B).

The relationship of sediment organic carbon to silt and clay is assessed in Figures 5-38 and 5-39 for Areas B and E, respectively. For Area B, the correlation is poor if all samples are included. Outliers with lower organic carbon than might be predicted based on the silt-clay content are mainly samples from habitat 3B, eroded flanks. The silt and clay present in these sediments is probably relict, resulting from older deposits exposed by the local erosion of the surficial sand sheet. Clay lumps were visible in most of these samples, but these relict fine sediments are depleted in organic

(TEXT CONTINUES ON PAGE 5-72)

Table 5-6. Sediment parameters and depth of each stratified random station sampled in the habitat delineation study of Area B.

Station	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter (ϕ)	Sorting Coefficient (ϕ)
Stratum 1									
BPO	41	3.1	36.6	54.9	4.8	0.6	0.25	1.12	0.64
BP1	41	11.7	34.4	49.4	4.4	0.1	0.49	1.05	0.93
BP2	41	1.2	39.5	54.3	4.9	0.0	0.26	0.98	0.66
BP3	42	10.0	28.8	56.7	4.5	0.0	0.24	1.20	0.79
BP4	46	7.8	26.7	63.5	1.8	0.2	0.77	1.18	0.83
BP5	48	4.7	25.7	65.7	3.8	0.1	0.33	1.26	0.58
BP6	45	0.9	30.7	65.4	3.0	0.1	0.36	1.19	0.40
BP7	47	3.5	30.9	60.8	4.8	0.1	0.30	1.24	0.68
BP8	45	1.0	17.8	75.2	5.9	0.1	0.29	1.37	0.43
BP9	42	2.2	23.3	63.1	10.7	0.7	0.25	1.34	0.54
BF1	52	6.1	52.6	37.6	3.8	0.0	0.29	0.72	0.89
BF2	54	2.6	38.9	52.6	5.8	0.0	0.31	1.16	0.91
B4	42	8.7	26.9	58.6	5.7	0.1	0.44	1.14	0.62
Stratum 2 Substratum 2A									
BR2	66	4.1	21.9	64.8	8.6	0.6	1.22	1.38	0.52
BR4	65	14.6	30.7	52.0	2.6	0.2	0.68	1.07	1.15
BR5	63	0.5	33.8	58.7	7.0	0.1	0.64	1.26	0.60
BF3	58	1.6	31.4	59.9	6.9	0.3	0.59	1.33	0.74
BM2	58	36.1	32.8	20.8	9.5	0.9	1.12	0.38	--
Substratum 2B									
BR6	66	1.8	17.6	68.5	11.7	0.4	1.75	1.47	0.52
BD1	62	0.4	7.0	82.6	10.0	0.1	1.16	1.51	0.38
BD2	64	0.2	17.9	68.6	12.9	0.4	1.48	1.48	0.52
BD4	64	5.3	10.4	72.6	11.3	0.4	0.84	1.58	0.49
BD5	65	2.9	9.7	77.6	9.7	0.1	0.44	1.61	0.41
BD7	64	1.3	23.6	64.9	9.8	0.3	0.47	1.39	0.52
B2	62	2.6	19.4	62.0	13.5	0.2	0.47	1.45	0.64

Table 5-6 (continued)

Station	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter (ϕ)	Sorting Coefficient (ϕ)
Stratum 3									
Substratum 3A									
BM1	56	0.9	0.9	15.0	77.8	5.4	2.15	2.39	0.37
BM3	56	3.1	6.7	71.3	17.1	1.8	0.55	1.61	0.45
BM4	56	0.7	2.0	51.4	45.4	0.5	0.81	1.98	0.27
BM6	63	0.6	1.0	67.0	27.7	3.4	1.16	1.87	0.36
BF4	58	2.4	2.9	45.2	48.1	1.4	1.67	2.00	0.48
BF5	59	1.1	1.0	60.0	35.8	0.4	0.95	1.92	0.31
BF6	62	1.2	3.9	73.4	19.6	2.0	1.12	1.76	0.34
BR1	62	0.6	1.9	41.9	51.4	4.3	1.60	2.04	0.30
BR8	65	3.3	8.3	50.6	33.1	4.7	0.29	1.85	0.57
BD3	66	2.7	7.6	68.4	19.0	2.3	0.96	1.63	0.49
BD8	64	0.6	1.0	69.0	28.6	0.7	1.14	1.74	0.41
BSO	71	0.8	--	--	--	7.0	1.36	--	--
BS5	66	4.1	10.8	64.7	14.4	6.0	1.48	1.67	0.53
B1	65	0.4	3.5	61.3	31.7	3.1	0.94	1.80	0.44
Substratum 3B									
BR7	64	11.0	24.9	49.8	11.2	3.1	0.40	1.29	1.02
BR9	62	11.3	14.5	53.1	12.9	8.2	0.46	1.57	1.10
BM5	63	0.7	25.2	61.9	9.7	2.6	0.54	1.35	0.57
BS2	69	7.7	26.4	42.2	19.3	4.4	1.05	1.39	1.09
BS4	64	8.1	11.8	43.0	29.5	7.5	1.11	1.79	0.91
BS7	68	12.9	31.8	43.0	9.9	4.4	0.90	1.13	1.29
B5	68	5.2	13.43	58.5	20.0	2.8	--	1.67	0.56
Stratum 4									
BR3	66	2.5	2.6	43.2	43.2	1.5	0.47	1.95	0.58
BS1	66	2.1	3.7	45.2	43.4	1.8	0.81	2.00	0.43
BS3	66	2.9	3.7	41.4	46.9	5.2	1.08	2.02	0.44
BS6	66	5.3	9.7	29.9	48.4	6.8	1.77	2.08	0.74

Table 5-6 (concluded)

Station	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter (ϕ)	Sorting Coefficient (ϕ)
Stratum 5									
BD6	74	3.0	5.7	36.8	51.9	2.7	2.14	2.07	0.54
BS8	75	0.5	2.8	27.6	61.6	7.5	1.85	2.25	0.52
BS9	74	1.9	3.7	23.0	65.4	6.1	1.72	2.26	0.52
B3	74	8.1	2.6	18.3	64.6	6.5	1.95	2.37	0.63

Table 5-7. Sediment parameters and depth of each stratified random station sampled in the habitat delineation study of Area A.

Station	Depth (m)	% Gravel	% Coarse Sand	% Medium Sand	% Fine Sand	% Silt & Clay	Organic Carbon (mg/g)	Median Diameter (ϕ)	Sorting Coefficient (ϕ)
Stratum 1									
Substratum 1A									
ER1	58	8.9	15.9	60.0	12.4	0.3	0.37	1.50	0.77
ER2	56	1.5	21.7	64.0	12.8	0.1	0.59	1.36	0.55
ER3	52	1.4	30.6	61.2	6.9	0.0	0.28	1.30	0.71
ER4	54	13.8	48.2	28.4	9.5	0.0	0.34	0.77	1.17
ER5	57	8.6	28.3	53.8	9.1	0.1	0.69	1.24	1.05
ER6	57	4.1	21.1	64.2	10.5	0.1	0.12	1.36	0.59
EF7	65	5.6	19.8	67.9	6.6	0.1	0.39	1.33	0.54
EF8	61	5.3	38.7	52.9	2.8	0.3	0.57	1.10	0.77
E1	63	3.4	18.3	60.4	17.9	0.1	0.42	1.43	0.61
E3	65	2.8	24.4	66.2	6.3	0.3	0.35	1.33	0.67
Substratum 1B									
ED7	74	12.1	34.5	50.1	1.7	1.4	0.70	1.05	1.09
Stratum 2									
EF1	57	3.0	3.9	45.4	47.4	0.4	0.58	1.98	0.45
EF2	58	4.0	9.6	54.6	31.6	0.2	0.35	1.78	0.53
EF3	62	1.9	1.0	10.7	85.9	0.5	0.61	2.38	0.30
EF4	62	0.4	0	13.9	85.4	0.3	0.54	2.23	0.25
EF5	66	7.1	6.5	26.7	59.0	0.7	0.86	2.14	0.66
EF6	68	3.1	1.9	82.1	12.6	0.3	0.57	1.68	0.26
ER7	67	1.8	5.9	79.2	12.7	0.4	0.64	1.57	0.39
ER8	66	6.3	6.5	80.2	6.5	0.5	0.20	1.56	0.38
ED3	70	4.9	24.2	47.5	21.4	1.9	1.34	1.51	0.75
ED5	69	0.2	0.5	66.2	32.9	0.3	0.77	1.89	0.25
ED6	71	0.6	2.0	81.3	14.7	1.4	0.57	1.69	0.30

Table 5-7 (concluded).

Station	Depth (m)	% Gravel	% Coarse Sand	% Median Sand	% Fine Sand	% Silt & Clay	Carbon (mg/g)	Median Diameter (ϕ)	Sorting oefficient (ϕ)
Stratum 3									
Substratum 3A									
ED1	69	5.6	10.8	36.0	43.2	4.5	1.06	1.96	0.71
ED2	70	8.3	5.2	27.3	55.5	3.6	1.16	2.14	0.67
ED4	70	0.8	2.9	6.8	87.4	2.1	0.93	2.50	0.31
Substratum 3B									
ED9	76	1.4	1.0	23.9	70.9	2.8	1.01	2.18	0.30
ES1	77	0.1	2.0	84.6	12.9	0.4	0.45	1.61	0.32
ES2	77	0.2	2.0	86.4	10.9	0.5	0.47	1.64	0.31
ES4	73	0.1	0	10.9	88.5	0.4	0.74	2.36	0.26
E2	72	2.5	2.3	63.2	31.2	0.2	0.43	1.78	0.39
Stratum 4									
ED8	76	4.6	18.8	34.1	36.7	5.8	2.27	1.85	1.01
ES3	76	6.9	1.7	25.7	58.2	7.6	2.20	2.24	0.66
ES5	78	15.7	14.5	40.7	13.8	15.2	2.32	1.49	2.02
ES6	77	11.3	11.7	56.2	15.9	4.9	0.28	1.54	0.89
E4	78	5.5	7.4	31.0	51.1	5.0	1.28	2.09	0.85
Stratum 5									
Substratum 5A									
EDO	77	6.6	4.7	78.2	10.3	0.3	--	1.58	0.39
ES7	80	3.2	18.3	70.3	7.7	0.5	0.68	1.39	0.45
ES8	79	2.9	8.7	75.6	12.6	0.2	1.14	1.47	0.43
EL1	74	3.7	25.9	63.4	6.7	0.3	0.33	1.29	0.58
EL2	78	0.9	9.9	73.1	15.8	0.3	0.45	1.58	0.42
EL3	80	0.5	7.0	78.4	13.9	0.2	0.51	1.60	0.39
EL6	79	0.7	5.0	63.3	30.7	0.6	0.66	1.80	0.46
Substratum 5B									
EL4	89	0.4	1.0	6.7	88.3	3.7	1.17	2.50	0.28
EL5	87	3.0	3.6	25.0	62.8	4.6	0.97	2.40	0.63

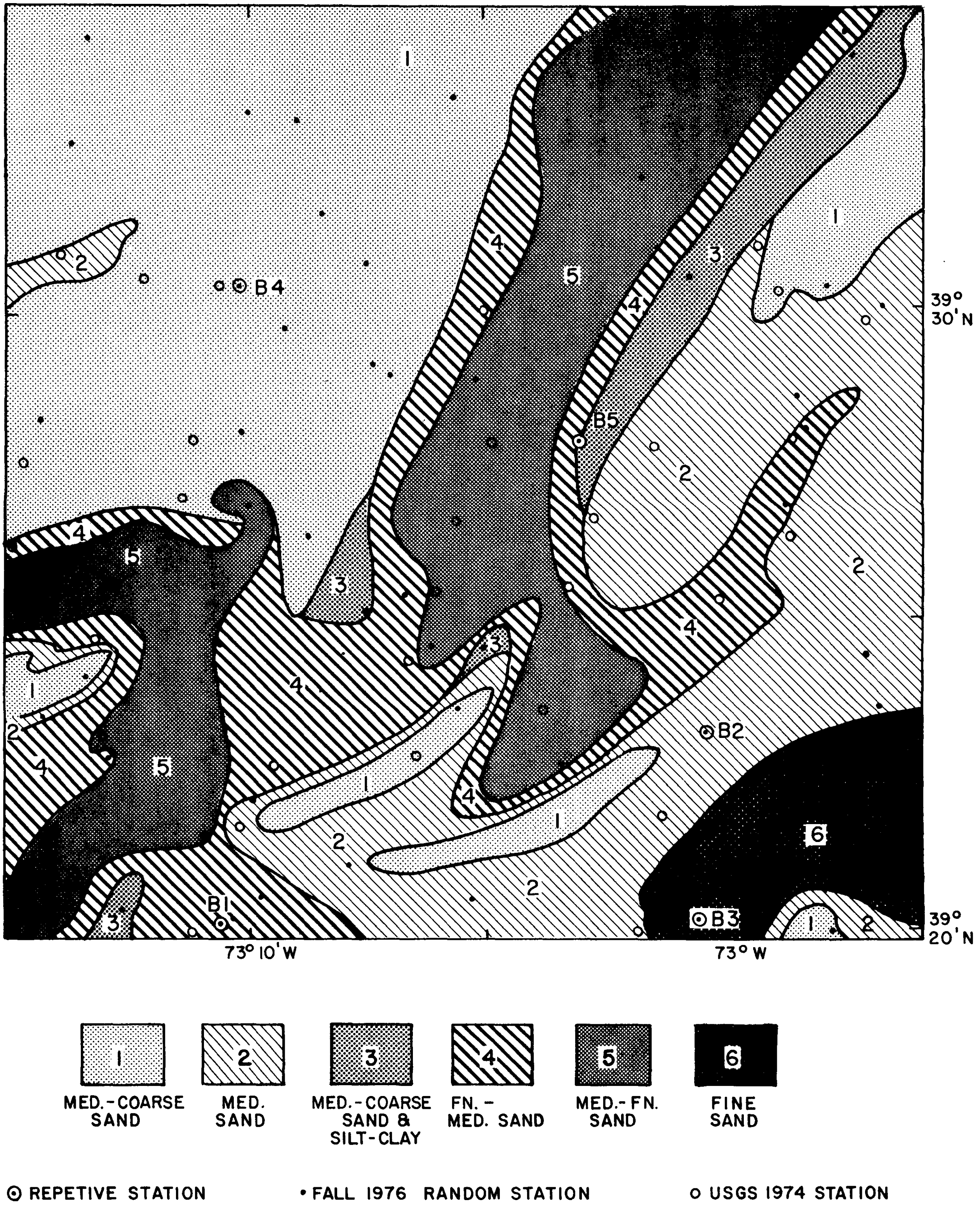

Figure 5-34. Distribution of sediment types in portion of Area B surveyed in the habitat delineation study.

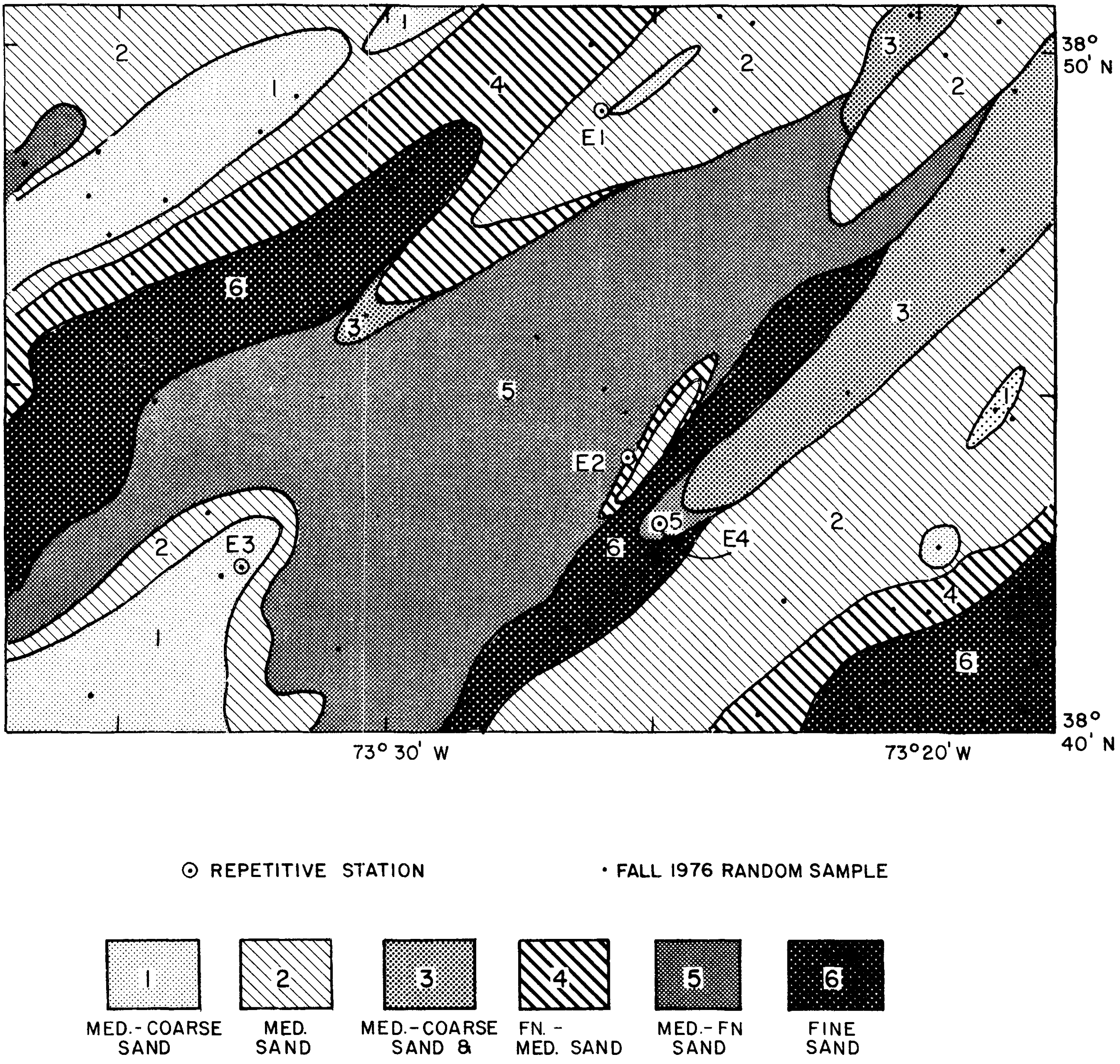

Figure 5-35. Distribution of sediment types in portion of Area E surveyed in the habitat delineation study.

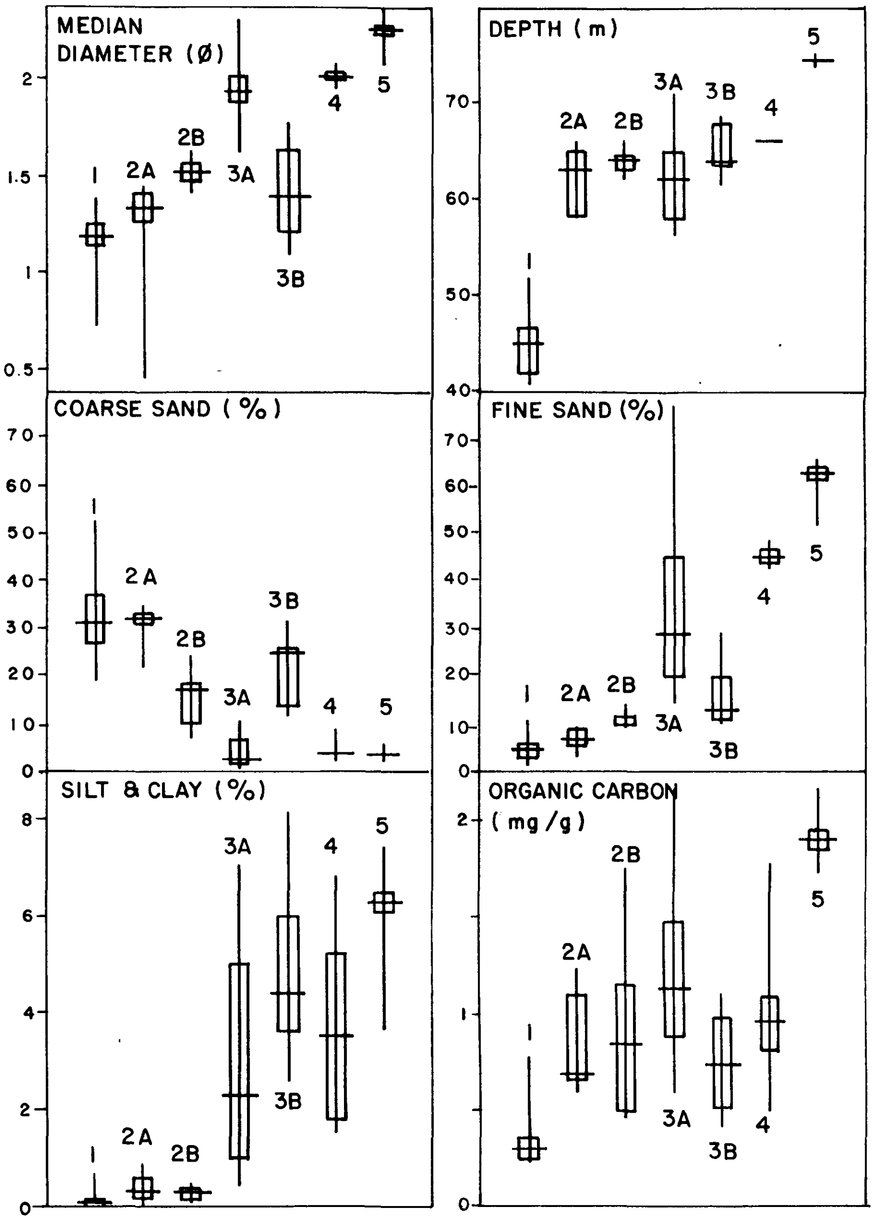

Figure 5-36. Variation of key sediment parameters and water depth at stratified random and repetitive stations in Area B classified into habitat strata on the basis of analysis of sediments and benthic biota (Chapter 6).

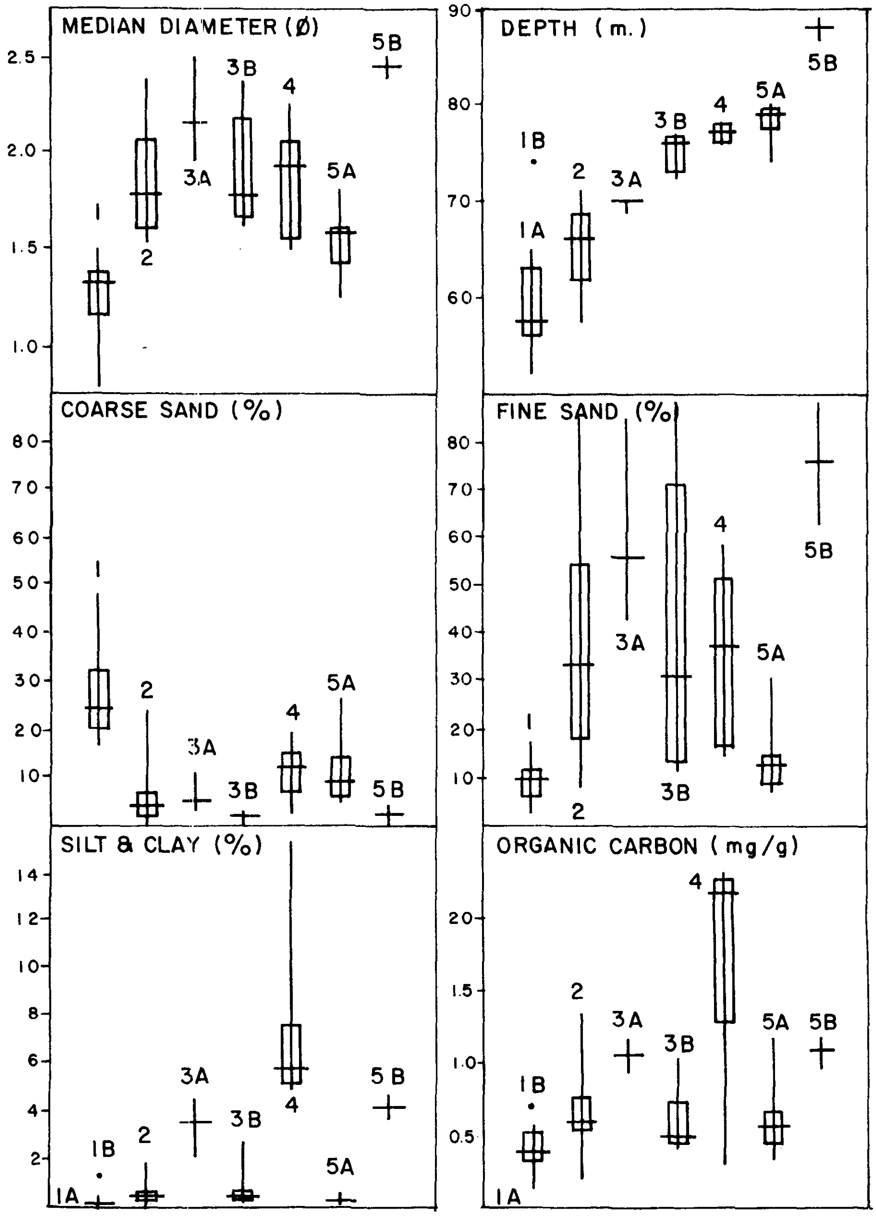

Figure 5-37. Variation of key sediment parameters and water depth at stratified random and repetitive stations in Area E classified into habitat strata on the basis of analysis of sediments and benthic biota (Chapter 6).

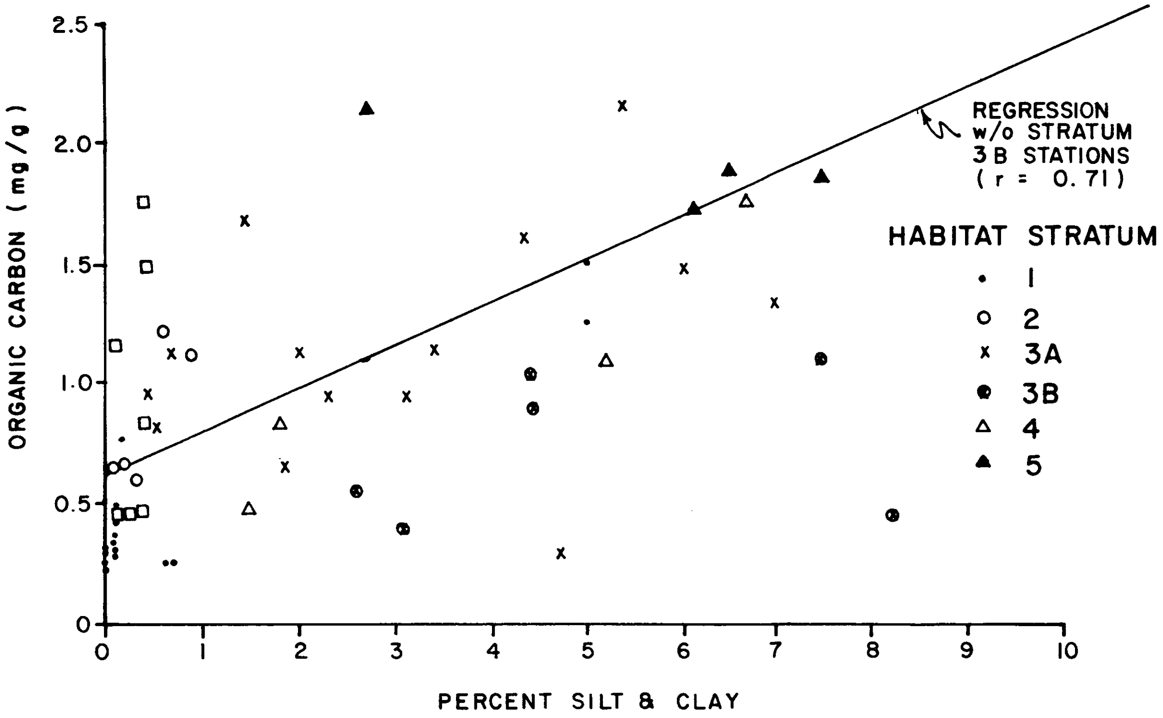

Figure 5-38. Relationship of sediment organic carbon content to percent silt and clay at stations sampled in habitat delineation study of Area B.

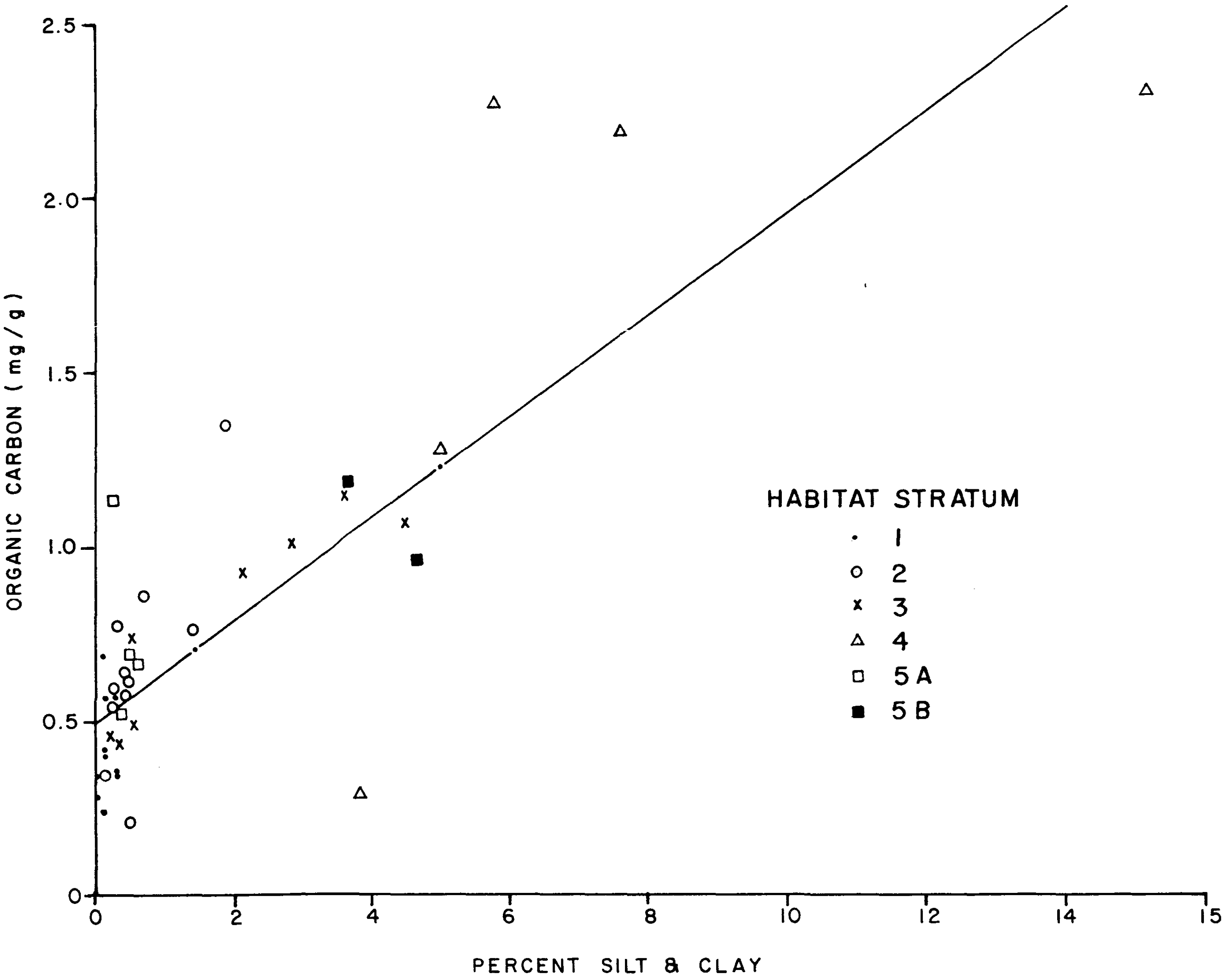

Figure 5-39. Relationship of sediment organic carbon content to percent silt and clay at stations sampled in habitat delineation study of Area E.

carbon. If habitat 3B samples are not considered, the correlation improves markedly ($r = 0.71$, $p < 0.001$). Nonetheless, there remain several samples which have relatively high organic carbon levels despite the lack of silt and clay. In Area E, organic carbon and silt and clay were strongly correlated (Figure 5-39). Again, outliers both below and above the least squares line were from mixed sediments of a presumably erosional environment (habitat 4).

The least square regression for the stratified-random samples in Area B and E are compared in Figure 5-40 with organic carbon, and silt clay levels found in sequential sampling of the fixed stations in those two areas. The three regressions were not significantly different. The comparison endorses the representativeness of the fixed stations and indicates the persistence of the relationship between organic carbon and silt and clay. It should be noted that the principal outliers are the deep swale stations, B3 and E4, where sediments contain more organic carbon than predicted by any of the three regressions.

DISCUSSION

The data on grain size and organic carbon conform well with those published in the literature on broad and local scales. A broad picture of Middle Atlantic shelf and slope sediments is available from data collected at stations on an 18 km grid by the Woods Hole Oceanographic Institution - U.S. Geological Survey continental margin program of the 1960's. Much of the resulting data is given in Hathaway (1971) and has been summarized by Emery and Uchupi (1972), Milliman (1972, 1973), Hollister (1973), and Trumbull (1972). From these and other sources, Johnson (1977) prepared a map of the distribution of median grain size for the continental shelf from northern New Jersey to Cape Charles.

The surficial sediments of the continental shelf of the study area are overwhelmingly sand, and it is only in isolated regions where coarser or finer sediments are found. Increased silt and clay content is found in the Hudson Shelf Valley and near the shelf break, particularly in the broad shelf-slope transition south of Hudson Canyon (Stanley and Freeland 1978). Stanley and Wear (1978) reported a transition from the sandy outer shelf facies (to depths of 130 m) to a slope facies (deeper than 250 to 300 m) along the shelf edge between Norfolk and Wilmington Canyons. The "mud line" located on the upper slope at about 250-300 m marks the substantially increased mud content of surficial sediments and the prevalence of sediment deposition.

Gross parameters such as percent sand and median grain size lack the specificity needed to relate grain-size to sediment dynamics or to benthic organisms (Chapter 6). Many examples can be found in the data reported here of predominantly sandy sediments with equivalent median diameters but quite different distribution within the sand fractions. Also, small amounts of silt and clay, of little consequence to the

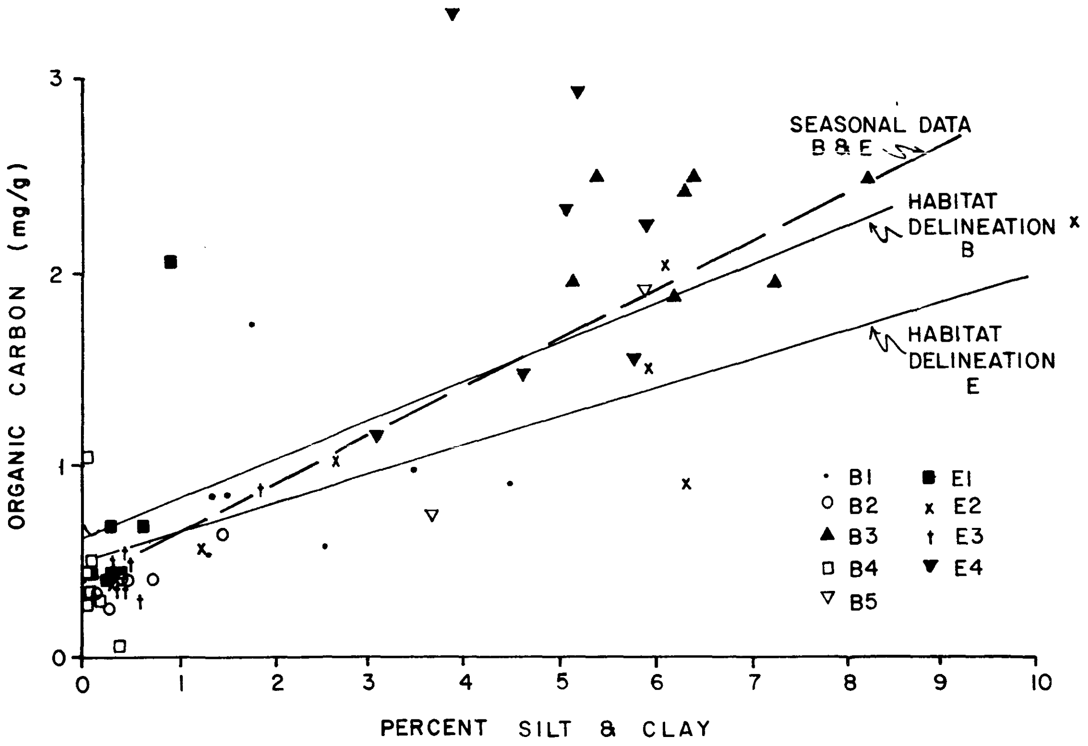

Figure 5-40. Relationship of sediment organic content to percent silt and clay in seasonal samples (means of 6 replicates) at repetitively sampled stations in Areas B and E. This is compared with regressions developed based on the habitat delineation study.

sediment mass, may be of extreme biological and geochemical importance. Because of the topographic and sedimentologic complexity of the Middle Atlantic shelf, the resolution of these broad scale characterizations is likewise inadequate for more localized sedimentological, biological, or chemical studies.

More detailed data on sediment distribution are available for several small areas within the study area (Stubblefield et al. 1974, 1975; Freeland et al. 1976; H. Knebel, unpublished data). These show more complicated granulometric distributions reflective of both the erosional source of sediments and the contemporary hydraulic regime. The sediment distribution is particularly related to ridge and swale topography as our data from repetitively-sampled fixed stations and the habitat delineation study clearly indicate. Finer sands with small amounts of silt and clay are found in swales. However erosional windows, often extending into older sediments beneath the surficial sand sheet (Stubblefield and Swift 1976; Knebel and Spiker 1977), locally winnow swale sediments leaving a coarse lag of sand, shell, gravel, and mud lumps. Most of the swale stations sampled here (except E4 and some samples at C4 and D4) were apparently in depositional rather than erosional sections of swales. Sediments seem invariable related to mesoscale shelf topography, although this relationship may be complex (Swift 1976; Swift et al. 1977, 1978; Hunt et al. 1977). Knebel and Twitchell (1978) examined the relationship of heavy mineral suites with topography in Area B. Hornblende dominated mineral suites were found primarily in swales and medium-fine sand flats and opaque or garnet mineral dominance was found on the terrace and ridges, where coarser sediments are found.

Organic carbon concentrations were also similar to those reported in literature (Hathaway 1971; Emery and Uchupi 1972; Hatcher and Keister 1976). Shelf sediments in the study area contain less than 5 mg/g total organic carbon except in the New York Bight apex and upper end of the Hudson Shelf Valley where concentrations up to 50 mg/g are found (Hatcher and Keister 1976). In those sediments containing less than 1% silt and clay, which includes most of the shelf, very low concentrations of 1 mg/g or less of organic carbon are found. However, where silt and clay became only slightly more important, either in depressions on the shelf or at the shelf break, organic carbon concentration increases dramatically.

Kjeldahl nitrogen concentrations are more variable than grain size distribution or organic carbon concentrations, but nonetheless show a high overall correlation with organic carbon. The nitrogen data are in general agreement with those Kjeldahl nitrogen concentrations reported by Emery and Uchupi (1972). Concentrations of less than 0.2 mg/g characterize most clean shelf sands. Kjeldahl nitrogen contrations > 0.5 mg/g are rare. The nitrogen: carbon ratio is generally lower in carbon-poor, low silt and clay sediments possibly reflecting that much of the organic carbon in these sediments is in fact living. Higher C/N ratios in depositional, fine-grained sediments reflects a build up of non-living and possibly more refractory organic material.

There was no clear cut evidence of seasonal changes in sediment parameters observed over two years of sampling. To be sure, temporal variability was great but seemed to be mostly related to the great spatial heterogeneity of sediments and the fact that precisely the same location could not be resampled. Biogenic deposition and binding of fine sediments was responsible for slightly increasing the silt-clay component on the inner shelf following hypoxia in summer 1976. There was also a suggestion of progressively finer sediments at a few stations during the second year. However, sediments in seasonal samples were quite persistent and characteristic of the station. This persistence is in agreement with Stubblefield et al. (1977) who found general constancy of grain size distribution and bedforms in the shallow shelf of the New York Bight Apex, based on six quarterly observation.

Summary of Significant Findings

1. The continental shelf of the Middle Atlantic Bight is topographically complex and is covered by sandy palimpsest sediments which reflect both ancient sources and contemporary redistribution. Although the scale of spatial variation in sedimentary parameters is essentially continuous, the widespread system of ridges and swales with spacing on the order of one kilometer particularly affects the distribution of sediments. Bottom currents due to surface waves and meteorological forcing are important in resuspending sediment over most of the shelf, which disallows the accumulation of the scarce silt and clay.

2. Analyses of sediments from 52 benchmark stations show the predominance of medium and coarse sand over much of the shelf and muddy finer sands in the shelf break region, grading into predominantly silt and clay sediment on the continental slope. Silt and clay were scarce at shelf stations except in topographic depressions and at the shelf break where this component makes up 5-10% of sediments. Higher amounts were found near Hudson Canyon. The sand component of the sediments tended to be finer in topographic depressions, at the shelf break and off the southern Delmarva Peninsula.

3. Organic carbon content was closely related to the distribution of silt and clay. Thus, organic carbon concentrations were very low (< 1 mg/g) over most of the shelf but higher (1-2 mg/g) in topographic depressions and at the shelf break. Still higher concentrations (to 10 mg/g) were found in muddy, slope stations. Nitrogen concentrations were variable but correlated with organic carbon concentrations. The lower carbon: nitrogen ratios in clean sands suggests that living organisms comprise much of the organic material in these sediments.

4. Variability in grain size distribution and carbon content both among replicate samples and among seasonal samples was low at most stations. Those instances of apparently great seasonal variability could mainly be explained in terms of variability in station location or great patchiness in the local distribution of sediments.

5. The distribution of grain size and organic carbon parameters among "habitats," recognized on the basis of the distribution of benthic organisms, in two topographically complex outer shelf regions also clearly distinguish the habitats. This emphasizes the strong relationship among shelf topography and resulting hydraulic regimes, sediment grain size distribution, sediment chemistry and the biota.

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CHAPTER 6

Benthic Ecological Studies: Macrobenthos

Donald F. Boesch

Special Report in Applied Marine Science
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CHAPTER 6

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*Provided on microfiche at the end of Volume II.

CHAPTER 6

BENTHIC ECOLOGICAL STUDIES: MACROBENTHOS

Donald F. Boesch

With Contributions By

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INTRODUCTION

Studies of benthic organisms comprise the major portion of the biological investigators in the Middle Atlantic Benchmark Studies Program. These studies have covered virtually the full spectrum of organisms represented in the benthos including bacteria, foraminiferans, meiobenthos, macrobenthos, and demersal fishes. The most extensive of these investigations concerned macrobenthos and is the subject of this chapter. The macrobenthos here is operationally considered to consist of those organisms living on or in the seabed which are retained by a 0.5 mm mesh sieve. This report will further distinguish the megabenthos, arbitrarily defined as those macroorganisms captured by dredge or trawl of relatively large mesh (4 mm), and the smaller macrobenthos (*sensu stricto*) collected from grab samples through a 0.5 mm mesh sieve.

The results of repetitive sampling of macrobenthos at fixed stations over the two year study period provide the main topics of presentation. Other results to be presented were derived from studies of the distribution of benthic communities within two intensively studied areas (habitat delineation study) and *in situ* experimental studies on the colonization of sediments from which living animals have been removed (recolonization study). The general objectives of these investigations are to determine the spatial distribution patterns of macrobenthos and their relationship to potentially causative abotic and biotic factors, to describe temporal variations of the macrobenthos over the two year study period; to determine the response of the benthos to catastrophic disturbance; and to deduce the interactions of the macrobenthos with other biotic components.

Background

The macrobenthos of the Middle Atlantic Bight has been relatively little studied and the results of most studies are unpublished or incompletely published. The locations of previous quantitative studies within the study region are indicated in Figure 6-1.

Extensive samples of macrobenthos were collected on an 18 km grid throughout the study area during the Woods Hole Oceanographic Institution - U. S. Geological Survey Continental margins program. Few results have been published, although a compilation of abundance and biomass data by major taxonomic group was produced (Wigley and Theroux 1976). Extensive sampling of macrobenthos has also taken place in the New York Bight apex in the assessment of the effects of solid and chemical waste disposal. Some results have been reported by National Marine Fisheries Service (1972), Pearce et al. (1976) and Rowe (1971) and others are contained in reports in press. Regional studies of the macrobenthos of the nearshore or inner shelf have been conducted off western Long Island, northern New Jersey (Pearce 1974), and northern Virginia (Boesch 1972). Maurer et al. (1976) reported on the composition of the macrobenthos in a number of small samples from the central shelf off Delaware and synthesized the faunistic similarities of the sand fauna of the shelf off the northeastern U. S. They suggested that the shelf benthic community was temporally highly variable. Studies of shelf macrobenthos in this same region have been carried out as part of the Environmental Protection Agency's monitoring of the sludge and acid dump sites. The results of these studies have not been published although some are included in Lear, O'Malley and Smith (1977). They report alterations in the composition of the communities in regions presumed to be contaminated by the sludge as indicated by high organic carbon and trace metals in sediments.

Few published reports relate to the benthic fauna of the outer continental shelf, shelf break, and slope areas which are the central focus of this study. Pearce (1975) and Pearce et al. (1976) report some data on density and diversity from stations in 40-70 m of water off New Jersey and Long Island, some included in the area sampled in this study. He concluded that the outer shelf communities were largely similar to those of the New York Bight apex in terms of species composition, diversity, and density. The zonation of the epibenthic macrofauna, including demersal fishes, on the continental slope south of New England was reported by Haedrich et al. (1975). Their collections were made by otter trawl and include only larger megabenthos. They concluded that sharp faunal changes took place between the upper (141-285 m) and middle (393-1095 m) continental slope.

Pratt (1973) proposed a three-tiered zonation scheme for the shelf benthic fauna of the Middle Atlantic Bight: a sand fauna zone extending from the littoral zone to 30-50 m and covered by clean, dynamic sands; a central silty-sand fauna zone with sediments of somewhat greater silt and clay and organic matter concentration and including more tube-building, suspension and deposit feeders than inshore; and an outer shelf zone beyond a variable "mud-line",

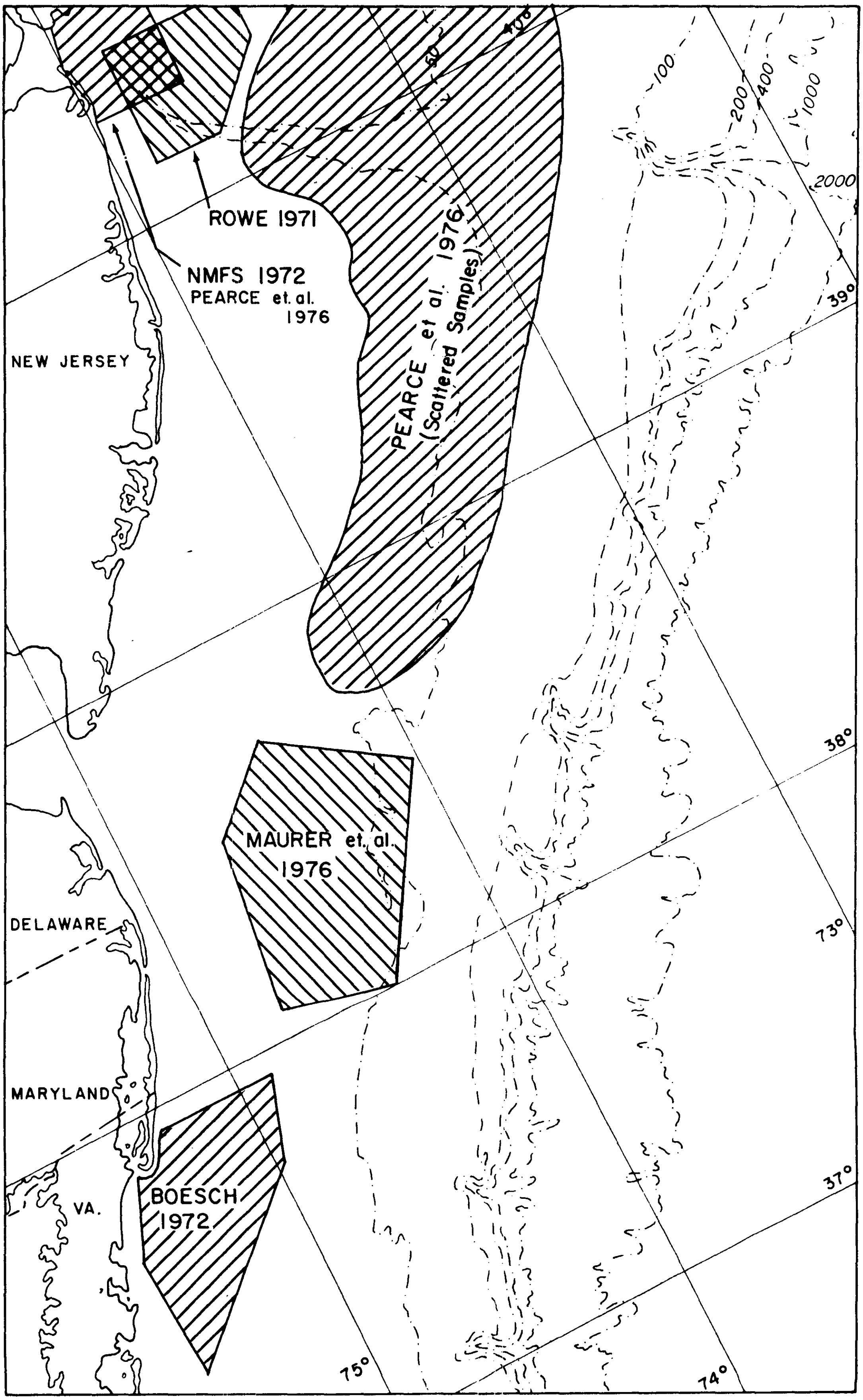


Figure 6-1. Location of previous studies of macrobenthos on the Middle Atlantic Continental Shelf. Wigley and Theroux (1976) sampled stations throughout the study area.

populated by a silt-clay fauna dominated by deposit feeding polychaetes, bivalves and echinoderms. His scheme was admittedly speculative and until the present study there was no comprehensive data base on which to base such a zonation scheme.

Findings during the first year of this study were reported in an earlier report (Boesch, Kraeuter, and Serafy 1977) and they comprise the most extensive documentation of the macrobenthos of the Middle Atlantic Continental shelf and upper slope to date. These preliminary findings were summarized:

1) Faunal changes of both macrobenthos and megabenthos were mainly continuous rather than abrupt, but five faunal zones could be distinguished: inner shelf (to 30 m), central shelf (30-50 m), outer shelf (50-100 m), shelf break (100-200 m) and continental slope (> 200 m). Shelf break and slope species assemblages were more discrete than those on the shelf.

2) This zonation pattern for macrobenthos was concordant throughout the 3 degrees of latitude represented in the study area. Assemblages within a depth zone were similar throughout the area and no strictly latitudinal trends were observed.

3) Macrobenthic communities displayed remarkably little seasonality over four seasonal sampling periods. Assemblages at specific stations generally retained qualitative similarity and consistancy of dominant species from season to season.

4) Although the biomass of macrobenthos was comparable to that reported in earlier studies in the Middle Atlantic Bight, numerical density was much higher owing to the use of finer sieve size than usually employed. Biomass of annelids and molluscs was highest on the outer shelf and in topographic depression, whereas echinoderm density was highest on the inner and central shelf. Total density of macrobenthos was highest on the outer shelf; on the continental slope biomass was one-third or less than typical on the shelf.

5) Species diversity of megabenthos and macrobenthos generally increased with depth. Highest Shannon diversity and numerical species richness of macrobenthos was found on the shelf break and continental slope and lowest on the inner shelf. Diversity on the outer shelf and shelf break was higher than previously reported.

6) Major differences occur in macrobenthic communities over short distances in relation to ridge and swale topography. Swales have generally finer sediments with more organic carbon than ridges and flanks. The benthos of swales is more abundant and has a greater biomass and species richness. Swale environments were therefore held to be relatively more valuable and susceptible shelf habitats.

7) The anoxic or hypoxic conditions of bottom waters of the central and inner shelf during the summer of 1976 resulted in mass mortalities of many megabenthic and macrobenthic species. Crustaceans and echinoderms were particularly affected.

8) Predominant abotic factors governing the distribution of the benthos include temperature and temperature constancy, sediment characteristics (grain size, organic content, etc.) and sediment mobility. These interact in a complex fashion with biotic factors to produce the observed patern of distribution and abundance.

This report relates the results of studies during a subsequent year and presents an integration of the results obtained during the two year period. The conclusions developed in the earlier report are reevaluated based both on continued sampling and new studies. In particular, results of second year studies considerably expand understanding of (1) relationship of macrobenthos to mesoscale sedimentary and topographic patterns; (2) temporal patterns and processes; (3) the response of benthos to catastrophic disturbance; and (4) biotic inter-relationships of the macrobenthos, particularly with the meiobenthos and demersal fishes.

METHODS

Sampling

Macrobenthos

Repetitive sampling for macrobenthos was accomplished at 52 stations over the two years of study (Figure 6-2). The rationale for selection of these stations and general shipboard procedures were described by Boesch and Brokaw (1977) and in Chapter 2. The schedule of sampling and the number of replicate samples collected are summarized in Table 6-1. Quarterly sampling over the two year period was accomplished at 20 stations clustered in six regions of the continental shelf off southern New Jersey. Other stations were variously sampled semiannually or during only one of the years of study. Six replicate grab samples were collected at most of the stations, except during the second year when replication was reduced to four at some of the semiannual stations.

A 0.1 m^2 Smith-McIntyre grab sampler (Figure 6-3) of stainless steel construction modified to accommodate a Benthos Edgerton 35 mm camera (Model 371) and flash (Model 381) was used. The camera's shutter was activated by a bottom trip switch when the camera was approximately 1 m off the bottom, except during the last two seasonal sampling periods when a focal distance of 0.6 m was used to enhance resolution of bottom features. Good quality black and white photographs were obtained for about 90 percent of successful grab hauls. Color-positive transparencies were also obtained on hauls made for samples for sediment chemistry. Maximum depth of penetration,

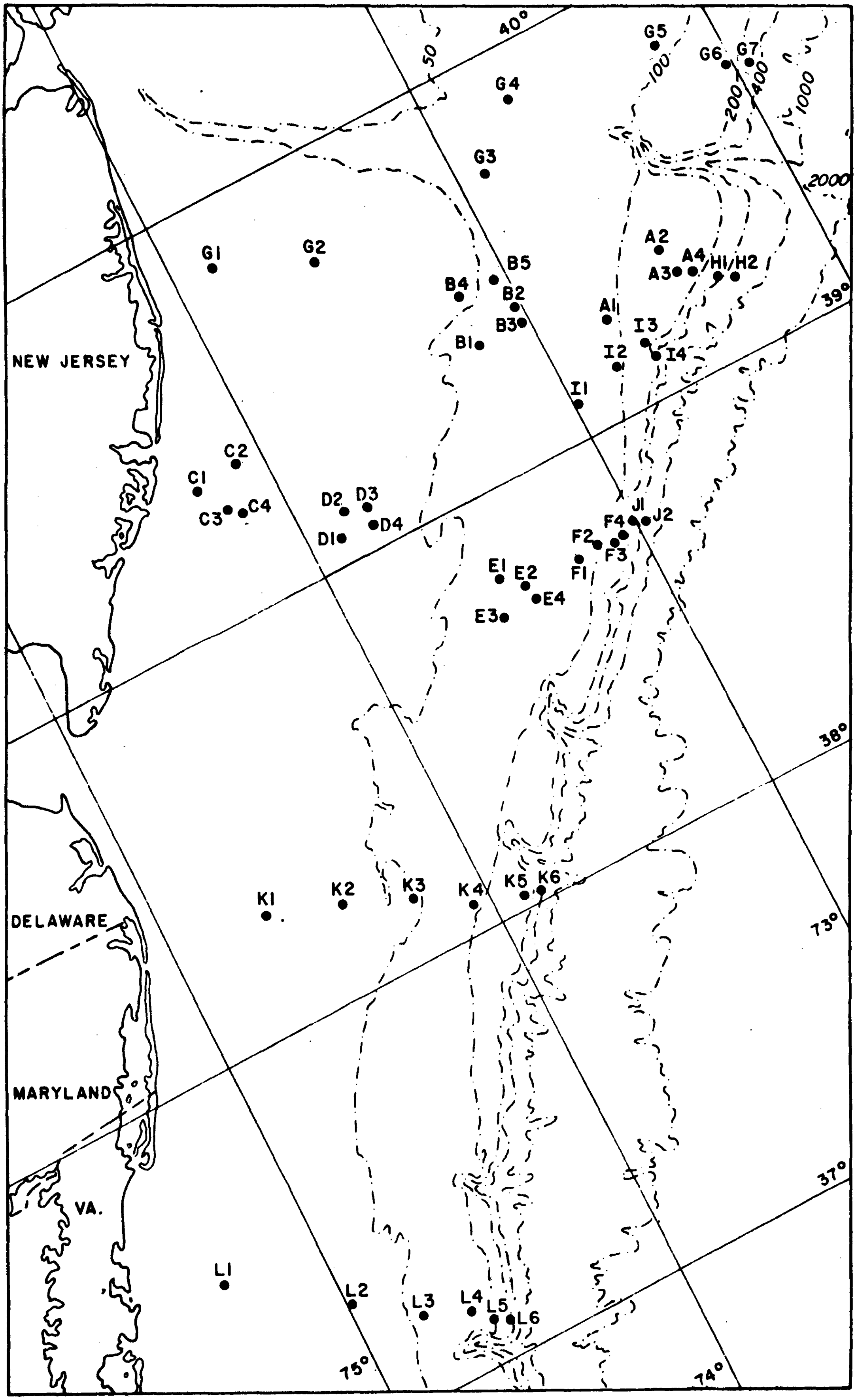
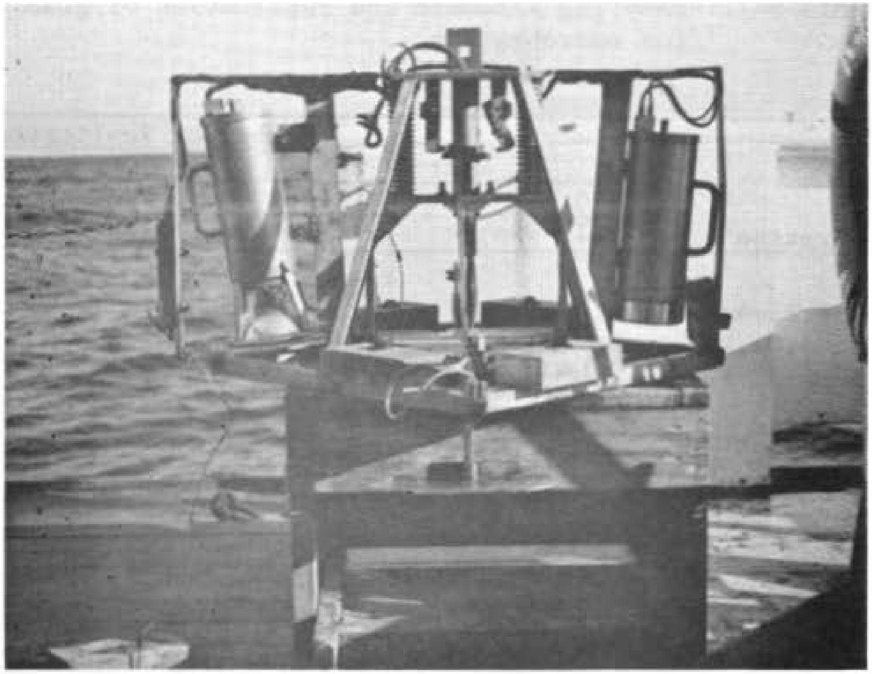


Figure 6-2. Stations sampled for macrobenthos.

Table 6-1. Sampling schedule and replication of grab samples taken for macrobenthos.

	Number of Replicates							
	Year 1				Year 2			
	1975	1976				1977		
Station	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
A1-4,B1-4, C2,C4,D1,D4 E1-E4,F1-F4	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				



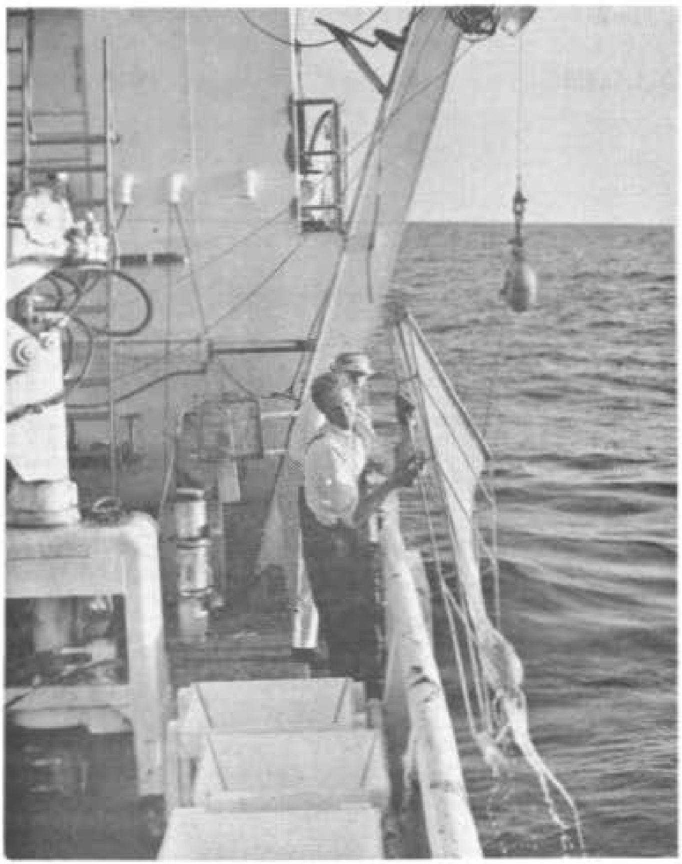


Figure 6-3. Top. Stainless steel Smith-McIntyre grab modified to accommodate a Benthos Edgerton 35 mm camera (right), strobe flash (left), and bottom trip switch (left). Bottom. Small biology trawl (SBT) or Menzies trawl being retrieved.

sediment temperature, and depth and appearance of the redox potential discontinuity (RPD) were measured and recorded for each grab sample. The Smith-McIntyre grab sampled to a sediment depth of 7-18 cm and generally depth of penetration exceeded 10 cm.

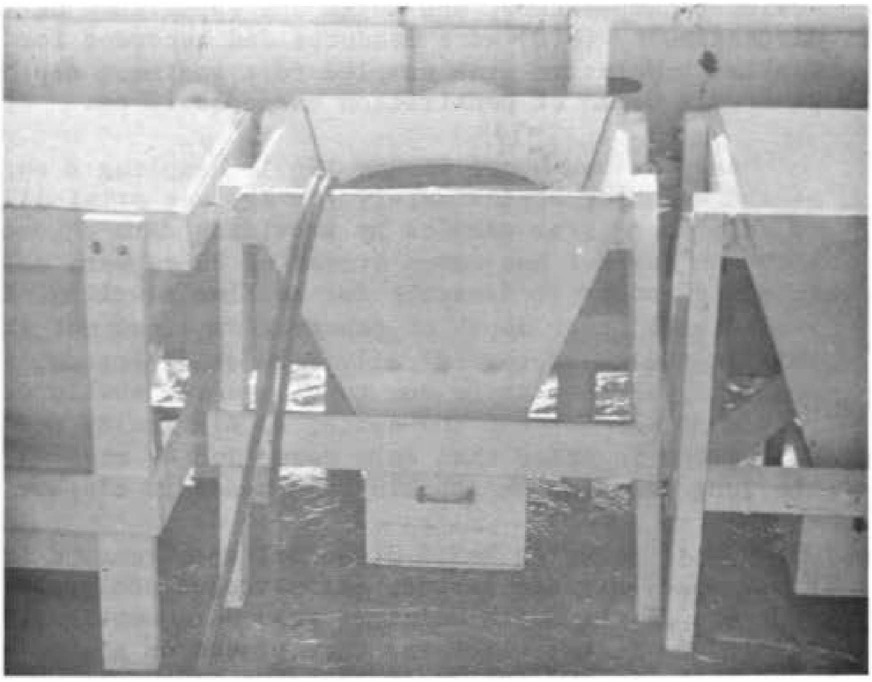
A spade box corer (Bouma 1969), sampling a surface area of 0.05 m^2 and weighing approximately 700 kg, was originally intended for use to supplement grab samples by providing data on deeper living infauna. Although several box cores exceeding 20 cm were collected, the box core did not prove feasible for routine sampling, for the following reasons: 1) poor depth of penetration often not exceeding that of grab in the characteristically firm sandy bottom, 2) the loss or winnowing of the sample due to stones and shells caught between the bottom of the box and the spade, 3) difficulty and safety risk of deployment in other than calm seas, and 4) rigging problems caused by the long lead to the shackle when spade is closed.

Small cores (2.2-3.5 diameter) were removed from each sample for grain size, organic carbon, and nitrogen analyses. The remaining contents of the Smith-McIntyre grab were emptied into a 5-gallon galvanized bucket which was then placed on a specially constructed elutriation stand (Figure 6-4). Sea water was run into the bucket and allowed to elutriate light-bodied organisms until no macrofauna was seen overflowing. The overflow was caught on a small 0.5 mm mesh Nitex screen in a frame at the bottom of the elutriator. This screen was then removed with the trapped organisms and debris and placed in a labeled cloth bag. The remaining sediment and heavy organisms in the bucket were sieved through a similar, but larger surface area, 0.5 mm Nitex screen (Figure 6-4), and the debris placed in a large cloth bag. Because of coarse sediments, a majority of the original sediment collected often remained on this screen after washing. The "light" and "heavy" fractions were anesthetized in isotonic $MgCl_2$ for about 30 minutes, then transferred to separate 30-gallon drums containing 10% buffered formalin with Rose Bengal as a vital stain.

Megabenthos

Megabenthos was sampled at nine stations: A1, B1, C2, D1, E1, F1, I1, J1, and N3 (Figure 6-5). Samples were also collected at D4 during the fall 1975 cruise.

Two pieces of equipment were utilized to sample the megabenthic fauna, a small biology (Menzies) trawl (SBT) (Figure 6-3) and a modified anchor dredge. The trawl was patterned after that used at the Duke University Marine Laboratory and was lined with 4 mm mesh fishing seine. The trawl mouth was 1 m wide and 10.5 cm high. The anchor dredge had a 39.5 cm wide and 10.5 cm high mouth (maximum cutting depth) and was modified by attaching a 1.35 m long tail section covered with a 4 mm stainless steel mesh to allow finer materials to winnow through.



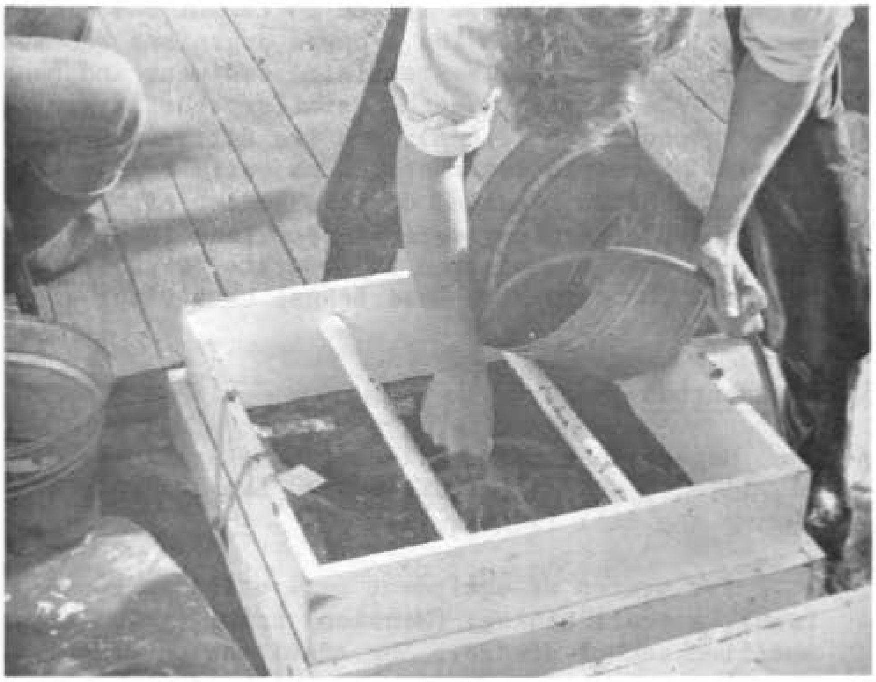


Figure 6-4. Top. Stand for elutriation of macrobenthos samples. Overflow from galvanized bucket falls down through 0.5 mm mesh screen in drawer below.
Bottom. Washing the "heavy" fraction remaining after elutriation through detachable 0.5 mm mesh Nitex screen.

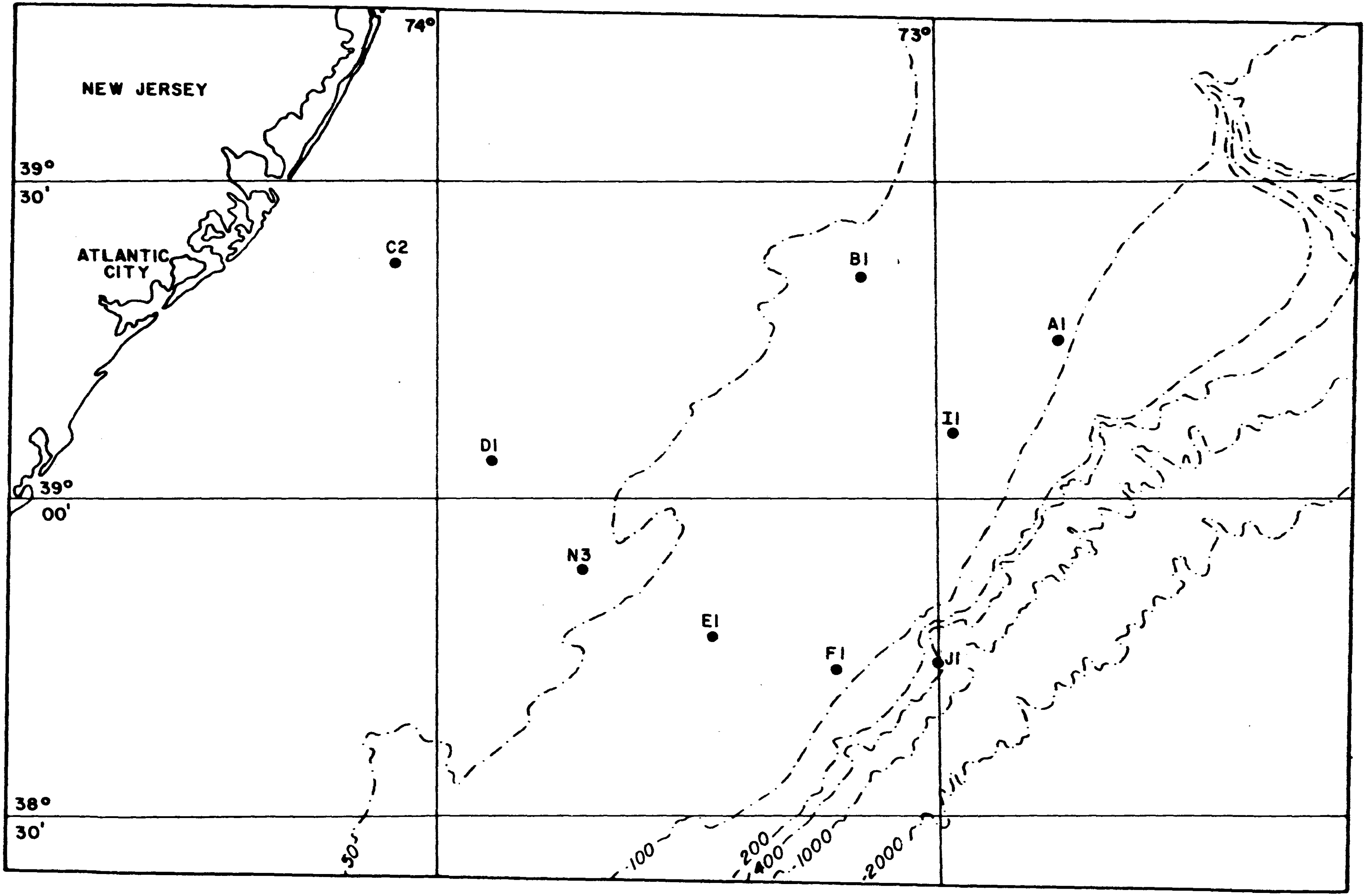


Figure 6-5. Stations sampled quarterly for megabenthos with dredge and trawl.

The two different samplers were used in order to provide accurate representation of both vagile, surface dwellers as well as the infauna. The SBT skimmed the surface layers and obtained shrimp and other motile forms as well as shallow infaunal species. The anchor dredge dug much deeper and thus sampled infaunal forms more efficiently.

Three samples were taken with both SBT and anchor dredge at each station. The only exceptions were on the first cruise when the anchor dredge was lost, when additional materials were required, when bad weather caused poor sample recovery, or at Station J1 where the muddy substrate was not suitable for anchor dredging. The SBT was towed for three minutes except at J1 where five minute tows were utilized. The anchor dredge was towed on the bottom for two minutes except where indicated. These tow times provided a sample as uniform as possible without filling the sampler, which greatly diminishes sampling efficiency and produces unknown sampling bias. A series of short tows produced more repeatable and interpretable data.

When the sampler was brought on board, the catch was placed in wooden buckets to prevent contamination of specimens to be used for chemical analysis. If the sample was large, an estimated proportion was removed for relaxing and preserving. Remainding specimens were utilized for histopathology and hydrocarbon and trace metal analysis. Small samples were preserved in their entirety except for specimens removed for histopathology and hydrocarbon and trace metal analysis which were noted on field data sheets. All animals were preserved in 10% buffered formalin. When additional specimens were required for histopathology or chemical analysis a 40-foot otter trawl was fished. Only voucher specimens were retained from the otter trawl catches and thus no data are presented for ecological interpretation.

Laboratory Procedure

Macrobenthos

Samples were first soaked for several hours in fresh water. The "light" fractions were sorted into major taxa by examination with a binocular dissecting microscope. The heavy fractions were processed by placing a small amount of sediment in a metal pan, elutriating and decanting repeatedly through a 0.5 mm Nitex screen. This material was examined as with the "light" fraction, while the remaining sediment was spread out in a white enamel pan and examined for the stained organisms with the naked eye. All organisms were sorted in major taxonomic groups, at a minimum, Annelida, Mollusca, Crustacea, Echinodermata, and other taxa, and stored in 70% ethanol.

Wet weight biomass was determined for each major group in each replicate grab sample following removal of external fluid by blotting on paper towels. The weights include skeletal material such as shells and tests and in some cases tubes and protective encrustations not easily removable.

Organisms were identified and counted for each replicate grab sample. Determinations were possible to species with most individuals; however, only genus, family, or higher taxon identifications were possible in some cases.

Megabenthos

Megabenthos samples were rinsed with fresh water to remove excess formalin and any remaining sediment. The samples were then spread in pans, the animals removed from the debris. The major groups (molluscs, echinoderms, and decapod Crustacea) and representatives of some minor groups were identified and counted while being sorted. Others were separated, placed in containers and stored or shipped to an appropriate taxonomic authority. Wet weight biomass for each species was determined euring the second year study after blotting excess liquid on paper towels. All identifications were to species unless there were taxonomic difficulties. Some of the minor groups have not been identified to species for all cruises, but are in the hands of specialists. The analyses of distribution and diversity and other data manipulations have taken these discrepancies into account.

Habitat Delineation Study

Design

The habitat delineation study was planned to delineate the mesoscale patterns of distribution of megabenthos, macrobenthos, and demersal fishes within two topographically complex regions on the outer continental shelf. For the purpose of this study the mesoscale encompasses horizontal distances of 10^2 to 10^4 m, i.e. larger than distances among replicate samples but generally smaller than distances between stations. This scale includes major topographic features of the shelf surface but is generally more extensive than the more transient features such as ripples, megaripples, and sand waves (Chapter 5). The areas chosen were portions of cluster areas B and E which included the repetitively sampled fixed stations in those areas. These areas were chosen because results of the first year's sampling showed major and consistent differences in the macrobenthos of the topographic features represented by the fixed stations and because these two areas include many of the prime lease tracts of BLM-OCS Sale 40.

The goals of the habitat delineation study were to determine whether one could extrapolate results based on limited fixed stations, to map or delineate the habitats and communities of macrobenthos and megabenthos, to uncover the causes of the mesoscale distribution patterns represented, and to relate the distribution of benthic invertebrates to the distribution of fishes and their food habits.

Both regions were stratified based on an interpretation of existing data on bathymetry and sediment distribution. Detailed charts contoured in meters developed by the U. S. Geological Survey, Woods Hole, were used. Sediment data from several stations sampled by USGS were available for area B, but sediment data for area E, except for the fixed stations, were scant. Area B was divided into six *a priori* habitat strata: the terrace atop Tiger Scarp, ridges below the scarp, shallow flanks and flats, deep flanks and flats, a muddy flat region, and swales. Area E was divided into five *a priori* strata: ridges, shallow flanks and flats, deep flanks and flats, swales, and the shelf break. Non-replicated samples of macrobenthos and megabenthos were collected at stations randomly positioned within each stratum during the fall 1976 sampling period (Figures 6-6 through 6-9).

Sampling

Locations of stations were determined by random selection of Y and Z Loran C coordinates with a certain number of stations assigned to each *a priori* stratum. At each station selected for sampling of macrobenthos, one Smith-McIntyre grab sample was collected. Sediment samples were removed and the sample was processed as usual. Stations sampled for megabenthos coincided with those sampled for demersal fishes during fall 1976. Three stations in each stratum were sampled during the night by a single three-minute SBT haul. Samples were processed as usual for the fixed station sampling. The stations sampled for megabenthos and macrobenthos did not always coincide.

Recolonization Study

Experimental Design

The recolonization study was designed to experimentally determine the response of outer shelf macrobenthos to catastrophic disturbance and the effects of incorporation of crude oil in the sediments on the recolonization process. The results would not only enhance the capability to predict the nature and duration of impacts which may be associated with oil and gas development, but would also provide insight into the role disturbances play in the natural community.

The experiment involved placement of boxes of sediment from which macroorganisms were artifically removed by freezing sediments collected *in situ* on the seabed for varying lengths of time. Sediments in some of the boxes were contaminated by mixing small quantities of crude South Louisiana oil with the sediments. Other boxes of azoic sediments were covered by screen to exclude or include epibenthic predators in order to test the hypothesis that cropping of infaunal prey by these predators had important effects on the structure of the macrobenthic community.

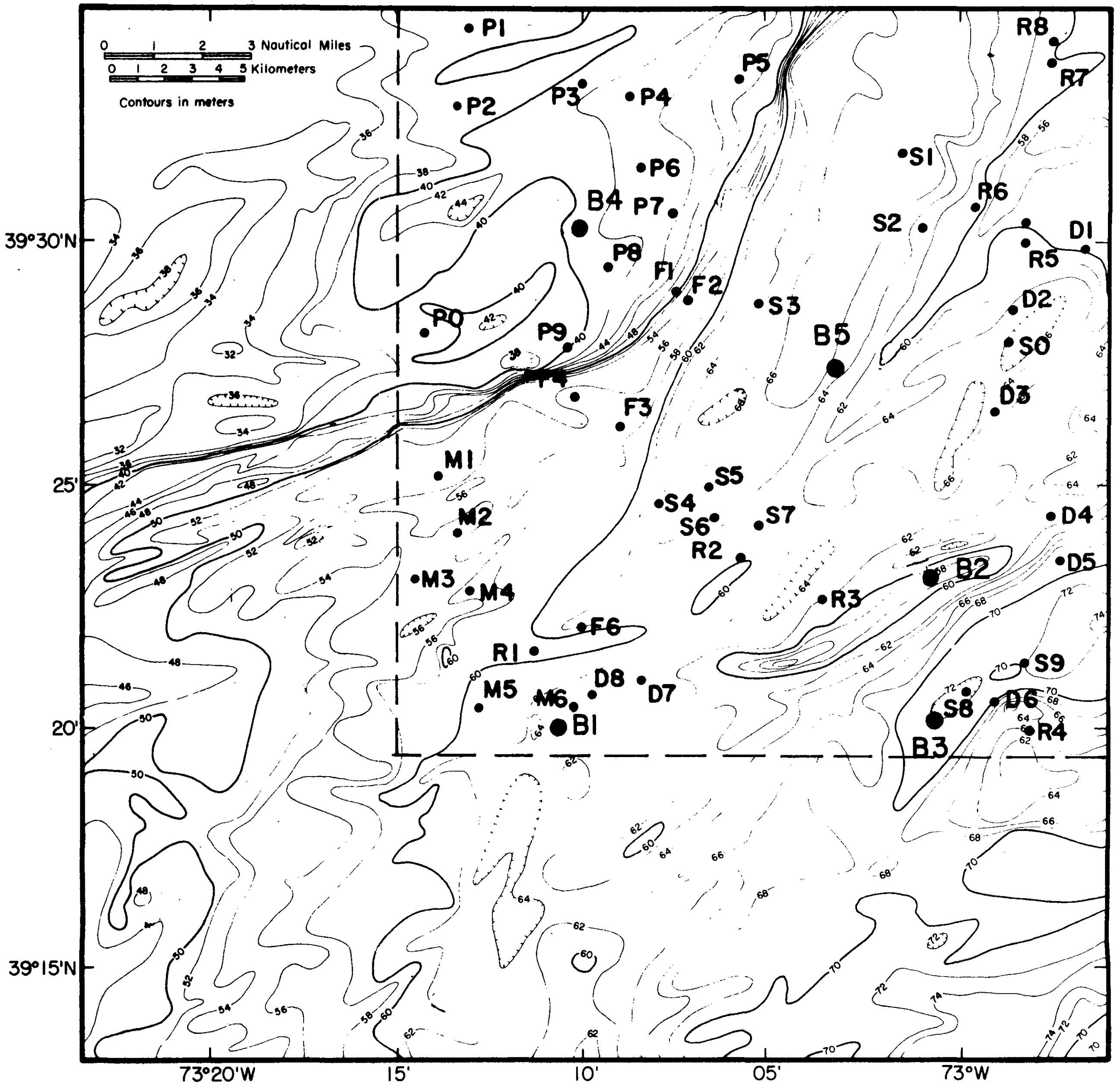


Figure 6-6. Habitat delineation study location of samples of macrobenthos located on a stratified-random basis in Area B.

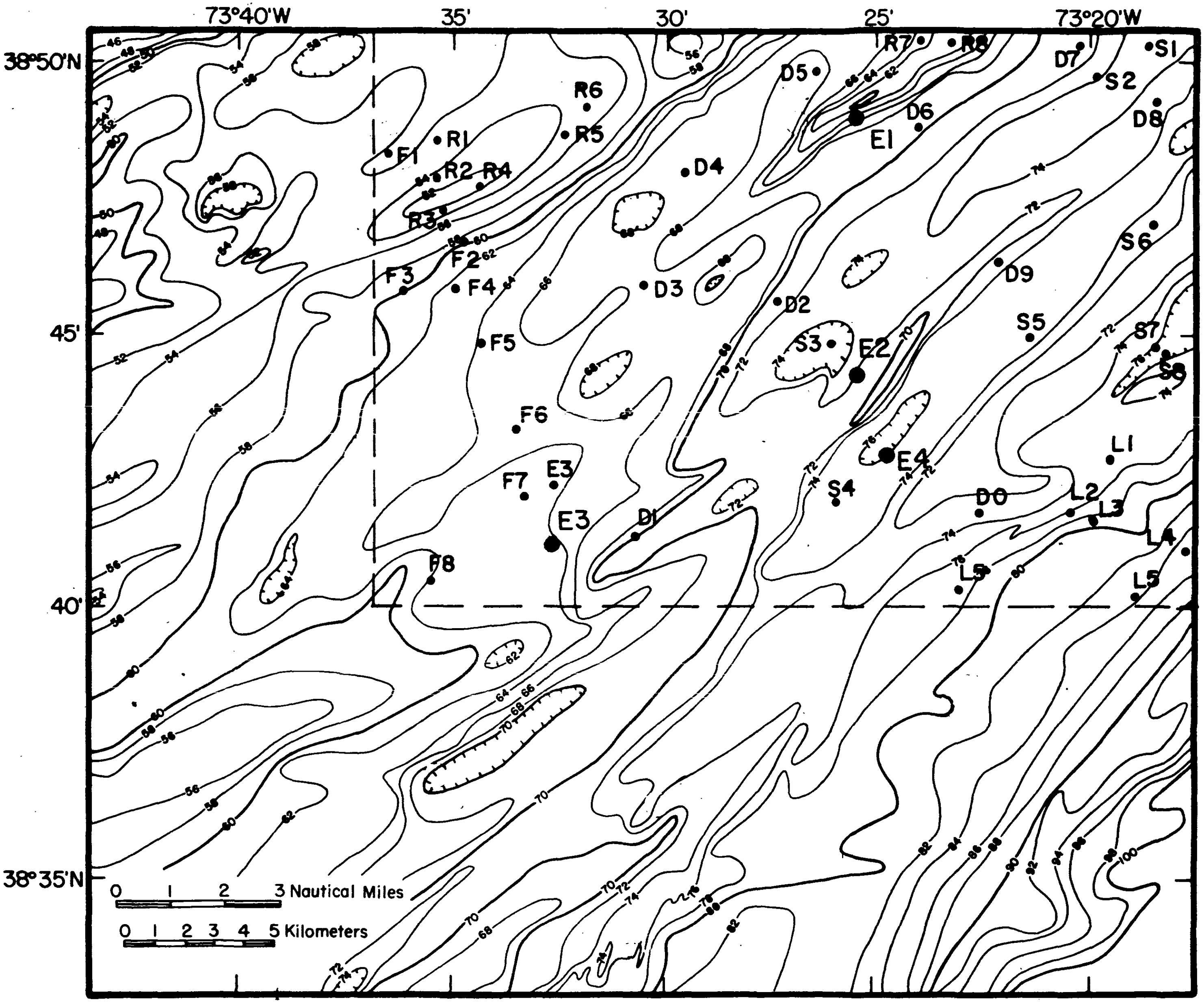


Figure 6-7. Habitat delineation study location of samples of macrobenthos located on a stratified-random basis in Area E.

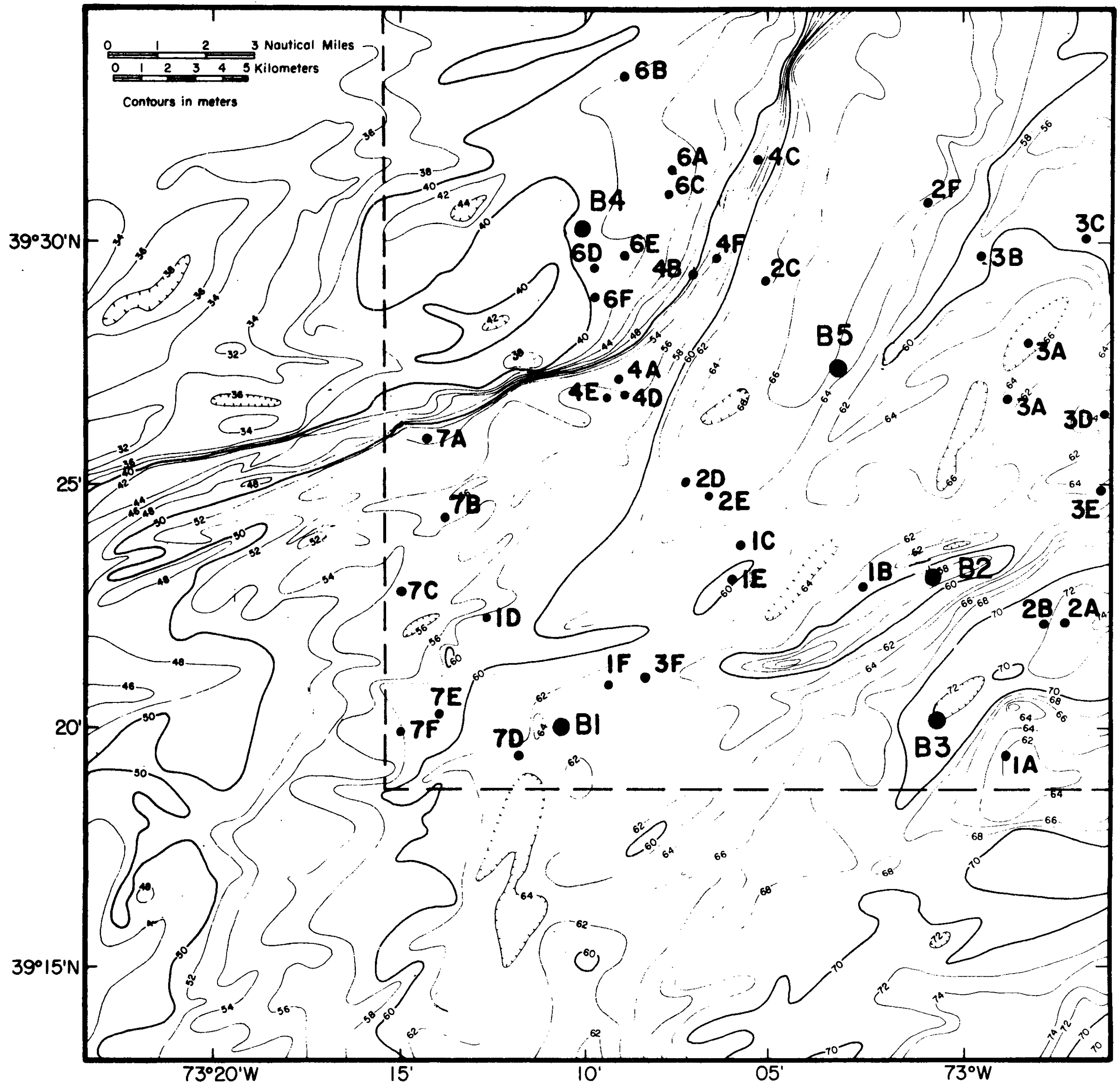


Figure 6-8. Habitat delineation study location of samples of megabenthos located on a stratified-random basis in Area B.

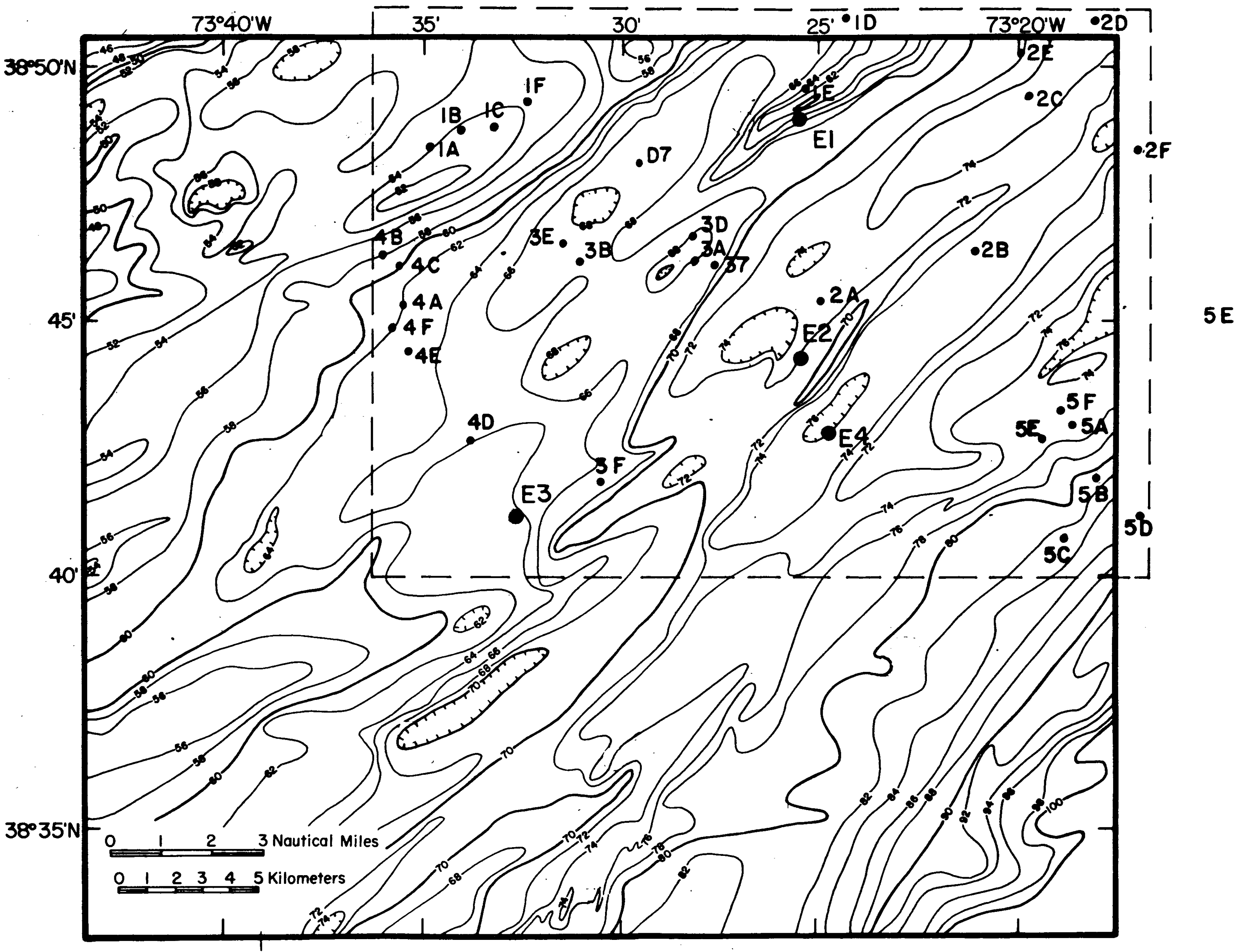


Figure 6-9. Habitat delineation study location of samples of megabenthos located on a stratified-random basis in Area E.

The site chosen for the recolonization study, Station B5, was located in the large depression in the center of area B at a depth of 65 m. The site was selected because it was argued that such depressions contained somewhat finer sediments with appreciable silt and clay content which could retain oil. Furthermore, the amphipods which are important constituents of swale communities are known to be relatively sensitive to the effects of petroleum hydrocarbons.

Boxes of sediment were scheduled to be deployed and retrieved on a staggered basis so that the time series of colonization and succession could be followed for the various experimental treatments (Table 6-2). Unfortunately, because of the problems discussed below associated with relocation of boxes and diving conditions, only seven of the 50 boxes deployed were successfully recovered, and they were recovered during August 1977.

Sediment Boxes and Treatments

Sediment was collected from B5 during the trawl cruises during fall 1976 and spring 1977 with an anchor dredge fitted with a reinforced vinyl bag. Ashore, batches of sediment were homogenized in a trough with a garden hoe. The homogenized sediment was placed in specially constructed fiberglass boxes whose inside dimensions were 50 cm x 50 cm x 15 cm deep. The boxes had skirts flared from their top to their base in order to reduce the chance that the box would be snagged by trawls or other objects dragged over the bottom. A well characterized South Louisiana crude oil (110 ml) was mixed into the sediment placed in those oil treatment boxes; yielding an expected concentration of approximately 2 mg/g dry weight of sediment.

In some azoic control boxes, layers of fluorescent dyed sand were placed in order to observe the extent of bioturbation and physical sediment mixing.

Sand particles were acid-cleaned with concentrated nitric acid, rinsed in distilled water and air dried. These sands were mixed with a small amount of fluorescent alkyd enamel, dried, and resieved to remove aggregated particles larger than 1 mm. Three colors were used, blaze orange, horizon blue, and saturn yellow. Thin layers of the colored sand were placed in certain boxes filled with natural sediment. The top layer of colored sands was covered with at least 1 cm of natural sediment. Cores (22 mm diameter) were taken to determine the vertical distribution of particles, but further compaction probably took place due to reorientation of the grains when the containers were placed in water.

Some boxes were loosely covered with 10 mm mesh screen to exclude large epibenthic predators. One or two specimens of the most common predatory asteroid at B5, Leptasterias tenera, were added just prior

Table 6-2. Description and status of boxes of sediments deployed during recolonization experiment. (NR=not recovered).

Treatment	Date Deployed	Box Number	Status
Azoic control	21 Nov. 76	A1	NR
Azoic control	1 Dec. 76	A2	NR
Azoic control	21 Nov. 76	A3	NR
Azoic control	21 Nov. 76	A4	NR
Azoic control	21 Nov. 76	A5	NR
Azoic control	1 Dec. 76	A6	NR
Azoic control	1 Dec. 76	A7	Recovered 13 Aug. 77
Azoic control	1 Dec. 76	A8	NR
Azoic control	21 Nov. 76	A9	NR
Azoic control	1 Dec. 76	A10	Recovered 13 Aug. 77
Oiled azoic	2 Dec. 76	01	NR
Oiled azoic	1 Dec. 76	02	Cover not removed
Oiled azoic	2 Dec. 76	03	NR
Oiled azoic	1 Dec. 76	04	Cover not removed
Oiled azoic	1 Dec. 76	05	Cover not removed
Oiled azoic	2 Dec. 76	06	NR
Oiled azoic	2 Dec. 76	07	NR
Oiled azoic	2 Dec. 76	08	NR
Oiled azoic	1 Dec. 76	09	Cover not removed
Oiled azoic	1 Dec. 76	010	Cover not removed
Screened azoic	1 Dec. 76	S1	NR
Screened azoic	1 Dec. 76	S2	NR
Screened azoic	1 Dec. 76	S3	NR
Screened azoic	1 Dec. 76	S4	NR
Screened azoic	1 Dec. 76	S5	NR
Screened azoic	1 Dec. 76	S6	Recovered 13 Aug. 77
Azoic control	4 June 77	A11	Located & covered but not recovered
Azoic control	4 June 77	A12	NR
Azoic control	4 June 77	A13	NR
Azoic control	4 June 77	A14	Recovered 16 Aug. 77
Azoic control	4 June 77	A15	Located & covered but not recovered
Azoic control	4 June 77	A16	NR
Azoic control	4 June 77	A17	NR
Azoic control	4 June 77	A18	Recovered 16 Aug. 77
Oiled azoic	4 June 77	011	NR
Oiled azoic	4 June 77	012	NR
Oiled azoic	4 June 77	013	NR
Oiled azoic	4 June 77	014	NR
Oiled azoic	4 June 77	015	NR
Oiled azoic	4 June 77	016	NR
Oiled azoic	4 June 77	017	NR
Oiled azoic	4 June 77	018	NR

Table 6-2. (concluded)

Treatment	Date Deployed	Box Number	Status
Screened azoic	4 June 77	S7	Located & covered but not recovered
Screened azoic	4 June 77	S8	NR
Screened azoic	4 June 77	S9	NR
Screened azoic	4 June 77	S10	Recovered 16 Aug. 77
Screened *Leptasterias* enclosed	4 June 77	E1	Located & covered but not recovered
Screened *Leptasterias* enclosed	4 June 77	E2	NR
Screened *Leptasterias* enclosed	4 June 77	E3	NR
Screened *Leptasterias* enclosed	4 June 77	E4	Recovered 16 Aug. 77

to deployment of some of the screened boxes during June 1977 as predator enclosure experiments.

Sediment samples were removed from each box for analysis of grain size, organic carbon and nitrogen, trace metals, and hydrocarbons. Boxes were then placed in a freezer truck and covered by dry ice. The boxes were kept in the truck at least overnight and were checked for complete freezing. Boxes containing frozen sediment were then placed on ship for deployment.

Deployment and Recovery

Professional divers were employed for placement and retrieval of the boxes. Divers used mixed gases (nitrogen, oxygen, and helium) and short bottom time (20 minutes or less) schedules. Time-consuming decompression on ascent, followed by recompression with prolonged decompression in a chamber on board the research vessel were required. During November and December 1976, divers placed individual boxes fitted with anchoring rods in the four corners on the bottom. During June 1977, boxes were placed in anchored racks of four boxes each in order to facilitate recovery. Boxes were deployed by lowering them to the bottom covered with lids to prevent washout of sediments. These lids were removed by divers.

Rough seas which made diving unsafe, frequently strong currents, and limited visibility on the bottom at 65 m combined to make deployment and recovery difficult. Furthermore, acoustic pingers marking the location of the boxes placed during the fall of 1976 either failed or were lost. Plans to recover boxes placed in the fall during June 1977 were thwarted because of inability to locate the boxes. Boxes placed during June 1977 were, however, located acoustically. One rack containing four boxes (two azoic controls and two screened boxes) was recovered after a diver secured a lid over the boxes and attached a lifting bridle. Another rack was secured but the lifting line parted because of rough seas. Three boxes deployed in the fall were also discovered by divers and recovered individually after securing lids and attaching lifting bridles. Attempts made early in December 1977 to recover boxes failed when, after fixing the pinger signal, divers were unable to safely descend to the bottom because of the moderately heavy seas prevailing.

On recovery, the contents of the box were sampled by inserting a template partitioning the contents with a 6 by 6 array of equal quadrants each 8 by 8 cm square. Certain squares were used for collection of sediment samples for grain size determination, chemical analyses, foraminifera, bacteriological characterization, and fluorescent particle distribution. The contents of the rest of the quadrants were spooned into jars labeled so that the position of the quadrants within the box was referenced. These samples were preserved with 10% buffered formalin. These samples were sieved at the shore laboratory through a 0.5 mm sieve for macrobenthos assessment.

Cores collected for fluorescent particle distribution were kept frozen until prepared for analysis. Cores collected before deployment and after recovery were extruded and allowed to thaw. The thawed core was cut in half and a portion was removed from the center of each half at 1 cm intervals from top to bottom. These samples were placed in plastic petrie dishes and dried at 60°C. The entire sample was counted except for those samples where particles were numerous, and then a subsample was placed in a new petrie dish. After counting, the dishes were weighed, the sediments removed, and the dish reweighed to determine the weight of sediments. Concentration of particles was expressed as number of dyed particles per gram of sediment.

Data Analysis

Data Processing

Abundance and biomass data for megabenthos and macrobenthos were entered on specially designed coding forms. Taxa were encoded using the 10-digit NODC code based on a scheme originally developed by (Swartz, et al. 1972). Once the data were machine readable, listings were carefully edited by the responsible technical staff and corrected data were entered into a tape file (Appendix IV). Subsequent listings and analyses were performed using these tape files.

Multivariate Analyses

Patterns of community similarity and species distribution were determined using numerical classification (cluster analysis) and ordination, as appropriate. Numerical classification attempts to optimally group entities whereas ordination develops a spatial model of the relationship among entities (Clifford and Stephenson 1975, Pielou 1977). Classification is usually more efficacious with large heterogeneous data sets where it is necessary to simplify relationships. Ordination is useful when the range of variation of entities is limited (more homogeneous data sets) and when it is helpful to view environment as gradational rather than discrete.

Data Reduction

Because the total number of species in any given set was too large for practical computation involved in classification or ordination, it was necessary to reduce the data to a subset of $\leq$ 200 species, an arbitrary, practical limit set for economy of computation time. Several criteria were used to accomplish this data reduction in various analyses. First, colonial species which were not enumerated were eliminated as were taxa not separated to species. Secondly, a score for each remaining species in the data set was computed as the sum of the number of stations at which it occurred, the number of replicates in which it occurred divided by the number of replicates, the number of stations at which it occurred in three or more replicates, and the number of replicates in which its abundance was $\geq$ 10, divided by six. Thus, this score reflects the composite ubiquity, constancy, and abundance of each species. The species were ranked by the score sum, and only data on the top or ranked species were selected from the total data set.

Numerical Classification. Normal classifications of collections and inverse classifications of species were produced for various data sets of mega- and macrobenthos using the VIMS program COMPAH. Algorithms used include, except where indicated, a combination of either log-transformation (log x+1) or square root transformation of species abundance, interentity resemblance expressed by the Bray-Curtis similarity measure, and either group-average or flexible sorting (Clifford and Stephenson 1975, Boesch 1977). Thus, the classifications are polythetic, agglomerative hierarchies based on quantitative data.

The Bray-Curtis similarity measure can be expressed as:

$$S_{jk} = 1- \frac{\sum_i |x_{ji}-x_{ki}|}{\sum_i (x_{ji}+x_{ki})}$$

where S_{jk} is the similarity between entities j and k; x_{ji} is the abundance of the i-th attribute for entity j; and x_{ki} the abundance of the i-th attribute for entity k. In the case of normal analysis (classification of collections) the collections are the entities and the species are attributes. In inverse analyses (classification of species) the species are the entities with collections as attributes.

The sorting strategy determines how the various entities are hierarchically grouped based on their similarities. The results of hierarchical classification are usually depicted in the form of a dendrogram. Group-average sorting was employed when small numbers of stations were being classified because it has desirable space-conserving properties. However, when large numbers of entities are considered, group-average sorting has a tendency to produce undesirable chaining in the hierarchical clustering route. In this case entities are fused to a few nuclear groups one at a time rather than forming new groups. This results in classifications in which many entities are not effectively clustered but must be considered as individuals. Therefore, when large numbers of entities were classified, as in the case of most inverse analyses, the space-dilating flexible sorting strategy was used to induce more discrete groupings. With this strategy, the intensity of clustering can be varied by varying the cluster intensity coefficient β. In these applications β was set at -0.25 which effects moderately intense clustering.

Nodal Analysis. Normal and inverse classifications were cross-related in order that the collection groups might be described in terms of their characteristic species and the species groups described in terms of the patterns of occurrence over the collection. Results of these comparisons, termed nodal analysis, were expressed in nodal diagrams (Boesch 1977). Coincidence was expressed in terms of nodal constancy, fidelity, and abundance concentration.

Simply stated, constancy is the degree to which a species is consistently found in a habitat. Highly constant species are found in most or all samples collected within the habitat. However, constancy implies nothing about the abundance of the species. In the context used here, group constancy refers to the average constancy of species in a species group in the collections within a habitat as defined by a site group. Constancy of species in a group within a collection group was computed as:

$$c_{ij} = a_{ij}/(n_i n_j),$$

where a_{ij} is the actual number of occurrences of members of species group i in the collection group j and the n_i and n_j are the numbers of entities in the respective groups. The index will take a value of 1 when all species occurred in all collections in the group and 0 when none of the species occurred in the collection.

Fidelity, a concept long in use in community ecology (Fager 1963; Westhoff and van der Maarel 1973), is the degree to which a species selects or is restricted to a habitat. Species with high fidelity, or faithful species, are found rarely outside of their preferred habitat. As with constancy, fidelity is qualitative and implies nothing about patterns of abundance. Group fidelity refers to the average fidelity of species in a species group in the collections within a habitat (site group) relative to the collections from all other habitats (site groups) sampled. The fidelity of species group i in collection group j was defined as:

$$F_{ij} = (a_{ij}\sum_j n_j)/(n_j\sum_j a_{ij})$$

using the same terms as in the constancy index. This index is unity when the constancy of a species group in a site group is equivalent to its overall constancy, greater than 1 when its constancy in that collection group is greater than that overall, and less than 1 when its constancy is less than its overall constancy. The significance of the deviation of the number of occurrences of members of a species group from that expected within a collection group assuming even distribution was tested by applying a chi-square test.

Some species may have high constancy in a range of habitats, and thus low fidelity, but be much more abundant in one habitat than elsewhere. To describe this aspect of distribution, abundance concentration was measured. Abundance concentration is computed for each species for each collection group by dividing the mean abundance of the species in the collection group by its mean abundance overall. These ratios are averaged over all species in the species group.

Ordination. Reciprocal averaging ordination (Hill 1973) was employed on reduced sets of square root transformed data. This technique, also known as correspondance analysis (Chardy, Glemarec and Laurec 1976), is an eigenvector method which seeks to maximize the amount of variation explained by initial axes derived from the complex species x collections space. Reciprocal averaging is particularly appealing because it is less prone to distortion (nonlinearity of linear factors) characteristic of most ordinations of ecological data (Gauch et al. 1977) and because it produces both normal and inverse ordinations in the same space. Thus, it is possible to explain the pattern of similarity among collections directly in terms of the species responsible for those patterns.

Computations involve extraction of eigenvectors and determination of collection and species scores on successive axes of variation. The program ORDIFLEX of the Cornell Ecology Program Series (Gauch 1977) was used to execute reciprocal averaging ordination.

Species Diversity

Species diversity was measured by the commonly used index of Shannon (Pielou 1975), which expressed the information content per individual. The index denotes the uncertainty in predicting the specific identity of a randomly chosen individual from a multispecies assemblage. The index H' is given by:

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

where s = number of species in the sample and p_i = proportion of the i-th species in the sample.

As considered above, species diversity is a composite of two components: species richness (the number of species in a community) and evenness (how evenly the individuals are distributed among the species). Species richness was measured in terms of area (areal richness) simply by the number of species in collections of standard area (0.6 m^2 or 0.4 m^2) and also as standardized in terms of numbers of individuals (numerical richness). Numerical richness was expressed using Hurlburt's (1971) modification of Sanders' (1968) rarefaction technique, by which the number of species in a rarefied sample of given size in terms of number of individuals is computed based on known abundance relationships. For a given sample size n the expected number of species is:

$$E_{S(n)} = \sum_{i=1}^{s} \left[\frac{\binom{N-N_i}{n}}{\binom{N}{n}} \right]$$

where N is the number of individuals, s is the number of species in the collection, and N_i is the number of individuals of the i-th species. In this case a sample size of 500 individuals was used since the number of specimens collected exceeded this at almost all of the stations.

Evenness was reflected by the ratio of Pielou (1975) expressed as

$$J = H'/\log_2 s$$

RESULTS

Bottom Photographs

The extensive bottom photographs taken during the two years of sampling serve as valuable tools in interpretation of the sedimentology and ecology of the benthos in the Middle Atlantic Bight. Selected photographs taken during the first year sampling were presented by Boesch et al. (1977) to illustrate salient bottom features and characteristic large epibenthos.

Over 580 black and white negatives and 360 color transparencies were obtained during the second year of this study. Photographs taken during fall 1976 and winter 1977 were exposed at a focal distance of

1.0 m. At this distance, the field of view was approximately 1.0 x 1.5 m, and this only enabled resolution of gross sediment surface features such as ripples, hummocks, and shell and gravel deposits and moderate to large epibenthos such as asteroids, echinoids, decapod crustaceans, and anthozoans. During spring 1977 and summer 1977 sampling, the focal distance was reduced to the limits of the camera (0.6 m) which resulted in a wide-angle field of view approximately 0.5 x 0.75 m. This enabled resolution of the smaller epifauna and the tubes and other surface biogenic structures of the infauna. Similarly, the fine-scale surface features, such as the presence of a flocculent surface veneer, could be better resolved.

The photographs were qualitatively helpful in a variety of ways as supplemental information to the quantitative species and sediment data. They enabled estimation of the composition and abundance of the epibenthic community and the infaunal commnity not adequately sampled by other gear (e.g. deep burrowing cerianthid anemones and bivalves). The photographs showed features of the sediment surface indicating sediment movement (e.g. ripples), biodeposition, bioturbation, and the presence of coarse substrate material, such as shell or gravel.

The photographs were particularly helpful in understanding the ecological role of substrate mobility. From inspection of the prevalence and nature of ripple marks one is able to get an impression of the bathymetric and seasonal distribution of mobilized sediment. For example, ripple marks on the outer shelf (>50 m) were generally only well developed during the winter, a result of increased frequency and severity of cyclonic storms (Butman et al. 1977). Furthermore, storm generated ripples degrade rather quickly (Butman et al. 1977), thus the presence of well formed ripples is indicative of recent mobility. The photographs were also useful in explaining between-replicate variations in grain size parameters or biotic composition. The photographs also provided insight to aspects of the biology of various benthic animals visible including living position, spatial dispersion and feeding behavior.

Several representative photographs are presented in Figures 6-10 - 6-22 which illustrate the cross shelf changes in the benthic environment as well as some of the common animals found in the study area.

The inner shelf sediments (<30 m) generally consist of medium to medium-coarse sand with only a trace of silt and clay (Figure 6-10, top). These sands are dynamic in nature and are constantly shifted and resuspended by oscillatory currents generated by surface waves. Species inhabiting these sediments were predominately small infauna or large motile predators such as crabs or sea stars (Figure 6-10, top). However, in July and August of 1976 a drastic decrease in dissolved oxygen caused severe mortalities of benthos on the inner shelf off New Jersey (Boesch et al. 1977 and below). This event caused considerable changes in the benthic communities and surface sediments. This

(TEXT CONTINUES ON PAGE 6-42)

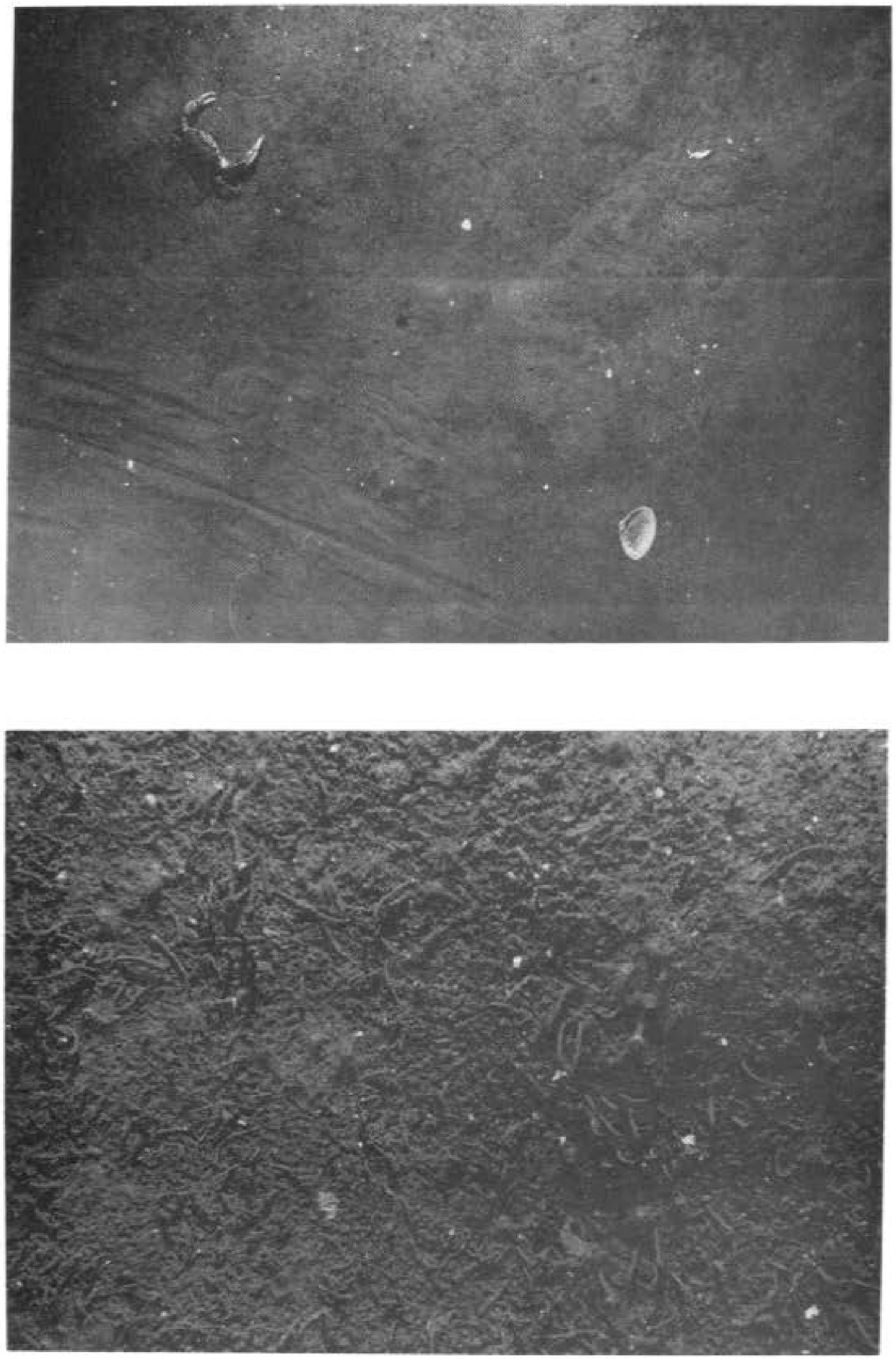
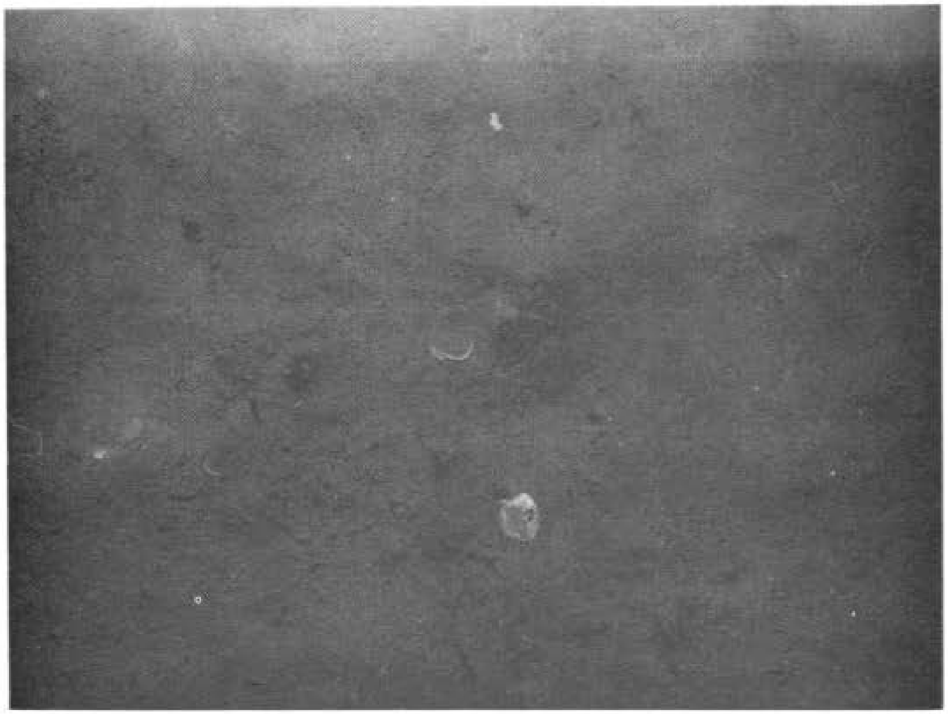


Figure 6-10. Top. Station C2, inner shelf off southern New Jersey, 26m, on 5 November 1975 about 9 months before hypoxia (1.0 m focal distance). Medium-coarse sand with no evidence of large tube builders. Predators such as the crab Ovalipes ocellatus, sea star Asterias forbesi, and a small flounder are seen in the photograph as well as the trail of the horseshoe crab Limulus polyphemus. Bottom. Station C2 on 30 May 1977, about 9 months after hypoxia (0.6 m focal distance). Bottom has been stabilized by tubes of Spiophanes bombyx and ampharetid polychaetes. Many cerianthid anemones are present and no large predators are seen.



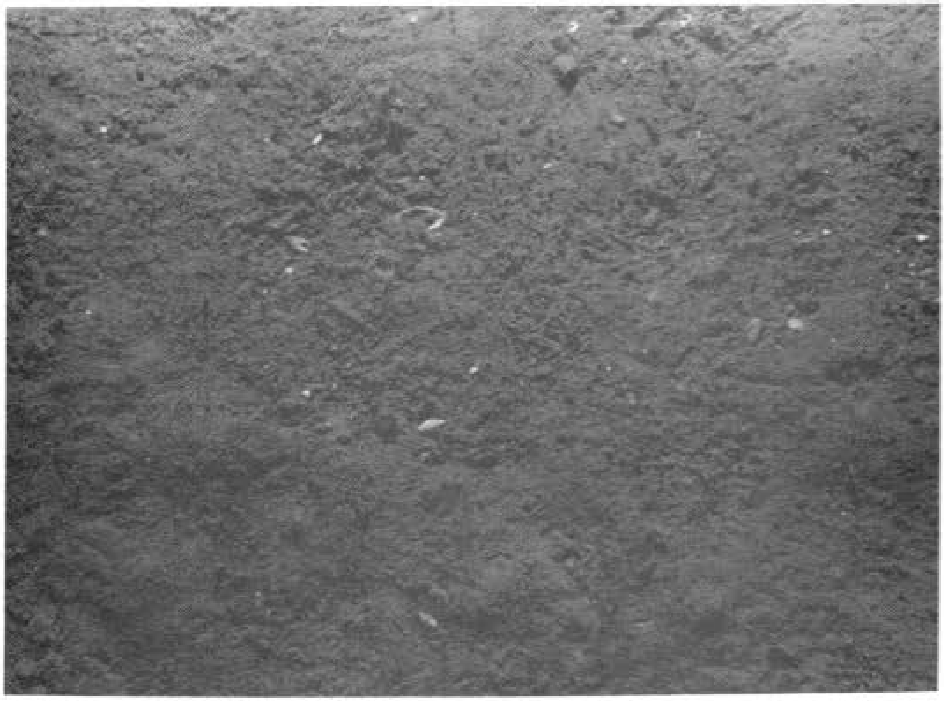


Figure 6-11. Top. Station C4, inner shelf swale off southern New Jersey, 34 m, on 16 June about 1 month before hypoxia (1.0 m focal) distance. Medium-fine sand with 5% silt-clay. Many cerianthid anemones, 1 Asterias forbesi, 1 hermit crab, several worm tubes and fecal castings can be seen.
Bottom. Station C4 on 12 August 1978 about 1 year after hypoxia (0.6 m focal distance). Tubes and fecal castings are more apparent, but cerianthid abundance is unchanged.

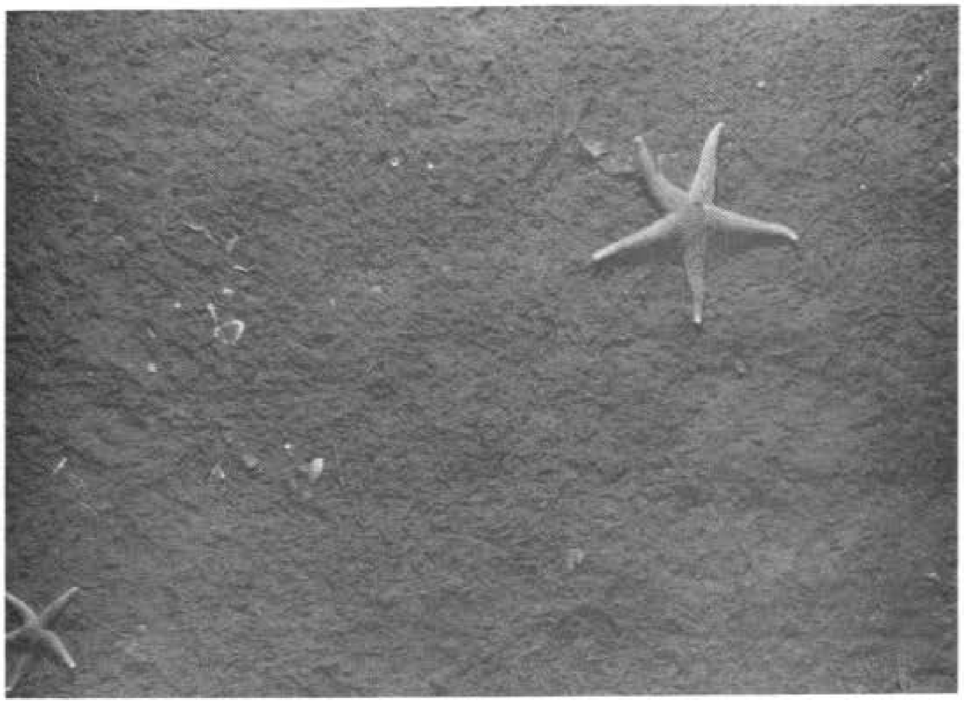


Figure 6-12. Top. Station D1, central shelf ridge off southern New Jersey, 31 m, on 12 August 1977 (0.6 m focal distance). Medium sand with scattered tubes. Large crab, Cancer irroratus, appears to be leaving an excavation. Bottom. Station D4, central shelf swale off southern New Jersey, 49 m, on 31 May 1977 (0.6 m focal distance). Fine sand with reworked surface sediments, many worm tubes, and two large Asterias vulgaris.

Figure 6-13. Top. Station G2, central shelf off northern New Jersey, 30 m on 13 August 1977, about one year after being stressed by hypoxia (0.6 m focal distance). Medium-coarse sand with cerianthid anemones, worm tubes, and biodeposits.
Bottom. Station L2, central shelf off Virginia, 43 m. Sands are finer than at comparible depths to the north and there are many worm tubes and evidence of reworked surface sediments.

Figure 6-14. Top. Station E1, outer shelf ridge off southern New Jersey, 61 m, on 9 February 1977 (1.0 m focal distance). Medium sand with ripples characteristically present during winter; shell fragments in troughs. Bottom. Station E1 on 11 August 1977 (0.6 m focal distance). There are no obvious ripples and a thin veneer of fine sediment seems to be present.

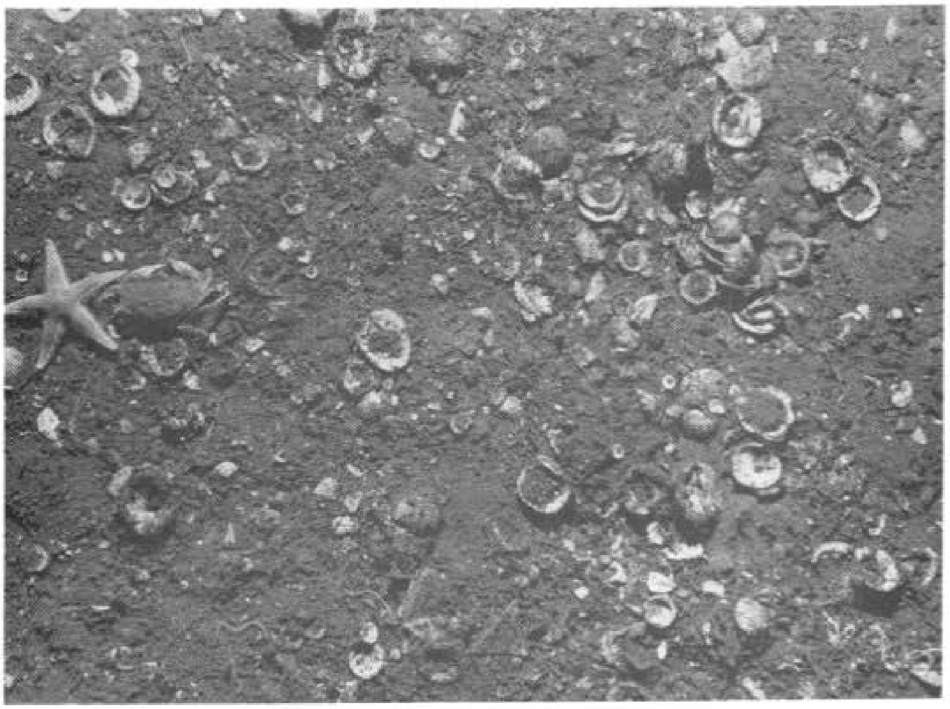


Figure 6-15. Top. Station E4, outer shelf swale off southern New Jersey, 80 m, on 11 August 1977 (0.6 m focal distance). Medium slightly muddy with many shells principally of Cyclocardia borealis. Numerous surface dwelling polychaetes, probably Typosyllis tegulum, Cancer irroratus, and the sea star Astropecten americanus are visible.
Bottom. Station G3 in the Hudson Shelf Valley off northern New Jersey, 73 m, on 14 August 1977 (0.6 m focal distance). Sediments are mixed slightly muddy sands. Amphipod tubes, principally of Ampelisca agassizi, Unciola irrorata, and Erichthonius rubricornis, form a surface mat interspersed with hummocks of biogenically reworked sediment.

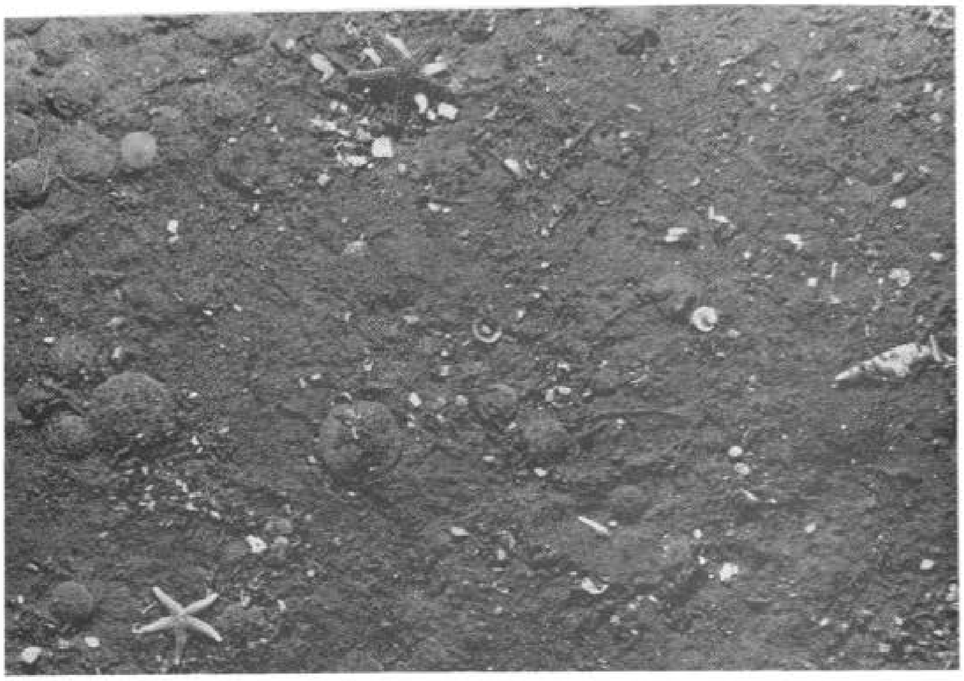


Figure 6-16. Top. Station B4 shelf on the terrace above Tiger Scarp off central New Jersey, 40 m, on 6 August 1977 (0.6 m focal distance). Very dynamic sediments with medium-coarse sand and gravel. A small Cancer irroratus, Asterias forbesi, and the shrimp Dichelopandalus leptoceras can be seen in the upper right.
Bottom. Station B2, outer shelf ridge off central New Jersey, 62 m, on 6 August 1977 (0.6 m focal distance). Dynamic environment with medium sand. Numerous sand dollars, Echinarachnius parma, partially covered with sediment can be seen along with a single Asterias vulgaris (lower left) and A. forbesi (upper center).

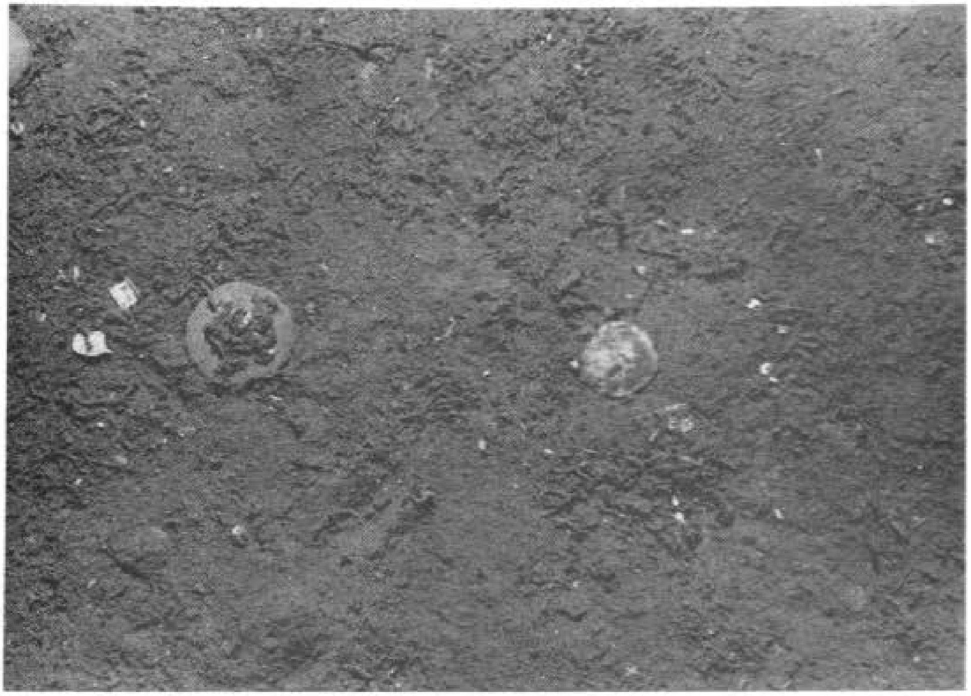
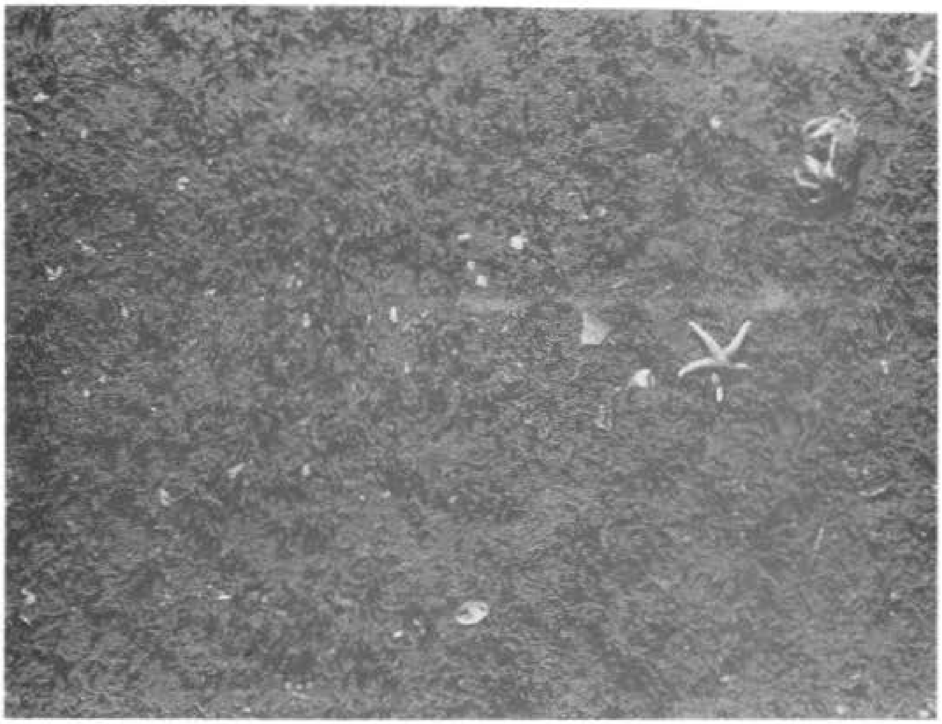


Figure 6-17. Top. Station B1, outer shelf flat off central New Jersey, 64 m, on 11 February 1977 (1.0 m focal distance). Medium sand with 1-2% silt-clay. The strings of mucus are of unknown origin but occurred over much of the central and outer shelf during the winter cruise. Several Echinarachnius parma, one Asterias vulgaris, several siphons of Arctica islandica, an opisthobranch mollusc, Pleurobranchia tarda (upper center), a few worm tubes and biodeposits can be seen.
Bottom. Station B1 on 6 August 1977, (0.6 m focal distance). More tubes, biodeposits, and evidence of biogenic reworking are evident than during the previous winter.



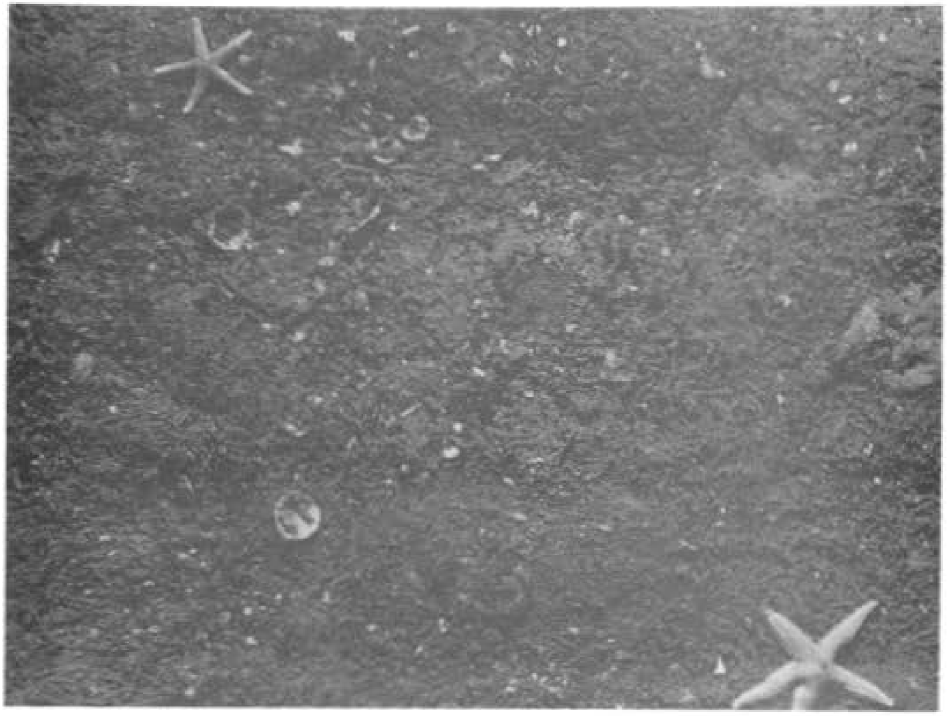


Figure 6-18. Top. Station B5, outer shelf swale off central New Jersey, 65 m, on 6 August 1977 (0.6 m focal distance). Medium sand bottom is covered by a dense mat of amphipod tubes, primarily Erichthonius rubricornis, but also Unciola irrorata and Ampelisca spp. Two Asterias vulgaris and one Cancer borealis can be seen. Bottom. Station B3, outer shelf swale off central New Jersey, 72 m, on 6 August 1977 (0.6 m focal distance). Sediments are slightly muddy fine sand. Dense mats of tubes of the amphipods Ampelisca agassizi and, to a lesser extent, Unciola irrorata, interspersed by mounds of reworked sediment around burrows, are apparent and Asterias vulgaris and Astropecten americanus are visible.

Figure 6-19. Top. Station A1, near the shelf break off central New Jersey, 91 m, on 7 August 1977 (0.6 m focal distance). Sediment is medium-fine muddy sand. Numerous arms of the brittle star Amphioplus macilentus, several cerianthid anemones, one Calliostoma bairdi and one burial trace of Astropecten americanus (upper right) can be seen.

Bottom. Station F1, near the shelf break off southern New Jersey, 85 m, on 10 August 1977, (0.6 m focal distance). Sediment is medium-fine sand. Numerous arms of Amphioplus macilentus, two Astropecten americanus (one buried), a striped maldanid polychaete, Praxillura longissima (left corner), and a snake eel, Pisodonophis cruentifer are visible.

Figure 6-20. Top. Station F2, shelf break off southern New Jersey, 110 m, on 1 June 1977 (0.6 m focal distance). Sediment is slightly muddy fine sand. A large cerianthid anemone can be seen along with two Astropecten americanus, a tubularian hydroid Corymorpha pendula, and several polychaete tubes.
Bottom. Station F3, shelf break off southern New Jersey, 155 m, on 10 February 1977 (1.0 m focal distance). Sediment is slightly muddy medium-fine sand. Many motile onuphid polychaetes, Nothria conchylega, several small cerianthid anemones, and Astropecten americanus can be seen.

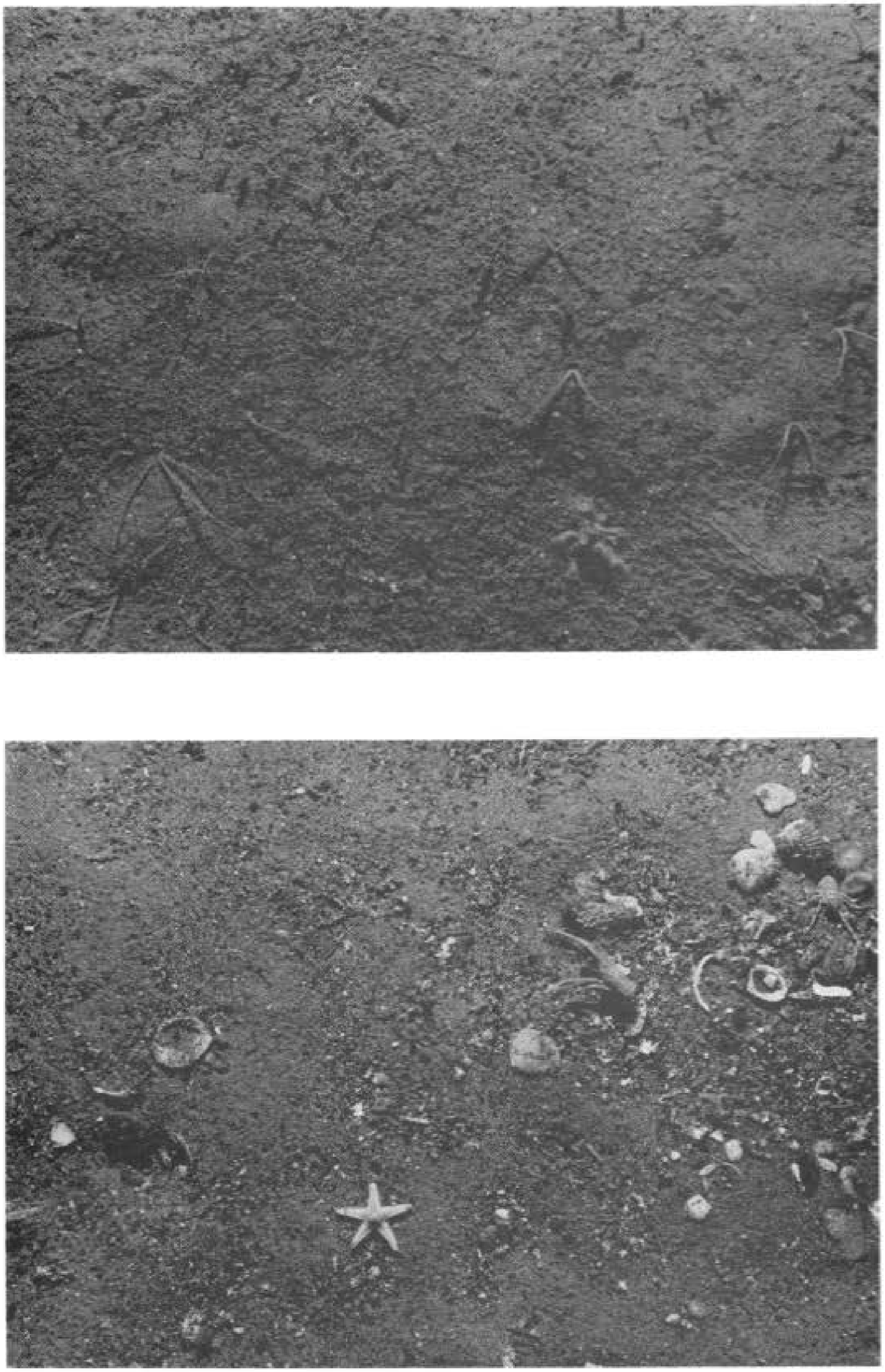


Figure 6-21. Top. Station A4, shelf break off northern New Jersey, 188 m, on 7 August 1977 (0.6 m focal distance). Sediment is muddy medium-fine sand. Many arms of *Amphilimna olivacea* (two arms projecting into water column), an arm of *Amphioplus macilentus* (single arm on sediment surface), a cluster of zoantharian anemones and a small spider crab, *Euprognatha rastellifera*, can be seen.
Bottom. Station K5, shelf break off Maryland, 150 m, on 15 August 1977 (0.6 m focal distance). Sediment is slightly muddy medium-fine sand with gravel. Three galatheid crabs, *Munida iris*, two solitary corals, *Desmosmylia lymani*, two zoantharians (*Epizoanthus* ?), one *Nothria conchylega*, and one *Astropecten americanus* are visible.

Figure 6-22. Top. Station L6, upper continental slope off Virginia, 380 m, on 5 August 1977 (0.6 m focal distance). Sediment is muddy sand with ca. 40% silt and clay. Numerous quill worms, Hyalinoecia artifex, two snails Colus pygmaeus, numerous polychaete tubes, and a few arms of the brittle star Amphiura otteri can be seen.
Bottom. Station H2, middle continental slope off central New Jersey, 740 m, on 8 August 1977 (0.6 m focal distance). Sediment is ca. 90% silt and clay. Sparse tubes and burrows and biogenically reworked deposits are visible.

drastic change can be seen at Station C2 just nine months after the hypoxia (Figure 6-10, bottom). The medium coarse sand had been stabilized by the introduction of large numbers of tube builders (e.g. Spiophanes bombyx, ampharetid polychaetes, and cerianthid anemones). Large predators, such as sea stars and crabs and surface grazers, such as Echinarachnius parma, which tend to destabilize sediments were killed and were slowly being recruited back into the area.

The swale station C4 on the inner shelf has sediments composed of somewhat muddy medium-fine sand. Large mortalities were also found at this station as a result of the hypoxia. Figure 6-11, top, shows the sediment surface in June 1976, a few weeks prior to the hypoxia. Numerous cerianthid anemones can be seen along with the sea star Asterias forbesi, a hermit crab, worm tubes, and fecal castings. The mortalities were not nearly as severe as those seen at C2, but Figure 6-11, bottom, shows the same station about one year after the die-off. There were still about the same numbers of cerianthids present, but the number of tubes and biogenic surface features had increased.

Benthic habitats of the central shelf off southern New Jersey (approximately 30-50 m) are represented in Figure 6-12. The top photograph is from D1, a ridge with dynamic clean medium sand, in August 1977. No mortality due to the hypoxia conditions was witnessed there and the sediment surface reflects rather quiescent summer conditions. Sediments at the central shelf swale at D4 are slightly muddy fine sand and are similar to those at the inner shelf swale at C4. Worm tubes, other biogenic structures and two large predatory sea stars (Asterias vulgaris) can be seen in Figure 6-12, bottom. Sediments at Station G2 on the central shelf (Figure 6-13, top) are medium-coarse sands. The hypoxia of 1976 caused extensive mortalities of echinoderms and crustaceans there. Many cerianthids are visible and there is evidence of increased biodepositional activity as at C2. The central shelf off Virginia (Figure 6-13, bottom) has sands very much finer than those found to be north off New Jersey. Many more worm tubes and biogenic surface features are apparent than usually seen at comparable depths to the north.

The outer shelf sediments are generally medium sands on mesotopographic ridges and flanks (Figures 6-14, 6-16, and 6-17) and finer sands with increased silt and clay in the swales (Figure 6-15, 6-18). Rippling of the surface sediment on ridges was more subdued on the outer shelf than on the inner and central shelf, and was most common during winter (Figure 6-14, top). The swale at E4 (Figure 6-15, top) is covered by a shell lag indicating an erosional history. Numerous polychaetes (Typosyllis tegulum) were commonly seen on the sediment surface (Figure 6-15, top) and submersible observations in the area indicate that demersal fishes, such as hake, ignore them. These polychaetes are easily visible, thus they must be distasteful to fishes. Other outer shelf swales, such as represented by B3 (Figure 6-18), and the topographic depression of the Hudson Shelf Valley (Figure 6-15, bottom) appear to be more depositional. These sites were characterized by dense mats of amphipod (Ampelisca, Unciola, and Erichthonius) tubes and much evidence of bioturbation. The slightly muddy medium sands present at B5 (Figure 6-18, top) were densely covered by amphipod tubes (Erichthonius rubricornis, with lesser numbers of Unciola irrorata and Ampelisca spp.). Station B3 (Figure 6-18, bottom) has sediments of muddy medium-fine sand which had dense populations of tubicolous Ampelisca aggassizi with many Unciola irrorata.

Within area B on the outer shelf there are a variety of topographic habitats grading from the shallow dynamic sediments on the terrace above Tiger Scarp (Figure 6-16, top) and ridges (Figure 6-16, bottom), to the moderately stable flanks and level bottom (Figure 6-17), and finally to the relatively quiescent swales (Figure 6-18). The grain size decreases along this gradient, while the percentages of silt and clay and fine sand and the organic carbon concentration increases.

The shelf-break transition begins at about 90-100 m where surface-generated oscillatory currents rarely reach the bottom. Sediments at the shelf break are muddier in the vicinity of Hudson Canyon than elsewhere. This can be seen by comparing the photographs from A1 to those at F1 (Figure 6-19). Arms of Amphioplus macilentus are seen in both of these photographs, but they are more abundant in the muddier sediments of A1 and A2. Figure 6-20, top, shows Station F2 which is deeper (110 m) in the shelf break zone. The sands become finer and the silt and clay increases with depth. The large cerianthid anemone visible occurred commonly along the shelf break and Astropecten americanus occurred on the shelf break (Figure 6-19, bottom; 6-20; 6-21, bottom) as well as in the outer shelf swales (Figure 6-15, top; 6-18, bottom). A large solitary hydroid, Corymorpha penderla, is seen in Figure 6-20, top. It is one of several species which were previously known only from north of Cape Cod, but have been found commonly in this study on the outer shelf of the Middle Atlantic Bight. Deeper (Station F3, 155 m) on the shelf break transition (Figure 6-20, bottom) the epifauna is dominated by the onuphid polychaete, Nothria conchylega. The muddier deep shelf-break habitat at Station A4 (188 m) (Figure 6-21, top) characteristically supported large numbers of brittle stars (Amphilimna olivacea) which extend two arms into the water column for feeding. Galatheid crabs (Munida iris) and solitary corals (Desmosylia lymani) were abundant as were worm tubes and anthozoans on the coarser sediments of the shelf break at K5 (Figure 6-21, bottom). The quill worm Hyalinoecia artifex and infaunal polychaete tubes were abundant on the muddier sediments of the upper slope (Figure 6-22, top) but the overall biomass and concentration of organisms is less than on the shelf break. At mid-slope stations (Figure 6-22, bottom) the very muddy sediments supported sparse epifauna. Worm tubes, bioturbated mounds, and trails of motile animals (e.g. the red crab Geryon quinquedens) can be seen, but the overall concentration of species and individuals is drastically reduced from that on the upper slope and shelf.

Macrobenthos

Composition of the Fauna

A total of 697 species of macrobenthic invertebrates was identified from the grab samples taken at 52 stations from fall 1975 through summer 1977 (Appendix 6-A). An additional 84 taxa were collected but could not be identified to species level. Many of these forms have been forwarded to appropriate taxonomic experts for further identification.

Polychaetous annelids numerically dominated the collections at most stations, usually comprising 40 to 60 percent and occasionally up to 90 percent of the individuals. A total of 250 species was separated while an additional 32 taxa were identified only to genus. It is estimated that 37 polychaete species are new to science.

The second most abundant group was the peracaridan crustaceans which included 157 species, of which at least 20 are new to science (1 cumacean, 3 tanaidaceans, 3 isopods, and 13 amphipods). Peracaridans generally comprised 10 to 30 percent of the individuals in collections at most stations. Amphipods were the most diverse group of peracaridans with 99 species, and at some of the outer shelf swale stations (e.g. B3, B5, G3), they accounted for more than 70 percent of the individuals by number.

Molluscs were the third most abundant and diverse group with a total of 115 species identified to date. They generally accounted for less than 10 percent of the individuals at most stations, but occasionally they accounted for up to 50 percent of the individuals in a collection.

The fourth most abundant group was the echinoderms. A total of 27 species was collected. Most of the individuals collected were amphiurid ophiuroids. Although echinoderms accounted for generally less than 5 percent of the individuals at a station, they comprised as much as 50 percent of the total at some stations (e.g. A2).

Ostracod crustaceans were occasionally abundant, particularly on the shelf break, and of the 29 species collected, three were new to science. One new species of hydrozoan was also obtained during this study.

It is clear from the species lists (Appendices 6-A and 6-B) that dredge and trawl sampling (megabenthos) and grab sampling (macrobenthos) captured largely different components of the benthic biota. The dredge and trawl sampling, because of the larger mesh size

(4 mm), selected for larger asteroids, echinoids, decapods, and molluscs, while the grab sampling (0.5 mm mesh) recovered the abundant but smaller annelids, peracaridans, and ophiuroids. The two approaches used in combination gave a good representation of the macroinvertebrate communities at any given site.

Taxonomic determinations of the diverse and previously poorly studied macrobenthos of the study area have evolved during the study and will continue to evolve as remaining taxonomic problems are resolved. Nomenclatural modifications effected since the preliminary report by Boesch et al. (1977) are listed in Table 6-3.

Abundance and Biomass

Abundance. Density patterns of total macrobenthos for various bathymetric zones are summarized in Figure 6-23 (detailed data are presented in Appendix 6-C). Justification for the division of habitats into inner, central, and outer continental shelf, shelf break, and upper and middle continental slope was given by Boesch et al. (1977) and is further supported by subsequent analyses presented in this report. Swale habitats on the continental shelf are also distinctive in terms of the qualitative composition and quantitative abundance of macrobenthos and are thus summarized separately.

Total densities ranged almost two orders of magnitude from 18,075 individuals/m^2 at G3 in winter 1976 to 250 individuals/m^2 at J2 in summer 1976. Density of macrobenthos was highest in swale habitats where half the estimates fall between 6,800 and 14,000 individuals/m^2 for outer shelf swales and between 5,000 and 8,200 for inner and central shelf swales. Outer shelf and shelf-break habitats outside of swales generally supported higher densities (medians 3800 and 3600 individuals/m^2, respectively) than did inner and central shelf environments (medians 2900 and 2500 individuals/m^2, respectively), although the distributions of density estimates for these four habitats broadly overlap. Densities in swales were about 2-3 higher than in adjacent shelf habitats.

Macrofaunal densities declined precipitously on the continental slope from about 2000 individuals/m^2 on the upper slope to less than 500 individuals/m^2 (median 390 individuals/m^2) on the middle slope.

Biomass. Wet weight biomass is not directly comparable among the various macrobenthic taxa because of the inclusion of skeletal material, tubes, and gut contents. Such data are, however, more comparable with a taxon, e.g. Annelida, Echinodermata, etc., which tends to have a relatively similar living matter to total bulk relationship. Thus, the biomass data are here treated separately by major taxon with no attempts to combine biomass over all taxa.

Table 6-3. Cross reference for taxa referred to in Boesch et al. (1977) for which different names are applied in this report.

Previous Reference (Boesch et al. 1977)	Current Reference
CNIDARIA	
Trochosmiliidae	*Dasmosilia lymani*
Caryophyllidae	*Dasmosilia lymani*
MOLLUSCA	
Gastropoda	
Rissoina sp. 1	*Odostomia bisuturalis*
Benthonella gaza	*Odostomia bisuturalis*
Crucibulum sp. 1	*Crucibulum striatum*
Mitrella sp.	*Astyris* sp.
Neptunea lyrata decemcostata	*Colus* sp. (juvenile)
Colus obesus	*Colus caelatus*
Colus parvus	*Colus* sp.
Olivella sp. 1	*Olivella bullata*
Ptychatractus ligatus	omit
Marginella sp. 1	*Marginella apicina*
Inodrillia sp.	*Inodrillia dalli*
Pleurotomella sp. 1	*Propobela pygmea*
Cylichna verrilli	*Cylichna alba*
Odostomia sp. 1	*Odostomia bisutralis*
Eulimella unifascata	*Eulimella smithi*
Dendronotus sp. 1	*Dendronotus frondosus*
Pelecypoda	
Lyonsia sp. 1	*Lyonsia arenosa*
Thracia sp.	*Thracia conradi*
Cardiomya striata	*Cardiomya perrostrata*
ANNELIDA	
Polychaeta	
Leanira tetragona	*Neoleanira tetragona*
Exogone gemmifera	*Exogone naidina*
Travisia parva	*Travisia forbesii*
Ophelina sp. A	*Opheliidae* sp. A
Asychis sp. A	*Asychis biceps*
Praxillella sp. A	*Clymenura* sp. A
Clymenella zonalis	*Euclymene collaris*
Rhodine loveni	*Rhodine gracilion*
Praxillura sp. A	*Praxillura longissima*
Praxillura ornata	*Praxillura longissima*
Aricidea suecica	*Aricidea catherinae*
Spio filicornis	*Spio setosa*
Lumbrineris cruzensis	*Lumbrineris latreilli*

Table 6-3. (Concluded)

Previous Reference (Boesch et al. 1977)	Current Reference
Ampharete acutifrons	*Ampharete arctica*
Amage auricula	*Amage tumida*
Amphicteis sp.	*Amphicteis gunneri*
Polycirrus medusa	*Polycirrus eximius*
Pherusa inflata	*Pherusa affinis*
Brada sp.	*Therochaeta collarifera*
CRUSTACEA	
Ostracoda	
Ostracoda sp. A	*Paracytheretta daniana*
Tanaidacea	
Tanaidacean 1	*Leptognathia* sp.
Tanaidacean 2	*Libanius* n sp.
Tanaidacean 3	*Typhlotanais* sp. 1
Leptochelia filum	*Pseudoleptochelia filum*
Amphipoda	
Idunella aequicornis	*Idunella* sp. C

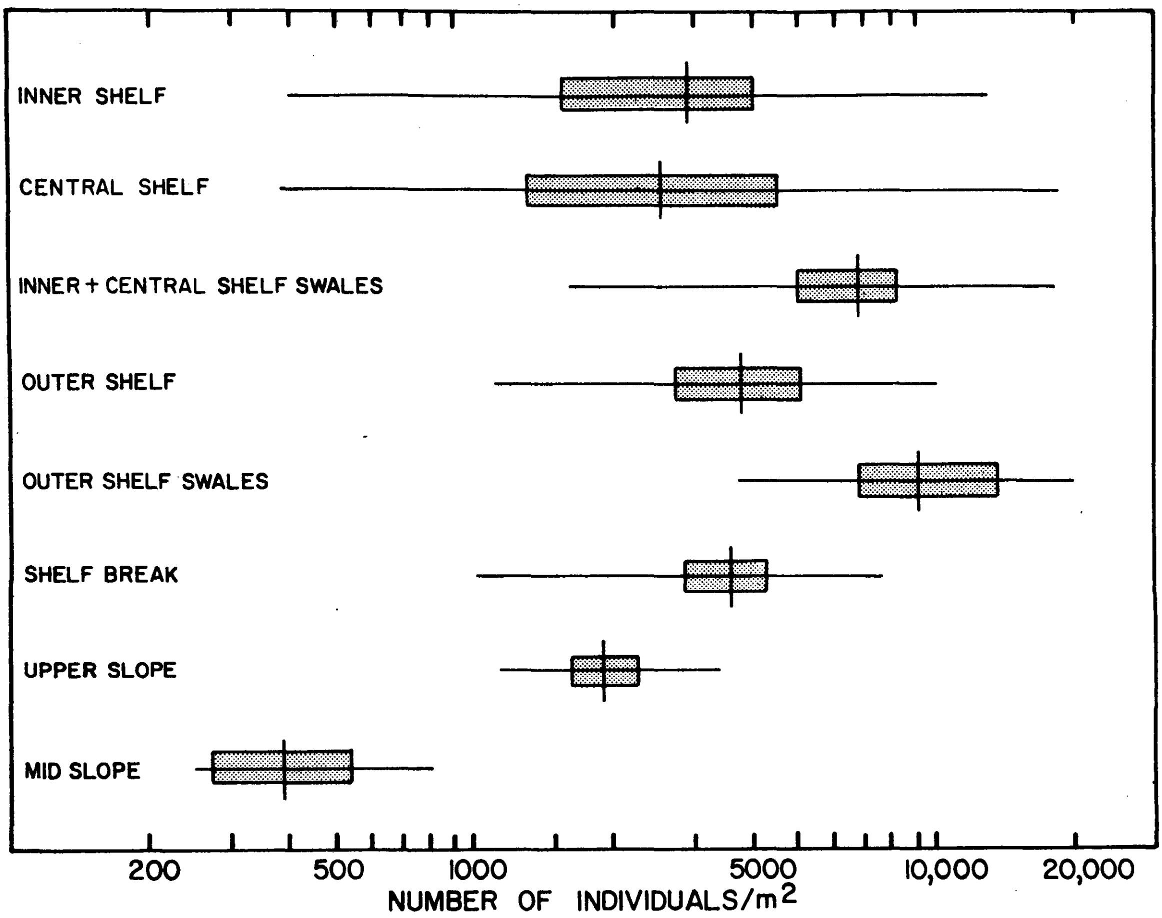


Figure 6-23. Distribution of total density of macrobenthos by major habitat. Horizontal lines represent ranges, bars represent the mid-ranges, and vertical lines represent medians.

Biomass data are summarized in Figures 6-24 to 6-27 in terms of the arithmetic means for each habitat type during each sampling period. These means were themselves computed on the geometric means of the biomass estimates from the replicate grab samples collected (Appendix 6-D). Geometric means are employed to reduce the effect on mean comparisons of the typically great variability in biomass.

Annelid biomass was the least variable from replicate to replicate because many individuals rather than a few large ones contribute to the biomass. Wet weight biomass was generally highest in the muddy fine sands of topographic depressions (swales and the Hudson Shelf Valley). The larger biomass in these habitats was attributable more to the presence of larger polychaete species than to increased density. Significant contributors to the biomass in these habitats include maldanid (e.g. *Clymenella torquata*), spionid (e.g. *Spio setosa* and *Spiophanes bombyx*), terebellid and ampharitid polychaetes. Mean biomass levels in the swales usually exceeded 20 g/m^2 but that level was seldom exceeded for other habitats. The exceedingly high biomass levels found at inner shelf stations including the swale station C4 was due to the elevated densities of *Spiophanes bombyx* and ampharetid polychaetes which irrupted following the hypoxic stress of the summer of 1976 (discussed in detail later in this report). Except for the elevated biomass of topographic depressions, the annelid biomass of the shelf and shelf break was fairly uniform. However, the biomass of annelids dropped significantly on the continental slope in response to attenuation of density to levels generally below 5 g/m^2 on the middle slope. The apparent decline of biomass during the second year on the outer shelf, shelf break, and upper slope remains unexplained.

Wet weight biomass of molluscs was consistently higher (generally >30 and frequently >60 g/m^2) in the outer and central shelf swales than on adjacent habitats (generally <20 g/m^2). The largest contributor to molluscan biomass in central and outer swales and occasionally elsewhere on the outer shelf was the bivalve *Arctica islandica*. *Astarte undata* and, especially at Station E4, *Cyclocardia borealis* were also important contributors to this biomass. *Astarte castanea* was the largest contributor to biomass on the inner shelf. Low molluscan biomass was found in the dynamic sands of the central shelf (generally below 10 g/m^2) and in the shelf-break zone and continental slope (declining to very low levels at the middle slope). As would be expected for large animals, there are no interpretable seasonal trends in the biomass of molluscs.

Biomass of crustaceans averaged less than 10 g/m^2 except in outer shelf swales where dense populations of amphipods, in particular *Ampelisca agassizi*, brought that level to 12-30 g/m^2. The low biomass at inner shelf stations during the second year was a result of the virtually complete elimination of crustaceans following the hypoxia of the summer of 1976. Biomass was reduced to generally below 2 g/m^2 at the shelf break and reduced even further on the continental slope.

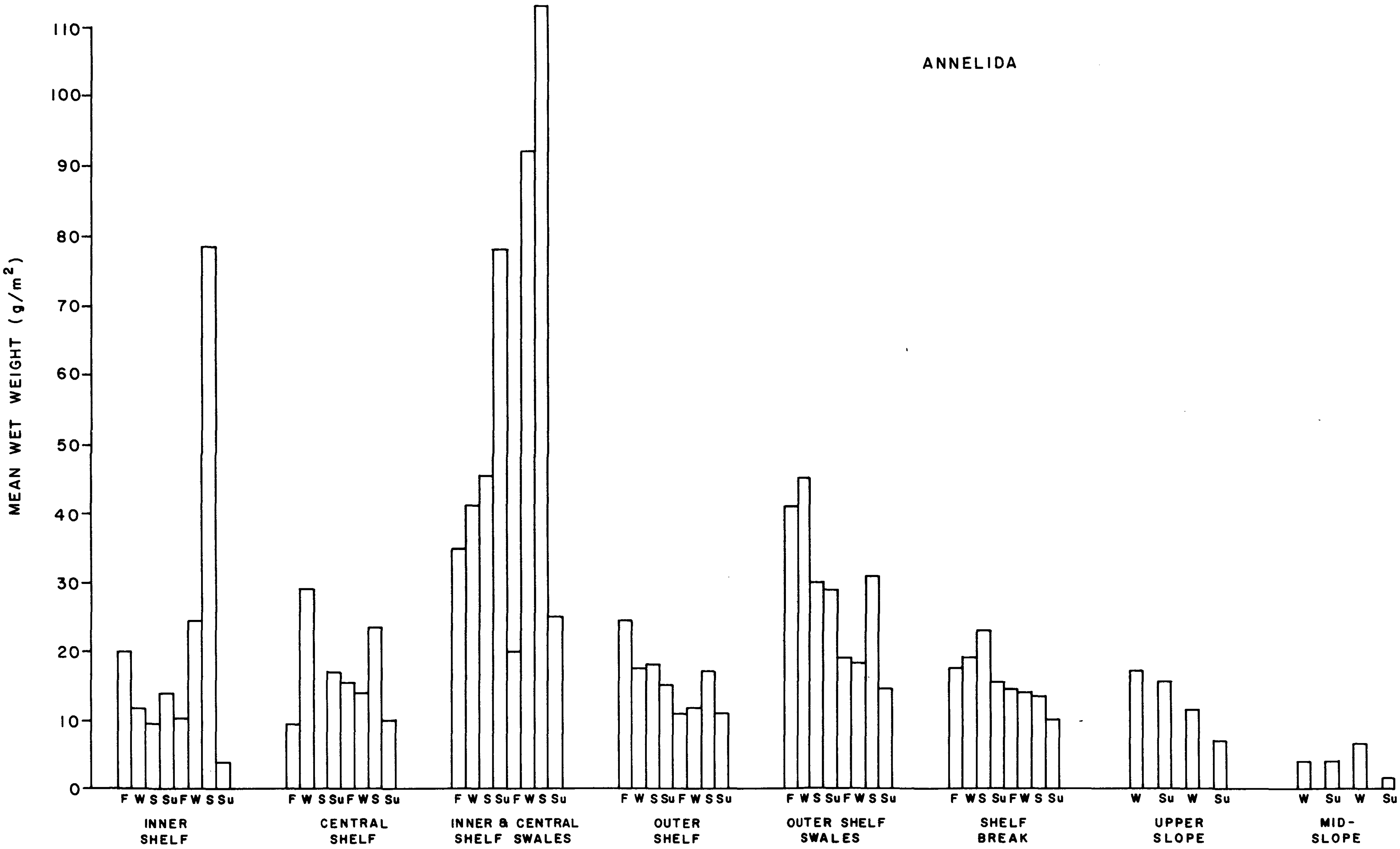


Figure 6-24. Geometric mean wet weight biomass of macrobenthic annelids by major habitat and season.

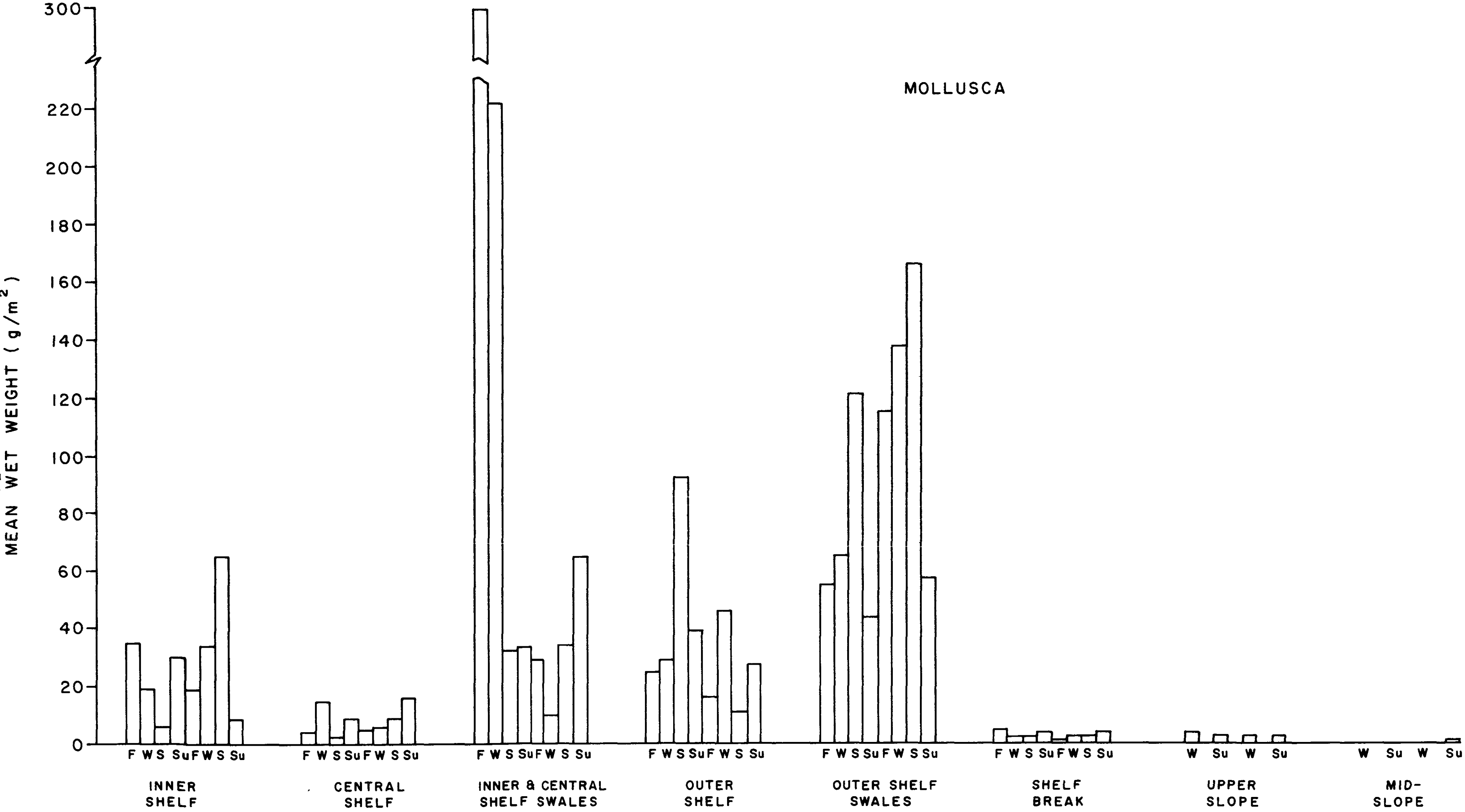


Figure 6-25. Geometric mean wet weight biomass of macrobenthic molluscs by major habitat and season.

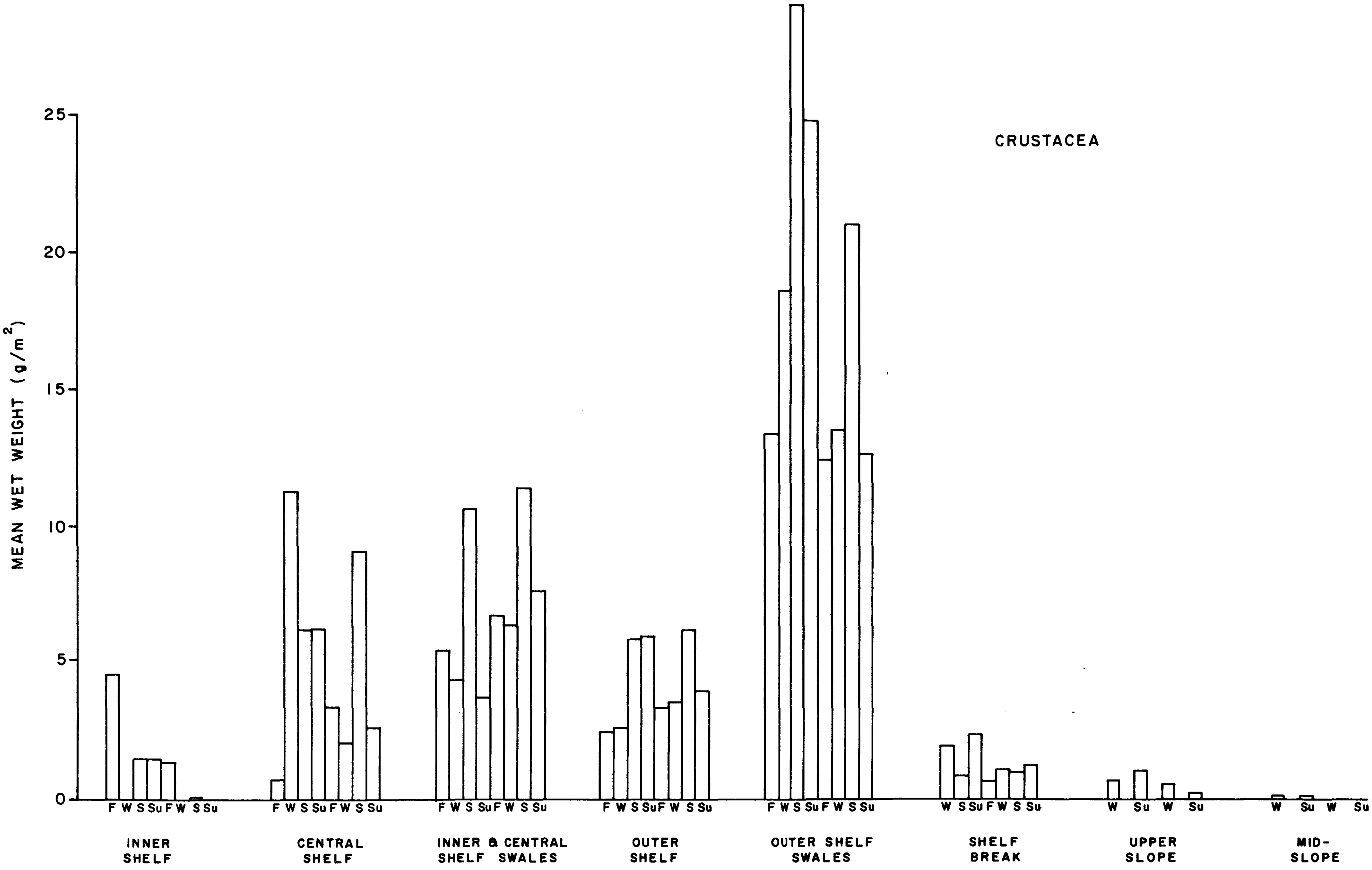


Figure 6-26. Geometric mean wet weight biomass of macrobenthic crustaceans by major habitat and season.

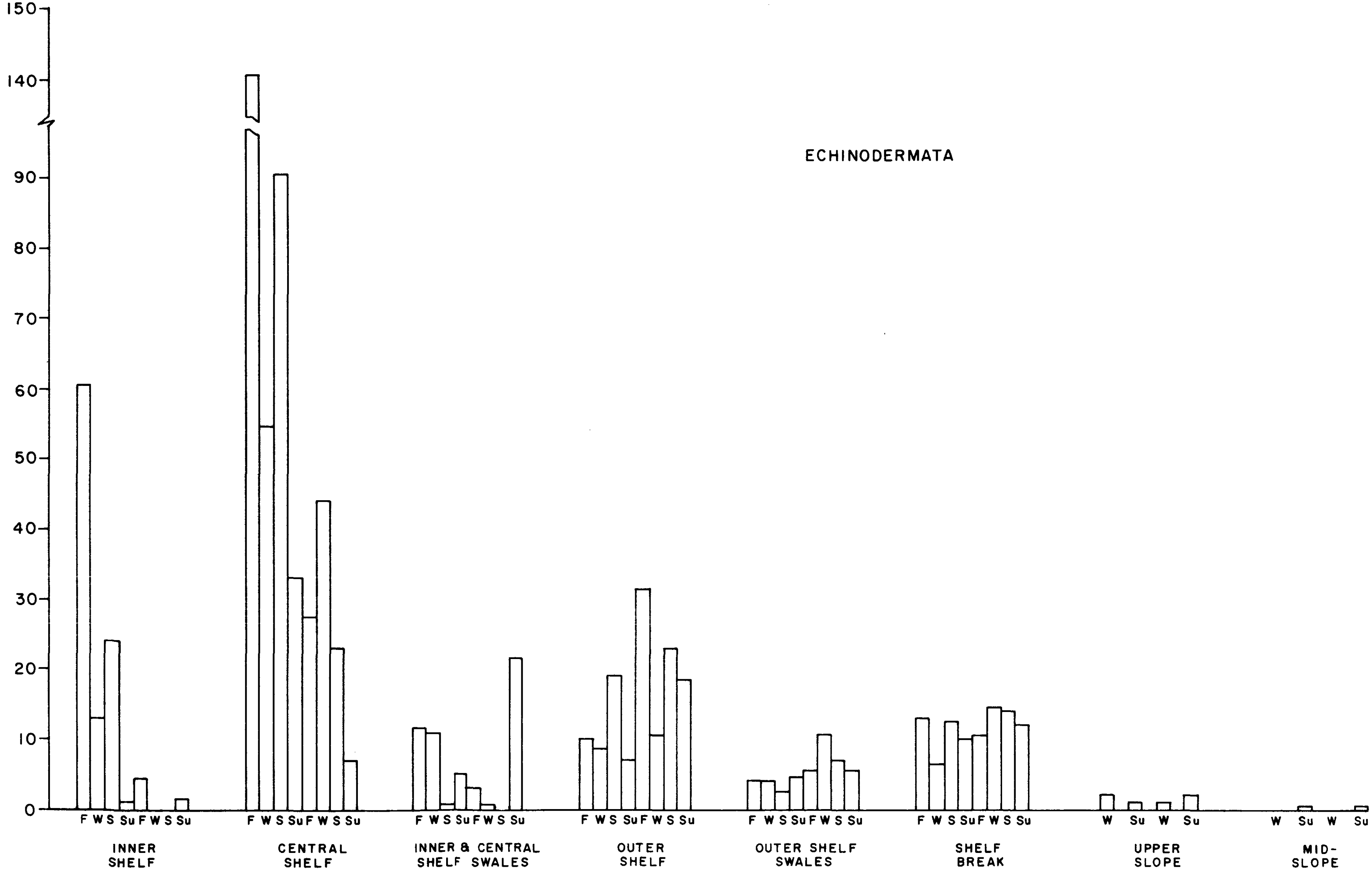


Figure 6-27. Geometric mean wet weight biomass of macrobenthic echinoderms by major habitat and season.

Crustacean biomass was concordantly highest during the spring across all shelf habitats except the inner shelf. This appears to be a period of reproduction and recruitment for many peracaridans and decapods.

Wet weight biomass of echinoderms was extremely variable reflecting variations in the capture of the sand dollar Echinarachnius parma on the shelf and the sea star Astropecten americanus at the shelf break. The biomass of echinoderms on the slope was very low. The biomass of shelf habitats consisted almost exclusively of Echinarachnius parma which was of reduced abundance in swales. The low biomass at the inner shelf stations during the last five sampling periods is due to the nearly complete elimination of echinoderms at the inner shelf stations off New Jersey during the summer of 1976.

The combined wet weight of remaining taxa of macrobenthos was generally less than 2 g/m^2, although occasionally the inclusion of cerianthid or zoanthid anemones or nemerteans raised this value to about 5-10 g/m^2.

Large Scale Patterns of Distribution

Two years of sampling produced an extremely large data set in which is represented spatial and temporal distribution patterns of various scales. In order to describe the basic spatial pattern of distribution of assemblages throughout the study area, the data for each station were combined over all seasons sampled by computing grand mean abundance for each species at each station (Appendix 6-G). These grand means were computed as the arithmetic mean of the geometric mean density (per 0.1 m^2 grab) for a given collection period. This produced a new data set of 52 stations vs. ca. 700 species. These data were further reduced to the most common, abundant, or characteristic species through a procedure in which an index of importance was computed for each species (taxa which were separated at the species level) and the top ranking species retained for further analyses. The importance index used was

$$R_i = \sum_j (f_{ij} + \log_{10} \bar{x}_{ij})$$

where f_{ij} and $\bar{x}_{ij}$ are the overall frequency (based on number of replicates) and the grand mean, respectively, of species i at station j.

Multivariate analyses were used to simplify and analyze the large scale spatial patterns. The 186 top-ranked species were included in normal and inverse numerical classification (square root transformation, Bray-Curtis similarity, group average sorting for normal analysis, flexible sorting for inverse analyses). The top 122 species were used in reciprocal averaging ordination (square root transformation). The numerical classification was intended to optimally group stations and species and, through nodal analyses, to describe the distributional bases for these groupings. Ordination was used to develop a continuum model of the large scale distribution patterns in which the overall relationships among assemblages should be better represented than in the classification.

Classification Results. The 52 stations were classified into 10 site groups (A-J) as indicated in Table 6-4 and the inverse analysis of 186 species was interpreted at the 22 group level (Table 6-5). The fusion hierarchies of these groups are given adjacent to the nodal diagrams in Figures 6-28 through 6-30. Note the differences in the similarity scales for normal and inverse dendrograms. The negative similarity values in the inverse agglomeration result from the use of flexible sorting. Group average sorting which is space conserving was used for the normal analysis, thus negative values are impossible. The less intensively clustering group average method was used in order to distort as little as possible the similarity relationships among sites.

Stations were clearly grouped in accordance with bathymetric and topographic position as evidenced by the geographical distribution of site groups (Figure 6-31) and by the depth ranges of the sites represented in each group (Table 6-3). Change of the macrobenthos across the shelf and onto the slope was very similar throughout the 3 degrees of latitude encompassed in the study area. Main station groupings represent inner and central shelf (A, B, C), inner and central shelf swales or other fine sands (D and E), outer shelf depressions and the shelf break (F, G, H), and upper (I) and middle (J) continental slope habitats. The apparently large differences between middle slope stations and the remaining stations is a result of the sparse collections included in this analysis for the middle slope. Faunal densities are very low on the middle slope and many species found only on the slope were not included in the analysis because of their low overall importance scores. Stations in swales and other topographic depressions (i.e. groups D and F) were generally more similar to stations in deeper bathymetric strata than to surrounding stations.

The distribution of species within the 22 species groups was investigated in nodal analyses in which these groups are directly related to the site groups in terms of constancy (Figure 6-28), fidelity (Figure 6-29), and abundance concentration (Figure 6-30). These presentations help simplify the discussion of distributional patterns and the explanation of biotic differences among the site groups.

Species in Group 1 were highly constant and faithful to the shelf. They were particularly more abundant at inner and central

(TEXT CONTINUES ON PAGE 6-64)

Table 6-4. Site groups selected from numerical classification of macrobenthos from 52 stations based on grand mean abundances over all sampling periods.

Site Group	Stations Included	Habitat	Depth Range (m)
A	L1	inner shelf, fine sand	24-26
B	C1,C2,C3,G1,K1	inner shelf	15-29
C	D1,D2,D3,G2	central shelf	31-39
D	C4,D4,L2	inner and central shelf swales, fine sand	34-51
E	B1,B2,B4,B5,E1, E3,G4,K2,K3,L3	outer shelf	40-66
F	B3,G3	outer shelf depressions	72-74
G	E2,E4,F1,I1,I2,L4	outer shelf-shelf break	64-94
H	A1,A2,A3,A4,F2,F3, F4,G5,G6,I3,K4,K5,L5	shelf break	90-201
I	G7,H1,I4,J1,K6,L6	upper slope	310-460
J	H2,J2	middle slope	680-760

Table 6-5. Species groups selected from numerical classification of macrobenthos occurrence over all stations based on grand mean abundance.

Species Group 1

Spisula solidissima
Tellina agilis
Nephtys picta
Sigalion arenicola
Pseudoleptocuma minor
Astarte castanea
Hemipodus roseus
Nephthys bucera
Chiridotea arenicola
Protodorvillea kefersteini
Protohaustorius wigleyi
Aricidea wassi
Pseudunciola obliquua
Corophium crassicorne

Species Group 2

Pandora inflata
Edotea montosa
Synchelidium americanum
Solariella obscura
Hippomedon serratus
Orbinia swani
Monoculodes sp. B
Cancer irroratus
Lyonsia hyalina
Drilonereis magna
Philine quadrata
Asterias vulgaris

Species Group 3

Nucula proxima
Cytheretta edwardsi
Pitar morrhuana
Sarsiella zostericola

Species Group 4

Goniadella gracilis
Lumbrinerides acuta
Polygordius sp. 1
Tanaissus lilljeborgi

Species Group 5

Spiophanes bombyx

Species Group 6

Lumbrineris impatiens
Chone infundibuliformis
Exogone verugera
Diastylis bispinosa
Scalibregma inflatum
Aricidae catherinae
Unciola irrorata
Erichthonius rubricornis
Ampelisca vadorum
Byblis serrata

Species Group 7

Ampelisca agassizi

Species Group 8

Euclymene collaris
Clymenura sp. A
Trichophoxus epistomus
Echinarachnius parma
Aglaophamus circinata
Cerastoderma pinnulatum

Species Group 9

Arctica islandica
Ensis directus
Harmothoe extenuata
Lumbrineris fragilis
Phyllodoce mucosa
Glycera dibranchiata
Sthenelais limicola
Ampharete arctica
Cirolana polita
Schistomeringos caeca
Aricidea cerrutii

Table 6-5. (Continued)

Species Group 10

Exogone hebes
Phoxocephalus holbolli
Euchone sp. A
Unciola inermis
Pholoe minuta
Aeginina longicornis
Cerebratulus lacteus
Pherusa affinis
Diastylis sculpta
Edotea triloba
Photis macrocoxa

Species Group 11

Scoloplos acmeceps
Marphysa bellii
Photis pugnator
Nucula delphinodonta

Species Group 12

Cyclocardia borealis
Melita dentata
Goniada brunnea
Golfingia minuta
Mysella ovata

Species Group 13

Cocculina sp. 1
Chaetopleura apiculata
Janira alta
Typosyllis tegulum
Crenella decussata
Pseudoleptochelia filum

Species Group 14

Polydora concharum
Melinna cristata
Nicolea venustula
Stenopleusies inermis
Cancer borealis
Sphaerosyllis erinaceus
Campylaspis rubicunda
Stenopleustes gracilis

Species Group 15

Nephtys incisa
Glycera capitata
Eulalia bilineata
Turbonilla interrupta
Golfingia catharinae
Terebellides stroemi
Alvania pelagica
Havelockia scabra
Harpinia n sp. 5

Species Group 16

Paraonis gracilis
Terebellides sp. A
Launice cirrata
Prionospio sp. A
Astropecten americanus
Nemertea sp. 5
Lumbrineris albidentata
Abra lioica
Macrocyprina sp. 1
Asychis carolinae
Echinocythereis echinata
Lucinoma filosa
Macrocypris sp. 1
Macrocypris sapeloensis
Thyasira trisinuata
Synasterope sp. 1

Species Group 17

Prionospio steenstrupi
Euchone incolor
Clymenella torquata
Ptilanthura tricarina
Phascolion strombi
Nereis grayi
Drilonereis longa
Cirrophorus lyriformis
Ninoe nigripes
Periploma fragilis
Leptocheirus pinguis

Table 6-5. (Concluded)

Species Group 18

Crenella glandula
Astarte undata
Polycirrus eximius
Cyclopecten nanus
Photis dentata
Eudorella pusilla
Notomastus latericeus
Axiognathus squamata
Ophelina acuminata
Harpinia sp. 2
Eriopisa elongata

Species Group 19

Nothria conchylega
Onuphis atlantisa
Harbansus bowenae
Harbansus dayi
Lumbrineris latreilli
Thyasira flexuosa
Spiophanes wigleyi
Onuphis pallidula
Aricidea neosuecica
Amphioplus macilentus

Species Group 20

Eunice vittata
Eunice antennata
Harpinia n sp. A
Platyishnopus sp. 1
Typhlotanais sp. 1
Malacoceros sp. A
Limatula subauriculata
Nephthys squamosa
Apanthura magnifica
Sarsiella sp. B
Dacrydium vitreum

Species Group 21

Amphilimna olivacea
Leiocapitella glabra
Myrtaea lens
Nuculana acuta
Paralacydonia paradoxa
Carlomya perrostrata
Lasaea rubra
Onchnesoma steenstrupi
Cossura longocirrata
Paradoneis lyra

Species Group 22

Paramphinome pulchella
Nucula tenuis
Lumbrineris tenuis
Thyasira pygmea
Ceratocephale loveni
Hyalinoecia artifex
Auchenoplax crinita
Brada villosa
Fauveliopsis sp. A
Portlandia inconspicua
Anobothrus gracilis

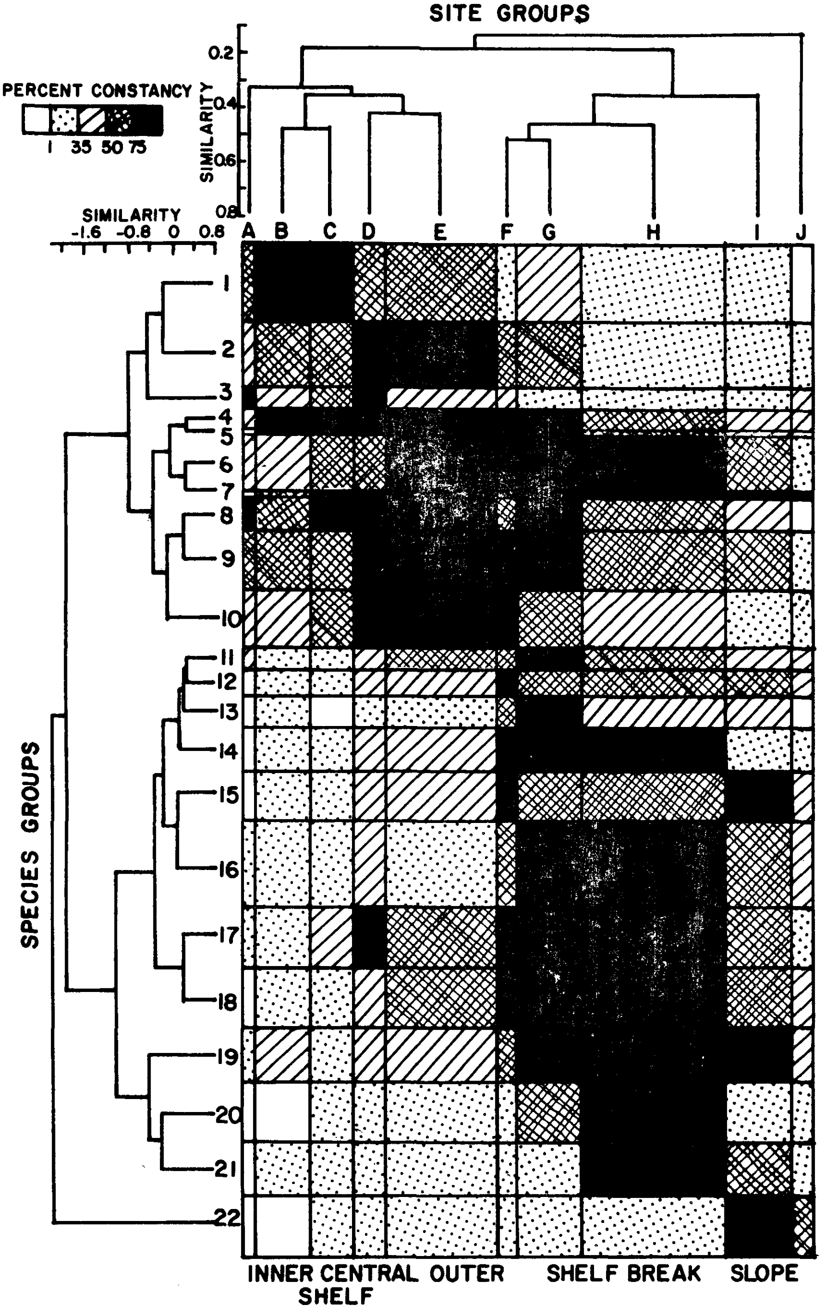


Figure 6-28. Normal and inverse classification hierarchies and nodal constancy for site-species group coincidence based on grand mean abundance data from macrobenthos from 52 stations.

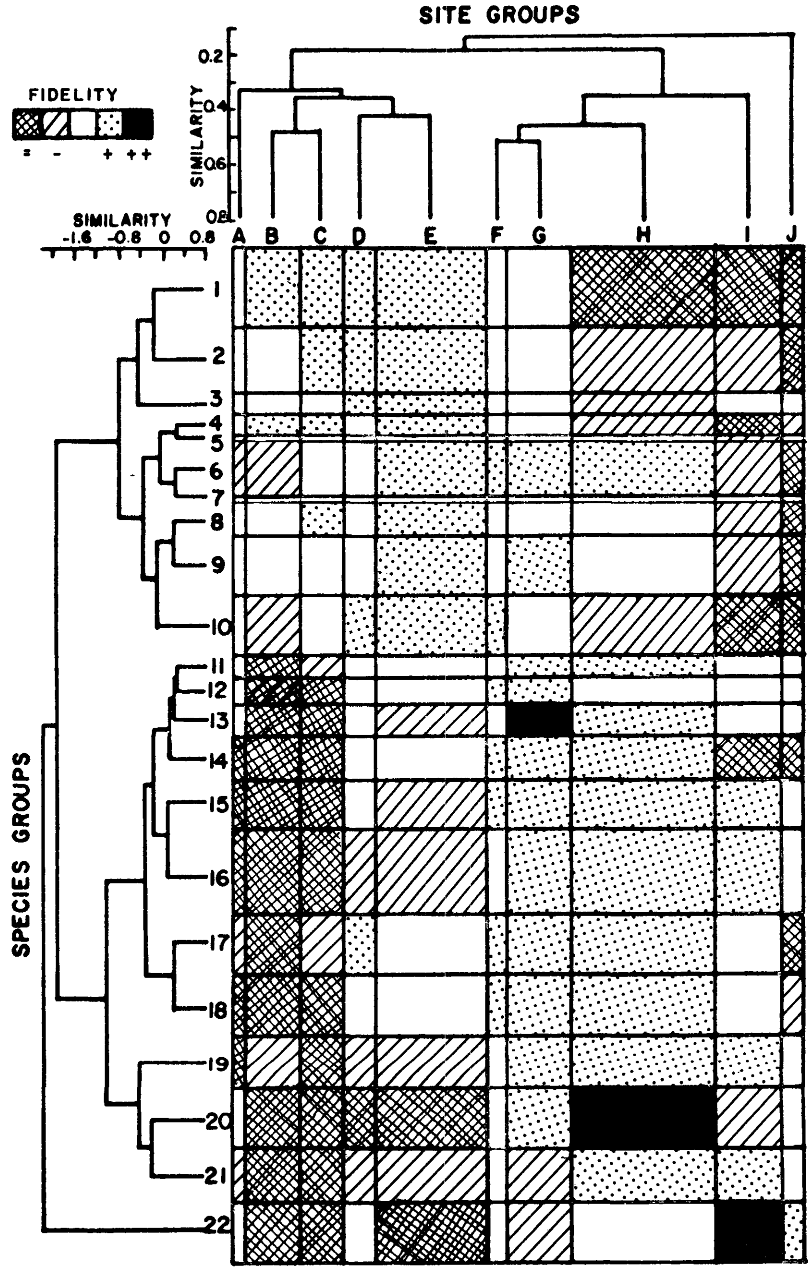


Figure 6-29. Nodal fidelity for classifications of macrobenthos from 52 stations as in Figure 6-28. Values indicate significant and highly significant fidelity and negative fidelity.

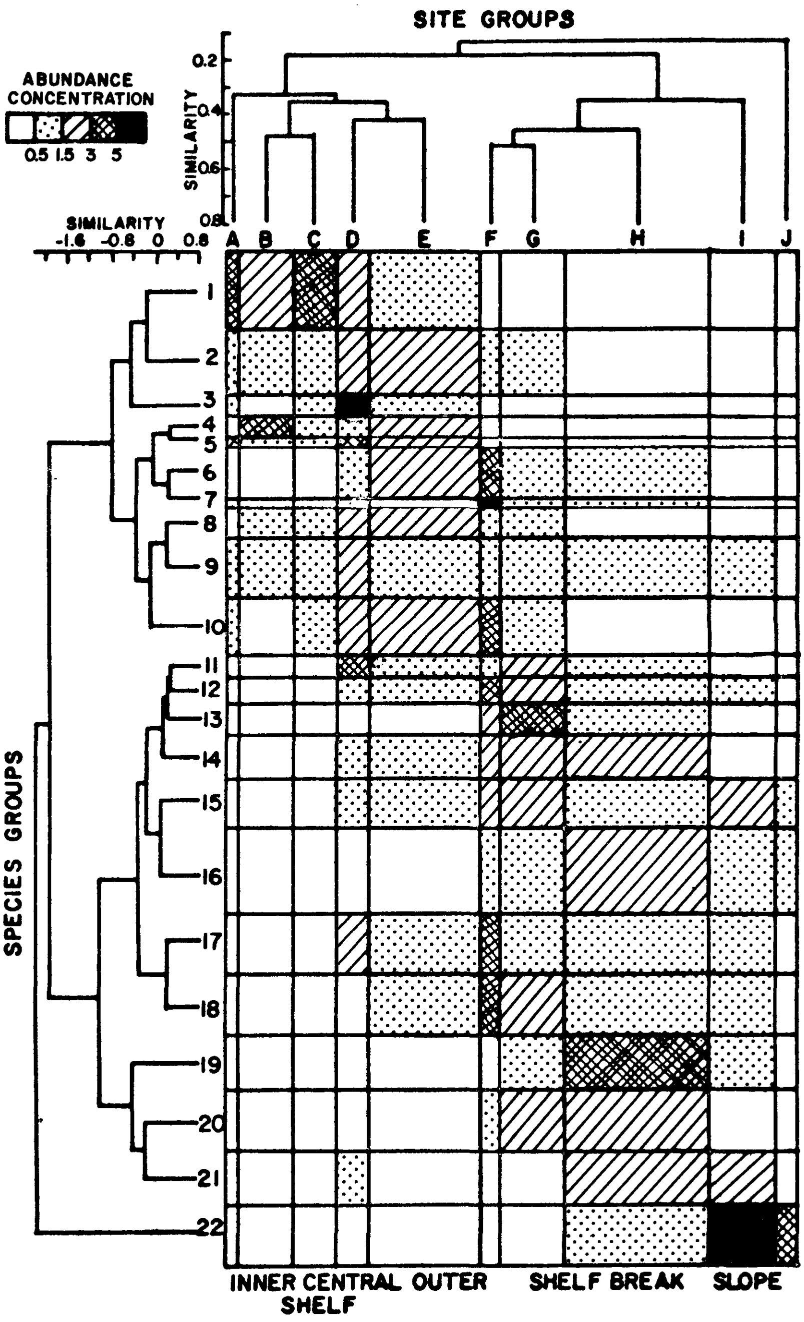


Figure 6-30. Nodal abundance concentration for macrobenthos from 52 stations as in Figure 6-28.

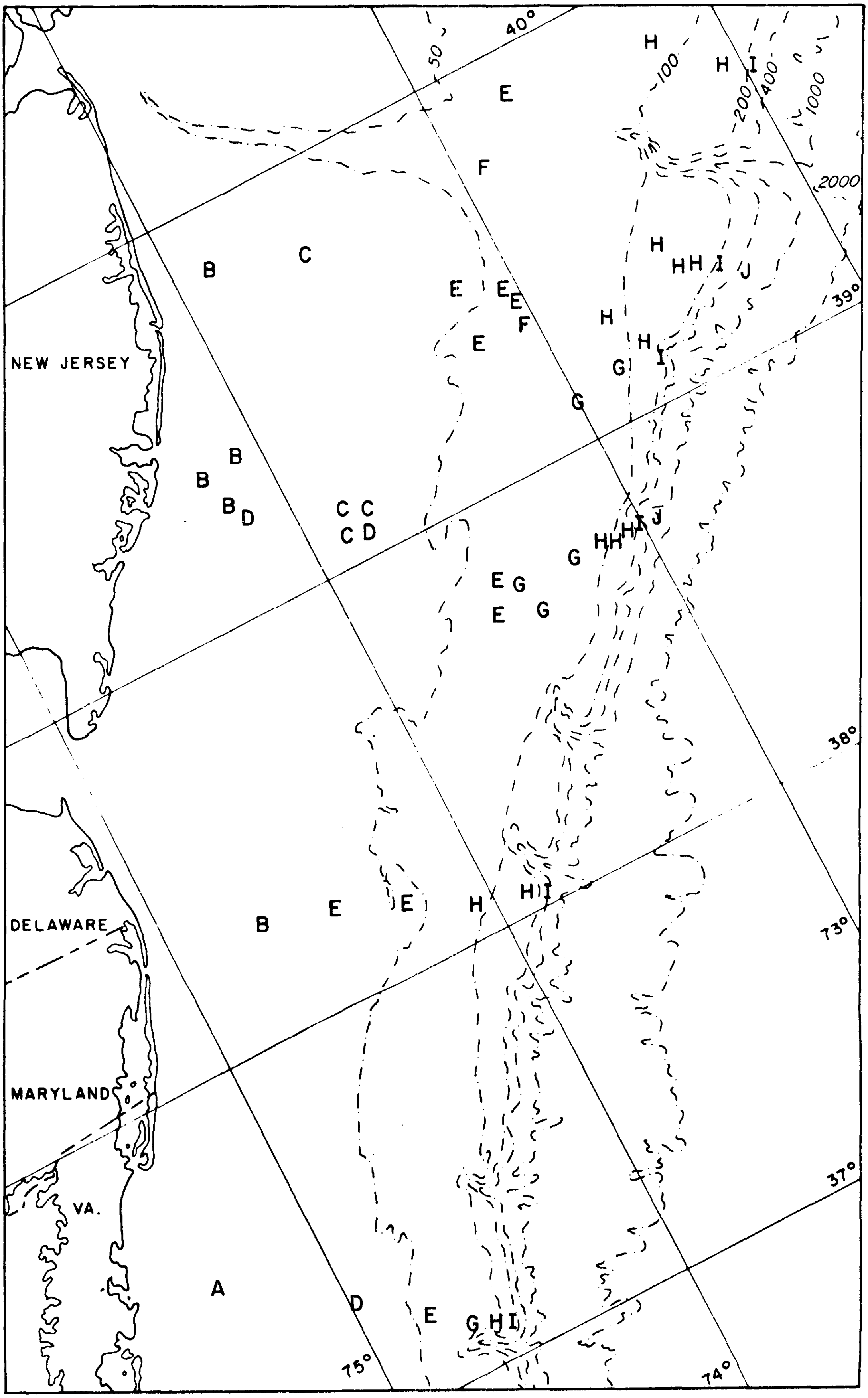


Figure 6-31. Geographical distribution of collection groups selected from numerical classification of macrobenthos assemblages.

shelf stations and never very abundant on the outer shelf or beyond. These species were generally restricted to nearshore, dynamic sand bottoms. While some species were widely distributed among all inner and central shelf stations (e.g. the bivalve Tellina agilis), others were more restricted to coarse (the polychaete Hemipodus roseus) or fine (the polychaete Nepthys picta) sands. Species in Group 2 had low mean abundance but occurred widely on the shelf. They were somewhat more frequent at inner and central shelf swale (Group D) and outer shelf (Group E) stations. Group 3 species occurred preferentially in the fine sands of the inner and central shelf swales (Group D), particularly at stations C4 and L2. At least two of these species, the bivalve Nucula proxima and the ostracod Sarsiella zostericola, also occur commonly in fine sands of coastal embayments. Species in Group 4 occurred widely on the shelf and were generally abundant on medium-coarse sands. Each of these species is very small and thin, an obvious adaptation for efficient burrowing and almost interstitial locomotion in coarse sediments. Because sediments were generally coarser on the inner shelf, this group showed high constancy and abundance concentration there; however, they also were abundant at outer shelf stations with coarser sediments (B2, B4, E3, G4, and K3). The polychaete Spiophanes bombyx is the sole member of Group 5. This species is widely distributed on the shelf and was found at all stations in Groups A-G and at most shelf break stations. S. bombyx was somewhat more abundant in finer sands and inner shelf stations stressed by hypoxia during the summer of 1976 (see below).

Species in Group 6 were rare on the inner shelf but were highly constant from the central shelf through the shelf break. They were most abundant in the more stable sands of the outer shelf and upper shelf break (Groups E, F, and G) where they constitute a characteristically occurring assemblage. Although the group shows significant negative fidelity on the inner shelf and continental slope, some more ubiquitous members such as the amphipod Unciola irrorata and the polychaete Aricidea catherinae were common, but not abundant, in both extreme habitats. The amphipod Ampelisca agassizi is the sole member of Group 7. It was the top scoring species in the data reduction ranking, a testimony both to its ubiquity and great local abundance. Ampelisca agassizi was found at all outer shelf, shelf-break, and slope stations and was absent in collections only from five inner and central shelf stations. However, it was only abundant in outer shelf depressions and at the shelf break. At B3 and G3 (site Group F) grand mean abundance of Ampelisca agassizi exceeded 5,000/m^2.

Species in Group 8 were widely distributed on the shelf and shelf break but were virtually absent on the slope. These species were seldom abundant, but were significantly more frequent at central and outer shelf stations and were most abundant at Station L2 (Group D) and at outer shelf stations (Group E). Group 9 species were also widely distributed, but not abundantly, on the shelf and upper slope. They were most common on the outer shelf (Group E and G), but showed no abundance concentration in any particular bathymetric zone. Group 10 species were relatively faithful to inner and central shelf swales and the outer shelf and showed negative fidelity to the inner shelf, shelf break and slope. They were seldom abundant, although several were relatively more abundant at G3 (Group F). Group 11 species were extremely rare on the inner and central shelf, but were more frequently collected on the outer shelf and shelf break. These species were generally not abundant, although the bivalve Nucula delphinodonta at L2 and the polychaete Scoloplos acmeceps at L3 had unusually dense populations.

Species in Group 12 characterized outer shelf depressions and the shelf break and were rare elsewhere on the shelf. Although generally present only in low densities, abundances were greatest at some outer shelf swales stations, in particular E4. Species in Group 13 were of a similar habitat preference, but were somewhat more restricted to Group G stations, in particular E4. Group 14 species were also similarly common but seldom abundant in outer shelf depressions and across the shelf break. Abundance was poorly concentrated in any site group and Group 14 species were more common in shelf-break site Group H than those of Groups 11-13.

Species in Group 15 occurred from the outer shelf swales to the upper slope, but were seldom abundant. They were rare or absent on the shelf and lower slope. Group 16 species were very common subdominants along the shelf break and showed significant fidelity to the shelf break and upper slope. Their abundance generally peaked at stations in Group H. Species in Group 17, like those in Group 15, were common at the shelf break and in shelf swales, where they were most abundant. They were also infrequent on the outer shelf, but in contrast were uncommon at slope stations. Several of these species, e.g. the polychaetes Clymenella torquata, Ninoe nigripes, and Notomastus latericeus, characteristically distinguished the central and outer shelf swale assemblages from those elsewhere on the shelf. Group 18 species were also widely distributed across the outer shelf to the upper continental slope. As with species in Groups 15 and 17, they were most abundant in outer shelf depressions. In contrast to those in Group 15 they were less frequent on the slope and in contrast to those in Group 17 they were rare at inner shelf swales (Group D).

Group 19 species were highly constant shelf-break and upper slope species and were rarely taken on the shelf. This group included many of the characteristic dominants of the shelf-break zone, e.g. the onuphid polychaetes Onuphis atlantisa, Onuphis pallidula and Nothria conchylega, the polychaetes Spiophanes wigleyi, Aricidea neosuecica, and Lumbrineris latreilli, the ophiuroid Amphioplus macilentus, and the two ostracods of the genus Harbansus. Group 20 species were subdominant in the shelf-break zone (Groups G and H) to which they were very faithful. They were less common on the upper slope than Group 19 species.

Species in Group 21 were faithful to the deeper, muddier shelf-break stations (Group H) and the upper slope stations (Group I) where they were dominants or subdominants. Conversely, Group 22 species were faithful to and characteristic of the slope stations. They were infrequent in the shelf-break zone and absent from the shelf.

The continual biotic change across the shelf-slope habitat gradient is strikingly apparent in the nodal diagrams (Figures 6-28 to 6-30). The species distributed themselves in complex patterns across the gradient with a zone of maximum occurrence and density grading off in either direction. The sharpest faunal change across this gradient occurred at the shelf break, underlying the major agglomeration of the normal dendrogram separating shelf stations (Groups A-E) from those in outer shelf depressions and along the shelf-slope transition (Groups F-I). The inverse dendrogram also distinguishes groups of species which were principally found on the shelf (Groups 1-10) and those principally found in the shelf break and slope zones (11-22).

Ordination Results. The community continuum, or coenocline, can perhaps better be seen in the reciprocal averaging ordination of the grand mean data (Figure 6-32). The shape of the coenocline in ordination space is curvilinear rather than linear, with a significant range of scores on axes past the first. This is more an artifact of ordination procedures, all of which distort the biotic continuum into horseshoe-shaped configurations in two dimensions (Gauch et al. 1977), than a representation of the effects of important factors other than those related to the bathymetric gradient. Even so, the first extracted axis explains 67 percent, and the first three, 76 percent of the total variation witnessed in the data set.

The stations are closely ordinated on the first axis according to depth from the inner shelf to the shelf break (rank correlation, $p < 0.01$). The slope stations are poorly separated from the shelf break stations by the first two axes. However, the third axis essentially separates the slope stations (which score low) from all others (which score high). The third axis also separates those inner and central shelf stations in fine sand (Groups A and D) from the other shelf stations. Thus, there is virtually no overlap of station groups defined by numerical classification in the three dimensional ordination.

As with the normal classification the principal hiatus in the coenocline appears at the shelf break, separating Groups F and G from E. This as well as the overall gradational nature of the coenocline is better illustrated in Figure 6-33 in which the ordination scores on the first axis are plotted against depth of the station. A hiatus in first axis score at about 65 m is apparent, separating the outer shelf swales with finer sands and the shelf break stations from those on the shelf.

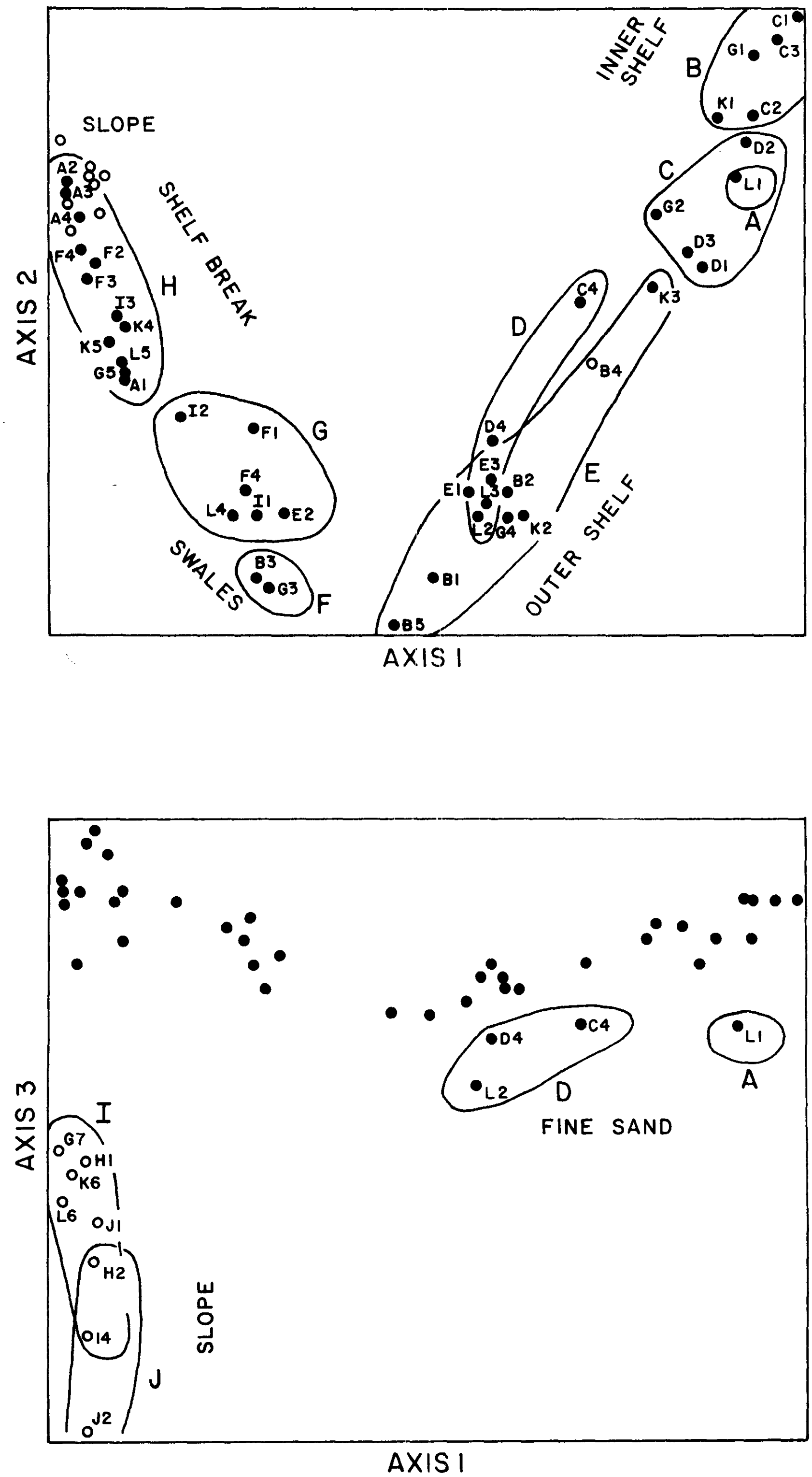


Figure 6-32. Reciprocal averaging ordination of collections of macrobenthos from 52 stations based on grand mean abundance data.

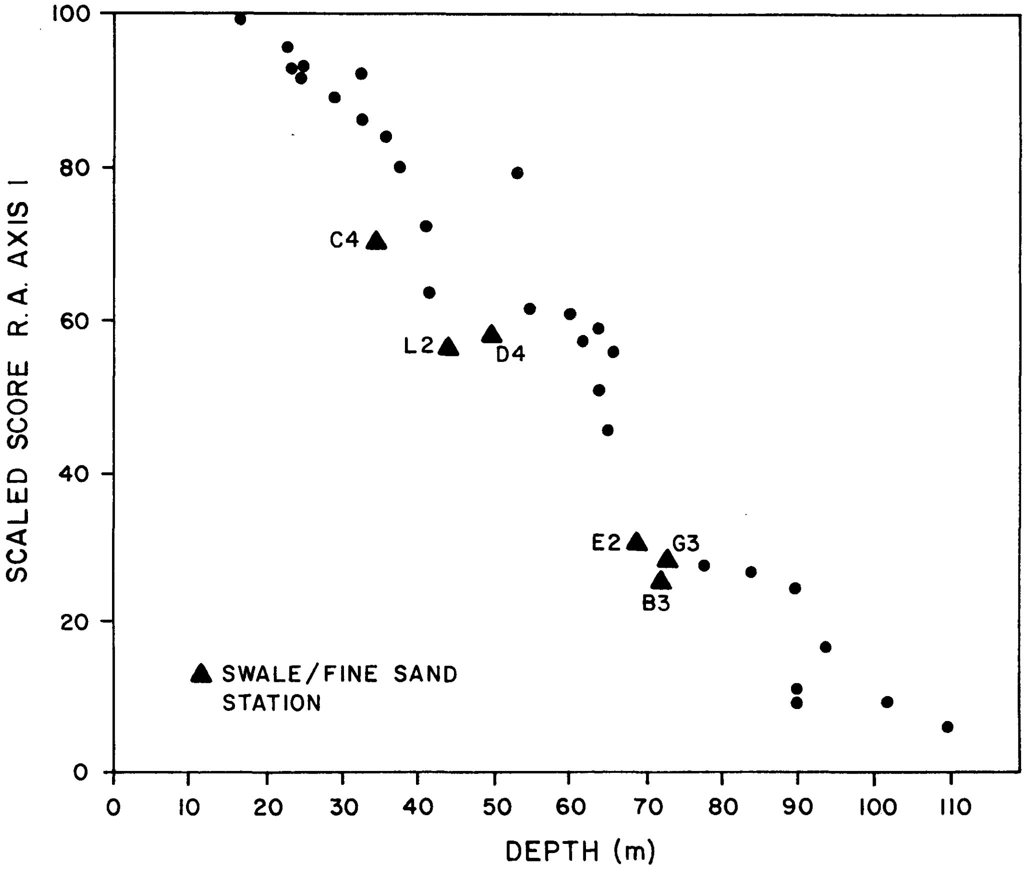


Figure 6-33. Relationship of scaled reciprocal averaging ordination scores for collections of macrobenthos to station depth. Triangles represent stations with finer sands, mainly in topographic depressions.

Reciprocal averaging ordination of species presented a somewhat different representation of the relationship of species distribution patterns than numerical classification. The classification grouped species based on their overall distribution patterns, thus a group of widely distributed species which were most abundant on the outer shelf would be discrete from a group of species faithful to the outer shelf. Reciprocal averaging ordination seeks to place species in ordinated space to reflect their geometric center of distribution along the coenocline. Thus, species in the two hypothetical groups mentioned above may actually be intermingled in ordination space, representing a commodium (Whittaker 1970) of species which have their maximum abundance in a particular segment of the coenocline.

To simplify the confused picture that results and enhance comparison with the classification, species groups were represented in the same ordination space in which stations were cast as the centroids of the points representing the species included in the group (Figure 6-34). Keep in mind that in many cases there was a considerable spread of the individual species points around these centroids. What emerged is a better depiction of the relationships of the species groups than the agglomerative hierarchy of the numerical classification. The basic separation of shelf species groups (1-5, 8-10) and shelf-break-slope species groups (11-22) remains, but the ubiquity and importance of species in Groups 6 and 7 is acknowledged by this placement on the shelf break side of the hiatus along axis 1. The species groups characterizing the various habitats can be clearly seen by superimposing or otherwise comparing the species group ordination on the ordination of stations. For example, species in Groups 19 and 20 were characteristic of stations in Group H, species Group 22 was characteristic of the slope habitat (Groups I, J) and species in Group 3 were characteristic of the fine sands on the inner and central shelf (Groups A, D).

Dominant Species. The foregoing analysis of distributional patterns were based on consideration of a large number (186) of species which made the application of multivariate analyses advantageous. However, consideration of just the numerically dominant species also shows striking differences among the bathymetric habitats on the shelf and slope.

The 10 most numerically important species in each site group produced by the numerical classification were determined by rank analysis in which the top 10 species at each station were rank-scored based on the arithmetic mean of the geometric mean seasonal estimates of abundance. The most abundant species scored 10 points, the second most abundant 9, etc. These scores were averaged over the stations in the site group to derive a rank index (possible range 0-10) for that species in that site group. Species were ranked by the index and the top 10 scoring species are included in Table 6-6.

The community of the inner shelf habitat (Site Groups A and B) was dominated by interstitial-burrowers and burrowing deposit feeders

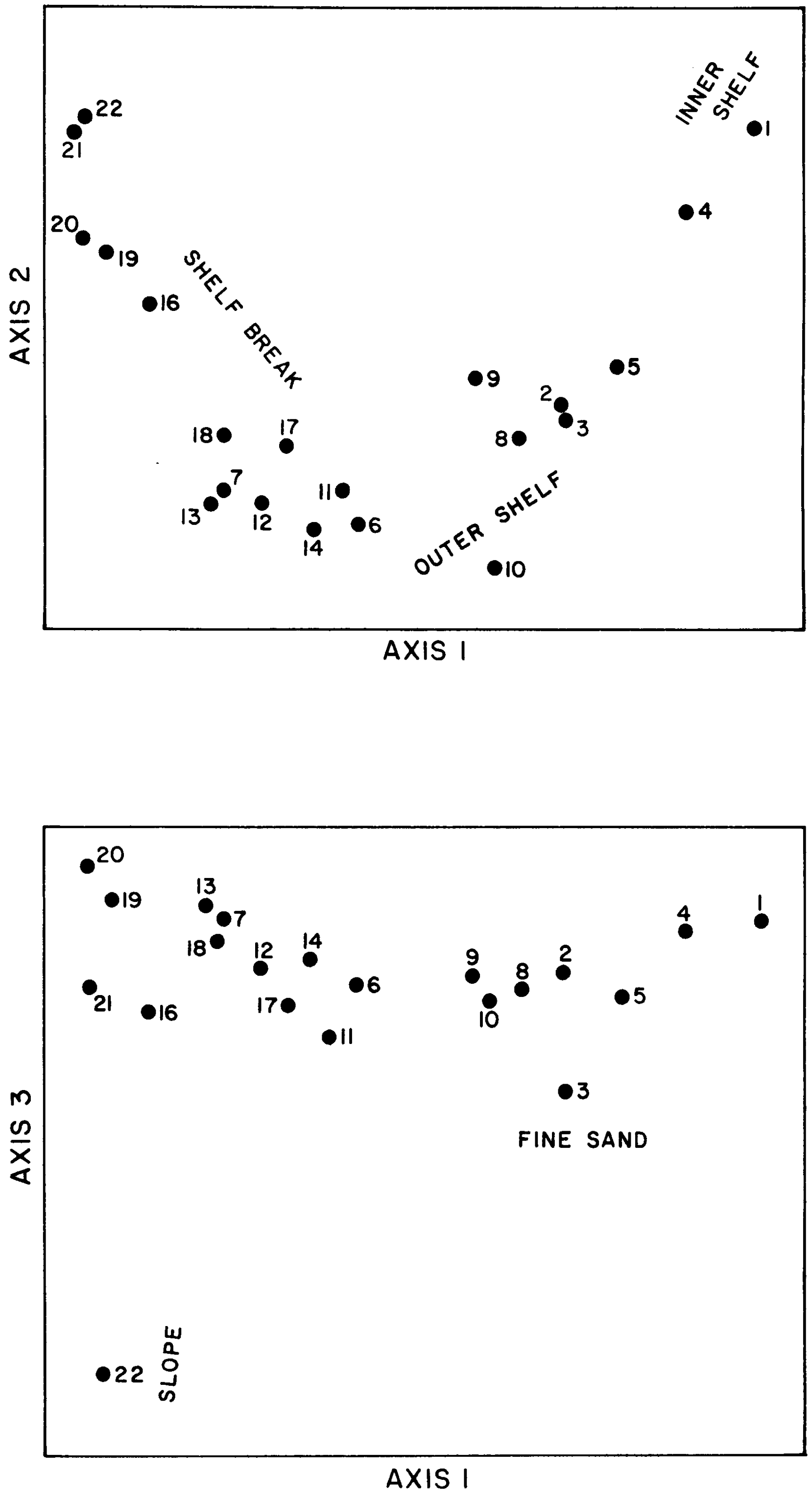


Figure 6-34. Reciprocal averaging ordination of species groups indicated in Table 6-5. Scores are centroids of individuals species scores.

Table 6-6 . Numerically dominant species in major bathymetric habitats (A=amphipod; B=bivalve; C=cumacean, E=echinoid, Op=ophuroid, Os=ostracod, P=polychaete). Species are ranked by average rank index (see text), also given are the numerical classificatory groups in which the species was placed, geometric mean density and living position-feeding category (B=burrower, D=subsurface deposit feeder, E=epifaunal, F=fossorial, I=interstitial feeders, P=suspension feeders, S=surface deposit feeder and T=tubicolous).

Species	Group	Rank Index	Mean Density(m^{-2})	Living-Position Feeding Category
INNER SHELF - GROUPS A & B				
Tanaissus liljeborgi (T)	4	7.2	227.5	I
Polygordius sp. (P)	4	7.0	315.4	I
Goniadella gracilis (P)	4	6.8	307.6	I
Tellina agilis (B)	1	6.7	132.9	B-S
Spiophanes bombyx (P)	5	4.5	276.3	T-S
Spisula solidissima (B)	1	4.2	56.2	B-P
Nephtys picta (P)	1	2.5	39.1	B-D
Lumbrinerides acuta (P)	4	2.3	83.8	I
Echinarachnius parma (E)	8	1.8	33.1	E-S
Pseudunciola obliquua (A)	1	1.7	55.6	T-S
CENTRAL SHELF - GROUP C				
Pseudunciola obliquua (A)	1	9.0	200.0	T-S
Tanaissus liljeborgi (T)	4	6.5	78.9	I
Trichophoxus epistomus (A)	8	6.3	92.3	F
Spiophanes bombyx (P)	5	5.3	219.1	T-S
Echinarachnius parma (E)	8	5.0	63.3	E-S
Goniadella gracilis (P)	4	4.5	113.7	I
Protohaustorius wigleyi (A)	1	5.5	53.9	F
Spisula solidissima (B)	1	3.0	88.6	B-P
Byblis serrata (A)	6	2.8	54.2	T-S
Lumbrinerides acuta (A)	4	2.3	25.3	I
CENTRAL AND INNER SHELF SWALES - GROUP D				
Spiophanes bombyx (P)	5	8.3	798.7	T-S
Lumbrineris impatiens (P)	6	6.0	292.5	B-D
Polygordius sp. (P)	4	6.0	276.0	I
Nucula proxima (B)	3	5.3	214.6	B-D
Cytheretta edwardsi (Os)	3	3.7	153.1	E-S
Tellina agilis (B)	1	3.7	195.8	B-S
Trichophoxus epistomus (A)	8	3.3	111.0	F
Nucula delphinodonta (B)	22	3.3	168.4	B-D
Clymenella torquata (P)	17	3.0	126.1	T-D
Unciola irrorata (A)	6	2.7	93.0	T-S

Table 6-6. (continued)

Species	Group	Rank Index	Mean Density (m^{-2})	Living-Position Feeding Category
OUTER SHELF - GROUP E				
Unciola irrorata (A)	6	7.5	260.0	T-S
Spiophanes bombyx (P)	5	5.8	329.0	T-S
Ampelisca vadorum (A)	6	4.4	460.4	T-S
Goniadella gracilis (P)	4	3.6	188.0	I
Lumbrinerides acuta (P)	4	3.6	91.0	I
Byblis serrata (A)	6	3.4	148.9	T-S
Trichophoxus epistomus (A)	8	3.1	63.7	F
Erichthonius rubricornis (A)	6	3.0	302.2	T-S
Euchone sp. A (P)	10	2.4	111.1	T-P
Ampelisca agassizi (A)	7	1.8	215.2	T-S
OUTER SHELF SWALES - GROUP F				
Ampelisca agassizi (A)	7	10.0	7054.2	T-S
Unciola irrorata (A)	6	8.5	552.7	T-S
Erichthonius rubricornis (A)	6	7.5	464.0	T-s
Diastylis bispinosa (C)	10	6.0	332.0	F
Photis dentata (A)	18	5.0	238.4	T-S
Notomastus latericeus (P)	18	3.5	189.0	B-D
Lumbrineris impatiens (P)	6	3.0	217.5	B-D
Eudorella pusilla (C)	18	2.5	149.5	F
Euchone sp. A (P)	10	2.0	172.5	T-P
Scalibregma inflatum (P)	6	1.5	60.3	B-D
SHELF SWALE-SHELF BREAK TRANSITION - GROUP G				
Notomastus latericeus (P)	18	7.7	180.4	B-D
Ampelisca agassizi (A)	7	7.5	685.3	T-S
Chone infundibuliformis (P)	6	6.7	301.8	T-P
Unciola irrorata (A)	6	5.0	122.3	T-S
Erichthonius rubricornis (A)	6	3.3	100.1	T-S
Onuphis pallidula (P)	19	3.2	86.1	T-S
Lumbrineris impatiens (P)	6	2.3	92.6	B-D
Axiognathus squamata (Op)	18	2.2	48.4	B-S
Ampelisca vadorum (A)	6	2.0	65.1	T-S
Scoloplos acmeceps (P)	11	1.8	50.2	B-D

Table 6-6. (concluded)

Species	Group	Rank Index	Mean Density(m^{-2})	Living-Position Feeding Category
SHELF BREAK - GROUP H				
Ampelisca agassizi (A)	7	8.2	566.2	T-S
Lumbrineris latreilli (P)	19	6.2	165.6	B-D
Thyasira flexuosa (B)	19	5.9	152.5	B-P
Onuphis pallidula (P)	19	5.7	157.8	T-S
Aricidea neosuecica (P)	19	5.4	405.9	B-D
Harbansus bowenae (Os)	19	3.2	101.5	E-S
Spiophanes wigleyi (P)	19	3.1	86.0	T-S
Amphioplus macilentus (Op)	19	2.8	232.1	B-P
Onuphis atlantisa (P)	19	2.3	63.5	T-S
Unciola irrorata (A)	6	1.8	70.0	T-S
UPPER SLOPE - GROUP I				
Thyasira flexuosa (B)	19	7.0	111.2	B-P
Lasaea rubra (B)	21	6.5	89.1	B-S
Onchnesoma steenstrupi (S)	21	6.0	99.4	B-S
Notomastus latericeus (P)	18	5.8	65.4	B-D
Paramphinome pulchella (P)	22	4.3	51.2	B-D
Auchenoplax crinita (B)	22	3.3	0.4	B-P
Lumbrineris latreilli (P)	19	2.5	33.6	B-D
Paraonis gracilis (P)	16	1.8	29.5	B-D
Harbansus bowenae (Os)	19	1.7	32.9	E-S
Nucula tenuis (B)		1.5	24.6	B-D
MIDDLE SLOPE - GROUP J				
Nucula delphinodonta (B)	22	7.5	20.2	B-S
Nucula tenuis (B)	22	6.5	11.7	B-S
Lumbrineris tenuis (P)	22	6.5	18.6	B-D
Ceratocephale loveni (P)	22	5.0	31.3	B-S
Thyasira pygmea (B)	22	5.0	19.6	B-P
Paranois gracilis (P)	16	4.5	9.0	B-D
Lumbrineris impatiens (P)	6	4.5	12.2	B-D
Harpinia sp.2. (A)	18	4.0	10.5	E-S
Paramphinome pulchella (P)	22	3.5	5.8	B-D
Mitrella diaphana (G)		3.5	8.3	E-C

in species groups 1 and 4. Only the widely distributed *Spiophanes bombyx* and *Echinarachnius parma* were not members of either of these groups. Many of the dominants in the central shelf station group were similar to those of the inner shelf (7 species are shared); species in groups 1 and 4 were also well represented. However, the interstitial-burrowers of group 4 were decidely less important in the slightly finer sands present at these stations. Two fossorial amphipods were abundant on the central shelf and there was a paucity of deposit feeders. The dominant species of the finer sediments of central and inner shelf swales (Group D) demonstrate the striking differences between the macrobenthic community of these depressions and those of the surrounding bottom of the inner and central shelf. Only four of the species were included among the dominants in either of the previous habitats and only one member each of species groups 1 and 4 are represented. Some of these species were also dominants in deeper water habitats (e.g. *Lumbrineris impatiens* and *Unciola irrorata*), while members of Group 3 were only abundant in the swales. The dominants at Group D stations included more subsurface deposit feeders than other shallow shelf communities.

The dominants of the outer shelf are in part similar to those of the central shelf (5 species shared). This is partially due to the fact that assemblages of the outer shelf are hetergeneous. The assemblages at some stations were similar to those inshore and included the interstitial-burrowers of Group 4. Other collections were dominated by the tubicolous amphipods in groups 6 and 7 as well as various deposit feeding polychaetes. Distributional patterns on the outer shelf are analyzed in detail under the following section on medium scale patterns of distribution. The importance of tubicolous amphipods on the outer shelf is noteworthy - 6 of the top 10 species are amphipods and 5 of these are surface-deposit feeding tube dwellers. Such organisms were not nearly as numerically important in the shallower habitats or on the shelf break.

Assemblages in topographic depressions on the outer shelf (Site Group F) were even more heavily dominated by pericaridan crustaceans - the top five species are four amphipods and one cumacean. Deposit feeders, including surface and subsurface feeders, strongly predominated in the organically richer sediments of the depressions. Several dominants were found widely on the outer shelf, but were much more abundant in the swales, e.g. *Ampelisca agassizi*, *Erichthonius rubricornis*, *Diastylis bispinosa*, *Eudorella pusilla*, and *Lumbrineris impatiens*. Other species were common shelf-break species which extended into the deeper swales, e.g. *Notomastus latericeus*.

In the outer shelf swale and shelf edge habitats represented in Group G, the dominants were intermediate between those at Group E and F stations (six species included) and those in shelf-break zone (Group H, three species included). The numerical importance of the polychaetes *Chone infundibuliformis* and *Scoloplos acmeceps* distinguished this transitional zone. Interstitial-burrowers were lacking from the dominants and tubicolous surface feeders and subsurface feeding burrowers predominated.

The dominants in the shelf-break habitat (Group H) were highly diagnostic. Eight of the top 10 species belonged to Group 19. Only one was among the dominants in site groups A-G and only three were among the dominants on the upper continental slope (Site Group H). Dominant species were tubicolous surface deposit feeders, burrowing subsurface deposit feeders or suspension feeders.

Dominance by two Group 21 species and three Group 22 species was specific to the upper slope habitat (Group H). Only three of the top 10 species were shared between the upper and middle slope (Group I). Bivalve molluscs were much more important on the continental slope than elsewhere. Predominant feeding strategies were suspension feeding and subsurface deposit feeding. Tubicolous animals were notably reduced in abundance. The dominants at the mud slope station were present in considerably lower densities than those in shallower habitats. Deposit feeding protobranch bivalves and burrowing polychaetes were the most abundant forms. Incompletely identified cirratulid (burrowing surface deposit feeders) and ampharetid (tubicolous surface deposit feeders) polychaetes were also abundant in the upper and middle slope, but are not included in Table 6-6. Five of the top 10 species belong to Group 22.

Temporal Effects. There remains a question as to whether the distributional patterns based on grand mean abundance are truly representative since important temporal variations may be obscured by averaging. Numerical classifications (square root transformation, Bray-Curtis similarity, and group average clustering) were produced for all seasonal collections from stations grouped by bathymetric stratum (15-50 m, 50-80 m, 80-200 m, and 300-750 m). These classifications (Figure 6-35) reveal the truly striking faunal similarity of seasonal collections from fixed stations relative to between station differences. Temporal collections grouped generally in no pattern consistent with season of collection. Those cases where collections from particular stations did not tightly cluster may be explained by a) differences between sampling periods in the composition of sediments sampled (Chapter 5), b) effects induced by hypoxic stress during and subsequent to the summer of 1976 (discussed at length below), or c) intense sampling (i.e. several stations) in relatively homogeneous areas, in particular the outer shelf.

Medium Scale Patterns of Distribution

The above analyses of large scale patterns indicate that great differences in faunal assemblages can occur within bathymetric zones of the shelf in response to mesoscale topography. To better describe and understand the causes of these mesoscale patterns the habitat

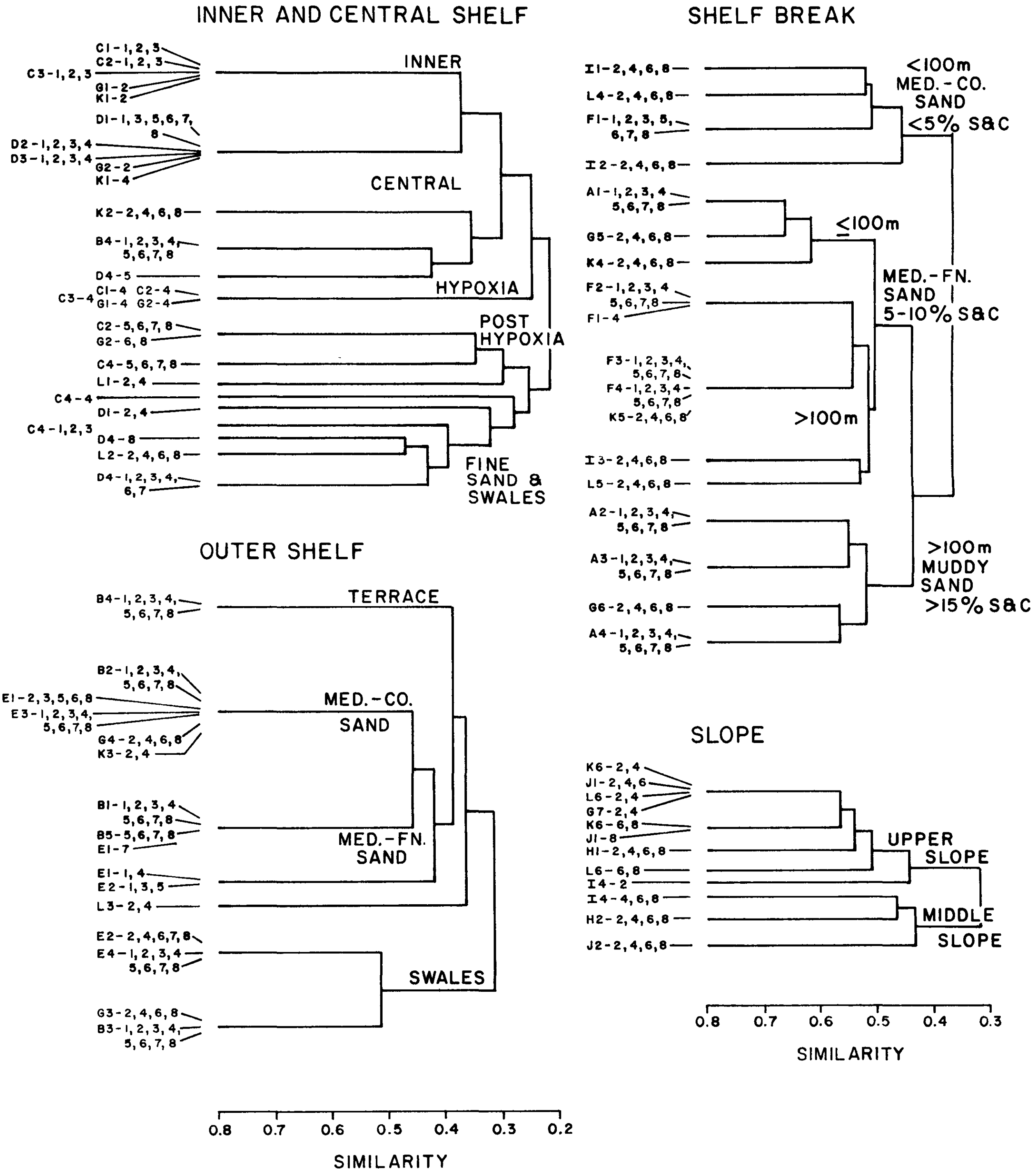


Figure 6-35. Hierarchies resulting from agglomerative classification of seasonal collections of macrobenthos grouped by major bathymetric habitat.

delineation study was conducted. Subsections of cluster areas E and B were sampled randomly within a priori habitat strata during fall 1976. These subsections included the fixed, repetitively sampled stations in those areas. The species abundance data from the six replicate samples from the fixed stations were standardized to 0.1 m^2. A total of 54 stations was sampled in Area B and 44 in Area E.

Numerical classification (square root transformation, Bray-Curtis similarity, group average sorting for normal analysis, flexible sorting for inverse analysis) was performed on reduced data sets consisting of all species occurring at five or more stations in Area B and four or more in Area E. Reciprocal averaging ordination was effected on square root transformed abundances of the 50 most common and abundant species in each area. Delineation of major habitats was based on the collective consideration of the results of normal classification and ordination of the biotic data, distribution of sediment grain-size composition (Chapter 5) and appearance of bottom photographs collected at the time of sampling. In order to delineate the recognized habitats, starting with the numerical classifications based on biotic data, the stations were reallocated where this seemed appropriate based on the station ordination. Further reallocation was effected for stations of intermediate affinities based on consideration of grain size distribution and bottom photographs. As will be seen, the resulting classifications were basically similar to that resulting from the initial numerical classification, reallocations mainly involved small groups of stations of intermediate affinities which were not instructively related in the group average agglomeration. Interpolation and extrapolation from the existing stations was made consistent with the topography by generally following isobaths.

Area B. Five major habitats, with subdivision of two of the habitats, were recognized for Area B (Figure 6-36). These were closely related to the topography and sediment composition. The sediment characteristics of each of the habitats are discussed in detail in Chapter 5. Generally, sediments on the terrace (Habitat 1) were coarse-skewed medium or medium-coarse sands; sediments in the ridge habitat (Habitat 2A) were coarse-skewed medium sands; sediments in Habitat 2B were nearly symmetrical medium sands; sediments in Habitat 3A were fine-skewed medium sands with a small amount of silt and clay; sediments in the eroded flank habitat were poorly sorted mixed sands with a small amount of silt and clay; sediments in the shallow swale (Habitat 4) were muddy, medium-fine sands; and sediments in the deep swale (Habitat 5) were muddy-fine sands.

The hierarchical classification of the 54 collections of macrobenthos is presented in Figure 6-37. Separation of the extreme habitats, the terrace and the deep swale, was very good, but collections from intermediate habitats (habitats 2-4) were grouped in a seemingly confused pattern. All Habitat 2 collections were

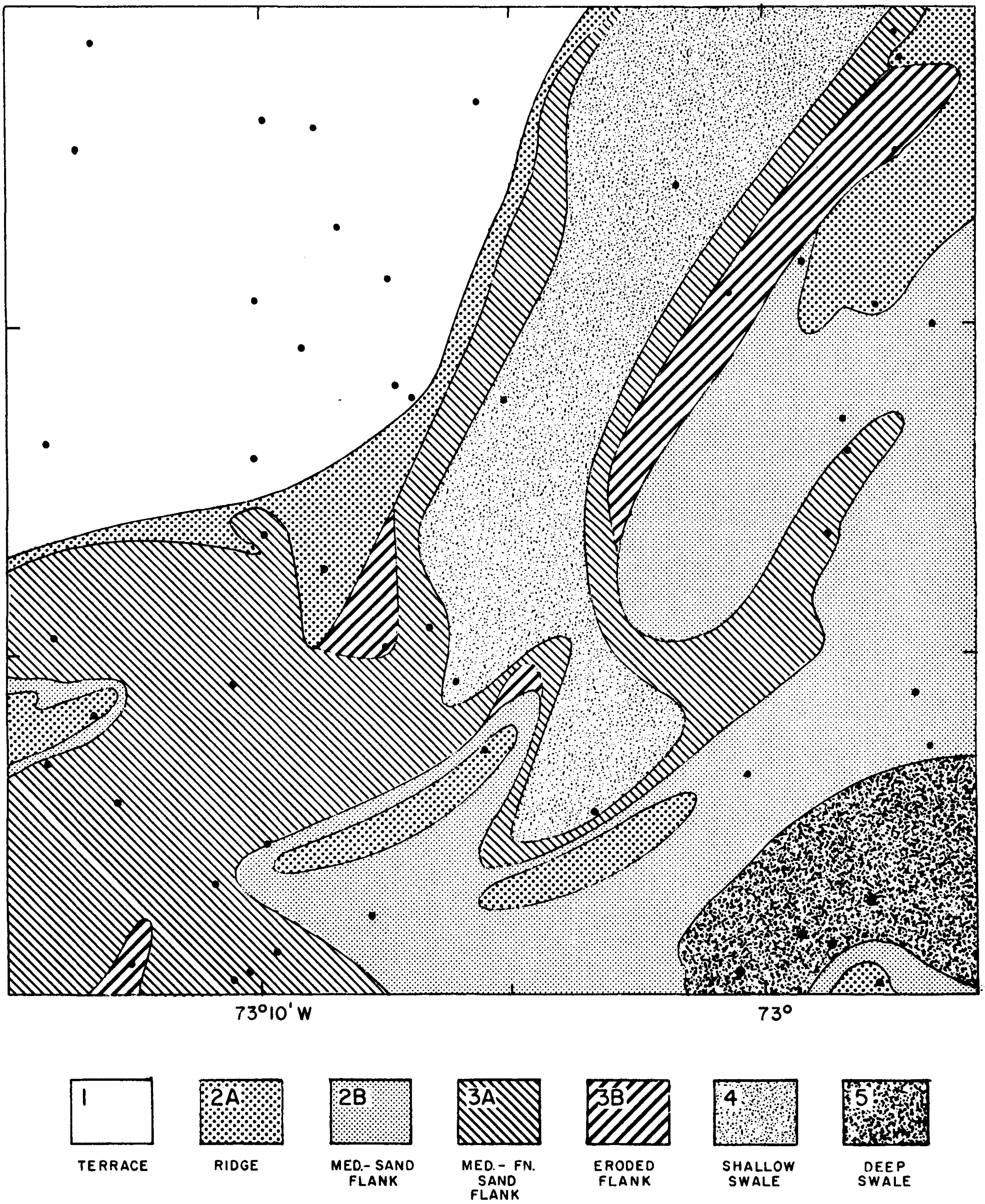


Figure 6-36. Distribution of major habitats identified in habitat delineation study of macrobenthos, area B.

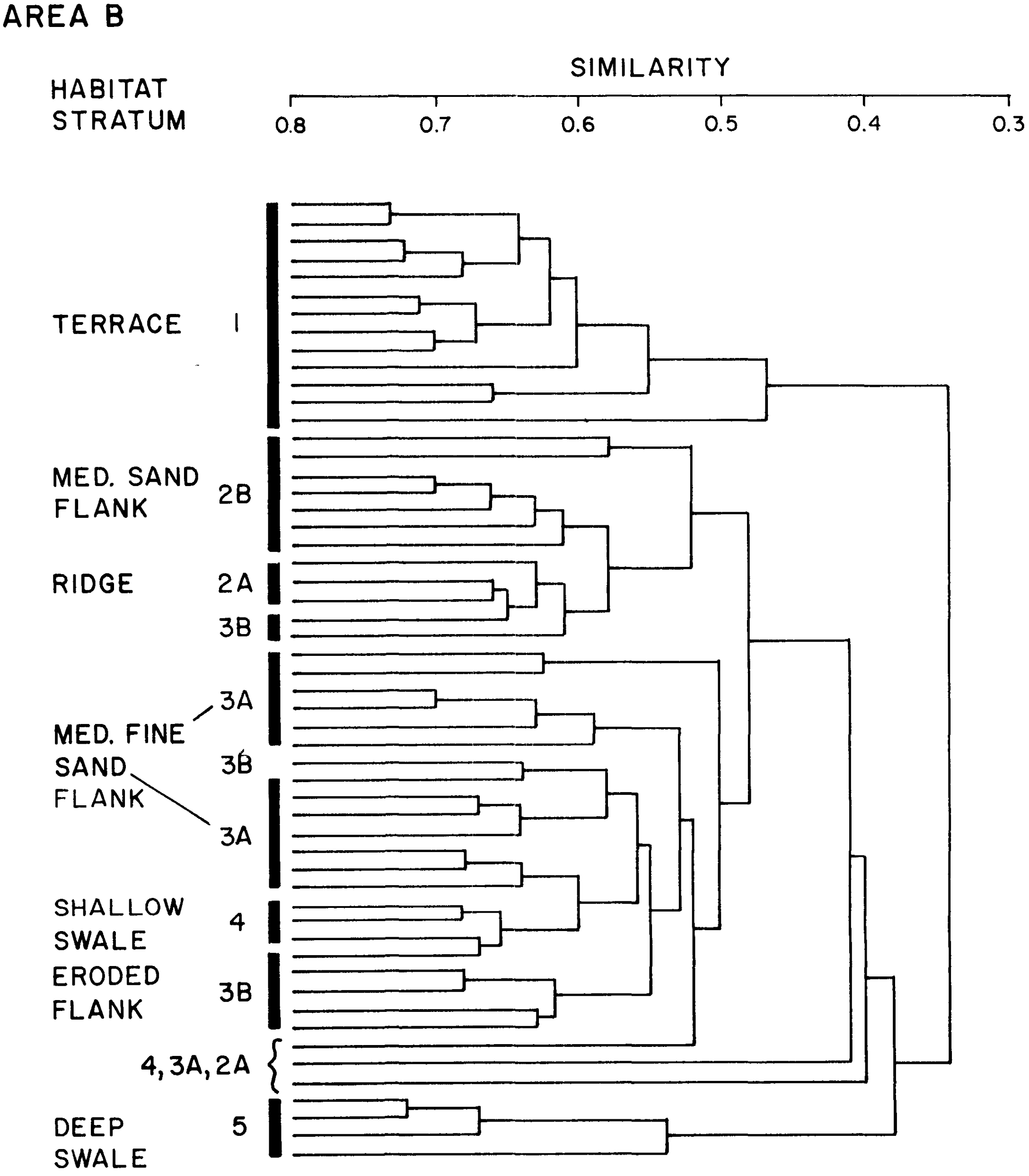


Figure 6-37. Classification hierarchies resulting from agglomeration of collections of macrobenthos from habitat delineation study of Area B. The final disposition of samples in recognized habitats is indicated.

separated in one main cluster together with some from the deeper eroded flank habitat where the sediments were relatively coarse. Collections from the finer sediment habitats 3 and 4 were more homogeneous. Although most Habitat 4 collections agglomerated in one group, collections from habitats 3A and 3B were interspersed. The distinction between these two habitats was made somewhat clearer in subsequent nodal analyses and ordination, and the separation was consistent with sediment differences.

The 110 species included in the inverse classification were interpreted at the 16 group level as indicated in Table 6-7. The distributional characteristics of these species groups are indicated in the nodal analyses represented in Figure 6-38.

Species in groups 1-4 were more common and abundant in the coarser sediments of the terrace, ridge and medium sand flanks. Group 1 members were characteristic inner shelf species which although seldom abundant, were virtually restricted to the terrace. Species in Group 2 were highly faithful to the terrace and include species characteristic of the coarse dynamic sand habitats on the inner and central shelf. These species are small, interstitial burrowers or fossorial forms adapted for life in shifting sands. Species in Group 3 were also more frequent on the terrace and were an average of 2-6 times more abundant there than overall in Area B. However, they were more widely distributed in coarse and medium sand habitats throughout the area. Group 4 species were widely distributed in Area B, but were more frequent and constant in the terrace habitat. This group included species which were generally characteristic of coarse to medium sand bottoms on the shelf, such as the polychaetes Goniadella gracilis, Lumbrinerides acuta, and Euclymene collaris and the tanaidacean Tanaissus liljeborgi. Members of this group were included in groups 4, 6, 8, and 9 of the grand mean analysis of all 51 stations (Table 6-5). Goniadella and Lumbrinerides were particularly good indicators of the coarser sands of habitats 1 and 2. Members of Group 4 are either interstitial, fossorial, or have deep-tubes or burrows to maintain purchase in dynamic sands.

Species in Groups 5-8 were generally ubiquitous, but showed low frequency and abundance in the terrace habitat. Group 5 species were seldom abundant, except for Caulleriella sp. They were less frequent on the terrace and swales than in intermediate habitats and were most common in Habitat 2B. The four amphipods and two polychaetes included in Group 6 were characteristic of relatively stable medium to medium-fine sand, and thus were very characteristic of Habitat 3A. They are all tubicolous surface feeders. Species in Group 7 were most ubiquitous and as a group show no significant fidelity or particular abundance concentration to any habitat. Some of these wide-spread species (e.g. the sand dollar Echinarachnius parma and the polychaete Spiophanes bombyx) were less common and reduced in abundance in the deep swale habitat. Species in Group 8 were widely distributed except on the terrace and were not very abundant on the ridges. They

Table 6-7. Species groups selected from numerical classification of macrobenthos collected in habitat delineation study of Area B.

Species Group 1

Nephtys bucera
Polydora caulleryi
Nemertea sp. 2
Astarte castanea

Species Group 2

Aricidea cerrutii
Protodorvillea kefersteini
Parapionosyllis sp. A
Streptosyllis arenae
Chiridotea arenicola
Retusa obtusa
Paradoneis lyra
Protohaustorius wigleyi

Species Group 3

Sthenelais limicola
Aphrodita hastata
Glycera robusta
Edotea triloba

Species Group 4

Drilonereis magna
Tanaissus lilijeborgi
Clymenura sp. A
Goniadella gracilis
Lumbrinerides acuta
Euclymene collaris
Cirolana polita
Arctica islandica
Ensis directus
Lumbrineris fragilis
Schistomeringos caeca
Cerastoderma pinnulatum

Species Group 5

Drilonereis longa
Siphonoecetes new sp.
Caulleriella sp.

Species Group 6

Phyllodoce mucosa
Trichophoxus floridanus
Byblis serrata
Erichtonius rubricornis
Ampelisca vadorum
Euchone incolor

Species Group 7

Unciola irrorata
Echinarachnius parma
Spiophanes bombyx
Polygordius sp. 1
Tharyx sp.
Exogone hebes
Aricidea catherinae
Ampharetidae

Species Group 8

Nereis grayi
Lumbrineris impatiens
Diastylis bispinosa
Phascolion strombi
Ptilanthora tricarina
Astyris sp.
Phoxocephalus holbolli
Scalibregma inflatum
Euchone sp. A
Aglaophamus circinata
Exogone verugera

Species Group 9

Cerebratulus lacteus
Aricidea wassi
Diastylis sculpta
Nicolea venustula
Phoronis psammophila

Species Group 10

Sphaerodoridium claparedii
Chaetozone sp.
Colus pygmaeus
Cytheretta edwardsi

Table 6-7. (Concluded)

Species Group 11

Harpinia sp. 2
Asterias vulgaris
Corophium crassicorne
Harpinia n sp. 5

Species Group 12
Prionospio sp. A
Thracia conradi
Glycera dibranchiata
Cerianthidae
Clymenella torquata
Nemertea sp. 5
Photis macrocoxa
Tubulanus sp.

Species Group 13

Scoloplos acmeceps
Solariella obscura
Lunatia triseriata
Leptocheirus pinguis

Species Group 14

Pherusa affinis
Edwardsia sp.
Cancer irroratus
Unciola inermis
Harmothoe extenuata
Chone infundibuliformis
Cirrophorus lyriformis
Ampelisca agassizi

Species Group 15

Polycirrus eximius
Cancer borealis
Axiognathus squamata
Cyclocardia borealis
Laonice cirrata
Potamilla reniformis
Pholoe minuta
Polydora concharum

Species Group 16

Spiophanes wigleyi
Nucula delphinodonta
Ophelina acuminata
Notomastus latericeus
Eudorella pusilla
Goniada brunnea
Golfingia minuta
Astarte undata
Photis dentata
Crenella glandula
Periploma fragile
Eriopisa elongata
Astropecten americanus

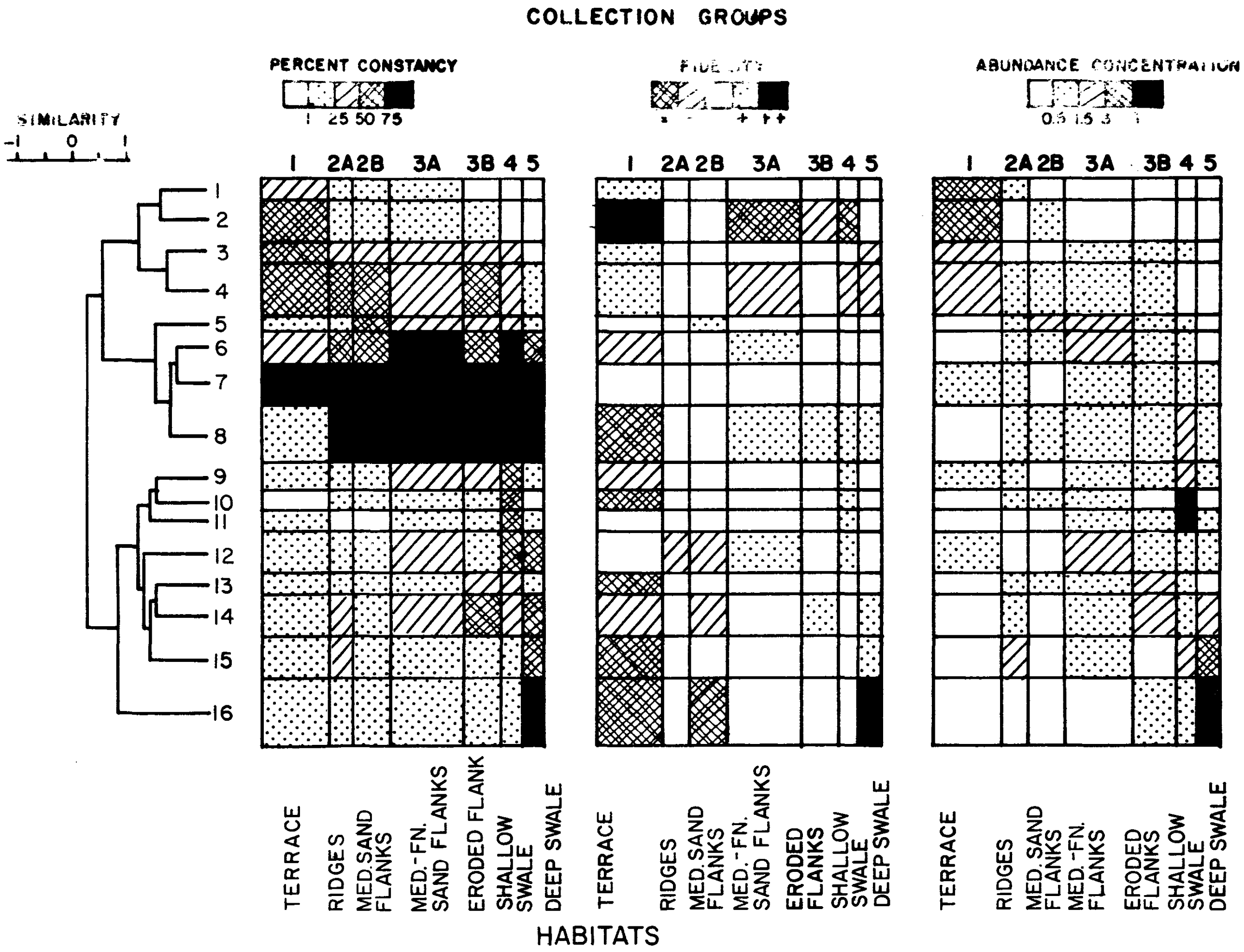


Figure 6-38. Hierarchical classification of species groups of macrobenthos and their nodal statistics in topographic habitat strata, Area B.

preferred deeper, finer-sediment habitats (habitats 3A, 3B, and 4) than species in Group 6.

The remaining species in groups 9-16 all showed varying degrees of preference for the finer sediments and more quiescent conditions of habitats 3-5. Species in groups 9, 10, and 11 were relatively infrequent and seldom abundant forms which were even rarer on the ridges and terrace. Several species in groups 10 and 11 were highly charcteristic of the shallow swale (Habitat 4).

Species in Group 12 were widely distributed, but seldom abundant. They were more frequent and abundant in the medium-fine-sand flank habitat (3A). Group 13 species were also rare, deep water species not found on the terrace, but were slightly more abundant in the eroded flank habitat. Species in Group 14 were relatively faithful to deeper flanks and swales although they were found widely below the terrace. The group includes the amphipod *Ampelisca agassizi* which was widely distributed but only very abundant in swale habitats. Species in Group 15 were widely distributed (except on the terrace) but were only common or abundant in swales. Group 16 species were frequent and highly faithful members of the deep swale assemblage. Most of the species included were characteristic of the shelf break, and many were included in Group 16 of the "grand mean" analysis of large scale shelf-slope patterns (Table 6-5). Their occurrence in the deep swale in Area B represents the shallowest intrusion for many of these species.

The assemblages of the recognized habitats can be clearly distinguished by their complements of species groups (Figure 6-38). The terrace community was characterized by species in groups 1-4, which are predominantly interstitial or fossorial animals. The fauna of the ridges consisted of elements of the terrace fauna, but also included some species characteristic of more stable substrates (e.g. species in groups 6 and 8). The deep swale assemblage was distinguished by a paucity of psammophiles characteristic of most shelf habitats and the presence of some shelf-break species (Group 16) and tubicolous outer shelf forms (Group 14). The medium-fine sands of flank and shallow swale habitats were populated by some elements of both extreme habitats, ubiquitous species and several other species which had a peak abundance in the stable sands of these habitats (e.g. groups 6, 10, 11, and 12). Many of these species are surface tube dwellers or burrowers which are not very active and thus require more stable substrate conditions. The fauna of eroded flanks contained a curious mixture of coarser sand forms (e.g. Group 4) and species more characteristic of stable substrates and deeper bottoms (e.g. groups 13 and 14).

The gradient of conditions from dynamic coarse sands of the shallow terrace to stable fine sands of the deep swales is represented on the first two axes of ordination space in the typical horseshoe shape (Figure 6-39), much like that for the "grand mean" analysis of

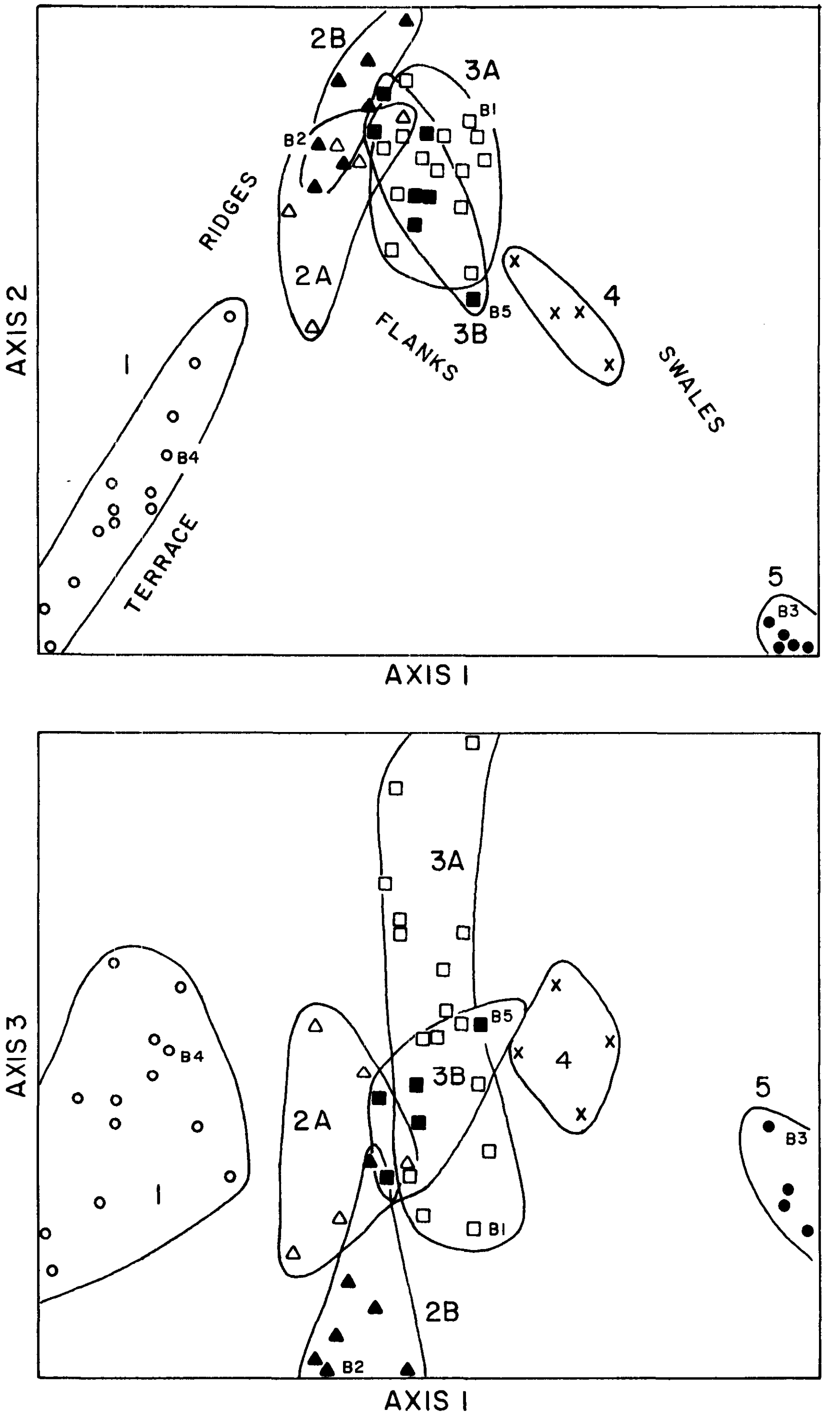


Figure 6-39. Reciprocal averaging ordination of collections of macrobenthos from habitat delineation study of Area B. The disposition of samples in habitats and the location of regular stations is indicated.

all 52 fixed stations (Figure 6-32). The first axis basically describes the coenocline, the second axis is probably artificial, and the third axis separates collections from intermediate habitats. These three axes account for 55% of the variation. As in the classification, the terrace and deep swale habitats (1 and 5) are distinct, but the intermediate habitats are intermingled. Habitat 4 is more discrete than implied by the classification. Habitats 2A and 2B are separated in three-dimensional space; however, habitats 3A and 3B overlap broadly.

The ordination emphasizes the continuum nature of the benthic assemblages over the range of habitats in Area B and reminds us that this, like many classifications, is a somewhat artificial dissection. Nevertheless, the five fixed, repetitively sampled stations in Area B well represent the range of sedimentary habitats and macrobenthic assemblages in Area B.

The ordination of species on the first two axes of the same space is shown in Figure 6-40. Species are positioned in the same area as the collections they characterize, thus this galaxy of points has the same horseshoe shape as that for the collections.

Species characteristic of coarser sands such as the polychaetes *Protodorvillea kefersteini*, *Euclymene collaris*, *Goniadella gracilis*,and *Lumbrinerides acuta* have low scores on axis 1. Ubiquitous species occurring on the terrace (e.g. the polychaete *Spiophanes bombyx* and the amphipod *Unciola irrorata*) have somewhat higher scores. Species found preferentially on more stable or finer sand bottoms (e.g. the polychaetes *Scalibregma inflatum*, *Lumbrineris impatiens*, and *Clymenella torquata* and the ampeliscid amphipods *Byblis serrata* and *Ampelisca vadorum*) have even higher scores. Species most abundant in or restricted to swales (e.g. the crustaceans *Eudorella pusilla*, *Ampelisca agassizi*, and *Photis dentata* and the polychaete *Notomastus latericeus*) scored high on the first axis.

Area E. Five major habitats, with subdivisions of three, were also recognized in Area E (Figure 6-41). As in Area B the habitats are closely related to topography and sediment distribution and range from ridge habitats to swales of various characteristics and shelf-break habitats not represented in Area B. Sediment and depth characteristics of each habitat are discussed in detail in Chapter 5. Habitat 1A is located on topographic ridges in less than 65 m where sediments are coarse-skewed medium sand. The one station placed in Habitat 1B is deeper (74 m) than stations in 1A and occurred in an area with unusually coarse sediment. Megaripples almost 1 m from crest to crest were present in this habitat and can be seen in the bottom photograph taken. This is obviously an area of strong currents, possibly related to tidal current exchange at the shelf edge. Areas classified in Habitat 2 are located on the flanks of ridges but have a variety of sediment types, mostly fine-skewed medium

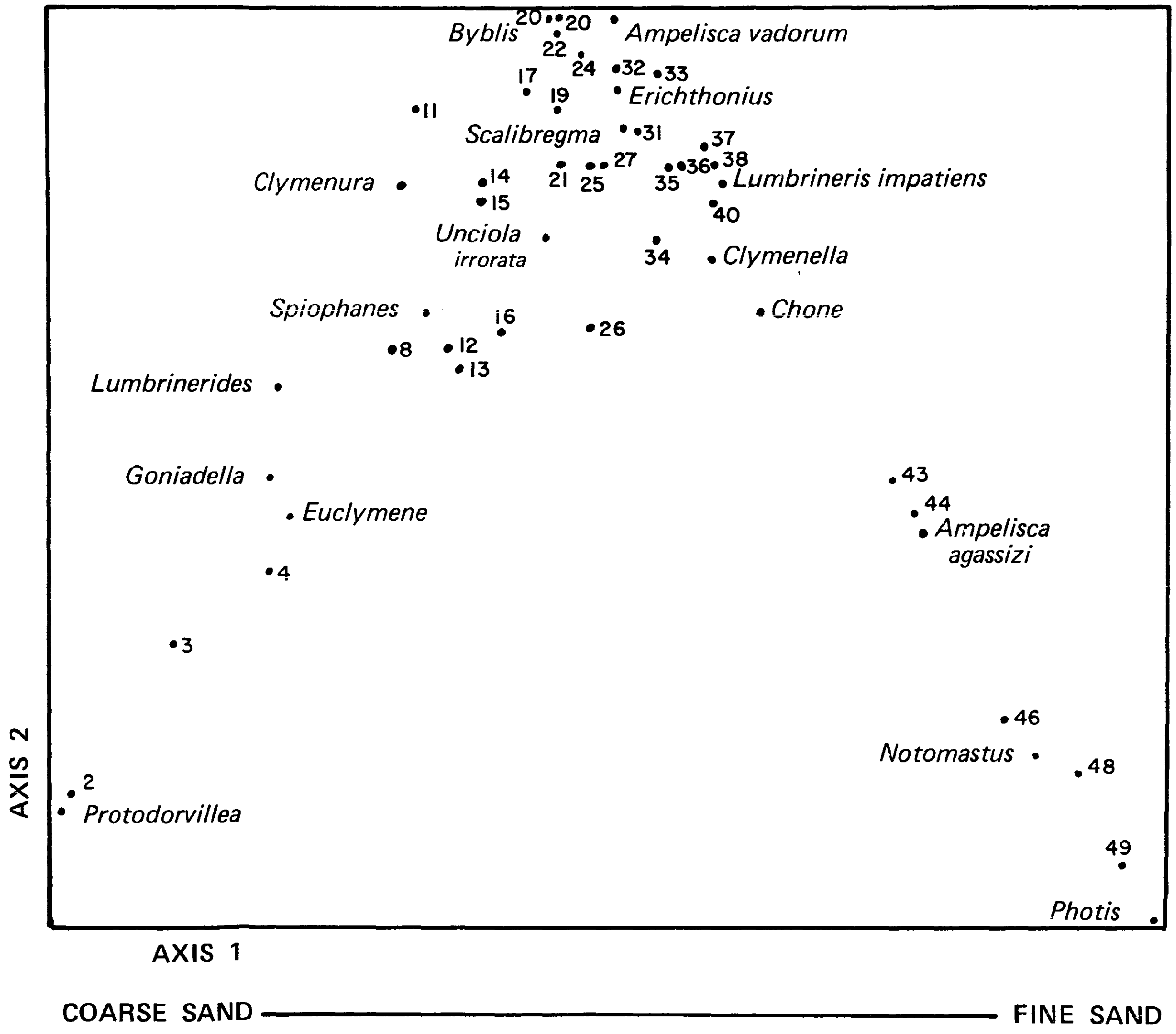


Figure 6-40. Reciprocal averaging ordination of species of macrobenthos from habitat delineation study of area B. Numbers refer to species as indicated in Table 6-8.

Table 6-8. Species used in reciprocal averaging ordination of collections from Area B, habitat delineation study. Numbers refer to Figure 6-40.

Reference Number	Species	Reference Number	Species
1	*Protodorvillea kefersteini*	40	*Phascolion strombi*
2	*Chiridotea arenicola*	41	*Lumbrineris impatiens*
3	*Aricidea cerrutii*	42	*Chone infundibuliformis*
4	*Glycera robusta*	43	*Eudorella pusilla*
5	*Goniadella gracilis*	44	*Ophelina acuminata*
6	*Lumbrinerides acuta*	45	*Ampelisca agassizi*
7	*Euclymene collaris*	46	*Eriopisa elongata*
8	*Aricidea catherinae*	47	*Notomastus latericeus*
9	*Clymenura* sp. A	48	*Periploma fragilis*
10	*Spiophanes bombyx*	49	*Astarte undata*
11	*Tanaissus lilljeborgi*	50	*Photis dentata*
12	Cerianthidae		
13	*Exogone hebes*		
14	*Echinarachnius parma*		
15	*Polygordius* sp. 1		
16	*Glycera dibranchiata*		
17	*Trichophoxus epistomus*		
18	*Unciola irrorata*		
19	*Unciola inermis*		
20	*Caulleriella* spp.		
21	*Tharyx* spp.		
22	*Drilonereis longa*		
23	*Byblis serrata*		
24	*Euchone* sp. A		
25	*Phyllodoce mucosa*		
26	*Prionospio* sp. A		
27	*Exogone verugera*		
28	*Ampelisca vadorum*		
29	*Erichthonius rubricornis*		
30	*Scalibregma inflatum*		
31	*Euchone incolor*		
32	*Aglaophamus circinata*		
33	*Astyris* sp.		
34	*Harmothoe extenuata*		
35	*Ptilanthura tricarina*		
36	*Phoxocephalus holbolli*		
37	*Nereis grayi*		
38	*Diastylis bispinosa*		
39	*Clymenella torquata*		

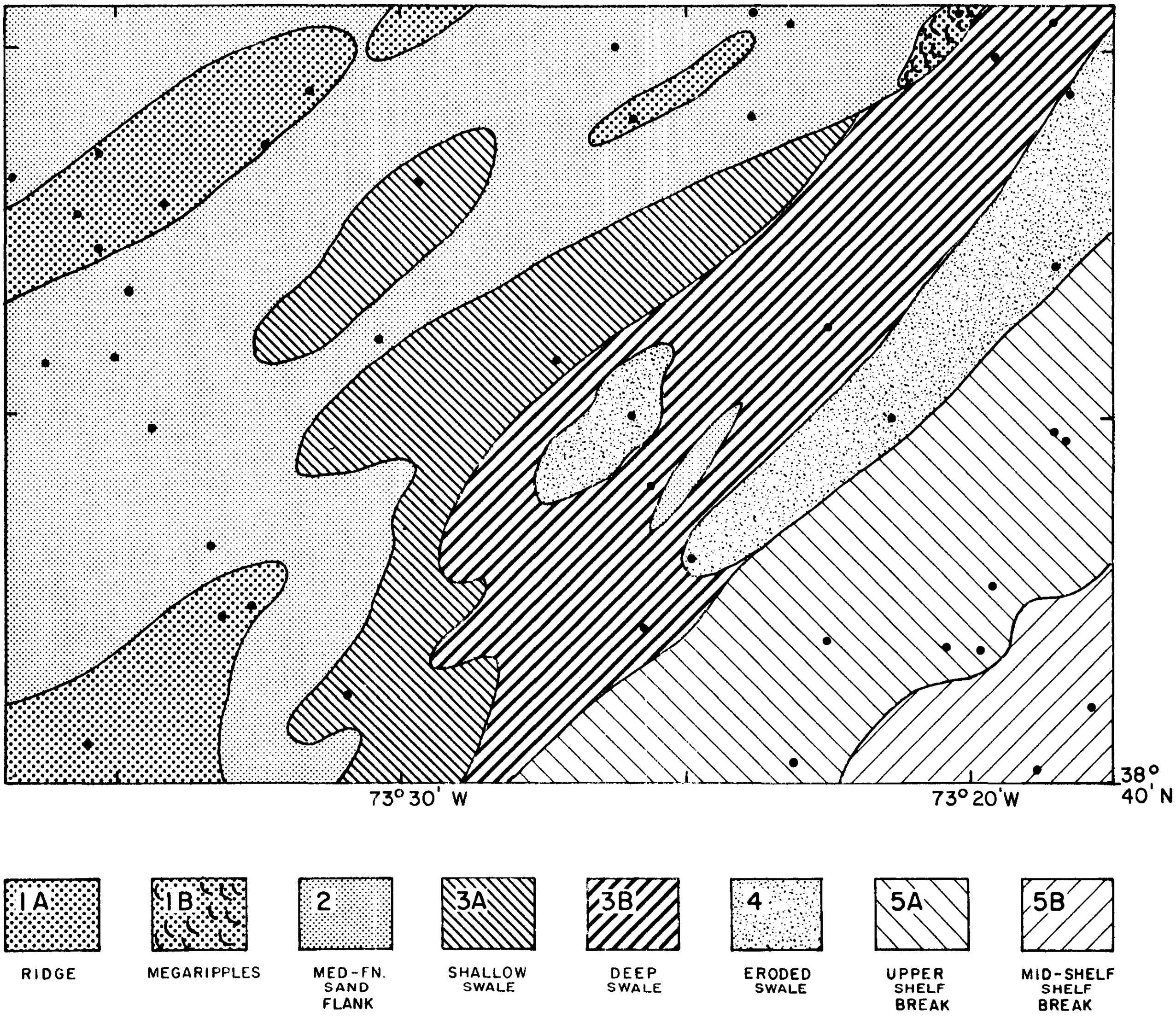


Figure 6-41. Distribution of major habitats identified in habitat delineation study of macrobenthos, area E.

to fine sands with little silt and clay. This habitat could not be consistently subdivided on the basis of both biotic and abiotic data and is thus retained as a heterogeneous habitat.

The swale environments fell into three habitat subdivisions: Habitat 3A has medium-fine sand, somewhat muddy sediments at water depths of 68-70 m; Habitat 3B has slightly cleaner sediments with less fine sand at water depths of 76-83 m; and Habitat 4 represents swales with an erosional history as evidenced by the presence of abundant dead shells on the surface sediments. Even though the sediments in Habitat 4 are poorly-sorted, silt-clay and organic carbon levels are higher there than elsewhere in Area E.

The shelf break zone was divided into two habitats, in recognition of the rather sharp sediment and biotic discontinuity at 80-85 m. The upper part of the shelf break zone (Habitat 5A) has rather symmetrical medium sands devoid of silt and clay, possibly a result of sorting by shelf edge currents or the shoaling of internal waves. The mid-shelf break (Habitat 5B) has considerably finer sands with higher silt and clay content (ca. 4 percent).

The hierarchical classification of the 44 collections of macrobenthos shows a clearer relationship to the habitats recognized than did the same analysis for Area B (Figure 6-42). Collections from all habitats are discrete, except for two from Habitat 2, which did not show a strong relationship to the others from this habitat. They were combined with the others on the basis of indistinct separation by the ordination and lack of obvious differences in sediment conditions.

The 127 species included in the inverse classification were interpreted at an 18 group level as indicated in Table 6-9. The distributional characteristics of these species groups are expressed in the nodal analysis represented in Figure 6-43.

Species in groups 1-6 were variously more frequent and abundant in shallower habitats. Those in Group 1 were constant in the medium-coarse sand of the ridge and megaripple habitats (Habitat 1) to which they were significantly faithful. They were generally over three times as dense in these habitats than overall. Included are the highly diagnostic polychaetes Goniadella gracilis, Lumbrinerides acuta, and Euclymene collaris (included in Group 4 in the analysis of Area B). Group 2 species were more widely distributed but were more frequent in and faithful to habitats 1 and 2. The amphipods Unciola irrorata and Trichophoxus epistomus were found commonly in virtually all habitats but were only abundant in habitats 1 and 2. Species in Group 3 were less common and found widely in shelf habitats, but were rare at the shelf break. They were more frequently collected in the ridge habitat. Members of Group 4, although widely distributed on the shelf, were significantly more common in Habitat 2 and less common in Habitat 5B. The widely distributed polychaete Spiophanes bombyx and

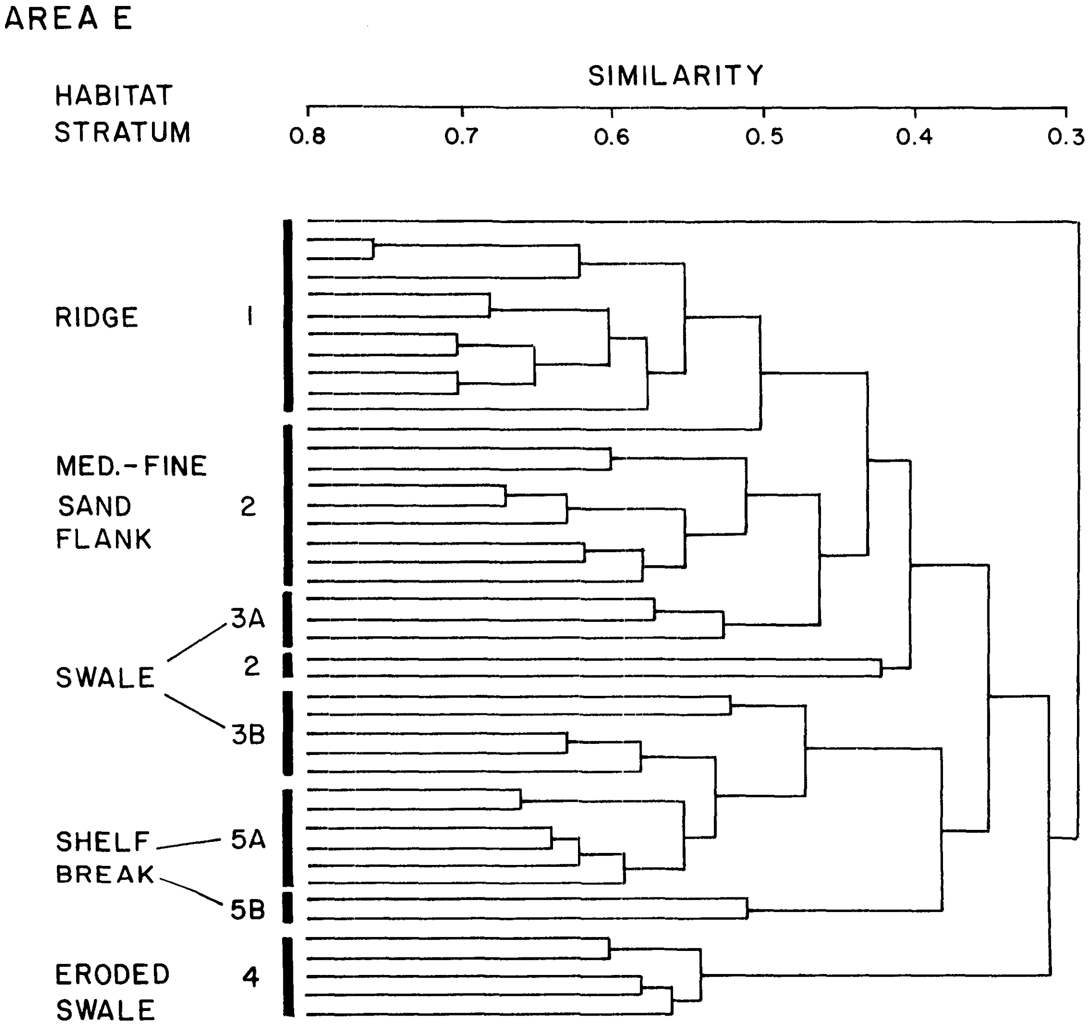


Figure 6-42. Classification hierarchies resulting from agglomeration of collections of macrobenthos from habitat delineation study of Area E. The final disposition of samples in recognized habitats is indicated.

Table 6-9. Species groups selected from numerical classification of macrobenthos collected in habitat delineation study, Area E.

Species Group 1

Goniadella gracilis
Lumbrinerides acuta
Polygordius sp. 1
Euclymene collaris

Species Group 2

Aricidea catherinae
Caulleriella sp.
Aglaophamus circinata
Trichophoxus epistomus
Unciola irrorata
Lumbrineris fragilis
Glycera dibranchiata
Byblis serrata
Euchone sp. A

Species Group 3

Harmothoe extenuata
Cirolana polita
Ampharetidae
Axiognathus squamata
Erichthonius rubricornis

Species Group 4

Phyllodoce mucosa
Spiophanes bombyx
Ampharete arctica
Phascolion strombi
Phoxocephalus holbolli
Astyris sp.
Echinarachnius parma

Species Group 5

Tanaissus liljeborgi
Exogone hebes
Clymenura sp. A
Marphysa bellii
Scoloplos acmeceps
Ampelisca vadorum
Scalibregma inflatum
Tharyx spp.
Lubrineris impatiens
Chone infundibuliformis

Species Group 6

Aricidea cerrutii
Schistomeringos caeca
Paradoneis lyra
Parapionosyllis sp. A
Lunatia triseriata
Solariella obscura
Sthenelais limicola
Sphaerosyllis erinaceus
Hippomedon serratus
Cerastoderma pinnulatum
Siphonoecetes smithianus
Arctica islandica
Cancer irroratus
Ensis directus
Drilonereis magna

Species Group 7

Anobothrus gracilis
Cytheretta edwardsi
Edotea acuta
Cerebratulus lacteus
Travisia forbesii
Clymenella torquata

Species Group 8

Aricidea wassi
Ophelina acuminata
Euchone incolor
Ptilanthura tricarina
Syllis sp.

Species Group 9

Eulalia bilineaia
Melita deniata
Prionospio dayi
Terebellides stroemi
Melinna cristata
Laonice cirrata

Table 6-9. (Concluded)

Species Group 10

Glycera capitata
Argissa hamatipes
Samytha sexcirrata
Cerianthidae
Unciola inermis
Pseudunciola obliquua
Corbula sp.

Species Group 11

Ascorhynchus pyrginospinum
Edwardsia sp.
Lumbrineris albidentata
Cadulus agassizi
Lumbrineris latreilli
Onuphis atlantisa
Amphioplus macilentus
Asychis carolinae
Aricidea neosuecica
Euclymene sp.

Species Group 12

Drilonereis longa
Nereis grayi
Cirrophorus lyriformis
Exogone verugera
Polydora concharum

Species Group 13

Diastylis bispinosa
Orbinia swani
Streptosyllis arenae

Species Group 14

Typosyllis tegulum
Jerbarnia n sp.
Notomastus latericeus
Onuphis pallidula
Spiophanes wigleyi
Polycirrus medusa

Species Group 15

Astropecten americanus
Abra lioica
Photis pugnator
Protohaustorius wigleyi

Species Group 16

Eudorella pusilla
Harpinia sp. 2
Ampelisca agassizi
Photis dentata
Periploma fragile
Goniada brunnea
Cancer borealis
Meiodorvillea minuta
Paraonis gracilis
Nicolea venustula

Species Group 17

Eriopisa elongata
Thyasira trisinuata
Chaetopleura apiculata
Golfingia minuta
Pseudoleptochelia filum
Lucinoma filosa
Thyasira flexuosa
Ninoe nigripes
Harbansus dayi

Species Group 18

Astarte undata
Cyclocardia borealis
Turbonilla interrupta
Nucula delphinodonta
Crenella glandula

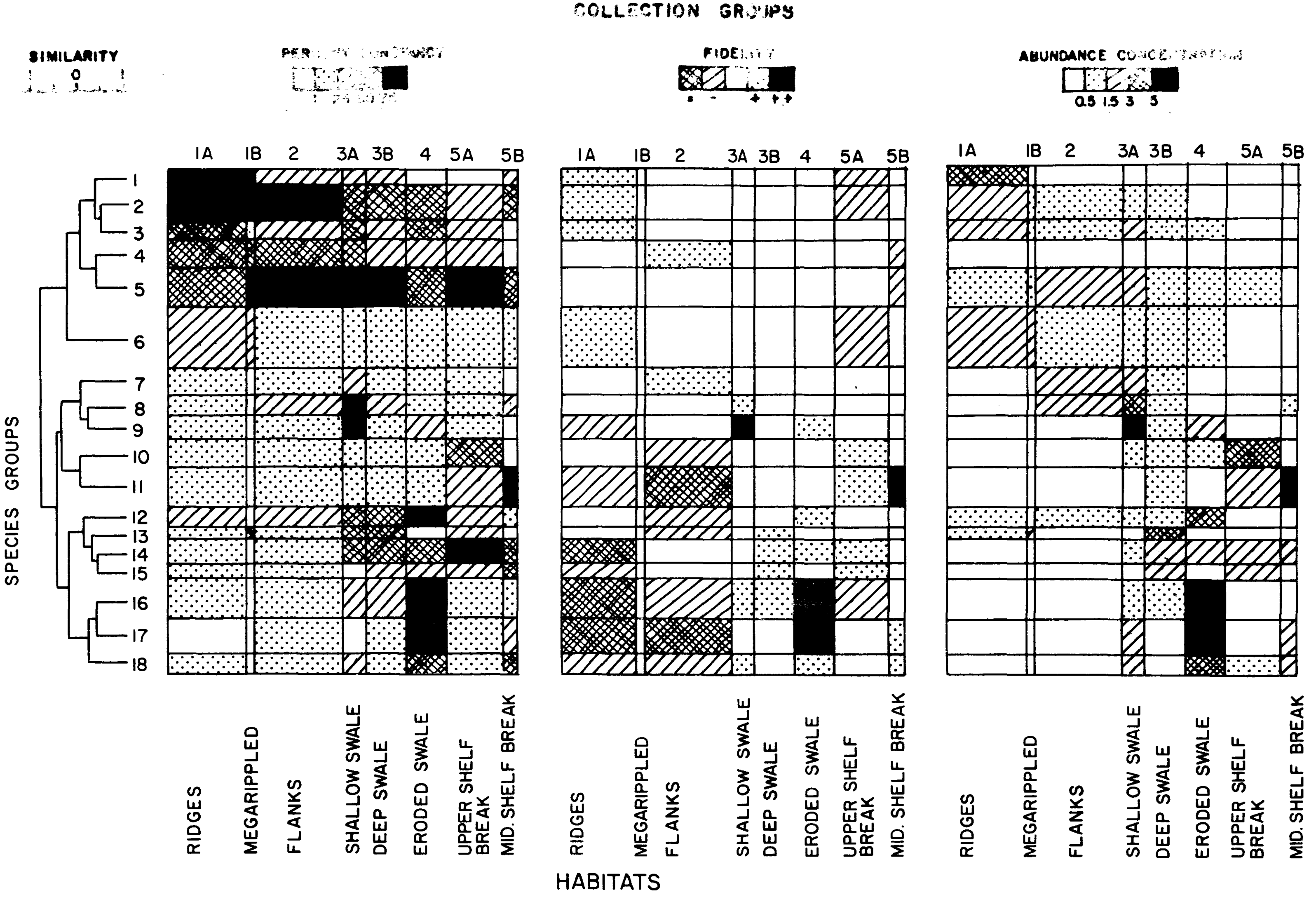


Figure 6-43. Hierarchical classification of species groups of macrobenthos and their nodal statistics in topographic habitat strata, Area E.

the sand dollar Echinarachnius parma were more than twice as abundant in Habitat 2 than overall.

Species in Group 5 were common in all habitats except the mid-shelf break and erosional swales. Some members were more common and abundant in the medium-fine sands of habitats 2 and 3 (e.g. the polychaetes Scalibregma inflatum, Lumbrineris impatiens, and Tharyx sp.), while others were more abundant in the somewhat coarser, more dynamic sands on ridges and at the shelf edge in Habitat 5A (e.g. the tanaidacean Tanaissus liljeborgi and the polychaete Clymenura sp.). Still others were found widely except on ridges (e.g. the polychaetes Marphysa belli and Scoloplos acmeceps).

Species included in Group 6 were less common than those in Group 5, preferred ridges and flanks (Habitats 1 and 2) and were very rare elsewhere.

Species in groups 7-9 were relatively uncommon, seldom abundant and seemed to prefer flank and swale habitats. Group 7 species were more common in flank and shallow swale habitats while species in Group 8 were similarly distributed but were more common in the mid-shelf break habitat. Group 9 species were found almost exclusively in swales, especially in habitats 3A and 4.

Species in groups 10 and 11 were characteristic of shelf-break habitats. Group 10 species were found mainly and most abundantly in the upper shelf-break habitat (5A). Species in Group 11 were very faithful shelf-break species. They were common but not abundant in Habitat 5A but were well represented in Habitat 5B collections. The group includes species characteristic of the shelf-break zone throughout the Middle Atlantic Bight: the polychaetes Lumbrineris latreilli, Onuphis atlantisa, Asychis carolinae, and Aricidea neosuecica and the ophiuroid Amphioplus macilentus.

Members of Groups 12-15 were variously restricted to the deeper swale habitats and the shelf break. Species in Group 12 were widely distributed but most occurrences were in the swale habitats. They averaged almost four times more abundant in Habitat 4 than overall. Group 13 species were also rather widely distributed but not very common or abundant in habitats 2, 3A, 4, and 5B. They were associated with somewhat coarser sediments irrespective of depth. Species in Group 14 were common and generally abundant in the deeper swales and in the shelf break habitat. The polychaetes Heteromastus latericeus and Typosyllis tegulum were more abundant in swales, but other typical shelf-break species (e.g. the polychaetes Onuphis pallidula and Spiophanes wigleyi) were found mainly in habitats 5A and 5B. Group 15 species were uncommon and never abundant. They were essentially restricted to the deeper swales and shelf-break stations except for the amphipod Protohaustorius wigleyi, a typical inner shelf species which found favorable a habitat in the dynamic sediments of the ridges and the shelf edge (Habitat 5A).

Species in groups 16-18 were faithful to swale habitats and some were also common in the mid-shelf break. They appeared to prefer the muddier sediments and were uncommon on the upper shelf break (Habitat 5A). Group 16 included faithful swale species (habitats 3 and 4) which were not common in the mid-shelf break habitat. Only the amphipod *Ampelisca agassizi* was very abundant. Many members of this group were also characteristic of the muddy fine sands of the deep swale in Area B. Group 17 species were faithful to the eroded swale and mid-shelf break habitats and rare in habitats 3 and 5A. The group includes typical subdominant and some dominant shelf-break species which also extend into some outer shelf swales. They were rare in the dynamic medium sands of the shelf edge (Habitat 5A) despite its depth regime. Species in Group 18 were uncommon but faithful to habitats 3A, 4, and 5B. They were only moderately abundant in Habitat 4.

The ridge habitat in Area E was similar to the ridge habitat of Area B and supported primarily interstitial or fossorial animals. Species from Groups 1, 2, 3, and 6, which were faithful to this habitat, and ubiquitous shelf species in Group 5 comprised most of the community. The assemblage of the deeper megarippled bottom (Habitat 1B) was similar but also contained some deeper water elements (e.g. species in Group 13).

The flank habitat contained more surface tube-dwellers and burrowing forms as well as some species also characteristic of the ridge habitat. Few common species were faithful to the flank habitat, and most members of the community consisted of species which were characteristic of both ridge and swale habitats.

The composition of the communities in swale environments reflected subtle variations in grain size of the sediments. In addition to the more ubiquitous species, the shallow, deep and eroded swale habitats each supported species more common and abundant in these particular habitats than elsewhere. Many of the characteristic species of the shallow swale habitat were also found in the flank habitat, those of the deep swales were generally also found in the upper shelf-break habitats, and many of those of the erosional swale were also common in the mid shelf-break habitat. Species in Group 16 were diagnostic for swale habitats in general.

The upper shelf-break habitat had coarser, apparently more dynamic sediments than the surrounding swale or mid-shelf-break habitats. Thus, it was populated by a mixture of "deeper water" species (Groups 11, 14, and 15) and species also characteristic of inner shelf sands (e.g. the crustaceans *Pseudunciola obliquua*, *Trichophoxous epistomus*, and *Tanaissus liljeborgi*). The characteristic and stenotopic shelf-break species (species in groups 11 and 14) become dominant in the mid-shelf break habitat (deeper than 80 m).

The reciprocal averaging ordination presented a clearer depiction of the complex gradational relationships of the communities in Area E (Figure 6-44) than did the same analysis of Area B collections. The ridge-swale continuum is also represented as a horseshoe-shaped galaxy in the first two dimensions, but there is an offshoot representing shelf-break communities. The net result is a Y-shape representation of the community-types present in Area E. Axis 1 is correlated with depth while axis 2 separates collections from habitats 3A and 3B and the erosional swale (Habitat 4) from the shelf break habitats. Axis 3 further separates the upper and mid-shelf break habitats (5A and 5B) and better distinguishes the ridge and flank collections. There is no spatial overlap of the galaxies representing the seven habitat types in three dimensions. The ordination better represents the overall relationships among the assemblages than does the normal dendrogram. In particular, the relationships of habitats 3A and 4 and 4 and 5B are better modeled.

The ordination of species in the same space (Figure 6-45) has a trumpet-shaped structure indicating that some species (those which have high scores on axis 1 and mid-range scores on axis 2, e.g. *Thyasira flexuosa* and *Notomastus latericeus*) characterize both shelf-break and swale habitats. As in Area B, species such as the polychaetes *Lumbrinerides acuta*, *Goniadella gracilis*, and *Euclymene collaris* characterize the shallow, coarse sand end of the spectrum. Ubiquitous shelf species, such as *Unciola irrorata* and *Spiophanes bombyx* are near the mid-range of axis 1. Similar species to those in Area B also characterize the swales, e.g. the crustaceans *Ampelisca agassizi* and *Eudorella pusilla*. The diagnostic status of the polychaetes *Lumbrineris latreilli*, *Onuphis atlantisa*, *Onuphis pallidula*, and *Spiophanes wigleyi* for the shelf-break habitat is well represented.

Dominant Species. The foregoing analyses of distributional patterns were based on a consideration of a large number of species (110 and 127 for Areas B and E, respectively), and thus it was advantageous to employ multivariate analyses. However, consideration of just the numerically dominant species also shows striking differences among habitats in these two outer shelf areas.

The top 10 species ranked by geometric mean abundance are listed in Tables 6-11 and 6-12. The frequency of occurrence of the species and living position and feeding categorization are also listed. Some species, such as the polychaete *Spiophanes bombyx* and the amphipod *Unciola irrorata* are prevalent in a wide variety of habitats in both regions and are thus characteristic of many habitats but not diagnostic for any one. The coarser, more dynamic sands of the terrace in Area B and the ridges in both areas are distinguished by the importance of the thin interstitial-burrowing polychaetes *Goniadella gracilis*, *Lumbrinerides acuta*, and to some extent, *Exogene hebes*. The abundance of the tubicolus maldanid polychaete *Euclymene*

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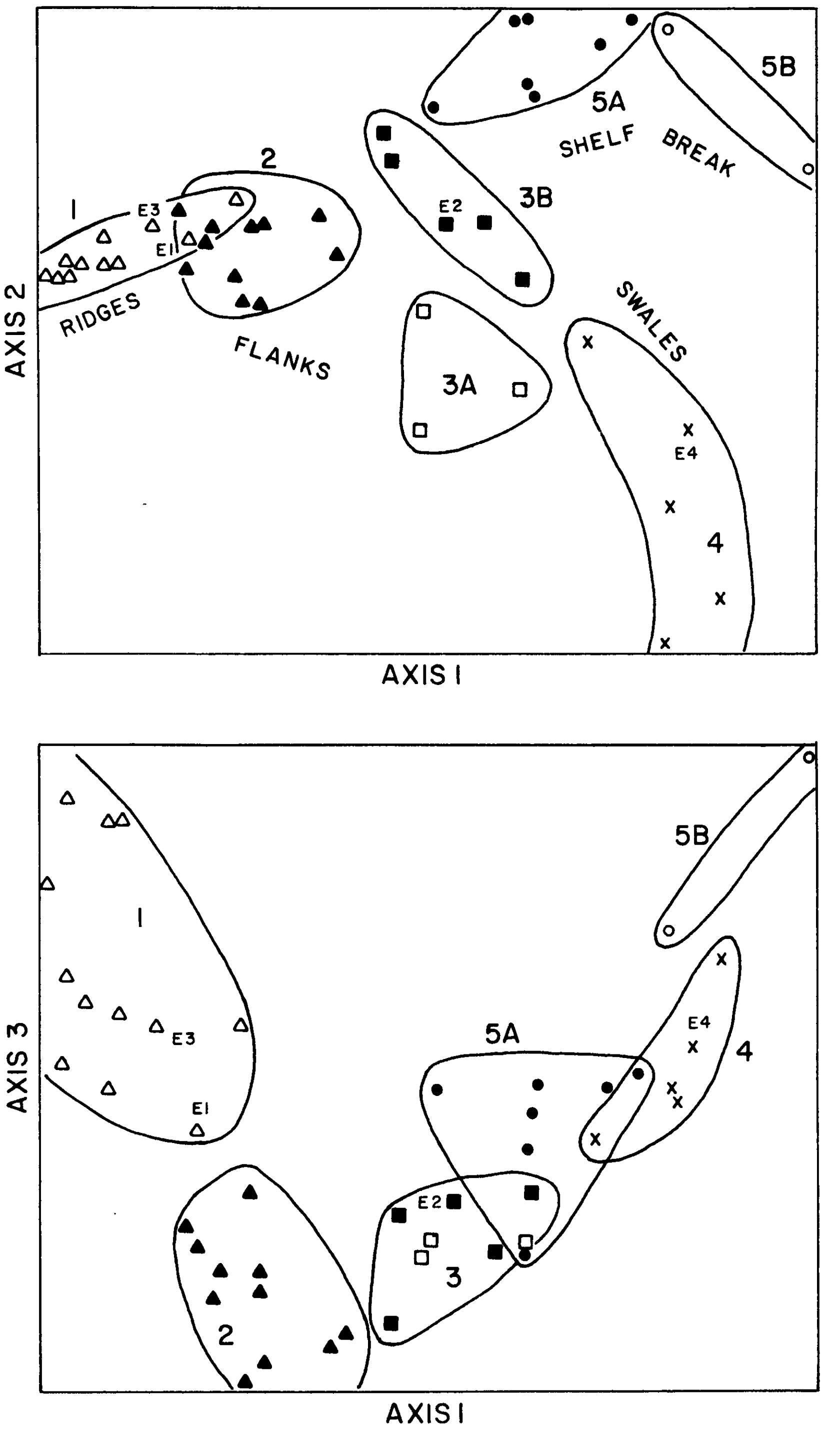

Figure 6-44. Reciprocal averaging ordination of collections of macrobenthos from habitat delineation study of Area E. The disposition of samples in habitats and the location of regular stations is indicated.

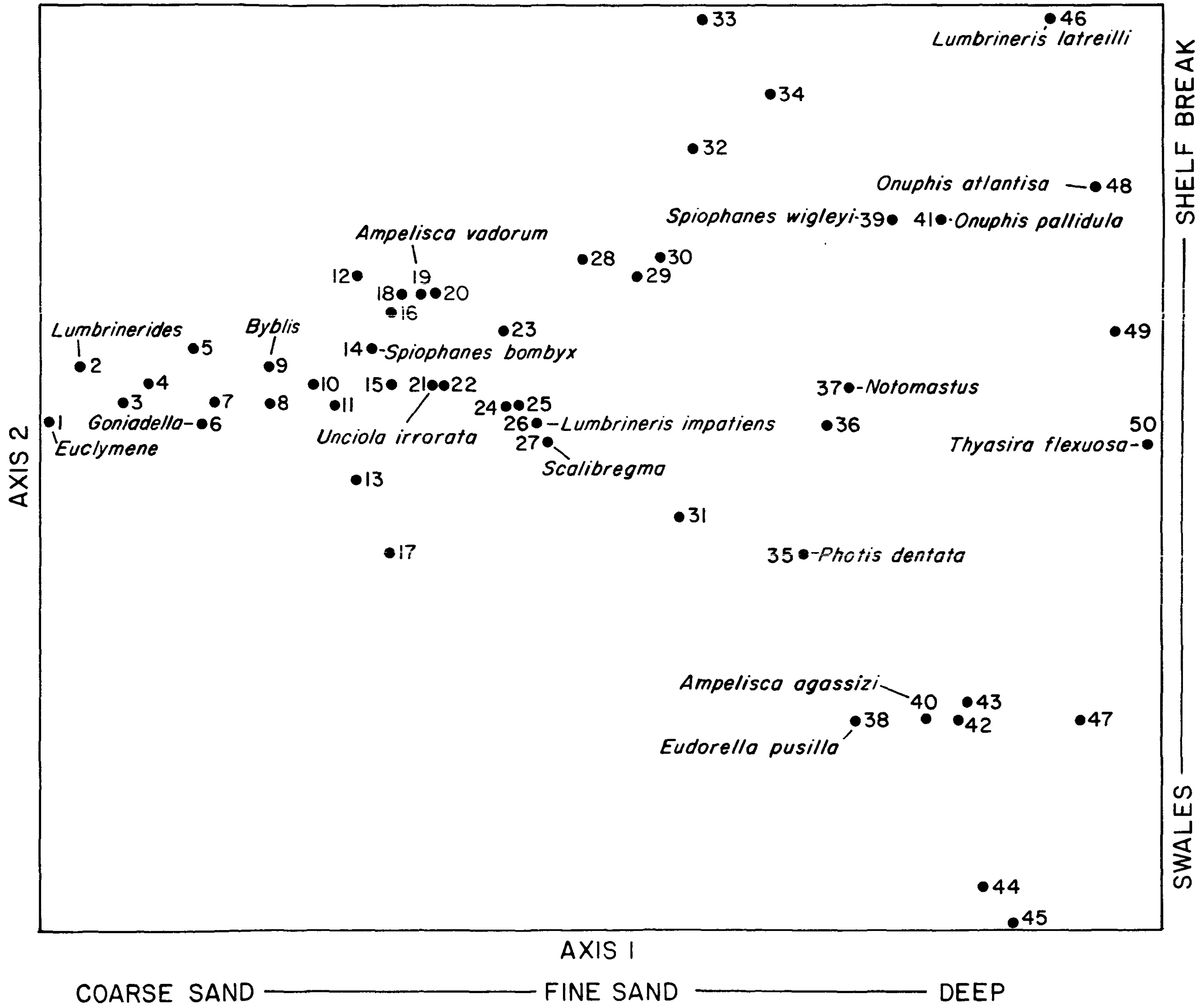

Figure 6-45. Reciprocal averaging ordination of species of macrobenthos from habitat delineation study of area E. Numbers refer to species as indicated in Table 6-10.

Table 6-10. Species used in reciprocal averaging ordination of collections from Area E, habitat delineation study. Numbers refer to Figure 6-45.

Reference Number	Species	Reference Number	Species
1	*Euclymene collaris*	40	*Ampelisca agassizi*
2	*Lumbrinerides acuta*	41	*Onuphis pallidula*
3	*Goniadella gracilis*	42	*Ninoe nigripes*
4	*Euchone* sp. A	43	*Chaetopleura apiculata*
5	*Echinarachnius parma*	44	*Harpinia* sp. 2
6	*Polygordius* sp. 1	45	*Eriopisa elongata*
7	*Caulleriella* sp.	46	*Lumbrineris latrielli*
8	*Cirolana polita*	47	*Harbansus dayi*
9	*Byblis serrata*	48	*Onuphis atlantisa*
10	*Exogone hebes*	49	*Amphioplus macilentus*
11	*Aricidea catherinae*	50	*Thyasira flexuosa*
12	*Tanaissus lilljeborgi*		
13	*Euchone incolor*		
14	*Spiophanes bombyx*		
15	*Aglaophamus circinata*		
16	*Trichophoxus epistomus*		
17	*Clymenella torquata*		
18	*Clymenura* sp. A		
19	*Ampelisca vadorum*		
20	*Phyllodoce mucosa*		
21	*Unciola irrorata*		
22	*Erichthonius rubricornis*		
23	*Aricidea wassi*		
24	*Tharyx* spp.		
25	*Phoxocephalus holbolli*		
26	*Lumbrineris impatiens*		
27	*Scalibregma inflatum*		
28	*Marphysa bellii*		
29	*Scoloplos acmeceps*		
30	*Aricidea neosuecica*		
31	*Exogone verugera*		
32	*Chone infundibuliformis*		
33	*Unciola inermis*		
34	*Pseudunciola obliquua*		
35	*Photis dentata*		
36	*Typosyllis tegulum*		
37	*Notomastus latericeus*		
38	*Eudorella pusilla*		
39	*Spiophanes wigleyi*		

Table 6-11. Numerically dominant species in habitats recognized in Area B. (A=amphipod, B=bivalve, C=cumacean, E=echinoid, Op=ophiuroid, Os=ostracod, P=polychaete). Species are ranked by geometric mean density ($\bar{x}$), also given are frequency of occurrence (f), and living-position-feeding category (B=burrower, D=subsurface deposit feeder, E=epifaunal, F=fossorial, I= interstitial feeders, P=suspension feeder, S=surface deposit feeder, and T=tubicolous).

Species	f	$\bar{x}$	Living-Feeding Category	Species	f	$\bar{x}$	Living-Feeding Category
HABITAT 1 - TERRACE				HABITAT 2A - RIDGES			
Spiophanes bombyx (P)	1.00	109.4	T-S	*Tharyx* sp. (P)	1.00	32.8	B-S
Goniadella gracilis (P)	1.00	40.7	I	*Unciola irrorata* (A)	1.00	21.7	T-S
Lumbrinerides acuta (P)	1.00	36.1	I	*Goniadella gracilis* (P)	1.00	10.5	I
Euclymene collaris (P)	1.00	15.8	T-D	*Spiophanes bombyx* (P)	1.00	10.3	T-S
Unciola irrorata (A)	1.00	11.7	T-S	*Byblis serrata* (A)	0.80	10.0	T-S
Exogone hebes (P)	1.00	10.9	I	*Scalibregma inflatum* (P)	1.00	9.2	B-D
Tharyx sp. (P)	0.92	8.3	B-S	*Lumbrinerides acuta* (P)	1.00	9.2	I
Aricidea catherinae (P)	0.92	7.8	B-S	*Ampelisca vadorum* (A)	0.80	8.2	T-S
Aricidea cerruti (P)	0.92	7.4	B-S	*Euchone* sp. A (P)	1.00	8.0	T-P
Polygordius sp. 1 (P)	0.92	5.5	I	*Erichthonius rubricornis* (A)	0.80	6.2	T-S
HABITAT 2B - MED. SAND FLANK				HABITAT 3A- MED. FINE SAND FLANK			
Ampelisca vadorum (A)	1.00	17.0	T-S	*Spiophanes bombyx* (P)	1.00	68.0	T-S
Caulleriella sp. (P)	1.00	16.1	I	*Tharyx* sp. (P)	0.93	33.8	B-S
Byblis serrata (P)	1.00	14.5	T-S	*Unciola irrorata* (A)	0.93	24.2	T-S
Spiophanes bombyx (P)	1.00	9.0	T-S	*Euchone* sp. A (P)	1.00	21.6	T-P
Scalibregma inflatum (P)	1.00	8.4	B-D	*Scalibregma inflatum* (P)	1.00	16.1	B-D
Lumbrinerides acuta (P)	1.00	8.3	I	*Byblis serrata* (A)	0.93	14.3	T-S
Unciola irrorata (A)	0.86	8.2	T-S	*Erichthonius rubricornis* (A)	0.93	13.6	T-S
Euchone sp. A (P)	0.86	5.6	T-P	*Ampelisca agassizi* (A)	0.86	10.5	T-S
Tharyx sp. (P)	0.86	4.7	B-S	*Euchone incolor* (P)	0.86	8.0	T-P
Goniadella gracilis (P)		4.5	I	*Trichophoxus epistomus* (A)	0.86	5.9	F

Table 6-11. (Concluded)

Species	f	$\bar{x}$	Living-Feeding Category	Species	f	$\bar{x}$	Living-Feeding Category
HABITAT 3B - ERODED FLANKS				HABITAT 4 - SHALLOW SWALE			
Tharyx sp. (P)	1.00	60.7	B-S	*Ampelisca agassizi* (A)	1.00	188.9	T-S
Spiophanes bombyx (P)	1.00	25.1	T-S	*Spiophanes bombyx* (P)	1.00	26.3	T-S
Euchone sp. A (P)	1.00	24.0	T-P	*Tharyx* sp. (P)	1.00	21.2	B-S
Unciola inermis (A)	1.00	14.1	T-S	*Unciola irrorata* (A)	1.00	19.1	T-S
Byblis serrata (A)	1.00	14.0	T-S	*Scalibregma inflatum* (P)	1.00	15.7	B-D
Unciola irrorata (A)	0.86	10.8	T-S	*Phoxocephalus holbolli* (A)	1.00	14.5	F
Scalibregma inflatum (P)	1.00	9.6	B-D	*Erichthonius rubricornis* (A)	1.00	13.9	T-S
Polygordius sp. 1 (P)	1.00	9.5	I	*Lumbrineris impatiens* (P)	1.00	13.6	B-D
Erichthonius rubricornis (A)	1.00	8.6	T-S	*Euchone* sp. A (P)	1.00	12.1	T-P
Exogone verrugera (P)	1.00	8.1	I	*Exogone verrugera* (P)	1.00	10.9	I
HABITAT 5 - DEEP SWALE							
Ampelisca agassizi (A)	1.00	564.0	T-S				
Notomastus latericeus (P)	1.00	34.4	B-D				
Unciola irrorata (A)	1.00	20.3	T-S				
Photis dentata (A)	1.00	20.3	T-S				
Lumbrineris impatiens (P)	1.00	10.3	B-D				
Tharyx sp. (P)	1.00	8.8	B-S				
Chone infundibuliformis (P)	1.00	8.6	T-P				
Scalibregma inflatum (P)	1.00	7.1	B-D				
Astarte undata (B)	1.00	4.3	B-P				
Nereis grayii (P)	1.00	4.0	B-S				

Table 6-12. Numerically dominant species in habitats recognized in Area E. (A=amphipod, B=bivalve, C=cumacean, E=echinoid, Op=ophiuroid, Os=ostracod, P=polychaete). Species are ranked by geometric mean density ($\overline{x}$), also given are frequency of occurrence (f), and living-position-feeding category (B=burrower, D=subsurface deposit feeder, E=epifaunal, F=fossorial, I=interstitial feeders, P=suspension feeder, S=surface deposit feeder, and T=tubicolous).

Species	f	$\overline{x}$	Living-Feeding Category	Species	f	$\overline{x}$	Living-Feeding Category
HABITAT 1A - RIDGES				HABITAT 1B - MEGARIPPLES			
Goniadella gracilis (P)	1.00	16.7	I	*Goniadella gracilis* (P)		24	I
Lumbrinerides acuta (P)	1.00	16.3	I	*Exogone hebes* (P)		21	I
Spiophanes bombyx (P)	1.00	13.3	T-S	*Lumbrinerides acuta* (P)		18	I
Trichophoxus epistomus (A)	1.00	12.7	F	*Spiophanes bombyx* (P)		17	T-S
Euclymene collaris (P)	0.90	11.8	T-D	*Chone infundibuliformis* (P)		17	T-P
Unciola irrorata (A)	1.00	11.1	T-S	*Marphysa belli* (P)		8	B-D
Ampelisca vadorum (A)	1.00	9.3	T-S	*Scalibregma inflatum* (P)		7	B-P
Euchone incolor (P)	0.90	9.1	T-P	*Ampelisca vadorum* (A)		7	T-S
Polygordius sp. 1 (P)	1.00	5.9	I	*Tharyx* spp. (P)		6	B-S
Caulleriella sp. (P)	0.80	5.4	I				
HABITAT 2 - FLANKS				HABITAT 3A - SHALLOW SWALES			
Spiophanes bombyx (P)	1.00	31.9	T-S	*Spiophanes bombyx* (P)	1.00	34.2	T-S
Ampelisca vadorum (A)	1.00	19.8	T-S	*Scalibregma inflatum* (P)	1.00	18.0	B-D
Trichophoxus epistomus (A)	1.00	12.5	F	*Ampelisca agassizi* (A)	1.00	18.0	T-S
Lumbrineris impatiens (P)	0.91	7.8	B-D	*Tharyx* sp. (P)	1.00	16.0	B-S
Aglaophamus circinata (P)	1.00	6.7	B-D	*Lumbrineris impatiens* (P)	0.67	11.8	B-D
Tharyx sp. (P)	0.91	6.7	B-S	*Notomastus latericeus* (P)	1.00	11.5	B-D
Euchone sp. A (P)	0.91	5.8	T-P	*Trichophoxus epistomus* (A)	1.00	8.3	F
Echinarachnius parma (E)	0.91	5.0	E-S	*Euchone incolor* (P)	1.00	7.8	T-P
Chone infundibuliformis (P)	1.00	4.8	T-P	*Chone infundibuliformis* (P)	1.00	7.4	T-P
Scalibregma inflatum (P)	0.91	4.7	B-D	*Ampelisca vadorum* (A)		4.8	T-S

Table 6-12. (Concluded)

Species	f	$\bar{x}$	Living-Feeding Category	Species	f	$\bar{x}$	Living-Feeding Category
HABITAT 3B - DEEP SWALES				HABITAT 4 - ERODED SWALES			
Chone infundibuliformis (P)	1.00	46.3	T-P	*Ampelisca agassizi* (A)	1.00	29.5	T-S
Spiophanes bombyx (P)	1.00	43.0	T-S	*Notomastus latericeus* (P)	1.00	24.4	B-D
Ampelisca vadorum (A)	1.00	18.3	T-S	*Tharyx* sp. (P)	1.00	8.0	B-S
Scoloplos acmeceps (P)	1.00	13.4	B-D	*Unciola irrorata* (A)	1.00	6.7	T-S
Lumbrineris impatiens (P)	1.00	8.7	B-D	*Polydora concharum* (P)	0.80	6.5	T-S
Notomastus latericeus (P)	0.80	7.2	B-D	*Lumbrineris impatiens* (P)	0.80	5.5	B-D
Trichophoxus epistomus (A)	1.00	6.7	F	*Scalibregma inflatum* (P)	1.00	4.1	B-D
Unciola irrorata (A)	1.00	6.0	T-S	*Eudorella pusilla* (C)	1.00	3.9	F
Scalibregma inflatum (P)	1.00	3.6	B-D	*Onuphis pallidula* (P)	0.80	3.6	T-S
Tharyx sp. (P)	0.60	3.4	B-S	*Harbansus dayi* (Os)	0.80	3.2	E-S
HABITAT 5A - UPPER SHELF BREAK				HABITAT 5B - MID-SHELF BREAK			
Chone infundibuliformis (P)	1.00	117.8	T-P	*Chone infundibuliformis* (P)	1.00	28.7	T-P
Notomastus latericeus (P)	1.00	11.7	B-D	*Onuphis pallidula* (P)	1.00	26.5	T-S
Ampelisca vadorum (A)	1.00	11.5	T-S	*Lumbrineris latreilli* (P)	1.00	26.5	B-D
Scoloplos acmeceps (P)	1.00	9.3	B-D	*Notomastus latericeus* (P)	1.00	17.7	B-D
Pseudunciola obliquua (A)	0.86	8.8	T-S	*Aricidea neosuecica* (P)	1.00	8.2	B-D
Trichophoxus epistomus (A)	0.86	8.3	F	*Trichophoxus epistomus* (A)	1.00	7.8	F
Onuphis pallidula (P)	1.00	6.2	T-S	*Scoloplos acmeceps* (P)	1.00	6.9	B-D
Marphysa belli (P)	1.00	5.9	B-D	*Tharyx* sp. (P)	1.00	5.5	B-S
Spiophanes bombyx (P)	0.86	4.5	T-S	*Thyasira flexuosa* (B)	1.00	5.0	B-P
Unciola inermis (A)		4.4	T-S	*Amphioplus macilentus* (Op)	1.00	5.0	B-P

collaris is also distinctive. Except for the ubiquitous *Spiophanes bombyx* and *Unciola irrorata*, the extremely dynamic habitats have a paucity of the tubicolus, surface deposit and suspension feeders so abundant in deeper, more stable substrates. On the deeper ridges in Area B and on the flanks in both areas, ampeliscid amphipods (*Ampelisca vadorum* and *Byblis serrata*) become important. These animals live in shallow membranous tubes and feed at the sediment-water interface.

As the sediments become relatively depleted of coarse sands down-flank, the interstitial-burrowers diminish in importance (Figure 6-46) such that they are non-existent in the fine sands of swales or the mid-shelf break. The aforementioned ampeliscids become important (Figure 6-48), however, *Byblis* is strangely much less abundant in area E. Other delicate tube dwellers, including two species of the sabellid polychaete genus *Euchone* become common in the finer, more stable sediments (Figure 6-49). Burrowing species which ingest deposits in subsurface sediments also are more prevalent. The polychaetes *Scalibregma inflatum*, which ingests sand somewhat non-selectively, and *Lumbrineris impatiens*, which feeds more selectively, are particularly good indicators of the finer, more stable sediments of those intermediate habitats (Figure 6-47).

The capitellid polychaete *Notomastus latericeus* is a very good indicator of swale habitats on the outer shelf (Figure 6-47). It ranked second in mean abundance on the extreme swale habitats both in Area B (Habitat 5) and Area E (Habitat 4), ranked sixth in the shallow and deep swale habitats in Area E, and was very rare in shallower habitats. *Notomastus* was also abundant in shelf-break habitats throughout the Middle Atlantic Bight. *Notomastus* feeds on subsurface sediments at the base of its burrow which are understandably richer in organic material in the muddier swale and shelf-break habitats.

Another characteristic dominant in the swales was the amphipod *Ampelisca agassizi* (Figure 6-48). Although it was widely distributed, it was very abundant in both swale habitats in Area B (habitats 4 and 5) and in the muddier swale habitats in Area E (habitats 3A and 4). The distribution of *Ampelisca agassizi* overlaps with that of its congener *Ampelisca vadorum*, however, there was a clear separation of their "optimal" habitats (Figure 6-48).

Area E is located near the shelf edge and habitats are somewhat deeper than those comparable habitats in Area B. Thus, there was a much stronger influence of shelf-break species among the dominants in Area E. The sabellid polychaete *Chone infundibuliformis* was present in moderate densities in the deep swale habitat in Area B, but was very abundant in the deep swale and shelf-break habitats of Area E (Figure 6-49). The polychaete *Scoloplos acmeceps* was common and a dominant or subdominant in all except the ridge habitat of Area E, but was extraordinarily rare in Area B (Figure 6-50). Other typical shelf-break species, e.g. the polychaetes *Onuphis pallidula*, were also

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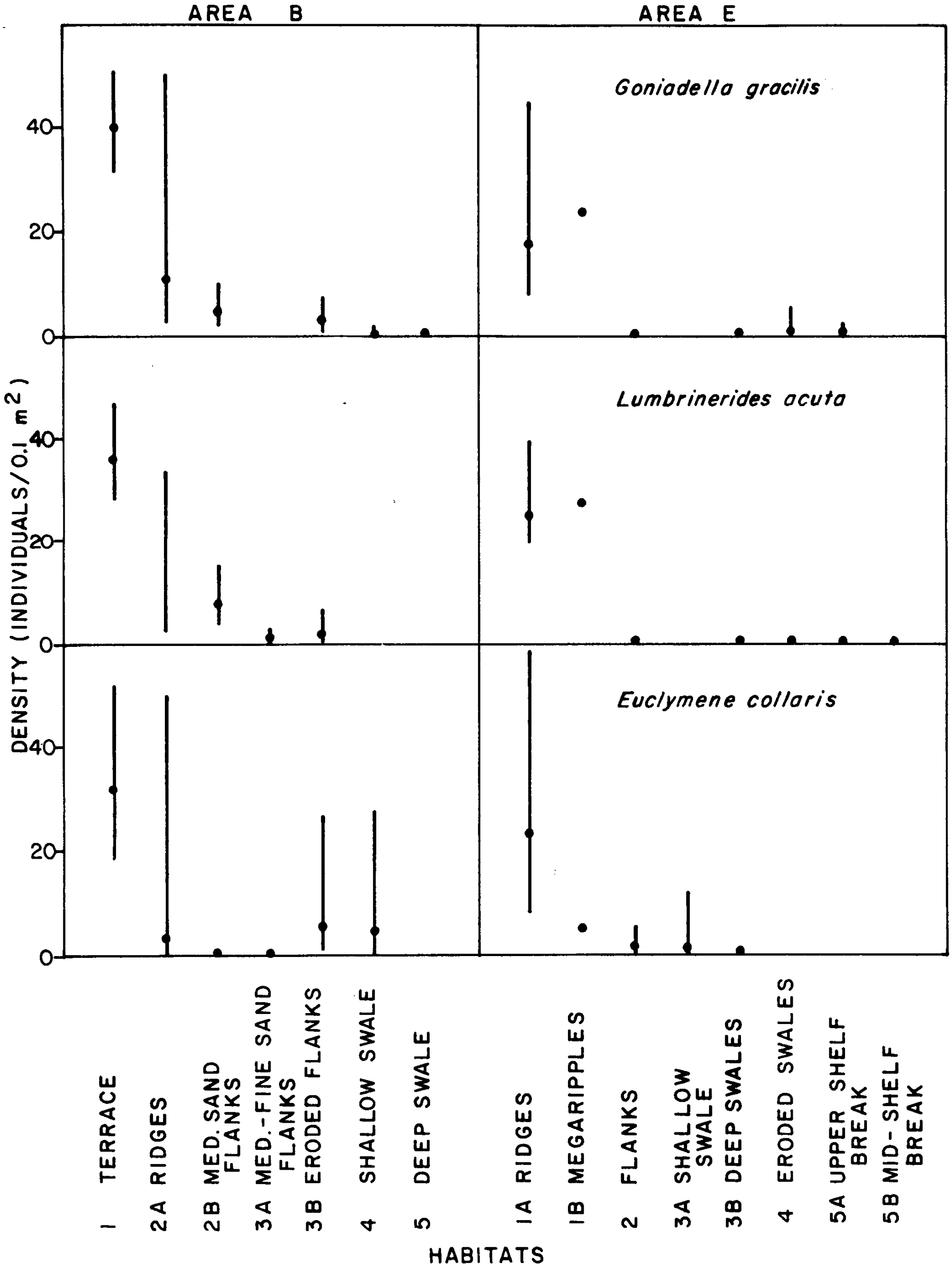

Figure 6-46. Geometric means and confidence limits on those means for population densities of species by topographic habitat in areas B and E.

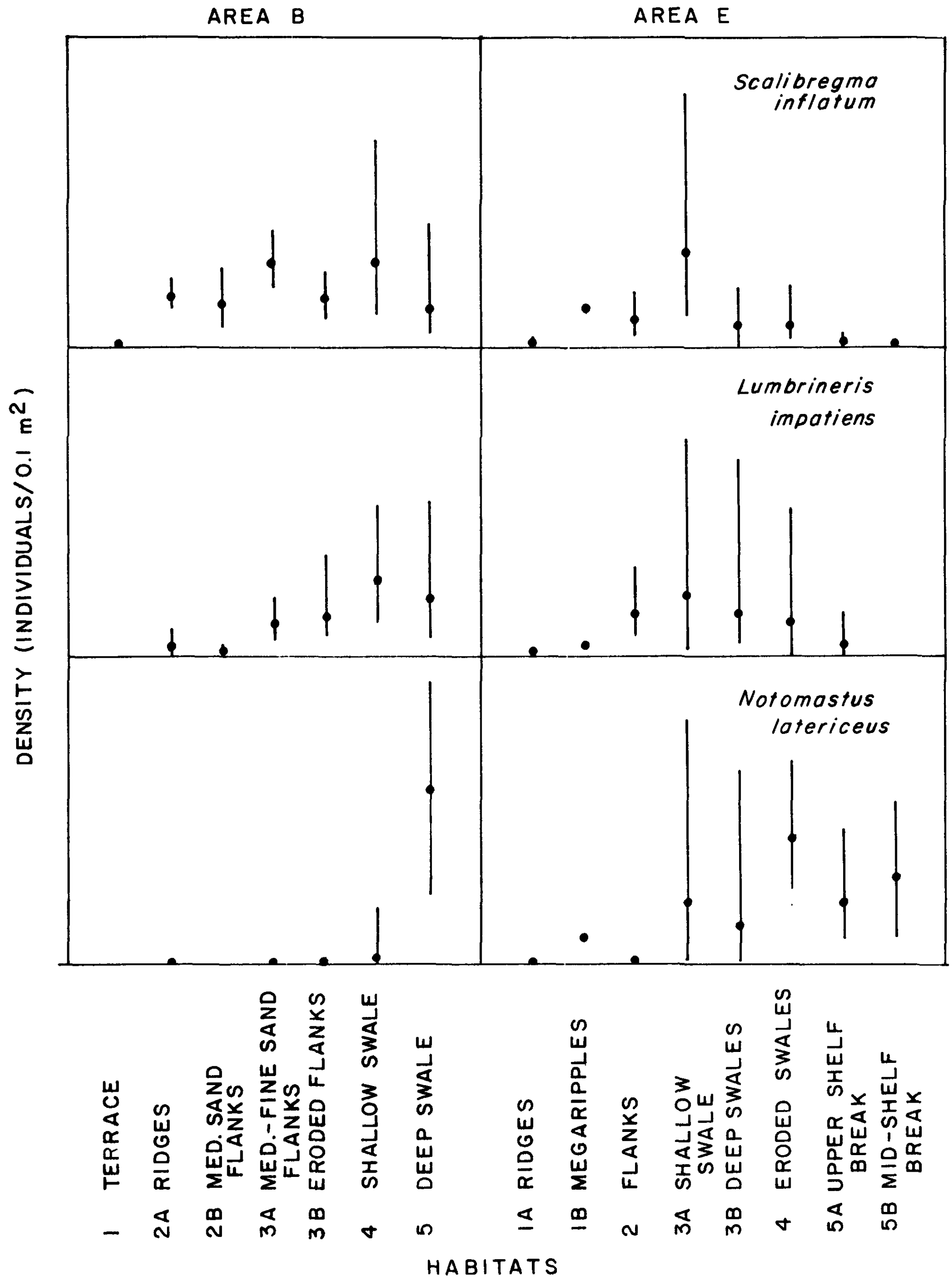

Figure 6-47. Geometric means and confidence limits on those means for population densities of species by topographic habitat in areas B and E.

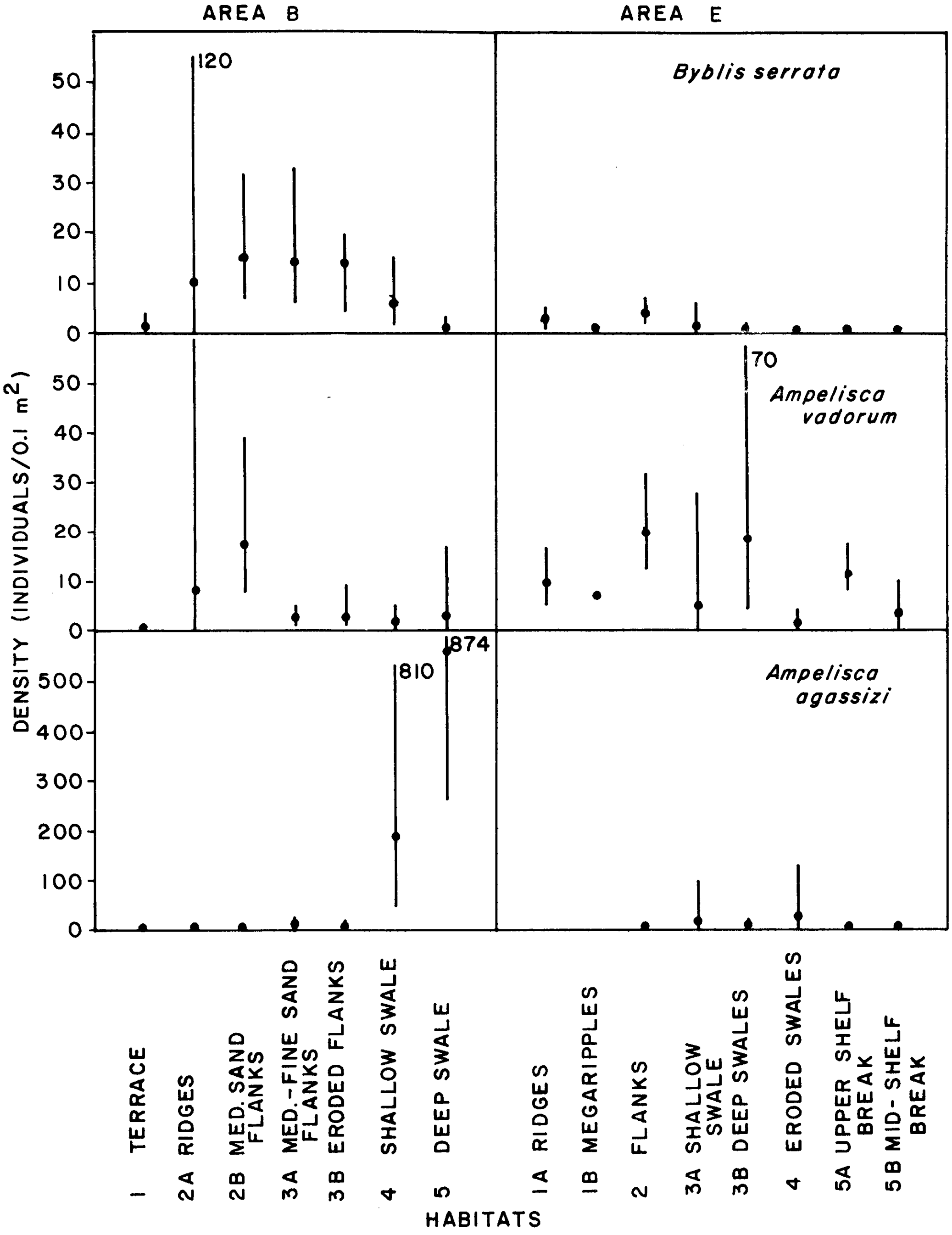

Figure 6-48. Geometric means and confidence limits on those means for population densities of species by topographic habitat in areas B and E.

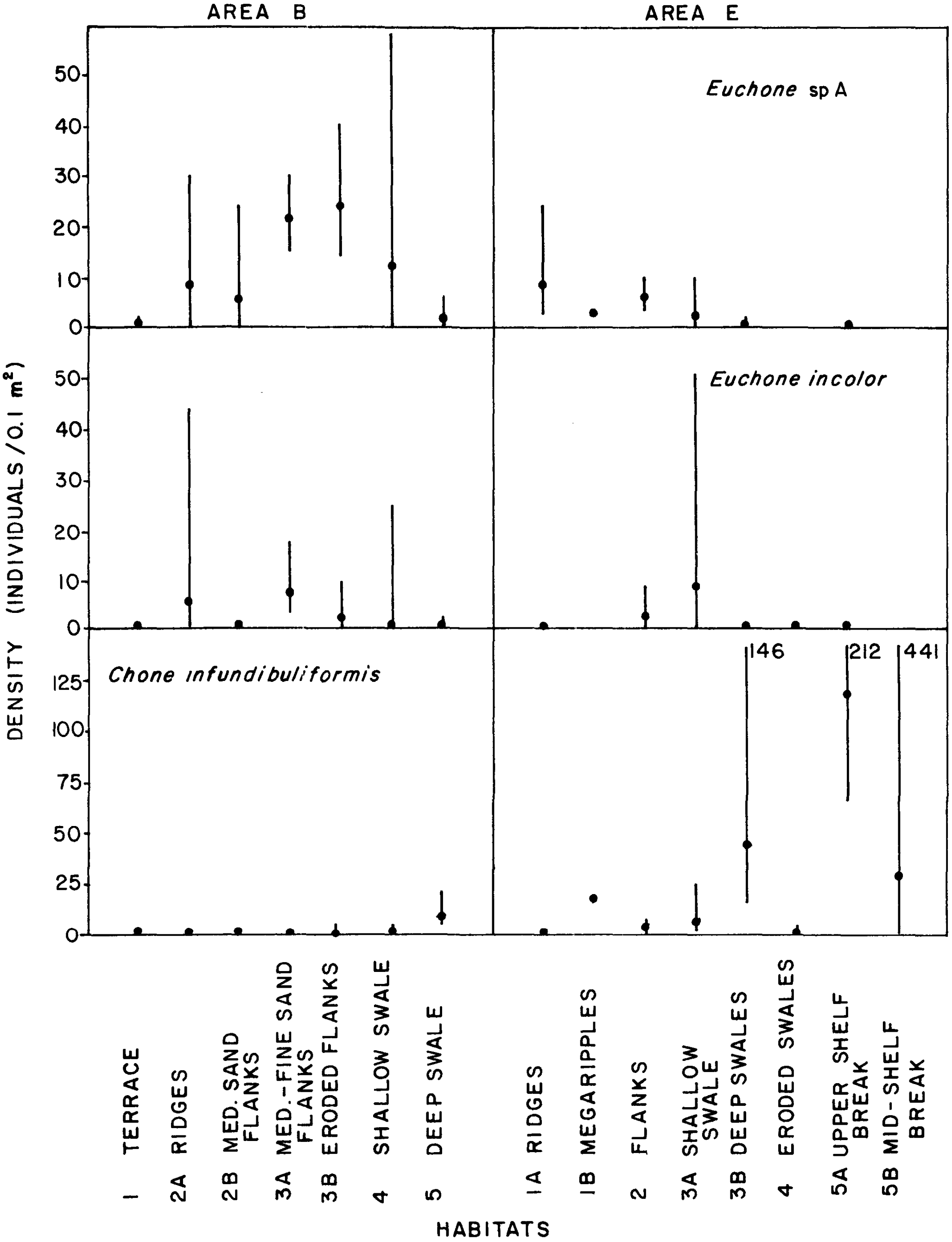

Figure 6-49. Geometric means and confidence limits on those means for population densities of species by topographic habitat in areas B and E.

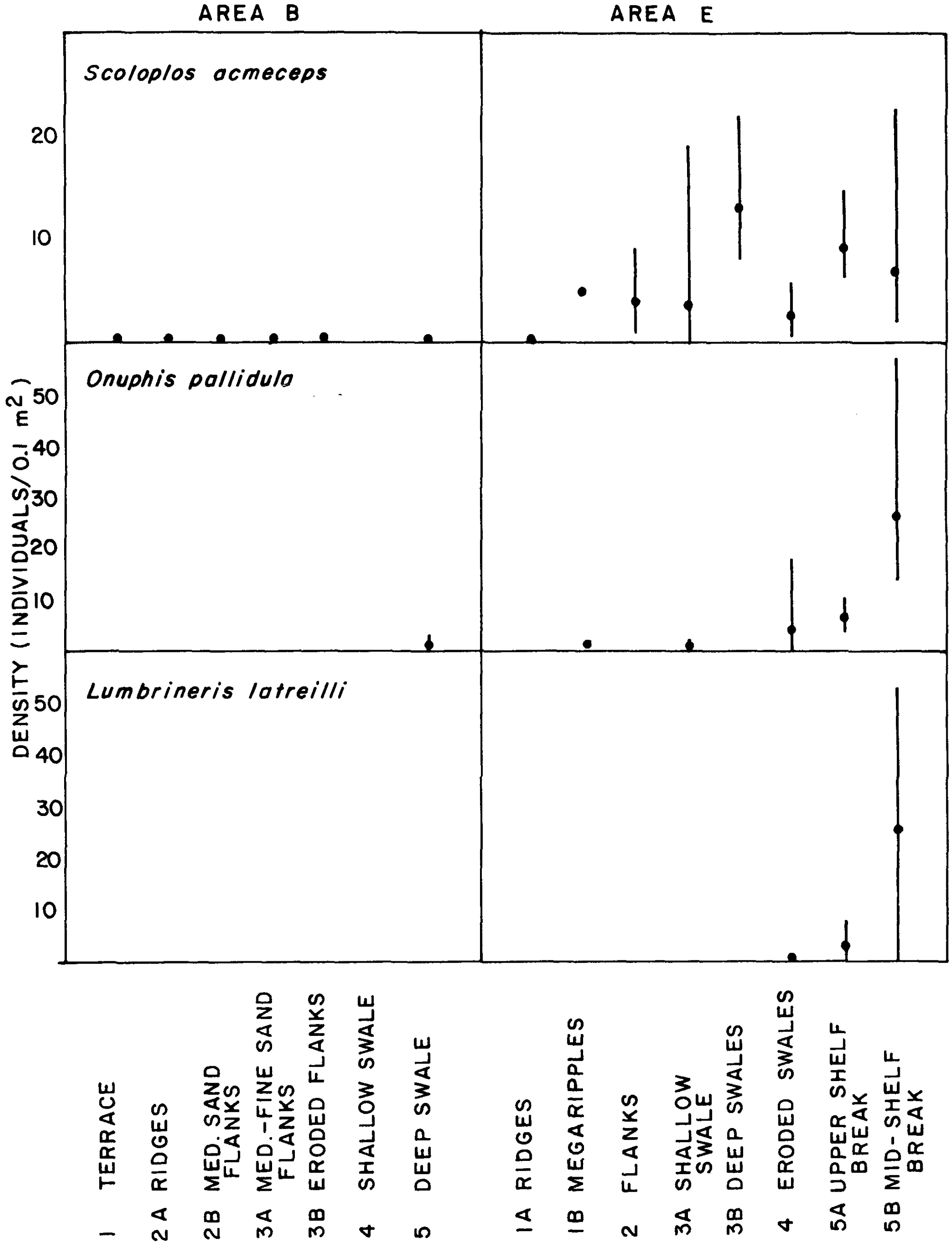

Figure 6-50. Geometric means and confidence limits on those means for population densities of species by topographic habitat in areas B and E.

found in reduced densities in swale habitats of Area E and even the deep swale in Area B.

The dominant species in deeper flank, swale, and shelf break habitats had diverse living positions and feeding strategies. Interstitial burrowers were rare but tube builders, burrowers, suspension, surface-deposit and subsurface deposit feeders were well represented.

Species Diversity

Large Scale Patterns. Community structure statistics, including measures of areal richness, Shannon diversity, numerical richness, and species evenness, are graphically summarized in Figures 6-51 and 6-52 based on values obtained for both sampling years (Appendix 6-C). For this summarization, collections were grouped by bathymetric habitat: inner shelf (15-30 m), central shelf (30-50 m), outer shelf (50-100 m), shelf-break (100-200 m), upper slope (200-500 m), and mid-slope (500-800 m). Collections from topographic depressions on the shelf are summarized separately. Separate summarizations are provided for the quarterly sampled cluster stations and semiannual stations. This is necessitated by the variable replication at the latter. The smaller sample size resulting from collection of four rather than six replicates at some stations during the second year affects diversity estimates. All data from semiannual stations were computed based on four replicates only.

Areal richness (number of species per unit area) increased across the shelf and was highest at outer shelf and shelf-break stations. Typically, between 40 and 50 species were taken at inner shelf stations and between 45 and 60 at central shelf stations. The swales at stations C4 and D4 supported areally richer assemblages, generally more than 60 species in 0.6 m^2 and in some instances in excess of 100 species. The fewest number of species was collected at inner shelf stations (C2, C4, and G2) affected by the hypoxic conditions of the summer of 1976. Outer shelf assemblages were very rich and most stations yielded in excess of 80 species in 0.6 m^2. A maximum of 150 species in 0.6 m^2 was collected at Station A1 on one occasion. Outer shelf swales were richer still with more than 100 species almost always taken. Shelf-break and upper slope communities were about as areally rich as those on the outer shelf. The number of species collected at mid-slope stations declined dramatically to generally less than 40 species in 0.4 m^2 sampled. This coincided with a very precipitous decline in the densities of macrobenthos. Thus, fewer species were collected mainly because fewer animals were collected in the area sampled.

Numerical richness expresses the number of species predicted, E_s, for a sample size of a set number of individuals, in this case 500.

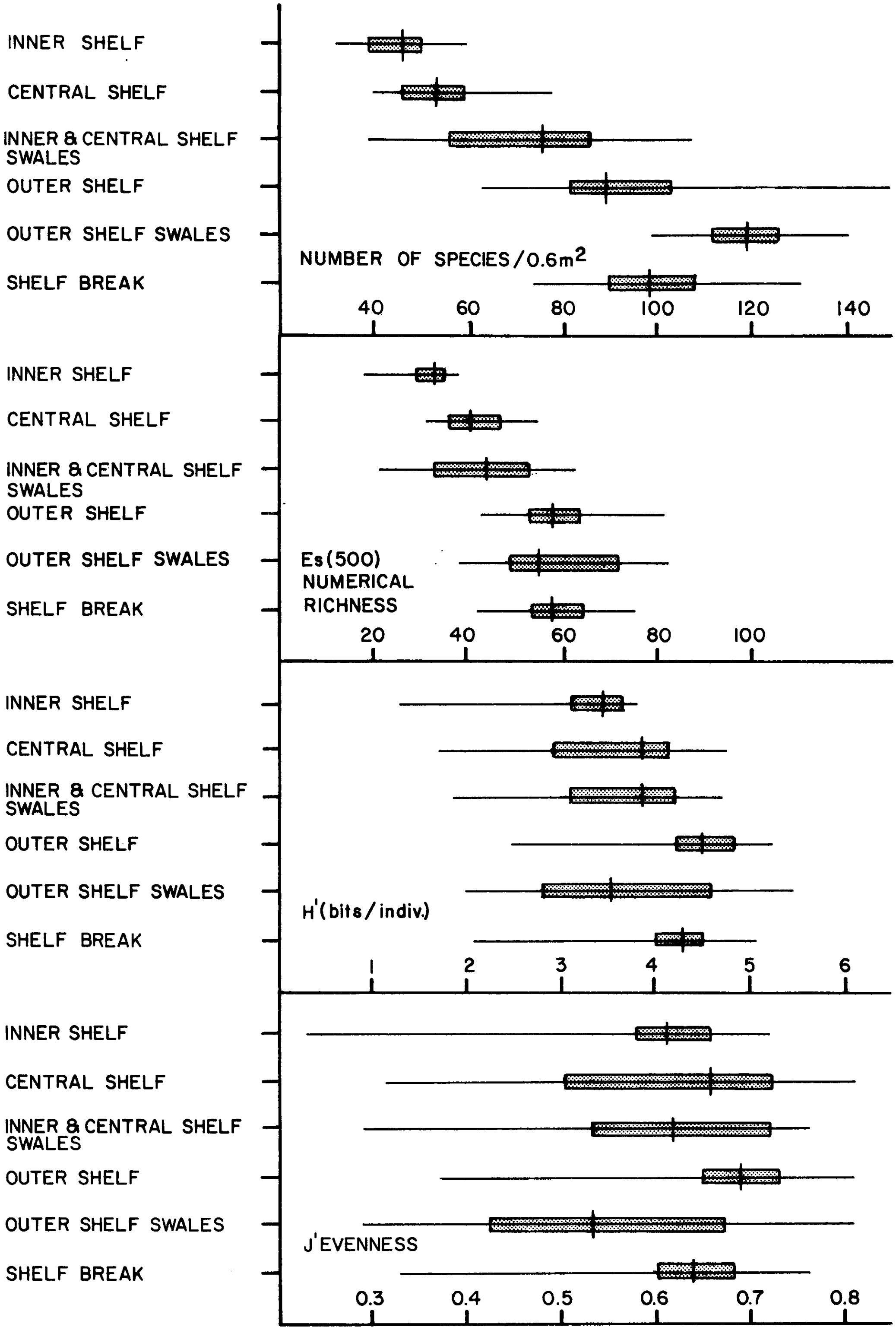

Figure 6-51. Distribution of areal and numerical species richness, Shannon diversity, and species evenness for collections of macrobenthos from quarterly stations, by major habitat. Horizontal lines represent the range of values measured, bars represent the mid-range, and vertical lines represent the median.

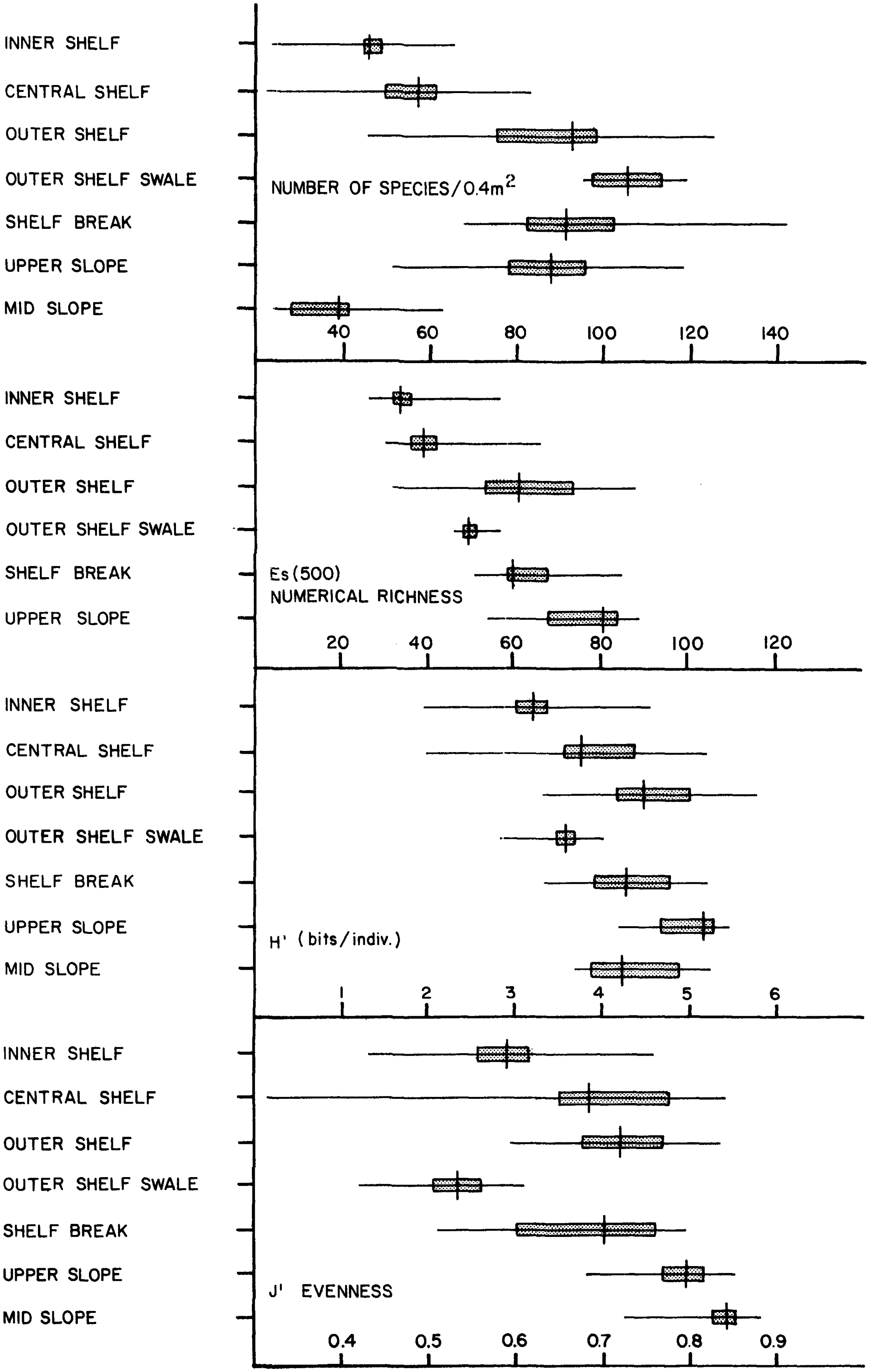

Figure 6-52. Distribution of areal and numerical species richness, Shannon diversity, and species evenness for collections of macrobenthos from semi-annual stations, by major habitat. Horizontal lines represent the range of values measured, bars represent the mid-range, and vertical lines represent the median.

This allows comparison of the richness of sparse assemblages with that of dense assemblages. However, like informational (Shannon) diversity, E_s is affected by the evenness of the distribution of individuals among species. Numerical richness increased nearly monotonically from inner shelf stations to the upper continental slope. The increase in E_s was less dramatic than that for areal richness. This is a reflection of the high abundance as well as richness of macrobenthos on the outer shelf and shelf-break. Outer shelf swale assemblages demonstrated slightly lower median values of E_s than did other outer shelf assemblages, a manifestation of the high density and dominance at swale stations. The expected number of species collected in a sample of 500 individuals could not be computed for mid-slope collections because they generally consisted of fewer than 500 individuals.

Median Shannon diversity increased across the shelf as did the richness measures. As with numerical richness, values were somewhat depressed in outer shelf swales due to heavy dominance by a few species despite the high areal richness. Values of H' within the bathymetric zones ranged widely, however, and the trend is not as clearcut as with the richness measures. Shannon diversity values found within the shelf-break zone were comparable with those of the outer shelf, although the median of the former was slightly lower. Highest Shannon diversity was found on the upper slope (median 5.4 bits/individuals) but diversity on the mid-slope was only just comparable with that on the shelf-break and outer shelf. Shannon diversity values might have been higher on the mid-slope if larger sample sizes were collected, because although relatively few species were collected, the assemblages were very even. In general terms, H' values for outer shelf, shelf-break, and slope communities were in excess of 4 bits/individual; whereas values for inner and central shelf and swale communities were mostly below 4 bits/individuals.

The distribution of species evenness as measured by J' shows the effect of high dominance (low evenness) on Shannon diversity and numerical richness at the swale stations, despite the high areal richness of these communities. A clear trend toward high evenness, due to the lack of clear dominants, on the continental shelf is also apparent. Otherwise, the medians and mid-ranges of J' values for outer shelf and shelf break assemblages are roughly similar.

Medium Scale Patterns. Mesoscale patterns of species diversity can be evaluated from the results of the habitat delineation study. Figures 6-53 and 6-54 display the distribution of diversity and abundance statistics for the major habitats recognized in areas B and E. These data are not directly comparable to those presented above because they are based on estimates from single grab samples rather than pooled replicates.

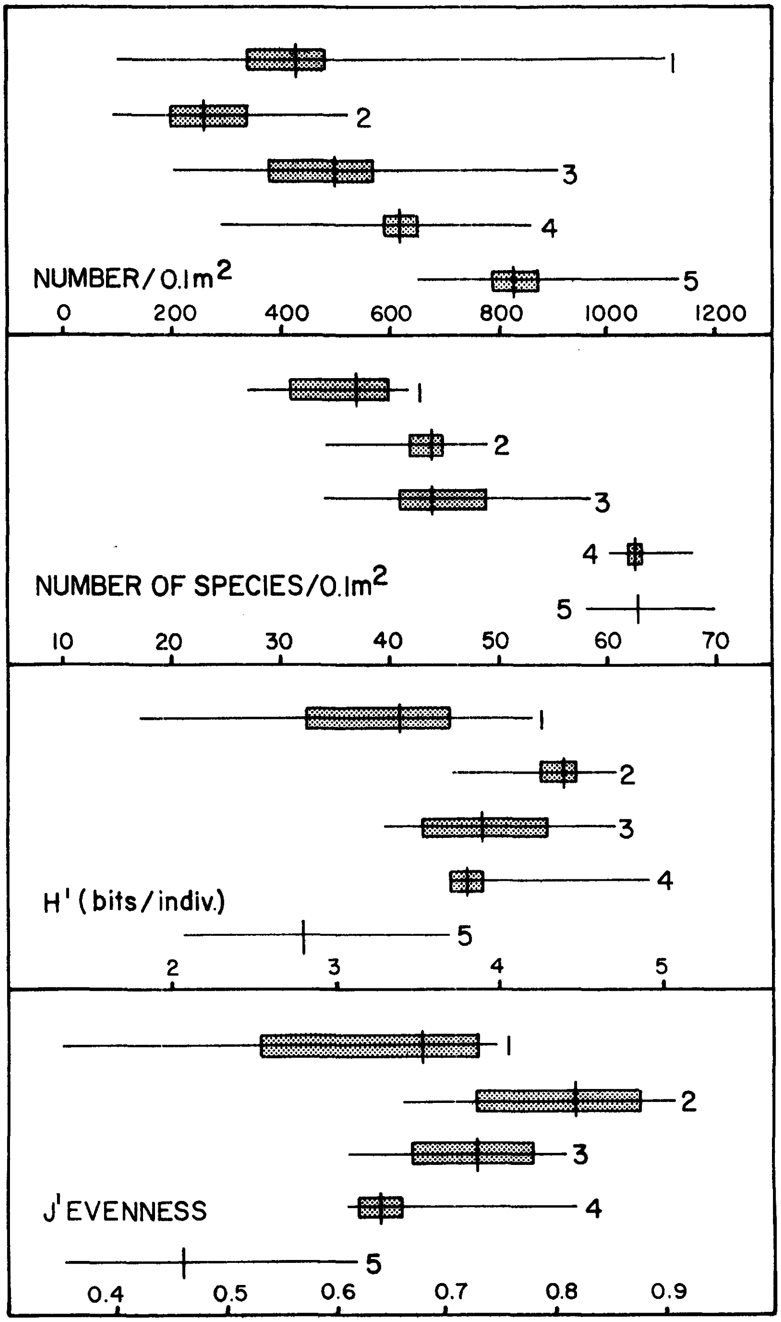

Figure 6-53. Distribution of density of total macrobenthos, areal species richness, Shannon diversity, and evenness by topographic habitat in area B. Horizontal lines represent the range of values measured, bars represent the mid-range, and vertical lines represent the median.

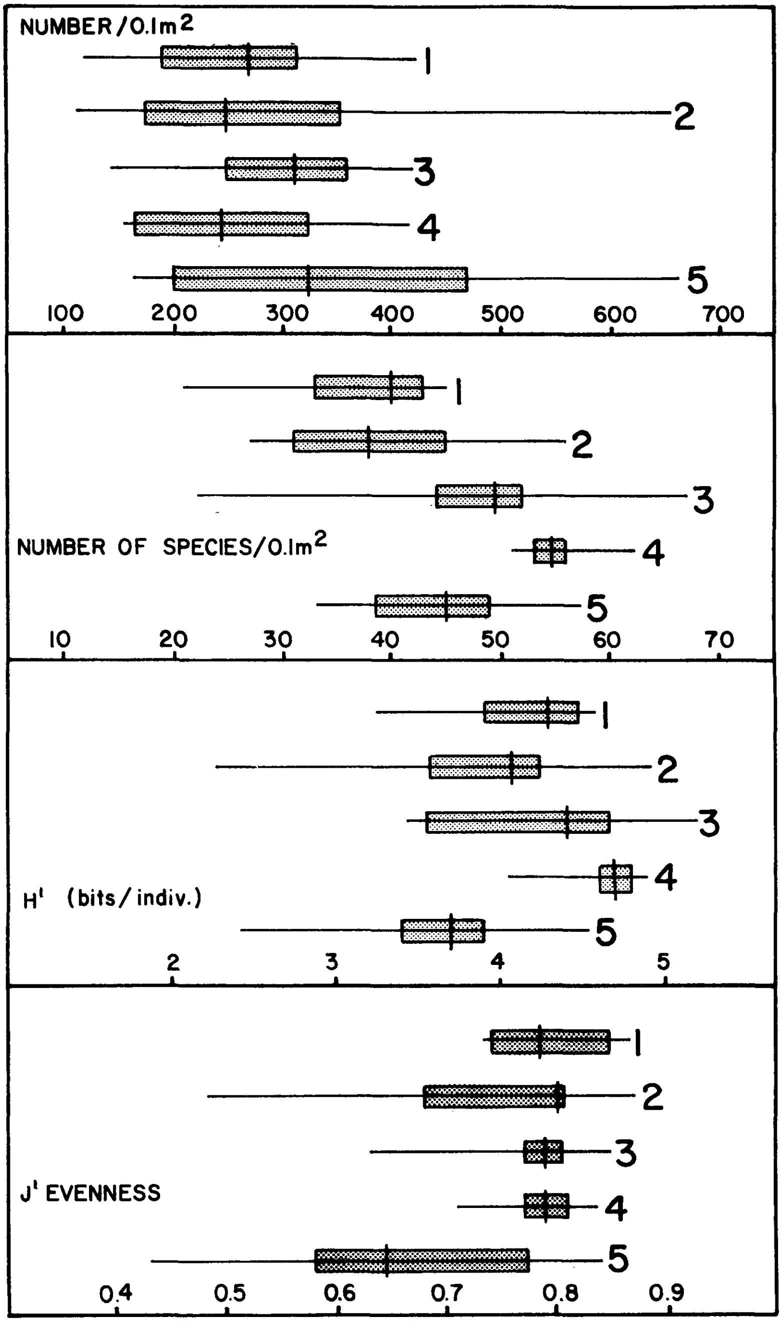

Figure 6-54. Distribution of density of total macrobenthos, areal species richness, Shannon diversity, and evenness by topographic habitat in area E. Horizontal lines represent the range of values measured, bars represent the mid-range, and vertical lines represent the median.

The terrace habitat supported a community of relatively high density but of low species richness. Evenness, and thus H', was low. Total densities of macrobenthos and areal richness showed a progressive increase from ridge to swale habitats (Habitats 2-5), however, the trend in evenness and Shannon diversity was just the opposite, i.e. highest values in the ridge habitat and lowest in the deep swale habitat. J' and H' were strongly related to the dominance by a few species, most strikingly to that by the amphipod *Ampelisca agassizi* in the swales.

The density of total macrobenthos in Area E showed no clearcut difference among major habitats. Highest densities were found in the upper shelf-break and swale habitats (habitats 3 and 5A). Densities were below, in some cases substantially, those in comparable habitats in Area B. Areal richness was lowest in the ridge and flank habitats, intermediate in the shelf-break habitat, and highest in the swales, paralleling the large scale pattern discussed above. H' and J' were similar in habitats 1-3; H' was considerably higher in the erosional swale, due to high richness, and lowest in the shelf-break habitat, due to low evenness resulting from high numerical dominance by the small polychaete *Chone infundibuliformis*.

In summary, there was a strong trend of increase in species richness of macrobenthos with increased depth throughout the Middle Atlantic Bight. Species richness was locally accentuated in topographic depressions where stable substrates and habitat complexity allowed population by species of a greater variety of niches. The derived diversity measure according to Shannon's formula (H') integrates species richness and evenness. On the broad scale H' reflected the bathymetric trend in species richness, except in the topographic depressions where large populations of a few species reduced evenness, thus Shannon diversity. On the local scale, however, species evenness was the predominant determinant of Shannon diversity.

Temporal Trends

Temporal variability of the macrobenthos at the cluster stations sampled repetitively for two years was examined at three levels: the relative persistence of the assemblages considered as a whole, variation in the "structural" indexes of species diversity, and fluctuations in the densities of populations of dominant species.

Assemblage Similarity. Measures of similarity computed between collections taken at a given station were used to reflect the relative persistence (*sensu* Boesch 1974) of the composition and abundance relationships within the community. Such an approach was previously employed by Peterson (1975) and Boesch et al. (1977). Bray-Curtis measures were computed between all pairs of collections (lumped replicates) taken at a station. The means of these similarity mesures were interpreted as indices of community persistence.

The persistence indices for all stations sampled are plotted versus depth in Figure 6-55 to demonstrate the increase in community persistence across the continental shelf. Lowest persistence was found at inner shelf stations affected by the hypoxia of the summer of 1976. Those affected stations at which sampling was continued during the second year, C2, C4, and G2, showed lower persistence than stations C1 and C3 at which the last samples were collected in August 1976. This reflects the repercussive changes in the communities witnessed at the former stations during the second year.

At the stations unaffected by hypoxic stress, the persistence increased from about 0.5 on the inner and central shelf to >0.6 at most outer shelf stations and peaked at over 0.7 for shelf-break stations shallower than 150 m. Communities in outer shelf swales (B3, E4, E2, B5, and G3) were more persistent than those elsewhere on the outer shelf and were roughly equivalent to shelf-break communities in persistence. Variations in the composition of sediments sampled among cruises considerably affected the measured persistence of the community. For example, considering only those collections at Station E2 in which fine sand was more abundant than medium sand (summer 1976 and winter, spring, and summer 1977), i.e. when the station was located in regional habitat 3B (swale) rather than 2 (flank), yielded a persistence index of 0.73 (labeled E2' in Figure 6-55), whereas the mean persistence of all collections at E2 was 0.58. Similarly, when fine sands were predominant in sediments collected at the E4 swale station (fall 1976 and spring and summer 1977) persistence averaged 0.73 versus 0.64 overall.

Deeper than 150 m the persistence index declined down the continental slope to about 0.57 at the middle slope stations. This at first appears to contradict hypothetical predictions that community persistence should increase into the deep sea (Sanders 1968; Grassle and Sanders 1976). However, two alternate explanations of the lowered mean similarity among collections at the deeper stations are suggested. Because of the very low densities and higher species evenness of the slope communities, random samples of a unit area should have inherently less similarity than samples drawn from dense populations. Secondly, because of the abrupt change in depth along the slope, collections from a station taken on different cruises, and even replicate samples from a single cruise, may range considerably in depth even though their horizontal displacement is no greater than for shelf samples.

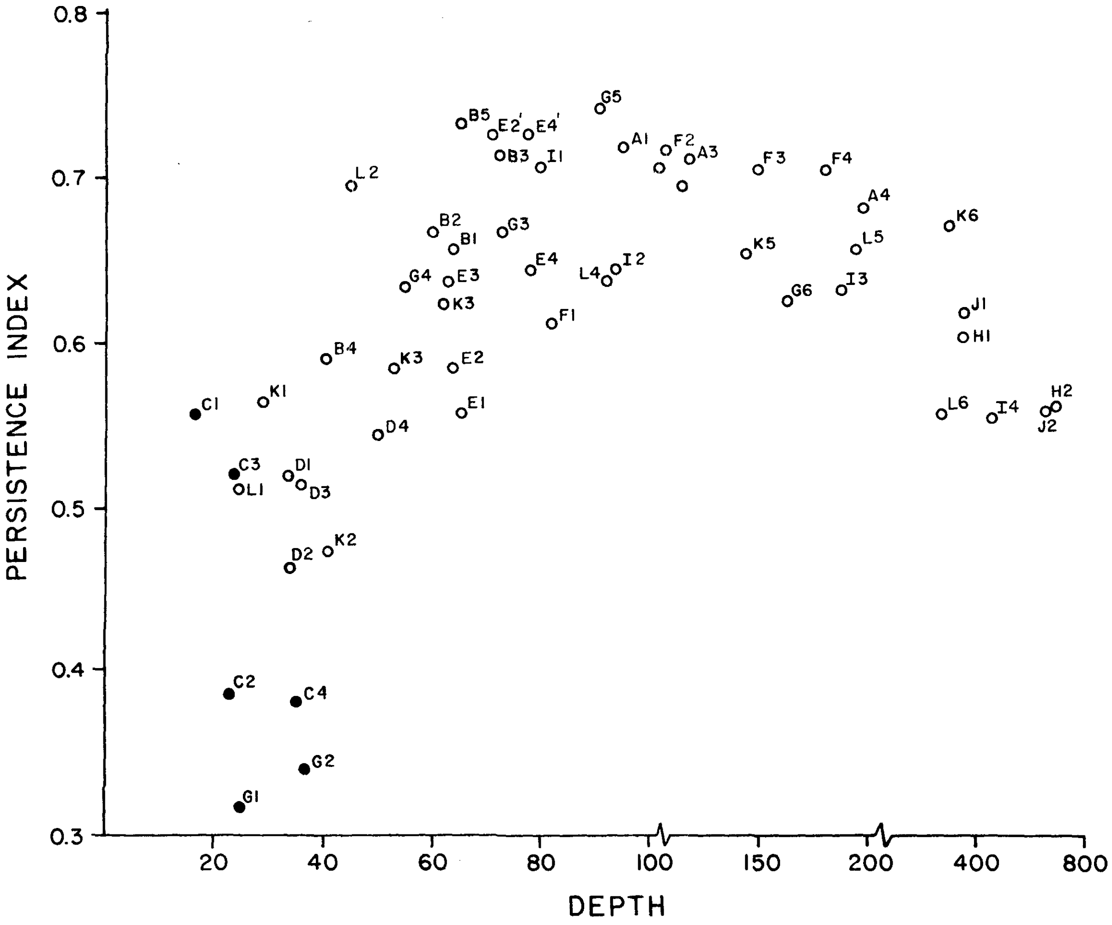

Figure 6-55. Persistence index (see text) of macrobenthos from each station versus depth. Solid circles represent stations affected by hypoxia during summer 1976. E2' and E4' represent only those collections at those stations from strictly swale habitats.

Species Diversity. The temporal trends in Shannon diversity are summarized by bathymetric zone in Figures 6-56 and 6-57. The mean diversity index was most variable on the inner and central shelf. The large fluctuations at the inner shelf stations were mainly due to repercussions resulting from the hypoxic stress of the summer of 1976 which included extremely low species evenness concomitant with the establishment of dense populations of the polychaete *Spiophanes bombyx*. However, H' fluctuated considerably at central shelf stations not experiencing mortalities from the hypoxia. The lowered diversity at some central shelf stations during fall 1976 was the result of lowered evenness due to dense setting of juveniles, notably the bivalve *Spisula solidissima* at Station D1.

Mean Shannon diversity was persistent at outer shelf and shelf break stations, mainly constrained between 4.1 and 4.6 bits/individual. Only the fall 1975 collections from the outer shelf cluster stations appreciably departed from these limits (mean of 3.6 bits/individual). At the outer shelf swale stations, mean H' was more variable (range of 3.1-4.3 bits/individual). The unusually low levels in summer 1976 and unusually high levels in fall 1976 were due to variations in the abundance of dominant species (i.e. evenness) rather than any changes in species richnes.

Slope communities yielded the most constant Shannon diversity levels. On the middle slope, mean Shannon diversity ranged only from 4.2 to 4.5 bits/individual (4.6-5.3 at H2 and 3.7-4.0 at J2). Mean values at the upper slope stations were even more uniform, ranging from 4.9 to 5.1 bits/individual.

Populations of Dominant Species. Twenty-five species were chosen for detailed examination of their temporal variation over the two year study period (Table 6-12). They were chosen on the basis of their dominance at two or more stations. The polychaete taxa Syllidae and *Tharyx*, although dominant at several stations, were not considered due to incomplete separation of species during the first year. *Spisula solidissima* was included because of its commerical importance in the area. Variability of these populations was quantified in three ways. The relationship of the variance attributable to among-season sample differences in population density (log-transformed) was compared to the variance among replicates within seasons. That is, temporal variance was compared to spatial variance in a one way model II analysis of variance. The resultant ratio, F, could then be used an an index of temporal variability and its significance tested. Secondly, the patterns of temporal variation for a species were compared for the stations (maximum of five stations) at which it was dominant. The ranks of the seasonal densities were tested for concordance using Kendall's coefficient. Finally, the Mann-Whitney U test was employed to determine any differences in the rank of the seasonal means between the two years of sampling. The temporal

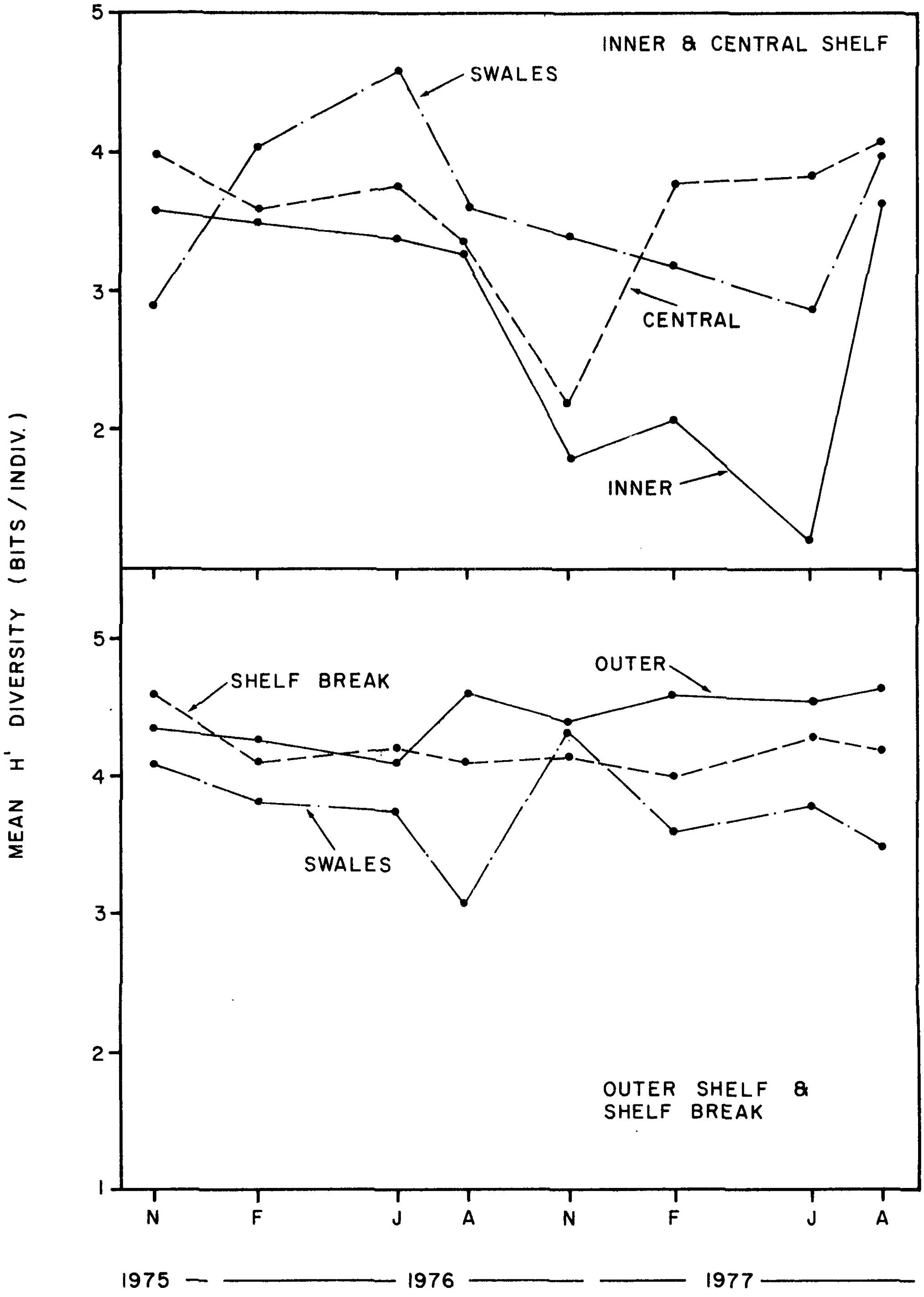

Figure 6-56. Temporal variation in Shannon diversity of macrobenthos averaged by major habitats for quarterly stations.

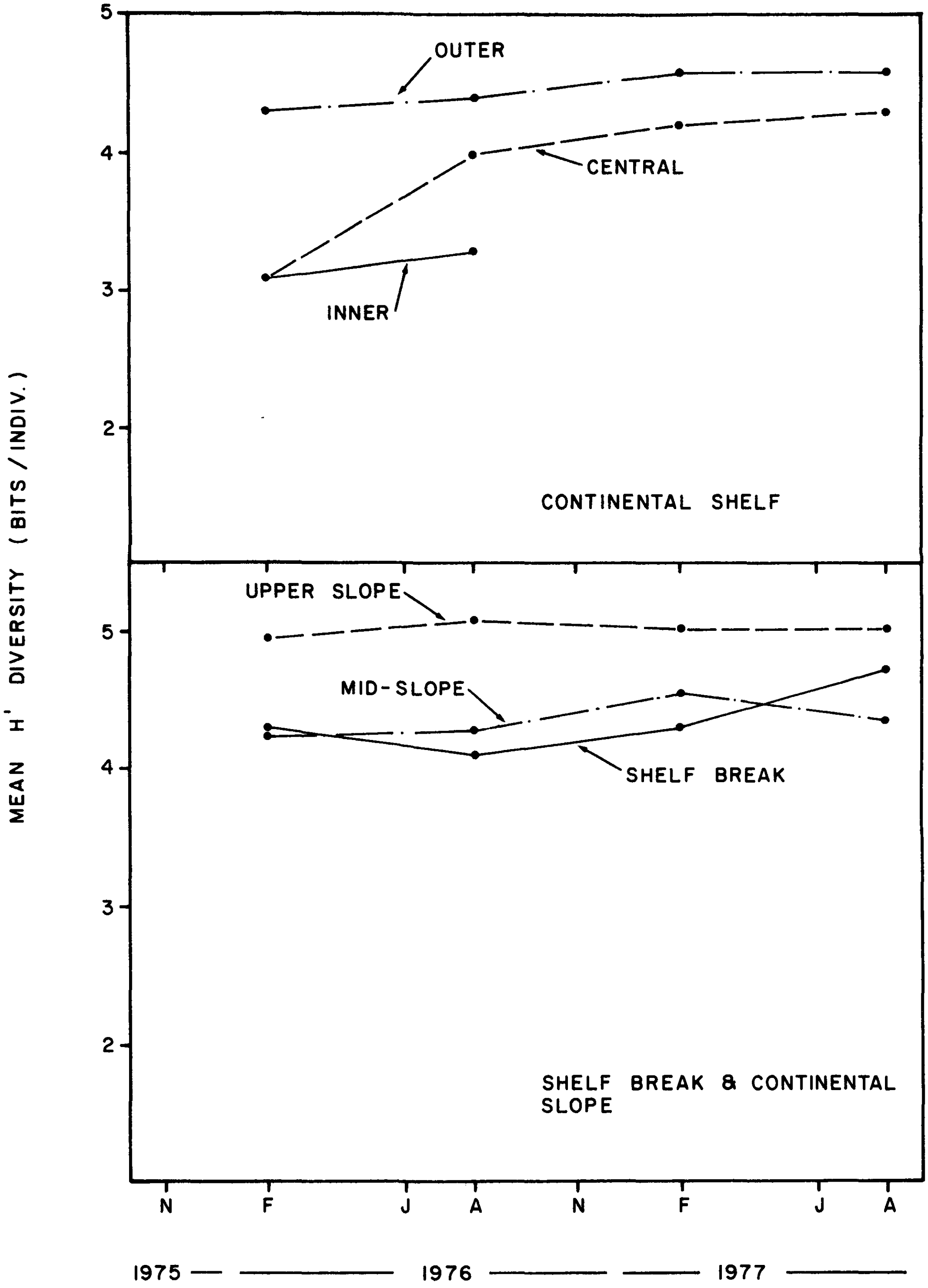

Figure 6-57. Temporal variation in Shannon diversity of macrobenthos averaged by major habitats for semiannual stations.

variations of nine of the 25 species are plotted in Figures 6-58 to 6-65.

Several groupings of the dominant species can be made on the basis of their temporal variability (Table 6-13). One group is characterized by having relatively persistent populations. The ampeliscid amphipod *Ampelisca agassizi* (Figure 6-58) had typically constant population levels. Population densities at Station E2 were the only exception. The much higher densities found at E2 in summer 1976 and winter and summer 1977 coincide with the muddy fine sands found during these periods related to variations in station location (Chapter 5). Despite the lack of sharp rises and falls there seems to be a concordant pattern of higher densities in the spring and summer, especially June 1977, possibly attributable to recruitment. Bousfield (1973) reports ovigerous females of *A. agassizi* in the summer in New England. The sibling species *Ampelisca abdita* and *A. vadorum* have two generations in New England, a winter population which breeds about mid-April and a summer generation which breeds in July (Mills 1967). *A. agassizi* was found in zooplankton samples in June of both years and it is known that ampeliscids (Mills 1967) leave their tubes to swim freely prior to mating.

Patterns for two shelf-break species, the bivalve *Thyasira flexuosa* (Figure 6-59) and the polychaete *Lumbrineris latrelli*, (Figure 6-60) and, to a lesser degree, two shelf species, the echinoid *Echinarachnius parma* (Figure 6-61) and the polychaete *Goniadella gracilis*, similarly lack extreme seasonal variations. *Thyasira flexuosa* showed a concordant rise in abundance in spring with a subsequent decline to a low in winter. The low value at Station F4 in summer 1976 may be due to the somewhat finer sediment found there (Chapter 5). A similar species, *Thyasira gouldi*, is reported to breed in late August through September in Greenland (Ockelmann 1958). It is fairly common for species that breed in late summer in higher latitudes to breed earlier in the lower latitudes (Thorson 1950).

Of the stations considered, *Echinarachnius parma* showed significant temporal variability at only D1 and E2 (Figure 6-61). This variability is largely attributable to unusually high densities in winter 1976 at D1 and in summer 1976 and spring and summer 1977 at E1. These coincide with off-feature location of these stations at these times and concomitant differences in sediment type (Chapter 5). There was a lack of concordant seasonality although densities during the second year were generally below those of the first. Cocanour (1969) found that *E. parma* in the intertidal zone of Maine spawned in September and October. Newly settled juveniles occurred in these samples throughout the summer and fall. However, recruitment of a new year class did not always correspond to an increase in densities and in some cases there was a decrease.

Two other species characteristic of the shelf break, the polychaete *Aricidea neosuecica* and the ostracod *Harbansus bowenae* also

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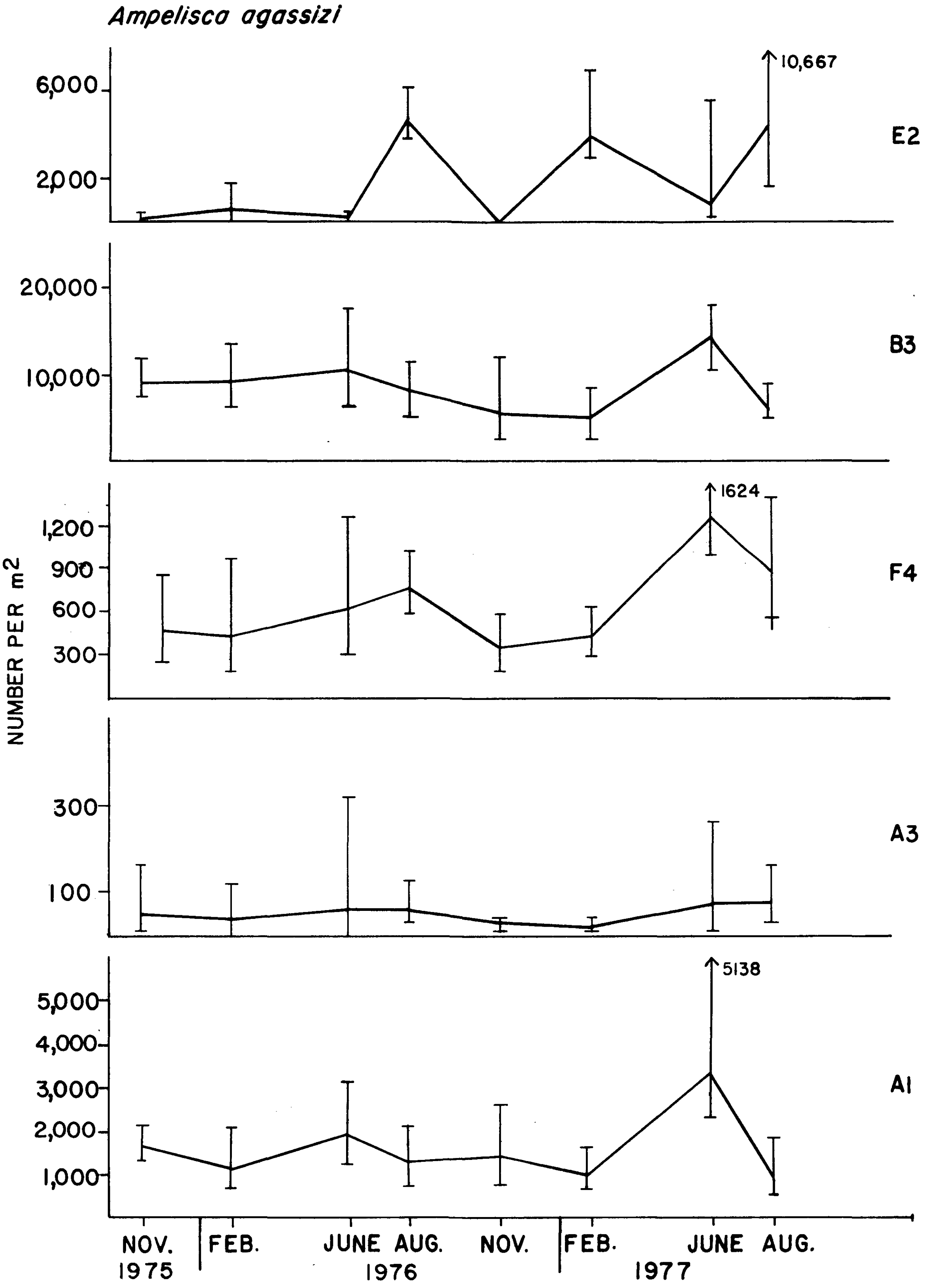

Figure 6-58. Temporal variation in the population densities of the amphipod Ampelisca agassizi at stations where it was most abundant.

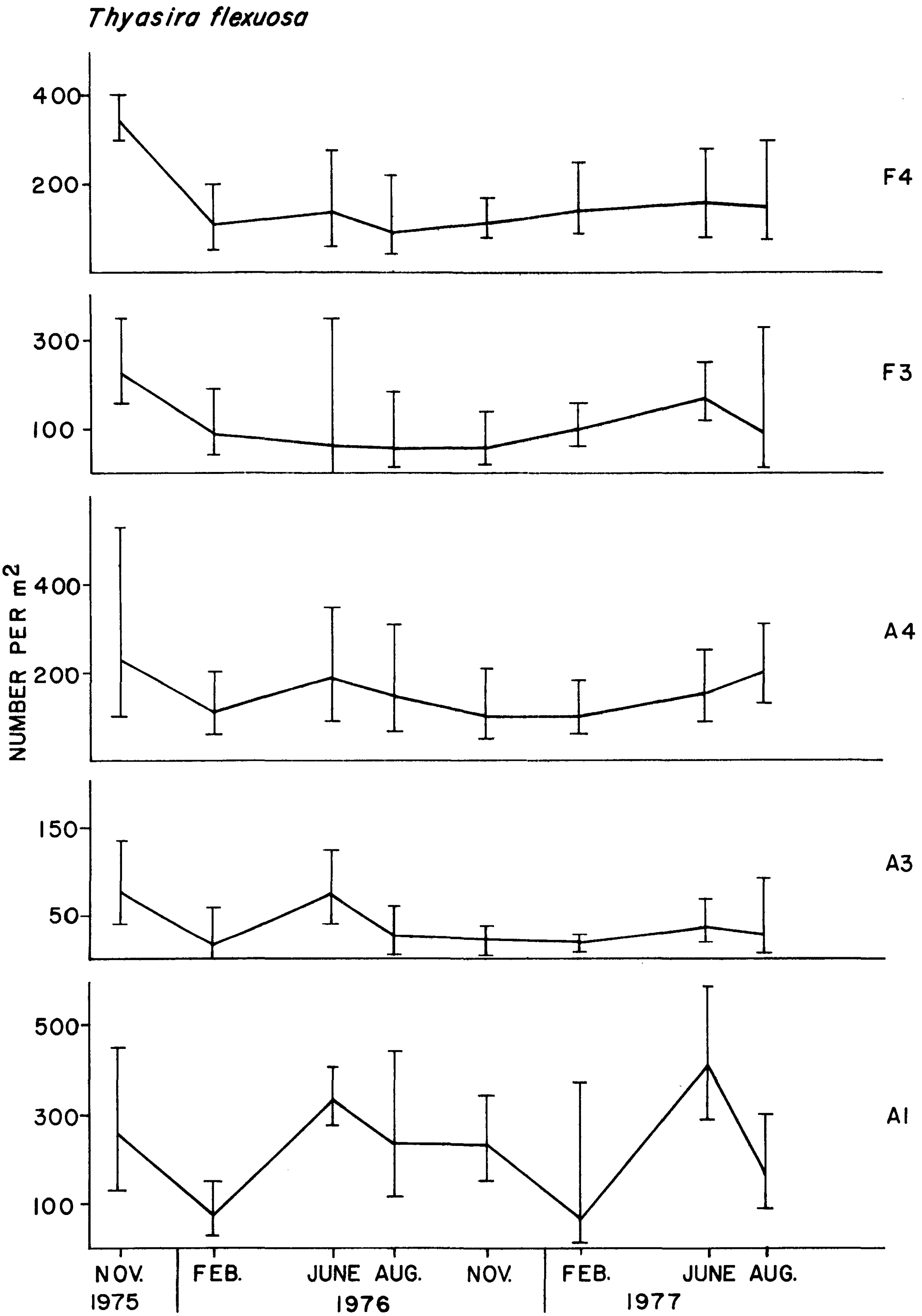

Figure 6-59. Temporal variation in population densities of the bivalve Thyasira flexuosa at stations where it was most abundant.

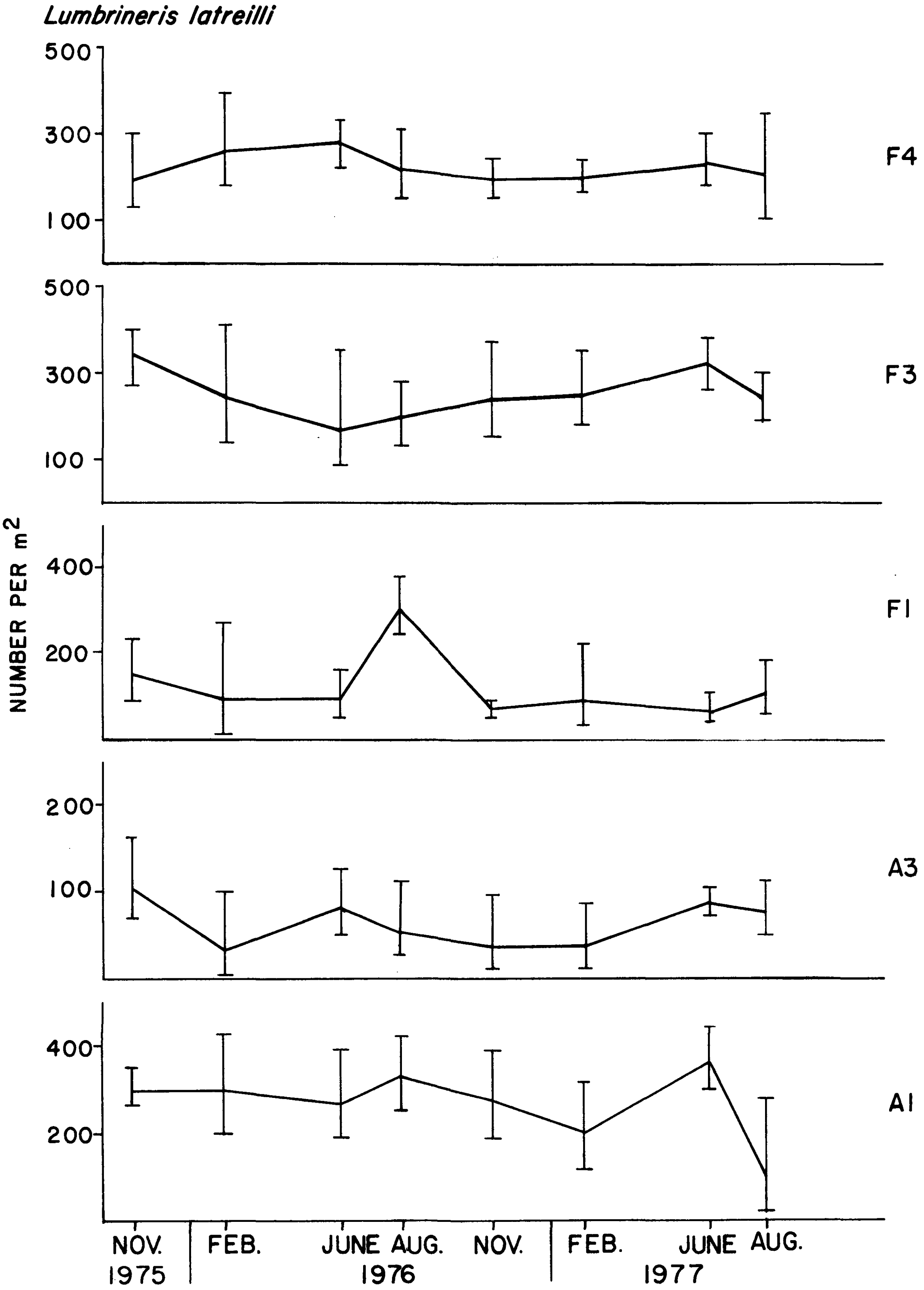

Figure 6-60. Temporal variation in population densities of the polychaete Lumbrineris latreilli at stations where it was most abundant.

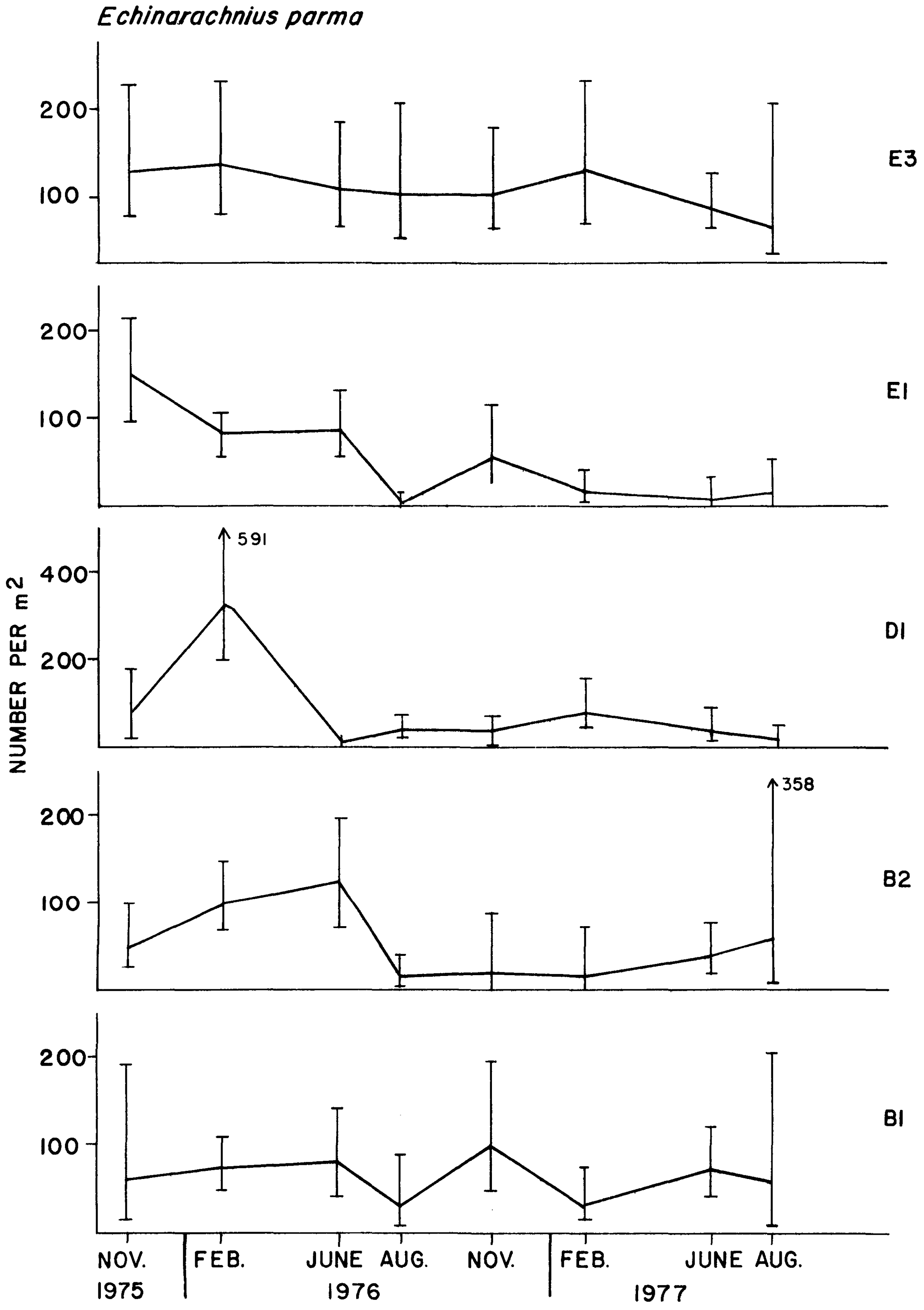

Figure 6-61. Temporal variation in the population densities of the echinoid Echinarchnius parma at stations where it was most abundant.

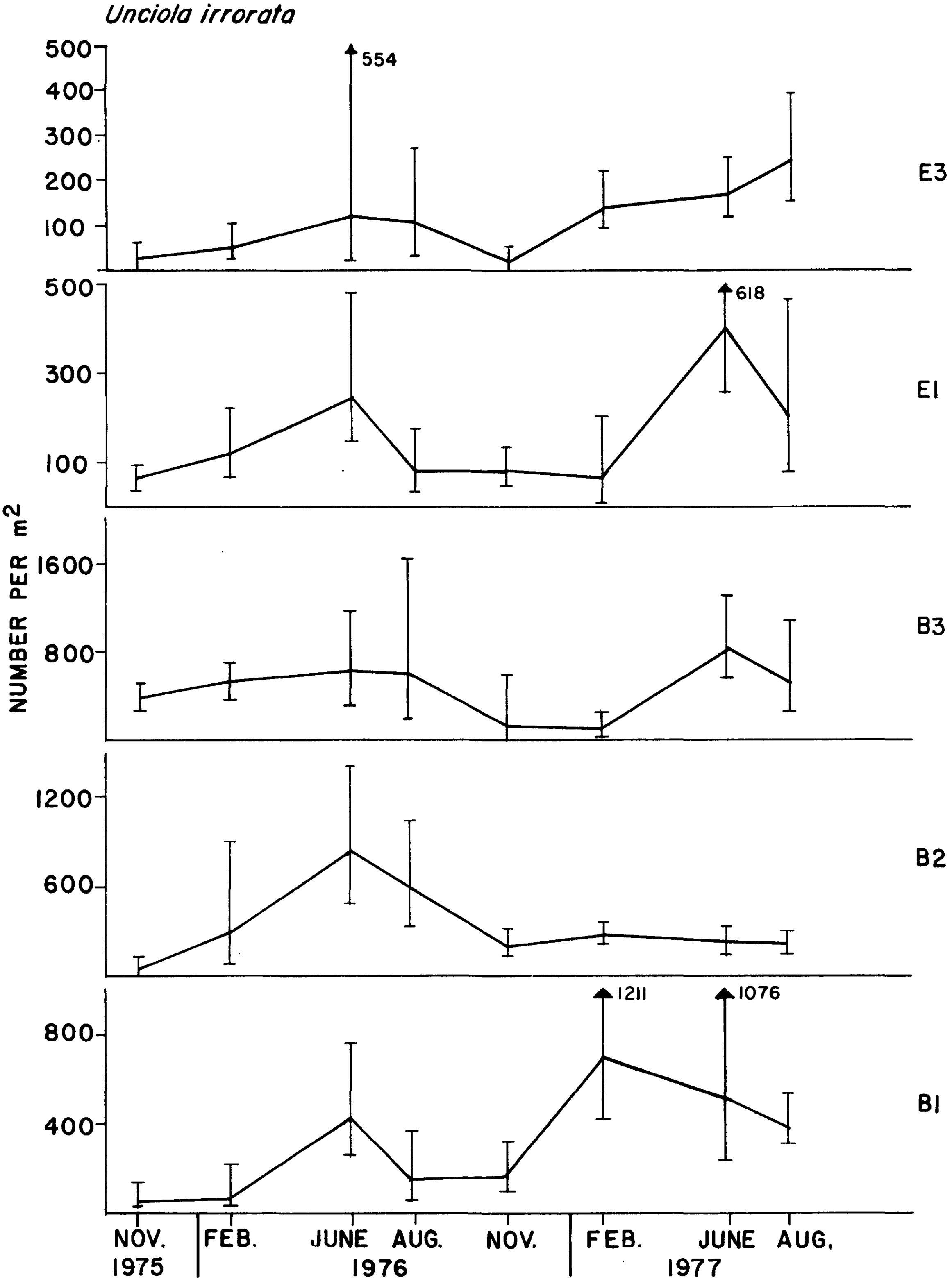

Figure 6-62. Temporal variation in population densities of the amphipod Unciola irrorata at stations where it was most abundant.

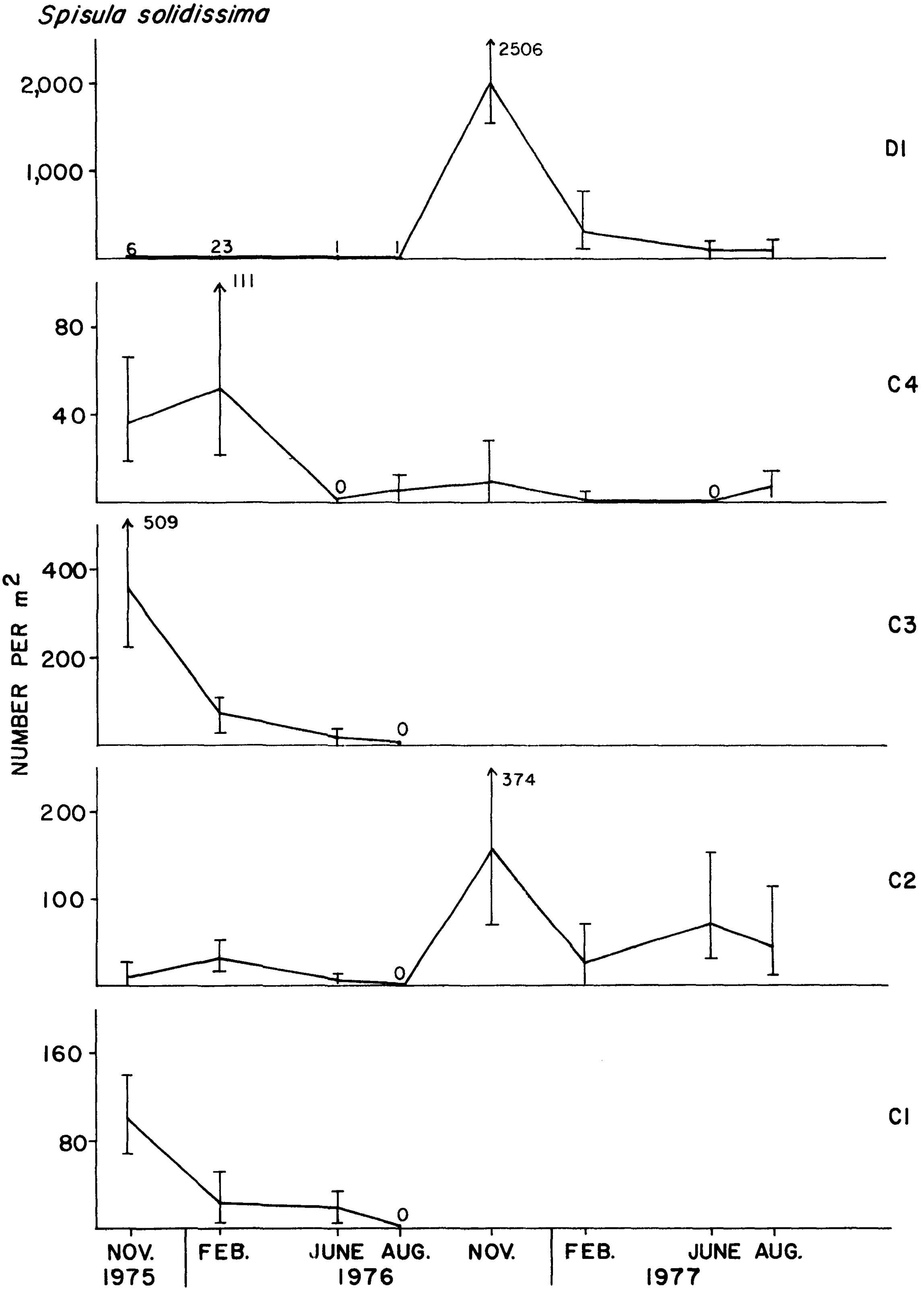

Figure 6-63. Temporal variation in population densities of the bivalve Spisula solidissima at stations where it was abundant.

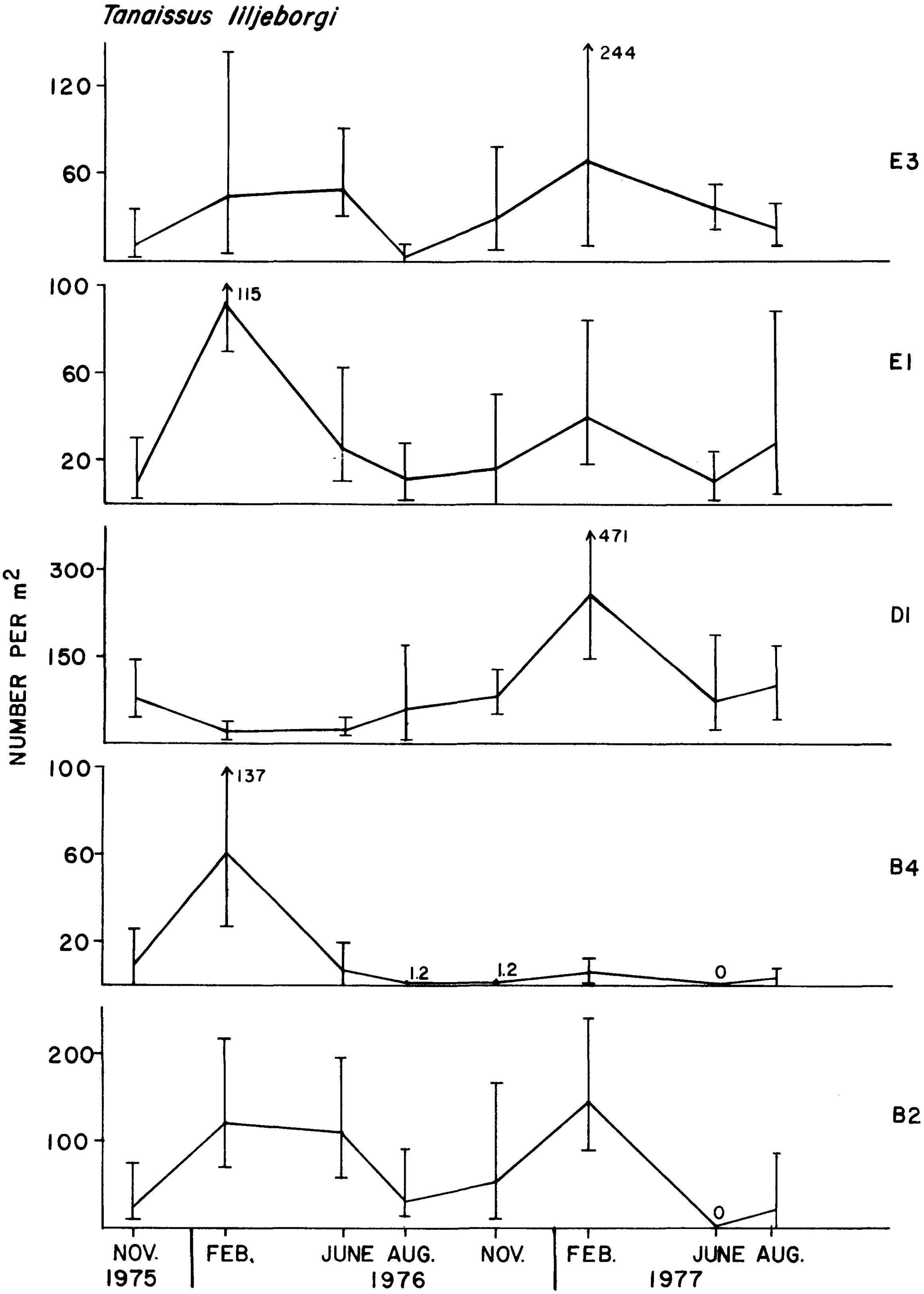

Figure 6-64. Temporal variation in the population densities of the tanaidacean Tanaissus liljeborgi at stations where it is most abundant.

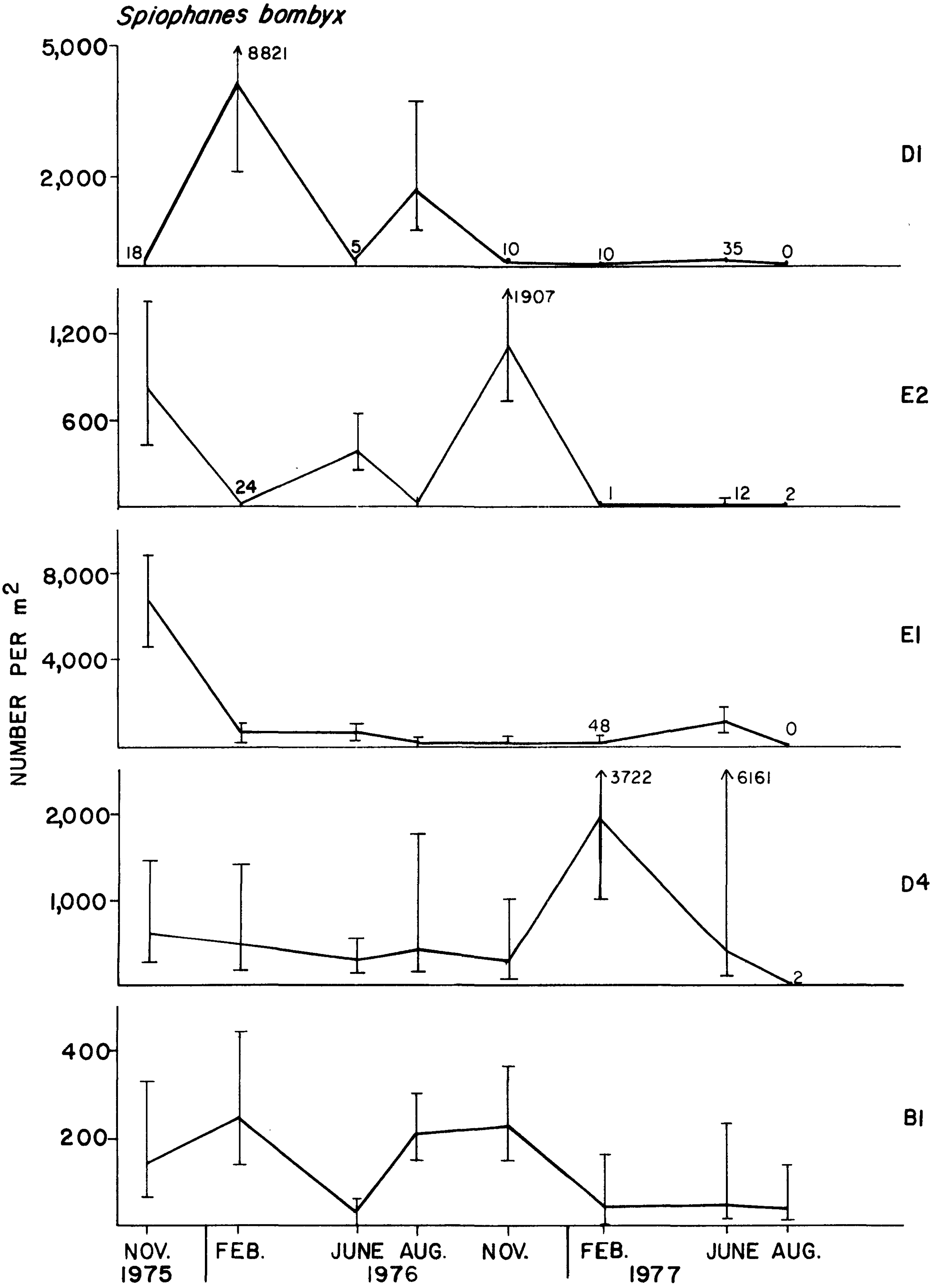

Figure 6-65. Temporal variation in the population densities of the polychaete Spiophanes bombyx at stations where it was most abundant.

Table 6-13. Results of statistical analyses of temporal variability of dominant, widely-occurring species of macrobenthos.

Species	Temporal Variation within Stations (F - Statistic)	Concordance among Stations (Kendall coefficient of Concordance: W)	Difference between Years (Mann-Whitney U Test)
Persistent species			
Aricidea neosuecica	A3(6.9)*, A4(2.6), F2(7.3)*, F3(1.6), B4(5.8)		
Lumbrineris latreilli	A1(4.8), A3(2.7), F1(6.7)*, F3(1.8), F4(2.1)		
Goniadella gracilis	B2(6.3)*, B4(3.2), C2(3.9), E3(5.0)		
Thyasira flexuosa	A1(4.9), A3(3.5), A4(1.4), F3(1.8), F4(3.0)	*	
Ampelisca agassizi	A1(4.4), A3(1.0), B3(3.9), E2(29.9)*, F4(4.50)	*	
Echinarachnius parma	B1(1.4), B2(2.9), D1(11.9)*, E1(13.4)*, E3(1.0)		*
Seasonal species			
Polygordius sp. 1	B2(10.7)*, B4(9.5)*, D4(12.3)*, E3(4.3)	*	
Nothria conchylega	A3(8.7)*, E4(5.0), F3(5.3), F4(11.0)*	*	
Chone infundibuliformis	D4(27.0)*, F1(22.8)*	*	
Spisula solidissima	C1(27.1)*, C2(14.1)*, C3(87.7)*, C4(16.8)*, D1(49.3)*	*	*
Tanaissus liljeborgi	B2(12.0)*, B4(12.6)*, D1(7.6)*, E1(4.5), E3(4.1)	*	
Ampelisca vadorum	B1(14.4)*, B2(5.5), D4(13.7)*, E1(12.8)*, E4(12.4)*	*	
Unciola irrorata	B1(10.9)*, B2(12.0)*, B3(5.4), E1(6.1)*, E3(6.1)*	*	
Variable but not seasonal species			
Spiophanes bombyx	B1(5.6), D1(101.0)*, D4(8.9)*, E1(112.6)*, E2(56.3)*		*
Scalibregma inflatum	B1(8.7)*, B2(6.7)*, B3(12.3)*, E1(7.5)*		*
Onuphis pallidula	A1(20.5)*, A2(22.4)*, A3(132.9)*, F2(8.4)*, F4(19.6)*		
Spiophanes wigelyi	A1(4.0), A3(6.8)*, F2(18.4)*, F3(10.5)*		
Lumbrineris impatiens	B1(1.4), D4(23.2)*, E1(20.9)*		
Lumbrinerides acuta	B2(7.31)*, B4(.74)		
Notomastus latericeus	B3(7.2)*, E2(4.7), E4(3.9), F1(9.4)*		
Euclymene collaris	B4(16.2)*, E3(5.4)		
Harbansus bowenae	A1(3.6), A2(3.5), A4(13.5)*, F2(4.8), F4(2.3)		
Trichophoxus epistomus	D1(21.4)*, D4(8.2)*, E1(3.4), E3(15.7)*, F1(2.4)		
Ericthonius rubricornis	B1(7.54)*, B3(12.6)*		
Amphioplus macilentus	A2(6.99)*, A3(2.1), E4(7.7)*, F2(6.4)*, F4(1.3)		
	* significant at 1% level	* significant at 5% level	* significant at 5% level

lacked significant temporal variability at most stations at which they were dominants. Variability at other stations could be explained in part by differences in the sediment composition in seasonal samples. For example, the increase of *A. neosuecica* in summer 1976 at F2 concided with finer than usual sediments.

A second group of species showed large and concordant increases in density during one season (Table 6-13, Figures 6-62 to 6-64). The density of the amphipod *Unciola irrorata* tended to rise in the spring and decline in the fall. Bousfield (1973) found ovigerous females of *Unciola irrorata* from March to July in coastal New England. *Spisula solidissima* populations were highest in the fall of 1977 at stations C2 and D1, reflecting a heavy spatfall in the inner and central shelf. *S. solidissima* populations spawn during July and August and may spawn again in mid-October through early November (Ropes 1969). Populations of the tanaidacean *Tanaissus liljeborgi* peaked in winter of each year with a nadir in spring. Ovigerous females and a few males were found in the spring of both years. This species is probably a protogynous hermaphrodite and males of the species have not been reported since 1880 (Sieg 1973). It is conceivable that, due to the small size of the adults, the juveniles released during the summer do not become large enough to be retained in numbers on the 0.5 mm sieve until winter. The archiannelid *Polygordius* sp. and the sabellid polychaete *Chone infundibuliformis* increased in abundance from fall to winter with a rapid decline in spring and summer. The reptant onuphid polychaete, *Nothria conchylega*, showed concordantly low densities in summer, but no concordant peaks of abundance. Populations of the amphipod *Ampelisca vadorum* usually increased from fall to winter and then declined by spring except at E1, where, due to the location of the spring 1977 collection in finer sediments (Chapter 5), *A. vadorum* was very abundant. As discussed above, *A. vadorum* has two breeding periods in coastal New England, one in April and the other in July (Mills 1967). The critical breeding temperature of 8°C is reached in the spring there, whereas this temperature is usually not reached until late summer or early fall in the outer shelf study region.

The remaining species showed large to moderate temporal variations in abundance which were not concordant among stations. Large temporal variability is exemplified by the polychaete *Spiophanes bombyx* (Figure 6-65). Large and sometimes sporadic irruptions of populations of *S. bombyx* have been reported by Ziegelmeier (1963) in the German Bight, by Frankenberg and Lieper (1977) on the shallow continental shelf off Georgia and by Boesch (1973) in the Chesapeake Bay. Simon and Brander (1967) found larvae from June to August and October to February at Cape Cod. Therefore, it probably has the potential for recruitment throughout most of the year. Other species which showed large population variations without a concordant or reoccurring pattern and which could not be largely explained by between-collection sediment differences include: the polychaetes *Notomastus latericeus*, *Spiophanes wigleyi*, *Lumbrineris impatiens*, *Lumbrinerides acuta*, and *Euclymene collaris* and the amphipod

Trichophoxus epistomus. Except for Spiophanes wigleyi these species are all characteristic of shelf habitats.

Several other species showed large temporal variability during one year and not the other. Populations of the polychaete Onuphis pallidula showed a characteristic increase through the summer of 1976 then declined to persistent levels during the second year at A1, A2, and A3. However, at F2 and F4 populations again increased through the summer. The polychaete Scalibregma inflatum decreased in density from fall 1975 to fall 1976 and remained at persistently low densities during the second year. Only four of the 21 species showed any significant yearly differences between the two years of study. Echinarachnius parma, Scalibregma inflatum, and Spiophanes bombyx had larger populations during the first year while Spisula solidissima had larger populations during the second year due to a large spat fall prior to the fall 1976 sampling.

Although the pattern is by no means clear, species dominant at shelf break stations (e.g. Thyasira flexuosa, Lumbrineris latreilli, Ampelisca agassizi, Aricidea neosuecica, Harbansus bowenae) showed more persistence than the shelf dominants. The temporal variability of Spiophanes wigleyi and Onuphis pallidula and the persistence of Goniadella gracilis and Echinarachnius parma are notable exceptions to this trend.

Effects of Catastrophic Disturbance: Hypoxia of Summer of 1976

Unusual conditions developed during the summer of 1976 resulting in depletion of dissolved oxygen of bottom waters below a sharp pycnocline. Hypoxic (dissolved oxygen <2 mg/l) conditions were widespread on the inner shelf off New Jersey, and anoxic conditions and the presence of hydrogen sulfide (H_2S) were experienced off central New Jersey (Figure 6-66). These conditions developed during early July and hypoxic stress continued into October 1976.

Several factors are thought to have contributed to the development of the hypoxia. Warmer than normal surface temperature during the winter, less than average winter storm mixing, and prevalent southwest winds in the spring (Diaz 1976) resulted in strong thermal stratification of shelf waters earlier than usual (Parker 1976). At the same time, an unusually large phytoplankton bloom dominated by the large dinoflagellate Ceratium tripos occurred in shelf waters from Georges Bank to Cape May, N. J. (Malone 1976; Smayda 1976). The degradation of bloom organisms sinking into bottom water depleted available oxygen below the pycnocline which effectively insulated the bottom layers from surface oxygenation. Following collapse of the bloom in June, the seabed of the inner shelf was covered by the dark flocculent detritus resulting from the bloom. The excess oxygen demand persisted through September, as the pycnocline was not broken down by Hurricane Belle which moved through the area in

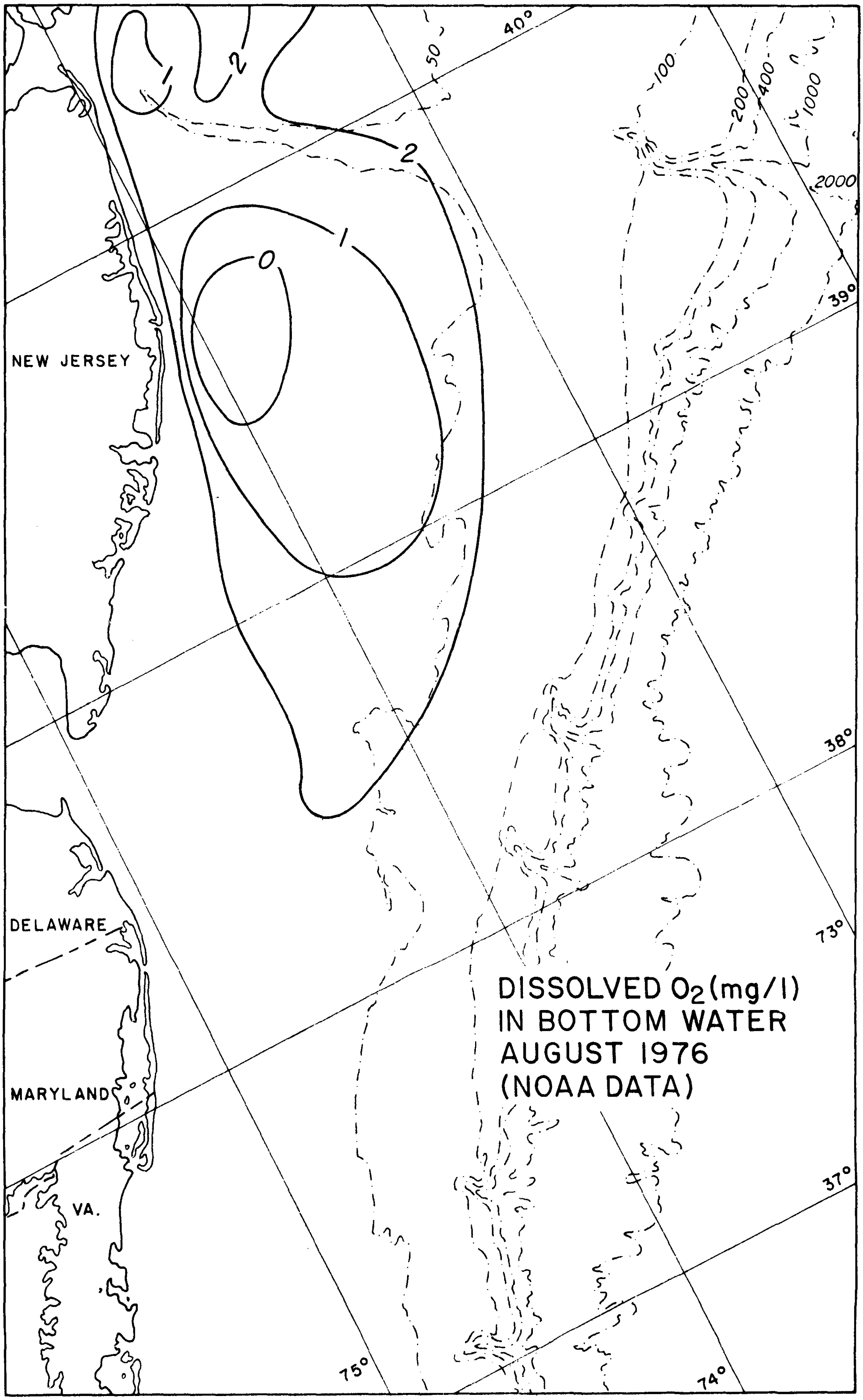

Figure 6-66. Distribution of dissolved oxygen in bottom waters on the continental shelf off New Jersey during August 1976, based on NOAA data (Sharp 1976).

was not broken down by Hurricane Belle which moved through the area in August, until oxygenation occurred with fall turnover of the water mass in October (Steimle 1976).

The hypoxia caused extensive mortalities of shellfish and death or avoidance by fishes (Steimle 1976). The most stressful conditions resulted in extensive but selective mortalities to the macrobenthos and megabenthos at the following stations: C1, C2, C3, C4, G1, G2, and N3. The immediate effects were reported by Boesch et al. (1977). This section of the report further documents these effects and the subsequent response of the communities. In addition to providing unique documentation of the biological effects of a natural disaster, these results enhance understanding of the resilient response of benthic communities to acute perturbations which may possibly result from petroleum development activities.

Physical Observations. Samples taken on four different cruises during August and early September 1976 at stations in Area C showed bottom water dissolved oxygen levels to be consistently <1 mg/l and in some cases immeasurable (Chapter 3). In comparison, dissolved oxygen levels in June 1976 were ca. 7 mg/l and in August 1977 were 2-5 mg/l. This area was in the most critically affected region whereas other affected stations (G1, G2, and N3) did not experience hypoxia as severe or persistent. Generally, bottom sediments on the inner shelf are well oxygenated, and a redox potential discontinuity (RPD), as evidenced by a darkening of sediment color, is not usually visible except in swales in the 10-15 cm depth of sediment sampled. Most samples taken at C2 during June 1976 showed the presence of an RPD. Samples taken in August 1976 showed the sediments to be reducing and with a strong odor of H_2S at all affected stations. An RPD was again located within the sampled depth of sediment during November 1976, but was seldom seen in subsequent samples.

Other important observations can be made from photographs of the seabed, although the photographic record is patchy because of poor visibility and camera malfunctions. Except at the swale station C4, the seabed usually appeared as clean rippled sand (Figure 6-10, top). Epibenthic organisms such as Cancer irroratus, Pagurus sp., Ovalipes ocellatus, Asterias vulgaris, and Echinarachnius parma were characteristically present. Photographs taken in November 1976 showed patches of dark floc overlying the coarse-medium sand at C2; no living organisms were visible. In February 1977 tubes of the polychaete Diopatra cuprea, rarely seen previously, appeared with an average of more than 30 tubes in each photograph although none was taken in the grab samples. In June 1977, Diopatra tubes were not apparent, but the bottom at C2 and G2 was covered with a dark mat of tubes of Spiophanes bombyx and ampharetid polychaetes (Figure 6-10, bottom). Many cerianthid anemones, not seen prior to the hypoxic stress, were also present. Epibenthic crustaceans were not seen again until August 1977. At the swale station C4, the same epibenthos and cerianthids

(<8 per photograph) were commonly visible on a heavily bioturbated finer sand bottom before the hypoxic incident. Photographs taken after the hypoxia showed an absence of epibenthos and a smooth, not obviously reworked seabed. In February and June 1977 the photographs showed evidence of colonization and tube building. Cerianthid anemones were very abundant in June and August 1977 (>20 per photograph).

Macrobenthos. Analysis of collections of macrobenthos show evidence of community alterations due to hypoxic stress only at C1, C2, C3, C4, G1, and G2 (Boesch et al. 1977), although mortalities may have also been caused over a wider area after the August 1976 sampling (e.g. on the central shelf at N3 which was sampled only for megabenthos). Detailed analysis will concentrate only on results from stations C2, C4, and G2 at which sampling continued after August 1976.

The acute effects of the hypoxic stress resulted in the nearly complete extirpation of macrobenthic crustaceans and echinoderms. The numbers and biomass of crustaceans and echinoderms (Appendix 6-D) declined drastically from June to August 1976. Annelids and molluscs were in general much less acutely impacted. Thus, the assemblages collected in August 1976 were similar to those found during previous sampling periods with a much reduced or non-existent component of crustaceans and echinoderms. Following the summer of 1976, however, the assemblages changed considerably from the pre-hypoxia condition during an extended "responsive phase".

These relationships of the assemblages over time are apparent in the numerical classification presented in Figure 6-67. The assemblages collected during the stress conditions in August 1976 are distinct from but relatively similar to those found earlier. Assemblages collected during the responsive phase are very different and cluster discretely.

Several patterns of species response accounted for the observed changes in assemblage similarity, and they are exemplified by the temporal variations in population densities of dominant species (Figures 6-68 to 6-71). The archiannelid Polygordius sp. was a temporally and spatially variable but abundant member of both the dynamic sand and swale communities on the inner shelf prior to August 1976 when only a few specimens were found (Figure 6-68, 6-71). Polygordius was very rarely collected in either environment after that time, although it may have been excluded from C4 during the second year because of the change to predominately fine sands from the medium sand predominant in earlier collections. The polychaete Goniadella gracilis, a characteristic dominant of dynamic medium-coarse sands, maintained relatively persistent population densities throughout the two years of sampling at C2, although abundance during the second year was somewhat below levels found during the first year (Figure 6-68). Populations of the polychaete Lumbrinerides acuta and the bivalve

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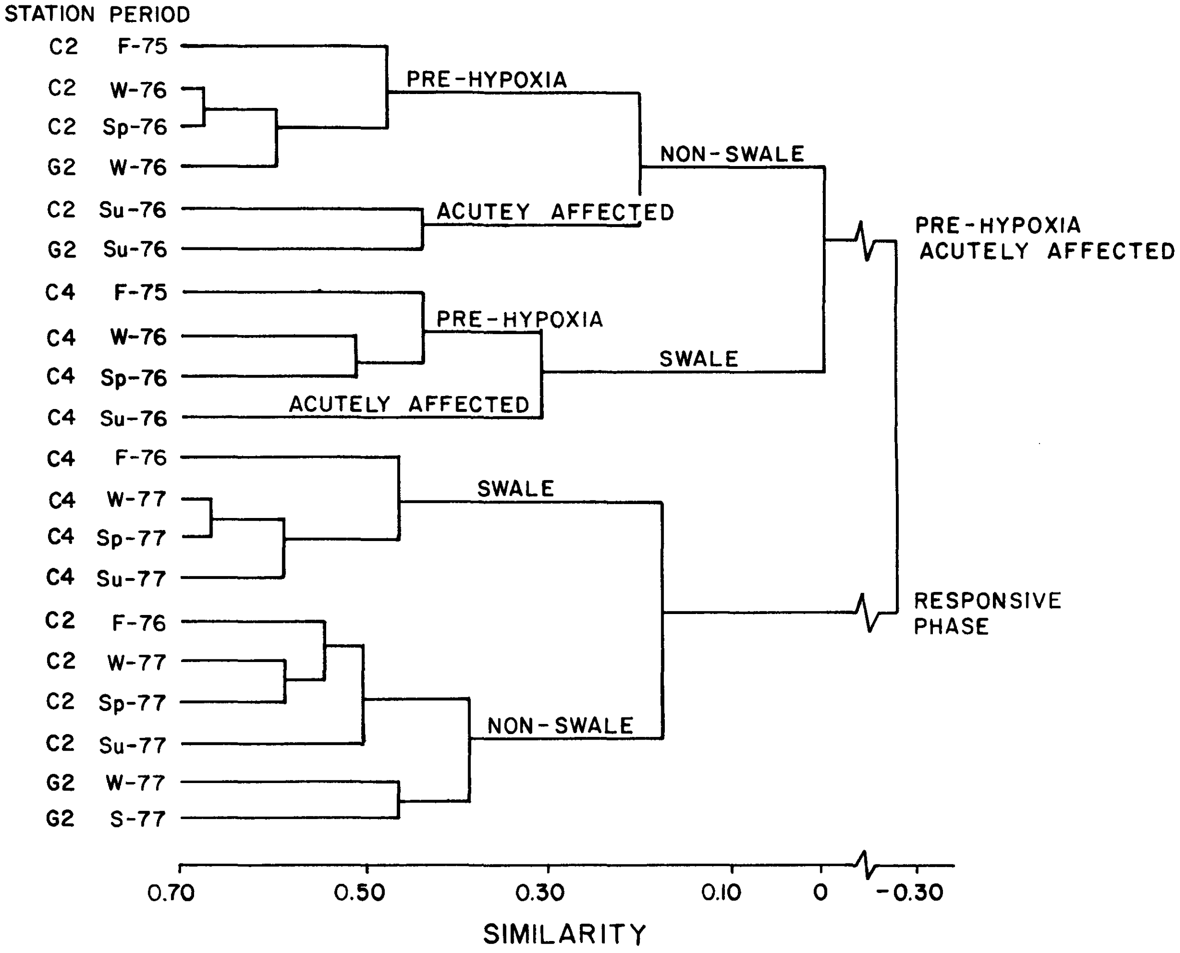

Figure 6-67. Normal classification of seasonal collections of macrobenthos from stations affected by hypoxia during the summer of 1976.

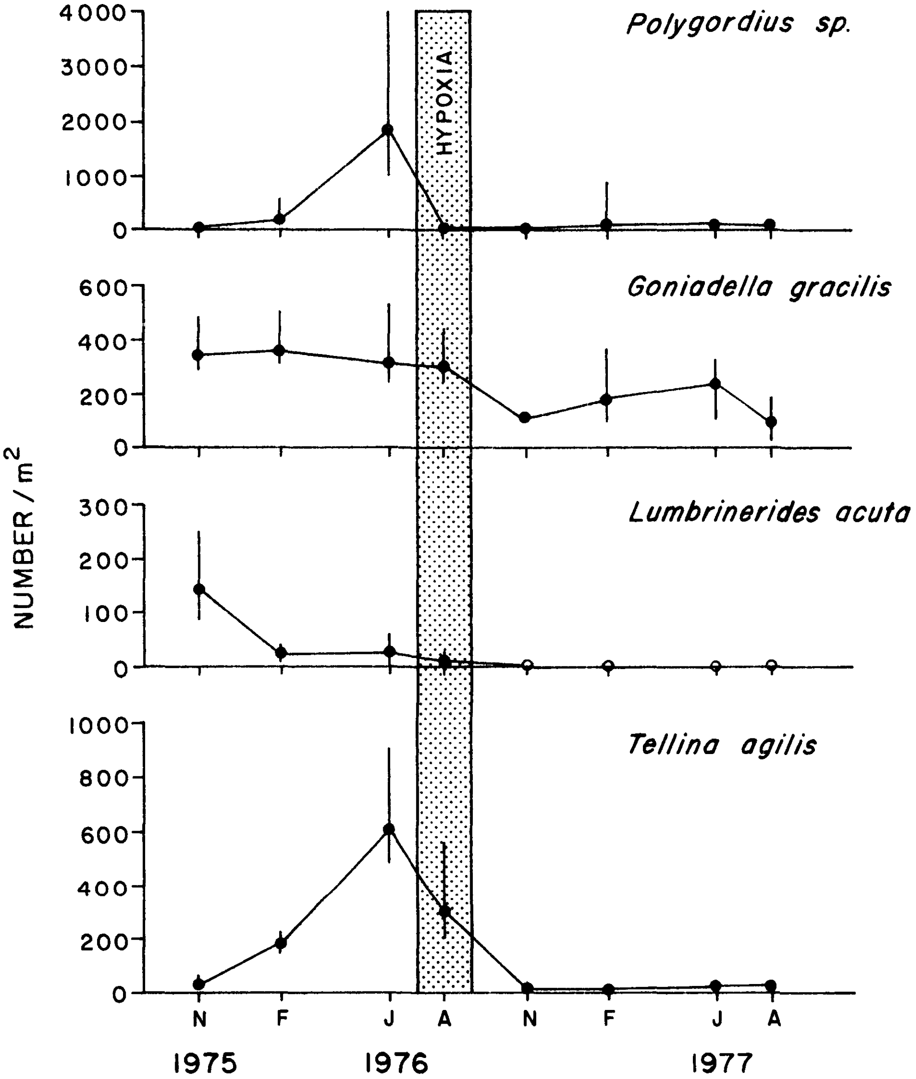

Figure 6-68. Temporal variations in population densities for dominant macrobenthic species at Station C2, which was affected by the hypoxia incident of the summer of 1976. Vertical lines are confidence limits ($\bar{x} \pm S_{\bar{x}}\, t_{.05}$) computed on log transformed values; levels connect geometric means. Open circles are zero estimates.

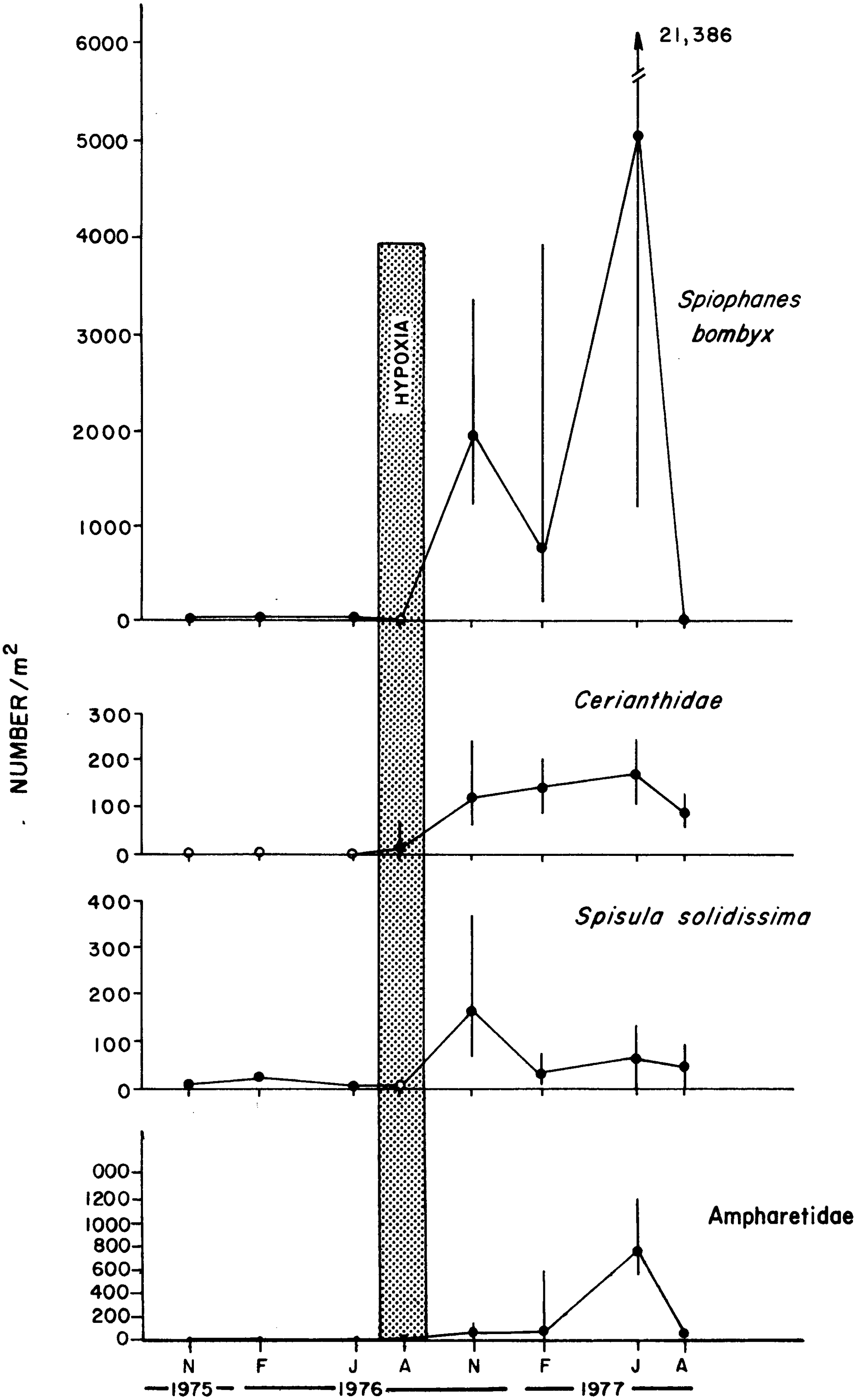

Figure 6-69. Temporal variations in population densities for dominant macrobenthic species at Station C2, which was affected by the hypoxia incident of the summer of 1976. Vertical lines are confidence limits ($\bar{x} \pm S_{\bar{x}}\ t_{.05}$) computed on log transformed values; levels connect geometric means. Open circles are zero estimates.

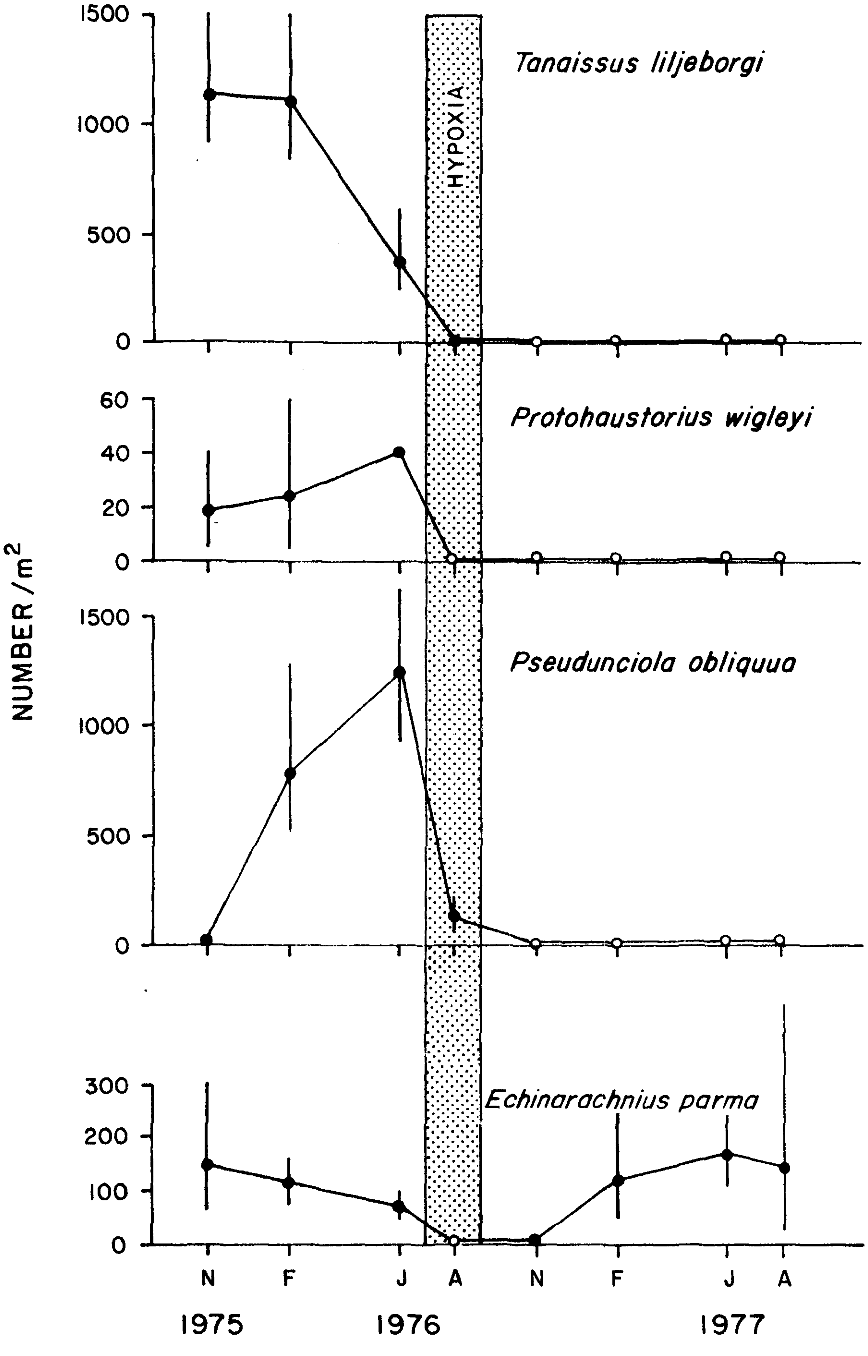

Figure 6-70. Temporal variations in population densities for dominant macrobenthic species at Station C2, which was affected by the hypoxia incident of the summer of 1976. Vertical lines are confidence limits ($\bar{x} \pm S_{\bar{x}}\, t_{.05}$) computed on log transformed values; levels connect geometric means. Open circles are zero estimates.

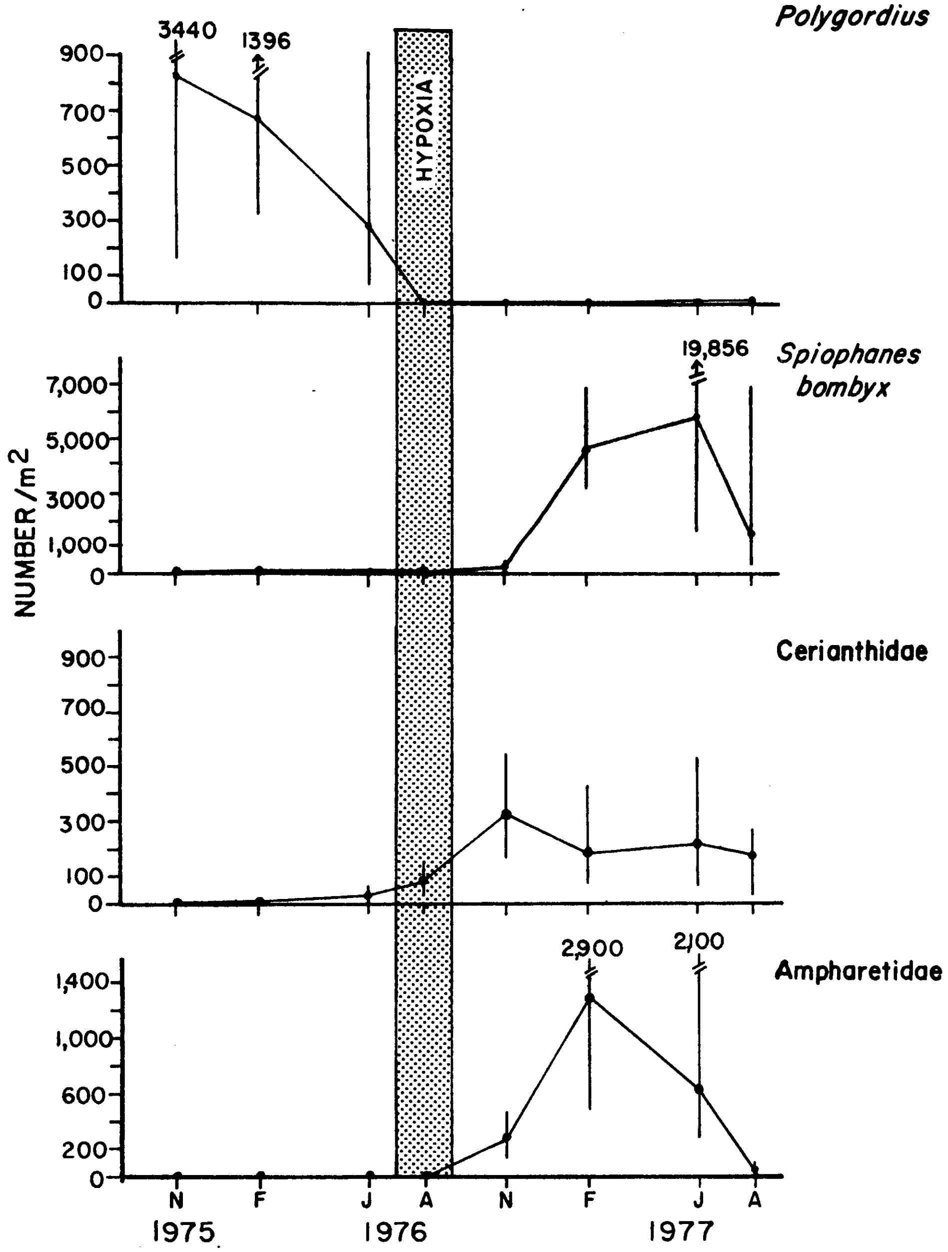

Figure 6-71. Temporal variations in population densities for dominant macrobenthic species at Station C4, which was affected by the hypoxia incident of the summer of 1976. Vertical lines are confidence limits ($\bar{x} \pm S_{\bar{x}}\ t_{.05}$) computed on log transformed values; levels connect geometric means. Open circles are zero estimates.

Tellina agilis were not immediately eliminated by the hypoxia at C2. However, Lumbrinerides was not found there subsequently, and Tellina did not increase in abundance in the spring of 1977 as it had the previous year. The most abundant crustaceans in the inner shelf flanks prior to summer of 1976 were the tanaidacean Tanaissus liljeborgi amd the amphipods Protohaustorius wigleyi and Pseudunciola obliquua. A few specimens of Pseudunciola were collected during August 1977, but otherwise no specimens of either of these species were taken after June 1976 (Figure 6-70). The sand dollar Echinarachnius parma was also eliminated by the hypoxia by August 1976 (Figure 6-70). Successful recruitment took place in the fall, such that at C2 population densities returned to pre-hypoxic levels by winter or spring of 1977. However, the population during this time consisted of very small specimens of this slow-growing species in comparison to the previous adult populations.

Most striking was the ascendancy of several species, uncommon before the hypoxia, during the responsive phase. Some species may have experienced a normal seasonal recruitment pulse in the fall. For example, the surf clam Spisula solidissima, which experienced heavy adult mortalities as a result of hypoxia, had a strong spatfall by November 1976 (Figure 6-69). Other species were much less common before the incident but established extremely dense and somewhat persistent populations following the incident. Notable among these are the polychaetes Spiophanes bombyx and Ampharetidae and a cerianthid anemone which exhibited population irruptions in both the coarser sands of C2 and G2 and the finer sands of the C4 swale station (Figures 6-69 and 6-71). As seen in the bottom photographs, these species effected considerable changes in the nature of the seabed by building dense mats of tubes and biogenically binding fine sediments.

The assemblages at stations affected by the hypoxia show similar trends in the aggregate properties of abundance and diversity (Figure 6-72). Total abundance of macrobenthos was lower in August 1976 than it had been previously and remained low in November 1976. Total densities increased through the winter and spring to show a maximum during the responsive phase in June 1977. These high densities were drastically reduced by August 1977. The number of species collected in each sampling period (areal richness) also showed a reduction (30-40%) in August 1976 from the high levels observed in June 1976. The areal richness increased in fall and winter but remained far below the levels observed before the hypoxia. On the other hand, relatively high values of Shannon diversity were measured during August 1976 and, as more species were recruited in winter and spring, H' declined drastically at C2 and C4. The diversity index increased abruptly in August 1977 to levels comparable with those observed prior to the summer of 1976. Comparison of the patterns of Shannon diversity with those for species evenness shows that the evenness component is the overwhelming determinant of Shannon diversity. Depressed diversity during the winter and spring of 1977 was the result of overwhelming numerical dominance by Spiophanes bombyx and the ampharetids.

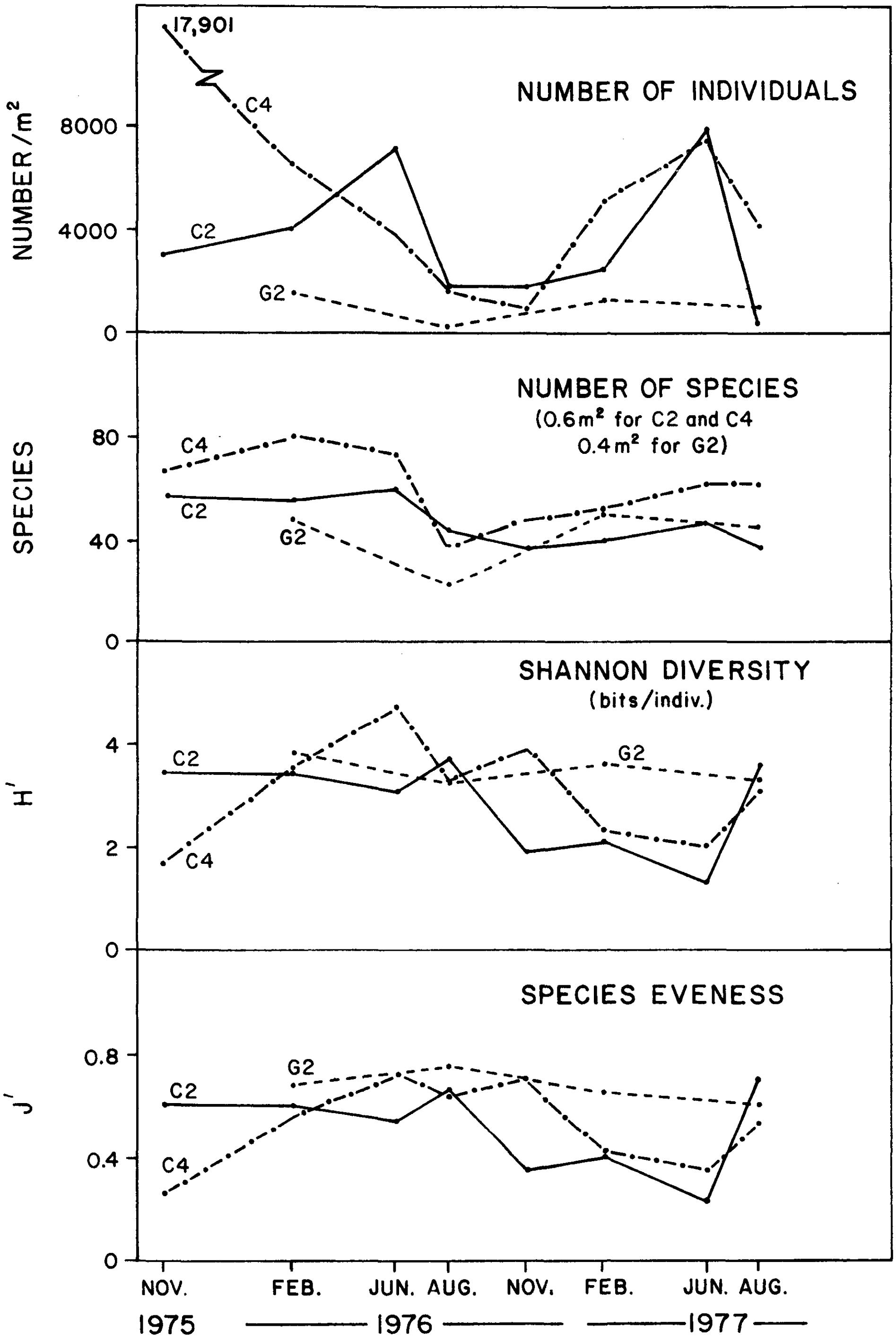

Figure 6-72. Total density, areal species richness, Shannon diversity, and species evenness of macrobenthos at stations affected by hypoxia during summer 1976.

Megabenthos. For the sake of continuity, the effects of the hypoxia on large benthic animals collected by dredge and trawl will be discussed here rather than under the full presentation of results on megabenthos.

Extensive mortalities were witnessed at the inner shelf stations C2 in August 1976. Mortalities apparently resulting from subsequent (probably in September) depletion of dissolved oxygen farther offshore were observed at Station N3 on the central shelf but, strangely, not at the intermediate central shelf station D1. As with the macrobenthos, immediate effects of the hypoxia resulted in the complete extirpation of echinoderms and crustaceans (decapods in this case) while molluscs were variously affected. Thus, neither the previously dominant decapod crustaceans, Crangon septemspinosa, Cancer irroratus, and Pagurus acadianus, nor echinoderms, Echinarachnius parma and Asterias forbesi, were collected in August 1976 small biology trawl (SBT) or anchor dredge samples from C2 (Figures 6-73 and 6-74). Paired, still-articulated valves ("gapers") and decaying flesh of commercially important surf clams, Spisula solidissima, were taken, but no live specimens were found. The bivalve Astarte castanea and the gastropod Nassarius trivittatus did not appear to be affected (Figure 6-75). Representatives of unsampled or infrequently sampled, deep dwelling species such as the polychaetes, Glycera dibranchiata and Sigalion arenicola; the sipunculan Phascolopsis gouldi; the stomatopod Platysquilla enodis; and a burrowing anemone, Edwardsia elegans?, were also found. These immediate effects caused a severe drop in the number of species and individuals taken at C2 as exemplified by SBT collections (Figures 6-76 and 6-77). A decline was similarly reflected in Shannon diversity, species evenness and species richness values (Figure 6-77).

The delayed offshore hypoxic stress caused severe effects at N3 without affecting the intermediate D1 station (Figures 6-77 and 6-78). The most seriously affected species at N3 were Echinarachnius parma, Cancer irroratus, and Pagurus acadianus (Figure 6-79). Other species which were severely affected at C2 such as Asterias vulgaris, Ensis directus, and Crangon septemspinosa showed only a minor decrease in abundance (Figure 6-80). No catches were made of decaying Spisula or unusual deep-dwelling species but this could have been due to the time lapsed since the hypoxic stress. A decrease in dominance caused by the loss of Echinarachnius at N3 resulted in an increase in diversity and evenness whereas species richness dropped slightly (Figures 6-77 and 6-78).

Following hypoxic conditions, recovery trends at stations C2 and N3 were observed. Crangon populations had recovered by fall 1976, only 10 weeks after complete extirpation at C2. Repopulation of this motile species was primarily by young individuals, although several mature adults were also present, suggesting recruitment by larvae from the plankton as well as immigration from adjacent ares. Cancer

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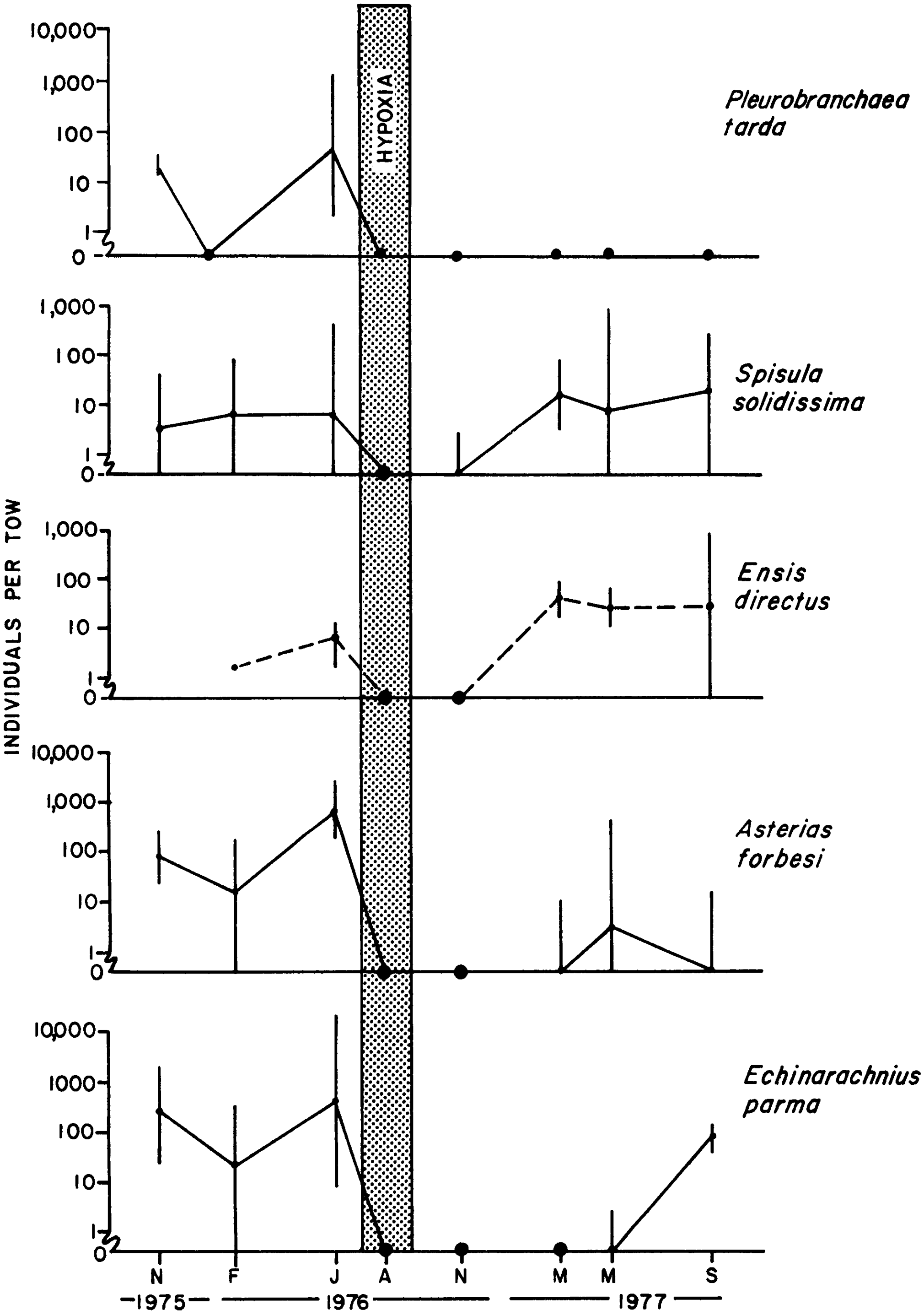


Figure 6-73. Fluctuations in the abundance of dominant megabenthos as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines) at Station C2.

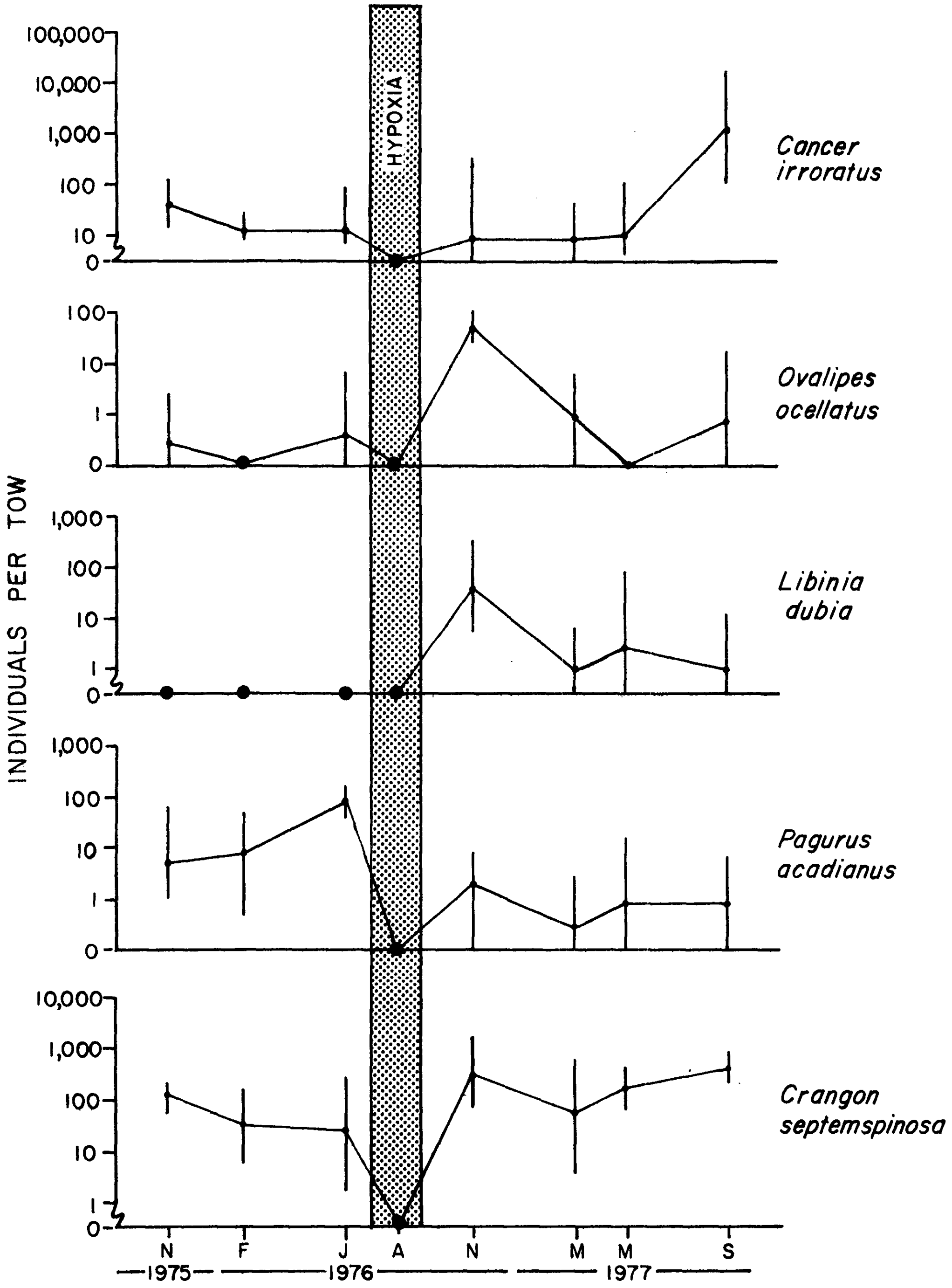


Figure 6-74. Fluctuations in the abundance of dominant megabenthos as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines) at Station C2.

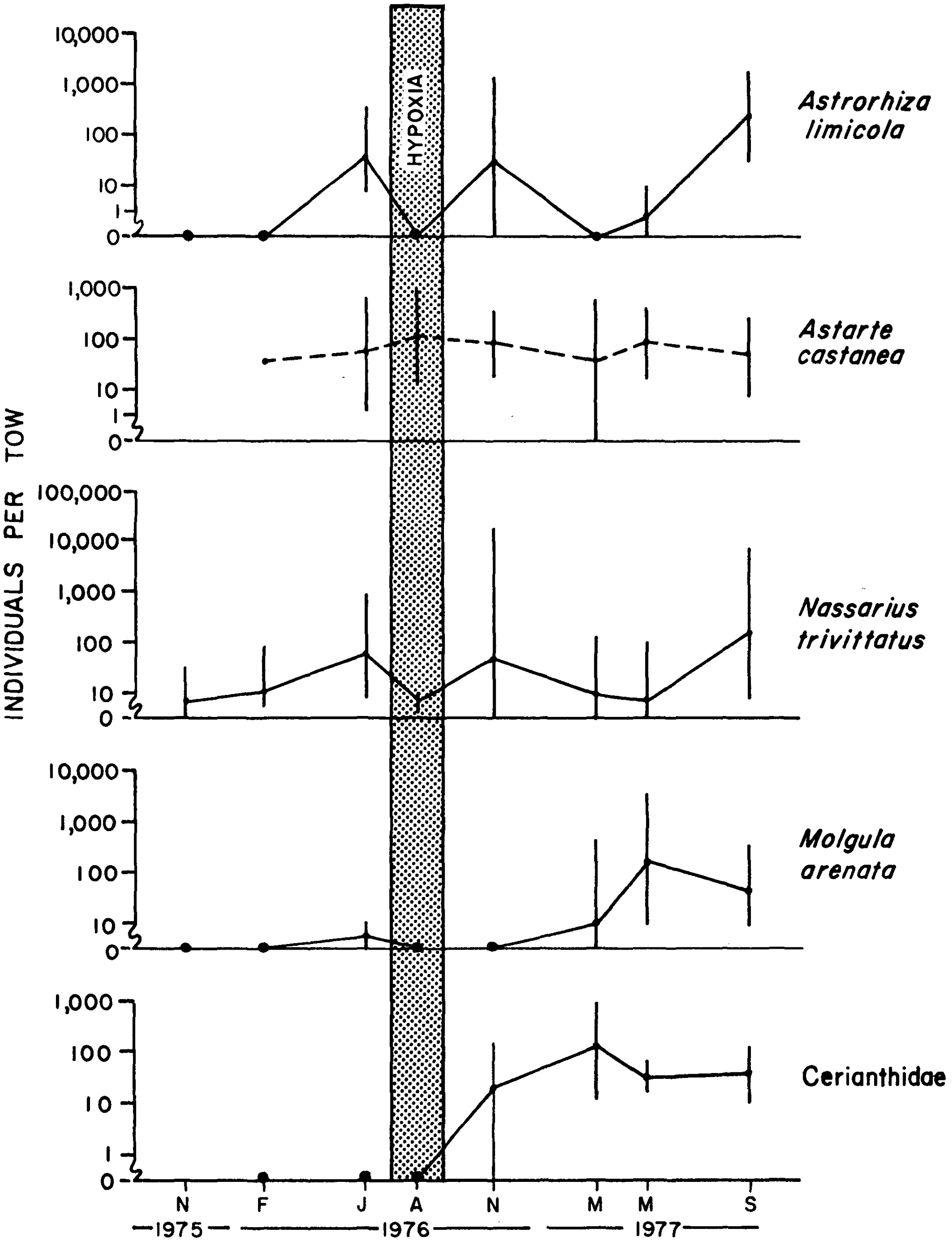


Figure 6-75. Fluctuations in the abundance of dominant megabenthos as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines) at Station C2.

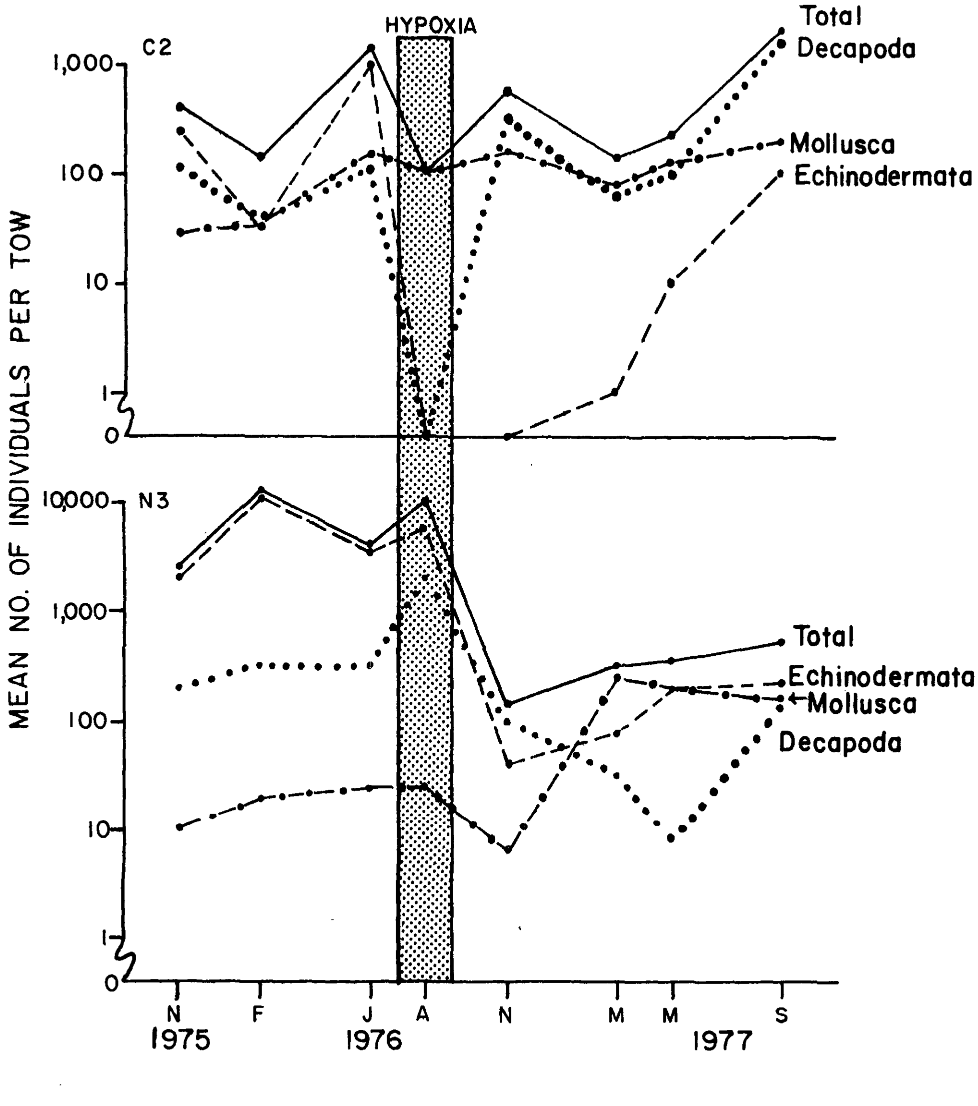


Figure 6-76. Fluctuations in the density of megabenthos as reflected in small biology trawl collections at stations C2 and N3.

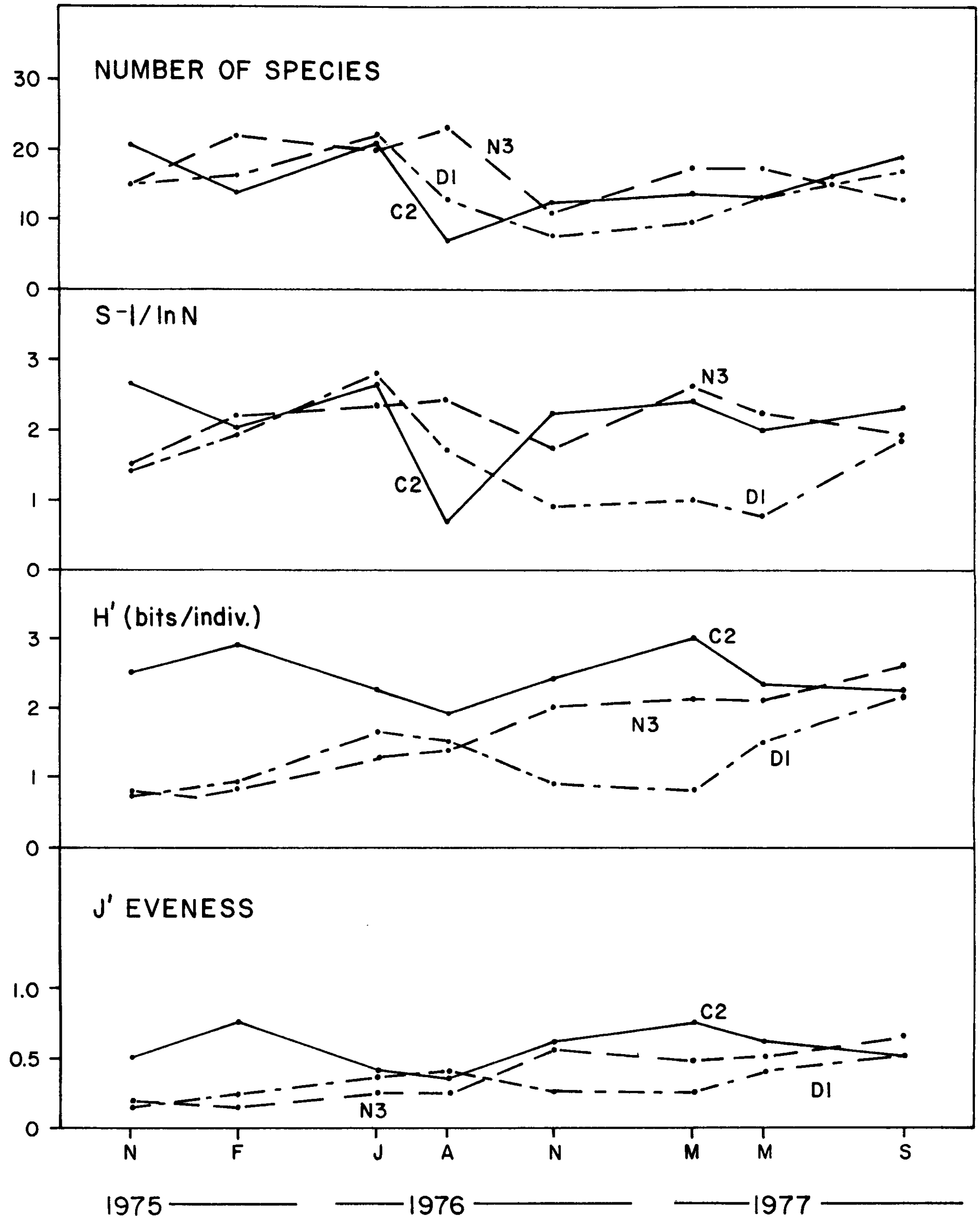


Figure 6-77. Species richness, Shannon diversity, and evenness of small biology trawl collections of megabenthos at Stations C2, D1, and N3.

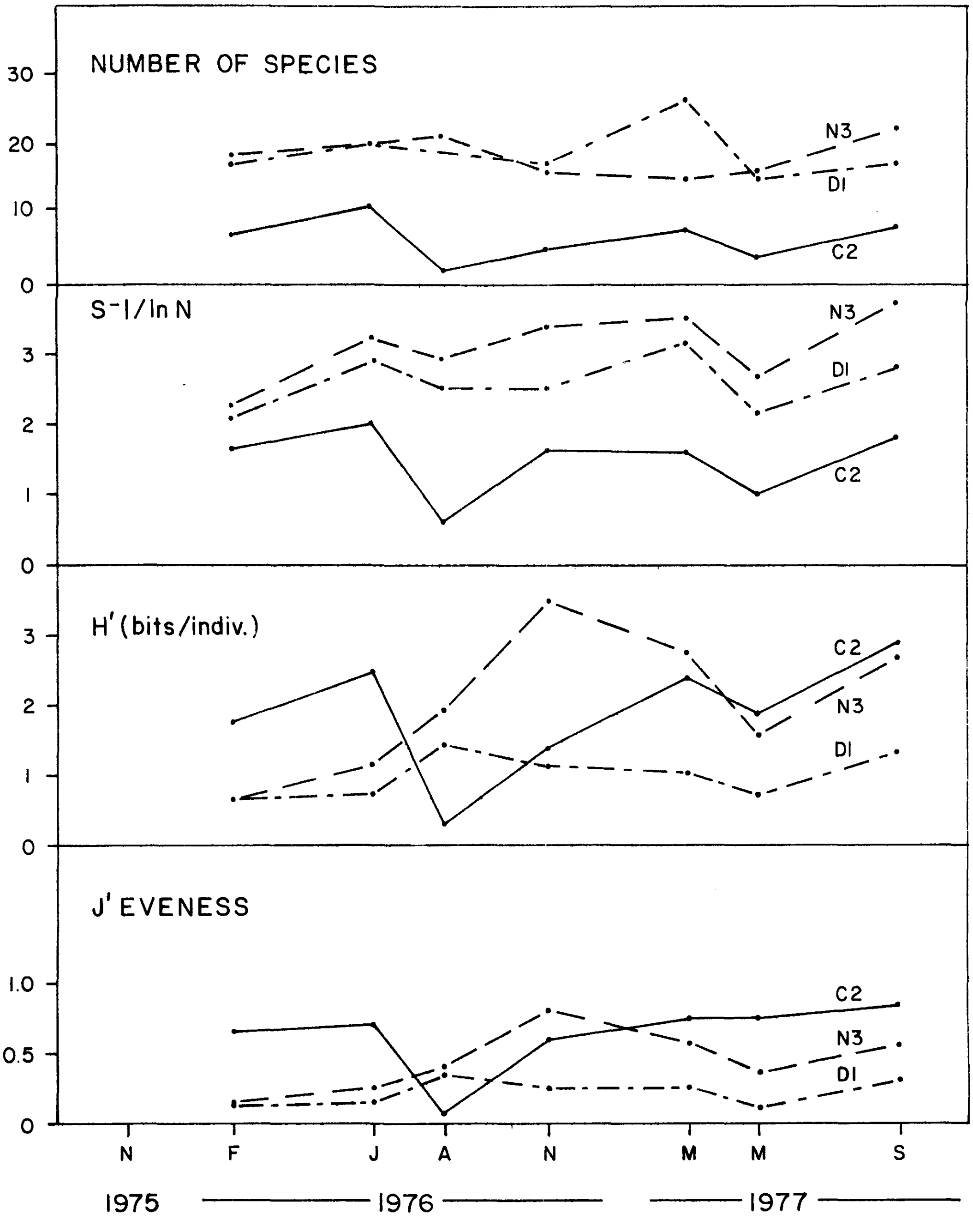


Figure 6-78. Species richness, Shannon diversity, and evenness of anchor dredge collections of megabenthos at stations C2, D1, and N3.

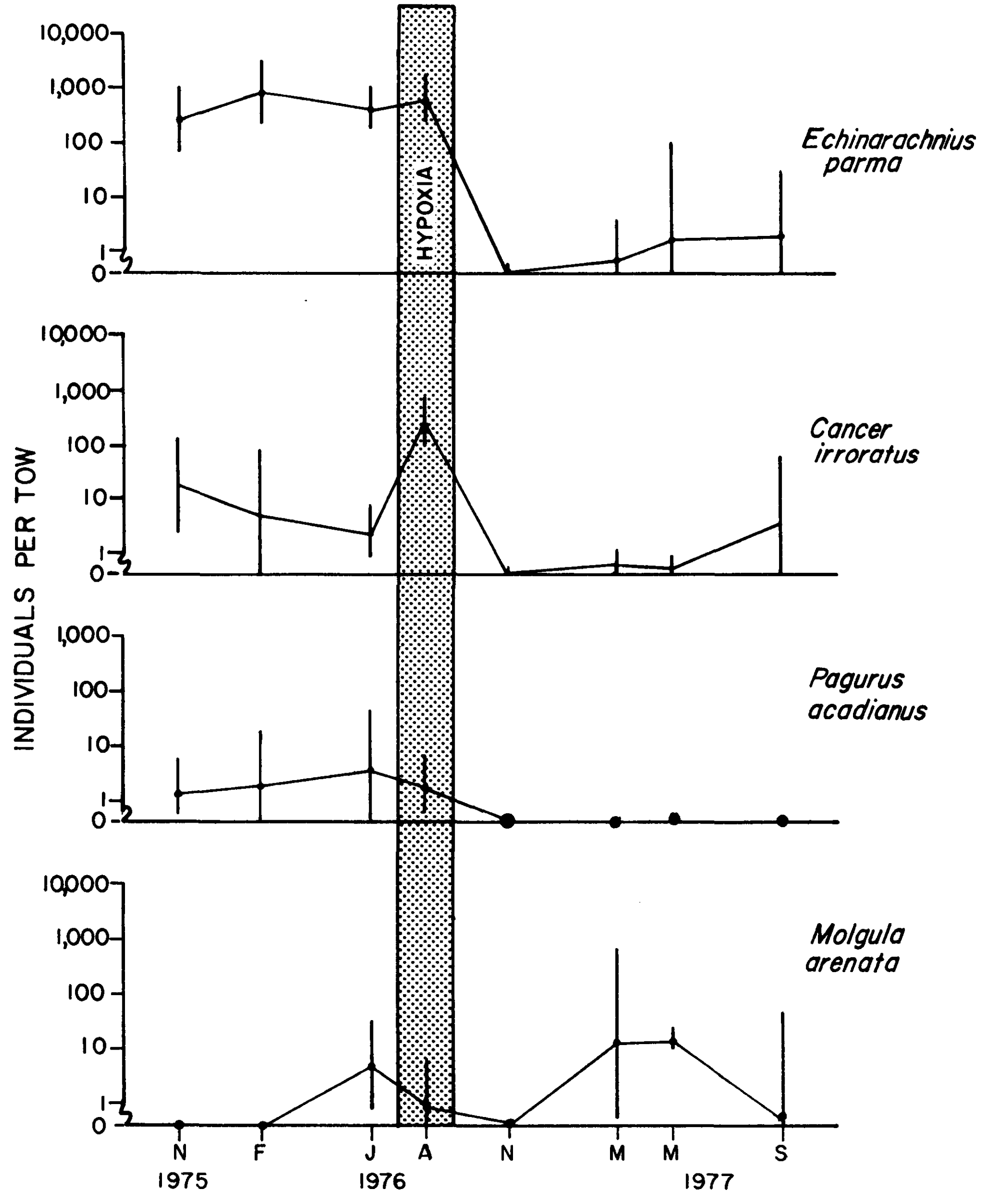


Figure 6-79. Fluctuations in the abundance of dominant megabenthos as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines) at Station N3.

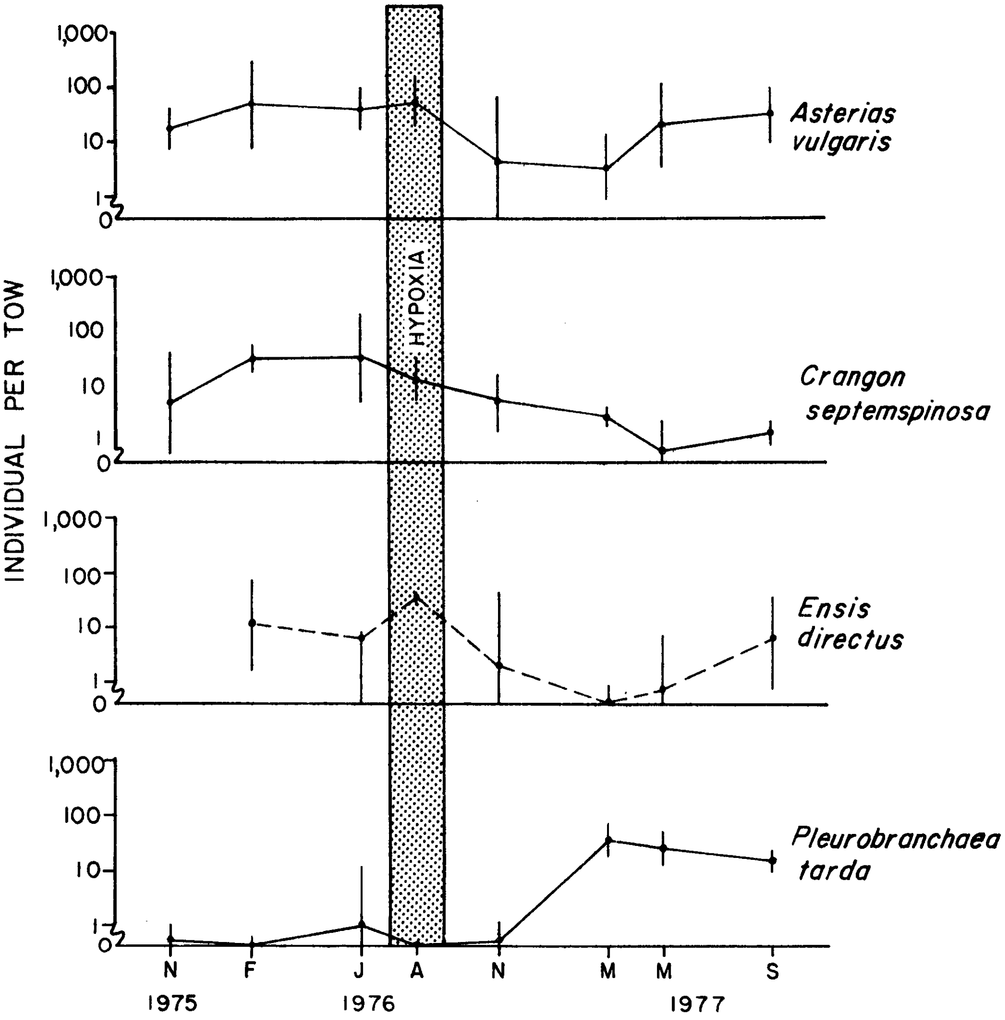


Figure 6-80. Fluctuations in the abundance of dominant megabenthos as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines) at Station N3.

irroratus started recovering in fall 1976, mainly through an influx of juveniles. A large number of *Cancer* was collected one year following the hypoxia. The geometric mean of 1266 individuals, most of which were recently metamorphosed juveniles, represents a 29 fold increase over the previously high mean of 44 specimens collected two years earlier (fall 1975). *Spisula solidissima* populations were restored by the settlement of a new year-class. By winter 1977, and thereafter, the numbers of small specimens reached higher levels than any time prior to the hypoxia (Figure 6-73). Razor clams, *Ensis directus*, which were sampled more effectively by the anchor dredge, followed the same pattern (Figure 6-73).

Other previously dominant species, *Echinarachnius parma* and *Asterias forbesi*, did not reappear in significant numbers until at least nine months after hypoxic conditions. Juvenile (24 mm) *Echinarachnius* were not collected until 13 months after extirpation. Newly set specimens were found in grab samples in fall 1976, but they did not reach sufficient size to be collected in large numbers in the SBT until September 1977. *Asterias forbesi* was similarly affected by the low oxygen but showed a much slower rate of recovery, never reaching pre-hypoxia densities during the second year of sampling. Similarly, *Pagurus acadianus*, common before the hypoxia, was not found at C2 in August 1976 and only a few juveniles occurred thereafter.

Some species increased in abundance after the hypoxia (Figures 6-74 and 6-75). The brachyurans *Ovalipes ocellatus* and *Libinia dubia* were either poorly represented (former) or absent (latter) prior to oxygen depletion. Both species displayed a sudden but short-lived increase in November 1976. The surge was caused by an influx of juveniles that later died or emigrated. The arenaceous ascidian *Molgula arenata* and burrowing cerianthid anemone were also more numerous after hypoxia and their numbers remained consistently high throughout the remainder of the study period. Both species were generally absent before the oxygen minimum.

Erratically occurring species such as the mollusc *Pleurobrachaea tarda* and the large arenaceous foraminiferan *Astrorhiza limicola* were intermittently numerous during the first year but showed different effects by hypoxia. *Pleurobranchaea* reached peak abundances in November 1975 and June 1976 but was not collected in the intervening period, during hypoxia or thereafter. *Astrorhiza* was not found until June 1976 and was not numerous again until November 1976 and September 1977. Unlike *Pleurobranchea*, *Astrorhiza* did not show long term elimination from C2.

Two dominant mollusc species did not appear to be affected by hypoxia, *Astarte castanea* and *Nassarius trivittatus* (Figure 6-75). Population levels of the bivalve *Astarte* increased between June and August 1976, even though several "gapers" of recently killed specimens were collected. Behavioral as well as physiological adaptions in *Astarte*, such as shell closing, possible metabolic shut-down, and the presence of red hemoglobin in the blood, enhanced this species' survival during minimal oxygen levels allowing its persistence. In addition, the presence of several small specimens in post-hypoxia samples implicates larval recruitment in maintaining post-hypoxia population levels. Although it appears that *Nassarius trivittatus* was able to survive hypoxia (Figure 6-75), an examination of specimen sizes and shell condition indicates that individuals present prior to and during the oxygen minimum were generally large and thick-shelled, whereas specimens collected subsequently were considerably smaller and thin-shelled. *Nassarius* survived beyond the August 1976 sampling period, but later collections contained only specimens newly recruited from the plankton. This species may therefore be able to survive only short term hypoxic stress. Juvenile recruitment was intense and, in this regard, the response of *Nassarius* resembles the response exhibited by *Crangon septemspinosa*.

Dominant species at N3 were variously affected by hypoxia. Three species showed severe declines suggesting intolerance to depressed oxygen levels. *Echinarachnius parma* which reached maximum cross shelf abundance at N3 prior to hypoxic conditions was almost totally decimated (Figure 6-79). Small specimens were found during the three post-hypoxia sampling periods. *Cancer irroratus* showed a considerable decline in November 1976, but eight months later approached pre-hypoxia abundances. The vast majority of specimens in second year samples were juveniles indicating a similar response to that observed for this species at C2. Finally, the hermit crab *Pagurus acadianus* which was consistently present prior to low oxygen, showed complete extirpation with virtually no recovery. Several other less abundant species, e.g. the polychaete *Aphrodita hastata* and the sea star *Leptasterias tenera*, showed reduced densities in November 1976 and thereafter.

Three other dominants which were severely affected at C2 showed somewhat reduced abundances during the fall and winter sampling periods at N3 but were not eliminated: *Asterias vulgaris*, *Ensis directus*, and *Crangon septemspinosa* (Figure 6-80). By September 1977 population levels had been restored due to immigration (*Asterias*), larval recruitment (*Ensis*), or both (*Crangon*). Other species, some of which were severely affected at C2 (e.g. *Pleurobranchea tarda*) showed no interpretable diminution of population densities. The cerianthid anemone, again previously rare at N3, increased in abundance in the responsive phase, although not as dramatically as at C2.

Effects of Catastrophic Disturbance: Experimental Recolonization Study

Three boxes, one a screened exclosure, deployed in early December 1976 (A7, A10, S6), and four boxes, including one screened exclosure and one in which one *Leptasterias tenera* was enclosed, deployed in early June 1977 (A14, A18, S10, E4), were recovered in mid-August 1977. The boxes were *in situ* 43 weeks and 10 weeks respectively. None of the boxes of oiled sediment was retrieved (Table 6-2). Grab samples taken at the experimental site B5 in fall 1976, winter, spring, and, in particular, at the time of recovery of the boxes in summer 1977 were used for comparisons to the natural community.

Sediments. Biotic and geochemical variables have been shown to be strongly related to subtle differences in bottom sediment texture on the continental shelf of the Middle Atlantic Bight. Any study designed to experimentally evaluate recolonization and succession of benthos or geochemical alterations must, therefore, pay careful attention to the nature of bottom sediments in the interpretation of results. Analysis of sediments during the recolonization experiments was designed to: a) determine whether sediment characteristics were altered by biological and physical processes while on the bottom; b) ultimately evaluate the possibility that faunal patterns in the boxes could be attributed to variability in sediments rather than experimental treatment; and c) determine the effects on chemical constituents, i.e. trace metals and hydrocarbons, of experimental treatment.

I. Grain size. With the exception of box A10, sediments in boxes deployed in December changed little during exposure (Figure 6-81). The sediments placed in the boxes were moderately well sorted medium-fine sand (>40 percent fine sand). On recovery in June, boxes A7 and S6 showed only slight coarsening while box A10 appeared to have lost a significant proportion of fine sand. The disparity might have been due to small-scale patchiness within the box or the winnowing of fine sediments during exposure. Silt and clay content (initially 4.5 percent) rose slightly in A7 (9.3 percent) and S6 (6.8 percent) but declined in A10 (1.6 percent). It is likely that erosion caused the observed coarsening of sediments in A10 because only 8 cm of sediment remained in this box (ca. 14 cm initially) as opposed to 10 cm in A7 and 13 cm in S6. Furthermore, the shallowest layer of dyed sediment was completely absent on retrieval (Figure 6-82).

Boxes deployed in June were filled with somewhat coarser sediments (25-30 percent fine sand). The experimental site, Station B5, is located in a zone of rapid transition from the eroded flank habitat (3B) characterized by poorly sorted, muddy sands, through the medium-fine sand flank habitat (3A) to the shallow swale habitat (4) characterized by over 40 percent fine sand (Figure 6-36). Sediments sampled within the small, well fixed area at the station varied during the sampling periods. Sediments sampled at B5 during November and August were coarser and represent the eroded flank habitat. Those collected during February and January represent the medium-fine sand flank or shallow swale habitats. Similar differences existed between the sediments placed in the boxes in December (finer) and those placed in June (coarser). Differences in biotic or chemical constituents between the experiental boxes and the natural habitat (as sampled at B5 in August) could only be explained on the basis of grain size composition for boxes A7 and S6 (Figure 6-81). It should be noted, however, that sediments in the eroded flank habitat of B5 were highly variable as indicated by broad confidence limits in Figure 6-81.

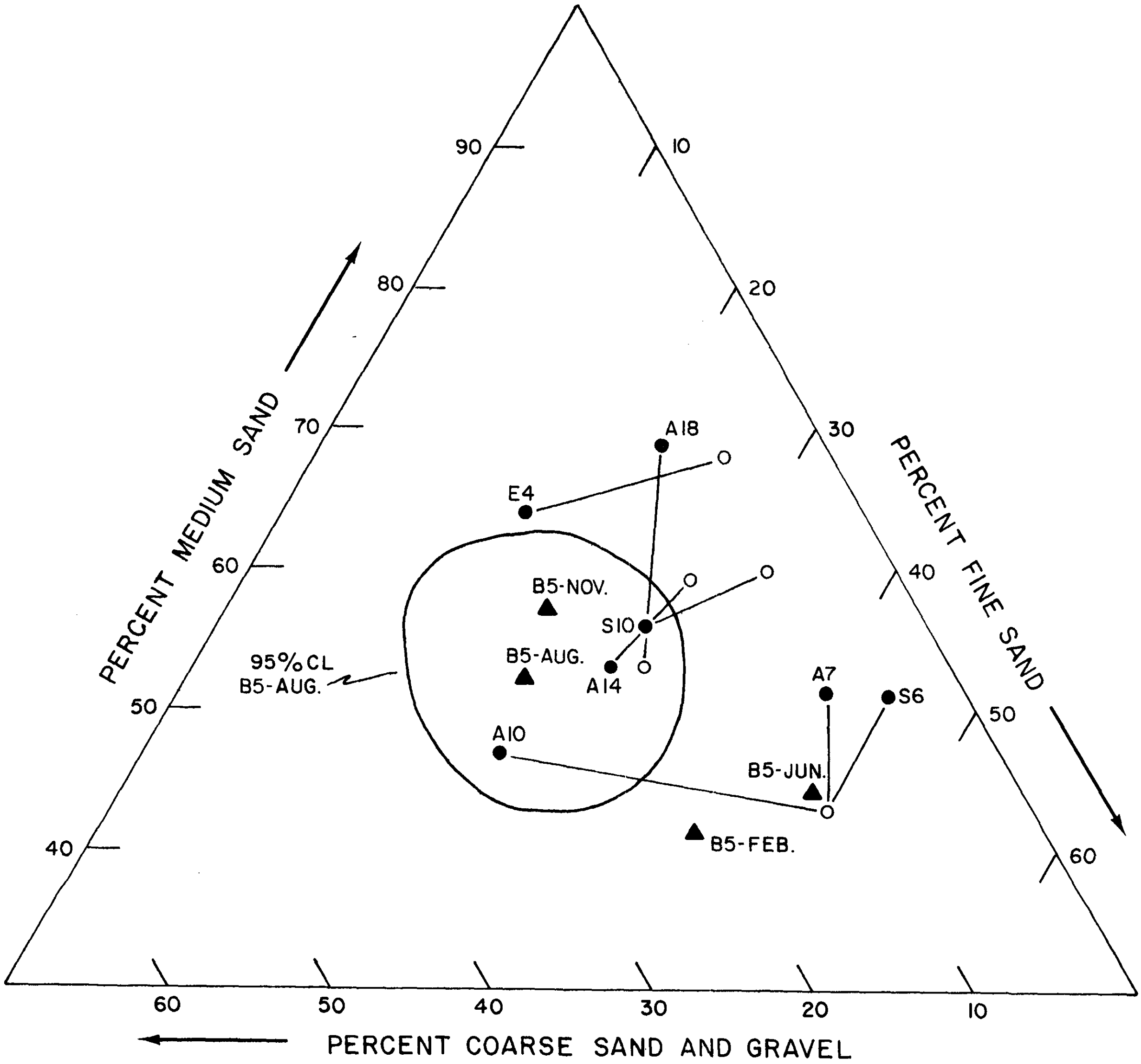


Figure 6-81. Changes of grain size distribution in sediment boxes deployed in recolonization experiments. Open circles represent size proportions based on samples taken before deployment. Closed circles are based on samples taken on recovery. Triangles represent mean proportions found at Station B5 during various sampling periods. The 95% confidence limits encircle the mean for B5 in August 1977.

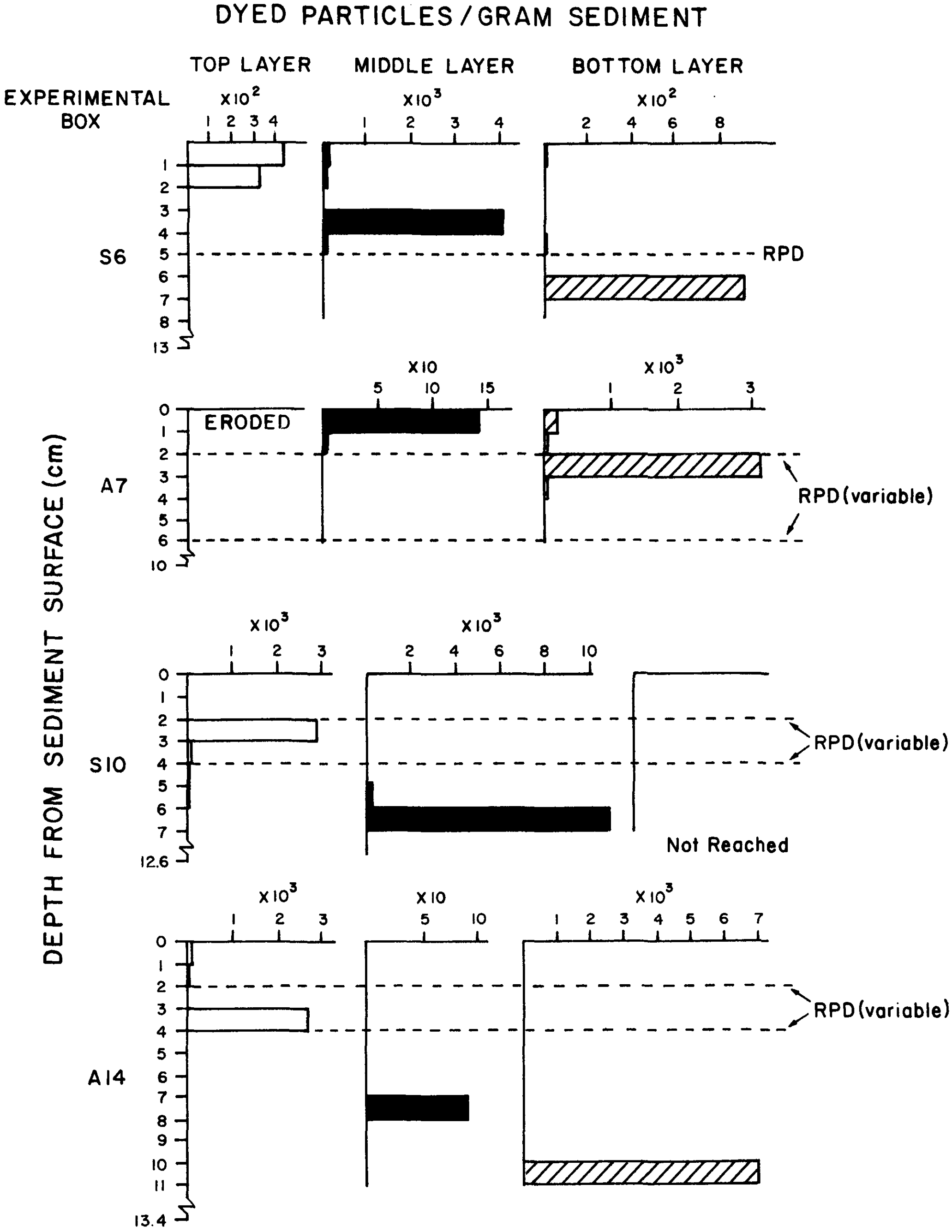


Figure 6-82. Distribution of dyed particles of sediment placed in three discrete layers in sediment boxes found on recovery.

Of the boxes deployed in June and exposed for 10 weeks, only box E4 showed appreciable reduction in the fine sand component. However, this apparent erosion was more likely due to patchiness of sediments within the box because there was little, if any, net sediment loss from this box (13.8 cm of sediment remained).

II. Organic carbon. As is true on both large and medium scales on the continental shelf (Chapter 5) organic carbon was related to the amount of silt and clay present in the sediment (Figure 6-83). Concentrations of organic carbon in the boxes were not unusual in relationship to the proportion of silt and clay in the sediments. The boxes with extreme values were in fact both 43 weeks azoic treatments (A7 and A10). Sediments in A10 which was badly eroded had the lowest organic carbon and silt and clay content of any box. Except for these extremes, it is unlikely that differences in chemical concentrations or biotic composition could be related to differences in silt and clay or organic carbon.

III. Sediment mixing. Analysis of the distribution of dyed sand grains placed in layers after exposure of sediments showed that, except for erosion of surface sediments in some of the boxes that "over-wintered", very little disturbance of bottom sediments took place (Figure 6-82). In particular there was relatively little vertical mixing of sediments by biotic or other agents.

There nonetheless was evidence of some vertical movement of sediments within 4 cm of the surface, probably by bioturbation. This is evident in the dispersal of the top colored layer and movement of a small number of particles from the middle layer in S6, surface displacement of the lowest layer in A7 and, possibly, the surface advection of particles from the top colored layer in A14. In no case was there anything like homogenization of the sediment in the boxes.

The depth of reworking (not deeper than 4 cm) coincided closely with the position of the redox potential discontinuity (RPD). This suggests that burrowing infauna may play a role in regulating the oxygen availability in the sediments and thus the depth of the RPD. The RPD in 43 week boxes was deeper (mostly 5-6 cm) than in the 10 week boxes (2-4 cm). The shallow depth of the RPD is in marked contrast with the natural habitat where an RPD is generally not apparent in the upper 10 cm of sediment. Possible causes of the shallower RPD in the boxes include: a) lack of large burrowing infauna which ventilate sediments; b) organic enrichment of sediments due to killing benthic organisms by freezing the sediments; and c) restriction of interstitial circulation due to enclosure of sediments in an impermeable container.

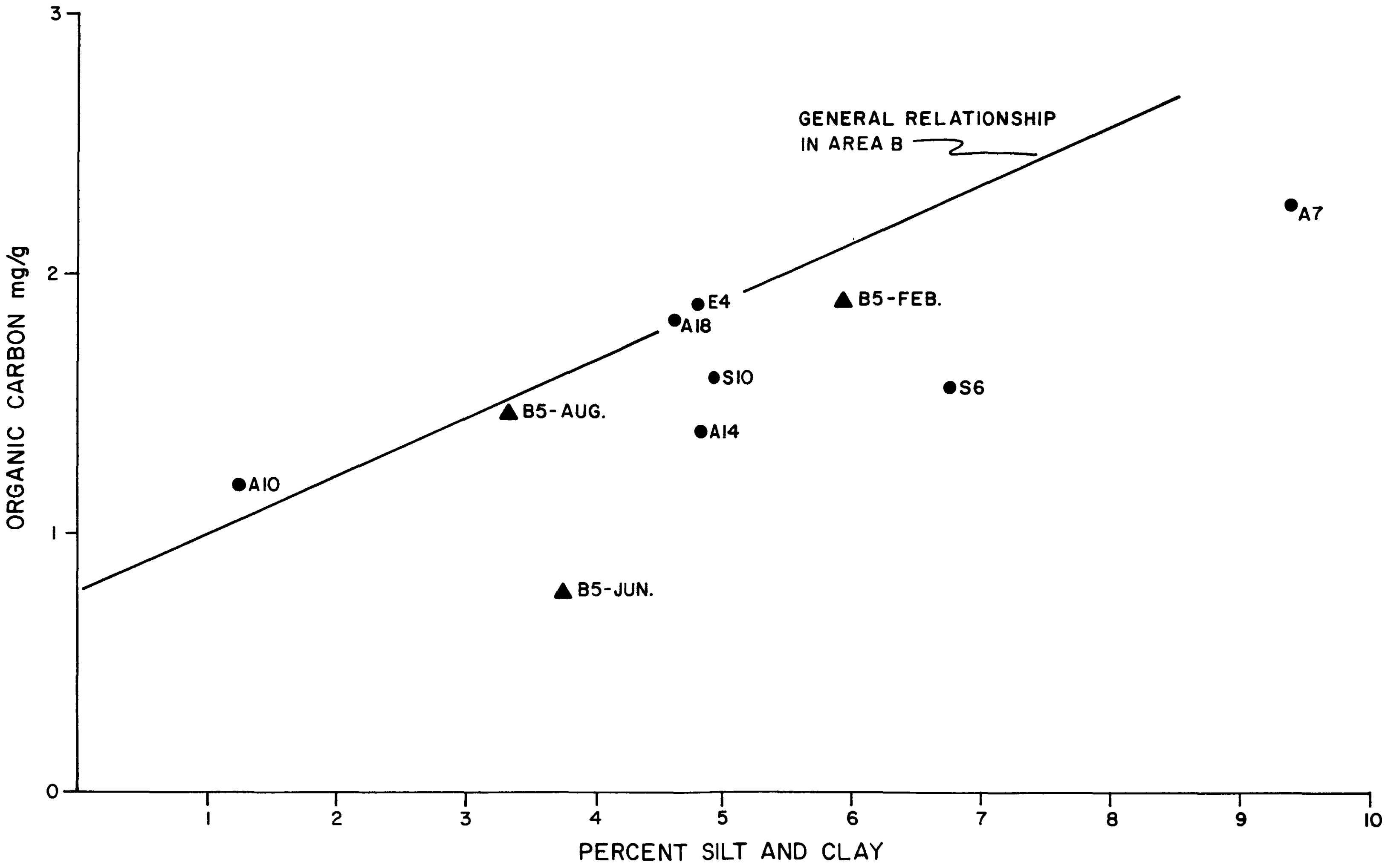


Figure 6-83. Relationship between silt and clay content and organic carbon in sediments from the experimental site B5 and in boxes recovered. These values are compared with the regression based on all samples from Area B (Chapter 5).

IV. Trace metals and hydrocarbons. Concentrations of leachable trace metals in sediments placed in and recovered from the experimental boxes were within or close to the ranges found in sediments at Station B5 based on seasonal sampling (Table 6-14). The concentrations of most leachable metals were highest in the November 1976 samples and lowest in the August 1977 samples, however, total metals showed no clear trend. This change is not correlated with a concomitant reduction in the percentage of silt and clay in the sediments.

Short term (10 week) exposure of sediments in the experimental boxes induced no consistent changes in the concentration of leachable or total trace metals (Tables 6-14 and 6-15). However, the leachable concentrations of many metals declined slightly in several of the sediments exposed for 43 weeks (boxes A7, A10, and S6). This reduction coincided with erosion of fine sediments from the boxes, particularly A10, however, sediments in A7 and S6 contained more silt and clay on retrieval than indicated in the initial sample. Concentrations of total trace metals showed consistent reduction only in the most severely eroded box A10.

Analyses of hydrocarbons in sediments placed in and retrieved from the experimental boxes indicated that the hydrocarbons appeared to be from a common source (Table 6-16). Concentrations of aliphatic and aromatic hydrocarbons, carbon preference index (CPI) and pristane/phytane, pristane/C_{17} and phytane/C_{18} ratios were more similar to each other than replicate samples at many stations (Chapter 14). The distribution of hydrocarbon compounds in the samples was characteristic of sediments of the Middle Atlantic continental shelf with a distinct but not prominent pristane peak, a large variable peak of a compound with a retention index of 2076 (probably a C_{25} cyclo-olefin), a suite of n-alkanes between C_{23} and C_{31}, and a fairly strong odd/even predominance and major peaks at C_{29} and C_{31}.

Concentrations of both aliphatic and aromatic hydrocarbons were well within the range characteristic of outer shelf sediments. There were only minor and inconsistent differences between samples taken before and after deployment suggesting that experimental treatment introduced no detectable contamination.

Abundance of Colonizing Biota. Although the total density of colonizing macrobenthos showed no pattern, faunal composition varied with both experimental treatment and time spent on the bottom. Crustaceans and annelids numerically dominated with approximately equal densities except in the 43 week exclosure (S6) where, as in the natural community, crustaceans comprised about 75 percent of the total macrobenthos (Figure 6-84). The dominance of crustaceans both in S6

Table 6-14. Concentration of leachable metals in ppm dry weight in sediments from the experimental site B5 and in recolonization boxes deployed and retrieved.

	Ba	Cd	Cr	Cu	Fe	Ni	Pb	V	Zn
Natural Environment									
B5 November 1976	ND	ND	3.3	0.67	2400	0.67	4.5	ND	6.7
B5 June 1977	ND	ND	2.4	0.64	1800	0.62	4.4	ND	5.7
B5 August 1977	ND	0.039	2.0	0.45	1400	0.61	3.0	3.6	4.2
43 Week Azoic									
Deployment (A6-A10)	1.2	0.054	3.1	0.56	2200	0.54	4.4	0.8	7.2
Retrieval A7	ND	ND	2.5	0.58	1900	0.59	4.8	ND	6.4
A10	ND	ND	2.3	0.44	1800	0.43	3.6	ND	6.1
43 Week Exclosure									
Deployment (S4-S6)	ND	ND	2.5	0.71	2000	0.83	5.1	1.3	8.4
Retrieval S6	2.3	ND	2.5	0.63	1900	0.75	5.0	ND	7.4
10 Week Azoic									
Deployment (A11-A14)	1.3	0.047	2.6	0.67	2000	0.73	5.1	1.2	6.1
Retrieval A14	2.1	ND	2.3	0.44	1700	0.65	3.6	ND	5.4
Deployment (A15-A18)	2.4	ND	2.6	0.75	2100	0.70	5.1	1.3	7.1
Retrieval A18	ND	ND	2.7	0.58	2100	0.83	4.8	ND	6.6
10 Week Exclosure									
Deployment (S7-S10)	ND	ND	2.6	0.63	2100	0.35	5.2	1.3	6.2
Retrieval S10	ND	ND	2.6	0.58	2100	0.81	4.9	ND	7.0
10 Week Enclosure									
Deployment (E1-E4)	ND	ND	2.8	0.61	2300	0.56	5.3	ND	7.1
Retrieval E4	1.8	ND	2.6	0.65	2200	0.89	5.0	ND	7.0

Table 6-15. Concentration of total metals in ppm dry weight, except for Iron (Fe) which is in percent dry weight, in sediments from the experimental site B5 and in recolonization boxes deployed and retrieved.

	Ba	Cd	Cr	Cu	Fe	Ni	Pb	V	Zn
Natural Environment									
B5 November 1976	90	0.26	15.0	3.4	1.2	8.0	7.0	12	16
B5 June 1977	270	0.16	7.3	3.5	1.5	6.2	14	55	41
B5 August 1977	240	ND	12.0	23.0	1.3	6.8	9.7	41	20
43 Week Azoic									
Deployment (A6-A10)	280	0.50	16.0	3.8	1.3	8.6	12	29	20
Retrieval A7	230	0.45	18.0	3.7	1.3	7.5	12	ND	20
A10	210	0.43	15.0	1.9	1.2	7.0	12	ND	16
43 Week Exclosure									
Deployment (S4-S6)	300	0.16	16.0	2.9	1.3	8.1	13	ND	21
Retrieval S6	220	0.17	7.3	1.5	1.4	ND	11	40	38
10 Week Azoic									
Deployment (A11-A14)	180	0.38	17.0	2.7	1.3	12.0	12	33	18
Retrieval A14	210	0.37	18.0	2.2	1.4	6.2	11	56	19
Deployment (A15-A18)	230	0.21	14.0	3.4	1.3	8.8	11	ND	19
Retrieval A18	220	0.42	18.0	3.4	1.3	7.0	12	42	18
10 Week Exclosure									
Deployment (S7-S10)	240	0.24	14.0	2.2	1.4	7.7	11	29	18
Retrieval S10	130	0.05	13.0	11.0	1.3	5.8	7.6	18	17
10 Week Enclosure									
Deployment (E1-E4)	300	0.43	15.0	3.0	1.4	7.4	14	26	21
Retrieval E4	210	0.30	12.0	1.5	1.4	ND	11	62	19

Table 6-16. Characterization and concentration of hydrocarbons in sediments from recolonization boxes deployed and retrieved.

	Pristane/ Phytane	Phytane/C_{18}	Pristane/C_{17}	CPI	Total Extractable Weight (µg/g)	Hydrocarbon Conc. (µg/g)		
						Aliphatics	Aromatic	Total
43 Week Azoic								
Deployment (A6-A10)	3.42	0.339	0.94	1.408	15.35	0.061	0.032	0.093
Retrieval A7	6.63	0.411	1.65	1.498	21.42	0.032	0.041	0.073
A10	2.75	0.355	1.22	1.713	16.41	0.029	0.053	0.082
43 Week Exclosure								
Retrieval S6	2.63	0.581	1.04	1.597	51.31	0.015	0.031	0.046
10 Week Azoic								
Deployment (A11-A14)	5.98	0.390	1.27	1.55	18.79	0.034	0.057	0.091
Retrieval A14	4.88	0.399	1.37	1.333	11.34	0.061	0.062	0.123
Deployment (A15-A18)	4.08	0.333	0.88	1.922	22.51	0.112	0.185	0.297
Retrieval A18	2.96	0.486	0.85	1.592	25.33	0.036	0.092	0.128
10 Week Exclosure								
Deployment (S7-S10)	2.46	0.439	0.99	1.828	14.52	0.017	0.068	0.085
Retrieval S10	7.79	0.421	1.58	1.973	21.32	0.050	0.027	0.077
10 Week Enclosure								
Deployment (E1-E4)	0.62	0.257	0.12	1.685	26.34	0.140	0.037	0.177
Retrieval E4	4.84	0.311	0.89	1.788	17.78	0.013	0.013	0.026

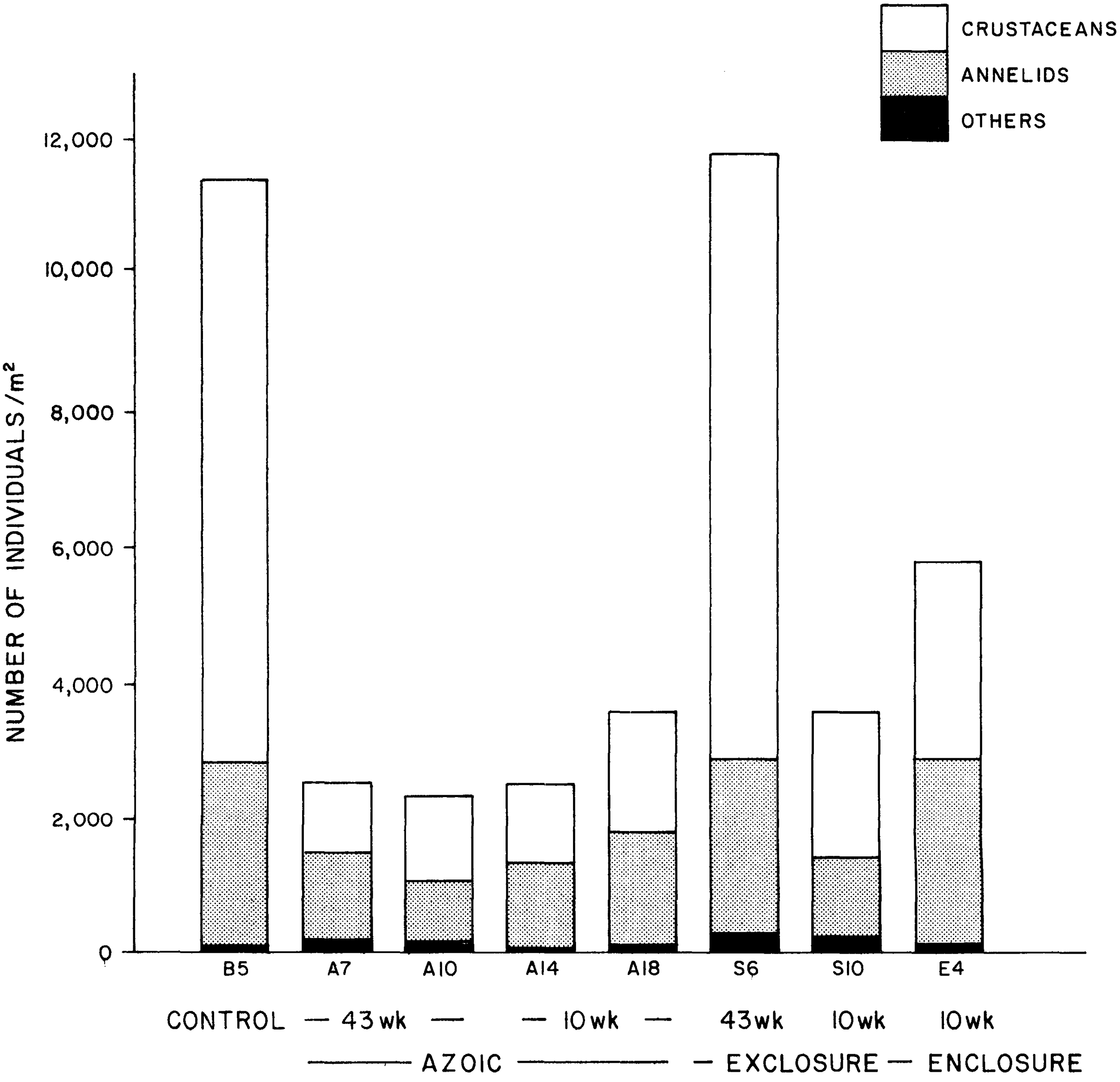


Figure 6-84. Density of macrobenthos in recovered sediment boxes and the control natural community (B5, August 1977).

and in the control samples was due to similarly high densities of the amphipod *Erichthonius rubricornis* and few other dominant species were otherwise shared (Figure 6-85).

Biomass. Total wet weight biomass of macrobenthos was higher in the boxes after 43 weeks than after 10 weeks, although all boxes supported less biomass than the natural community (Figure 6-86). In the B5 samples, molluscs, particularly the relatively large bivalve *Arctica islandica*, comprised the largest portion of wet weight biomass. Little molluscan biomass was found in any of the boxes except for A10 and S10 where the gastropod *Buccinum undatum* was found. The biomass of annelids was also higher in the natural community than in any of the boxes, mainly due to the presence of the large polychaete *Aphrodite hastata*. The relatively higher biomass of annelids in boxes A7, A10, and S6 was due to the polychaetes *Glycera dibranchiata* and *Aglophamus circinata* in A7 and A10 and *Glycera* and *Scalibregma inflatum* at S6. The peracaridan crustaceans, although numerically dominant, contributed little biomass and the large crustacean biomass in A7 and S6 was due to the presence of the crab *Cancer borealis*.

Assemblage Composition. Patterns of similarity in the macrobenthos of experimental treatments and the natural community were investigated with the use of numerical classification (species occurring only once not included, square root transformation, Bray-Curtis similarity, group average sorting normal analysis, and flexible sorting inverse analysis). The similarity matrix between pairs of treatments and the control samples and the agglomeration of these collections is represented in Figure 6-87.

The assemblages grouped on the basis of duration of exposure of the sediment and, secondarily, on the basis of the screening treatment. The natural community showed relatively low similarity to any of the assemblages established in the boxes. The 10 week predator enclosure, E4, showed strong similarity to the 10 week exclosure, S10. The enclosed predator, a single *Leptasterias tenera*, was absent when the box was retrieved. It may have died or escaped soon after deployment and, in any case, evidently had little effect on the macrobenthos. The assemblages of one of the 10 week azoic boxes (A18) was more similar to the 10 week screened boxes (S10 and E4) than it was to the other box receiving the same treatment (A14), which was poorer in species than the other boxes.

The fauna of the 43 week azoic controls (A7 and A10) was more similar to that of the 10 week boxes than to that of the 43 week exclosure box (S6). This is largely a reflection of the great abundance of the amphipod *Erichthonius rubricornis* in S6.

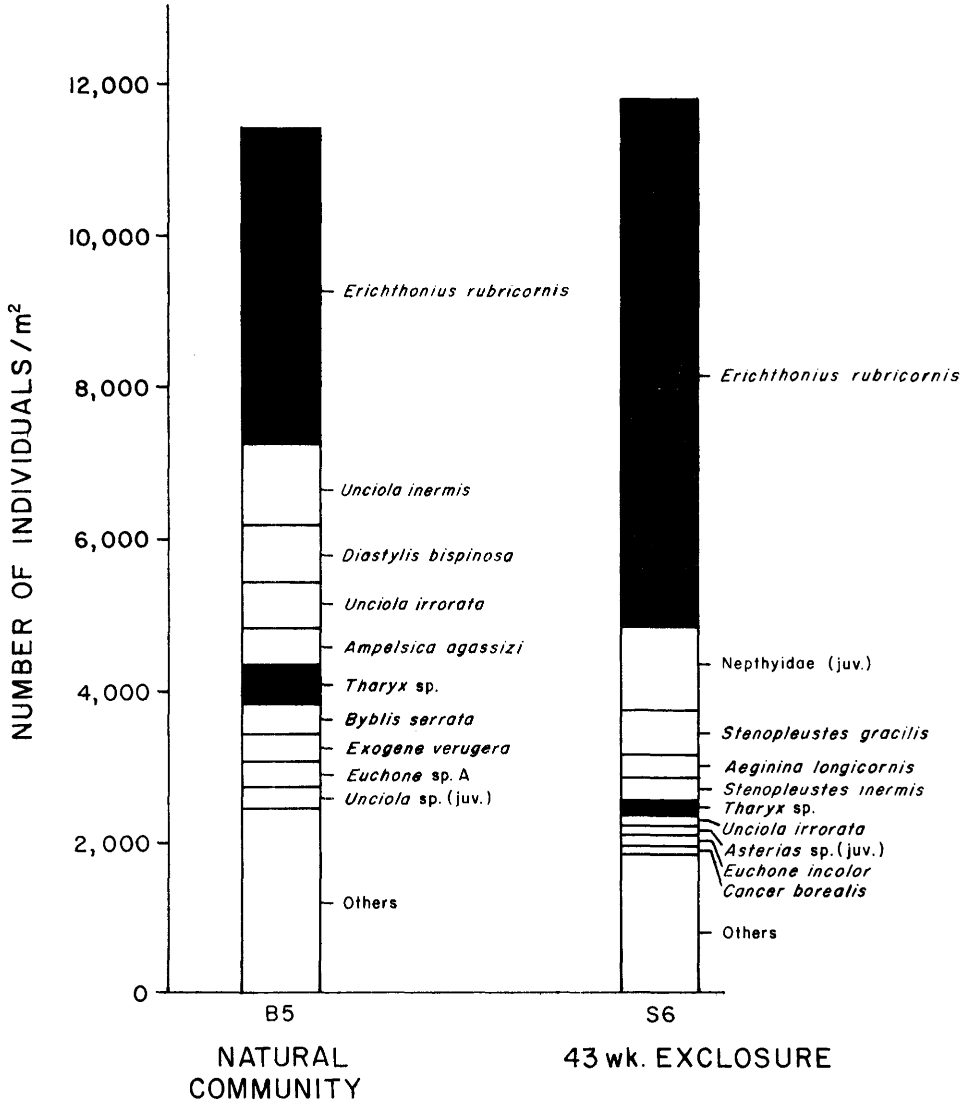


Figure 6-85. Comparison in composition of dominant species in the sediment box exposed for 43 weeks and from which large predators were excluded and the natural community at B5 in August 1977. Species in common are represented by black bars.

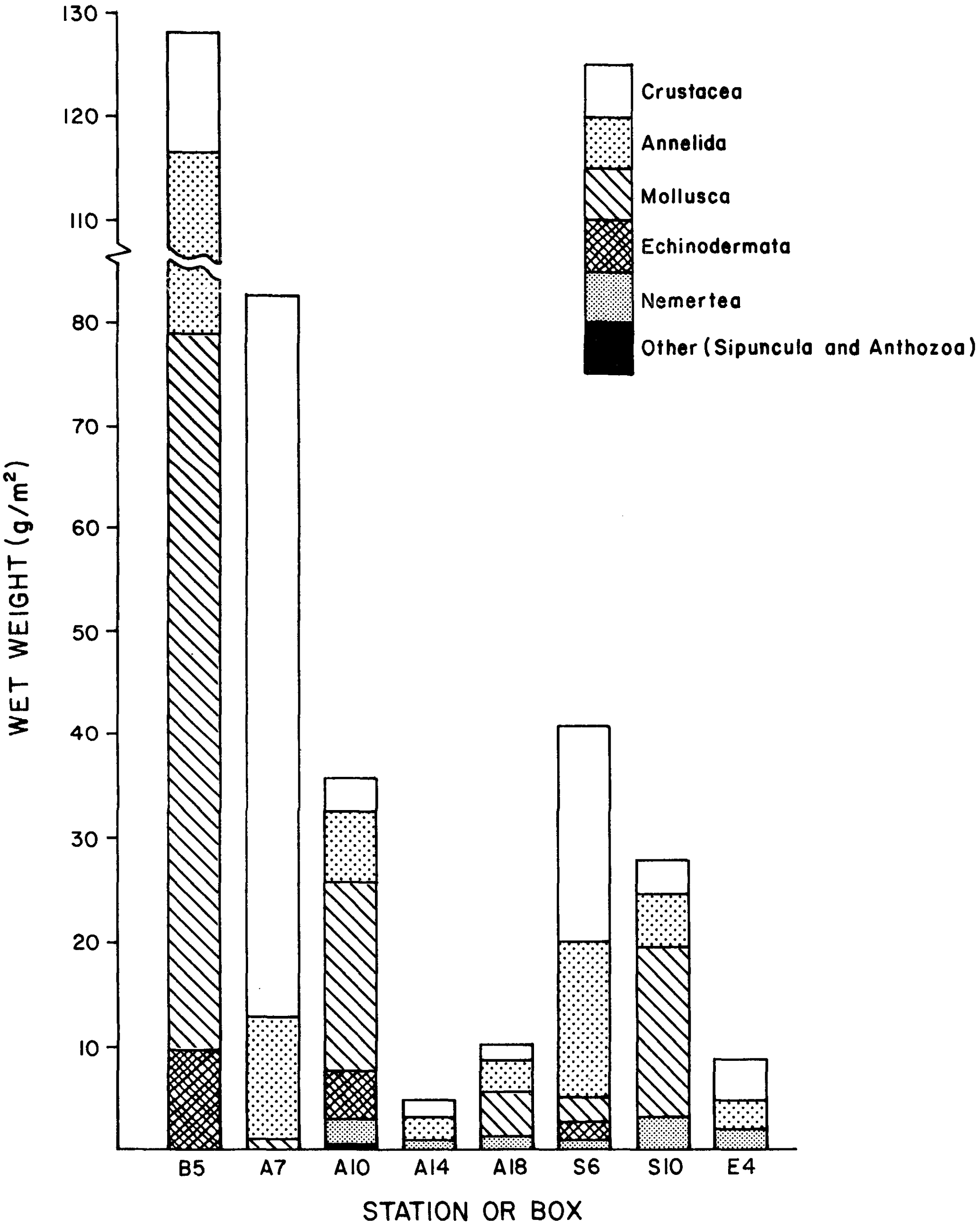
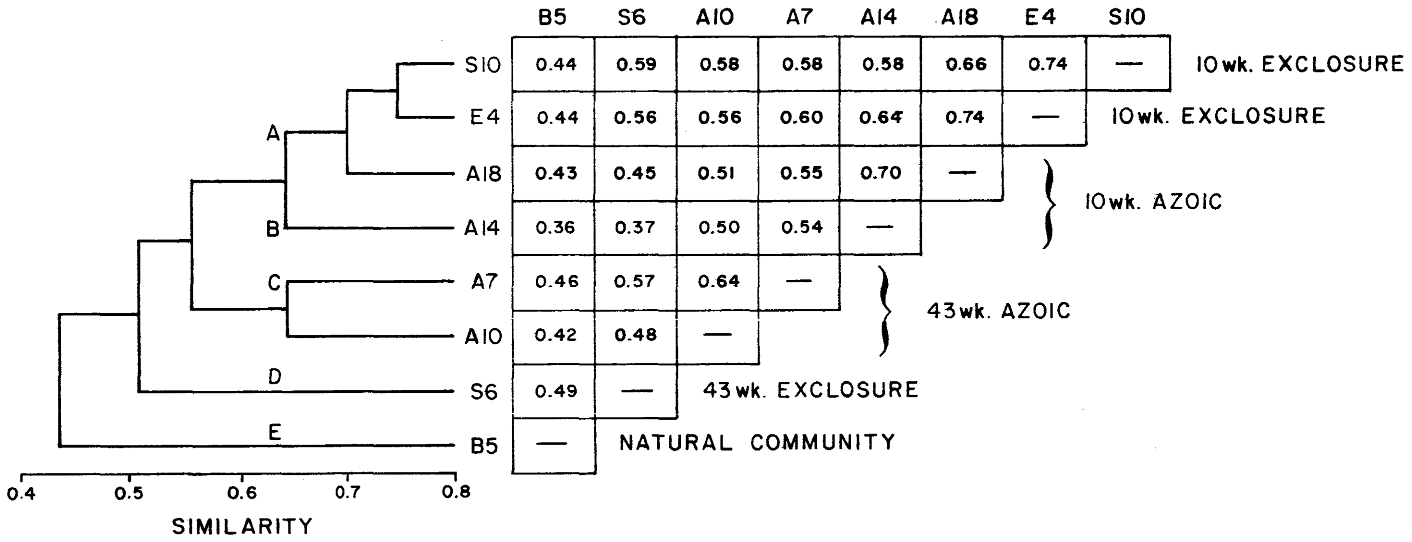


Figure 6-86. Biomass of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.



	B5	S6	A10	A7	A14	A18	E4	S10	
S10	0.44	0.59	0.58	0.58	0.58	0.66	0.74	—	10wk. EXCLOSURE
E4	0.44	0.56	0.56	0.60	0.64	0.74	—		10wk. EXCLOSURE
A18	0.43	0.45	0.51	0.55	0.70	—			10wk. AZOIC
A14	0.36	0.37	0.50	0.54	—				
A7	0.46	0.57	0.64	—					43wk. AZOIC
A10	0.42	0.48	—						
S6	0.49	—	43wk. EXCLOSURE						
B5	—	NATURAL COMMUNITY							

Figure 6-87. Similarities of the macrobenthos assemblages in recovered sediment boxes and the natural community at B5.

Species which were found in at least two boxes were numerically classified on the basis of their patterns of occurrence in the boxes; 13 species groups are interpreted (Table 6-17). Nodal diagrams (Figure 6-88) demonstrate the constancy, fidelity, and abundance concentration of the species groups to the groups of collections recognized from the normal analysis.

Species in groups 1-7 generally occurred in low abundances. Group 1 species were found significantly more frequently in the 43 week boxes. Species in Group 2 were only found in the 43 week unscreened boxes. Those in Group 3 were rare but did all occur in screened boxes E4 and S6. Similarly, species in Group 4 were rare but co-occurred in A14. Group 5 species did not occur in the 43 week unscreened boxes but were common in the 43 week screened box (S6) and some of the 10 week boxes. Presence in most boxes except S6 characterized the species of Group 6. Species in Group 7 were for the most part found in boxes exposed for 43 weeks or in shorter term exclosure boxes. These species in groups 1-7 were generally rare or low in abundance in the natural community as well as in the boxes. However, the polychaetes *Euclymene collaris* and *Euchone* sp. A and the cumacean *Eudorella pusilla* were present at densities in excess of 100/m^2 at B5 in August 1977.

Group 8 species were common but seldom abundant in each of the experimental sediment boxes. They include species found commonly in the natural community, such as the amphipod *Ampelisca agassizi* and the polychaete *Exogone verugera*, and some rarely found at B5, including the polychaete *Sphaerosyllis erinaceus* and the nemertean *Cerebratulus lacteus*. Group 9 was similar to Group 8 in that the species were found in most boxes, however, they were slightly more abundant in exclosures. The most notable members of this group are the polychaetes *Phyllodoce mucosa* and *Prionospio* sp. which were rare in the natural community.

Species in Group 10 and 11 exhibited especially high population levels in the boxes. Populations of the polychaete *Capitella capitata* and amphipod *Unciola inermis* were high in the 10 week boxes but were much less abundant in the 43 week boxes. The reduced populations of *Unciola inermis* in the older sediment is surprising because it was abundant in the natural community. The greater abundance of *Capitella*, which was not found in the natural community in the more recently defaunated sediment is consistent with its reputation as a fugitive species (Grassle and Grassle 1974; McCall 1977). The two species in Group 11 were also found in all the boxes, but they were more abundant in exclosures than in unprotected boxes exposed for comparable periods. Both species were found in S6 at population densities in excess of those found in the natural community.

The two congeneric amphipods comprising Group 12 were common except in A14, however, they were only abundant in the 43 week

Table 6-17. Species groups selected from numerical classification of macrobenthos from experimental recolonization boxes.

Species Group 1

Euclymene collaris
Echinarachnius parma
Maldanidae
Edwardsia sp.
Chone infundibuliformis
Nereis grayi
Pleurogonium inerme
Metopa sp.
Exogone hebes
Monoculodes sp. B
Glycera dibranchiata
Thracia conradi
Photis macrocoxa
Orchomenella minuta
Phyllodoce sp.
Musculus discors
Harmothoe extenuata
Euchone sp. A
Polycirrus eximius
Placopecten magellanicus
Euchone incolor
Spio pettiboneae

Species Group 2

Lyonsia hyalina
Crangon septemspinosa
Ptilanthura tricarina
Edotea triloba

Species Group 3

Ensis directus
Ampharetidae
Tetrastemma sp.

Species Group 4

Streptosyllis arenae
Colus sp.
Nicolea venustula
Phascolion strombi
Sthenelais limicola

Species Group 5

Terebellides sp. A
Ampharete arctica
Arctica islandica
Eudorella pusilla
Diastylis sculpta
Lunatia triseriata

Species Group 6

Cerianthidae
Terebellidae
Melita dentata

Species Group 7

Cancer irroratus
Crenella glandula
Crucibulum striatum
Actinocythereis vineyardensis
Buccinum undatum
Siphonoecetes sp.

Species Group 8

Lumbrineris impatiens
Ampelisca agassizi
Sphaerosyllis erinaceus
Exogone verugera
Ampelisca vadorum
Cerebratulus lacteus
Spiophanes bombyx
Leptocheirus pinguis
Pherura affinis
Unciola sp. (juveniles)
Corophium crassicorne

Table 6-17. (Concluded)

Species Group 9

Astyris sp.
Cerastoderma pinnulatum
Typosyllis tegulum
Polygordius sp.
Phyllodoce mucosa
Diastylis bispinosa
Prionospio sp.
Ophelina acuminata
Schistomeringos caeca
Scalibregma inflatum
Aglaophamus circinata
Asterias sp.

Species Group 10

Capitella capitata
Unciola inermis

Species Group 11

Nepthyidae (juveniles)
Ericthonius rubricornis

Species Group 12

Stenopleustes gracilis
Stenopleustes inermis

Species Group 13

Unciola irrorata
Phoxocephalus holbolli
Tharyx sp.
Byblis serrata
Aeginina longicornis
Cancer borealis

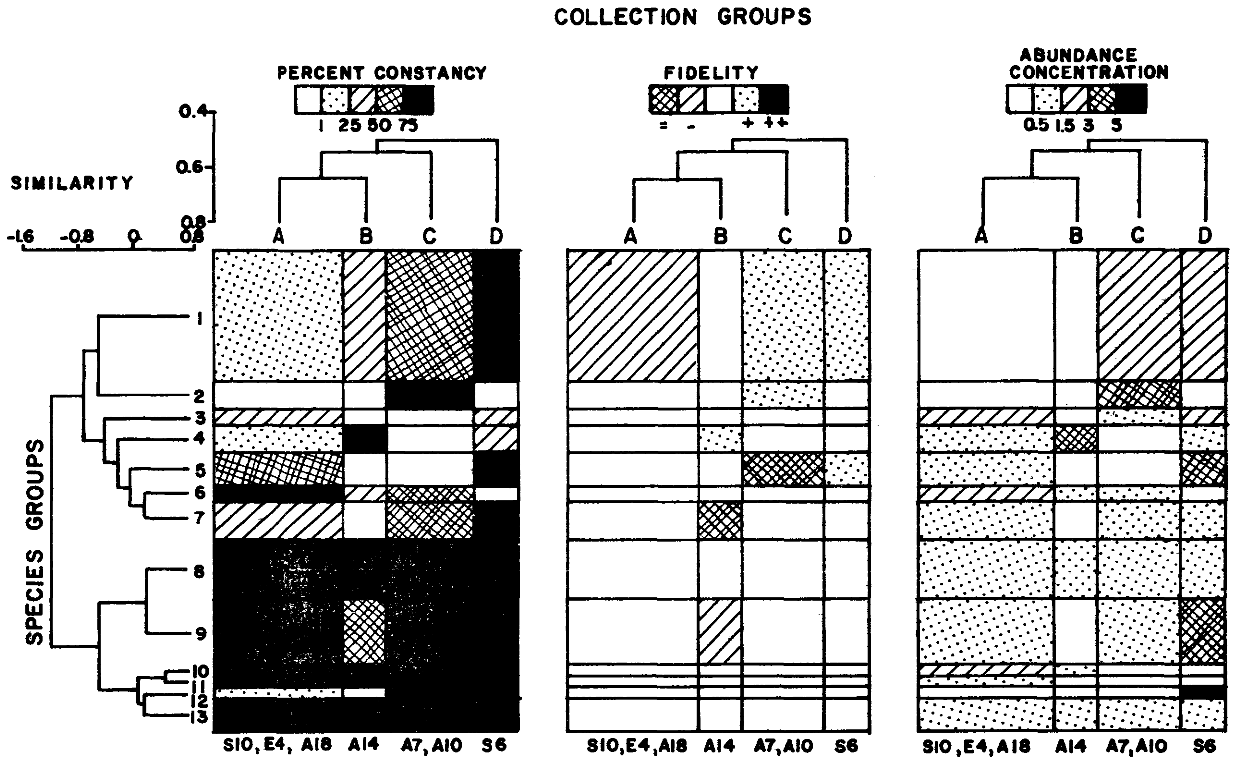


Figure 6-88. Hierarchies resulting from numerical classification of macrobenthic species and collections represented in recolonization experiments and nodal statistics.

exclosure. Species in Group 13 were very widely distributed among the boxes. Although as a group they showed no concentration of abundance in one treatment or another, some member species were more abundant in the exclosures. The caprellid amphipod *Aeginina longicornis*, generally epifaunal on hydroids, was observed clinging to screens at the time of retrieval. The crab *Cancer irroratus* was slightly more abundant in screened boxes, possibly an indication that the exclosures acted as a refuge from predation.

Individual Species Patterns. Patterns of individual species abundance in boxes varied with time of exposure and exclosure treatment. Comparison of boxes with others receiving the same type of treatment indicated three discernible trends in abundance.

Species more abundant in 10 week old boxes than in 43 week old boxes include the polychaete *Capitella capitata* and the amphipods *Erichthonius rubricornis* and *Unciola inermis* (Figure 6-89). The super-opportunist, *Capitella capitata*, which occurred in high densities in A14, A18, and E4 and to a lesser extent in S10, was not found in any of over 1600 grab samples collected from the shelf and slope during the study! Population levels in the boxes retrieved after 43 weeks were very low in comparison to the 10 week boxes. *Unciola inermis*, a species which naturally exhibited high population densities at Station B5, followed the same general trends in population levels as *C. capitata*, but to lesser extremes. *Erichthonius rubricornis* was more abundant in A14 and A18 than in A7 and A10, but unlike *Capitella* and *Unciola inermis* it was more abundant in the 43 week screened box than in the 10 week screened boxes.

A less readily distinguishable pattern is exemplified by juvenile nepthyids, *Tharyx* sp. (polychaete) and *Unciola irrorata* (Figure 6-90). These animals were found in lower numbers in boxes exposed for 10 weeks than in 43 week old boxes. Juvenile nepthyids show the most marked difference, being particularly abundant in the 43 week exclosure. These juvenile nepthyids were more abundant in the boxes than in the natural community but the reverse is true for *Tharyx* sp. and *Unciola irrorata*.

Species important in B5 control samples, but not in the boxes are shown in Figures 6-91 to 6-94. Included are the ampeliscid amphipods *Ampelisca agassizi*, *Ampelisca vadorum*, and *Byblis serrata*, the cumacean *Diastylis bispinosa* and juvenile *Unciola*. Polychaete species abundant in the natural community but not found in high numbers in the boxes include *Exogene verugera*, *Euchone* sp. A, *Euclymene collaris*, *Lumbrineris impatiens*, *Goniadella gracilis*, and the archiannelid *Polygordius* sp. *Goniadella* was not found in any of the boxes and *Euclymene collaris* and *Euchone* sp. A were not found or were very rare in the 10 week boxes.

Almost all numerically important members of the natural community were established in the experimental boxes. However, many species were present in reduced densities. Only juvenile nepthyids, *Capitella capitata* and some subdominant epifaunal amphipods were consistently more abundant in sediment boxes than in the natural community.

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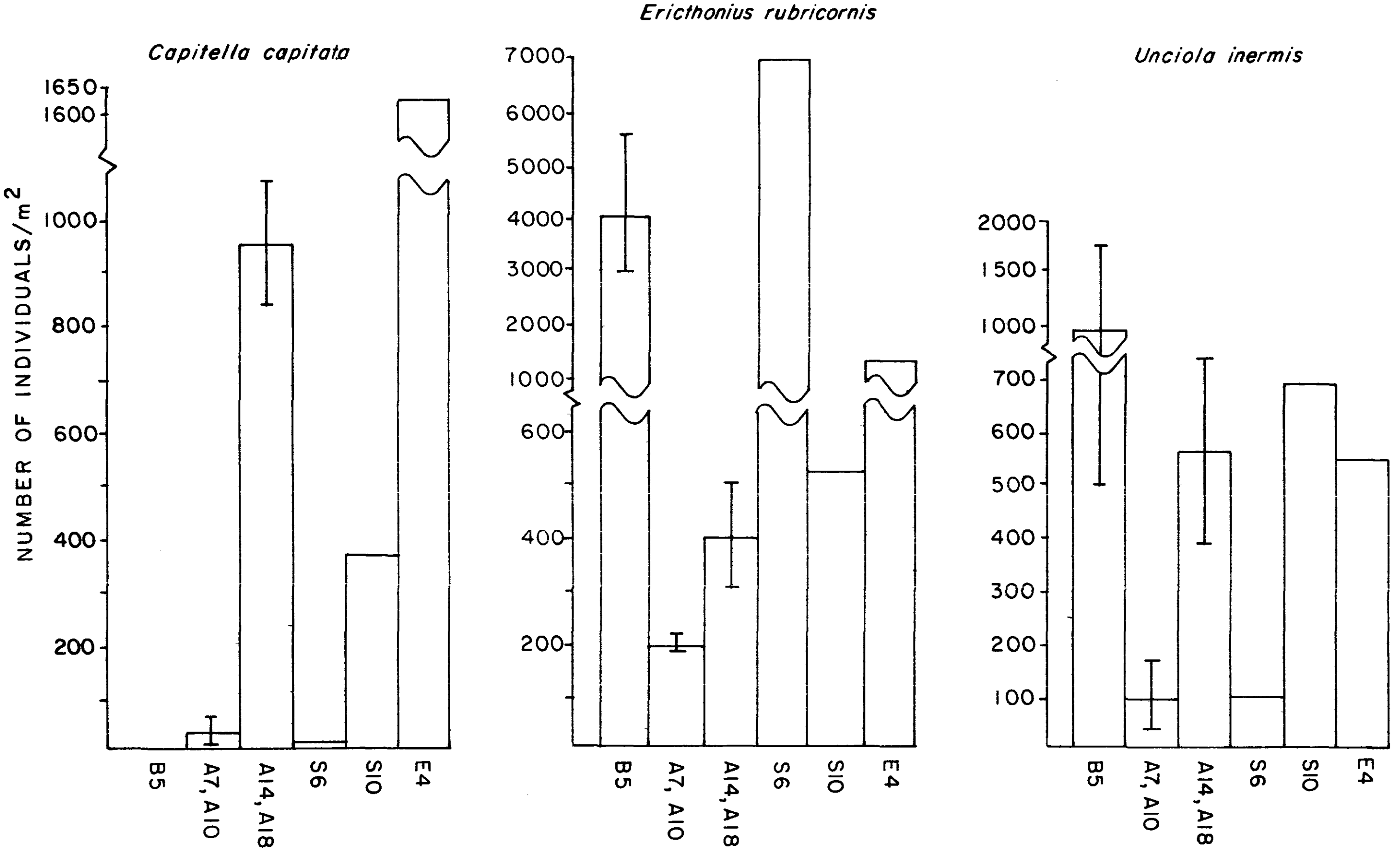

Figure 6-89. Population densities of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

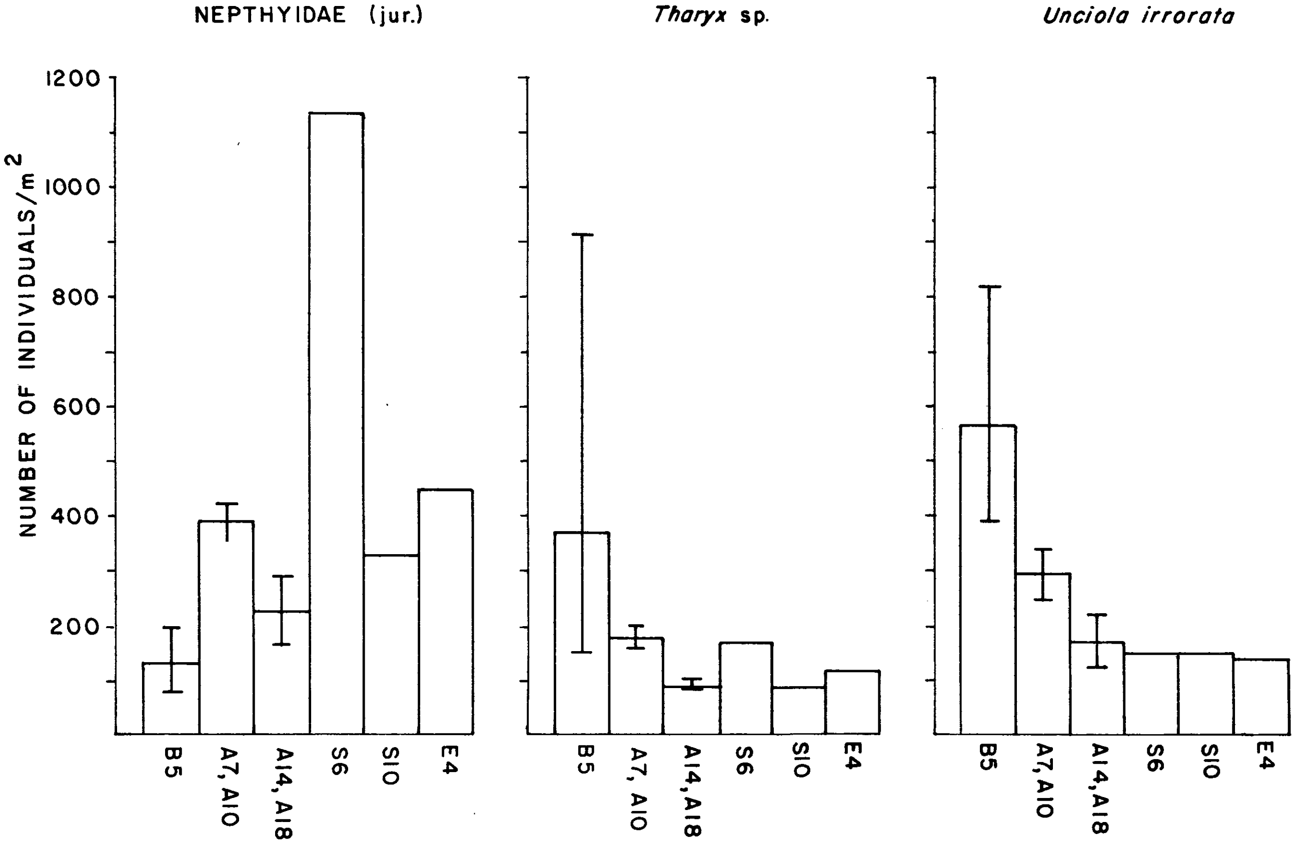

Figure 6-90. Population densities of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

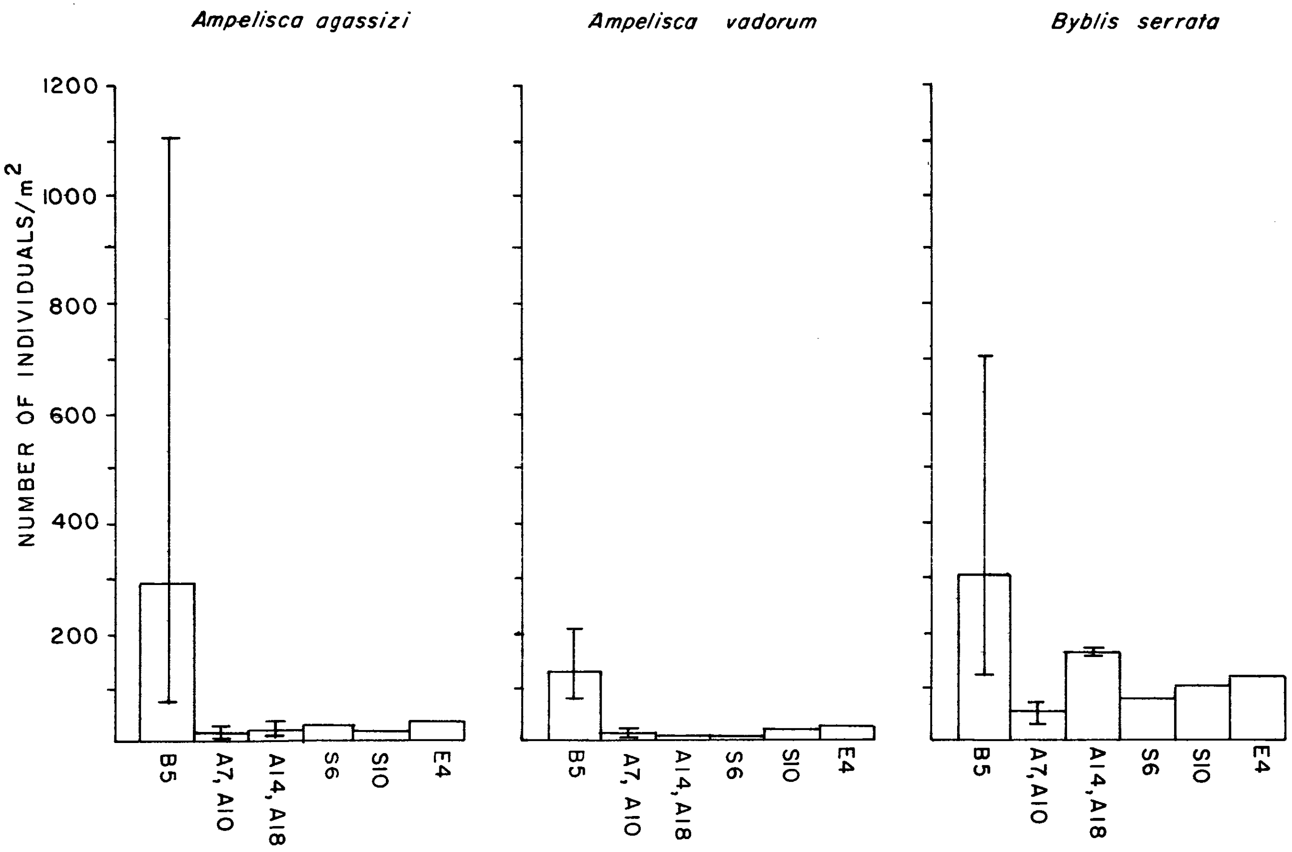

Figure 6-91. Population densitites of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

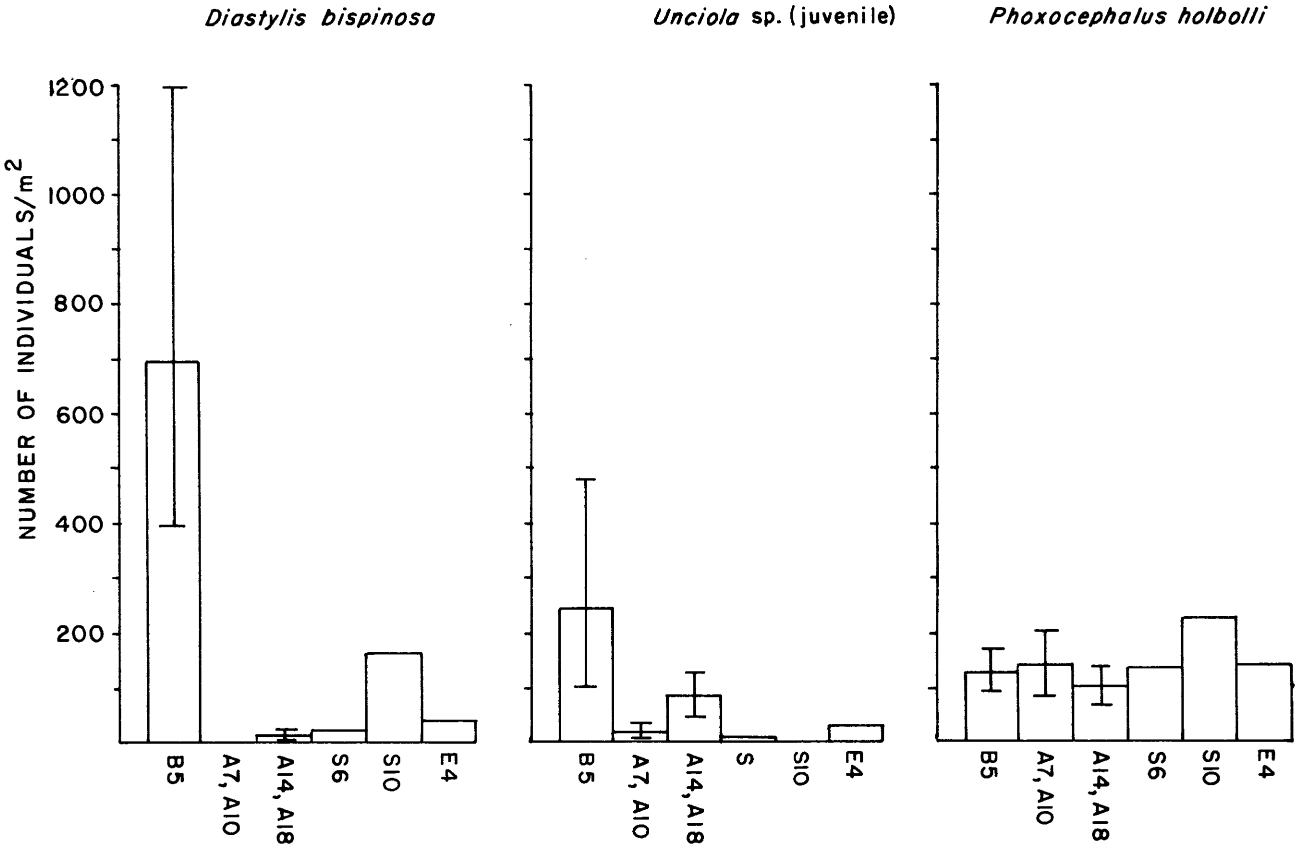

Figure 6-92. Population densitites of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

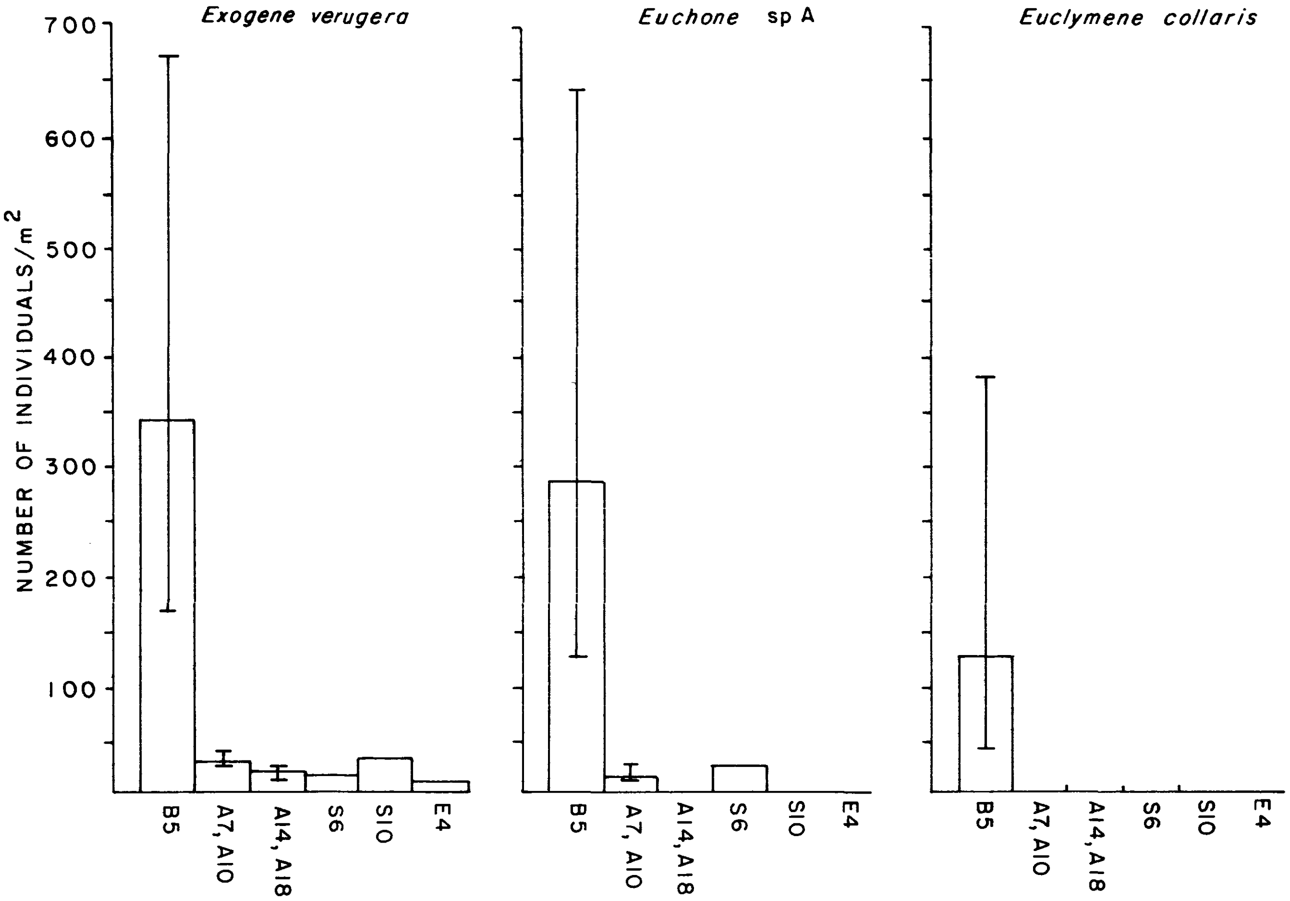

Figure 6-93. Population densitites of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

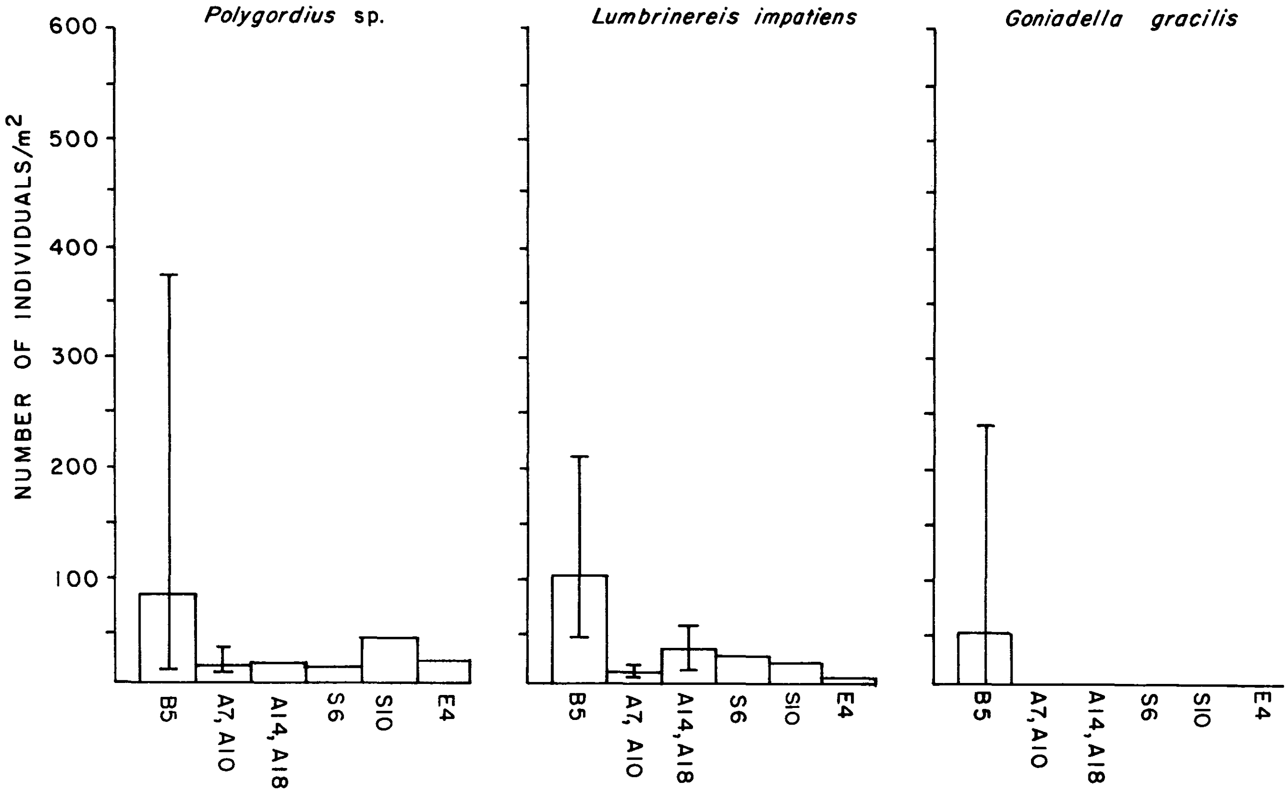

Figure 6-94. Population densities of various species of macrobenthos in recovered sediment boxes and in the natural community at B5 in August 1977.

Species Diversity. Areal species richness was higher in sediments exposed longer (i.e. 43 week boxes and the natural seabed) and sediments in screened exclosures than in unprotected sediments exposed for the same time (Figure 6-95). Boxes exposed for 43 weeks contained about 40 percent more species than those similar treatments exposed for 10 weeks. Exclosure boxes supported 30-40 percent more species than unscreened boxes. The areal richness of the assemblage in the 43 week exclosure approached that of the natural community.

Shannon diversity was higher in the 43 week azoic boxes than in the comparable 10 week boxes. However, diversity in the 43 week exclosure and in the natural community, the two richest assemblages, was lowered because of the reduced evenness brought about by the strong numerical dominance by *Erichthonius rubricornis*. Thus, species evenness was the dominant component of Shannon diversity in these collections (Figure 6-95). The numerical richness measure also shows a strong effect of species evenness and its pattern was thus very similar to that of H', although it was slightly more sensitive to areal species richness than H'.

Megabenthos

Composition of the Fauna

Megabenthic fauna collected by anchor dredge and small biology trawl was dominated in numbers of individuals, numbers of species, and biomass by echinoderms, molluscs, and decapod crustaceans. Species identified from collections made during the two years of study are listed in Appendix 6-B. Identifications are incomplete for some other taxonomic groups such a hydroids and peracaridan crustaceans, but neither of these taxa was abundant. The polychaetous annelids, which comprise a dominant taxon of the macrobenthos (0.5 mm sieve) were represented only sparsely in collections of megabenthos (4 mm mesh), but three species were relatively important. Two of the three, *Nothria conchylega* and *Hyalinoecia artifex*, were important in the shelf break and slope habitats, respectively, while the third, *Aphrodita hastata*, was more widely distributed on the central and outer shelf. Four other minor taxa had species which were numerically important in the megabenthos. These taxa and the species are: foraminifera, *Astrorhiza limnicola* (a large, widely distributed arenaceous form); Anthozoa, the zoantharian anemones *Epizoanthus incrustans*, *Epizoanthus paguralilis* and *Isozoanthus* sp., cerianthid anemones, and the solitary coral *Dasmosmilia lymani*; Sipuncula, *Phascolion strombi*; and Ascidacea, *Molgula arenata*.

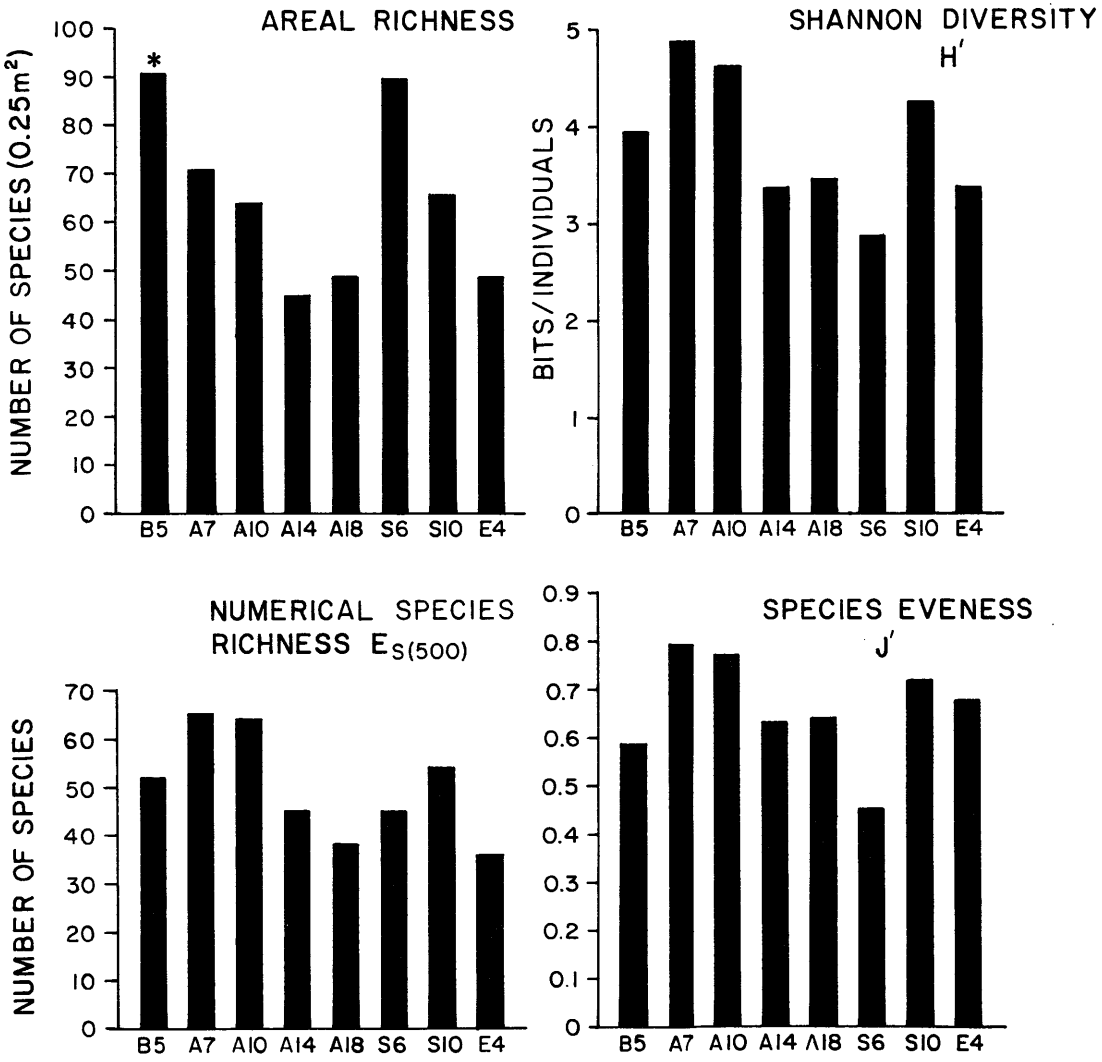

Figure 6-95. Species richness, Shannon diversity, and species evenness of assemblages of macrobenthos represented in sediment boxes and the natural community at B5, August 1977.

These collections represent a considerably different portion of the benthos than that sampled by bottom grab. Although many species captured by dredge or trawl were also taken in grab samples, most were infrequent in grab samples. On the other hand, a large portion of the fauna sampled by grab (0.5 mm mesh), particularly the small annelids and peracaridans which dominate those collections, was not sampled by dredge and trawl samples (4 mm mesh), which were dominated by echinoderms, molluscs, and decapod crustaceans.

The megabenthic species sampled by the SBT and anchor dredge are surface dwellers or near-surface infauna. Neither sampler penetrated deeply enough into the sediment to reliably collect large bivalves, e.g. Spisula solidissima and Arctica islandica, and other deep dwelling infauna. Sampling this component would require massive mechanical or hydraulic dredges and much coarser screening of sediments.

Sampling Variability

Tows of trawls and dredges produce notoriously variable catches due to differences in sampling efficiency and area from tow to tow as well as natural patchiness. For this reason, these data are considered semi-quantitative in that the spatial and temporal trends may be deduced from species abundances, but considerable caution must be applied to interpretations. The data collected indicate that tow times and sampler efficiency remained reasonably consistent at least within a cruise and in most cases between cruises (Boesch et al. 1977). Still, the variance in the abundance of these species was generally rather large with respect to the mean.

The one exception to the overall sampling consistency was at the continental slope station J1, where because of abrupt bathymetric and faunal change, catches were produced which were quantitatively and, frequently, qualitatively variable from tow to tow and cruise to cruise.

Comparison of Sampling Equipment

Both SBT and anchor dredge were used in order to sample two components of the biota, epifauna and infauna, respectively. Although there was considerable overlap in the fauna sampled by either device, the anchor dredge usually caught more species of molluscs and fewer echinoderms and decapod crustaceans at all stations than did the SBT. When catch data are adjusted for difference in mouth width and tow duration, differences in density estimates among abundant species can also be observed. For example, when adjusted abundances of mollusc species at stations C2 and D1 were compared for the two samplers (Table 6-18), the estimates of deeper dwelling bivalves (e.g. Ensis, Arctica, and Astarte) were higher with the anchor dredge. On the

Table 6-18. Adjusted abundance of molluscs collected in the SBT and anchor dredge at stations C2 and D1. Data are the sums of the averages for winter and spring 1976. The anchor dredge data were adjusted relative to the SBT to compensate for difference in mouth width and tow length.

	Station			
	C2		D1	
	SBT	Anchor Dredge	SBT	Anchor Dredge
Ensis directus	2	15		958
Spisula solidissima	17	15		58
Arctica islandica				203
Cyclocardia borealis			1	7
Astarte castanea	46	254	1	22
Pandora gouldiana	4	7	2	152
Cerastoderma pinnulatum	13	7	14	58
Lyonsia hyalina	4		4	29
Crenella glandula	1			
Placopecten magellanicus			1	15
Lunatia heros	2		8	29
Nassarius trivittatus	95	36	29	275
Colus pygmaeus			7	160
Polinices immaculatus			1	7
Solariella obscura				22
Pleurobranchaea tarda	66			
Crepidula plana	1		8	

other hand epifaunal or shallow infaunal molluscs show minor or inconsistent differences between the SBT and anchor dredge.

Biomass

Wet weight biomass was recorded for individual species from all of megabenthos collections made during the second year of sampling (fall 1976-summer 1977). For summarization of results, biomass was summed for each of the dominant phyla: Mollusca, Echinodermata, and the decapod Crustacea (Figures 6-96 and 6-97, Appendix 6-F). The biomass of tubicolous polychaetes is also reported for Station J1 (continental slope) where it contributed significantly.

Anchor dredge data were standardized to compensate for differences with the SBT in tow length and mouth width. Geometric means of the three replicate tows were calculated for both sets of gear.

No attempt was made to sum biomass values across major taxa because species variously included skeletal material, gut contents, and tubes, and these discrepancies make between-taxa comparisons meaningless. Additional problems were associated with large bivalves where only the posterior portions of the animal or simply siphons were collected rather than the entire animal. In spite of these difficulties, the data support utilization of two types of sampling devices. Except at Station A1 anchor dredge molluscan biomass was generally higher than equivalent SBT values. This was caused by the presence of large *Spisula solidissima* or *Arctica islandica* or the presence of more numerous smaller *Astarte* spp. or *Cyclocardia borealis*, all burrowing bivalves. The occurrence of the epibenthic *Calliostoma bairdii* in the SBT samples at Station A1 as well as the absence of any large infaunal bivalves accounts for the discrepancy at this station. In contrast to the molluscan biomass values, biomass estimates for epifaunal species such as the decapod crustaceans and the majority of the echinoderms were generally higher with the SBT. Even when SBT and anchor dredge samples were combined, estimation of biomass within major bathymetric zones was difficult because of the disruptive effects of hypoxia. In general, molluscs comprised a higher percentage of the biomass on the inner shelf due to better survival through hypoxia, but seem to be major contributers chiefly on the outer shelf. Echinoderm biomass peaked on the central shelf due to *Echinarachnius* and would have averaged higher had hypoxia not affected Station N3. In general, biomass increased from inner to central to outer shelf and then declined at the shelf break, but this may reflect skeletal contributions rather than actual organic matter. In addition, the large standing crop biomass for the slow growing molluscs and echinoderms may not be indicative of actual biomass production trends.

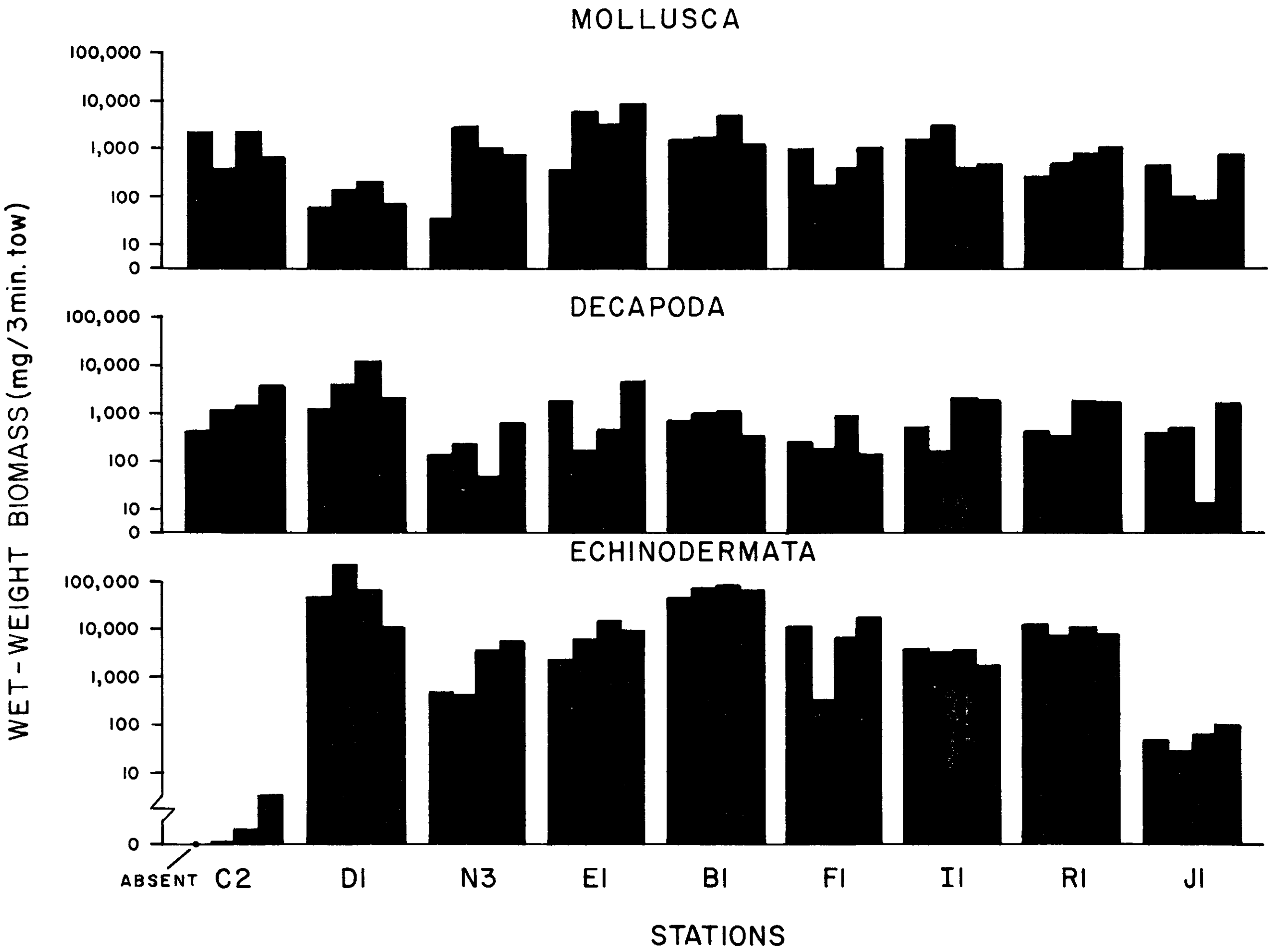

Figure 6-96. Geometric mean wet-weight biomass of the three dominant taxa of megabenthos collected by small biology trawl, by station and season, fall 1976-summer 1977.

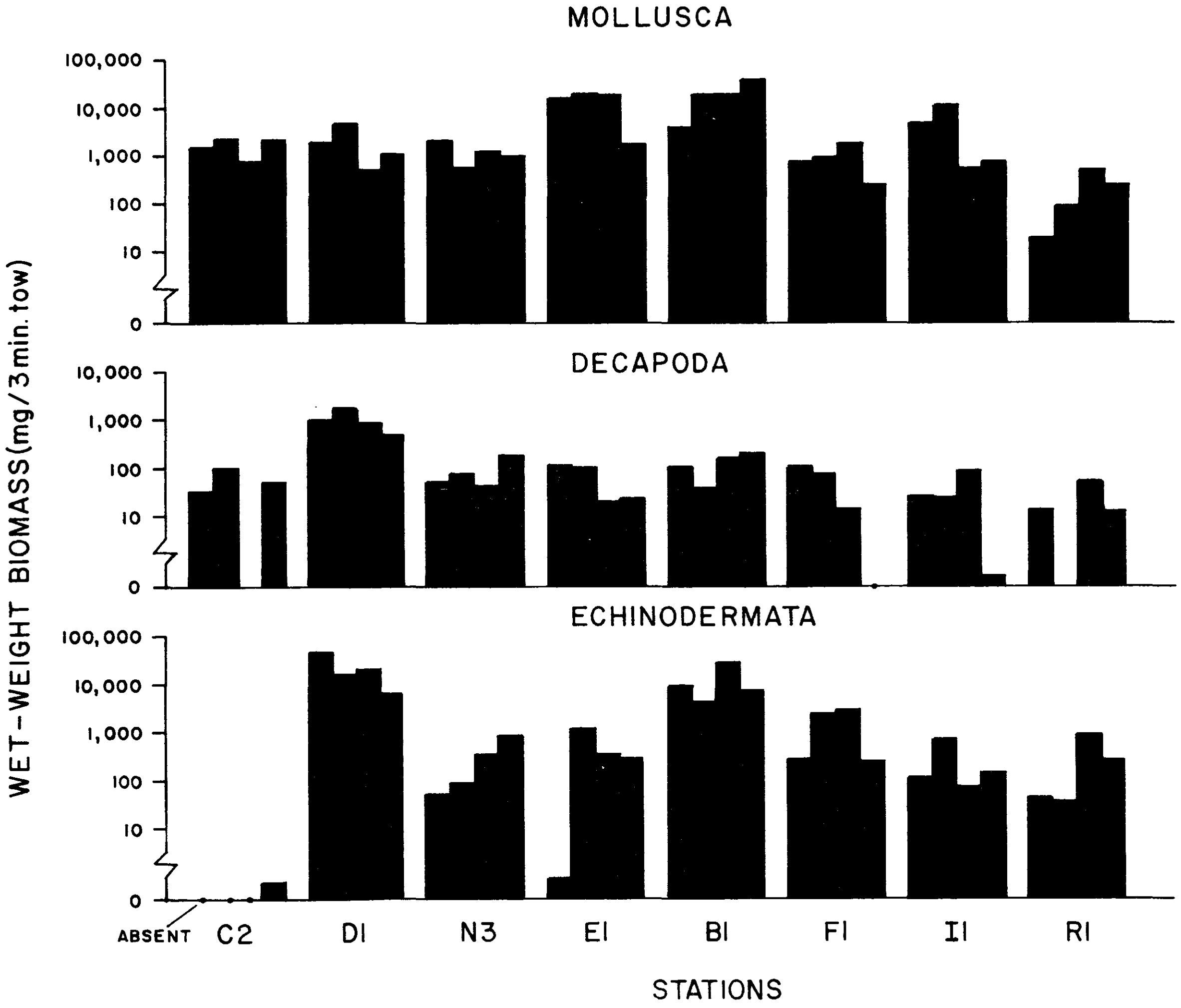

Figure 6-97. Geometric mean wet-weight biomass of the three dominant taxa of megabenthos collected by anchor dredge, by station and season, fall 1976-summer 1977.

Large Scale Patterns of Distribution

To discern cross-shelf distributional patterns represented in the megabenthos, normal and inverse numerical classifications were applied separately to reduced data sets from small biology trawl (SBT) and anchor dredge collections. Data from individual seasonal collections at each station were reduced by elimination of species not represented in at least three collections and by restriction to decapod crustaceans, molluscs, echinoderms, and several minor taxa which were identified from all collections. Log-transformed data were subjected to cluster analyses incorporating Bray-Curtis similarity and flexible sorting.

Small Biology Trawl Collections. Thirteen groups are interpreted from the clustering of SBT collections (Table 6-19). The five main agglomerations represent: a) C2 during the hypoxic stress of summer 1976 and the subsequent recovery phase (Group A); b) collections from the inner and central shelf stations C2, D1 and N3 (groups B and C); c) collections from central and outer shelf stations D1, D4, N3, B1 and E1 (groups E, F, and G); d) collections from shelf break stations A1, F1 and I1 (groups H, I, and J, respectively); and e) collections from the slope station J1 (Group K). Variability among seasonal collections from shelf break and slope stations was such that collections from each of these stations grouped discretely. The grouping of seasonal collections from shelf stations was less discrete because of the effects of hypoxic stress (C2 and D1) or because of sampling variability, despite large scale biotic homogeneity.

The agglomeration of the 99 species included in the analyses is interpreted at the 19 group level (Table 6-20) with the assistance of nodal analyses. The nodal diagrams (Figures 6-98 to 6-108) show clear cross shelf patterns of distribution. Species in Group 1 and, to a lesser degree, Group 6 were primarily found on the inner and central shelf. Other species (e.g. Group 15) were found broadly except on the inner shelf. Species groups 2, 3, and 10 were ubiquitous but showed differing patterns of abundance. Those inhabiting the central and, primarily, outer shelf are included in groups 4 and 5, whereas species showing affinity for the outer shelf and shelf-break make up groups 9 and 13. Group 11 species were more widely distributed but showed a greater affinity for the shelf-break, slope, and, to a lesser degree, outer shelf. Those forms characteristic of the shelf-break are included in groups 8, 12, and 14 while those restricted primarily to the upper continental slope are contained in groups 16-19.

Closer examination of the species groups in terms of constancy, fidelity and abundance concentration and of patterns of distribution of some individual species is required to separate the more subtle cross-shelf or within-zone patterns.

(TEXT CONTINUES ON PAGE 6-203)

Table 6-19. Allocation of collection groups selected from numerical classification of megabenthos collected by small biology trawl.

	Season							
	1975	1976				1977		
Station	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer
C2	B	B	B	A	A	A	A	A
D1	C	E	E	C	C	C	C	C
D4	E	–	–	–	–	–	–	–
N3	C	E	E	E	D	D	D	D
B1	F	F	F	F	F	F	F	F
E1	E	G	G	F	G	G	G	G
I1	H	H	H	H	H	H	H	H
F1	I	I	I	I	I	I	I	I
A1	J	J	J	J	J	J	J	J
J1	K	K	K	K	K	K	K	K

Table 6-20. Species groups selected from numerical classification of megabenthos collected by small biology trawl (SBT).

Species Group 1

Ovalipes ocellatus
Libinia dubia
Ensis directus
Cerianthidae sp. 1
Astarte castanea
Spisula solidissima
Nassarias trivittatus
Asterias forbesi

Species Group 2

Crangon septemspinosa
Cancer irroratus
Dichelopandalus leptocerus
Astrorhiza limicola
Echinarachnius parma
Pleurobranchaea tarda

Species Group 3

Cerastroderma pinnulatum
Pagurus acadianus
Pagurus arcuatus
Leptasterias tenera
Solariella obscura
Lyonsia hyalina
Aphrodita hastata

Species Group 4

Buccinum undatum
Arctica islandica
Stereoderma unisemita
Lunatia triseriata

Species Group 5

Polinices immaculatus
Strongylocentrotus droebachiensis
Crucibulum striatum
Placopecten magellanicus
Rossia tenera
Axiognathus squamata

Species Group 6

Lunatia heros
Pandora gouldiana
Crepidula plana
Raja erinacea

Species Group 7

Dendroda carnea
Musculus niger
Pitar morrhuana

Species Group 8

Crenella glandula
Amphioplus macilentus
Epitonium dallianum
Collodes robustus
Cadulus agassizi
Eualus pusiolus

Species Group 9

Turbonilla interrupta
Ascidia callosa
Modiolus modiolus
Cyclopecten nanus
Anomia simplex
Anomia squamula
Hyas coarctatus
Ophiopholis aculeata

Species Group 10

Molgula arenata

Species Group 11

Cancer borealis
Astropecten americanus

Species Group 12

Nothria conchylega
Astarte undata
Pontophilus brevirostris

Table 6-20. (Concluded)

Species Group 13

Calliostoma bairdii
Cyclocardia borealis
Astarte crenata subequilatera
Henricia sanguinolenta

Species Group 14

Euprognatha rastellifera
Sclerasterias tanneri
Pandora inflata
Bythocaris nana
Dasmosmilia lymani
Munida iris iris
Amphilimna olivacea
Epizoanthus paguraphilus

Species Group 15

Phascolion strombi
Colus pygmaeus

Species Group 16

Isozoanthus sp.
Astyris diaphana
Stephanasterias albula
Oenopota harpularia
Meganyctiphanes norvegica
Yoldia sapotilla
Havelockia scarbra

Species Group 17

Lucinoma filosa
Periploma fragilis
Catapagurus sharreri
Catapagurus gracilis

Species Group 18

Epizoanthus incrustatus
Hyalinoecia artifex

Species Group 19

Geryon quinquedens
Colus stimpsoni
Pagurus politus
Nuculana caudata
Dentalium occidentale
Odontaster setosus
Sergestes arcticus
Parapagurus arcuatus
Golfingia catharinae
Philine quadrata
Bathynectes superbus
Myxine glutinosa
Cuspidaria rostrata

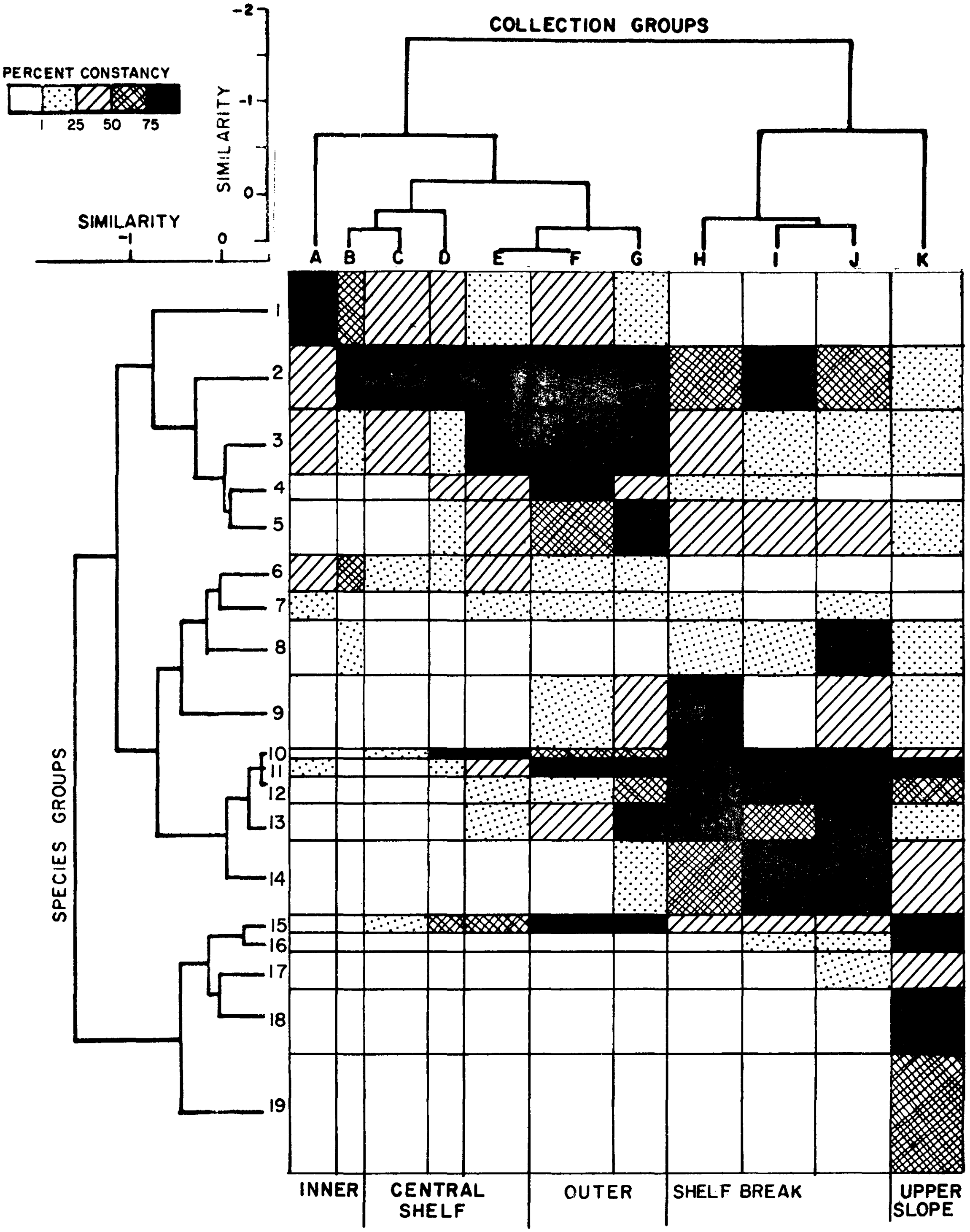

Figure 6-98. Normal and inverse classification hierarchies and nodal constancy for site-species group coincidence based on all small biology trawl collections.

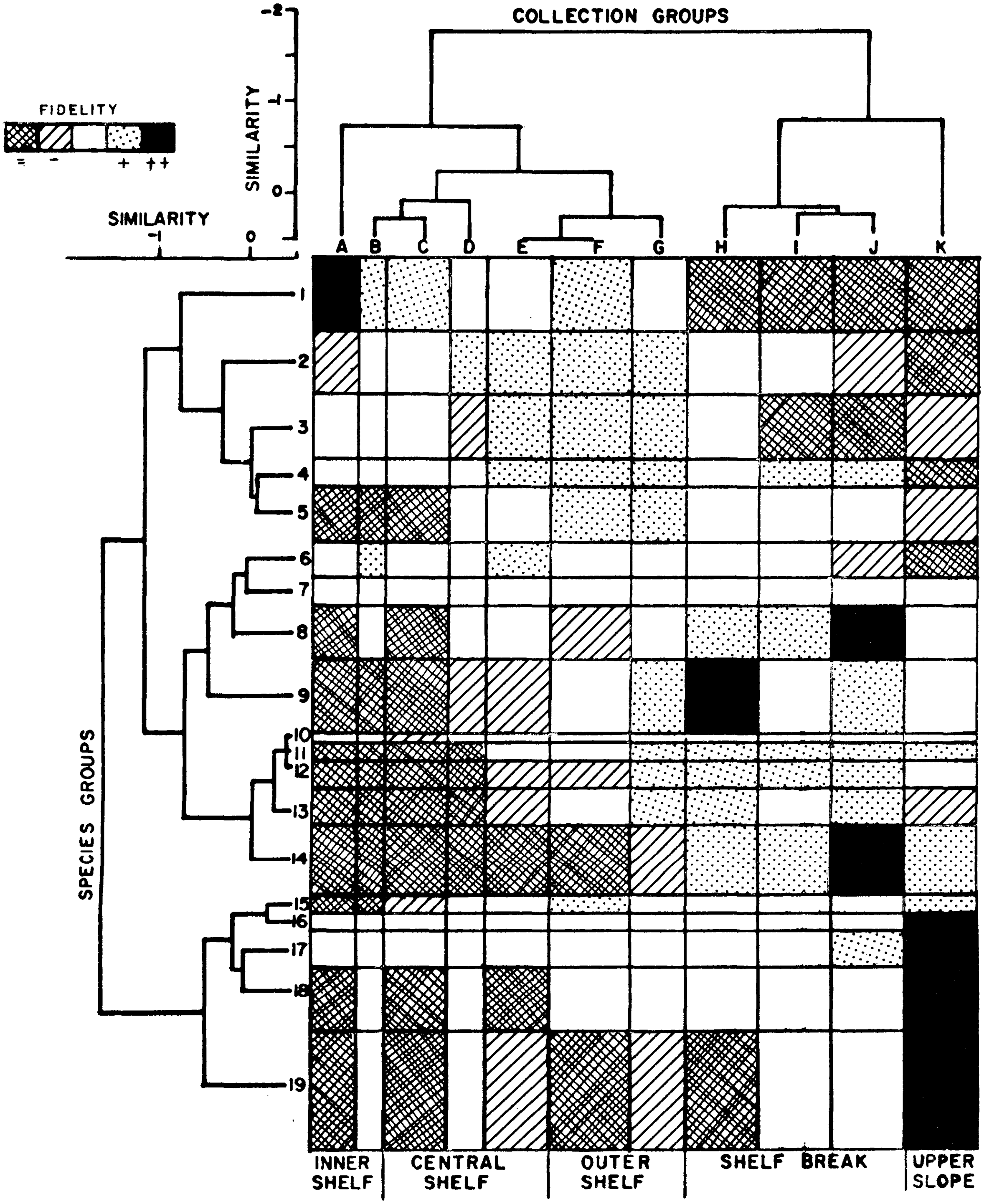

Figure 6-99. Nodal fidelity for classification of megabenthos from small biology trawl samples as in Figure 6-98. Values indicate significant and highly significant fidelity and negative fidelity.

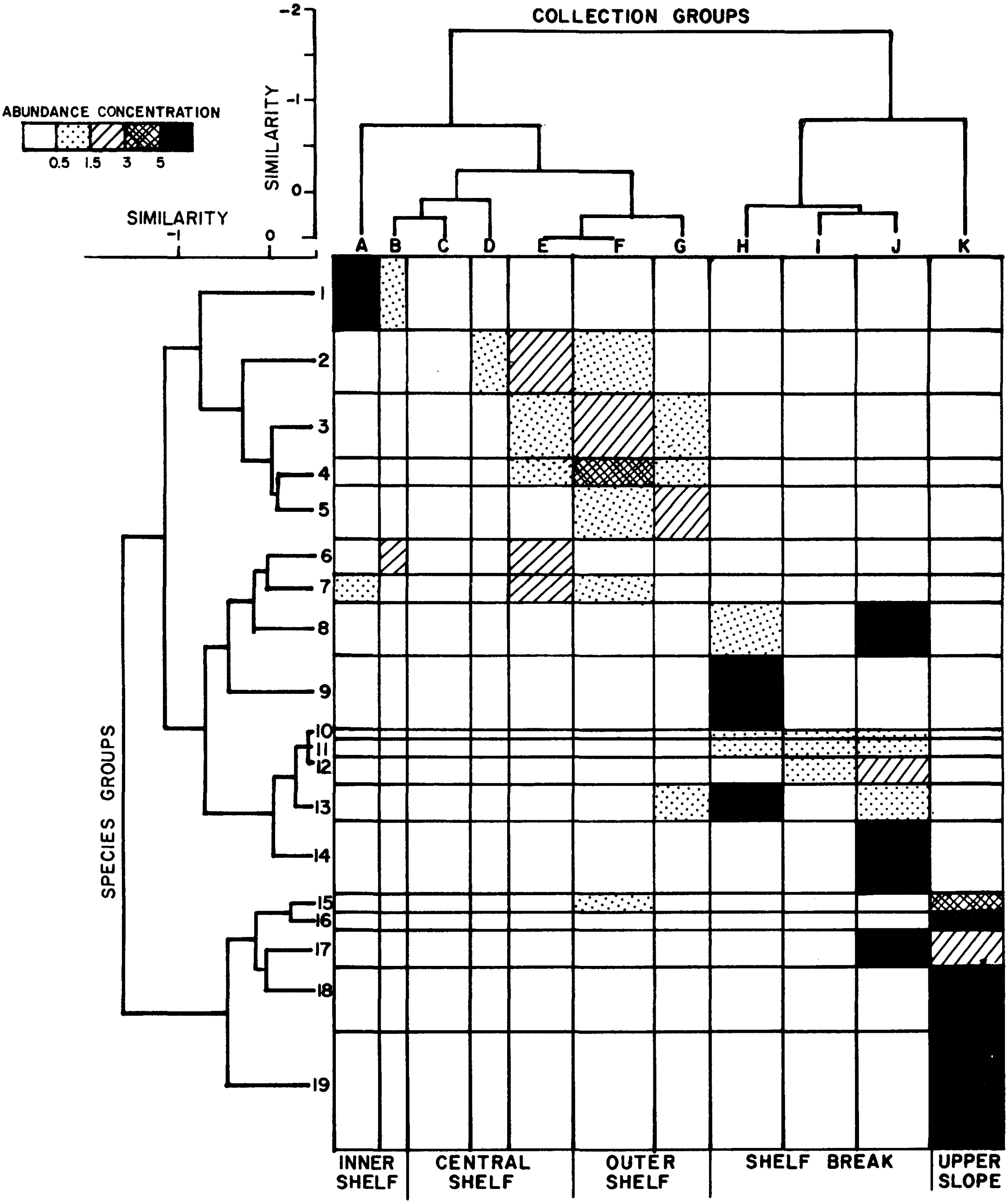

Figure 6-100. Nodal abundance concentration for classification of megabenthos from small biology trawl samples as in Figure 6-98.

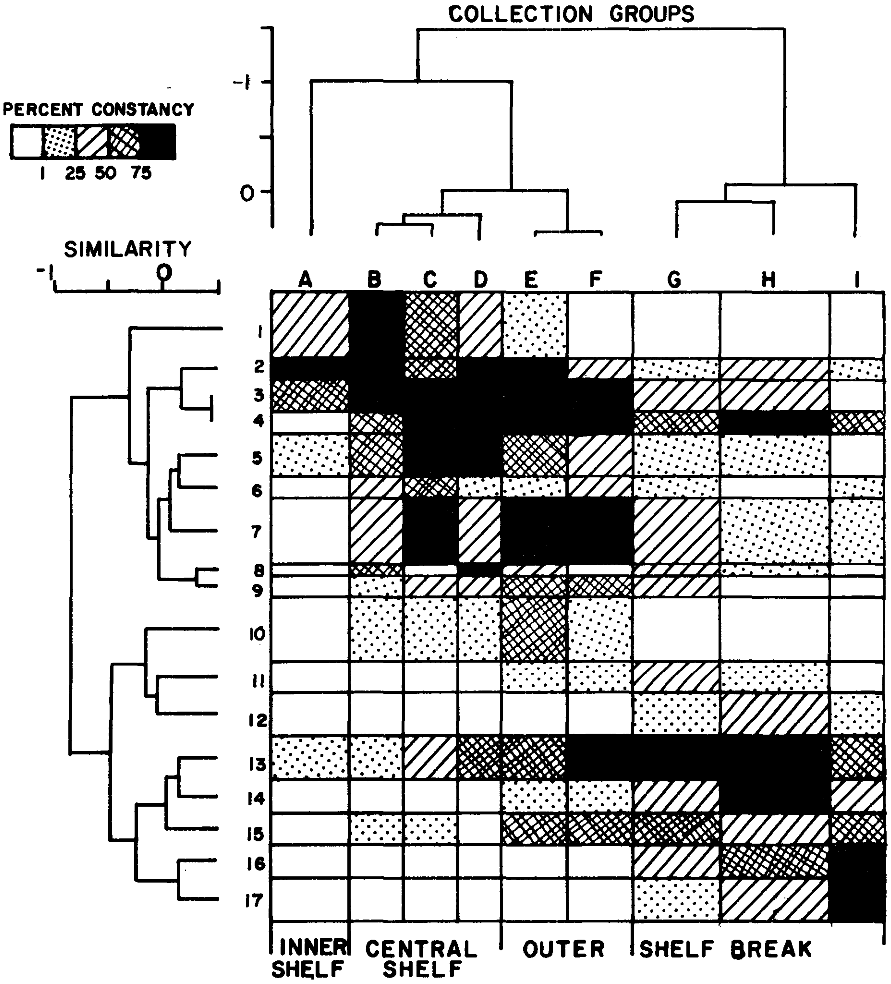

Figure 6-101. Normal and inverse classification hierarchies and nodal constancy for site-species group coincidence based on all anchor dredge collections.

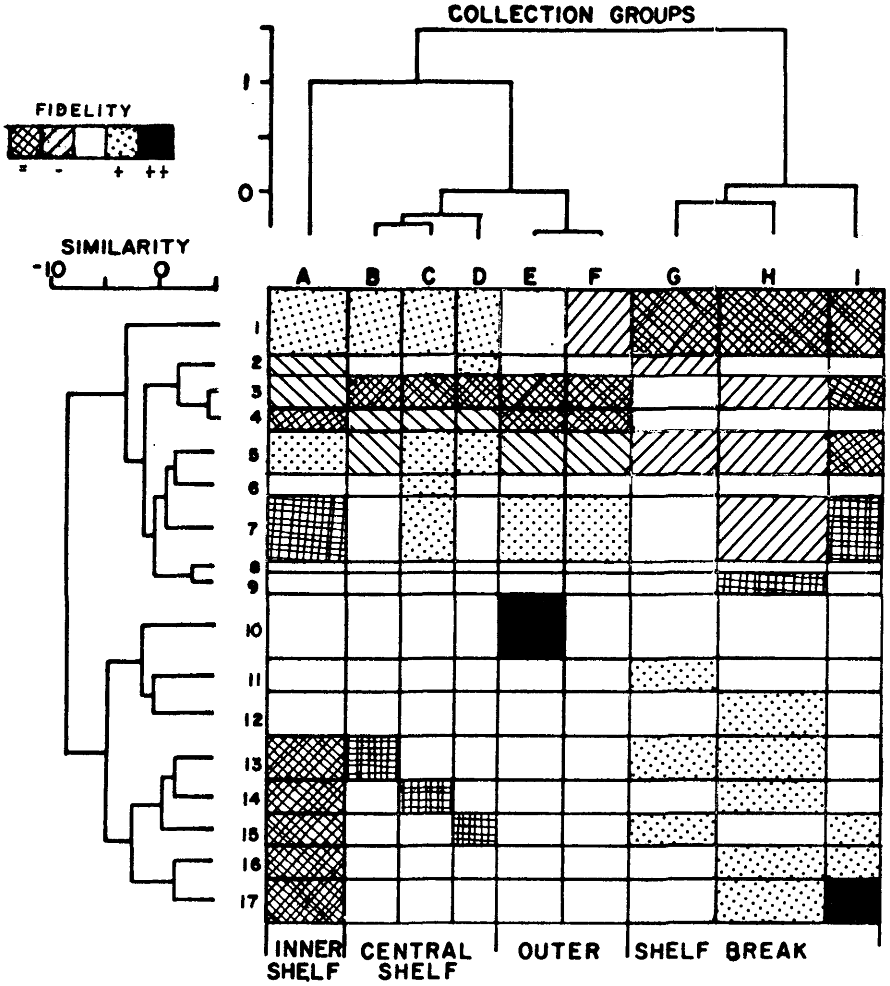

Figure 6-102. Nodal fidelity for classification of megabenthos from anchor dredge samples as in Figure 6-101. Values indicate significant and highly significant fidelity and negative fidelity.

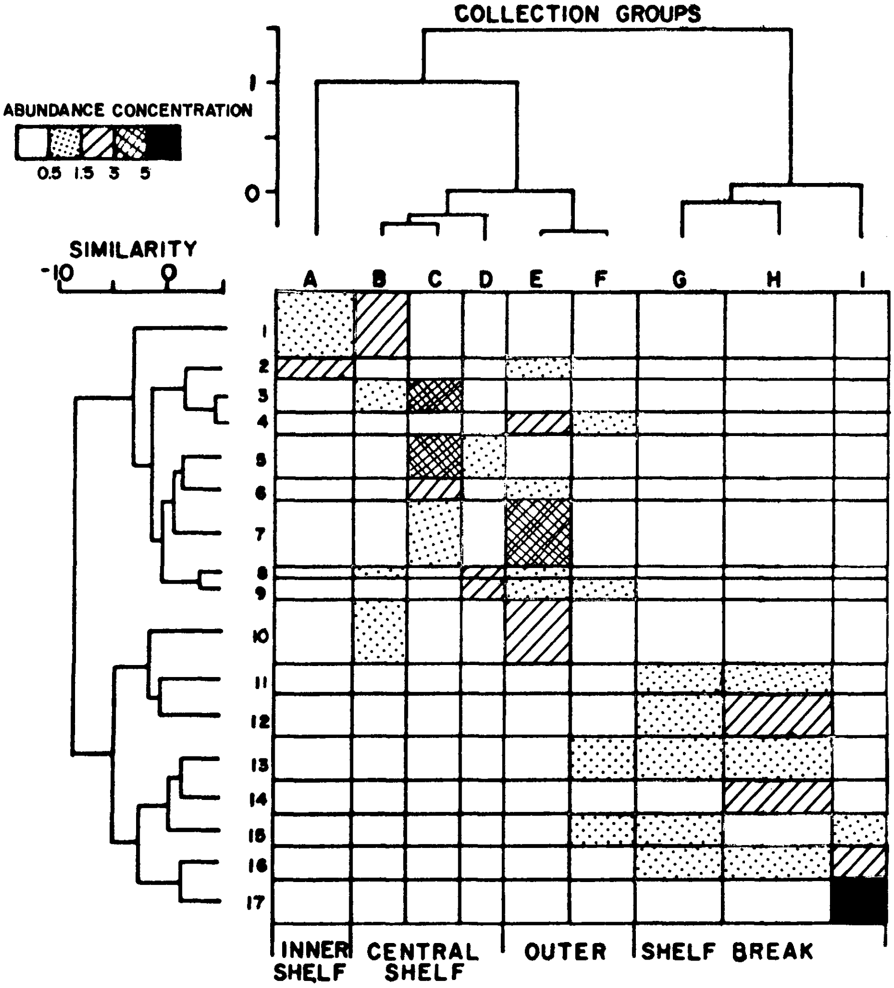

Figure 6-103. Nodal abundance concentration for classification of megabenthos from anchor dredge samples as in Figure 6-101.

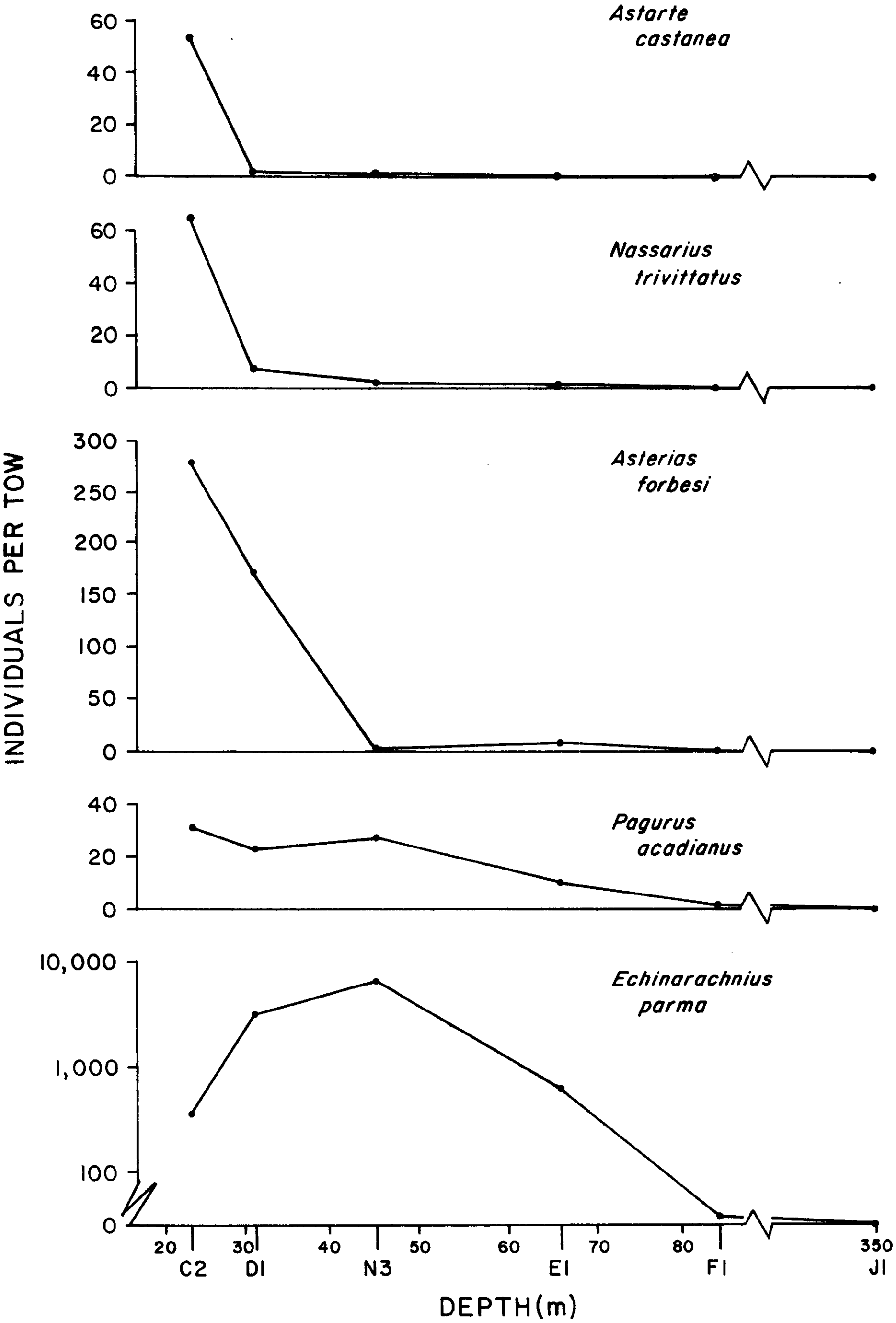

Figure 6-104. Cross shelf patterns of distribution of dominant megabenthos based on abundances averaged over 8 seasons.

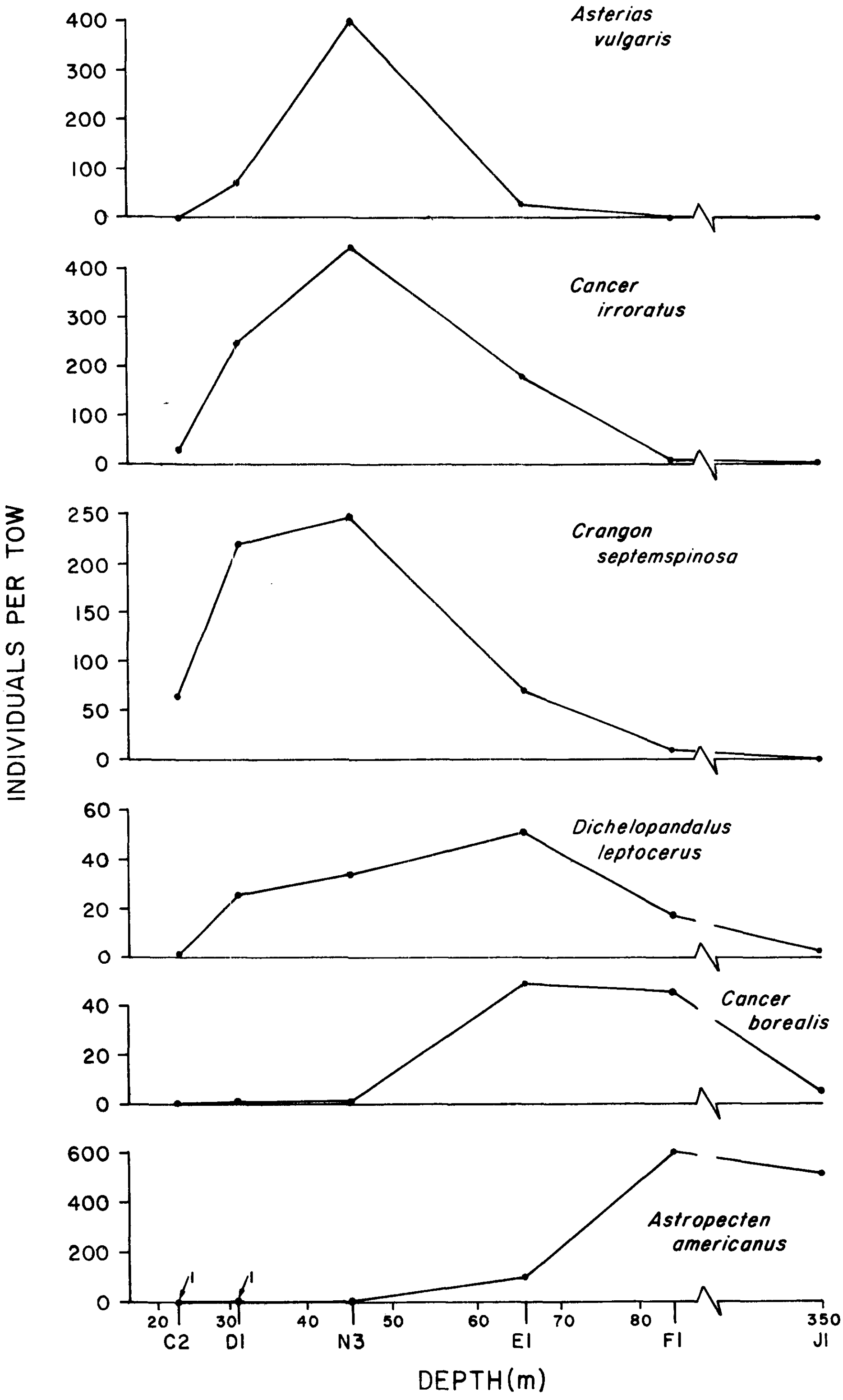

Figure 6-105. Cross-shelf patterns of distribution of dominant megabenthos based on abundance averaged over all 8 seasons.

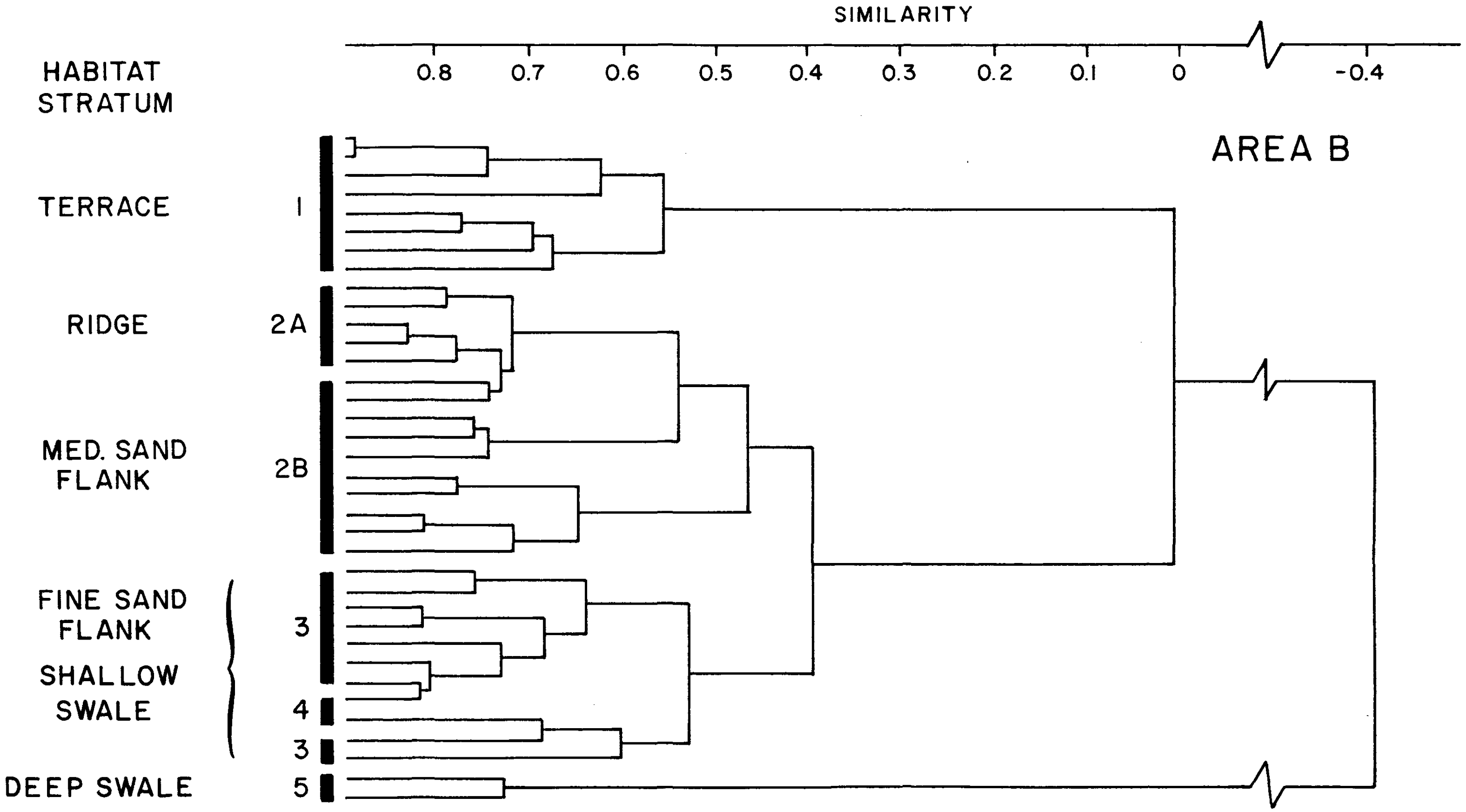

Figure 6-106. Classification hierarchies resulting from agglomeration of collections of megabenthos from habitat delineation study of Area B. Habitat strata recognized on the basis of sediments and macrobenthos are indicated.

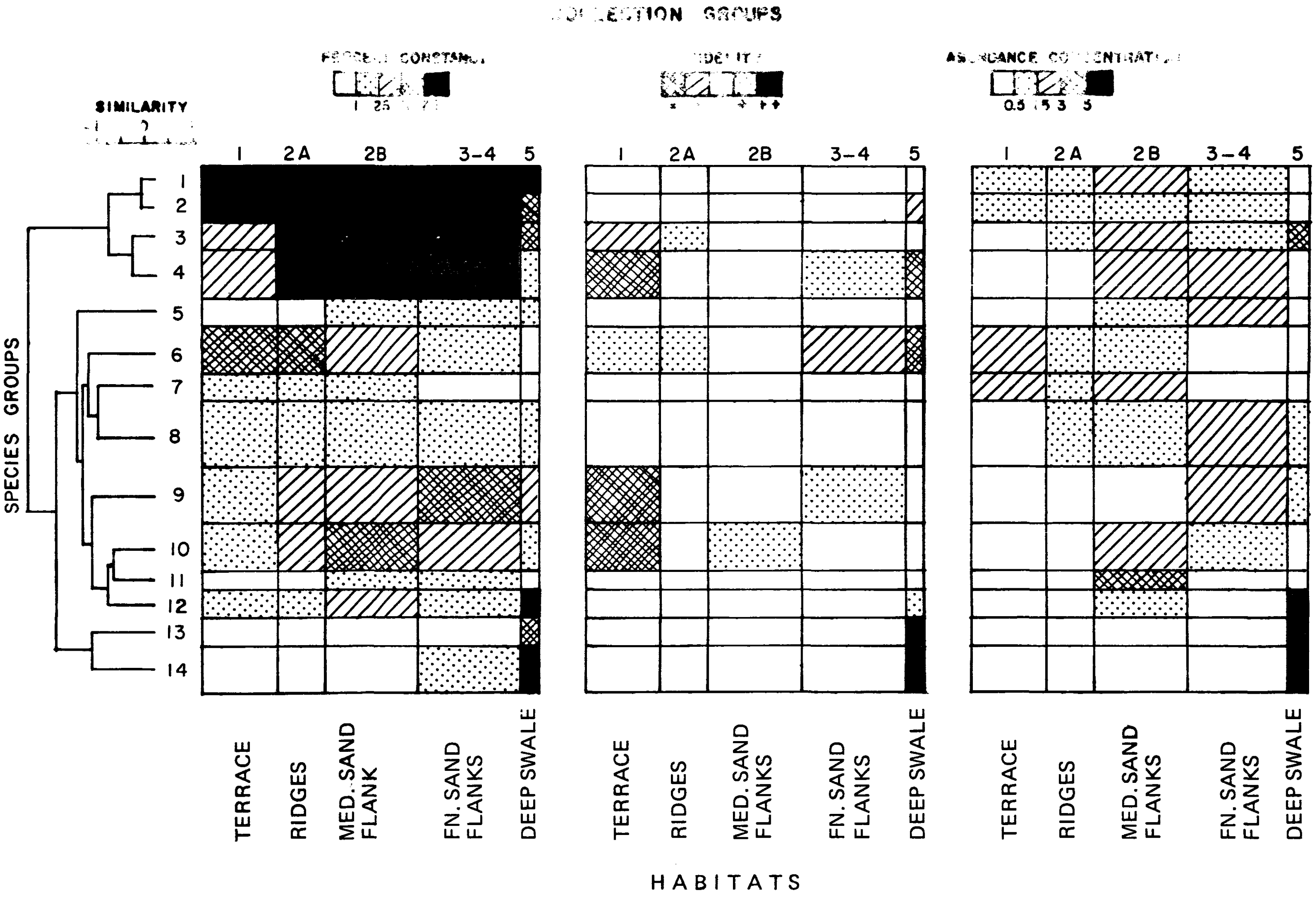

Figure 6-107. Hierarchical classification of species groups of megabenthos and other nodal statistics in topographic habitat strata, Area B.

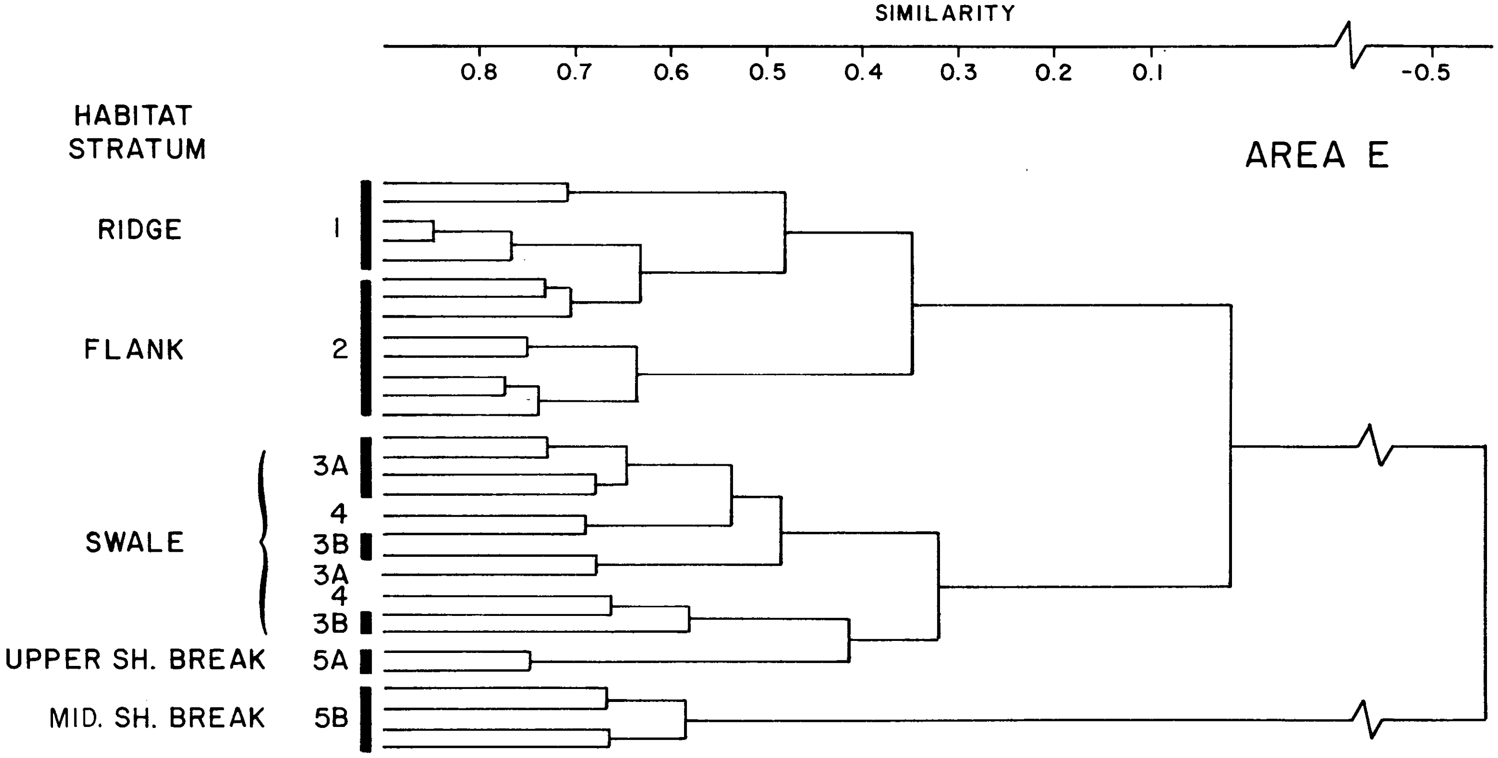

Figure 6-108. Classification hierarchies resulting from agglomeration of collections of megabenthos from habitat delineation study of Area E. Habitat strata recognized on the basis of sediments and macrobenthos are indicated.

Species in Group 1 were greatly affected by hypoxic conditions. Recolonization patterns caused post hypoxia increases for many of these species resulting in high fidelity, abundance concentration and constancy in these C2 collections (Group A). Some Group 1 species are typically found near shore along ocean beaches (Ovalipes ocellatus) and higher salinity sandy embayments (Ensis directus, Libinia dubia, Asterias forbesi). Others are more characteristic of dynamic sandy bottoms of the inner shelf (Spisula solidissima, Astarte castanea, Nassarius trivittatus). Group 6 species, although exhibiting higher constancy at inner and central shelf sites, were more frequent and abundant before the hypoxia (group B and E). Species in Group 6 were generally rarer than Group 1 species.

The widespread abundance of species in Group 2 is indicated by the high group constancy from the inner shelf through the shelf-break. Group 2 is composed of natant (Crangon septemspinosa, Dichelopandalus leptocerus) or otherwise mobile benthic decapods (Cancer irroratus), an ubiquitous arenaceous foraminiferan (Astrorhiza limicola), echinoderms (Asterias forbesi, Echinarachnius parma) and molluscs (Pleurobranchaea tarda). Many of these were numerically important at several sites across the continental shelf. Less abundant species more restricted to the central and outer shelf are included in Group 3. Species in both groups 2 and 3 display moderate fidelity and concentration of abundance at central and outer shelf sites. The monotypic Group 10 (Molgula arenata) was regularly numerous and lacks fidelity for any particular site group although it shows very slight abundance concentration at central shelf (Group D) and shelf-break (groups H, I, J) habitats.

Species in groups 4 and 5 were found primarily on the central and outer continental shelf and include the commerically important ocean quohog (Arctica islandica) and sea scallop (Placopecten magellanicus).

The crab Cancer borealis and the sea star Astropecten americanus comprise Group 11 and, although constant in all collection groups except B and C, were relatively faithful to outer shelf, shelf-break and upper slope areas. These species were also more abundant in shelf-break collections.

Negative or highly negative fidelity for the inner and central shelf is displayed in groups 9 and 13. Both species groups show very high concentration of abundance and constancy in collection group H (Station I1). Species group 9 was particularly characteristic of Station I1 as exemplified by a highly significant chi square statistic (Figure 6-98). The bivalve Clyclopecten nannus which was found only in collections from I1 was primarily responsible for this phenomenon. Species in groups 9 and 13 apparently prefer the coarser sediments found at Station I1.

Station A1 collections at the shelf-break showed significantly high fidelity of species in groups 8 and 14. Amphioplus macilentus, *Cadulus agassizi*, and *Eualus pusiolus* were largely restricted to outer shelf stations. Species group 14 contains the more numerous shelf-break species and these show an even more striking avoidance of all inner, central, and, to some extent, outer shelf zones. Unlike shelf break group 8 species, group 14 species were somewhat selective for the upper slope. The characteristic group 14 species included, in part, very common decapods, *Euprognatha*, *Bythocaris*; echinoderms, *Sclerasterias tanneri*, and *Amphilimna olivacea*; a mollusc, *Pandora inflata*; and a solitary coral *Dasmosmilia lymani*. This group exhibits a narrow bathymetric range that may be linked to the relatively warm, more thermally stable, slope water which bathes the shelf break. Species in Group 12 were also characteristic and numerous at shelf break stations where they display significant fidelity but no striking concentration of abundance.

Species group 15 consists of the sipunculan *Phascolion strombi* and the gastropod *Colus pygmaeus* which avoid the inner shelf (groups A and B) and the central shelf (Group C). These species have a wide cross-shelf distribution as indicated by variable constancy in the remaining collection groups. The similarity in the distribution and abundance of these two species is a reflection of use of *Colus pygmaeus* shells by *Phascolion strombi*. *Phascolion* inhabitation of other gastropod shells (e.g. *Nassarius trivittatus* and *Solariella obscura*) and occasionally serpulid polychaete tubes coupled with the scanty *Colus pygmaeus* populations on the central shelf are responsible for the reduced occurrence of Group 15 in this zone.

The remaining species groups were constant, faithful, and of concentrated abundance on the continental slope. These groups comprise over 25 percent of the total species included in the analyses and serves to emphasize the uniqueness of this habitat relative to shelf and shelf break.

Anchor Dredge Collections. Nine groups are interpreted from clustering of the anchor dredge collections (Table 6-21). The four main agglomerations represent: a) collections from the inner shelf station C2 (Group A); b) collections from the central shelf stations D1 and N3 (groups B, C, and D); c) most collections from the outer shelf stations B1 and E1 (groups E and F); and d) collections principally from the shelf-break stations I1, F1, and A1 (groups G, H, and I). Anchor dredge samples were not collected at the slope station J1, thus there is no slope assemblage paralleling the unique assemblage collected by SBT at J1. Group A contained all collections from the inner shelf station C2, which were quite dissimilar from the collections at other stations. Collections taken before and after hypoxic stress at C2 were different but more similar to each other than to collections from other stations. Groups B and C defined the central shelf assemblage and Group D represented that assemblage following hypoxia at N3, which occurred at this station in the late summer. The anchor dredge collections from outer shelf stations

Table 6-21. Allocation of collection groups selected from numerical classification of megabenthos collected by anchor dredge.

	Season						
	1976				1977		
Station	Winter	Spring	Summer	Fall	Winter	Spring	Summer
C2	A	A	A	A	A	A	A
D1	C	C	B	B	B	B	B
N3	C	C	C	D	D	D	D
B1	F	E	E	E	E	E	E
E1	F	F	F	G	G	G	F
I1	G	G	G	F	G	H	G
F1	H	H	H	H	H	H	H
A1	I	I	H	I	I	H	I

Table 6-22. Species groups selected from numerical classification of megabenthos collected by anchor dredge.

Species Group 1

Crangon septemspinosa
Nassarias trivittatus
Asterias forbesi
Tellina agilis
Spisula solidissima
Libinia dubia

Species Group 2

Astarte castanea
Cerianthidae

Species Group 3

Ensis directus
Cancer irroratus
Echinarachnius parma

Species Group 4

Phascolion strombi
Astrorhiza limicola

Species Group 5

Cerastoderma pinnulatum
Pagurus acadianus
Asterias vulgaris
Pandora gouldiana

Species Group 6

Lunatia heros
Pitar morrhuana

Species Group 7

Solariella obscura
Lyonsia hyalina
Aphrodita hastata
Colus pygmaeus
Arctica islandica
Lunatia triseriata

Species Group 8

Pleurobranchaea tarda

Species Group 9

Crucibulum striatum
Placopecten magellanicus

Species Group 10

Dichelopandalus leptocerus
Stereoderma unisemita
Dendroda carnea
Pagurus arcuatus
Axiognathus squamata
Anomia simplex

Species Group 11

Crenella glandula
Cyclopecten nanus
Rossia tenera

Species Group 12

Calliostoma bairdii
Euprognatha rastellifera
Sclerasterias tanneri
Yoldia sapotilla

Species Group 13

Astarte undata
Cyclocardia borealis
Astropecten americanus
Molgula arenata

Species Group 14

Nothria conchylega
Cancer borealis
Epizoanthus paguriphilus

Table 6-22. (Concluded)

Species Group 15

Astarte crenata subequilateria
Polinices immaculatus
Havelockia scabra

Species Group 16

Pontophilus brevirostris
Amphilimna olivacea
Pandora inflata

Species Group 17

Dasmosmilia lymani
Lucinoma filosa
Amphioplus macilentus
Periploma fragile

(groups E and F) were more discretely different from the central shelf collections than were SBT collections. Furthermore, the grouping of collections from shelf-break stations was not discrete by site as was the classification of SBT collections. The classification of the 59 species included in the analysis is interpreted at the 17 group level using nodal anlyses. These nodal diagrams (Figures 6-101 to 6-103) also show clear cross-shelf patterns of distribution. Many of the species responsible for delineating bathymetric habitats based on SBT collections show similar cross-shelf distributions indicated by their classification based on anchor dredge (AD) collections, although there are some variations.

Species showing fidelity for the inner and mid-shelf regions are included in AD Group 1. Several are the same as those found in SBT Group 1 (i.e. Nassarius trivittatus, Spisula solidissima, Asterias forbesi, Libinia dubia). Also included were the more widely distributed shrimp, Crangon septemspinosa, which was a member of SBT Group 2, and the bivalve Tellina agilis, which was poorly sampled by the SBT and therefore not included in the classification of SBT data. Members of this group were moderately to highly constant on the inner and central shelf and exhibited some degree of abundance concentration in collection AD groups A and B. Species in Group 2 (Astarte castanea and cerianthid anemones) were widely distributed in the AD collections but showed a slight abundance concentration in inner and outer shelf collections (groups A and E).

Other more or less ubiquitous species that were characteristic of the central and/or outer shelf include those in groups 3-8 and 10. Species in groups 3 and 7 showed an affinity for both central and outer shelf sites whereas those in groups 5, 6, and 8 were more restricted to the central shelf (Group C). Outer shelf species are indicated by high fidelity in collection group E and include species in Group 10. Species in Group 4 showed moderated fidelity for both outer shelf collections groups (E and F).

Species group 9, consisting of the commercially important sea scallop, Placopecten magellanicus, and its commensal, the gastropod Crucibulum striatum, showed highly negative fidelity for shelf-break collection group H. These species were most frequent and abundant on the central and outer shelf showing a similar pattern to that found based on SBT collections.

The remaining groups (11-17) contained characteristic shelf-break species. Groups 13-17 in particular were significantly infrequent at inner shelf stations and are moderately (13-15) to highly (17) selective for the shelf-break. The latter group contains the solitary coral Dasmosmilia lymani which also characterized the SBT shelf-break collections from Station A1.

The zonation schemes resultant from classification of macrobenthos collections and megabenthos collections by SBT and anchor dredge are all in close agreement. Inner, central, and outer shelf, shelf-break and slope assemblages can be recognized in the bathymetric coenocline. The classification based on SBT collections indicated that consistent differences existed in the larger epibenthos at shelf-break stations, i.e. SBT collections from A1, F1, and I1 were grouped discretely. The differences among collections of larger infauna were apparently less consistent, as indicated by the distribution of anchor dredge collections from shelf-break stations into several groups. However, the distribution of central and outer shelf assemblages was more consistent based on anchor dredge collections.

Bathymetric Distribution of Dominant Megabenthos. In addition to the classificatory analyses of large scale distributional patterns, examination of the bathymetric (cross-shelf) distributions of individuals species further elucidates distributional patterns of megabenthos. Grand mean abundances over the eight seasonal sampling periods are plotted from six stations along the bathymetric gradient represented from stations C2 to J1 for dominant megabenthos in Figures 6-104 and 6-105. Only data from the first three or four sampling periods were used to compute these respective means for stations C2 and N3, which were affected by hypoxia.

Two inshore species were primarily restricted to inner shelf station C2, *Astarte castanea* and *Nassarias trivittatus*, while another, *Asterias forbesi*, showed a steady decline in abundance through central shelf stations D1 and N3. All three were virtually absent beyond the central shelf region. *Pagurus acadianus*, which reached maximum abundances on the inner and central shelf, was found in low numbers on the outer shelf (Station E1) and was rarely, if ever, encountered at greater depths.

A number of widely distributed, more eurybathic species showed peak abundances at central shelf station N3. The generally Gaussian cross-shelf abundance curves for *Asterias vulgaris*, *Echinarachnius parma*, *Cancer irroratus*, and *Crangon septemspinosa* are similar but reflect minor differences in bathymetric abundance patterns. *Asterias vulgaris* was very numerous at moderate depths (Station N3), but its abundance declined sharply both shoreward and seaward. *Echinarachnius*, *Cancer irroratus*, and *Crangon* displayed a more gradual decline from Sation N3 throughout the inner and outer shelf region. All four species exhibited very low abundances or were absent at the deeper shelf break (F1) and slope (J1) stations.

Dichelopandalus leptocerus, although widely distributed, was most numerous at outer shelf station E1. *Cancer borealis* was similarly more abundant at Station E1 as well as at the deeper shelf break station F1. The restriction of *C. borealis* to the outer shelf and shelf break reflects the phenomenon of tropical submergence displayed by this species in the more southern extent of its range (Williams 1974).

A dominant species showing preference for the shelf-break and upper slope stations was *Astropecten americanus*. This species had its most suitable habitat at the shelf break (Station F1) where specimens were considerably larger, although only slightly more numerous, than on the upper slope (Station J1). The small size of *Astropecten* at J1 during all eight sampling periods indicated less than optimal conditions for this species on the upper slope.

Although the bathymetric distributions of species along this transect clearly show cross-shelf abundance patterns, these data should be interpreted with caution. An analysis of ridge and swale topography on the outer shelf (see section on medium scale distribution patterns) showed that several characteristically inshore species can also be found on the coarser sediment ridges of the outer continental shelf.

Medium Scale Patterns of Distribution

Habitat delineation studies were conducted in parallel with those described for macrobenthos in subsections of areas B and E. The same *a priori* stratification scheme was employed and 35 randomly allocated SBT tows were made in area B and 30 in area E during fall 1976. Three day and three night tows were made in each *a priori* stratum in order to account for diel movements of some species. The only species to show consistent differences in day and night tows was the small squid *Rossia tenera*. Significant numbers of *Rossia* were only caught in day tows as the squid evidently leaves the bottom at night to feed.

Numerical classification (log-transformation, Bray-Curtis similarity, and flexible sorting for normal and inverse analyses) was performed on complete data sets. These classifications were related to the habitats delineated on the basis of distributions of macrobenthos and sediments as described in the previous section on macrobenthos.

Area B. The classification of collections of megabenthos agreed very closely with the classification of habitat strata (based on macrobenthos) from which the collections were taken (Figure 6-106). The deep swale assemblage was most dissimilar and collections from the terrace were clearly separated from those below. Collections from ridges (Habitat 2A) and medium sand flanks (Habitat 2B) were sorted together and overlapped to a degree. Collections from the fine sand flanks (Habitat 3A), erosional flanks (Habitat 3B), and shallow swale (Habitat 4) were poorly differentiated and thus grouped in subsequent analysis.

The numerical classification of species is interpreted at the 14 group level, with the assistance of nodal analyses (Table 6-23, Figure 6-107). Species in Group 6 were more frequent and abundant in the

Table 6-23. Species groups selected from numerical classification of megabenthos collected in habitat delineation study of Area B.

Species Group 1

Cancer irroratus
Asterias vulgaris
Echinarachnius parma

Species Group 2

Dichelopandalus leptocerus
Crangon septemspinosa
Astrorhiza limicola

Species Group 3

Aphrodita hastata
Solariella obscura
Cancer borealis

Species Group 4

Pleurobranchaea tarda
Leptasterias tenera
Colus pygmaeus
Pagurus acadianus
Citharichthys arctifrons

Species Group 5

Musculus niger
Havelockia scabra
Crenella glandula

Species Group 6

Nassarius trivitattus
Pandora gouldiana
Ensis directus
Stereoderma unisemita
Astarte castanea

Species Group 7

Edwardsia elegans
Axiognathus squamata
Spisula solidissima

Species Group 8

Anomia simplex
Amphioplus macilentus
Pisodonophis cruentifer
Lunatia heros
Liparis inquilinus
Macrozoarces americanus
Caridion gordoni

Species Group 9

Crucibulum striatum
Strongylocentrotus droebachiensis
Buccinum undatum
Placopecten magellanicus
Rossia tenera
Pagurus arcuatus
Henricia sanguinolenta

Species Group 10

Arctica islandica
Cerastoderma pinnulatum
Lunatia triseriata
Lyonsia hyalina
Asterias forbesi

Species Group 11

Polinices immaculatus
Colus stimpsoni

Species Group 12

Cyclocardia borealis
Pontophilus brevirostris
Astropecten americanus

Species Group 13

Nothria conchylega
Molgula arenata
Modiolus modiolus

Table 6-23. (Concluded)

Species Group 14

Astarte crenata subequilatera
Hyas coarctatus
Astarte undata
Lepophidium cervinum
Calliostoma bairdii

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coarser sediments of the terrace and ridge habitats and include species characteristic of the inner and central shelf (e.g. the molluscs *Astarte castanea* and *Nassarius trivittatus*). Group 7 species were very rare but were only found in the coarser sediments of the terrace, ridges, and medium sand flanks.

Species in groups 1-4 were very common, widely distributed, and abundant. Those in groups 1 and 2 were extremely ubiquitous but were not abundant in the deep swale (except *Cancer irroratus*). Species in groups 3 and 4 were widely distributed but were less abundant than those in groups 1 and 2. They were rare and never abundant on the terrace. All Group 4 species were rare in the deep swale but the crab *Cancer borealis*, a member of Group 3, had its peak abundance in the deep swale in comparison with *Cancer irroratus* which was abundant in all habitats, but in particular in Habitat 2B.

Species in groups 8, 9, and 10 were widely occurring except on the terrace but most were uncommon and never abundant. Group 8 species were very rare throughout the area with no discernible pattern of occurrence. Group 9 species were moderately faithful and were an average of more than 2.5 times more abundant in habitats 3 and 4 than overall. Species in Group 10 were moderately frequent in all habitats except the extremes of the terrace and deep swale. Several (e.g. *Lyonsia hyalina* and *Cerastoderma pinnulatum*) were more abundant in Habitat 2B than elsewhere. Species in groups 5 and 11 were very rare and essentially restricted to flank habitats.

Species in groups 12, 13, and 14 showed a strong preference for the deep swale habitat. Species in Group 12 were occasionally found in other habitats but were much more abundant in the deep swale (the sea star *Astropecten americanus* in particular). Species in groups 13 and 14 were only found in the two collections from the deep swale but were not abundant. Species of the latter three groups are mostly shelf-break species at their inner limits of their bathymetric distribution in the deep swales of the outer shelf.

Area E. The classification of collections of megabenthos from Area E also agreed remarkably well with the classification of the habitats from which they were collected (Figure 6-108). Collections from the ridge and flank habitats were clearly gradational, and several Habitat 2 collections were grouped with those from Habitat 1. Collections from the mid-shelf break (Habitat 5B) were quite discrete from the others. However, collections from various swale habitats (3A, 3B, and 4) and from the upper shelf-break habitat (5A) were distinctly allocated. Collections from ridge (1), flank (2), swale (3 and 4), upper shelf-break (5A), and mid-shelf break (5B) habitats were recognized in subsequent analyses.

The numerical classification of species is interpreted at the 16 group level using nodal analyses (Table 6-24, Figure 6-109). As with

Table 6-24. Species groups selected from numerical classification of megabenthos collected in habitat delineation study of Area E.

Species Group 1

Pleurobranchaea tarda
Cancer borealis
Astropecten americanus

Species Group 2

Cancer irroratus
Asterias vulgaris

Species Group 3

Dichelopandalus leptocerus
Crangon septemspinosa

Species Group 4

Astrorhiza limicola
Echinarachnius parma

Species Group 5

Pagurus acadianus
Leptasterias tenera
Aphrodita hastata
Placopecten magellanicus
Rossia tenera
Citharichthys arctifrons
Cyclocardia borealis

Species Group 6

Crucibulum striatum
Pagurus arcuatus
Nothria conchylega
Henricia sanguinolenta
Astarte undata

Species Group 7

Solariella obscura
Lyonsia hyalina
Colus pygmaeus
Astarte castanea
Cerastoderma pinnulatum

Species Group 8

Ensis directus
Havelockia scabra

Species Group 9

Lunatia triseriata
Stereoderma unisemita
Anomia squamula
Amphioplus macilentus
Modiolus modiolus

Species Group 10

Buccinum undatum
Dendroda carnea
Hyas coarctatus
Ophiopholis aculeata

Species Group 11

Ascidia callosa
Liparis inquilinus
Asterias forbesi
Pisodonophis cruentifer
Arctica islandica

Species Group 12

Strongylocentrotus droebachiensis
Axiognathus squamata
Lunatia heros
Anomia simplex

Species Group 13

Bythocaris nana
Sclerasterias tanneri
Hippoglossina oblonga

Species Group 14

Caridion gordoni
Amphilimna ovalacea
Nassarius trivitattus
Pitar morrhuana

Table 6-24. (Concluded)

Species Group 15

Cyclopecten nanus
Pandora gouldiana
Astarte crenata subequilatera
Munida iris iris

Species Group 16

Pontophilus brevirostris
Molgula arenata
Calliostoma bairdii
Pandora inflata
Euprognatha rastellifera
Polinices immaculatus

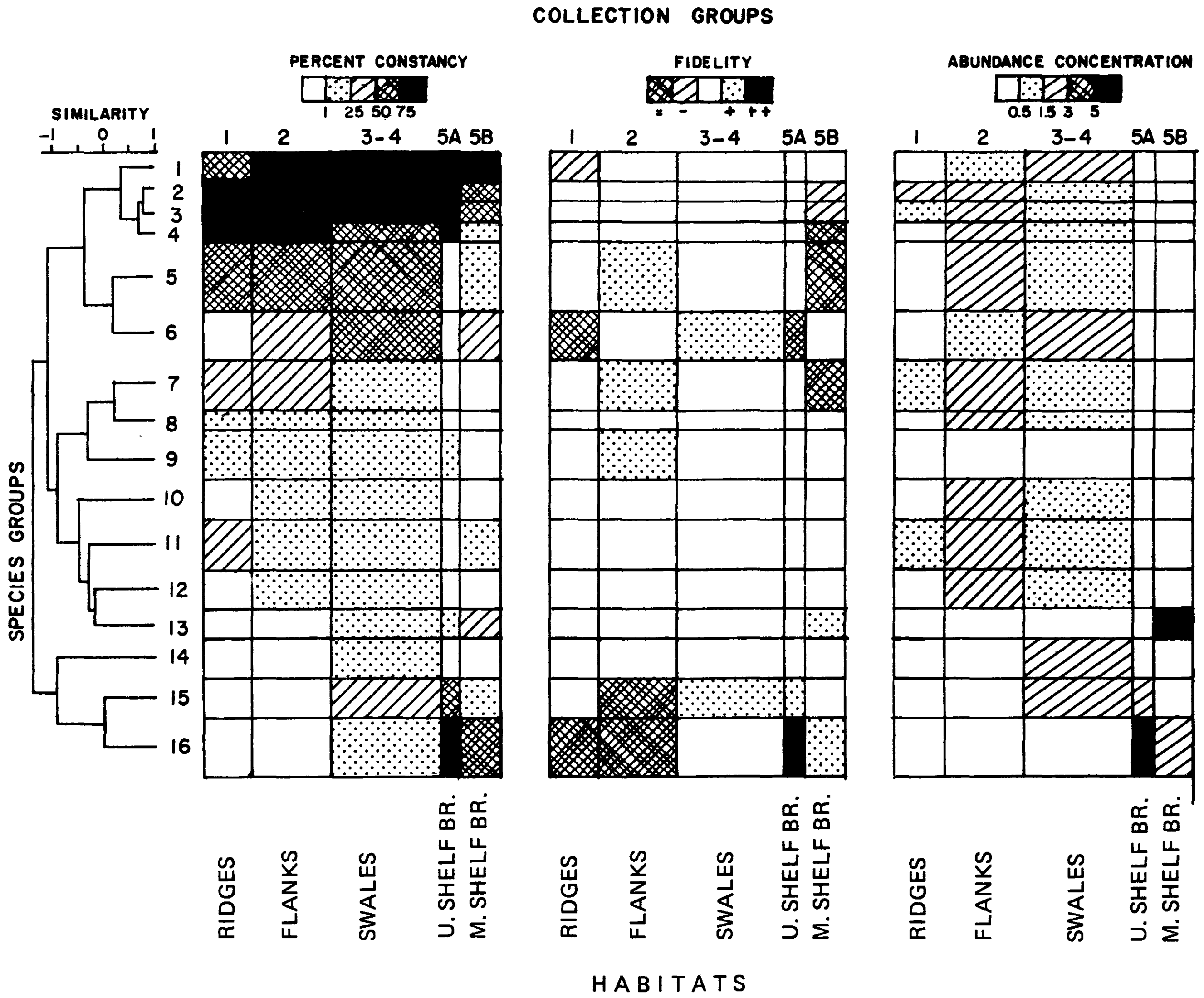

Figure 6-109. Hierarchical classification of species groups of megabenthos and nodal statistics in topographic habitat strata, Area E.

the classification of species based on Area B collections, groups 1-4 include the widely distributed dominant species. Each of these except Astropecten americanus is also included in groups 1-4 recognized from Area B. Groups 2-4 include species typically found broadly over the continental shelf. They were generally much less frequent and abundant in the shelf-break habitat (5A and 5B). On the other hand, species in Group 1, which includes the typical outer shelf and shelf-break species, Astropecten americanus and Cancer borealis, were rare on the ridges and most abundant in the swales.

Species in groups 5 and 6 were also widely distributed but were less frequent and abundant than the previous species. Members of Group 5 were very rare on the mid-shelf-break and were most abundant in the flank habitat. Group 6 species were absent from the dynamic clean sands of the ridges and the upper shelf-break and were most abundant in swales.

Species in groups 7-12 were infrequent in any habitat and were almost completely absent from the shelf-break habitats (5A and 5B). All groups showed abundance concentration in the flank habitat. Some groups consisted of species reasonably common in the ridge habitat (groups 7 and 11) while the members of others were not found on ridges at all (groups 10 and 12).

Species in groups 13-16 were virtually absent from the ridges and flanks but variously showed some preference for swale and/or shelf-break habitats. Group 13 was characteristic of the mid-shelf-break, Group 14 was restricted to swales; Group 15 was found in swales and the upper shelf-break, and Group 16 characterized the upper- and, to a lesser degree, the mid-shelf-break.

In summary, the distribution of megabenthos in both areas B and E represented a transitional mozaic of assemblages characteristic of central shelf, those characteristic of the outer shelf, and those characteristic of the shelf-break. The coarser, more dynamic sediments of the terrace in Area B and the ridge habitat in both areas supported megabenthic assemblages similar to that characteristic of the central shelf fixed stations (D1 and N3). The flanks and shallow swales were populated by assemblages similar to those characteristic of the outer shelf habitat (such as at E1 and B1). The deeper swales supported assemblages which were similar to the outer shelf community but with some faunal elements of the shelf-break community. Finally as the edge of the shelf is approached, the assemblages become more clearly like those characterizing the shelf-break (cf. fixed stations A1, I1, and F1).

Species Diversity

Values of species diversity indices are summarized by station in Figures 6-110 and 6-111 for SBT and anchor dredge collections,

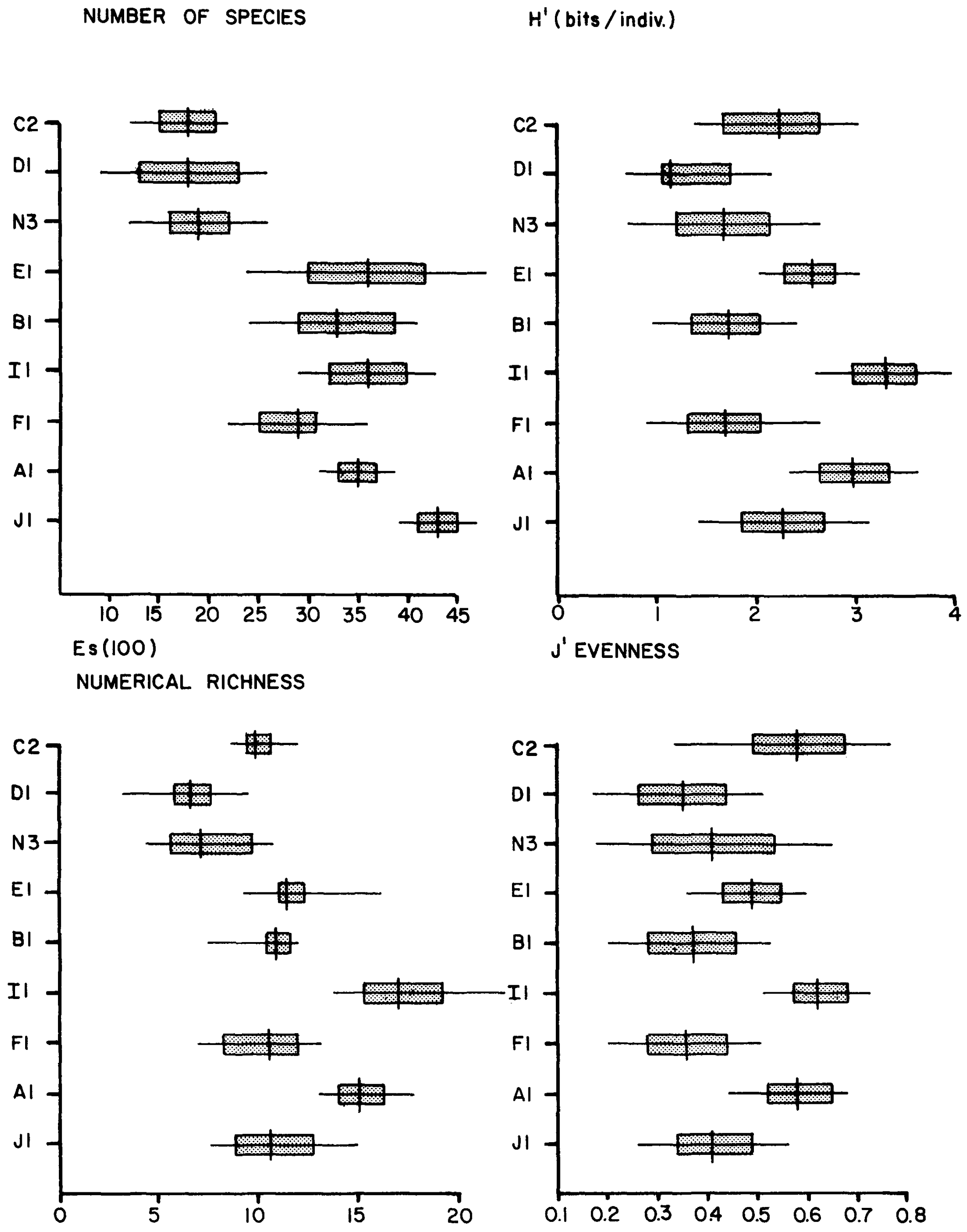

Figure 6-110. Distribution of species richness, evenness, and Shannon diversity of megabenthos (small biology trawl collections) by station. Horizontal lines represent ranges, bars represent mid-ranges, and vertical lines represent medians.

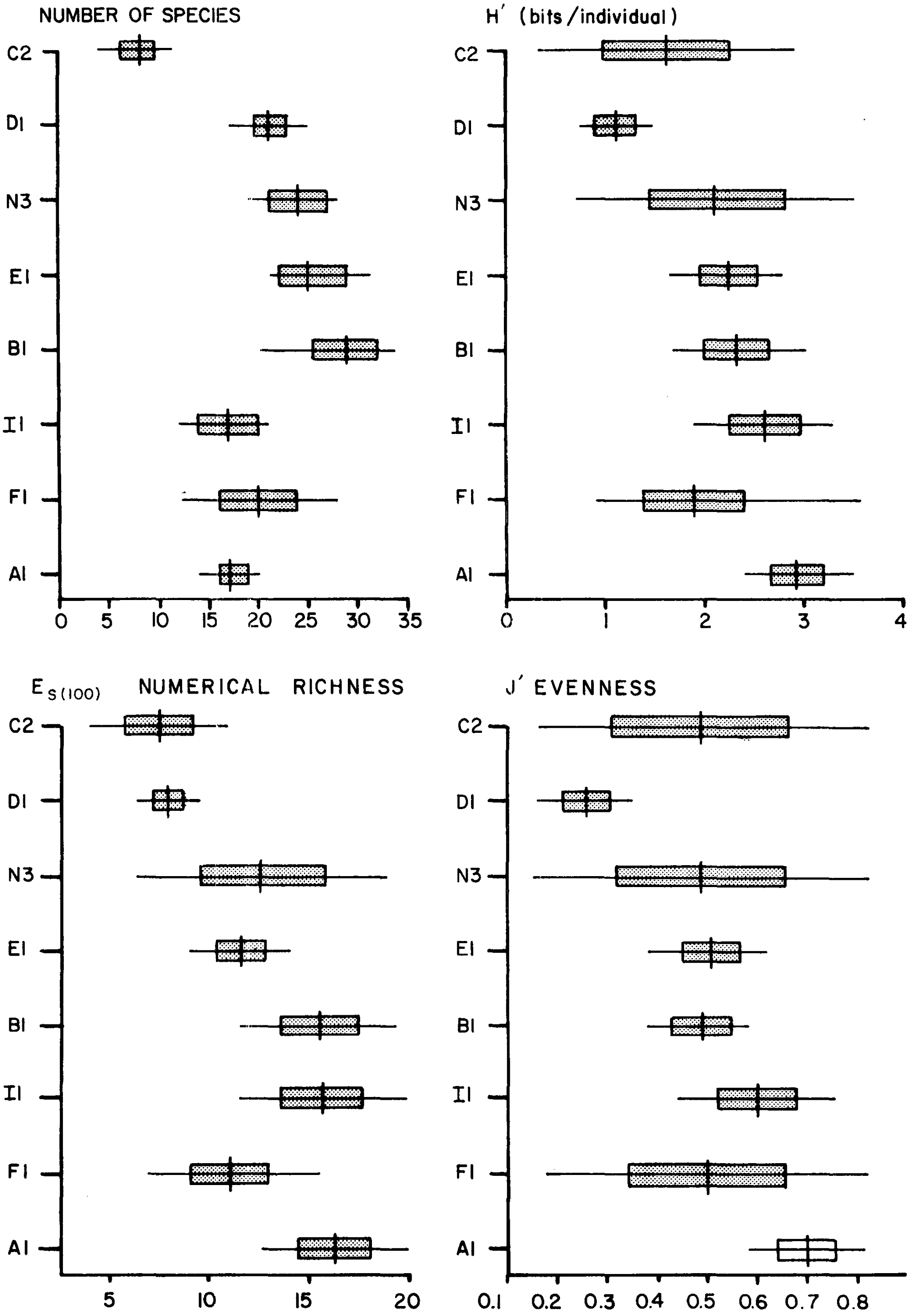

Figure 6-111. Distribution of species richness, evenness and Shannon diversity of megabenthos (anchor dredge collection) by station. Horizontal lines represent ranges, bars represent mid-ranges, and vertical lines represent medians.

respectively (see also Appendix 6-E). No attempt has been made to adjust for differences in sampling effort between the two different samplers.

Shannon diversity (H') of SBT collections was lowest at central shelf stations D1 and N3 due to the very low evenness compared to those from inner shelf station C2 and the much lower richness compared to deeper stations. Species richness expressed both as number of species collected and rarefied numerical richness ($E_{S(500)}$) was nearly uniform over the inner and central shelf. On the other hand, richness of anchor dredge collections increased from the inner shelf station C2 to the central shelf stations, however, lowered evenness depressed the Shannon diversity of the latter collections.

Species richness of SBT collections showed a substantial increase from the central to the outer shelf from values of generally less than 20 species collected to generally more than 30 species (of <15 species/500 individuals to >20 species/500 individuals). This resulted in higher Shannon diversity except where it was depressed by low species evenness, i.e. stations B1 and F1. However, anchor dredge collections did not show a consistent increase in richness from the central to the outer shelf. Anchor dredge collections from stations E1 and F1 were of comparable richness to those from the central shelf. Anchor dredge collections from Station B1 were considerably richer, however, and those from A1 and I1, although yielding numbers of species comparable with the central shelf stations, contained fewer individuals and thus, had higher numerical richness.

SBT collections from the slope station J1 were considerably richer in species than those from the shelf-break, however, because of lowered evenness, H' and numerical richness values were not as high as at some of the shelf-break stations, i.e. A1 and I1.

In all habitats except the central shelf, the SBT caught more species than the anchor dredge, however, when collections from both samplers are rarefied to a common 100 individuals, the numerical richness of anchor dredge collections is greater at the central and outer shelf stations and roughly equivalent at the shelf break stations.

Temporal Trends

Assessment of seasonal fluctuations in abundance of megabenthos is made difficult by several factors: a) the high variability in catch from replicate to replicate and collection period to collection period due to the semi-quantitative nature of dredge sampling and the apparently patchy nature of distributions; b) the longevity of many species of megabenthos which has the result that resident adult populations dominate and mask recruitment of juveniles; c) the potential migration of some more motile forms; and d) the disruptive effects of the hypoxia of the summer of 1976. Time and resources have not permitted the analyses of size-frequency distributions which would clarify the population dynamics of dominant megabenthos.

Fluctuations in the mean catch of dominant species of megabenthos are represented in Figures 6-112 to 6-117 for all the stations (except J1) which were unaffected by mortalities attributable to hypoxia. Few clearly repeatable seasonal fluctuations are apparent. Populations of molluscs and echinoderms, in particular, were either temporally persistent (e.g. Astropecten americanus at Station I1, Figure 6-116) or varied with no apparent seasonal pattern. The only convincing examples of population fluctuations due to seasonal dynamics are the two Cancer species. At outer shelf and shelf-break stations, both Cancer irroratus (Station B1, Figure 6-113 and E1, Figure 6-114) and Cancer borealis (Station F1, Figure 6-117 and I1, Figure 6-116) were most abundant during summer and fall and least abundant in winter. Ovigerous females were common in the winter and planktonic larvae were abundant in spring (Chapter 4). Spring recruits grew to a size at which they could be captured abundantly by late summer and fall (August-November). Other dominant decapod crustaceans also showed some indication of seasonality, but it was much less clear-cut. Juvenile Crangon septemspinosa were heavily recruited into inner shelf areas affected by hypoxia in fall 1976 (Figure 6-74) but similarly heavy recruitment was not observed elsewhere and could be masked by the densities of resident adults. Crangon larvae are found in the plankton during most of the year but are not abundant during summer (Chapter 4). There is also evidence of seasonal migration and recruitment of the shrimp Dichelopandalus leptocerus which were not abundant on the inner and central shelf during summer and fall. Individuals collected at the shelf break and upper slope were generally larger than those found inshore, suggesting offshore migration of adults. Dichelopandalus was most abundant as larvae in the plankton in the winter and early spring (Chapter 4) and may be recruited to offshore benthic populations by the summer and subsequently migrate inshore during the winter.

Other fluctuations in populations which may appear seasonal are apparently not related to patterns of recruitment but may be simply due to sampling variability or imprecise station relocation. For example, both Asterias vulgaris and Asterias forbesi were most abundant at Station D1 during the winters of both sampling years. However, this increase was not accompanied by a notable increase in proportion of juveniles.

Temporal variability of the recruitment of megabenthos may be greater than that indicated by species seasonal abundance curves. However, due to the relatively long life of most species, recruitment patterns are masked by the relatively small numbers of recruits compared to the abundance of resident adult populations. To more accurately evaluate recruitment patterns of megabenthos, interpretation of the age structure of populations is necessary. At

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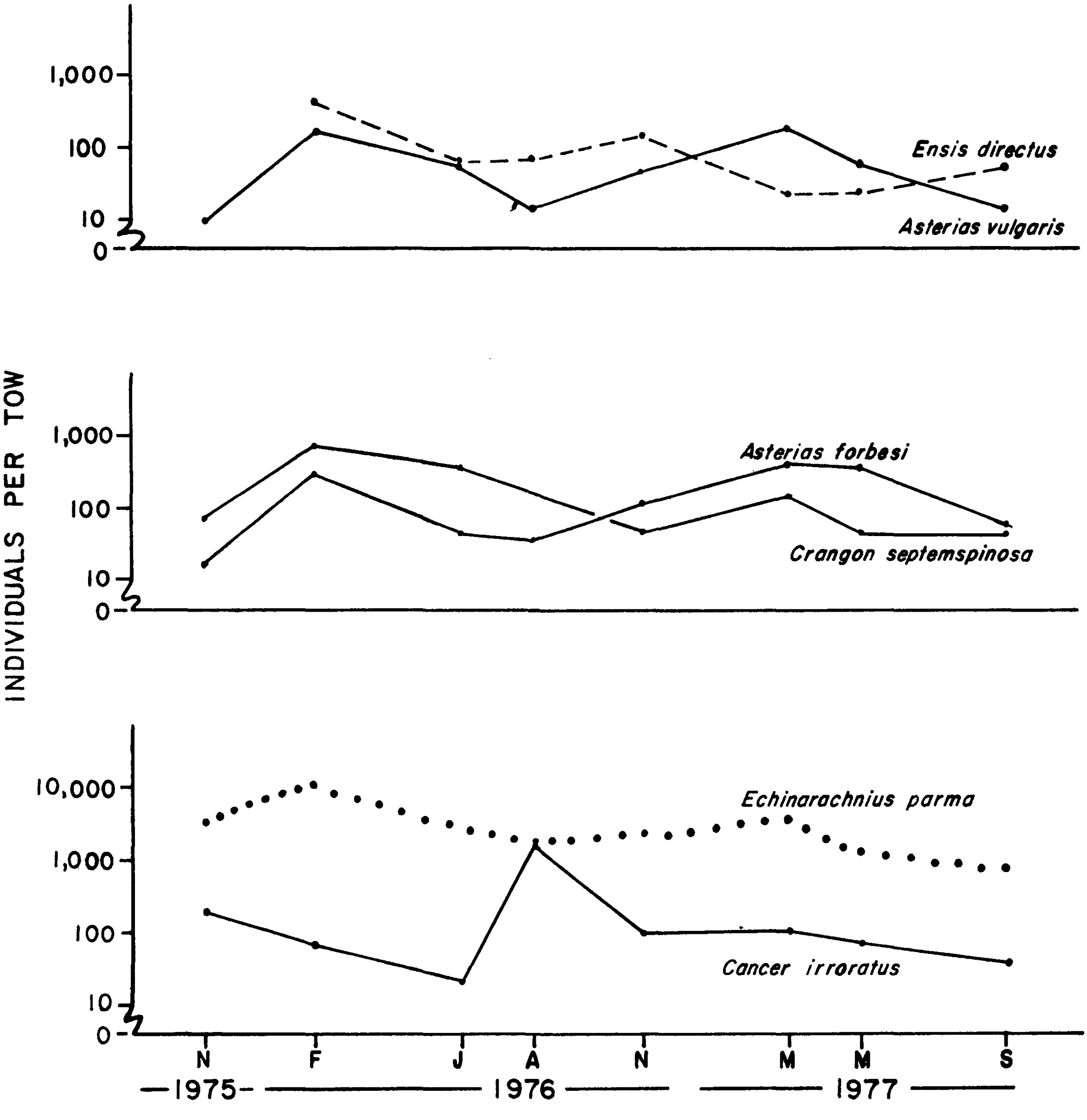

Figure 6-112. Fluctuations in the abundance of dominant megabenthos at Station D1 as reflected in catches by small biology trawl (solid lines), anchor dredge (dashed lines), or combined total (dotted line).

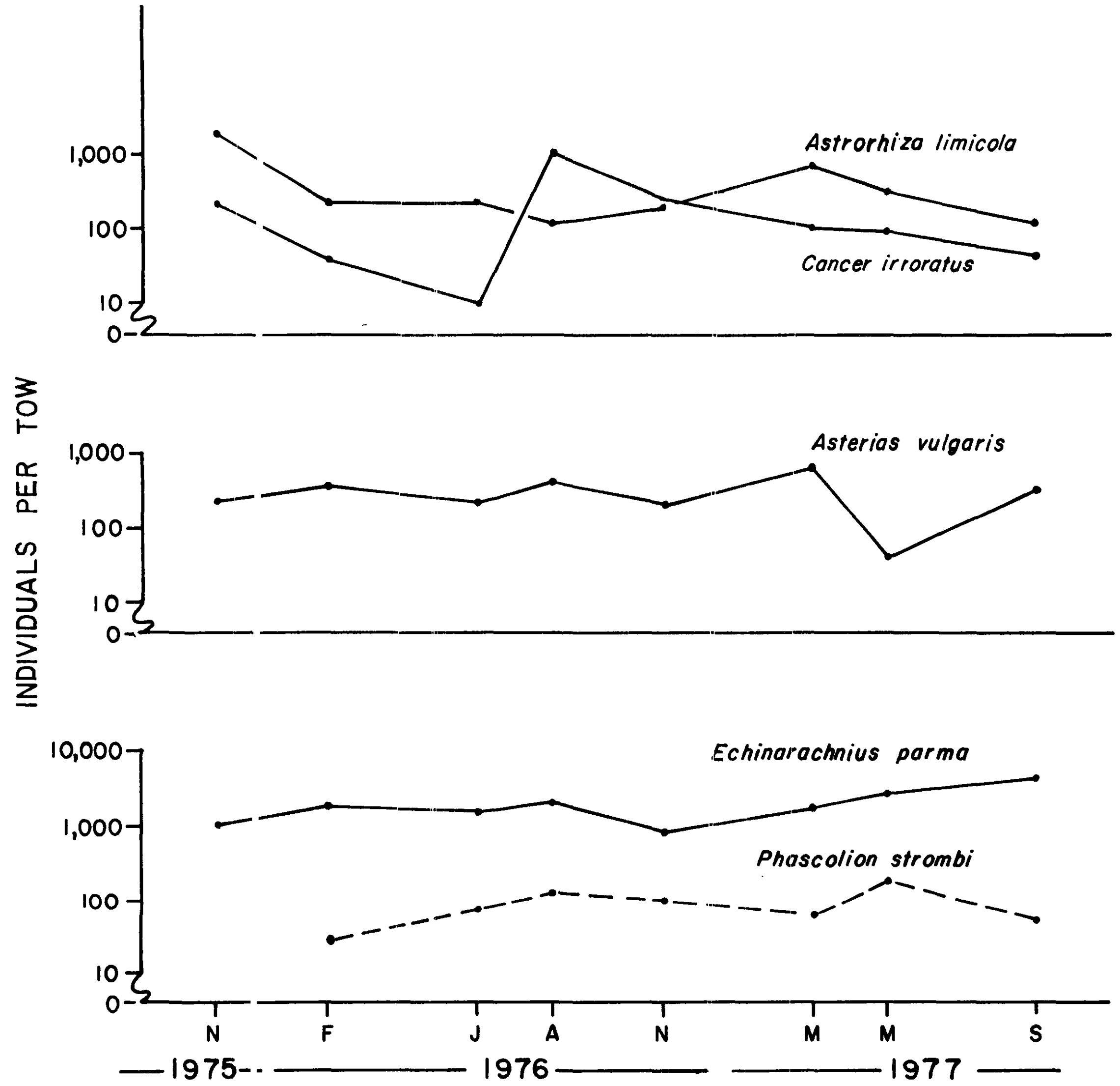

Figure 6-113. Fluctuations in the abundance of dominant megabenthos at Station B1 as reflected in catches by small biology trawl (solid line) or anchor dredge (dashed lines).

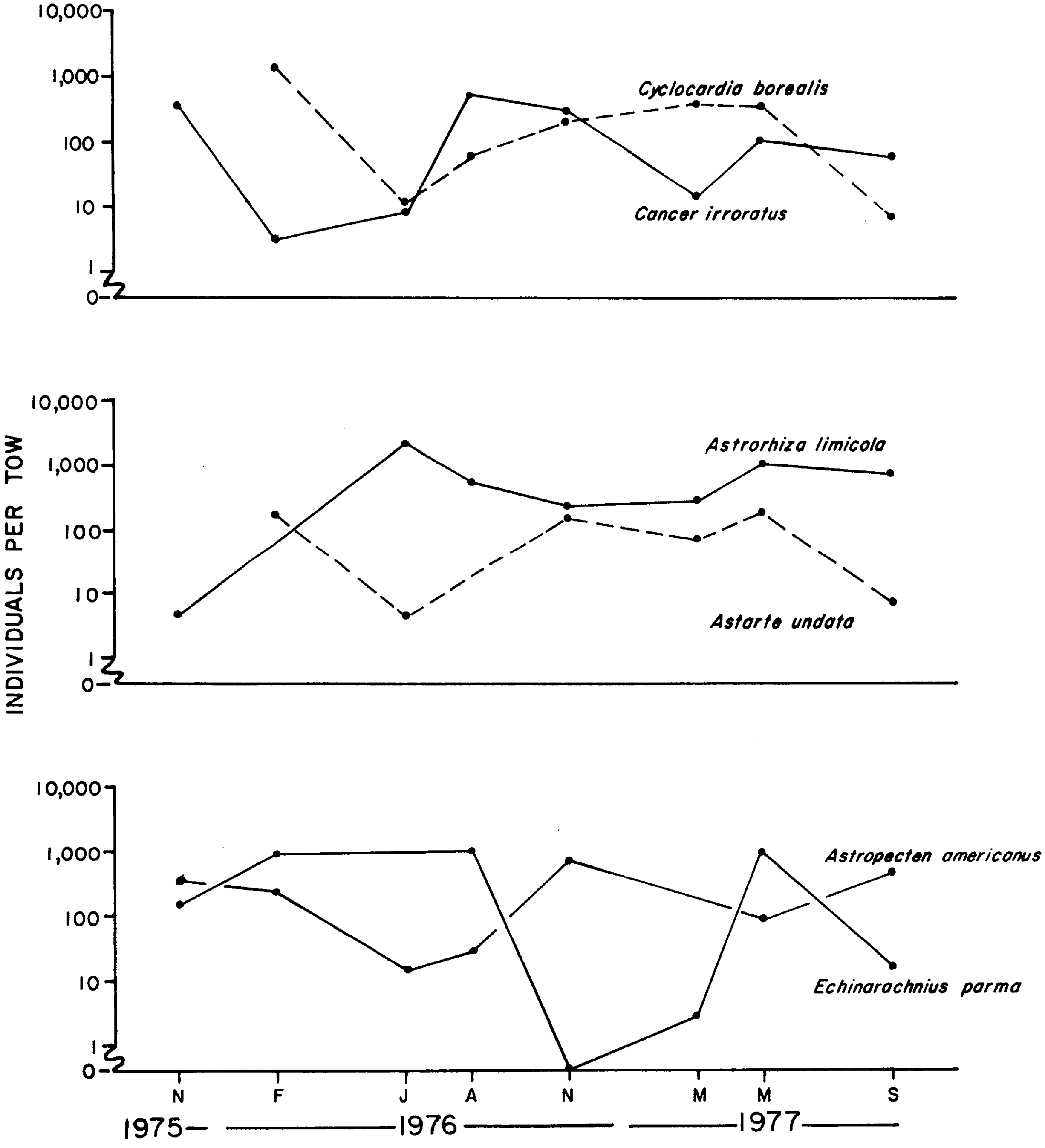

Figure 6-114. Fluctuations in the abundance of dominant megabenthos at Station E1 as reflected in catches by small biology trawl (solid lines) or anchor dredge (dashed lines).

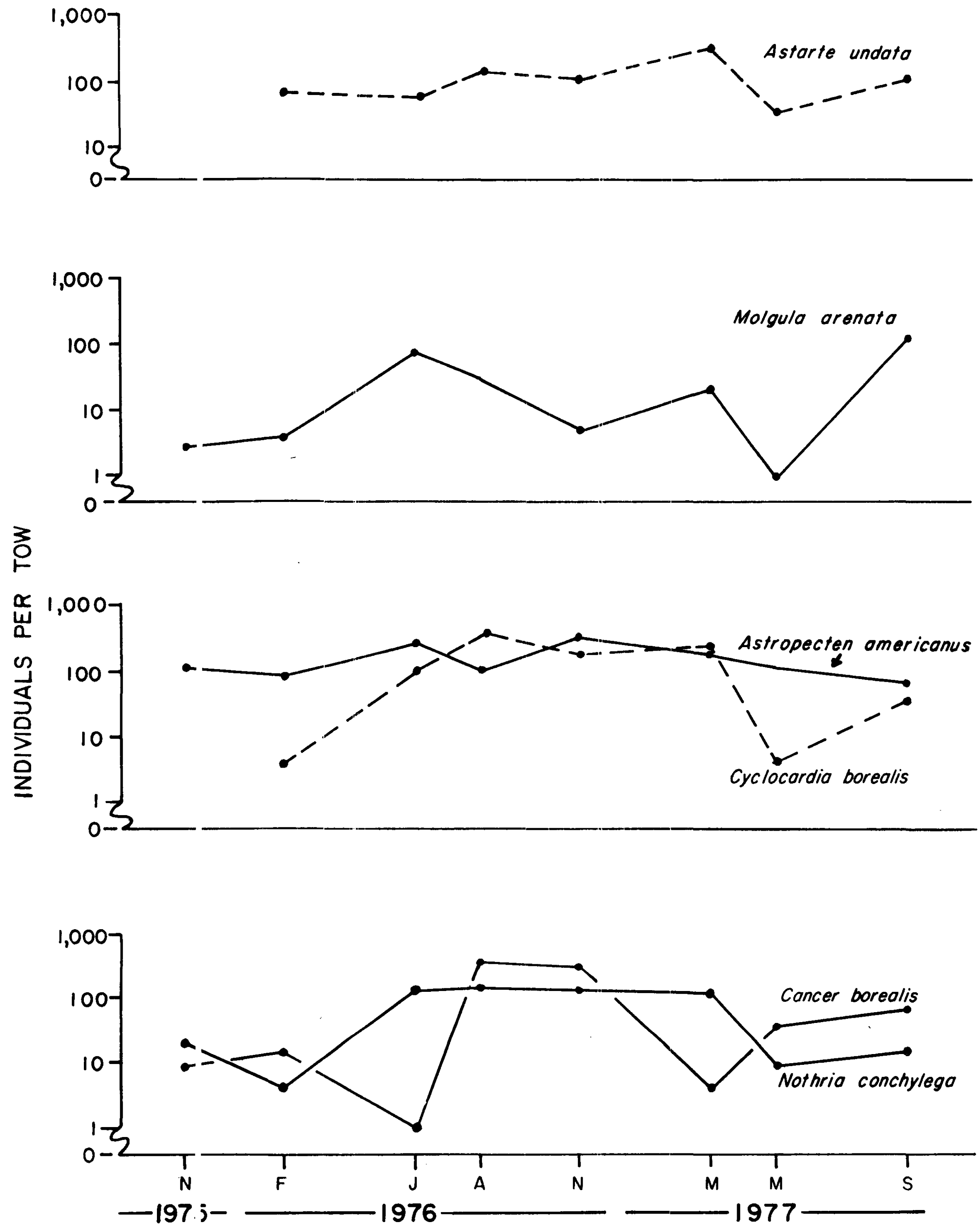

Figure 6-115. Fluctuations in the abundance of dominant megabenthos at Station I1 as reflected in catches by small biology trawl (solid line) or anchor dredge (dashed lines).

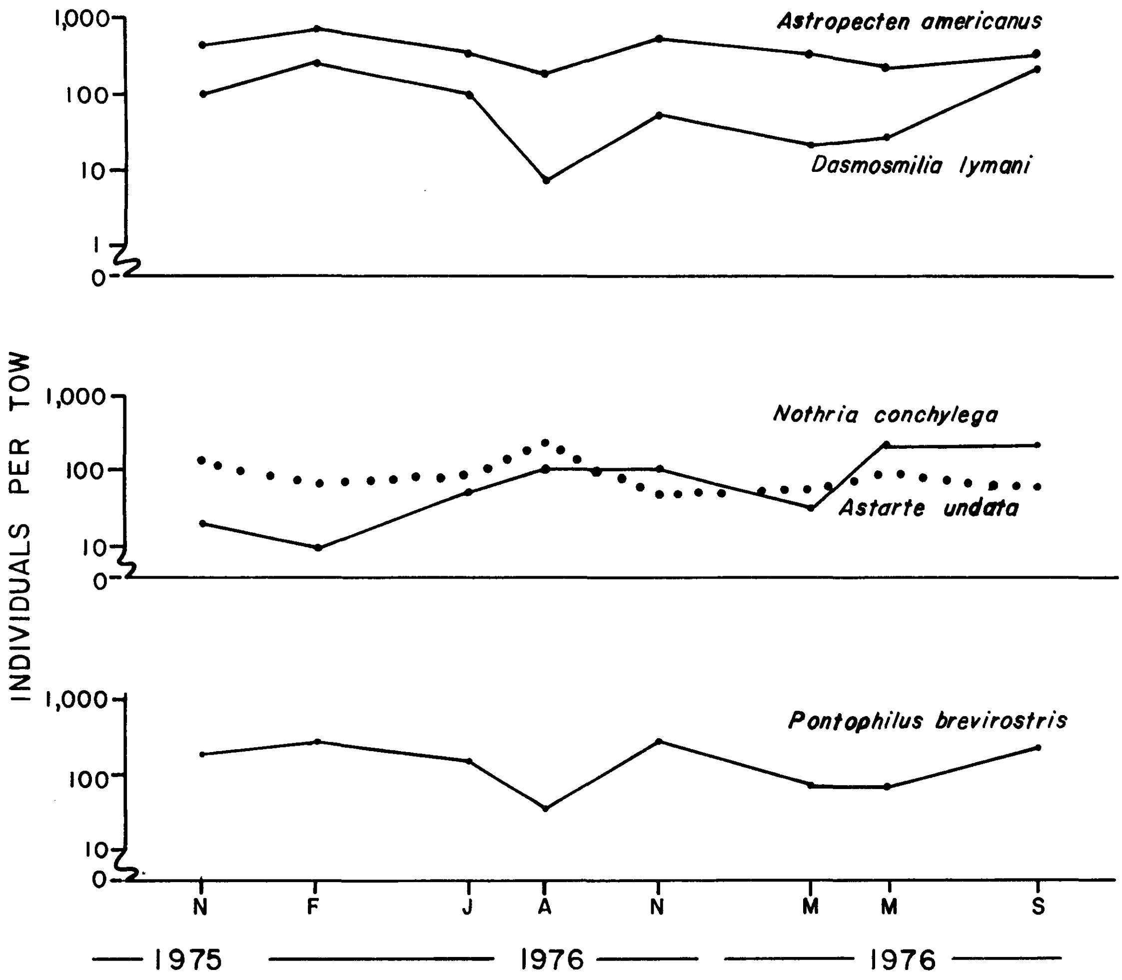

Figure 6-116. Fluctuations in the abundance of dominant megabenthos at Station A1 as reflected in catches by small biology trawl (solid lines) or anchor dredge (dotted line).

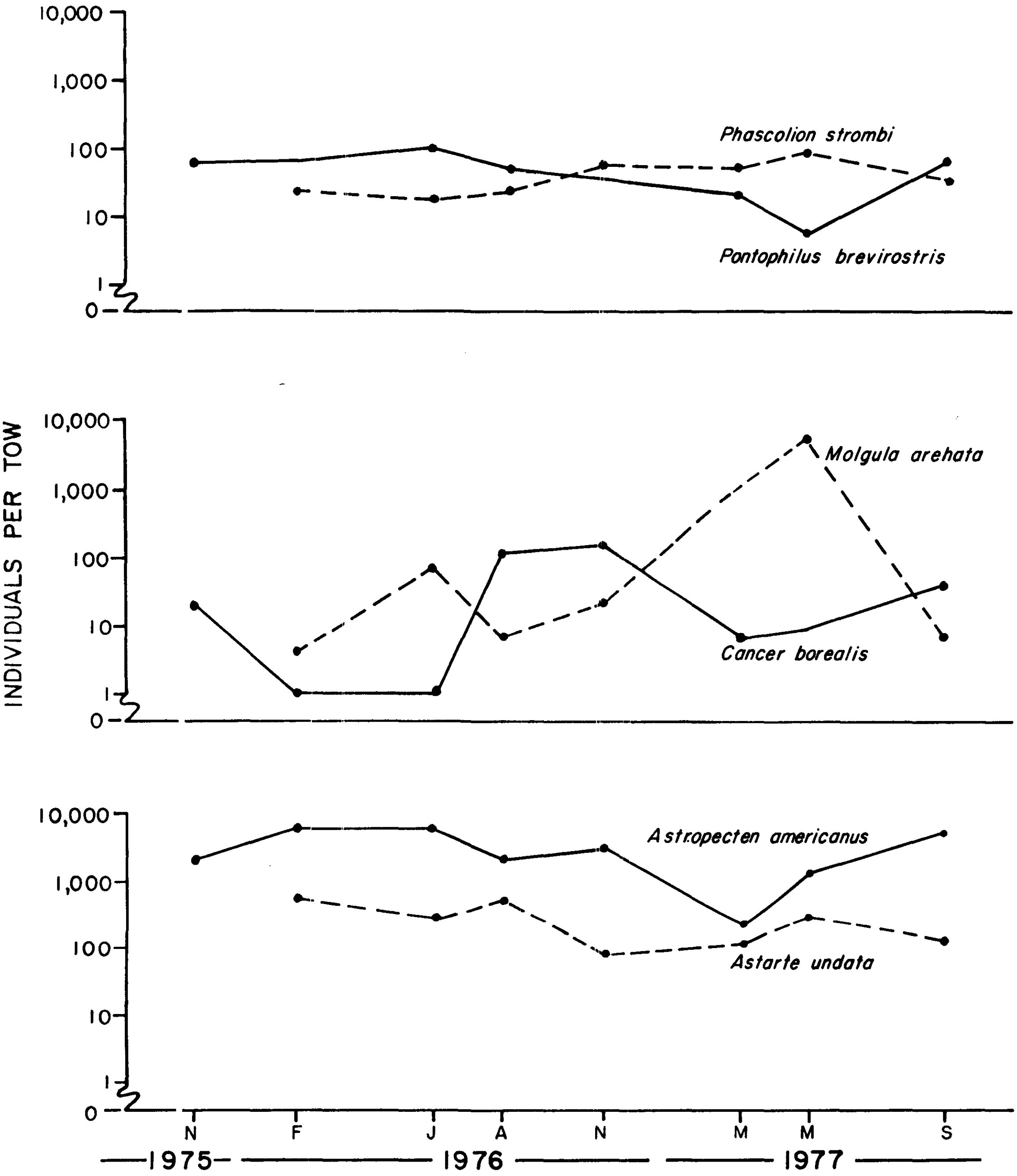

Figure 6-117. Fluctuations in the abundance of dominant megabenthos at Station F1 as reflected in catches by small biology trawl (solid line) or anchor dredge (dashed lines) samples.

stations C2 and N3 where adult populations of most species were eliminated by hypoxia, recruitment was obviously intense. Similar, although less obvious recruitment, probably occurs throughout the entire shelf but could not be detected from seasonal collections of most species of megabenthos.

DISCUSSION

Abundance and Diversity

The spatial patterns of macrobenthos abundance, biomass, and species diversity found during the second year of investigation were essentially the same as those found after one year and reported by Boesch et al. (1977). Only the repercussions of anoxia during the summer of 1976 on the inner shelf benthic communities produced any significant alterations in abundance or diversity.

There are few comprehensive data sets on the density, biomass and diversity of macrobenthos for the Middle Atlantic continental shelf, although localized regions have been intensively studied. In the earlier report, Boesch et al. (1977) compared their findings with those of Wigley and Theroux (1976) for the New York Bight (Montauk Point to Cape May). The mean density values reported by bathymetric stratum by Wigley and Theroux were generally substantially below those found for similar depths ranges during this study, particularly for annelids and small crustaceans. This is certainly in part due to the coarser mesh sieve (1 mm) employed by Wigley and Theroux. Futhermore, Boesch et al. (1977) concluded that Wigley and Theroux's (1976) generalizations regarding decreased density and biomass (1) from shallow to deep water, (2) from north to south within the Middle Atlantic Bight, (3) from coarse-grained to fine-grained sediments, and (4) from areas with wide to areas with narrow temperature range were not entirely applicable within the present study area (continental shelf and upper slope). Although density and biomass rapidly declined from the shelf break down the continental slope concomitant with stenothermy and reduction of sediment grain size, density and biomass was higher on the outer shelf and in finer shelf sediments than on the inner shelf (Figures 6-23 through 6-26). In addition, no consistent latitudinal trends in the density or biomass of macrobenthos were found within the present study area, which admittedly is not as extensive as that studied by Wigley and Theroux. Although differences exist in the density of macrobenthos for some comparable habitats in areas B and E (Figures 6-53 and 6-54), these seem to be local differences related more to sedimentary conditions than to latitudinal.

Comparisons of abundance and diversity with the results of other studies of macrobenthos are possible, but they must be cautioned because of important methodological differences. Most notably, investigators have used different means of separating the macrobenthos from the sediment. Coarser sieves, generally 1 mm mesh, have generally been used than that used here (0.5 mm). On the other hand, some investigators have removed macrofauna from small sediment samples without sieving (Maurer et al. 1976). No attempts were made in this study to separate 1 mm and 0.5 mm fractions of macrobenthos, however, extensive fractionation was employed in surveys of proposed alternate dump site on the outer shelf north of the Hudson Shelf Valley (Raytheon 1977). The sediments and benthos of this site are similar to those over much of the study area. Raytheon found that, on the average, the number of macrobenthos retained by a 1 mm sieve was 57% of the total that would be retained on a 0.5 mm sieve (1 mm and 0.5 mm fractions combined). Thus by applying conversion factor of 1.75 to densities reported based on 1 mm sieve collections one can develop a crude approximation of what the 0.5 mm sieve densities would be. This ratio may undoubtedly vary considerably with habitat type and season but serves for restricted comparisons.

Table 6-25 compares the central tendency of total macrobenthos density values reported by various investigators, including estimated 0.5 mm sieve densities. The median densities by bathymetric stratum found in this study remain very much higher (2.5 to 5 times) than the estimated 0.5 mm sieve-equivalents of those densities reported by Wigley and Theroux (1976) or Steimle and Stone (1973). On the other hand densities found on the outer shelf are comparable with those found at the alternate New York and Philadelphia dump sites which were studied using equally fine screens. Even these comparisons are difficult, because of the variable inclusion of meiobenthic taxa (e.g. foraminifera and nematodes) excluded in this study. In Table 6-26 total macrofaunal densities are compared by topographic habitat for areas B and E (shelf break only) for the results of the habitat delineation study and those of investigators from the National Marine Fisheries Service (Radosh et al. 1978) who sampled these areas in 1974. The NMFS results are also based on 1 mm sieve samples but 0.5 mm sieve densities may be roughly estimated based on the comparisons of Raytheon (1977). The estimated densities of macrobenthos are very similar and rank-correlated among habitats (only terrace and ridge-medium sand habitats are in juxtaposed order). Densities in swales were greatest by far for both data sets.

In summary, total densities of macrobenthos (0.5 mm seive) typically range from 2,000 to 10,000 individuals per square meter on the Middle Atlantic shelf, but can be locally higher in topographic depressions or during ephemeral proliferation of one or a few species.

Species diversity is even harder to compare among studies. Not only is it susceptible to the same methodological differences which confound density comparisons, but all diversity measures are sample size dependent in a non-linear fashion, and the numbers of species recognized depends on taxonomic experience of staff.

Table 6-25. Densities of total macrobenthos (individuals/m^2) reported for the Middle Atlantic Bight.

	Middle Atlantic Bight BLM Benchmark Studies (median, 0.5 mm)	New York Bight Wigley & Therous (1976) (mean, 0.5 mm)	Alternate N.Y. Dumpsite Raytheon (1977) (mean, 0.5 mm)	Philadelphia Dump Site Marine Research (1975) (median, unsieved)	Southwestern Long Island Steimle & Stone (1973) (median, 1.0 mm)
Inner & Central Shelf (20-49 m)	3149	752(1316)*			499(873)*
Outer Shelf (50-99 m)	4320	1390(2433)	5515**	7500***	
Shelf Break (100-199 m)	3575	442(774)			
Continental Slope	1690	230(403)			

* Values in parentheses are estimates of 0.5 mm sieve population assuming 1 mm sieve fraction represents 57% of population (Raytheon 1977)

** Excluding foraminifera, nematodes, and unidentified fragments

*** 1974-1975 surveys only, includes some meiobenthos

Table 6-26. Densities and number of species of total macrobenthos for outer shelf habitats (Area B except for shelf break, Area E) found in the habitat delineation study (VIMS) and by an earlier National Marine Fisheries Service study (Radosh et al. 1978).

Habitat	Equivalent NMFS Station Groupings (Radosh et al. 1978)	Species/0.1 m^2		Individuals/0.1 m^2	
		VIMS	NMFS	VIMS	NMFS
Terrace	9	37	19	435	147(257)*
Ridge/Med. Sand Flank	1,3	43	34	225	226(396)
Med.-Fine Sand Flank	2,4,8	43	39	495	242(424)
Swale	5,6	62	39	720	406(711)
Shelf Break	7	46	39	324	197(345)

* Values in parentheses are estimates of 0.5 mm sieve population assuming 1 mm sieve fraction represents 57% of population (Raytheon 1977)

Wigley and Theroux (1976) present no data on species diversity or richness, but conclude that portions of the Middle Atlantic Bight experiencing marked seasonal changes in bottom temperature supported "diverse forms", whereas areas with uniform temperatures throughout the year (bathyal habitats) support only "a moderate variety of species". Their characterization of bottom temperature variability is based on long-term extremes and not seasonal variation within two years, as in this study. Zones described as varying in bottom temperature from 12-16°C varied only 2-5°C during this study.

Day et al. (1971) sampled macrobenthos on a cross-shelf transect off Cape Lookout, North Carolina, and reported greatest numerical species richness in the 20-120 m zone, but reduced richness at 160 and 200 m stations.

By comparison, these data generally indicate increased species richness and diversity with reduced seasonal variation in bottom water temperature and increased depth. Areal richness declined from the shelf break to the continental slope (Figure 6-52) due to the reduced densities of macrobenthos, but numerical richness and Shannon diversity did not. Thus, our results agree with those of Hessler and Sanders (1967) who found increasing diversity from the outer continental shelf, across the shelf break, and down the slope off southern New England.

Pearce et al. (1976) describe the distribution of Shannon diversity (H') from collection of macrobenthos from the central and outer continental shelf in the New York Bight. Their values (<3) are generally much below those reported here, although the units employed (base logarithms) are not stated. Their collections were not replicated, thus their values are probably underestimates of the true (asymptotic) diversity of the 1 mm sieve populations. However, higher H' values were found by Radosh et al. (1978) for the outer shelf employing a 1 mm sieve and for the unreplicated 0.5 mm sieve samples collected in the habitat delineation study. Boesch (1972) reported values of H' for macrobenthos (1 mm sieve) from the inner shelf off the Delmarva Peninsula and the shelf break of the Virginia-North Carolina shelf which are within the range of those values reported for these respective environments in this study.

Areal richness (number of species taken in a sample of a fixed area sampled) is perhaps the most conservative and straightforward component of species diversity. Raytheon (1977) collected 5 replicate 0.1 m^2 Smith-McIntyre grab samples and also employed a 0.5 mm sieve. The median areal richness of these collections was 98 species/0.5 m^2, which is very comparable (Figure 6-51) to the richness reported in this study for outer shelf habitats (0.6 m^2 should produce only a few more species than 0.5 m^2). Also, the mean areal richness reported for Raytheon station 2, which had a characteristic swale assemblage with Ampelisca agassizi dominance, was 120 species, essentially identical with the median for outer shelf swales. The uniformly lower number of species taken in single 0.1 m^2 grabs by Radosh et al. (1978) is probably in large part a result of sieve size differences (Table 6-25).

To summarize, numerical species richness had a pattern consistent with the predictions of Sanders (1968) with richness higher in habitats with stable temperature and sediments. Areal richness, on the other hand, declines somewhat down the continental slope as a result of greatly reduced faunal densities. Diversity measures which have a strong evenness component, including Shannon diversity (H'), show departures from the pattern of species richness where extreme numerical dominance by one on a few species reduces evenness. The pattern of diversity is temporally persistent except that population fluctuations of dominants, principally on the inner and central shelf, may effect temporal variations in species evenness.

Large Scale Patterns of Distribution

Bathymetric Distribution

A clear bathymetric gradient in distribution was apparent for both megabenthos and macrobenthos. Even though most of the analyses performed were, because of necessary simplicity, designed to dissect this gradient it should be conceptualized as a coenocline, or community continuum, rather than as discrete faunal zones. Reasonable classification of the distribution of even the more common species shows a pattern of overlapping distributions across the continental shelf and slope. Thus, the bounds of the artificial zones should coincide with somewhat sharper biotic change across the continuum.

In terms of assemblage similarity, the sharpest changes occurred at or near the shelf break. Change on the upper slope and the continental shelf was more gradual. Thus, the apparently optimal subdivisions of the bathymetric coenocline conform to the following geographic subdivisions: inner shelf (to ca. 30 m), central shelf (30 - 50 m), and outer shelf (50 - 100 m), shelf beak (100 - ca. 200 m), and continental slope (<200 m).

The bathymetric coenocline is controlled by several environmental factors acting across the bathymetric complex-gradient (sensu Whittaker 1971). The principal cause of the biotic change is not the effect of depth (pressure) itself but rather the complex effects of hydrography and sediment characteristics.

Temperature is the principal hydrographic factor affecting distribution of macrobenthos. Not only the absolute extremes, but also the temperature range, are certainly important. The temperature regime on the inner shelf is influenced by the continental climate and bottom water in Area C experienced a 17°C range during the two years of sampling (Chapter 3). Coldest temperatures were about 0°C during the very cold winter of 1977, and warmest were about 17°C in summer 1976. On the central shelf, bottom temperature was less variable, with the warmest temperatures in fall 1975 (16°C) and the coldest in winter 1977 (3°C). Bottom temperatures on the outer shelf are, however, usually much more constant with a range during the first year of sampling of only 3-4°C. During the first year the temperatures were warmest in the fall (ca. 11°C), following vertical mixing concomitant with the break up of the thermocline, and coldest during spring and summer (8-9°C). During the spring and summer the outer shelf is covered by the "cold pool" of southward traveling water formed off New England during the winter (Beardsley et al. 1976). More variable bottom temperatures were experienced on the outer shelf during the second year of study. This resulted from an intrusion of warm (ca. 14°C), higher salinity (>35 o/oo) slope water onto the shelf (Chapter 3) in the fall of 1977 and the colder than usual (ca. 4°C) cold pool water which extended down part of the shelf in spring 1977. Except for the period of slope water intrusion and the fall warming of bottom waters on the outer shelf, the bottom temperatures in the shelf-break region were warmer than those on the outer shelf. At the shelf break the bottom temperatures were extremely constant, varying at most 4°C and typically 11-12°C. The constancy of the temperature in bottom waters along the shelf break is maintained despite the highly dynamic hydrographic conditions of the shelf water-slope water interface. This interface may move offshore or onshore and is scalloped by warm core eddies moving southwesterly within the slope water mass. Slope water is intruded and shelf water is pulled offshore by such mesoscale hydrodynamic forces. This activity scarcely affects water below the permanent thermocline, however. Although slope water from below the thermocline may be advected onshore, the mass of shelf water moving offshore is insufficient to displace the large column of slope water. As a consequence, the shelf water is restricted to floating offshore atop the saltier surface water over the slope.

The variable temperature conditions of the inner and central shelf no doubt restrict some cold stenothermal species found on the outer shelf. Moreover, sooouthwesterly flow of water masses carrying larval drift from off New England allows the existence of boreal species farther south than previously expected. The shelf-break assemblages probably contain stenothermal species, restricted by temperatures below 8-9°C, which have broad latitudinal distributions. Thus, differences in temperature regime are probably the prime cause of the sharper faunal change at the outer shelf-shelf break transition than elsewhere.

Salinity and other hydrographic factors are thought to have an insignificant effect on the distribution of macrobenthos in the study area. Although lowered dissolved oxygen levels during the summer of 1976 altered distribution patterns, dissolved oxygen is not thought to be a limiting factor under usual conditions.

The bathymetric coenocline, as conceived, bears resemblance to the more rigid schemes of zonation of shelf benthos popular among French workers (Peres 1957; Guille 1970; Glemarec 1973). Glemarec (1973) summarized data on zonation of benthos of the shelf of Europe and identified three major bathymetric zones, or etages: infralittoral, (bottom temperatures may reach 18°C, seasonal variation more than 10°C), coastal (maximum 16°C, variation 7-8°C) and open sea (generally 10-12°C, below 70-90 m). These etages correspond roughly to the inner shelf, outer shelf and shelf break of this study, except that the cold, relatively stenothermal outer shelf habitat has no direct parallel in European waters.

Latitudinal Distribution

The study area is usually described as part of the Virginian biogeographic province which extends from Cape Cod to Cape Hatteras and is thought to be inhabited mainly by eurythermal warm temperate species (Ekman 1953; Briggs 1974). Few tropical species, most of which extend no further north than Cape Hatteras, and few arctic or boreal species, most of which extend no further south than Cape Cod, presumably occur in the region. However, this characterization is based primarily on epifaunal echinoderms, decapod crustacans, molluscs, and fishes and primarily on littoral or shallow water biota. Some of the dominant infaunal taxa, in particular polychaetes and peracarideans, demonstrate less clear-cut biogeographic patterns. Polychaetes, for example, tend to have notoriously wide latitudinal and bathymetric ranges. Furthermore, the biogeography of outer shelf, shelf-break, and continental slope regions is not well known, but often does not bear much resemblance to that of the littoral biota.

The latitudinal distribution of macrobenthos within the study area is overwhelmed by strong bathymetric trends such that there are no apparent faunal differences from north to south. Communities seem to be qualitatively and quantitatively similar within a given depth zone over the 3° latitude studied. This is in part due to the dominant along-shelf flow of shelf currents and the general lack of direct influence of oceanic circulation (e.g. the Gulf Stream) on shelf waters. As a consequence, bottom temperatures within a depth zone are fairly uniform (Chapter 3) and are dominated by the advection of relatively cold water from the north and slope water intrusion which may affect the entire study area. Because of this and strong seasonal stratification, bottom temperatures on the outer shelf remain cold throughout the year and apparently support many boreal species previously thought limited north of Cape Cod. Many of these species, restricted to the outer shelf off New Jersey are found inshore in relatively shallow water in northern New England and Maritime Canada. They display the classic pattern of tropical submergence, well characterized for the benthic communities of the continental shelf of the eastern North Atlantic by Glemarec (1973). As a whole, the macrobenthos of the Middle Atlantic continental shelf shares many species with the boreal sand assemblages of 10° higher latitudes described by Ledoyer (1975a, 1975b).

Relationship to Sediments

The distribution of benthic animals is strongly tied to substrate characteristics (Gray 1974), and the benthos of the Middle Atlantic Bight is no exception. On many continental shelves there is a cross shelf transition from sandy to muddy sand to mud. Thus the effects of depth related factors (principally temperature) and substrate-type operate in consort (Guille 1970). In the Middle Atlantic Bight, however, sediments remain uniformly sandy over the shelf because of the transgressive history of the shelf (Chapter 5). The progression to silts and clays does not take place until the shelf break-continental slope transition. The distribution of sediments nonetheless plays a large role in the distribution of benthos, both on a large scale (with depth and latitude) and a smaller scale (with shelf topography). Detailed discussion of animal-sediment relationships, particularly with respect to mesoscale topography, is reserved for a subsequent section, however it is necessary to discuss the effects of sediments on large scale distribution patterns.

Substrate characteristics related to depth were important in the outer shelf-shelf break-slope transition. Of probable but unquantified importance is the dynamic, rather than static, sediment property of mobility. The reduced frequency of disturbance of bottom sediments by waves and currents on the outer compared to the central shelf looms very important. Predictions of the bottom orbital velocites propagated by waves (Chapter 15) confirm the impression of much less frequent bottom disturbance of bottoms deeper than 50 m. Sediments become consistently finer (finer sand and gradually increasing silt and clay content) across the shelf break and slope. It thus becomes difficult to separate the effects of depth and sediment on distributional patterns. Both factors are obviously important as there are important differences and important similarities in the communities of habitats with disparate sediment composition (e.g. the muddier stations A2, A3, and A4) within the shelf-break zone.

Overall Distribution

A generalized distribtuion scheme of shelf benthic biotopes is given in Figure 6-118). This is based on data collected during the study and extrapolations from sediment distribution in areas not sampled. Because of the scale, the detailed influence of ridge and swale topography could not be included in this figure, but it should be kept in mind that local topography can effect biological differences as great as those of the depth zones.

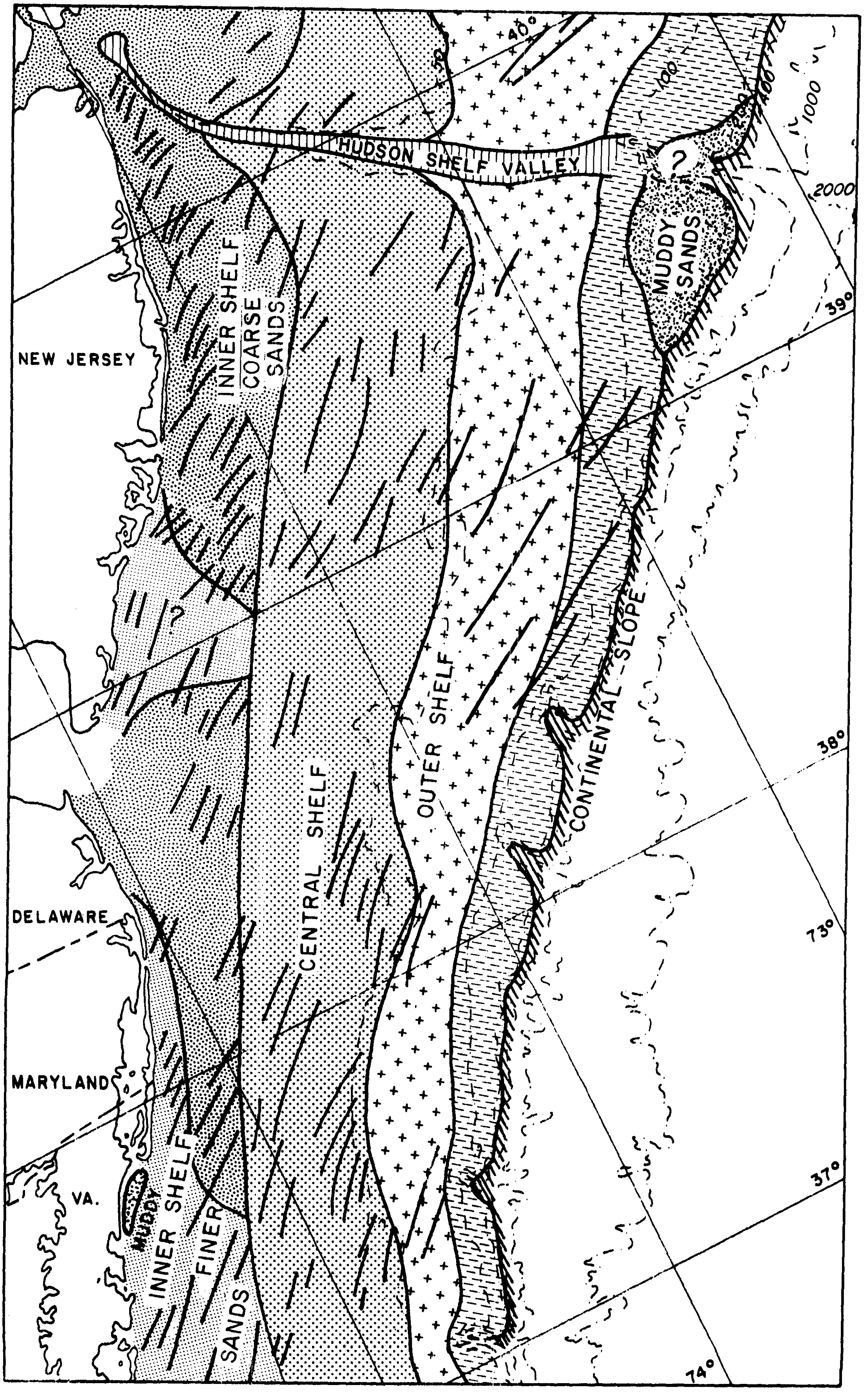

Figure 6-118. Schematic zonation of macrobenthic biotopes in the middle portion of the Middle Atlantic Bight. Major ridge fields are indicated.

The data on which to base such biotope characterizations have heretofore been scant, and conclusions were thus speculative (see Introduction). Pratt's (1973) conception of latitudinally homogeneous bathymetric zone bears some relationship to the observed distribution of benthos in this study, although the relationship of his zonation scheme to sediment type was somewhat misconceived. Changes in benthic communities occur on the outer shelf even if sediments are not silty. Also, although sediments do have somewhat higher silt and clay content at the shelf break, the great faunal changes found there are probably more the result of temperature differences than the existence of a "mud line". Pearce (1975, Pearce et al. 1976) emphasized the homogeneity in the distribution of macrobenthos across the Middle Atlantic continental shelf by referring to species found widely across the shelf. Our results demonstrate that the composition and structure of the benthic communities are, in fact, greatly different from the inner to the outer shelf. Although there are several notable ubiquitous species, there are large numbers of species restricted to the inner or outer shelf.

Maurer et al. (1976) listed characteristic sand fauna species on the inner and central shelf of the Middle Atlantic Bight based on their studies and others. Although they recognized the effect of local sediment differences on the benthic communities off the mouth of Delaware Bay and the possible influence of microtopography, their qualitative characterization leaves the impression of greater homogeneity than observed in this study. The species listed by them are in fact characteristic of much of the inner and central shelf; however, their patterns of distribution and abundance are strongly influenced by bottom topography and subtle differences in sand size distribution.

Animal-Sediment Interrelationships

The relationship of the benthos of the continental shelf to sediment characteristics has been underestimated by many investigators. Community differences may be striking where there is a wide range of sediment types represented (Sanders 1958; Jones 1969; Guille 1970; Glemarec 1973) but most investigators have been content to describe a sand community, or a coarse sand and a fine sand community. These results for megabenthos and macrobenthos, as well as those for meiobenthos, demonstrate a very finely tuned relationship between benthic communities and the sandy sediments of the Middle Atlantic shelf. In comparison, one gets the impression that the benthos, despite the notorious variability of biological parameters and the sampling and analytical imprecision, is a more consistent and reliable an indicator of sedimentary conditions than more "basic" chemical and microbiological parameters. As Thorson (1957) suggested, "the bottom animals can give a much finer analysis of the bottom than we can..."

Relationship to Shelf Topography

The relationships of animals to sediment is best exemplified when the effects of depth are minimized, as in the habitat delineation study in which mesoscale topography with a relief of about 20 m creates a subtle patterns of sediment distribution. The macrobenthic communities of swale habitats of fine-medium sands are considerably and consistently different than those on ridges (coarse-medium sands) or their flanks (medium sands).

The predictable relationship of sediments as distributed with respect to ridge and swale topography to benthos has heretofore been unrecognized. Maurer et al. (1976) refer to the possible relationships to "ridge and swale microtopography", but it is clear that they refer to ripples or megaripples of 30-100 cm wavelength and not linear shoals or sandwaves, which are much larger and more persistent features. The sampling networks of Wigley and Theroux (1976) and Pearce et al. (1976) were too widely spaced to effectively reflect patterns related to regional topography. Raytheon (1977) sampled 12 stations on three occasions within a rectangular area on the outer shelf north of Hudson Shelf Valley which is of a similar depth and about the same size as area B. Although one station (station 2) obviously represented a swale habitat because of the medium-fine sands and abundance of such good faunal indicators as the amphipod *Ampelisca agassizi* and the cumacean *Eudorella emarginata* (=*pusilla*), they failed to recognize the habitat amd community distinction. Rather they "conclude that there is no major geographic division of the infauna community within the Study Area".

The importance of understanding the mesoscale habitat distribution is illustrated in the results of studies of the benthos of the Philadelphia dumpsite off Delaware Bay (Lear et al. 1977). Lear et al. found patterns of species distribution which they could relate to sediment properties, organic carbon levels and trace metals concentrations they felt were related to contamination by sewage sludge. The dark, more organic sediments containing higher metals concentrations lay in two principal pools south of the dumpsite, apparently indicating down current deposits of sludge remnants. Although meaurements of cellulose and cuprostanol support a contention of sewage contamination, carbon and metals levels were mostly in the range of those found in these studies to be characteristic of swale habitats (Chapters 5 and 13). These pools of presumed contaminants essentially correspond to topographic depressions later recognized by Lear et al. Indeed, the distribution of infaunal species which seemed to be related to degree of contamination (e.g. *Goniadella gracilis* and *Lumbrinerides acuta* avoiding the contaminants and *Lumbrineris impatiens* and *Ampelisca vadorum* "stimulated in the high organic areas"), is parallel to their distribution along the sediment-topography gradient in areas B and E. The danger realized in Lear et al.'s interpretation is confusion of natural distributional patterns with those alterations due to contamination.

Given an understanding of the topographic framework, however, investigators will find important differences in the benthos related to subtle sediment distribution patterns. Radosh et al. (1978) reported on the macrobenthos of samples taken principally from area B during 1974. Their analysis was based in part on comparisons to results of fixed station sampling during the first year of this study and to preliminary results of the habitat delineation study. The agreement in the pattern of community composition between these two studies is striking and becomes even closer if taxonomic discrepancices are adjusted. Such species as the polychaetes *Goniadella gracilis*, *Lumbrinerides acuta*, and *Aricidea cerruti* proved to be good indicators of coarse-medium sediments of the terrace, ridge, and exposed flank habitats. The crustaceans *Ampelisca agassizi* and *Eudorella pusilla* and the polychaetes *Clymenella torquata* and *Notomastus latericeus* proved good indicators of the medium-fine sands of swales.

Differences between communities found by Radosh et al. (1978) in 1974 and those found during 1975-77 may be summarized: a) some dominant taxa were referred to by different names, e.g. *Mitrella dissimilus* (Radosh et al.) = *Astyris dissimilis* (this study), *Lumbrineris tenuis* = *L. impatiens*, *Leiochone dispar* = *Clymenura* sp. A, *Macroclymene zonalis* = *Euclymene collaris*, *Tharyx acutus* = *Tharyx* sp., and *Diastylis quadraspinosa* = *D. bispinosa* (see Table 6-2 for name changes since Boesch et al. 1977); b) some small species were more poorly represented in Radosh et al.'s 1mm screen samples, e.g. *Exogone* spp., *Euchone* spp. and possibly juvenile amphipods such as *Unciola* and *Erichthonius*; c) some species were generally more abundant in 1974 possibly due to seasonal recruitment, e.g. *Echinarachnius parma*, or ephemeral population irruptions, e.g. *Polydora socialis*, and, in swales, *Filograna implexa*; d) some species, principally the amphipods *Unciola* spp., *Erichthonius rubricornis*, *Ampelisca vadorum* and *Byblis serrata* were apparently much more abundant during 1975-1977.

The communities of macrobenthos within reasonably small areas of the Middle Atlantic continental shelf respond to subtle patterns of sediment distribution in a predictable fashion. Species distribution patterns with respect to substrate are similar in broadly separated areas of the same approximate depth regime. The communities of coarse to medium sand habitats are characterized by species identified by Pratt (1973) as members of the sand fauna and some of those characteristic of the medium to fine sands of deeper flanks and swales were identified as members of deeper silty-sand environments. However, these latter habitats are scarcely silty and are interspersed with the coarser sediment habitats. The result is an interdigitating mosaic of benthic habitats across the shelf rather than a progression of increasingly fine sediments.

The biotic response to this environmental heterogeneity can be exemplified by considering the distribution of feeding types and the distribution of closely related species which appear to partition the sedimentary continuum. Coarser sediments of dynamic bottoms are populated by interstitial feeders and deposit feeders which exploit the recently sedimented organic-mineral aggregates in this otherwise detritus poor habitat. The finer, more stable sediments of swales preclude interstitial forms because of the small lacunae available in the sediment, but are populated by a greater variety of deposit-feeding forms allowed by the availability of sedimented organic matter.

Closely related species, congeners or members of the same family, are adapted to exploit different portions of this sediment continuum. This can be illustrated by considering the relative positions of the species in ordination space. Since in both areas B and E, reciprocal averaging axis 1 basically paralleled the grain size continuum, the relative rank of a species score on axis 1 can be taken to indicate the "optimum" sediment conditions for a species. Table 6-27 compares the ranks on axis 1 in areas B and E of abundant species in several families of amphipods and polychaetes. In every case except one, the rank orders are identical. The ranks, of course, are different because they are relative to the total suite of species considered in each analysis and the two sets of samples cover different, but over lapping, intervals of the complex gradient - terrace to swale in area B and ridge to shelf break in area E. Similar partitioning of sediment gradients by closely related species has been reported by Guille (1971) for the continental shelf of the western Mediterranean.

Sediment Mobility

Results suggest that not only are the static properties of grain size and organic carbon content important in affecting the distribution of macrobenthos, but the dynamic property of sediment mobility must also be important. Relative sediment mobility can be inferred from observations of bedforms in bottom photographs and from submersible observations (Folger 1977), direct observations of movement such as those made during the USGS studies in the area (Butman et al. 1977), and theoretical considerations based on water depth and bottom topography (e.g. Chapter 12 and Stubblefield et al. 1975).

Disturbance on the inner and central shelf is frequent and is due primarily to oscillatory bottom currents created by surface waves. Sediments in swales in this region are less affected by surface waves but may be occasionally resuspended by meteorologically-forced bottom currents moving down the swales (Stubblefield et al. 1975). Surface waves are less effective in moving bottom sediments on the outer shelf, and sediments at many of the sites sampled apparently undergo long periods of quiescence (Chapter 5). Major disturbances occur here during winter storms and apparently little resuspension takes place during the remainder of the year (Butman et al. 1977). Although bedforms in evidence of physical disturbance are visible in

Table 6-27. Habitat partitioning of closely related species along the topographic-sediment gradient as exemplifed by the ranks of reciprocal averaging ordination scores.

Taxa	Rank (of 50) of Score on Axis 1	
	Area B	Area E
POLYCHAETA: SYLLIDAE		
Exogone hebes	13	10
Exogone verugera	27	31
POLYCHAETA: LUMBRINERIDAE		
Lumbrinerides acuta	6	2
Lumbrineris impatiens	42	26
Lumbrineris latreilli	*	46
POLYCHAETA: PARAONIDAE		
Aricidea cerruti	3	*
Aricidea catherinae	8	11
Aricidea wassi	*	23
Aricidea neosuecica	*	30
POLYCHAETA: MALDANIDAE		
Euclymene collaris	7	1
Clymenura sp. A	9	18
Clymenura torquata	39	17**
POLYCHAETA: SABELLIDAE		
Euchone sp. A	24	4
Euchone incolor	31	13
Chone infundibuliformis	42	32
AMPHIPODA: AMPELISCIDAE		
Byblis serrata	20	9
Ampelisca vadorum	28	19
Ampelisca agassizi	45	40

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* Not included in ordination analysis

** Low score on axis 1 attributable to bifurcation of ordination constellation into shelf-break and swale community (Figure 6-44), i.e. at the deep end of the gradient (high score), finer sediment habitats are distinguished by low scores on axis 2.

photographs of bottoms deeper than 100 m, sediments in the shelf-break region must be much less dynamic than on the shelf.

Major changes in the frequency of sediment mobility seem to take place in the same portions of the shelf gradient as the biological and temperature range changes, namely between the central and outer shelf and outer shelf and shelf-break region. Thus, it is difficult to determine the relative importance of sediment size and mobility and temperature regime to the distribution of benthos. Again the habitat delineation studies of areas B and E shed light on this subject. Within the outer shelf temperature regime, major differences in communities seem to be related to sediment properties and mobility. Characteristic shelf-break species penetrate into the more stable swales of the outer shelf. On the other hand, the upper shelf break habitat in area E has coarser, presumably dynamic sediments which accommodate a curious mixture of psammophiles found in dynamic sediments across the shelf and some stenothermal shelf-break species. This suggests that sedimentologic factors are more important than temperature regime over much of the shelf. However, at the deeper shelf break stations, sediment characteristics appear less important than on the shelf. For example, the muddy stations in area A had a slightly different fauna than the much less muddy stations in area F. However, these differences are less than would be expected from equivalently different sediment characteristics on the shelf. This suggests that the effect of temperature is preeminent at the shelf break and continental slope.

Implications for Environmental Impact Assessment

The potential effects of oil and gas exploration and development on benthos depend on the potential for disturbance and contamination of bottom sediments, the relative susceptibility of the biota and the rate at which the biota recovers from perturbation. Furthermore, more concern should be placed with regard to limited or "unique" benthic communities and those which are more productive or are of greater value in supporting resources exploited by man.

The dynamic, sandy sediments found over much of the Middle Atlantic continental shelf are less likely to become contaminated with toxicants such as petroleum hydrocarbons than the fine sediments of more depositional environments. Thus, the sediments of shelf swales and the shelf edge are more susceptible to persistent contamination than the coarser shelf sediments. Among the benthos, it appears generally true that crustaceans, particularly amphipods, and harpacticoid copepods, are among the most sensitive to the toxic effects of petroleum hydrocarbons (Sanders 1978, Cabioch et al. 1978). The Middle Atlantic outer continental shelf habitats, particularly topographic depressions, support high densities of benthic amphipods, other peracaridans and microcrustaceans (harpacticoids and ostracods).

Furthermore, the predominant importance of benthic Crustacea as prey of demersal fishes has been demonstrated (Chapter 9).

Because they support high biomass of benthos, are densely populated by Crustacea and have fine sediments, swale habitats (including other topographic depressions such as shelf valleys) are considered to be relatively productive, biological fragile and susceptible to contamination. The fine sediments found in shelf-break habitats may also enhance their susceptibility to contamination, although increased water depth may serve to reduce the potential of contaminants reaching the sea bed. Unfortunately, little direct evidence exists concerning the relative resilience (ability to recover from perturbation) of shelf and slope communities. Considerations based on theory and the empirical results of recolonization experiments similar to the one conducted here (Boesch and Rosenberg in press) suggest that continental slope and shelf-break communities are less biologically resilient than those on the continental shelf.

Finally, the communities discovered in this study were broadly distributed in the Middle Atlantic Bight. Although some valuable habitats are of limited extent (e.g. topographic depressions) none can be considered "unique" in any restricted sense of the word. However, the hard substrate and pueblo communities of the walls of submarine canyons which were not sampled in this study may be so limited in extent and faunally distinctive to be classified as "unique" and considered for preservation.

Temporal Trends

Seasonality and Persistence

The results of two years of sampling the macrobenthos of the continental shelf and slope of the Middle Atlantic Bight indicated that the communities have general persistent composition and structure. Furthermore, community persistence tends to increase with water depth. Moreover, most of the dominant species maintained populations in which the temporal variation witnessed was not significantly greater than small scale spatial variation or at least did not demonstrate concordant fluctuations at several stations which might indicate strong seasonality. For those species which did demonstrate concordant seasonality over two years there was no single season of population increases such as common in inshore waters. Rather, some peaked in spring, some in summer, and some in fall. The time of greatest reproductive activity on the outer shelf appears to be from late spring (June) to early fall (October).

The seasonal persistence of the outer shelf macrobenthos is at variance with several reports suggesting considerable temporal variability in the Atlantic shelf benthos. Maurer et al. (1976) suggested that the macrobenthos of the central and outer shelf off Delaware Bay was subject to large variations in the populations of dominants, although the trophic structure remained persistent. Their data are based on two sampling periods (May and November) and are presented based on combined small samples (portions of a Shipek grab sample). The differences are largely the result of larger collections of the annelids *Polygordius* sp., *Exogone verugera* and *Spiophanes bombyx* in November. Because of the presentation of data combined over many stations, the semi-quantitative sampling procedures and susceptibility of estimates of populations of small polychaetes to sorting techniques, these data must be viewed cautiously. Raytheon (1977) also reports large increases in densities of several species of outer shelf benthos from September-October 1974 to March-April 1975 to July-August 1975. Their conclusions are also potentially misled by probable variability in sample analysis as suggested by the dramatic increases of foraminifera, *Polygordius* and *Exogone* spp. upon modification of sample processing procedures. For macrofaunal species reliably sampled, densities found for the last two sampling periods, during which the same procedures were employed, are quite comparable. There are, however, clear cases of seasonal increases for a few species, e.g. *Scalibregma inflatum*.

Comparisons with the results of NMFS sampling of areas B and E as discussed above further supports the perception of persistence. The communities have maintained the same composition and the populations of dominant characterizing species remained relatively constant over more than three years. Occasionally high abundances of irruptive species, such as *Spiophanes bombyx*, and recently set juveniles, such as *Echinarachnius parma*, occur. These may give a false impression of temporally varying structure if data are relativized as percent composition of each species or as ranked dominants. However, if absolute densities of the consistent dominants are compared the communities appear persistent.

Of course, the mesoscale habitat complexity makes the assessment of temporal variability difficult. Relocation errors of the order of scores of meters can place the sampler in a different habitat than previously sampled and the faunal differences observed may be due to spatial rather than temporal variation. Environmental impact assessment strategies which attempt to follow time series of impacts or recovery must take into account the substantial biological variation introduced by spatial heterogeneity on scales requiring precise navigation.

Few data exist on the persistence of shelf benthos. The best information comes from shallow shelf communities off Georgia (Frankenberg and Leiper 1977) and in the North Sea (Ziegelmeier 1963, 1970; Buchanan et al. 1974). The benthos of the inner Georgia shelf shows dramatic seasonal and annual variations of populations of dominant species. Some species had similar seasonal variations from year to year, e.g. the polychaete Spiophanes bombyx, the cumacean Oxyurostylis smithi and the bivalve Ensis directus; others showed a particular seasonal pattern in some years and not others, while still others were found in abundance during only one year. On the other hand, Day et al. (1968) concluded that the macrobenthos of the North Carolina shelf showed little seasonal variation during a one year study, although few data are presented to support their conclusions. The continental shelf, particularly the inner shelf of the South Atlantic Bight, is bathed by warm waters and inshore areas experience a considerable seasonal temperature range. This drives growth and reproduction rates theromodynamically, increasing r, the intrinsic rate of increase of populations. From theoretical considerations related to population growth alone, one can conclude that populations with a large r are "condemned to track environmental fluctuation, where as those with relatively small r [benthos of the boreal Middle Atlantic Bight] may average over essentially all fluctuations" (May 1977).

Seasonal and long term variations are also known for North Sea benthos. Zeiglemeier's (1963, 1970) data suggest long term persistence but with some definite seasonal variation for sand bottom macrobenthos of the German Bight. However, disruptions caused by intense winters, for example, may cause irruptions of some species, e.g. again Spiophanes bombyx. Buchanan et al. (1974) found persistent diversity and production of a mud bottom community off Northumberland. However, in terms of constituent populations, there were "conservative" species with persistent populations, "volatile" species which were subject to great fluctuations in abundance from year to year, and "opportunistic" species which can rapidly increase their numbers in response to the elimination of a highly productive volatile. Clearly, there is a mix of species displaying various temporal responses in most benthic communities. The assemblages of the outer shelf and upper slope of the Middle Atlantic Bight have a high proportion of apparently "conservative" species and relatively few opportunists or "volatile" forms.

Highly dynamic macrobenthic communities appear to be the rule in coastal and estuarine habitats. Most of the relevant literature has been reviewed by Boesch et al. (1976) to which must be added Levings (1975), McCall (1977), Whitlatch (1977), Holland et al. (1977), Rachor and Salzwedel (1975) and Rachor (1977). Persistent populations seem to exist among longevous species such as large infaunal bivalves (Peterson 1975) or in cold stenothermal habitats (Lie and Evans 1973; Richardson 1977; Lowry 1977). The offshore increase in community persistence found on the Middle Atlantic shelf parallels increased stenothermal conditions and reduced frequency of sediment disturbances.

Implications for Impact Assessment

A major difficulty in establishing biological "baseline" conditions is the determination of temporal patterns of variability against which changes can be measured. Highly variable and dynamic communities present a particular problem because it often becomes impossible to determine if changes witnessed in impact investigations are due to effects of man's activities or natural variations. The two years of sampling have shown the benthic communities of the outer Middle Atlantic shelf have persistent integrity. If these communities are truly persistent in the long term then confidence in impact detection will be high. Furthermore, this persistence implies that baseline monitoring need not entail extensive multi-year sampling. Rather, more efficient long-term studies should be limited in scope, otherwise, the information gained to cost ratio will decline drastically.

Response of the Benthos to Catastrophic Disturbance

It has become increasingly apparent that disturbances are important in the structuring of biotic communities and that even such "benign" epitomes of biotic diversity as tropical rain forests and coral reefs are structured by disturbances (Connell 1978). It was hypothesized in the preliminary report on these studies (Boesch et al. 1977) that small scale disturbances attributable to sediment movement and predator cropping were important structuring mechanisms for the benthos of the Middle Atlantic continental shelf. It was, in part, to collect evidence regarding these hypotheses that the recolonization and fish food habit studies were undertaken during the second year. The recolonization study simulated a small scale catastrophic disturbance and the hypoxia incident of the summer of 1976 provided a large scale catastrophic disturbance of a different mode, but which nonetheless proved instructive of responses to disturbances in general.

The results of both of these investigations have important implications in understanding the potential impacts of anthroprogenic stress resulting from oil and gas development. For example, estimates of the recovery rates assuming complete extirpation of the benthos have been used in environmental assessments of the effects of oil spills (Offshore Oil Task Group, Massachusetts Institute of Technology 1973). These predictions have been based on little or no direct evidence and often naive assumptions based strictly on growth rates. The results of the recolonization and response to hypoxia studies provide the first direct evidence of the recovery of continental shelf benthos from such catastrophic disturbance.

Effects of the Hypoxia of the Summer of 1976

The widespread low dissolved oxygen conditions which developed during the summer of 1976 were apparently unprecedented during the history of measurement or recollection (Sharp 1976), although localized depletions in the New York Bight Apex in 1968 and 1971 also resulted in fish kills (Ogden and Chess 1968; Young 1973). The anoxic or nearly anoxic conditions which prevailed at the heavily affected C-stations during parts of July, August, and September 1976 produced substantial mortalities of the resident benthos which parallel those found by other investigators in oxygen stressed habitats (Dean and Haskin 1964; Tukki 1965; Reish 1966; Leppakowski 1968, 1969; Rosenberg 1972, 1977; Boesch et al. 1976; Arntz 1977; Rachor 1977; Holland et al. 1977).

Crustaceans, including the small peracaridans and the epibenthic crabs and shrimp, suffered essentially complete mortalities in the most severely impacted inner shelf habitats. Crustaceans are active with a high metabolism and have generally not developed respiratory adaptations to cope with hypoxic conditions or H_2S toxicity (Theede et al. 1969). Echinoderms also suffered nearly complete mortalities. Echinoderms are generally lacking in oxygen stressed shallow water habitats (Rosenberg 1972). The physiological inability of *Echinarachnius parma* to tolerate very low dissolved oxygen conditions has been demonstrated by Mangum and Van Winkle (1973). The European *Asterias rubens* was found to be intermediate in comparison with other invertebrates in its resistance to oxygen depletion and H_2S (Theede et al. 1969). Large mortalities of *E. parma* and *Asterias forbesi* were also found by other investigating the 1976 hypoxia (Milstein et al. 1977).

Molluscs were generally more tolerant of hypoxia. Many common species on the inner shelf (*Tellina agilis*, *Astarte castanea*, *Nucula proxima*, *Pitar morrhuana*, and *Nassarius trivittatus*) survived. However, the surf clam, *Spisula solidissima*, apparently suffered nearly-complete mortalities in the areas affected by persistent hypoxia (Steimle 1976). *Spisula* is known to have poor resistance to hypoxia (Theede et al. 1969) and in experiments lost burrowing activity after three days at 0.8 mg/l O_2 (Savage 1976). On the contrary, the respiratory pigment adaptation of the bivalve genus *Astarte* allows its survival at extremely low oxygen levels (Tukki 1965; Leppakowski 1968, 1969; Theede et al. 1969; Arntz 1977).

Annelids varied in their response to hypoxic stress, while some species (e.g. *Lumbrinerides acuta* and *Polygordius* sp.) suffered apparent mortalities, for others (e.g. *Goniadella gracilis* and *Clymenella torquata*) there was no indication of substantial reductions in population density in August 1976. Many marine annelids are facultative anaerobes (Mangum 1970) and the survival of some species during anoxia is not surprising. However, those forms adapted for life in well aerated, coarse dynamic sands are probably maladapted for resistance to hypoxia. Cerianthid anemones increased in abundance after the hypoxia but also appeared to survive relatively well the immediate stress (Milstein et al. 1977; Radosh et al. 1977), although some other investigators reported mortalities or other evidence of stress in cerianthids as a result of hypoxia (Steimle 1977; Bullock 1976).

As would be expected, immediate response of the macrobenthic community to hypoxic stress was a reduction in species (areal) richness and overall density and biomass. However, the effect on Shannon diversity (H') of the community was ambiguous. The diversity of megabenthos at Station C2 declined but increased at Station N3. The diversity of macrobenthos declined at Station C4 in August, but increased at stations C2 and G2. These disparate adjustments resulted largely from changes in the evenness component of diversity. Where diversity was low before hypoxic stress due to heavy dominance by species whose populations were reduced by the stress, the Shannon diversity index increased due to enhanced evenness. Where diversity was high or moderate due to high evenness, Shannon diversity declined due to reduced species richness. Ambiguous response of such composite diversity indices in response to stress is frequently found (Swartz in press) and it underscores the need to assess the components of species diversity and not to simply rely on interpretation of a composite diversity.

Parallels Between Recolonization after Hypoxia and Artificial Defaunation

In many ways the information which was gathered on the response of benthos following hypoxic stress and in artificially defaunated sediments of the recolonization study are parallel "experiments" on the recuperation and organization of benthic communities. However, several important differences should be pointed out: a) the hypoxia caused partial not complete elimination of macrobenthos; b) the spatial extent of the disturbances; c) differences in the habitats affected; d) the plankton blooms and hypoxia probably resulted in greater organic enrichment of the sediments; and e) differences in timing of the perturbation. In addition to habitat differences, the differences in scale of the perturbations are most important to consider. Small scale disturbances are frequent in most environments and they lead to patchiness which is an important mechanism structuring communities (Levin 1974; Levin and Paine 1974; Connell 1978). As a consequence, many members of natural communities have adaptations to respond to or recover from local disturbance. Spatially extensive disturbances, however, may select for a considerably different suite of species.

Initial Response

There is an extensive theoretical and empirical literature on responses to disturbance in communities (see Gadgil and Solbrig 1972). Treatments of the marine benthos (Boesch 1974; Grassle and Grassle 1974; McCall 1977) indicate that small surface-resource (surface deposit feeding and suspension feeding) forms are the earliest colonizers and that these forms have life history adaptations which allow their rapid exploitation of the resources made available by disturbance. The life histories of these "opportunistic" species emphasize reproductive rather than maintenance processes and are the product of what is termed r-selection (Gadgil and Bossert 1970). Opportunists are characterized by rapid growth and maturation, high fecundity and great capabilities for dispersal of offspring. Some opportunists produce large numbers of planktonic larvae, while other produce smaller numbers in a given spawning but offer some brood protection. Although many of these differences result from phylogenetic patterns (e.g. few bivalves brood larvae and peracaridan crustaceans all offer brood protection and thus have no free larval dispersal in the plankton), r-selection tends to maximize reproduction within the phylogenetic framework at the "expense" of longevity.

Other species in communities may be relatively K-selected or equilibrium species. Such species generally have more persistent populations of more longevous individuals with lowered fecundity. In benthic communities these generally include the larger deeper-living macrobenthos and those which utilize subsurface resources.

Following substantial disturbance one might expect the most rapid colonization by opportunists, some of which may be such poor competitors as to be extremely rare in the unperturbed community, i.e. fugitive species (Hutchinson 1957), others of which are normally found in the natural community. Subsequent colonization would be by progressively more equilibrium species, which have limited recruitment (low resilience, sensu Boesch 1974) but, once established, experience lower adult mortality.

The early colonizers following hypoxia on the inner shelf and artificial defaunation of the outer shelf exhibited characteristics of opportunists. The polychaete *Spiophanes bombyx* developed large populations which persisted for approximately one year on the inner shelf. The cosmopolitan species is known to demonstrate irruptive and ephemeral population dynamics in the German Bight (Ziegelmeier 1970), the Chesapeake Bay (Boesch 1973), the Georgia continental shelf (Frankenberg and Lieper 1977), and the Oregon continental shelf (M. Richardson, personal communication). It is very widely distributed on the continental shelf and polyhaline coastal waters in the Middle Atlantic and, *Spiophanes* larvae have been found in the plankton at Woods Hole nearly continuously from June to February (Simon and Brander 1967). Spionid polychaetes, in general, seem to be opportunists as the family contains several well known opportunistic species: *Polydora ligni* (Grassle and Grassle 1974 and Boesch 1977), *Paraprionospo pinnata* (Dauer and Simon 1976; Boesch et al. 1977; Holland et al. 1977), *Streblospio benedicti* (Grassle and Grassle 1974; Boesch 1977; Whitlatch 1977) and *Scololepis fulginosa* (Leppakowski 1968; Rosenberg 1972). Reproduction in spionids generally involves brooding followed by a variable planktonic larval existence. Ampharetid polychaetes are not known to be opportunists, but their development generally includes some brood protection (Zottoli 1974). Similarly, ceriantheid anemones are not generally characterized as opportunists and may, in fact, be quite long-lived. The bivalves *Spisula solidissima* and *Tellina agilis*, unlike the aforementioned species, were common in dynamic sand bottoms before the hypoxia of 1976. It appeared that their subsequent setting success was greater than usual, but this is speculative. Mactrid and tellinid bivalves and these species in particular are known for high fecundity and occasionally very dense setting.

In addition to the evident dispersal powers of the early colonizers of hypoxia-affected habitats, what factors allowed their populations to establish and persist for at least a year or more when several of these species were previously excluded or limited in population density? This question cannot be definitely answered and it is probable that a combination of factors were responsible. The following explanations commend themselves: 1) relaxation of competitive pressures because of mortalities caused by the hypoxia; 2) reduction or elimination of predators, which through predation or physical disturbance of the substrate regulated the colonist species; 3) organic enrichment resulting from the sedimentation of plankton blooms or mass mortalities of benthos; 4) enhanced stability of the sediment due to quiescent hydraulic conditions and/or biogenic stabilization by tubes.

Those macroinfaunal species which were eliminated by the hypoxia, e.g. amphipods, tanaidaceans, and small polychaetes, would not appear to be direct competitors of the opportunistic colonizers, e.g. *Spiophanes bombyx* and ampharetid polychaetes. The latter group was dominated by sedentary tubicolous animals which feed on surface deposits while the former are discretely motile (Jumars and Fauchald 1977) or burrowing forms which exploit both interstitial and surface resources. Pre-hypoxia infaunal densities were low, suggesting that populations were not controlled by competition and thus that mass mortalities did not offer a relief to this competition.

It is increasingly recognized that macroinfaunal populations are strongly regulated by large predators (Virnstein 1977; Peterson, in press). The elimination of the abundant megabenthic crabs, sea stars, shrimp, and *Echinarachnius parma* may have allowed opportunists excluded or controlled by the activities of these animals to become established. The activities include consumptive predation *per se* and sediment disturbance due to movement or foraging which may cause mortalities of recently set infauna in particular. Although Crangon, Cancer, Asterias, and Echinarachnius were recruited quickly (by November 1976) into affected inner shelf habitats, the recruits remained much smaller than previous inhabitants, thus exerting less of an influence than their relative abundance might indicate.

Although analyses indicated only a slight or no increase in sediment organic carbon concentrations associated with the hypoxia, observations indicate that there was an enriched surface layer, at first a floc resulting from sedimentation of the plankton bloom (Steimle 1976) and later biogenically bound fine particulate matter. The analyses performed on sediments did not adequately reflect these because they were performed on a homogenized sample of the top 6 cm of sediment. R. C. Swartz (personal communication, U.S.E.P.A., Newport, Oregon) sampled macrobenthos at a site off Fire Island, Long Island, during this same period and found similar irruptions of Spiophanes and ampharetids. There, however, they were not preceded by mass mortalities of indigenous benthos because severe hypoxia had not developed. The seabed off Fire Island was probably enriched by the spring phytoplankton bloom.

Given, for whatever reason, the dense recruitment of early colonizing macrobenthos, it seems likely that the stabilization of sediments by thick masses of polychaete and cerianthid tubes enhanced the survival of the opportunists. Bottom photographs taken at the inner shelf station C2 showed that the rippled "barren" sand characteristic of this habitat was covered and stabilized by worm tubes until the winter of 1978 when it appears that a severe "northeaster" moving along the Middle Atlantic coast broke up the biogenic binding.

In summary, it appears most likely that in inner shelf habitats severly impacted by hypoxia, a combination of eliminating motile megabenthos and organic enrichment allowed establishment and habitation by macrobenthos previously uncommon in these habitats. Furthermore, the activities of these early colonists may have enhanced their survival and played some role in delaying the return of some indigenous species.

At first examination, it seems that the early colonists in the recolonization experiments conducted on the outer shelf bear few, if any, similarities with those colonizing inner shelf habitats following hypoxia. Amphipods, notably absent following the hypoxia, were important immigrants to the sediment boxes. The polychaete Capitella capitata, the archetype marine fugitive species (Grassle and Grassle 1974), was the only important colonist which was rare in the natural environment.

However, when differences in the mode of disturbances are accounted, certain similarities in repopulation become apparent. An important difference between the two disturbances is their scale.

Peracaridan crustaceans, including amphipods, brood their young and thus do not have broad planktonic dispersal. Thus, the amphipods and tanaidaceans previously abundant on the inner shelf must slowly reestablish themselves by "leaps and bounds" through several generations of short range dispersal. It is interesting to note that several species of adult cumaceans did colonize hypoxia-affected habitats by fall 1976, for these peracaridans have greater long-range dispersal abilities because of their tychopelagic migrations, often on a diel basis. Similarly, the cumacean *Diastylis rathkii* rapidly colonizes hypoxia stressed or artificially defaunated habitats in the Baltic (Tukki et al. 1965; Brunswig et al. 1976; Arntz et al. 1977). Many amphipods are, however, admirably suited to repopulate following local disturbances because they remained reasonably motile as juveniles or adults. Their recolonization potential is not so limited by the timing of the disturbance as many bivalves or polychaetes, for example, which must recruit via planktonic larvae which may be only seasonally available. Thus, there are two strategies for opportunists adapted to respond to local disturbance (environmental patchiness): a) brood protection and either nearly continuous reproduction (e.g. *Capitella*) or post-larval dispersal (e.g. amphipods), or b) long range planktonic dispersal coupled with high fecundity and nearly continuous reproduction (e.g. *Spiophanes*).

The rapid population of azoic sediment boxes by corophiid amphipods (*Unciola* and *Erichthonius*) compared with the slow population by ampeliscid amphipods which are also abundant in the natural community appears to be a result of the relative motility of the two forms. While both are tubicolous, corophiids seem to be more vagrant and can more quickly occupy tubes and can survive outside of tubes while the ampeliscids seem to be obligately domestic and less able to reconstruct tubes if dislodged. Ampeliscids have, however, been reported as early colonizers of disturbed habitats including dredge spoils (Saila et al. 1972) and defaunated sediment (McCall 1977). Their ability to colonize disturbed habitats may depend on the timing of spawning, or the immigration of young, which may be more capable of dispersal.

Succession

Subsequent to early colonization of these disturbed habitats, is there a predictable or even interpretable (*ex post facto*) pattern of subsequent community development, i.e. a successional sequence? The application of the classical concepts of succession developed mainly by terrestrial plant ecologists (Odum 1969) to marine benthic communities has been recently questioned (Connell and Slayter 1977; Sutherland and Karlson 1977). Implicit in the classical concept (Connell and Slayter's model 1) is that early colonists are exclusively capable of utilizing a newly available habitat and that they alter the habitat in such a way as to make it suitable for subsequent arrivals, i.e. "prepare" it. Alternate models have received increasing support by evidence. Under Connell and Slayter's model 2, all species are equally capable of utilizing the habitat following disturbance but arrive at varying rates depending on their life history strategies. Under model 3, initial colonizers inhibit rather than enhance the influx of subsequent arrivals until they are themselves eliminated by disturbance, predation, etc.

The responses to disturbance witnessed in our investigations also offer little support for the classical concept of succession. Instead, more random processes were observed in which colonization sequences were determined by availability and life history strategies (model 2). Although the early colonists could have exerted an inhibitory influence on later arrivals (e.g. dense Spiophanes populations consuming larvae or modifying the previously dynamic sand bottom through tube construction (Woodin 1976), the evidence supporting model 3 is equivocal. Rather it appeared, both from the fragmentary results of the predator exclosures in the recolonization experiment and from the possible effects of predator decimation in hypoxia-affected habitats, that predator control may be most important in determining the course of community development.

In any case, the path of community development is complex and of limited predictability, possibly resulting in several different outcomes or "multiple stable points" (Sutherland 1974). However, against this rather nihilistic view must be balanced the remarkable predictibility of spatial and temporal patterns of natural communities on the continental shelf and slope.

Implications for Environmental Impact Assessment

The observations made here have some very important implications both in predicting the severity of impacts of man's activities and in detecting these impacts in the environment. The results demonstrate the inappropriateness of applying simple models based on individual maturation time or longevity to assess time for community recovery following catastrophe, such as those applied by the Offshore Oil Task Group, Massachusetts Institute of Technology (1973) and others in environmental impact statements. When the slate is wiped clean, species other than those originally present may crop up and there may be a considerable period of time for the original occupants to return. Species life histories vary. Complex biotic interactions occur. Different scales and modes of disturbance may produce different results.

It is impossible to definitively conclude that a certain period of time is required for community "recovery". The criterion of recovery is, of course, debatable. However, by any reasonably criteria, the inner shelf communities had not recovered 18 months (February 1978) after the hypoxia and the outer shelf communities in sediment boxes had not "recovered" 43 weeks after defaunation.

More encouraging are the implications these results have regarding detection of environmental impact. Disturbed communities were clearly different from unaffected communities for a considerable period of time after the disturbance. Such differences should be statistically detectable by properly designed survey or monitoring, especially on the biotically predictable outer continental shelf. Secondly, despite technical difficulties, the concept of manipulative field experiments involving continental shelf sediments yielded useful results. Although oil treated sediments were not recovered, results of chemical and sedimentological analyses indicate that sediments can be collected, treated, deployed, and recovered without contamination or serious artificial effects. The biological results have shed some light on the basic question of recovery rates and, furthermore, yielded important insight into processes of recruitment and biotic interactions, materially enhancing interpretation of benchmark sampling.

Experience with these preliminary recolonization experiments indicates that more reliable deployment and recovery systems are required for operation at depths in excess of 50 m than afforded by use of non-saturation diving systems. Submersibles, diver lock-out systems or saturation diving systems would allow longer bottom time and greater mobility in locating and retrieving experiments. All these approaches are very expensive, however. Rather, development of surface-retrievable experimental arrays is desirable. In this manner experimental sediment boxes could be deployed and recovered from a surface vessel by the use of acoustic releases coupled with effective uncovering and covering apparatus.

Biotic Interactions

Relationship with the Plankton

The macrobenthos of the Middle Atlantic Bight interacts with the plankton in two basic ways: the plankton serves as a direct or indirect food source and many members of the benthos are temporary inhabitants of the plankton in some stage of their life cycle.

The nearly exclusive source of organic matter in the outer shelf beyond the zone of direct coastal influence is protophyte production. Primary production by benthic protophytes undoubtedly occurs over the inner and central shelf but is believed to be quantitatively unimportant on the outer shelf. Rather, production by phytoplankton is the basis of benthic food webs. The benthic faunal communities are, however, deposit-feeder dominated and it is unlikely that suspension feeding on living plankton drifting over the bottom is quantitatively important in the flux of carbon through the benthos. Rather, it is suggested that sedimentation of planktonic detritus serves as the main input to the dominant surface deposit feeders and suspension feeders which filter the rich surface flux. Following seasonal phytoplankton blooms a significant portion of the production may settle to the bottom (Stephens et al. 1967; Bodungen et al. 1975). Thus seasonal input of particulate detritus serves as an enriching, potentially destabilizing force. While microbial metabolic rates might be expected to respond to such seasonal inputs and companion investigations of meiobenthos suggest that micrometazoans may have characteristic increases in populations in response to seasonal enrichment (Chapter 7), the macrobenthos shows no such pattern. The macrobenthos must either be unable to respond because of population growth (i.e. life history) constraints or their populations may be controlled by other factors (e.g. predation) and the deposit feeders are not generally food limited.

Although no comprehensive review of the literature has been attempted, it appears that the majority of macrobenthos of the outer shelf comprises species with planktonic larval dispersal. Some groups, such as the important peracaridan crustaceans, are not truly meroplanktonic, but some of these are temporarily pelagic as larval or adults. Clearly, the benthos and plankton are linked because of the importance of pelagic dispersal, however, the relationship is hard to elucidate because the larvae of many species, including polychaetes, molluscs, and echinoderms, were not sampled or identified during the investigations of zooplankton and neuston (Chapter 4). The only clear relationship between dispersal of larvae in the plankton and recruitment to the benthos appeared for decapod crustaceans. Large collections consisting of small juveniles of the shrimp *Crangon septemspinosa* and the crab *Cancer* spp. were taken on the seasonal cruise after their larvae were abundant in the plankton.

Macrobenthos-Meiobenthos Interactions

The interactions of macro- and meiobenthos remain speculative (Coull 1973). Meiobenthos has traditionally been viewed as a "trophic dead end", providing little nutrition to the macrobenthos. Although the relationship remains unquantified, it now appears that the meiobenthos may provide some of the food, perhaps a significant portion, of the macrobenthos (Elmgren 1977; Sikora et al. 1977; Gerlach 1978). Typically, this is viewed as the ingestion of meiofauna non-selectively with deposits, since it now appears that the biomass of meiobenthos is significant with respect to that of bacteria (Sikora et al. 1977; Gerlach 1978). This may be the case for the abundant surface deposit feeders of the outer shelf. However, it is possible that, especially in coarse grained habitats, specialist meiobenthic predators may exist among the macrobenthos, i.e. in the form of interstitial feeders such as the polychaetes *Goniadella gracilis*, *Lumbrinerides acuta* and diverse syllids. The populations of these species were most abundant in those habitats that also supported the highest densities of interstitial meiobenthos (Chapter 7) suggesting a possible trophic relationship, not simply a coincident adaptation to the prevalence and size of interstices.

The other side of the coin is the role of macrobenthic "predators" (including deposit feeders) in regulating the meiobenthos. Our combined studies yielded no direct evidence on this, however, the emerging opinion of many students of the meiobenthos suggests such regulation is widely important.

Role of Predation on Macrobenthos

The control of community structure of soft bottom benthos by epibenthic predators is an emerging paradigm (Virnstein 1977; Peterson in press). Although somewhat limited, the results of predator exclosure in the recolonization experiments lend evidence that the outer shelf communities are, in part, predator controlled. Populations of several species, notably corophiid amphipods, were denser in screened sediments than in azoic sediments exposed for an equivalent period of time. The structure of the colonizing community offered some predator protection more rapidly approached that of the natural community than in unprotected boxes. Furthermore, the species which were favored by protection were found to be important prey items of bottom feeding fishes (Chapter 9).

There is a diverse array of epibenthic predators on the outer continental shelf. Of the benthic fishes, red hake, *Urophycis chuss*; little skate, *Raja erinacea*; scup, *Stenotomus chrysops*; gulf stream flounder, *Citharichthys arctifrons*; fourspot flounder, *Hippoglossina oblonga*; and ocean pout, *Macrozoarces americanus* are important predators of benthic invertebrates (Chapter 9). Epibenthic invertebrates including the brachyuran crabs *Cancer irroratus* and *C. borealis*, the caridean shrimps *Crangon septemspinosa* and *Dichelopandalus leptoceras*, naticid gastropods, and the asteroids *Asterias* spp. and *Astropecten americanus* are also important predators of infauna. There is no one keystone, preeminent predator. Predation pressures are diverse but apparently intense as judged by the abundance of predators.

The food habits of the invertebrate predators remain unknown, but parallel investigations of the food habits of fishes in areas B and E (Chapter 9) have yielded much insight into the predation pressures exerted by fishes on the macrobenthos. Fish predation does not impact the benthos uniformly but certain components are more intensively preyed due to the selective feeding behavior of the prey fish. Decapod and peracaridan crustacans are the most important food items of bottom feeding fishes on the outer shelf, whereas the generally numerically dominant polychaetes are not heavily consumed. The disproportionate predation on the peracaridan crustacean (particularly amphipod) component of the infauna is depicted in Figure 6-119 which illustrates the basic trophic structure of the higher consumers of the outer shelf. Ampeliscids, and, in particular, corophiid amphipods are consumed far out of proportion with their numbers in the infauna. These forms live in tubes near the sediment surface and are thus more vulnerable than the more deeply burrowing or smaller infaunal forms represented in the polychaetes and molluscs. Such abundant polychaetes as Spiophanes bombyx, cirratulids, sabellids, Goniadella gracilis and Lumbrinerides acuta were extremely rare in fish stomachs.

Within the peracaridans, moreover, there are predator specific patterns of prey selectivity (Table 6-28). The two common corophiids Erichthonius rubricornis and Unciola irrorata were important items in the diets of all strictly bottom-feeding fishes. Ampeliscids were of only significant importance to Raja, Stenotomus, and Citharichthys. Ampelisca agassizi, which is tremendously abundant in swale habitats, was seldom consumed except by scup (Stenotomus). Other less abundant ampeliscids were consumed in greater amounts even in habitats where A. agassizi was abundant. This could be related to tube structure which may offer A. agassizi greater protection than the other ampeliscids. The heavy predation on Erichthonius and Unciola is interesting to consider in light of their early colonization of azoic sediment in the recolonization experiment. To extend the argument made earlier, these amphipods can tolerate the intense cropping and still remain abundant by their life history characteristics which allow rapid recovery from local disturbance. Short generation time, brooding, and post-larval dispersal are advantageous attributes of intensely cropped prey.

The diets of fishes did not very closely reflect the differences in prey communities in the topographic habitats in which they were captured. Although some fishes did reflect some prey differences related to topography, e.g. scup preyed on Ampelisca agassizi in swales and Chone infundibuliformis at the shelf break, the main prey items are more-or-less ubiquitous species which are found widely, but in variable density, among outer shelf habitats.

Summary of Significant Findings

1. The macrobenthos (collected by grab and sieved through a 0.5 mm mesh) of the study area was dominated by small polychaetous annelids and peracaridan crustaceans and to a lesser degree by molluscs and echinoderms (echinoids and ophuroids). The megabenthos (collected by dredge or trawl with a 4 mm mesh bag) was dominated by decapod crustaceans, echinoderms (asteroids and echinoids) and bivalve molluscs.

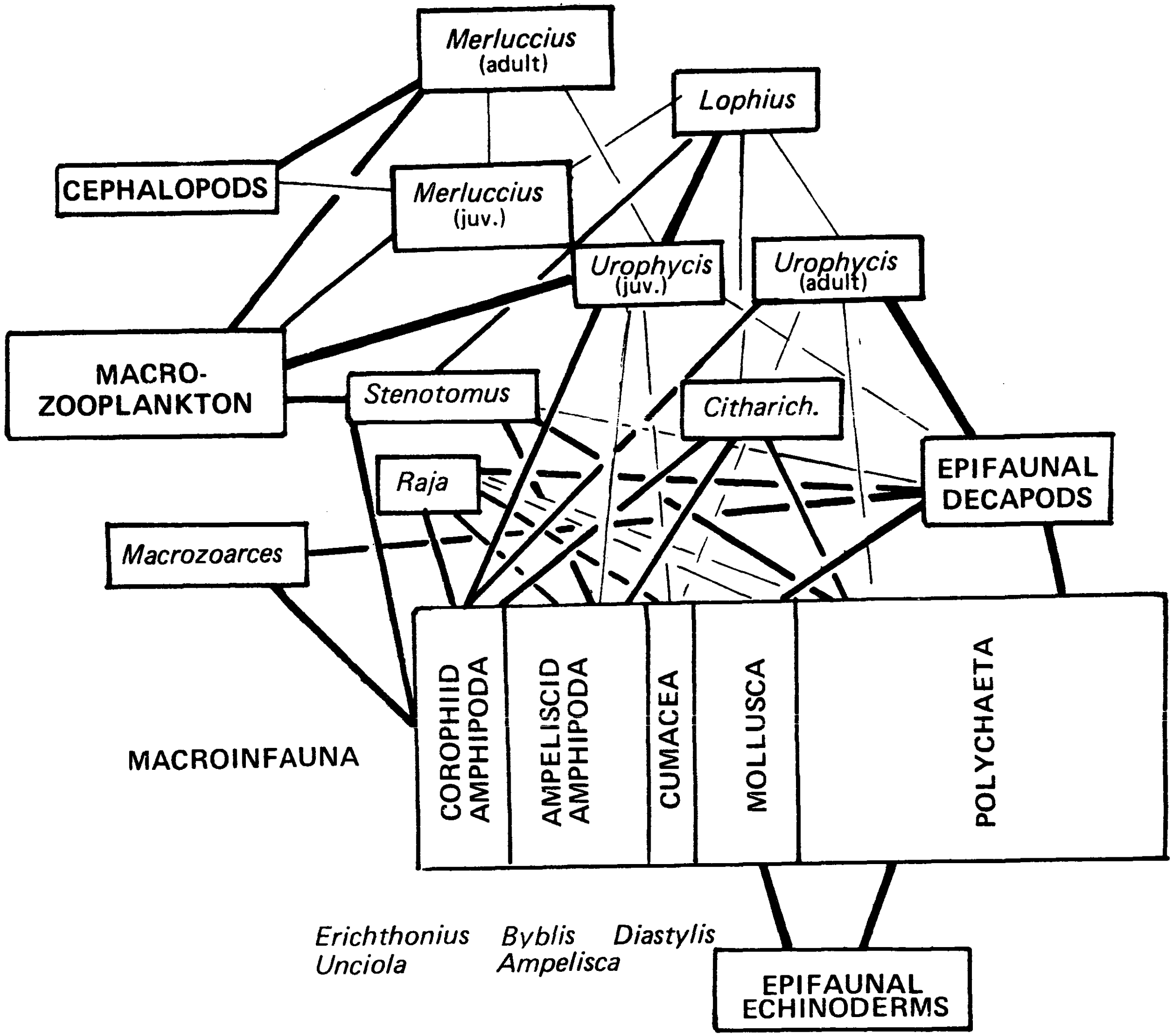

Figure 6-119. Schematic food web connecting macrobenthos and dominant bottom feeding fishes on the outer shelf. Macroinfauna partitioned according to the relative abundance of major taxa, emphasizing disproportionate predation on Amphipods. Wide lines indicate major prey items, narrow lines indicate subordinate prey.

Table 6-28. Importance of species of pericaridan crustaceans as prey for bottom feeding fishes on the outer continental shelf as indicated by their index of relative importance (Chapter 9).

	Predator Species									
Prey Species	*Raja erinacea*	*Urophycis chuss*		*Urophycis regius*	*Merluccius bilinearis*	*Macrozoarces americanus*	*Stenotomus chrysops*	*Citharichtys arctifrons*	*Hippoglossina oblonga*	
		JUV.	ADULT		JUV.				JUV.	ADULT
AMPHIPODA										
Ampeliscidae										
Byblis serrata	xxx	x	x	x	xx		x	xx	xx	x
Ampelisca agassizi							xx			
Ampelisca vadorum	xx		x		x	x	x	xx		
Corophiidae										
Erichthonius rubricornis	xxx	xx	xxx	x		xxx	xxx	xxx	xx	
Unciola irrorata	xxx	xxx	xxx	xx		xxx	xx	xxx	xxx	x
Leptocheirus pinguis	x									
Phoxocephalidae										
Trichophoxus epistomus	x		x	x						
Phoxocephalus holbolli							x			
Lysianassidae										
Hippomedon serratus				x						
Hyperiidae										
Parathemisto gaudichaudi		xxx		xx	xxx		xx	x		
CUMACEA										
Diastylis bispinosa	xx	x			x			x		
Diastylis sculpta	xx					x		x		
ISOPODA										
Cirolana polita			x	x						

x - minor importance
xx - secondary importance
xxx - major importance

2. Biomass of macrobenthos was similar to that reported in other studies in the Middle Atlantic Bight. Numerical density, however, was much greater than reported in most studies, owing in part to the finer sieve mesh size used in this study. Comparable densities have been reported in studies employing similarly fine sieves and careful sorting. Biomass distribution patterns varied among the higher taxa. Biomass of annelids and molluscs was highest on the outer shelf and in topographic depressions, whereas echinoderm biomass, dominated by the sand dollar *Echinarachnius parma* was highest on the central shelf.

3. The megabenthos and macrobenthos demonstrated similar distribution patterns across the continental shelf and upper continental slope. Faunal changes were mainly continuous rather than abrupt, but five faunal zones could be distinguished: inner shelf (to 30 m), central shelf (30-50 m), outer shelf (50-100 m), shelf break (100-200 m) and continental slope (>200 m). Inner and central shelf assemblages were relatively similar, and outer shelf assemblages contained both inshore and offshore species overlapping in distribution, but shelf break and continental slope assemblages were more discrete.

4. The macrobenthos demonstrated faunal similarity within bathymetric habitats throughout the study area (37°N-40°N latitude). Along-shelf differences were attributable mainly to sediment differences (e.g. the inner shelf off the southern Delmarva Peninsula has finer sands).

5. Major faunal differences occur over small distances in relation to shelf topography and its effect on sediment distribution. The most pervasive of such topographic habitats are those related to ridge and swale topography. Swales generally have finer sediments containing higher carbon content than ridges and flanks. The benthos of swales is more abundant, has a greater biomass and species richness and is composed of more deposit-feeding animals. Within each of two outer shelf areas containing many of the tracts currently leased for oil and gas development at least five topographic habitats and associated faunal assemblages can be recognized. Because of the relative richness of the benthic biota and the deposition of fine sediments in topographic depressions, such as swales, these environments must be regarded as relatively more valuable and susceptible shelf habitats.

6. Species diversity of both macrobenthos and megabenthos generally increased with depth. Highest Shannon diversity and numerical species richness of macrobenthos was found on the shelf break and continental slope and lowest was found on the inner shelf. Species richness in topographic depressions on the shelf was also high, but Shannon diversity was not, because of typically heavy dominance. Species diversity on the outer shelf and shelf break was higher than previously reported.

7. Anoxic or hypoxic conditions developed in bottom waters over a broad area of the inner and central shelf off New Jersey during the summer of 1976. The oxygen stress resulted in mass mortalities of many megabenthic and macrobenthic species. Crustaceans and echinoderms were particularly affected; however, some species of molluscs and annelids demonstrated no reduction in population density. Species which have a planktonic dispersal phase including echinoderms, decapod crustaceans, and some polychaetes returned quickly following elimination. Several opportunistic macrobenthic species not previously abundant proliferated following the perturbation, but their populations were reduced by winter 1978. Many species without a planktonic dispersal phase (i.e. larvae) such as peracaridan crustaceans had not significantly recolonized one and one-half years following their elimination.

8. Experiments designed to assess the recolonization rates of sediments in which all animals had been killed validated the efficacy of such an approach despite poor recovery success. Several experiments were recovered and they indicated that treatment and deployment did not introduce chemical contamination of sediments, which were not seriously eroded from the containers. Some colonization by macrobenthos occurred in sediments exposed for 10 weeks and substantial colonization occurred after 43 weeks. The recolonization rate was enhanced by protection from large predators. The fauna of even the most thoroughly colonized sediments (43 weeks exposed with predators excluded) was qualitatively different from that in the natural community. Tubicolous amphipods were the quickest and most successful recolonizers. One species, the notoriously opportunistic polychaete *Capitella capitata*, was found in defaunated sediments but not in the natural community.

9. Considerable interactions take place among the major components of the benthos. Correlative evidence suggests significant predation on meiobenthos in coarer sediments by interstitial feeding macrobenthos. Dense populations of epibenthic invertebrate predators (e.g. crabs and starfishes) occur in the study area and they must exert considerable predation pressure on infauna. Finally, fish food habit studies on the outer shelf indicate the heavy dependence of demersal fishes on benthic invertebrates, especially tubicolous, surface dwelling amphipods, crabs and shrimp. Only fishes which can excavate prey such as skates and, to some extent, flatfishes prey on deeper dwelling infauna.

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Appendix 6-A. Macrobenthic Taxa Collected in Grab Samples at 52 Stations, Fall 1975 to Summer 1977.

- PORIFERA
      - Porifera sp. 1
      - Porifera sp. 2
      - Porifera sp. 4
  - Calcarea
    - Heterocoelidae
      - *Scypha* sp.
  - Desmospongiae
    - Haliclonidae
      - *Haliclona permollis*
    - Microcionidae
      - *Eurypon clavata*

- CNIDARIA
  - Hydrozoa
    - Tubulariidae
      - *Tubularia larynx*
      - *Tubularia* sp.
    - Halecidae
      - *Halecium halecinum*
      - *Halecium articulosum*
      - *Halecium muricatum*
      - *Halecium beanii*
    - Campanularidae
      - *Clytia* sp.
      - *Clytia hemisphaerica*
      - *Clytia paulensis*
      - *Obelia longissima*
      - *Obelia* sp.
      - *Obelia bidentata*
      - *Gonothyraea loveni*
      - *Campanularia verticillata*
      - *Eulaomedea gelatinosa*
    - Lovenellidae
      - *Lovenella grandis*
    - Sertulariidae
      - *Sertularia cupressina*
      - *Sertularia latiuscula*
    - Plumularidae
      - *Cladocarpus flexilis*
      - *Nemertesia antennina*
    - Campanulinidae
      - *Stegopoma fastigatum*
      - *Cuspidella* sp.
    - Lafoeidae
      - *Lafoea dumosa*
    - Hydractiniidae
      - *Hydractinia echinata*
    - Bougainvilliidae
      - *Garveia* sp.
    - Eudendriidae
      - *Eudendrium* sp.
  - Anthozoa
    - Pennatulidae
      - Pennatulidae sp. 1
      - Pennatulidae sp. 2
    - Edwardsiidae
      - *Edwardsia* sp.
    - Metridiidae
      - *Metridium senile*
    - Halicampoididae
      - *Eloactis* sp.
      - *Eloactis producta*
    - Halcampidae
      - *Bicidium* sp.
    - Caryophylliidae
      - *Dasmosmilia lymani*
    - Zoanthidae
      - *Isozoanthus* sp.
      - *Epizoanthus incrustatus*
    - Cerianthidae sp.

- RHYNCHOCOELA
      - Nemertea sp. 1

Appendix 6-A. (continued)

- Nemertea sp. 2
- Nemertea sp. 3
- Nemertea sp. 4
- Nemertea sp. 5
- Nemertea sp. 6
- Nemertea sp. 7
- Anopla
  - Tubulanidae
    - *Tubulanus* sp.
  - Carinomidae
    - *Carinoma* sp.
  - Lineidae
    - *Cerebratulus lacteus*
    - *Cerebratulus luridus*
    - *Cerebratulus* sp.
    - *Micrura rubra*
    - *Micrura* sp.
    - *Zygeupolia rubens*
- Enopla
  - Amphiporidae
    - *Amphiporus* sp. 1

- ANNELIDA
  - Archiannelida
    - Polygordiidae
      - *Polygordius* sp. 1
  - Polychaeta
      - Polychaeta sp. A
    - Aphroditidae
      - *Aphrodita hastata*
      - *Laetmonice filicornis*
      - *Aphrodita* sp.
    - Polynoidae
      - *Alentiana aurantiaca*
      - *Austrolaenilla mollis*
      - *Harmothoe extenuata*
      - *Harmothoe imbricata*
      - *Harmothoe* sp.
      - *Lepidonotus sublevis*
      - *Antinoella sarsi*
    - Sigalionidae
      - *Sthenelais limicola*
      - *Sigalion arenicola*
      - *Pholoe minuta*
      - *Neoleanira tetragona*
    - Phyllodocidae
      - *Eteone lactea*
      - *Eteone heteropoda*
      - *Eteone spetsbergensis*
      - *Eteone* sp. A
      - *Eumida sanguinea*
      - *Eumida* sp. A
      - *Notophyllum foliosum*
      - *Paranaitis speciosa*
      - *Paranaitis kosteriensis*
      - *Phyllodoce arenae*
      - *Phyllodoce longipes*
      - *Phyllodoce mucosa*
      - *Phyllodoce maculata*
      - *Eulalia bilineata*
      - *Eulalia viridis*
      - *Eulalia* sp. A
      - *Mystides rarica*
      - *Mystides borealis*
    - Hesionidae
      - *Gyptis vittata*
      - *Gyptis* sp.
      - *Podarke obscura*
      - *Hesionidae* sp. A
    - Pilargidae
      - *Ancistrosyllis groenlandica*
      - *Synelmis albini*
    - Syllidae
      - *Autolytus alexandri*
      - *Autolytus* sp.
      - *Brania wellfleetensis*
      - *Brania* sp.
      - *Exogone verugera*

Appendix 6-A. (continued)

  - *Exogone dispar*
  - *Exogone hebes*
  - *Exogone* sp. A
  - *Exogone naidina*
  - *Odontosyllis longiseta*
  - *Parapionosyllis longicirrata*
  - *Pionosyllis* sp. A
  - *Syllis cornuta*
  - *Syllides convoluta*
  - *Syllides* sp.
  - *Proceraea* sp.
  - *Eusyllis lamelligera*
  - *Eusyllis* sp. A
  - *Streptosyllis varians*
  - *Streptosyllis arenae*
  - *Streptosyllis websteri*
  - *Sphaerosyllis erinaceus*
  - *Typosyllis tegulum*
  - *Typosyllis hyalina*
  - *Langerhansia cornuta*
- Nereidae
  - *Nereis grayi*
  - *Nereis succinea*
  - *Nereis zonata*
  - *Nereis* sp.
  - *Ceratocephale loveni*
- Nephtyidae
  - *Aglaophamus circinata*
  - *Nephtys bucera*
  - *Nephtys caeca*
  - *Nephtys incisa*
  - *Nephtys picta*
  - *Nephtys squamosa*
  - *Nephtys* sp.
- Glyceridae
  - *Glycera dibranchiata*
  - *Glycera robusta*
  - *Glycera oxycephala*
  - *Glycera papillosa*
  - *Glycera capitata*
  - *Glycera* sp. A
  - *Glycera* sp. B
  - *Hemipodus roseus*
- Goniadidae
  - *Goniada maculata*
  - *Goniada norvegica*
  - *Goniada brunnea*
  - *Goniada teres*
  - *Goniadella gracilis*
- Pisionidae
  - *Pisione remota*
- Sphaerodoridae
  - *Sphaerodoridium claparedii*
  - *Sphaerodoropsis corrugata*
  - *Sphaerodoropsis minuta*
- Euphrosinidae
  - *Euphrosine armadillo*
  - *Euphrosine* sp.
- Paralacydoniidae
  - *Paralacydonia paradoxa*
- Scalibregmidae
  - *Scalibregma inflatum*
  - *Scalibregma* sp.
- Opheliidae
  - *Ophelia denticulata*
  - *Travisia carnea*
  - *Travisia forbesii*
  - *Travisia parva*
  - *Travisia* sp. A
  - *Ophelina acuminata*
  - *Ophelina* sp. A
  - *Opheliidae* sp. A
- Capitellidae
  - *Heteromastus filiformis*
  - *Notomastus latericeus*
  - *Branchiocapitella* sp.
  - *Notomastus teres*
  - *Notomastus* sp. A

Appendix 6-A. (continued)

  - *Mediomastus ambiseta*
  - *Mediomastus* sp. A
  - *Leiocapitella glabra*
- Maldanidae
  - *Clymenella torquata*
  - *Clymenella zonalis*
  - *Clymenura* sp. A
  - *Maldane* sp. A
  - *Asychis carolinae*
  - *Asychis biceps*
  - *Praxillella* sp.
  - *Praxillella gracilis*
  - *Rhodine gracilior*
  - *Axiothella zonalis*
  - *Praxillura longissima*
- Sternaspidae
  - *Sternaspis scutata*
- Paraonidae
  - *Aricidea wassi*
  - *Aricidea catherinae*
  - *Aricidea suecica*
  - *Aricidea neosuecica*
  - *Aricidea abranchiata*
  - *Aricidea cerrutii*
  - *Aricidea* sp. A
  - *Aricidea* sp. B
  - *Aricidea quadrilobata*
  - *Aricidea* sp.
  - *Paraonis gracilis*
  - *Paraonis fulgens*
  - *Paraonis pygoenigmatica*
  - *Paraonis* sp. A
  - *Paraonis* sp. B
  - *Paraonis* sp.
  - *Aedicira* sp. A
  - *Cirrophorus lyriformis*
  - *Paradoneis lyra*
- Spionidae
  - *Polydora concharum*
  - *Polydora caulleryi*
  - *Polydora socialis*
  - *Polydora* sp.
  - *Prionospio steenstrupi*
  - *Prionospio cirrobranchiata*
  - *Prionospio cristata*
  - *Prionospio* sp. A
  - *Prionospio dayi*
  - *Prionospio cirrifera*
  - *Prionospio* sp.
  - *Prionospio pygmaea*
  - *Scolelepis squamata*
  - *Spio setosa*
  - *Spio* sp.
  - *Spio pettiboneae*
  - *Spiophanes bombyx*
  - *Spiophanes wigleyi*
  - *Spiophanes* sp. A
  - *Laonice cirrata*
  - *Malacoceros* sp. A
- Chaetopteridae
  - *Spiochaetopterus oculatus*
  - *Spiochaetopterus* sp.
- Poecilochaetidae
  - *Poecilochaetus* sp. A
- Onuphidae
  - *Diopatra cuprea*
  - *Diopatra* sp.
  - *Onuphis eremita*
  - *Onuphis opalina*
  - *Onuphis pallidula*
  - *Onuphis nebulosa*
  - *Onuphis atlantisa*
  - *Onuphis* sp.
  - *Rhamphobrachium atlanticum*
  - *Rhamphobrachium* sp. A
  - *Hyalinoecia artifex*
- Eunicidae
  - *Marphysa sanguinea*

Appendix 6-A. (continued)

- *Marphysa bellii*
- *Eunice pennata*
- *Eunice vittata*
- *Eunice antennata*
- *Eunice norvegica*
- *Eunice* sp.
- *Lysidice ninetta*
- *Nematonereis unicornis*
- Lumbrineridae
  - *Lumbrineris tenuis*
  - *Lumbrineris fragilis*
  - *Lumbrineris latreilli*
  - *Lumbrineris cruzensis*
  - *Lumbrineris impatiens*
  - *Lumbrineris albidentata*
  - *Lumbrineris* sp.
  - *Ninoe nigripes*
  - *Ninoe brevipes*
  - *Lumbrinerides acuta*
  - *Lumbrineriopsis paradoxa*
- Arabellidae
  - *Arabella iricolor*
  - *Arabella mutans*
  - *Drilonereis longa*
  - *Drilonereis magna*
  - *Drilonereis caulleryi*
  - *Notocirrus spiniferus*
- Dorvilleidae
  - *Protodorvillea gaspeensis*
  - *Protodorvillea kefersteini*
  - *Schistomeringos caeca*
  - *Schistomeringos* sp. A
  - *Meiodorvillea minuta*
- Amphinomidae
  - *Paramphinome pulchella*
- Magelonidae
  - *Magelona* sp.
- Apistobranchidae
  - *Apistobranchus tullbergi*
- Orbiniidae
  - *Orbina ornata*
  - *Orbina swani*
  - *Orbina michaelseni*
  - *Scoloplos fragilis*
  - *Scoloplos robustus*
  - *Scoloplos armiger*
  - *Scoloplos acmeceps*
  - *Scoloplos foliosus*
  - *Scoloplos* sp.
- Cirratulidae
  - Cirratulidae sp. A
  - *Tharyx* sp.
  - *Dodecaceria* sp.
  - *Caulleriella* sp.
  - *Chaetozone* sp.
- Cossuridae
  - *Cossura longocirrata*
- Oweniidae
  - *Myriochele heeri*
  - *Myriowenia* sp. A.
  - *Owenia fusiformis*
- Amphictenidae
  - *Cistena gouldii*
  - *Cistena hyperborea*
- Ampharetidae
  - *Melinna cristata*
  - *Ampharete arctica*
  - *Ampharete* sp.
  - *Anobothrus gracilis*
  - *Amphicteis vestis*
  - *Asabellides oculata*
  - *Lysippe labiata*
  - *Samythella* sp.
  - *Sabellides octocirrata*
  - Ampharetidae sp. y
  - Ampharetidae sp. z
  - *Amage tumida*
  - *Auchenoplax crinita*
  - *Samytha sexcirrata*
  - *Amphicteis gunneri*

Appendix 6-A. (continued)

- Terebellidae
  - *Lysilla alba*
  - *Polycirrus eximius*
  - *Polycirrus phosphoreus*
  - *Polycirrus* sp.
  - *Nicolea venustula*
  - *Amaeana trilobata*
  - *Artacama* sp. A
  - *Streblosoma spiralis*
- Trichobranchidae
  - *Terebellides stroemi*
  - *Terebellides* sp. A
- Flabelligeridae
  - *Flabelligeridae* sp. A
  - *Pherusa affinis*
  - *Brada villosa*
  - *Brada granosa*
  - *Therochaeta collarifera*
  - *Fauveliopsis* sp. A
- Sabellidae
  - *Fabricia sabella*
  - *Potamilla reniformis*
  - *Euchone incolor*
  - *Euchone* sp. A
  - *Euchone* sp.
  - *Chone infundibuliformis*
  - *Chone* sp.
  - *Jasmineira filiformis*
  - *Myxicola infundibulum*
  - *Megalomma bioculatum*
- Serpulidae
  - *Serpulidae* sp. A
  - *Hydroides protulicola*
  - *Hydroides* sp.
  - *Filograma implexa*

Oligochaeta

- Tubificidae
  - *Peloscolex dukei*
  - *Smithsonidrilus marinus*
  - *Clitello arenarius*
- Naididae
- Enchytraeidae
  - *Enchytraeus capitatus*
  - *Hemigrania postclitellochaeta*
  - *Lumbricillus codensis*

MOLLUSCA

- Polyplacophora
  - Ischnochitonidae
    - *Chaetopleura apiculata*
- Scaphopoda
  - Dentaliidae
    - *Dentalium occidentale*
  - Siphonodentallidae
    - *Siphonodentalium* sp.
    - *Cadulus aggassizii*
    - *Cadulus pandionis*
    - *Cadulus verrilli*
- Gastropoda
  - Scissurellidae
    - *Scissurella crispata*
  - Cocculinidae
    - *Cocculina* sp. 1
  - Lepetellidae
    - *Addisonia paradoxa*
  - Trochidae
    - *Solariella obscura*
    - *Calliostoma bairdii*
  - Rissoidae
    - *Alvania pelagica*
    - *Alvania brychia*
    - *Alvania castanea*
    - *Alvania harpa*
    - *Alvania* sp. 1
  - Thiaridae
    - *Melanella* sp. 1
    - *Melanella* sp. 2

Appendix 6-A. (continued)

- Epitoniidae
  - *Epitonium* sp.
  - *Epitonium multistriatum*
  - *Epitonium greenlandicum*
  - *Epitonium dallianum*
- Capulidae
  - *Capulus ungaricus*
- Calyptraeidae
  - *Crepidula fornicata*
  - *Crucibulum striatum*
- Naticidae
  - *Polinices immaculatus*
  - *Polinices duplicatus*
  - *Lunatia heros*
  - *Lunatia triseriata*
  - *Natica pusilla*
- Columbellidae
  - *Astyris* sp.
  - *Astyris diaphana*
  - *Astyris lunata*
- Buccinidae
  - *Colus pygmaeus*
  - *Colus caelatus*
  - *Colus* sp.
  - *Colus stimpsoni*
  - *Plicifuscus kroyeri*
- Nassariidae
  - *Nassarius trivittatus*
- Olividae
  - *Olivella mutica*
- Vasidae
- Marginellidae
  - *Marginella apicina*
  - *Marginella* sp. 1
  - *Granulina ovuliformis*
- Turridae
  - *Taranis cirrata*
  - *Eulimella smithi*
  - *Inodrillia dalli*
  - *Propobela pygmea*
  - *Propobela* sp. 1
  - *Propobela rathbuni*
- Aclididae
  - *Aclis* sp.
- Ringiculidae
  - *Ringicula nitida*
- Scaphandridae
  - *Cylichna alba*
  - *Cylichna gouldi*
- Philinidae
  - *Philine quadrata*
- Bullidae
  - *Haminoea solitaria*
- Retusidae
  - *Retusa obtusa*
  - *Volvulella* sp. 1
- Pyramidellidae
  - *Odostomia* sp.
  - *Odostomia bisuturalis*
  - *Turbonilla interrupta*
  - *Turbonilla* sp. 1
- Pleurobranchidae
  - *Pleurobranchaea tarda*
- Dorididae
  - *Cadlina laevis*
- Dendronotidae
  - *Dendronotus frondosus*
- Dotonidae
  - *Doto coronata*

Pelecypoda

- Solemyidae
  - *Solemya velum*
- Nuculidae
  - *Nucula proxima*
  - *Nucula delphinodonta*
  - *Nucula tenuis*
- Nuculanidae
  - *Yoldia limatula*

Appendix 6-A. (continued)

  - *Yoldia sapotilla*
  - *Nuculana acuta*
  - *Nuculana tenuisulcata*
  - *Portlandia inconspicua*
- Arcidae
  - *Bathyarca pectunculoides*
- Mytilidae
  - *Modiolus modiolus*
  - *Crenella glandula*
  - *Crenella decussata*
  - *Crenella* sp.
  - *Musculus discors*
  - *Dacrydium vitreum*
- Pectinidae
  - *Placopecten magellanicus*
  - *Cyclopecten nanus*
- Limidae
  - *Limatula subauriculata*
- Anomiidae
  - *Anomia simplex*
  - *Anomia squamula*
- Astartidae
  - *Astarte castanea*
  - *Astarte undata*
  - *Astarte crenata subequilatera*
- Carditidae
  - *Cyclocardia borealis*
- Arcticidae
  - *Arctica islandica*
- Lucinidae
  - *Lucinoma filosa*
  - *Myrtea lens*
- Leptonidae
  - *Kellia suborbicularis*
- Montacutidae
  - *Mysella ovata*
- Cardiidae
  - *Cerastoderma pinnulatum*
- Veneridae
  - *Pitar morrhuana*
  - *Liocyma fluctuosa*
- Petriocolidae
  - *Petricola pholadiformis*
- Tellinidae
  - *Tellina agilis*
  - *Macoma* sp.
  - *Macoma tenta*
- Semelidae
  - *Abra lioica*
- Lasaeidae
  - *Lasaea rubra*
- Solenidae
  - *Ensis directus*
  - *Siliqua costata*
- Mactridae
  - *Spisula solidissima*
- Corbulidae
  - *Corbula* sp.
  - *Varicorbula operculata*
- Hiatellidae
  - *Hiatella arctica*
- Lyonsiidae
  - *Lyonsia hyalina*
  - *Lyonsia arenosa*
- Pandoridae
  - *Pandora gouldiana*
  - *Pandora inflata*
  - *Pandora* sp.
- Thraciidae
  - *Thracia conradi*
- Periplomatidae
  - *Periploma fragile*
  - *Periploma leanum*
- Poromyidae
  - *Poromya granulata*
  - *Poromya tornata*

Appendix 6-A. (continued)

- Cuspidariidae
  - *Cardiomya perrostrata*
  - *Cuspidaria media*
  - *Cuspidaria* sp.
- Thyasiridae
  - *Thyasira flexuosa*
  - *Thyasira trisinuata*
  - *Thyasira pygmaea*
- Cephalopoda
  - Sepiolidae
    - *Rossia tenera*
- Aplacophora
  - Neomeniidae
  - Chaetodermidae
    - *Chaetoderma* sp.

ARACHNIDA

- Halacaridae

PYCNOGONIDAE

- Pallenidae
  - *Callipallene* sp.
- Phoxichiliidae
  - *Anoplodactylus lentus*
- Ammotheidae
  - *Ascorhynchus pyrginospinum*

CRUSTACEA

- Cephalocarida
  - *Hutchinsoniella macracantha*
- Ostracoda
  - Ostracod sp. E
  - Cylindroleberidae
    - *Synasterope* sp. 1
    - *Parasterope lata*
  - Sarsiellidae
    - *Sarsiella zostericola*
    - *Sarsiella greyi*
    - *Sarsiella georgiana*
    - *Sarsiella* sp. A
    - *Sarsiella* sp. B
  - Halocypridae
  - Philomedidae
    - *Harbansus dayi*
    - *Harbansus bowenae*
  - Pseudophilomedidae
    - *Pseudophilomedes ferulana*
  - Polycopidae
  - Cytherellidae
    - *Cytherella* sp. 1
  - Bairdiidae
    - *Bythocypris* sp. 1
  - Bythocytheridae
    - *Bythocythere* sp. 1
    - *Jonesia acuminata*
  - Paradoxostomatidae
    - *Xiphichilus* sp. 1
  - Cushmanideidae
    - *Pontocythere* sp. 1
  - Macrocyprididae
    - *Macrocypris sapeloensis*
    - *Macrocypris* "*labutisi*"
    - *Macrocyprina* "*atlantica*"
  - Hemicytheridae
    - *Muellerina canadensis*
    - *Bensonocythere arenicola*
    - *Bensonocythere* sp. A
  - Trachyleberididae
    - *Echinocythereis planibasalis*
    - *Echinocythereis margaritifera*
    - *Pseudocytheretta edwardsi*
    - *Pterygocythereis americana inexpecta*
    - *Actinocythereis vineyardensis*
    - *Paracytheretta daniana*
  - Cytheruridae
    - *Cytheropteron* cf.*latissimum*
  - Pontocyprididae
    - *Pontocypris* sp. 1

Appendix 6-A. (continued)

- Copepoda
  - Harpacticidae
    - *Harpacticus* sp.
  - Caligidae
    - *Lepeophtheirus edwardsi*
- Nebaliacea
    - *Nebalia* sp.
- Stomatopoda
  - Lysiosquillidae
    - *Platysquilla enodis*
    - *Heterosquilla armata*
  - Squillidae
    - *Squilla prasinolineata*
- Mysidacea
  - Mysidae
    - *Neomysis americana*
    - *Heteromysis formosa*
- Cumacea
  - Bodotriidae
    - *Manocuma stellifera*
    - *Pseudoleptocuma minor*
    - *Pseudoleptocuma* new sp.
    - *Cyclaspis* sp.
  - Leuconidae
    - *Eudorella pusilla*
    - *Eudorella hispida*
    - *Eudroellopsis deformis*
  - Diastylidae
    - *Diastylis sculpta*
    - *Diastylis bispinosa*
    - *Diastylis* sp. A
    - *Diastylis abbreviata*
    - *Oxyurostylis smithi*
    - *Leptostylis longimana*
    - *Leptostylis* sp.
    - Diastylidae sp. 1
  - Nannastacidae
    - *Cumella* sp.
    - *Campylaspsis rubicunda*
  - Lampropridae
    - *Hemilamprops cristata*
  - Pseudocumidae
    - *Petalosarsia declivis*
- Tanaidacea
    - Tanaidacean 4
    - Tanaidacean 6
    - Tanaidacean 7
    - Tanaidacean 11
  - Paratanaidae
    - *Pseudoleptochelia filum*
    - *Leptochelia* sp.
  - Leptognathiidae
    - *Libanius* new sp.
    - *Leptognathia* sp.
    - *Typhlotanais* sp.
  - Nototanaidae
    - *Tanaissus liljeborgi*
  - Pseudotanaidae
    - *Pseudotanais* sp.
  - Agathotanaidae
    - *Agathotanais* sp.
- Isopoda
  - Idoteidae
    - *Chiridotea tuftsi*
    - *Chiridotea arenicola*
    - *Edotea triloba*
    - *Idotea metallica*
  - Anthuridae
    - *Ptilanthura tricarina*
    - *Apanthura magnifica*
    - *Leptanthura* sp.
    - *Oscanthura vimsae*
  - Cirolanidae
    - *Cirolana polita*
    - *Cirolana concharum*
    - *Cirolana impressa*
  - Gnathidae
    - *Gnathia* sp.

Appendix 6-A. (continued)

- Macrostylidae
  - *Macrostylis spinifera*
- Desmosomatidae
  - *Desmosoma* sp.
  - *Desmosoma intermedium*
  - *Desmosoma latipes*
- Janiridae
  - *Ianiropsis* sp.
  - *Janira alta*
- Munnidae
  - *Pleurogonium* new sp. A
  - *Pleurogonium inerme*
  - *Pleurogonium rubicundum*
  - *Pleurogonium spinosissimum*
  - *Austrosignum* sp.
- Eurycopidae
- Ilyarachinidae
  - *Ilyarachna longicornis*
- Limnoridae
  - *Limnoria lignorum*

Amphipoda

- Ampeliscidae
  - *Ampelisca vadorum*
  - *Ampelisca verrilli*
  - *Ampelisca macrocephala*
  - *Ampelisca agassizi*
  - *Ampelisca aequicornis*
  - *Ampelisca declivitatus*
  - *Byblis serrata*
- Amphilochidae
  - *Amphilochoides odontonyx*
- Aoridae
  - *Lembos websteri*
  - *Leptocheirus pinguis*
  - *Microdeutopus anomalus*
  - *Rudilemboides* sp. 1
- Argissidae
  - *Argissa hamatipes*
- Corophiidae
  - *Corophium insidiosum*
  - *Corophium crassicorne*
  - *Erichthonius rubricornis*
  - *Erichthonius* sp. A
  - *Neohela monstrosa*
  - *Unciola* sp. A
  - *Unciola inermis*
  - *Unciola irrorata*
  - *Unciola serrata*
  - *Unciola spicata*
  - *Unciola dissimilis*
  - *Unciola leucopis*
  - *Pseudunciola obliquua*
  - *Siphonoecetes smithianus*
- Cressidae
  - *Cressa abyssicola*
- Eusiridae
  - *Pontogenia inermis*
  - *Rhachotropis inflata*
- Gammaridae
  - *Melita dentata*
  - *Maera danae*
  - *Maera loveni*
  - *Eriopisa elongata*
  - *Casco bigelowi*
  - *Jerbarnia* sp. 1
- Haustoriidae
  - *Acanthohaustorius intermedius*
  - *Acanthohaustorius* "*similis*"
  - *Acanthohaustorius spinosus*
  - *Acanthohaustorius shoemakeri*
  - *Bathyporeia quoddyensis*
  - *Parahaustorius attenuatus*
  - *Protohaustorius wigleyi*
  - *Platyishnopus* sp. 1
  - *Pseudohaustorius borealis*
  - *Pseudohaustorius* sp. 1
  - *Pseudohaustorius caroliniensis*

Appendix 6-A. (continued)

- Isaeidae
  - *Photis pugnator*
  - *Photis dentata*
  - *Photis macrocoxa*
  - *Photis reinhardi*
  - *Gammaropsis* sp. 1
  - *Gammaropsis nitida*
  - *Protomedia fasciata*
  - *Microprotopus maculatus*
- Ischyroceridae
  - *Ischyrocerus anguipes*
- Liljeborgiidae
  - *Idunella* sp. A
  - *Idunella* sp. B
  - *Idunella* sp. C
  - *Listriella barnardi*
  - *Liljeborgia fissicornis*
  - *Liljeborgia* sp. 1
- Lysianassidae
  - *Pasammonyx nobilis*
  - *Orchonomella pinguis*
  - *Hippomedon serratus*
  - *Hippomedon propingquus*
  - *Anonyx sarsi*
- Melphidippidae
  - *Melphidippa* sp. A
- Pardaliscidae
- Oedicerotidae
  - *Monoculodes* sp. A
  - *Monoculodes edwardsi*
  - *Synchelidium americanum*
- Phoxocephalidae
  - *Paraphoxus spinosus*
  - *Phoxocephalus holbolli*
  - *Trichophoxus epistomus*
  - *Harpinia antennaria*
  - *Harpinia truncata*
  - *Harpinia* new sp. A
  - *Harpinia* new sp. 2
  - *Harpinia* new sp. 3
  - *Harpinia* new sp. 4
  - *Harpinia* new sp. 5
  - *Harpinia* new sp. 6
  - *Heterophoxus oculata*
- Pleustidae
  - *Stenopleustes gracilis*
  - *Stenopleustes inermis*
- Stenothoidae
  - Stenothoidae sp. 1
  - Stenothoidae sp. 2
  - *Parametopella cypris*
  - *Parametopella* sp. A
  - *Metopa* sp.
  - *Stenothoe tenella*
- Stegocephalidae
- Synopiidae
  - *Synopiidae* sp. 1
  - *Tiron spiniferum*
- Podoceridae
  - *Dyopedos monacanthus*
  - *Dyopedos porrectus*
- Hyperiidae
  - *Parathemisto gaudichaudi*
  - *Lestrigonis bengalensis*
- Oxycephalidae
  - *Rhabdosoma* sp.
- Caprellidae
  - *Aeginina longicornis*
  - *Caprella equilibra*
  - *Mayerella limicola*
- Euphausidae
  - *Stylocheiron* sp.

Decapoda
- Sergestidae
  - *Lucifer faxoni*
- Pasaphaeidae
  - *Leptochela bermudensis*

Appendix 6-A. (continued)

SIPUNCULA
- Sipunculan 2
- Sipunculan 3
- Sipunculan 4
- Sipunculan 5
- *Phascolopsis gouldi*
- *Phascolion strombi*
- *Golfingia minuta*
- *Golfingia abyssorum*
- *Golfingia catharinae*
- *Golfingia trichocephala*
- *Golfingia elongata*
- *Golfingia* sp.
- *Onchnesoma steenstrupi*

ECHIURIDA
- Thallasemidae
  - *Echiurus echiurus*

PRIAPULIDA
- *Priapulida* sp.

PHORONIDA
- *Phoronis psammophila*

ECTOPROCTA
- Cheilostomata
  - Celloporinidae
    - *Cellopora americana*
  - Scrupariidae
    - *Scruparia clavata*
  - Porinidae
    - *Porina tubulosa*
  - Microporellidae
    - *Microporella ciliata*
  - Schizoporellidae
    - *Schizoporella unicornus*
    - *Schizoporella cornuta*
  - Membraniporidae

- Hippolytidae
  - *Eualus pusiolus*
- Penaeidae
  - *Parapanaeus longirostris*
- Pandalidae
  - *Dichelopandalus leptoceras*
- Paleomonidae
  - *Leander tenucornis*
- Crangonidae
  - *Crangon septemspinosa*
  - *Pontophilus brevirostris*
- Axiidae
  - *Axius serratus*
- Galatheidae
  - *Munida iris*
  - *Munida valida*
- Calappidae
- Goneplacidae
  - *Gonaplax hirsuita*
- Paguridae
  - *Catapagurus sharreri*
  - *Catapagurus* sp.
  - *Pagurus acadianus*
  - *Pagurus longicarpus*
  - *Pagurus arcuatus*
  - *Pagurus pubescens*
  - *Pagurus annulipes*
- Albuneidae
  - *Albunea paretii*
- Portunidae
  - *Ovalipes ocellatus*
- Cancridae
  - *Cancer borealis*
  - *Cancer irroratus*
- Pinnotheridae
  - *Dissodactylus mellitae*
- Majidae
  - *Euprognatha rastellifera*
  - *Hyas araneus*

Appendix 6-A. (continued)

Membranipora tenuis
Electridae
Electra hastingsae
Bugulidae
Bugula neritina
Bugula murrayana
Hippithoidae
Hippothoa hyalina
Hippothoa divaricata
Chorizopora brongniarti
Cheiloporinidae
Costazia ignota
Hippoporinidae
Hippoporina americana
Hippoporina verrilli
Cleidochasma contractum
Cribrilinidae
Cribrilaria radiata
Cribrilina punctata
Calloporidae
Amphiblestrum flemingii
Callopora aurita
Callopora craticula
Callopora americana
Smittinidae
Porella acutirostris
Porella concinna
Escharellidae
Escharella sp. 1
Petraliidae
Petraliella bisinvata
Gigantoporidae
Cylindroporella tubulosa
Cellariidae
Cellaria fistulosa
Cellaria sp. A
Stenolaemata
Lunulariidae
Cupuladria doma
Tubuliporidae
Tubulipora atlantica
Diaperoeciidae
Diaperoecia floridana
Cyclostomata
Lichenopora verrucaria

CHAETOGNATHA

ECHINODERMATA
Asteroidea
Astropectinidae
Astropecten americanus
Asteriidae
Asterias forbesi
Asterias vulgaris
Sclerasterias tanneri
Leptasterias tenera
Stephanasterias albula
Echinasteridae
Henricia sanguinolenta
Echinoidea
Arbaciidae
Coelopleurus floridanus
Temnopleuridae
Genocidaris maculata
Strongylocentrotidae
Strongylocentrotus droebachiensis
Echinarachniidae
Echinarachnius parma
Schizasteridae
Briaster fragilis
Schizaster orbignyanus
Brissidae
Brissopsis mediterranea
Loveniidae
Echinocardium cordatum
Ophiuroidea
Amphiuridae

Appendix 6-A. (continued)

Amphiuridae sp. A
Amphioplus macilentus
Axiognathus squamata
Amphiura otteri
Ophiuridae
Ophiura sp.
Ophiactidae
Ophiopholis aculeata
Ophiacanthidae
Amphilima ovalacea
Holothuroidea
Caudinidae
Caudina arenata
Cucumariidae
Stereoderma unisemita
Phyllophoridae
Havelockia scabra
Synaptidae
Leptosynapta tenuis
Labidoplax buski

HEMICHORDATA

UROCHORDATA
Ascidiacea
Pyuridae
Pyura torqueti
Molgulidae
Aplidium (Amaroucium) constellatum
Aplidium (Amaroucium) fuegiense
Fungulus cinereus
Molgula sp.
Molgula citrina
Molgula lutulenta
Molgula platana
Rhizomolgula globularis
unidentified ascideans
Larvacea

CEPHALOCHORDATA
Branchiostoma caribaeum

Appendix 6-B. Megabenthic taxa collected and the stations at which each occurred. Collection by small biology trawl (S) or anchor dredge (A) and stations at which taxon was numerically dominant (underlined) are indicated.

Taxon	SBT Anchor	Station(s)
PROTOZOA		
Sarcodina		
Astrorhizidae		
Astrorhiza limicola	SA	*B1*,C2,D1,D4,*E1*,F1,I1,N3
PORIFERA		
Calcarea		
Heterocoelidae		
Scypha ciliata	S	I1
Desmospongiae		
Keratosa		
Keratosa sp. 1	S	E1
Suberitidae		
Polymastia robusta	S	J1
Suberites ficus	S	C2,D4
Myxillidae		
Mixilla fimbriata	SA	A1,I1
Mixilla incrustans	S	A1
Halichondridae		
Halichondria sp.	S	E1,I1,J1
Clionidae		
Cliona sp.	S	N3
CINDARIA		
Hydrozoa		
Tubulariidae		
Tubularia sp.	S	I1
Corymorpha pendula	S	A1,F1
Hydractiniidae		
Hydractinia sp.	SA	B1,F1,N3
Bougainvilliidae		
Garveia sp.	S	D1
Eudendriidae		
Eudendrium ramosum	S	A1,F1,I1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Haleciidae		
Halecium sp.	S	A1,B1,D1,I1
Halecium halecium	S	A1,I1
Campanulariidae		
Clytia sp.	S	B1,C2,D1
Clytia hemisphaerica	S	A1,B1,I1
Clytia paulensis	S	I1
Obelia longissima	SA	A1,B1,C2,D1,D4,E1,I1,N3,J1
Obelia geniculata	S	D1,D4
Campanularia sp.	S	A1,E1
Campanularia verticillata	SA	B1,D1,D4,I1,N3
Sertulariidae		
Sertularia cupressina	SA	A1,B1,C2,D1,D4,E1,F1,I1,N3
Sertularia polyzonias	S	D4
Plumularidae		
Cladocarpus flexilis	SA	A1,I1
Nemertesia antennina	SA	B1,E1,I1
Campanuliidae		
Cuspidella sp.	S	I1
Cuspidella grandis	S	I1
Stegopoma fastigatum	S	A1,F1,I1
Lafoeidae		
Lafoea dumosa	S	A1,I1
Anthozoa		
Alcyoniidae		
Alcyonium digitatum	SA	A1,I1
Virgulariidae		
Virgularia sp.	SA	A1,B1,F1
Edwardsiidae		
Edwardsia elegans	S	C2
Hormathiidae		
Actinauge rugosa	S	J1
Caryophyllidae		
Dasmosmilia lymani	SA	A1,B1,F1,I1,J1
Cerianthidae		
Cerianthidae sp.	SA	A1,B1,C2,D1,F1,I1,N3
Zoanthidae		
Epizoanthus incrustatus	SA	A1,F1,I1,J1
Epizoanthus paguraphilus	S	A1,B1,F1,J1
Isozoanthus sp.	SA	F1,J1
ENTOPROCTA		
Pedicellinida		

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Pedicellinidae		
Pedicellina sp.	S	I1
ANNELIDA - (POLYCHAETA)		
Phyllodocida		
Aphroditidae		
Aphrodita hastata	SA	A1,B1,D1,D4,E1,I1,N3
Laetomnice filicornis	S	J1
Eunicida		
Onuphidae		
Hyalinoecia artifex	SA	J1
Nothria conchylega	SA	A1,F1,I1,J1
Diopatra cuprea	A	C2
MOLLUSCA		
Scaphopoda		
Dentaliidae		
Dentalium occidentale	S	J1
Siphonodentaliidae		
Cadulus agassizi	S	I1,J1
Cadulus pandionis	S	J1
Gastropoda		
Trochidae		
Solariella infundibulum	SA	D1,N3,J1
Solariella obscura	SA	B1,D1,D4,E1,N3,J1
Calliostoma bairdii	SA	A1,E1,F1,I1,J1
Calliostoma occidentale	S	J1
Architectonicidae		
Heliacus borealis	S	J1
Epitoniidae		
Epitonium dallianum	SA	A1,I1
Calptraeidae		
Crepidula plana	S	C2,D1
Crucibulum striatum	SA	B1,D4,E1,N3
Naticidae		
Polinices immaculatus	SA	B1,D1,D4,E1,F1,I1,N3
Polinices uberinus	S	B1
Lunatia heros	SA	A1,B1,C2,D1,E1,N3
Lunatia triseriata	SA	B1,D4,E1,N3
Tonnidae		
Eudolium crosseanum	S	J1
Columbellidae		
Astyris diaphana	S	I1,J1
Anachis lafresnayi	S	J1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Buccinidae		
Buccinum undatum	SA	B1,N3
Colus pygmaeus	SA	B1,D1,E1,J1,N3
Colus pubescens	S	J1
Colus stimpsoni	S	J1
Nassariidae		
Nassarius trivittatus	SA	B1,C2,D1,D4,E1,N3
Nassarius albus	S	J1
Turridae		
Eulimella smithi	S	A1,E1,I1
Inodrilla dalli	S	J1
Propebela harpularia	S	J1
Eubella limacina	S	J1
Scaphandridae		
Cylichna alba	SA	F1,J1
Cylichna verrilli	SA	F1
Ringiculidae		
Ringicula nitida	S	J1
Philinidae		
Philine quadrata	S	A1,D1,E1,J1
Pyramidellidae		
Turbonilla interrupta	SA	B1,E1,F1,I1,J1
Pleurobranchidae		
Pleurobranchaea tarda	S	A1,B1,C2,D1,E1,F1,J1,N3
Dendronotidae		
Dendronotus frondosus	S	F1
Pelecypoda		
Nuculidae		
Nucula proxima	A	E1
Nuculanidae		
Yoldia sapotilla	SA	A1,F1,J1
Nuculana acuta	S	J1
Nuculana caudata	S	J1
Arcidae		
Bathyarca pectunculoides	S	J1
Mytilidae		
Modiolus modiolus	SA	A1,E1,F1,I1
Musculus niger	SA	B1,D4,I1,N3
Crenella glandula	SA	A1,B1,C2,F1,I1
Pectinidae		
Placopecten magellanicus	SA	A1,B1,D1,D4,E1,F1,I1,N3
Cyclopecten nanus	SA	A1,E1,F1,I1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Anomiidae		
Anomia simplex	SA	B1,E1,I1
Anomia squamula	S	B1,E1,I1,N3
Astartidae		
Astarte castanea	SA	B1,C2,D1,D4,E1,F1,I1,N3
Astarte undata	SA	A1,B1,D4,E1,F1,I1,J1
Astarte crenata subequilatera	SA	A1,B1,E1,F1,I1,J1,N3
Carditidae		
Cyclocardia borealis	SA	A1,B1,D1,D4,E1,F1,I1,N3
Arcticidae		
Arctica islandica	SA	A1,B1,D1,E1,F1,I1,N3
Lucinidae		
Lucinoma filosa	SA	A1,J1
Myrtaea lens	S	J1
Cardiidae		
Cerastoderma pinnulatum	SA	B1,C2,D1,D4,E1,I1,N3
Veneridae		
Pitar morrhuana	SA	A1,B1,C2,D1,D4,E1,N3
Tellinidae		
Tellina agilis	SA	C2,D1,N3
Tellina versicolor	S	C2
Semelidae		
Abra liocia	S	J1
Solenidae		
Ensis directus	SA	B1,C2,D1,D4,E1,I1,N3
Mactridae		
Spisula solidissima	SA	C2,D1,D4,N3
Lyonsiidae		
Lyonsia hyalina	SA	B1,C2,D1,D4,E1,N3
Pandoridae		
Pandora gouldiana	SA	B1,C2,D1,D4,E1,F1,I1,N3
Pandora inflata	SA	A1,F1,I1
Periplomatidae		
Periploma fragile	SA	A1,C2,F1,J1
Periploma leanum	A	F1,I1
Poromyidae		
Poromya granulata	S	J1
Cuspidariidae		
Cardiomya perrostrata	S	J1
Cuspidaria rostrata	S	A1,F1,J1
Thyasiridae		
Thyasira flexuosa	S	A1,J1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Cephalopoda		
Loliginidae		
Loligo pealeii	S	I1
Sepiolidae		
Rossia tenera	SA	A1,B1,D4,E1,F1,I1,J1,N3
Octopodidae		
Bathypolypus arcticus	S	J1
Octopus vulgaris	S	C2
PYCNOGONIDA		
Phoxichiliidae		
Anoplodactylus lentus	S	F1
Anoplodactylus petiolatus	S	A1,F1,I1,J1
Anoplodactylus iuleus	S	J1
Ammotheidae		
Ascorhynchus pyrginospinum	A1	
Nymphonidae		
Nymphon grossipes	A	D4,J1
CRUSTACEA		
Stomatopoda		
Lysiosquillidae		
Platysquilla enodis	S	C2
Mysidacea		
Mysidae		
Neomysis americana	SA	C2
Cumacea		
Diastylidae		
Diastylis bispinosa	SA	A1,B1,E1,F1,I1,J1
Diastylis cornuifer	S	J1
Diastylis sculpta	SA	E1,N3
Tanaidacea		
Isopoda		
Idoteidae		
Edotea triloba	SA	A1,B1,C2,D1,N3
Anthuridae		
Calathura branchiata	S	J1
Ptilanthura tricarina	S	I1
Cirolanidae		
Cirolana polita	SA	A1,B1,C2,D1,E1,F1,I1,J1,N3
Cirolana concharum	S	C2
Cirolana impressa	SA	J1
Aegidae		
Syscenus infelix	S	J1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Janiridae		
Janira alta	S	I1
Amphipoda		
Ampeliscidae		
Ampelisca vadorum	SA	A1,B1,D1,D4,E1,F1,I1
Ampelisca verrilli	S	A1,D4
Ampelisca macrocephala	S	B1
Ampelisca agassizi	S	A1,B1,E1,F1,J1
Byblis serrata	SA	B1,D4,N3
Aoridae		
Leptocheirus pinguis	SA	A1,B1,D1,D4
Leptocheirus new sp.	A	B1
Corophiidae		
Erichthonius brasiliensis	S	B1
Erichthonius rubricornis	S	B1,E1,I1,J1,N3
Unciola inermis	SA	B1,E1,F1,I1,N3
Unciola irrorata	SA	A1,B1,D1,E1,F1,I1,N3
Unciola crassipes	S	J1
Unciola spicata	SA	A1,D4,F1,I1,J1
Unciola dissimilis	S	D4,E1
Pseudunciola obliquua	A	E1
Siphonoecetes colletti	S	D1
Siphonoecetes new sp.	S	B1,D1,I1
Eusiridae		
Rhachotropis sp. 1	S	J1
Pontogenia inermis	S	C2,D1
Gammaridae		
Melita dentata	SA	B1,D1,D4,E1,I1
Melita new sp.	SA	E1
Casco bigelowi	S	D4,E1
Jerbarnia sp.	S	F1
Haustoriidae		
Parahaustorius attenuatus	SA	D1
Protohaustorius wigleyi	S	N3
Acanthohaustorius spinosus	A	D1
Parahaustorius attenuatus	A	C2
Protohaustoris wigleyi	SA	N3
Isaeidae		
Photis dentata	SA	E1,F1,J1
Gammaropsis nitida	S	N3
Lysianassidae		
Lysianassidae sp. 1	A	I1
Hippimedon serratus	S	B1
Anonyx sarsi	SA	C2,N3

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Oedicerotidae		
Monoculodes edwardsi	S	C2,I1
Monoculodes sp. A	S	I1
Phoxocephalidae		
Trichophoxus epistomus	SA	E1,I1
Paramphithoidae		
Epimeria loricata	S	J1
Epimeria new sp.	S	F1,J1
Caprellidae		
Aeginina longicornis	S	B1,D1,D4,E1,I1,N3
Caprella unica	S	B1
Euphausiacea		
Euphausiidae		
Meganyctiphanes norvegica	S	J1
Decapoda		
Penaeidae		
Gennadas scuttatus	S	J1
Sergestidae		
Sergestes arcticus	S	J1
Palaemonidae		
Periclimenes pandionis	S	F1
Hippolytidae		
Caridion gordoni	S	E1,I1
Eualus pusiolus	S	A1,D1,D4,F1,I1,J1
Spirontocaris lilljeborgii	S	J1
Bythocaris nana	S	A1,F1,I1,J1
Bythocaris sp.(cf. *B. nana*)	S	J1
Processidae		
Processa profunda	S	J1
Pandalidae		
Dichelopandalus leptocerus	SA	A1,*B1*,C2,D1,D4,E1,F1,I1,J1,*N3*
Parapandalus willisi	S	J1
Pandalus montagui	S	J1
Pandalus propinquus	S	J1
Plesionika holthusi	S	J1
Crangonidae		
Crangon septemspinosa	SA	A1,*B1*,*C2*,*D1*,D4,*E1*,F1,I1,*N3*
Pontophilus brevirostris	SA	*A1*,B1,*F1*,I1,J1
Pontophilus norvegicus	S	J1
Homaridae		
Homarus americanus	S	J1
Scyllaridae		
Scyllarus depressus	S	A1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Galatheidae		
Munida iris	S	A1,E1,F1,I1,J1
Munida valida	S	J1
Diogenidae		
Dardanus insignis	S	F1
Paguridae		
Catapagurus sharreri	S	A1,J1
Catapagurus gracilis	S	A1,J1
Pagurus acadianus	SA	B1,C2,D1,D4,E1,I1,N3
Pagurus longicarpus	S	C2
Pagurus politus	S	J1
Pagurus pollicaris	S	C2
Pagurus arcuatus	SA	A1,B1,C2,D1,D4,E1,F1,I1,N3
Pagurus pubescens	S	C2
Parapaguridae		
Parapagurus arcuatus	S	J1
Pylochelidae		
Parapylocheles new sp.	S	E1,N3
Calappidae		
Acanthocarpus alexandri	S	J1
Calappa angusta	S	C2
Portunidae		
Bathynectes superbus	S	F1,J1
Ovalipes ocellatus	S	C2
Ovalipes stephensoni	A	D1
Ovalipes sp.	S	B1
Portunus sp.	S	C2
Cancridae		
Cancer borealis	SA	A1,B1,D1,D4,E1,F1,I1,J1,N3
Cancer irroratus	SA	A1,B1,C2,D1,D4,E1,F1,I1,N3
Geryonidae		
Geryon quinquedens	S	J1
Goneplacidae		
Goneplax hirsuta	S	A1
Pinnotheridae		
Dissodactylus mellitae	S	C2
Palicidae		
Palicus cursor	S	J1
Majidae		
Collodes robustus	A	A1,F1,I1
Euprognatha rastellifera	SA	A1,F1,I1,J1
Hyas coarctatus	S	A1,B1,E1,I1,J1,N3
Hyas araneus	S	B1,N3
Libinia dubia	SA	C2,D1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Parthenopidae		
Parthenope pourtalesi	S	A1
SIPUNCULIDA		
Phascolopsis gouldii	S	C2
Phascolion strombi	SA	A1,B1,D1,E1,F1,I1,J1,N3
ECHINODERMATA		
Asteroidea		
Unidentified Asteroid sp.	S	J1
Astropectinidae		
Astropecten americanus	SA	A1,B1,C2,D1,E1,F1,I1,J1,N3
Odontasteridae		
Odontaster setosus	S	J1
Echinasteridae		
Henricia sanguinolenta	SA	A1,B1,E1,F1,I1,N3
Asteriidae		
Asterias forbesi	SA	B1,C2,D1,E1,F1,N3
Asterias vulgaris	SA	A1,B1,C2,D1,D4,E1,F1,I1,N3
Sclerasterias tanneri	SA	B1,D1,E1,I1,N3
Leptasterias tenera	SA	A1,E1,F1,I1,J1
Coronaster briareus	S	I1,J1
Stephanasterias albula	S	J1
Echinoidea		
Strongylocentrotidae		
Strongylocentrotus droebachiensis	S	B1,E1,I1,N3
Echinarachiniidae		
Echinarachnius parma	SA	A1,B1,C2,D1,S4,E1,F1,I1,N3
Ophiuroidea		
Amphiuridae		
Amphiura otteri	S	J1
Amphioplus macilentus	SA	A1,E1,F1,I1
Axiognathus squamata	SA	A1,B1,E1,F1,I1,J1
Ophiactidae		
Ophiopholis aculeata	S	D1,E1,I1
Ophiacanthidae		
Amphilimna ovalacea	SA	A1,E1,F1,I1,J1
Ophiuridae		
Ophiura sarsi	SA	F1,J1
Holothuroidea		
Holothuroidea sp. 1	S	J1
Cucumariidae		
Stereoderma unisemita	SA	A1,B1,C2,E1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Phyllophoridae		
Havelockia scabra	SA	A1,B1,E1,I1,J1
UROCHORDATA		
Ascidiacea		
Molgulidae		
Molgula arenata	SA	A1,B1,C2,D1,E1,F1,I1,J1,N3
Styelidae		
Dendroda carnea	SA	A1,B1,D1,D4,E1,I1,N3
Ascidiidae		
Ascidia callosa	S	A1,I1
CHORDATA		
Agnatha		
Pteraspidomorphi		
Myxiniformes		
Myxinidae		
Myxine glutinosa	S	J1
Gnathostomata		
Chondrichthys		
Rajiformes		
Rajidae		
Raja radiata	S	J1
Raja erinacea	SA	B1,C2,D1,D4,E1,I1
Osteichthys		
Anguilliformes		
Ophichthidae		
Pisodonophis cruentifer	SA	A1,B1,E1,F1,I1,J1,N3
Synaphobranchidae		
Synaphobranchus kaupi	S	J1
Lophiiformes		
Lophiidae		
Lophius americanus	S	A1,I1
Ogcocephalidae		
Dibranchus atlanticus	S	J1
Gadiformes		
Gadidae		
Phycis chesteri	S	J1
Urophycis chuss	SA	B1,C2,D1,D4,E1,I1,J1,N3
Urophycis regius	SA	D1,I1,J1,N3
Enchelyopus cimbrius	S	J1
Merlucciidae		
Merluccius albidus	S	J1
Merluccius bilinearis	S	A1,B1,D1,E1,F1,I1,J1

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Ophidiidae		
Lepophidium cervinum	S	A1,B1,E1,F1
Macruridae		
Nezumia bairdii	S	J1
Coelorhynchus c. carminatus	S	J1
Zoarcidae		
Macrozoarces americanus	S	E1
Lycenchelys verrilli	S	J1
Gasterosteiformes		
Syngnathidae		
Hippocampus erectus	S	C2,D4
Sygnathus sp.	S	C2,D1
Sygnathus fuscus	S	C2
Scorpaeniformes		
Scorpaenidae		
Helicolenus dactylopterus	S	J1
Triglidae		
Prionotus carolinus	S	C2
Prionotus evolans	S	A1
Peristedion miniatum	S	J1
Cyclopteridae		
Liparis enquilinus	SA	B1, D1, E1, N3
Perciformes		
Serranidae		
Centropristis striata	S	D1,I1
Sparidae		
Stenotomus versicolor	S	N3
Labridae		
Tautogolabrus adspersus	S	D1
Pholididae		
Pholis gunnellus	S	B1,D1
Ammodytidae		
Ammodytes americanus	SA	C2,D1,E1,N3
Gobeisociformes		
Gobiidae		
Gobiosoma ginsburgi	S	C2,D1
Callionymidae		
Callionymus agassizi	S	C2
Pleuronectiformes		
Bothidae		
Citharichthys arctifroms	SA	A1,B1,C2,D1,D4,E1,F1,I1,N3
Hippoglossina oblonga	S	B1,I1,J1
Monolene sessilicauda	S	J1
Etropus microtomus	S	C2

Appendix 6-B (continued).

Taxon	SBT Anchor	Station(s)
Bothus ocellatus	S	C2
Pleuronectidae		
Glyptocephalus cynoglossus	S	J1
Tetradontiformes		
Tetradontidae		
Sphaeroides maculatus	S	C2

CHAPTER 7

Benthic Ecological Studies: Meiobenthos

D. J. Hartzband, D. F. Boesch

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CHAPTER 7

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CHAPTER 7

BENTHIC ECOLOGICAL STUDIES: MEIOBENTHOS

D. J. Hartzband
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INTRODUCTION

Studies of the Middle Atlantic Bight outer continental shelf meiobenthos were initiated during the second year of the BLM-OCS Benchmark Descriptive Studies. The meiobenthos is considered here to include those metazoans passing through a 0.5 mm sieve and retained on a 0.063 mm sieve. Although postlarval and juvenile individuals of macrobenthos are included in this size category, the meiobenthos is dominated by animal groups quite different from those of the macrobenthos. Thus, this investigation fills a large and important gap in the comprehensive investigations of the benthos, from microbes to demersal fishes, carried out as a central part of the Benchmark Studies.

Findings of the first year studies of the Middle Atlantic OCS benthos suggested the potential value of meiobenthos investigations in meeting the objectives of the Bureau of Land Management's Environmental Studies. The macrobenthos of the shelf proved to be closely "tuned" to sedimentary conditions, and it was reasoned that because of their small size the meiobenthos should be even more sensitive indicators of environmental conditions in the benthic habitat. Wieser et al. (1974) equated the meiofauna to "micro-probes" which greatly extend the range of man-made instruments in the study of sediments. Hypotheses concerning the trophic ecology of the macrobenthos (Boesch et al. 1977) suggested potentially important trophic interactions with the meiobenthos. Thus, to some extent, these studies are supportive of the more extensive investigation of macrofauna. Finally, because of the small size and rapid turn-over of the meiobenthos, this component is potentially more "responsive" to subtle and/or short term impacts of oil and gas development.

Specific objectives of the Middle Atlantic OCS meiobenthos study were: 1) to describe the composition and abundance of the meiobenthos of the outer shelf and shelf break region off New Jersey (in the area of potential development); 2) to determine the relationship of meiobenthic community composition and structure to sediments, bottom topography, and other environmental conditions; 3) to develop an understanding of the relationship of the meiobenthos to other components of the benthos; and 4) to assess the feasibility of baseline and monitoring investigations of meiobenthos in the outer continental shelf environment with respect to the evaluation of impact.

Previous Investigations of Meiobenthos of the Region

Previous studies on continental shelf meiofauna in the western North Atlantic have concentrated on the area south of the present study area. Tietjen (1971, 1976) focused on the nematode taxocene in the area off North Carolina; Coull (1972) emphasized harpacticoid copepods in a transect study from Cape Lookout, North Carolina to Bermuda; and R. Rieger (personal communication) has studied the soft-bodied meiofauna, primarily the Turbellaria, off the North Carolina capes. These studies confirm the great abundance of meiofauna in subtidal marine sediments, and each related meiofaunal species abundance and distribution with depth to a suite of other physico-chemical factors.

Areas to the north of the present study area were sampled by Wigley and MacIntyre (1964), who sampled both macrobenthos and meiobenthos along a depth gradient (45-179 m) off Cape Cod, and found the greatest abundance of meiofauna and the highest meiofauna/ macrofauna ratio (380:1) at their deepest shelf station. They associated this with the presence of fine sediments. Tietjen (personal communication) has also studied nematode assemblages in the New York Bight apex. Published studies on subtidal meiobenthos of the Middle Atlantic region are limited to bays and estuaries rather than the shelf. Noteworthy are those of Wieser (1960) on mud bottoms in Buzzards Bay; Tietjen (1969) on two shallow estuaries in southern New England; and Tietjen (1977) on the nematodes of Long Island Sound.

Bases of Design of this Study

Information available from first year BLM-OCS Middle Atlantic Benchmark Studies on sediments and macrobenthos (Boesch 1977; Boesch et al. 1977) provided a basis for understanding the complex benthic environment and enabled the development for informed strategy of investigation for meiofauna. The importance of mesoscale (over distances of 10^2 - 10^4m) topography in determining the distribution of sediments and associated meiobenthos was a critical design factor. Specifically, the macrobenthos found within topographic depressions in the Middle Atlantic OCS is qualitatively and quantitatively different from that at nearby sites not located in such depressions. These faunal distribution patterns generally coincide with important sedimentologic and physico-chemical differences between ridge and swale habitats. Sediments on ridges are generally coarser and contain very little silt and clay (<1%) and organic carbon (<1 mg/g), whereas sediments in swales are generally finer and contain >5% silt and clay and more organic carbon (1-2 mg/g). It therefore seemed clear that differences in meiofaunal species distribution and abundance could be expected in relation to differences in topography and that sampling design would have to reflect this.

Many studies (Thiel 1972; Arlt 1973; Dinet 1973) have shown that meiofauna species often occur in patches of specific sizes. Patch sizes for the greatest population sizes range from 100 cm^2 for ciliates to 25 cm^2 for ostracods. Coull et al. (1977) have suggested that densities of meiofauna are homogeneous within large areas at specific depths and that patchiness is a small scale phenomenon at the level of small subsamples. This indicated that small scale subsampling was required to account for this variability. The delineation of spatial and temporal patterns was necessary in order to integrate the meiobenthos into an overall characterization of the benthos and in order to establish a "baseline" against which changes could be measured. The highly dynamic nature of meiofaunal populations complicates the analysis and interpretation of spatial and, especially, temporal patterns. Previous work on nematodes (Gerlach and Schrage 1971; Tietjen and Lee 1972, 1973) has shown that generation times in marine free living forms average about 25 days, clutch size averages 25 eggs, and time from hatching until sexual maturity is about 20 days. Similar data for harpacticoid copepods (Johnson and Olsen 1948) show generation times of about 20 days in the laboratory, about 40 eggs/clutch and time until sexual maturity of 14 days. Even if these figures are adjusted for in situ seasonal effects, it is evident that population changes can take place very quickly and that large changes in species abundance and distribution between cruises could be accounted for almost entirely by the dynamics of meiofaunal populations. The frequency of sampling could not be increased to better account for the scale of the dynamics, and because of this, caution must be applied in the interpretation of apparent temporal trends.

METHODS

Shipboard Procedure

Sampling

Meiobenthos was sampled at eight (8) stations during each of the four (4) biological seasons (Figure 7-1). Stations sampled were A3 (depth 136 m), B2 (60 m), B3 (72 m), B4 (40 m), E1 (67 m), E3 (63 m), E4 (77 m), and F3 (147 m). All of these stations were previously occupied for macrofaunal sampling during the first year of the BLM Middle Atlantic Benchmark Sampling Program, and all of them are located within the central cluster areas established for first year sampling. The stations were selected to encompass the range of sedimentary and hydrodynamic conditions in the Middle Atlantic lease sale 40 area. Stations E1, E3, and B2 are located on ridges, and stations B3 and E4 in swales. Station B4 is located on a shallower, more dynamic bottom on the terrace east of the Tiger Scarp. Figures

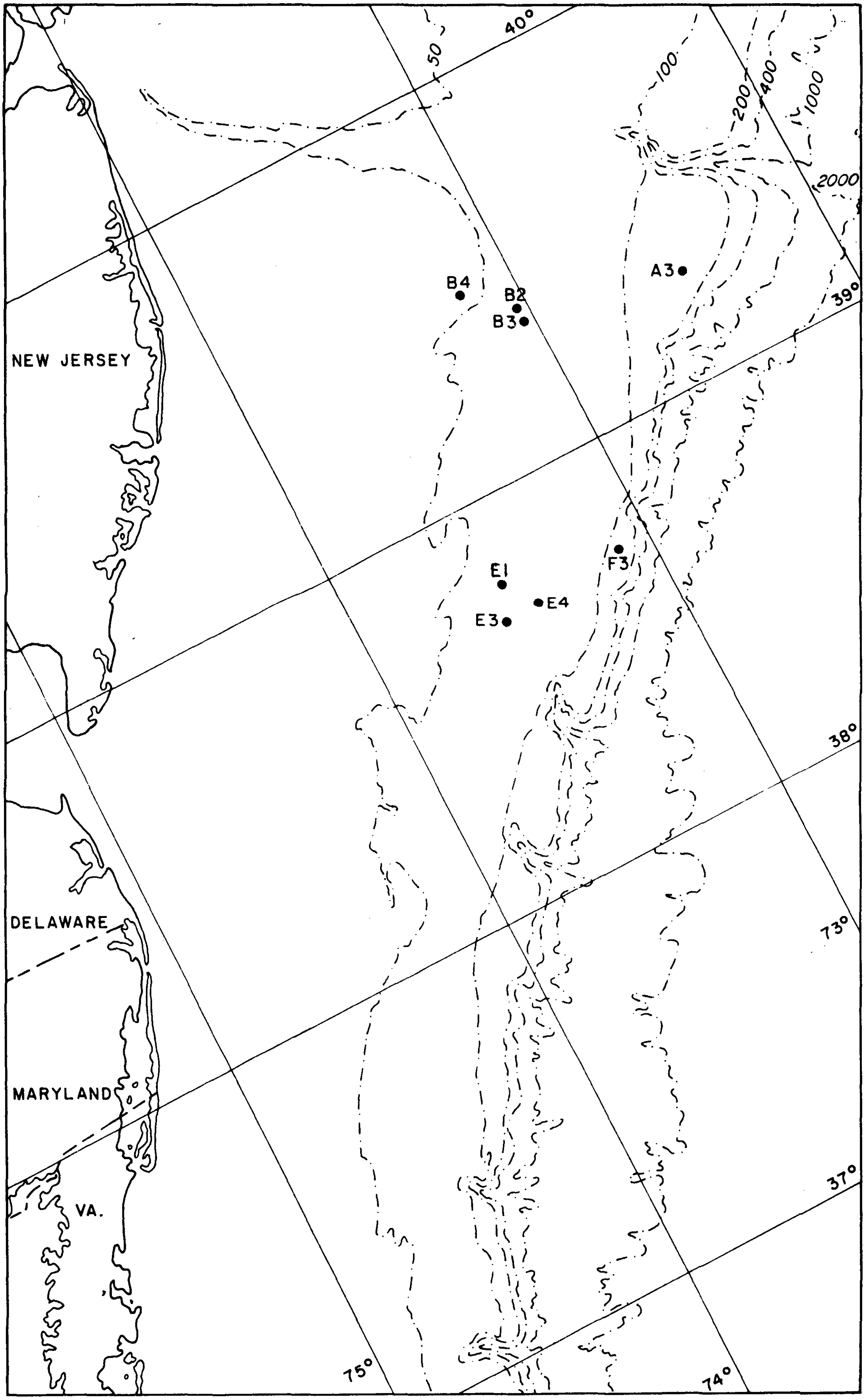


Figure 7-1. Stations sampled for meiobenthos.

7-2 and 7-3 show the bottom topography of cluster areas B and E in greater detail. Areas B and E are emphasized because they are the areas of highest expected developmental activity, and because they display topographic features which affect important mesoscale patterns of macrobenthos (Chapter 6). Stations A3 and F3 are located in similar depths near the shelf break, but they exhibit different hydrographic and sedimentary conditions. These stations were selected as representative of the different topographic features and correspondingly different sedimentary and oceanographic regimes found on the outer shelf.

Samples of meiobenthos were taken at each station as subsamples from a single 0.1 m^2 Smith-McIntyre grab (as described in Chapter 6). Maximum penetration depth and appearance of the redox potential discontinuity (RPD) were measured and recorded. The Smith-McIntyre grab sampled to a depth of 7-18 cm into the sediment, but any grab that did not penetrate at least 8 cm was not subsampled for meiobenthos.

Subsampling methodology was designed in order to elucidate small scale spatial patterns in the distribution and abundance of meiofaunal taxa. Samples were taken with a series of 12 contiguous square corers arranged in a three by four (3 x 4) array. Each core was 2.5 x 2.5 cm or 6.25 cm^2. Cores 1-9 were evaluated for hard-bodied meiofauna, cores 10 and 11 were archived in 5% formalin (buffered with $CaCO_3$), and core 12 was used for analysis of sediments (Figure 7-4). The total area of the 3 x 3 array used for taxonomic evaluation was 56.25 cm^2. Theoretical considerations indicate that, with respect to the definition of patch size, samples should be half the size of the actual patch in order to define the size of the patches without overlapping (Pielou 1969). The configuration used should be able to resolve patch sizes from 12.5 cm^2 to 112.5 cm^2 and thus provide information about the small scale spatial heterogeneity of distributions of meiobenthos.

Shipboard Processing

The 12 square corers were inserted into the sediment obtained with the Smith-McIntyre grab to a depth of at least 8 cm and withdrawn with as little disturbance as possible. Cores 1-11 were then rinsed into separate, labeled containers with an isotonic solution of magnesium chloride ($MgCl_2$) and allowed to relax for 15-20 minutes. Core 12 was extruded into a labeled Whirlpak and frozen prior to analysis of sediment. Cores 1-11 were then processed to remove the animals from the sediment by a $MgCl_2$ decantation method (Hulings and Gray 1971). Each individual core was agitated with $MgCl_2$ and the supernatant decanted through a 0.5 mm and a 0.063 mm sieve. This was repeated 6-8 times or until very little fine material was left in each sample. The material retained on the 0.063 mm sieve was then carefully washed into a prelabeled jar with 5% buffered formalin and

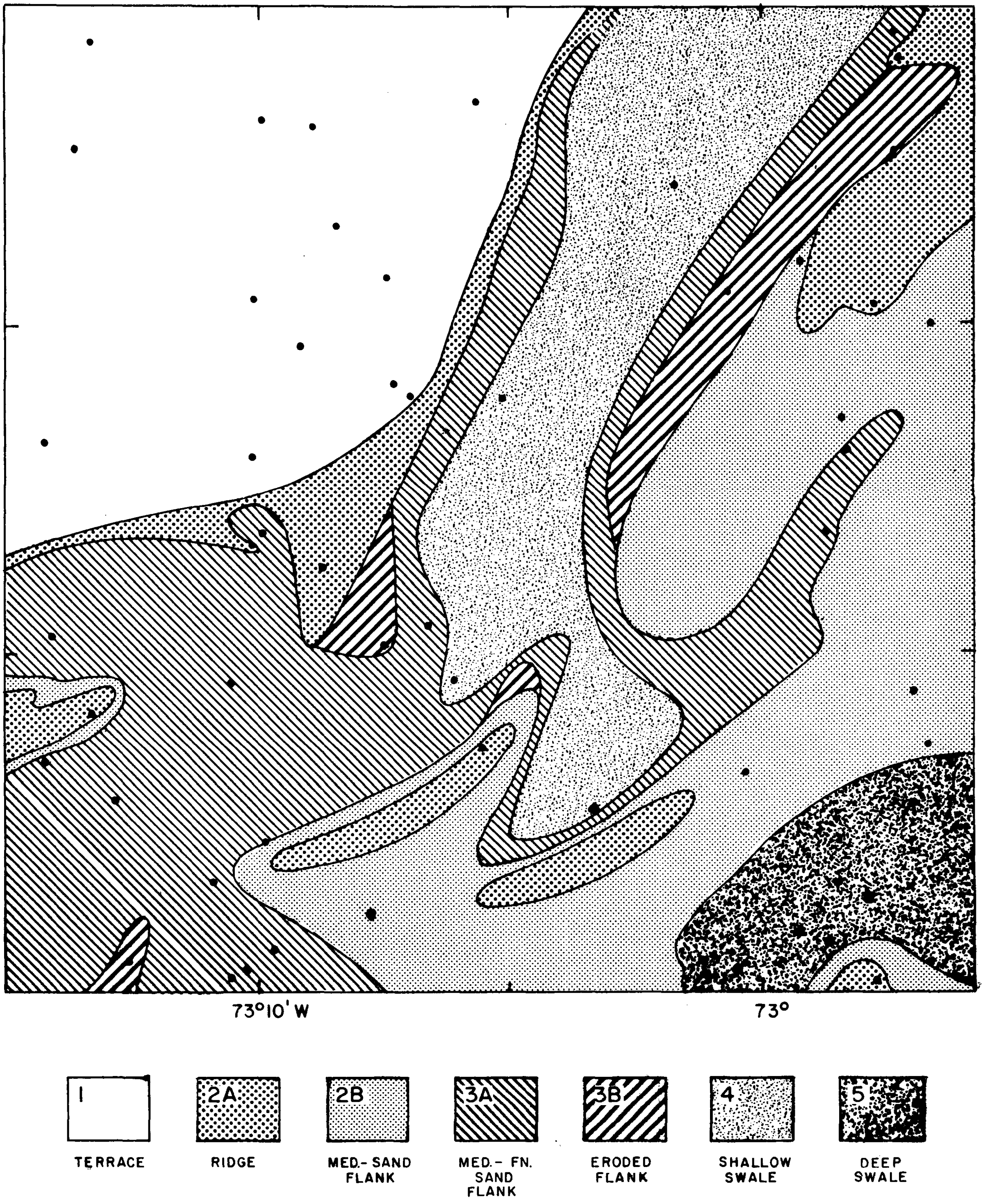


Figure 7-2. Distribution of major habitats identified in habitat delineation study of macrobenthos, area B.

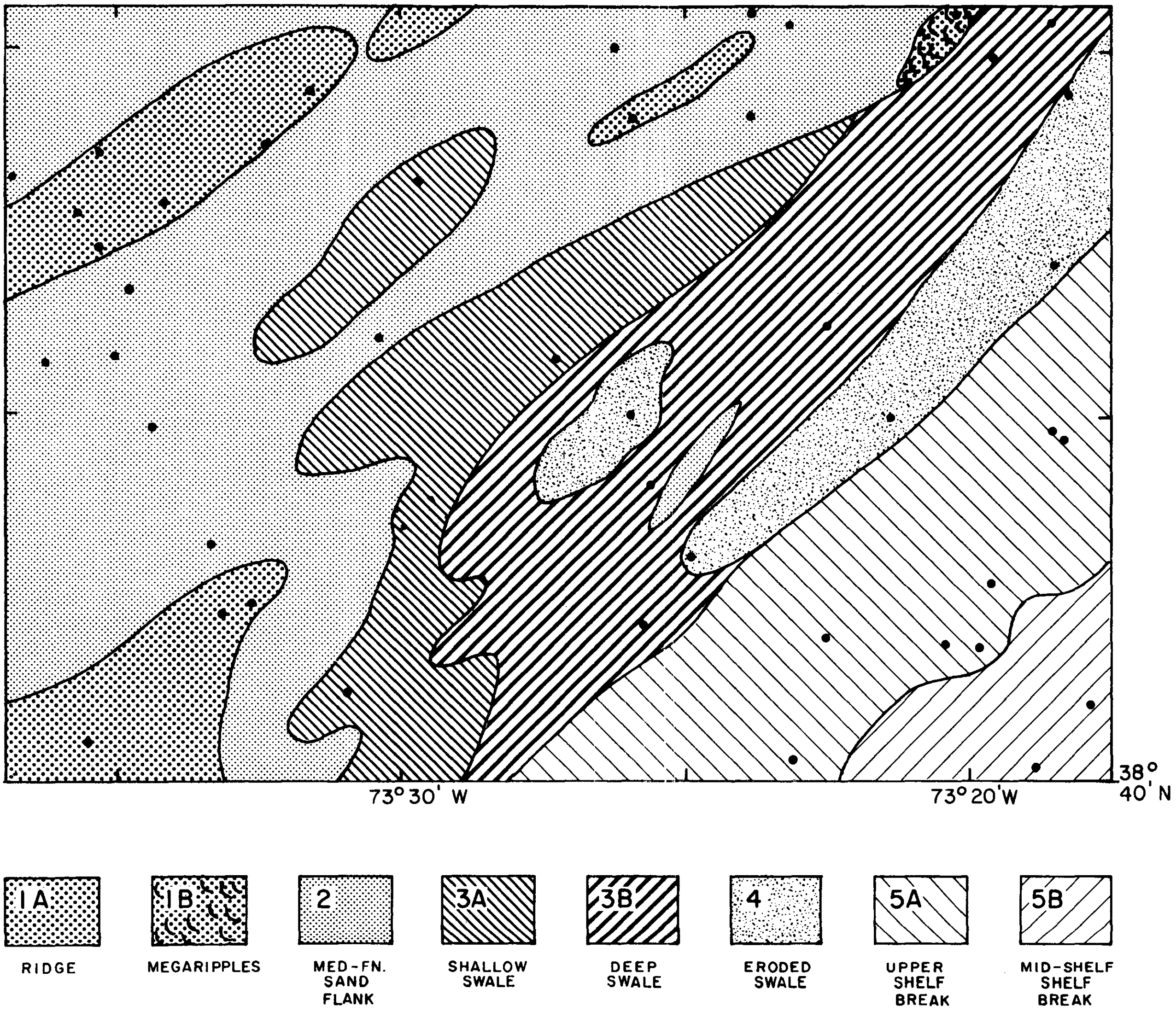
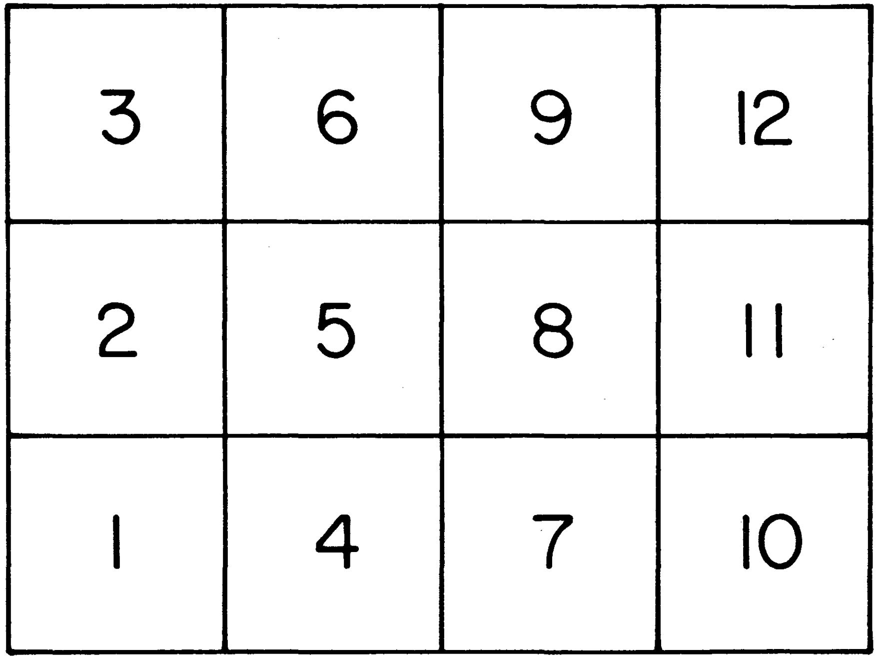


Figure 7-3. Distribution of major habitats identified in habitat delineation study of macrobenthos, area E.



CORES 1-9 QUANTITATIVE TAXONOMIC ANALYSIS

CORES 10-11 FORMALIN ARCHIVING

CORE 12 GRANULOMETRIC ANALYSIS

Figure 7-4. Arrangement of contiguous replicate cores taken for meiobenthos.

held for taxonomic analysis. This extraction technique is between 90-99% effective based on both estimates based on extraction efficiency tests performed on some of these samples and personal communications from other workers. The 0.5 mm sieve fraction was retained but not analyzed. Figure 7-5 summarizes the shipboard procedure for collection and initial processing of meiofaunal samples.

Laboratory Processing

The analytic protocol was designed to provide 1) quantitative, 2) summary, and 3) interpretive information as part of an ongoing procedure. Quantitative information was obtained by sorting and enumeration of samples and by estimation of biomass. Summary and interpretive information was obtained by analysis of these "raw data".

Laboratory processing was initiated by sorting meiofauna from cores 1-9 from each station and season into major taxa. The abundance of each major taxon was determined during sorting and recorded by core for each station and season. Biomass values for each major taxon and total biomass values for each core were also computed. Biomass values were not directly measured but were estimates based on empirical mass/individual values obtained from other studies. Table 7-1 gives the values used to compute biomass for each taxon and the source of these values. This method was chosen because of the inherent difficulties of consistently measuring the mass of organisms which might be as small as 0.5 μg.

Taxonomic determination of dominant organisms was carried out to genus and, where possible, species level. These determinations were accomplished by microscopic morphologic differentiation at high magnification (up to 1250x) using phase contrast optics. This procedure proved to be very time consuming. Nomenclature of marine free-living nematodes has been summarized several times in the last five years, but the system of Gerlach and Riemann (1973) was followed in this work. The recent summarization of Coull (1977) was followed for harpacticoid copepods. The only other taxa that made up substantial portions of sample collections were ostracods, polychaetes, and larvae. Many of the larval forms and polychaetes were temporary meiofauna, i.e., developmental stages of macrofaunal organisms which spend only a small part of their lives as members of the meiofauna. In many cases it was not possible to identify these juvenile organisms at even the genus level. Further taxonomic determinations of specific groups (Ostracoda, Tardigrada, Kinorhyncha, Gastrotricha) are planned.

Data Analysis

Figure 7-6 shows the general protocol of data analysis which can be broken down into the following categories: 1) data reporting, 2) determination of abundance patterns and community structure, 3)

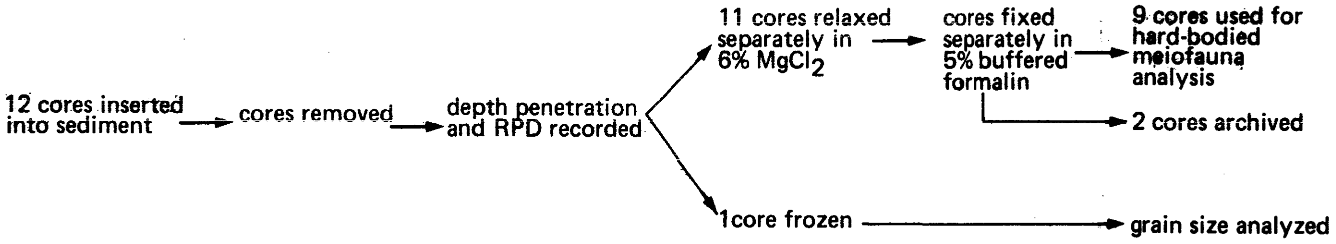


Figure 7-5. Synopsis for shipboard procedure for processing meiobenthos samples.

Table 7-1. Values for computation of meiobenthic biomass.

Taxon	Weight/individual (μg)	Source
Nematoda	0.6	Coull, personal communication
Harpacticoida	1.2	Coull, personal communication
Gastrotricha	0.5	Coull, personal communication
Tardigrada	0.5	Coull, personal communication
Ostracoda	0.5	Coull, personal communication
Larvae	0.4	Coull, personal communication
Turbellaria	1.0	Coull, personal communication
Polychaeta	6.2	Juario 1975
Bivalve juveniles	5.7	Juario 1975

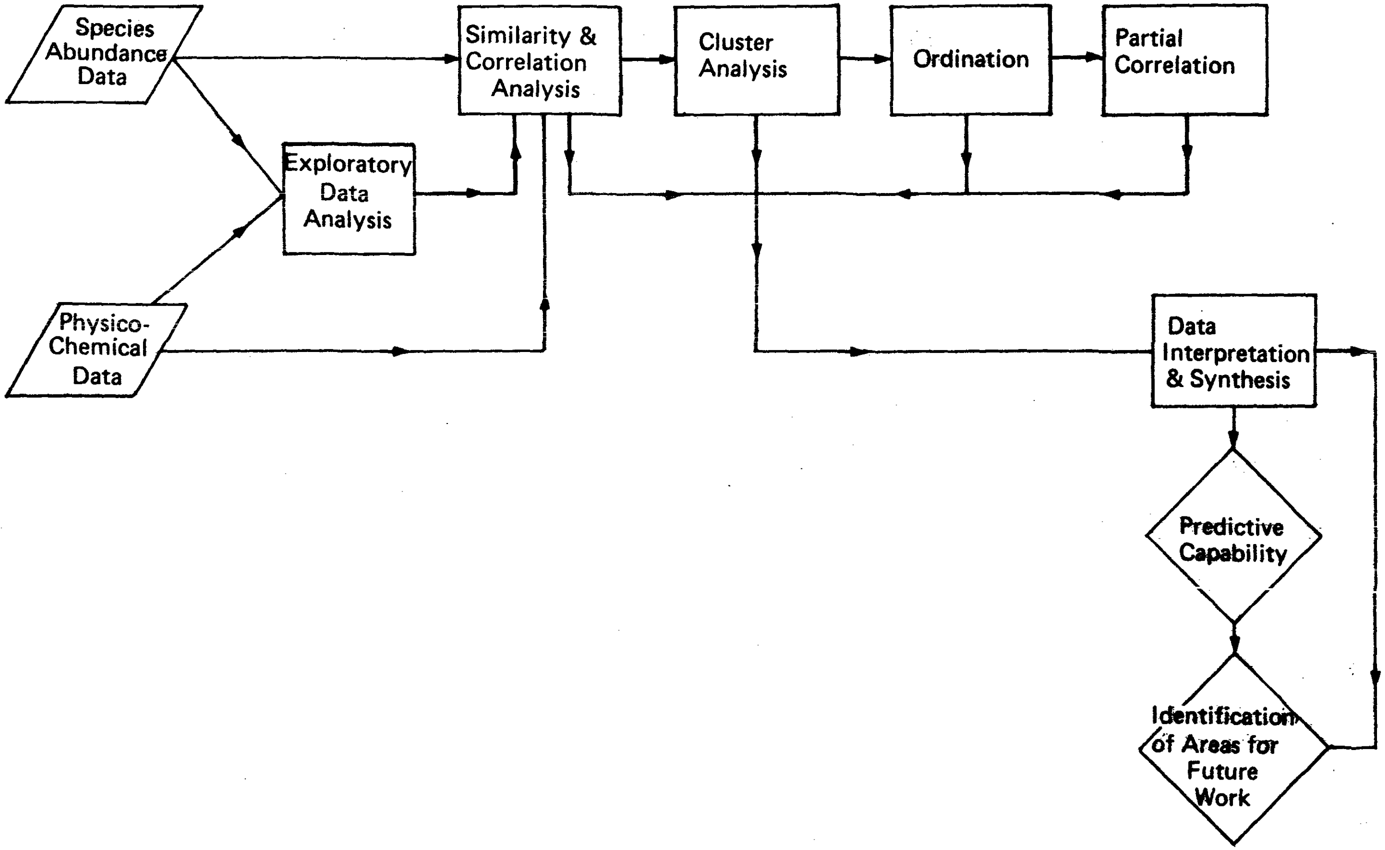


Figure 7-6. General outline of data analyses employed in meiobenthos study.

analysis of seasonal trends, 4) analysis of small spatial heterogeneity (patchiness), and 5) the analysis of these trends and patterns with respect to the physical and chemical parameters of the environment.

Determination of Abundance Patterns and Community Structure

Several indices were computed from species abundance data. A harpacticoid/nematode ratio was computed as

$$\frac{H}{N} = R$$

where H is the abundance per core of harpacticoid copepods and N is the abundance per core of nematodes. This ratio has been used previously (Pequegnat 1975) as an indicator of environmental perturbation. It was used here in a strictly comparative sense. The rationale for this use is that both taxonomic groups react to changes in the habitat differently and so similarities in patterns of abundance as shown by this ratio could be related to similarities in physico-chemical parameters in a habitat.

Species diversity as reflected by the Shannon-Wiener information function H' (bits/individual) was computed by sample for both nematodes and harpacticoid copepods. Species evenness, J' (Pielou 1966, 1969, 1975), was also calculated by sample for nematodes and harpacticoid copepods. These taxa were selected because of their overwhelming dominance of the permanent meiobenthos. The analyses were performed on Nematoda and Harpacticoida separately because the level of identification varied between the groups and for reasons of comparability with results of other investigators.

Various multivariate analyses were used to define between-station and between-cruise patterns in multi-species assemblages. Again, Nematoda and Harpacticoida were treated separately. Taxa included in the analyses were those identified at least to genus. Extremely rare taxa represented by only a few specimens were excluded from the analyses. The multivariate analyses employed are discussed in more detail in Boesch et al. (1977) and in Chapter 6 of this report. Numerical classification (cluster analysis) was employed followed by nodal analysis (Boesch 1977). The classification strategy used consisted of log-transformation of abundance measures, calculation of Bray-Curtis resemblance, and flexible agglomerative clustering. Because of the limited number of stations, however, ordination proved to be a more useful technique. Reciprocal averaging ordination (Hill 1974), an eigenvector technique which has desirable properties for the analysis of ecological data (Fasham 1977; Gauch et al. 1977), was applied. A principal advantage of this method is that it casts collections (normal analysis) and species (inverse analysis) in the same spatial model such that differences in assemblages among stations can be directly interpreted by characterizing species (inverse analysis).

Analysis of Seasonal Trends

Analysis of seasonal patterns was accomplished primarily by graphical comparisons. Five value batch summaries (Tukey 1977) were graphed for each station and displayed to show within habitat similarity. This allowed immediate visual comparisons of seasonal patterns of Nematoda, Harpacticoida, Ostracoda, Polychaeta, and total meiofauna, and pinpointed those taxa which had discernible seasonal patterns. As previously indicated, the accelerated population dynamics of meiofuanal organisms may mask seasonal patterns with respect to quarterly sampling.

Analysis of Small Scale Spatial Heterogeneity

The analysis of these spatial patterns was approached in a number of ways. Patterns of raw data were mapped for nematodes and harpacticoids among the nine core samples at each station. These patterns were visually compared and assessed by computing a coefficient of dispersion (Sokal and Rohlf 1969) and determining the distribution type of these taxa with respect to a Poisson model. Potential biological interactions on the spatial scale of the replicate cores was identified and tested by spatial autocorrelation (Jumars et al. 1977). This is a technique which correlates the spatial location of species occurrence within a sampling grid and was used by Jumars et al. (1977) to characterize the spatial pattern of a single species in an array. A technique was derived similar to Cliff and Ord (1972) to compare the spatial autocorrelation of two taxa at the same time. Species abundance values were first standardized with respect to sample variance as

$$\frac{x_i - \bar{x}}{\sigma^2 \bar{x}}$$

and then the standardized difference between species abundance was determined as

$$\left[\frac{x_i - \bar{x}}{\sigma^2 \bar{x}} - \frac{y_i - \bar{y}}{\sigma^2 \bar{y}} \right]$$

where x values refer to nematode abundances and y values refer to harpacticoid abundances, and autocorrelation was computed on the standard differences. The interpretation of this statistic gives an indication of the amount of influence one taxon may have had on the spatial location of another taxon within the sampling grid.

Spatial heterogeneity was also examined with reference to the hypothesis of Coull et al. (1977) already explained. During the summer 1977 cruise a duplicate set of samples (cores 1-12) was taken at each of the B cluster stations. These cores were taken from separate grab samples and were evaluated exactly the same as the first set. A non-parametric Mann-Whitney test (Conover 1971) was then carried out to determine if the two sets of samples at each station could have been drawn from the same overall population.

Trend Analysis with Respect to Physical and Chemical Parameters

Product-moment correlation coefficients (Sokal and Rohlf 1969) were computed between total meiofaunal abundance, abundance of selected taxa, biological indices (H/N, H', and J') and sedimentary, physical, and chemical parameters. This analysis was performed in order to elucidate strong association within the data, but because of the nature of the statistical test used, no causality can be inferred from these associations. As always with correlation analysis, the possibility of illusory correlation exists. The series of sedimentary, physical, and chemical data collected is probably highly autocorrelated so that strong associations can be statistically shown between variables which are actually related to an exterior or unmeasured causal factor. For this reason the strong associations indicated by high correlation must be interpreted with care. Only those high correlations which are consistent and appear to have clear ecological meaning will be interpreted and further analyzed.

One method to insure more realistic correlation in a multivariate data set is to use a partial correlation model. Partial correlation computes the strong association between variables while holding the effects of other variables constant (i.e., eliminating these effects). Conover (1971) presents arguments extending the partial correlation model to the non-parametric case for the Spearman's rho statistic. This non-parametric partial correlation model was used to try to identify the variables most effective in scaling the ordination analysis along each axis, and to show strong associations between meiofaunal occurrence and the occurrence of both bacteria and foraminifera.

RESULTS

Figure 7-7 shows the range of total density of meiobenthos found on the outer continental shelf in several studies including the present one. The range of 59 to 1123 organisms/$10cm^2$ found in this

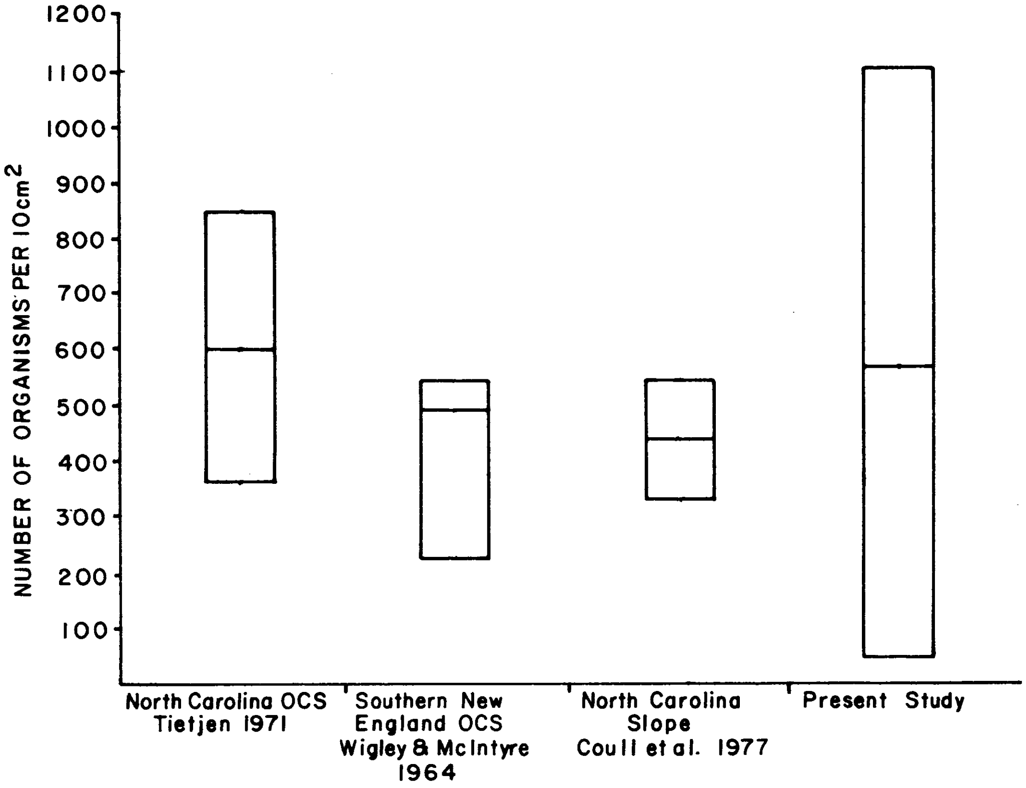


Figure 7-7. Comparison of densities of meiobenthos reported on the Atlantic continental shelf. Bars represent range and horizontal lines mean.

study encompasses the other values and suggests that the sampling and extraction methods were effective. This is especially significant as several of these other studies used deeper digging box corers and/or direct count enumeration without extraction.

Composition of the Fauna

Over 80 genera or species of dominant nematodes and harpacticoid copepods were identified along with members of 13 other higher taxonomic groups. Appendix 7-A lists the taxonomic determinations of each sample by station and sampling period. Tables 7-2 through 7-5 list the dominant species by station and sampling period, and Table 7-6 lists the proportions of total meiofauna comprised of nematodes and harpacticoid copepods in each collection.

Nematodes numerically dominated the collections at all stations (except Station E4, winter 1977) usually comprising 40-80% and occasionally up to 88% of the individuals. Fifty-eight nematode taxa (Tables 7-7 to 7-10) were recorded and a number of the species are apparently new to science.

Harpacticoid copepods comprised between 5 and 30% of the individuals in all collections, although in one sample (Station E4, winter 1977) they comprised 51% of the individuals collected. Twenty-two harpacticoid taxa were recorded and most of the species are already described.

Together these two taxa made up 60-90% of all individuals in all samples during this study. The only other taxa which occurred in significant numbers in these collections were Ostracoda and Polychaeta. The ostracods and polychaetes were generally juveniles of species which were taken as adults in the macrobenthos (>0.5 mm) samples (Chapter 6). Larvae sometimes made up a large but not dominant proportion of individuals. The larvae were generally comprised of decapod crustaceans, although both winter and spring 1977 samples contained large numbers of harpacticoid larvae.

Biomass and Abundance

Data on total meiofaunal biomass and abundance are summarized in Figures 7-8 and 7-9 (Data are presented in Appendix 7-C.). Biomass values ranged from 0.15-1.5 mg/10 cm^2, and total abundance values ranged from 59-1123 individuals/10 cm^2. In general, biomass and abundance showed similar patterns. This was primarily because of the dominance pattern already reported with respect to the nematodes and harpacticoid copepods. It seemed clear that, except in a few instances, both biomass and abundance patterns of total meiofauna were determined by these dominant taxa. Figures 7-10 and 7-11 summarize

(TEXT CONTINUES ON PAGE 7-36)

Table 7-2. Dominant Species, Fall 1976

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
A3					
Sabatieria sp.	68.70	12.8	*Stenhelia normani*	75.00	0.3
Tershellinga sp.	9.71		*Enhydrosoma longifurcata*	25.00	0.1
Sabatieria chitwoodi	8.84				
Theristus sp.	5.94				
B2					
Microlaimus sp.	42.89	16.6	*Enhydrosoma longifurcata*	38.29	9.
Desmodora sp.	12.66	4.	*Stenhelia normani*	27.48	6.
Biarmifer sp.	5.68				
Leptolaimus sp.	5.43				
B3					
Tershellinga sp.	24.63	18.	*Stenhelia normani*	56.46	5.
Paramonohystera sp.	21.72	16.	*Enhydrosoma longifurcata*	30.61	
Sabatieria sp.	19.70	14.			
Latronema sp.	9.63				
B4					
Microlaimus sp.	33.39	13.	*Leptocaris brevicornis*	39.35	7.
Oncholaimus sp.	31.77	13.	*Enhydrosoma longifurcata*	24.19	
Mesacanthion sp.	20.76				
Biarmifer sp.	9.21				
E1					
Tricoma sp.	30.10	11.	*Enhydrosoma longifurcata*	36.33	9.
Microlaimus sp.	18.66		*Leptocaris brevicornis*	30.55	
Desmodora sp.	14.43				
Actinonema sp.	12.94				
E3					
Microlaimus sp.	36.24	21.	*Enhydrosoma longifurcata*	18.53	6.
Desmodora sp.	28.80	17.	*Leptastacus macronyx*	18.53	6.
Tricoma sp.	12.75				
Rhynconema sp.	6.06				

Table 7-2. (concluded)

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
E4					
Tershellinga sp.	36.23	23.	*Robertgurneya rostrata*	28.97	0.9
Sabatieria sp.	20.03	12.	*Stenhelia normani*	28.04	
Neotonchus sp.	12.52				
Everta sp.	9.46				
F3					
Sabatieria sp.	41.26	30.5	*Schizopera carolinensis*	41.73	1.
Microlaimus sp.	11.86	9.	*Leptastacus macronyx*	26.62	
Paramonohystera sp.	10.47				
Theristus sp.	6.96				

Table 7-3. Dominant Species, Winter 1977

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
A3					
Tershellinga sp.	35.37	29.	*Enhydrosoma longifurcata*	34.92	3.
Sabatieria sp.	11.43	9.	*Stenhelia normani*	32.28	
Theristus sp.	11.09				
Latronema sp.	9.54				
B2					
Microlaimus sp.	43.12	14.	*Enhydrosoma longifurcata*	38.33	9.5
Mesacanthoides sp.	14.15	5.	*Stenhelia normani*	28.57	
Tricoma absidata	12.45				
Halichoanolaimus sp.	11.14				
B3					
Theristus sp.	25.03	15.	*Stenhelia normani*	47.15	15.
Sabatieria sp.	16.53	10.	*Enhydrosoma longifurcata*	24.66	10.
Viscosia sp.	10.73				
Sabatieria chitwoodi	8.57				
B4					
Viscosia sp.	28.10	12.	*Enhydrosoma longifurcata*	32.42	7.
Microlaimus sp.	13.76	6.	*Leptocaris brevicornis*	28.84	
Latronema sp.	12.16				
Microlaimus kauri	9.56				
E1					
Halichoanolaimus sp.	17.53	6.7	*Enhydrosoma longifurcata*	47.30	9.8
Ascolaimus sp.	11.64		*Leptocaris brevicornis*	24.68	
Microlaimus sp.	10.00				
Viscosia sp.	9.86				
E3					
Monoposthia sp.	19.81	9.	*Enhydrosoma longifurcata*	47.96	9.6
Viscosia sp.	17.99		*Leptocaris brevicornis*	17.04	
Microlaimus sp.	8.34				
Latronema sp.	7.45				

Table 7-3. (concluded)

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
E4					
Southernia sp.	23.45	5.	*Halectinosoma* sp.	26.28	13.
Latronema sp.	11.86		*Ameira* sp.	25.30	12.5
Microlaimus sp.	9.84				
Monoposthia sp.	9.70				
F3					
Sabatieria sp.	48.11	40.	*Schizopera carolinensis*	49.25	3.
Tershellinga sp.	11.20	9.	*Leptastacus macronyx*	26.12	
Chromaspirina sp.	8.90				
Viscosia sp.	7.80				

Table 7-4. Dominant Species, Spring 1977

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
A3					
Sabatieria sp.	42.09	35.	*Stenhelia normani*	43.37	4.
Monoposthia sp.	11.35	9.	*Halectinosoma* sp.	23.47	2.
Tershellinga sp.	9.07				
Paramonohystera sp.	7.52				
B2					
Microlaimus sp.	35.32	21.	*Leptocaris brevicornis*	22.39	3.
Chromadora sp.	14.58	8.	*Cletodes* sp.	18.44	
Latronema sp.	13.02				
Monoposthia sp.	6.36				
B3					
Sabatieria sp.	26.12	18.9	*Mesochra pygmaea*	21.73	3.
Tershellinga sp.	14.49	11.	*Schizopera carolinensis*	19.92	
Chromadora sp.	13.73				
Theristus sp.	7.87				
B4					
Monoposthia sp.	34.62	20.	*Apodopsyllus* sp.	20.00	3.
Mesacanthion sp.	18.82	11.	*Leptocaris brevicornis*	18.82	
Latronema sp.	16.21				
Ceramonema sp.	14.08				
E1					
Microlaimus sp.	36.15	13.	*Robertgurneya rostrata*	43.51	3.
Southernia sp.	16.45	6.	*Leptocaris brevicornis*	16.03	
Tricoma absidata	10.82				
Theristus sp.	9.52				
E3					
Microlaimus sp.	24.00	11.	*Cletodes* sp.	23.11	6.
Mesacanthion sp.	13.01		*Leptocaris brevicornis*	14.39	
Tricoma absidata	12.11				
Epsilonematidae	11.63				

Table 7-4. (concluded)

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
E4					
Theristus sp.	28.62	19.	*Apodopsyllus* sp.	27.09	5.
Paramonohystera sp.	15.83		*Halectinosoma* sp.	26.27	
Mesacanthion sp.	11.96				
Odontophora sp.	9.54				
F3					
Theristus sp.	29.30	26.	*Ameira* sp.	46.15	3.
Paramonohystera sp.	14.74	13.	*Stenhelia normani*	21.54	
Chromadora sp.	12.02	11.			
Tershellinga sp.	11.27	9.9			

Table 7-5. Dominant Species Summer 1977

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
A3					
Sabatieria sp.	20.44	17.	*Halectinosoma* sp.	33.58	4.
Tershellinga sp.	14.00	12.	*Schizopera carolinensis*	29.52	
Sabatieria chitwoodi	13.95	12.			
Theristus sp.	12.68	10.6			
B2					
Monoposthia sp.	33.04	19.	*Ameira* sp.	32.25	4.
Theristus sp.	16.98	9.6	*Leptocaris brevicornis*	29.96	
Viscosia sp.	12.55				
Microlaimus sp.	7.50				
B3					
Sabatieria chitwoodi	34.49	25.	*Leptocaris brevicornis*	25.99	3.
Theristus sp.	17.90	13.	*Amphiascus minutus*	16.25	
Monoposthia sp.	12.81	9.5			
Latronema sp.	6.83				
B4					
Ascolaimus sp.	26.31	13.	*Ameira* sp.	37.28	6.
Desmodora sp.	25.73	13.	*Leptocaris brevicornis*	29.95	
Viscosia sp.	15.88	8.			
Hypodontolaimus	10.43				
E1					
Euchromadora sp.	25.71	11.	*Enhydrosoma longifurcata*	46.08	13.
Microlaimus sp.	21.25	9.3	*Leptocaris brevicornis*	24.51	7.
Didelta sp.	9.21				
Odontophora sp. & *Mesacanthion* sp.	6.67				
E3					
Microlaimus sp.	21.16	8.	*Leptocaris brevicornis*	25.68	6.
Epsilonematidae	14.82		*Leptastacus macronyx*	17.39	
Desmodora sp.	13.10				
Tricoma pellucida	9.00				

Table 7-5. (concluded)

Nematoda	% Nematoda	% Total	Harpacticoida	% Harpacticoida	% Total
E4					
Theristus sp.	21.28	16.	*Enhydrosoma longifurcata*	33.33	3.
Odontophora sp.	16.69	13.	*Amphiascus minutus*	20.33	
Hypodontolaimus sp.	9.22	7.			
Mesacanthion sp.	9.02				
F3					
Sabatieria sp.	30.94	24.	*Schizopera carolinensis*	26.95	4.
Therisus sp.	14.82	11.	*Pseudobradya* sp.	26.95	4.
Tershellinga sp.	11.65				
Viscosia sp.	7.76				

Table 7-6. Proportion dominant taxa, Nematoda and Harpacticoida, 1976-1977.

Station	Season	Year	Nematoda	Harpacticoida	Nematoda & Harpacticoida	Mean of Nematoda & Harpacticoida	S.D. of Nematoda & Harpacticoida
A3	Fall	1976	0.1858	0.004	0.1898		
	Winter	1977	0.8313	0.0783	0.9096		
	Spring	1977	0.8439	0.1010	0.9449		
	Summer	1977	0.8336	0.1168	0.9504	0.935*	0.022*
B2	Fall	1976	0.3872	0.2256	0.6128		
	Winter	1977	0.3279	0.2478	0.5757		
	Spring	1977	0.6056	0.142	0.7476		
	Summer	1977	0.5653	0.1357	0.7010	0.659	0.079
B3	Fall	1976	0.737	0.0811	0.8181		
	Winter	1977	0.6138	0.1333	0.7471		
	Spring	1977	0.7259	0.1531	0.879		
	Summer	1977	0.7383	0.1229	0.8612	0.824	0.056
B4	Fall	1976	0.4027	0.182	0.5847		
	Winter	1977	0.4283	0.2143	0.6426		
	Spring	1977	0.5789	0.1707	0.7496		
	Summer	1977	0.4973	0.1718	0.6691	0.061	0.068
E1	Fall	1976	0.3672	0.2612	0.6284		
	Winter	1977	0.3849	0.2085	0.5935		
	Spring	1977	0.3555	0.0613	0.4168		
	Summer	1977	0.4362	0.2798	0.7159	0.589	0.126
E3	Fall	1976	0.5935	0.3174	0.9107		
	Winter	1977	0.4416	0.2022	0.6438		
	Spring	1977	0.4646	0.2519	0.7166		
	Summer	1977	0.3851	0.2321	0.6172	0.722	0.133

Table 7-6. (concluded)

Station	Season	Year	Nematoda	Harpacticoida	Nematoda & Harpacticoida	Mean of Nematoda & Harpacticoida	S.D. of Nematoda & Harpacticoida
E4	Fall	1976	0.6382	0.0306	0.6688		
	Winter	1977	0.2352	0.5075	0.7427		
	Spring	1977	0.6609	0.1973	0.8582		
	Summer	1977	0.7683	0.1028	0.8712	0.785	0.097
F3	Fall	1976	0.7405	0.0482	0.7887		
	Winter	1977	0.8349	0.0557	0.8906		
	Spring	1977	0.8828	0.0604	0.9433		
	Summer	1977	0.7659	0.1470	0.9129	0.884	0.067

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* Does not include Fall 1976 values.

Table 7-7. Species identification list, Nematoda, Fall 1976.

1. *Choniolaimus*
2. *Neotonchus*
3. *Halalaimus*
4. *Sabatieria chitwoodi*
5. *Tershellinga*
6. *Disconema*
7. *Latronema*
8. Unknown #2
9. *Araeolaimus*
10. *Diplopeltis*
11. *Sabatieria*
12. *Odontophora*
13. *Paramonohystera*
14. Unknown #1
15. *Sabatieria* sp. 2
16. *Theristus*
17. *Anticoma*
18. *Ascolaimus*
19. *Porocoma*
20. *Mesacanthion*
21. *Oncholaimus*
22. *Biarmifer*
23. *Rhynconema*
24. *Desmodora*
25. *Microlaimus*
26. *Tricoma*
27. *Xyala*
28. *Paracyatholaimus*
29. *Ceramonema*
30. *Leptolaimus*
31. *Tricoma absidata*
32. *Actinonema*
33. Epsilonematidae

Table 7-8. Species identification list, Nematoda, Winter 1977.

1. *Paramonohystera elliptícus*
2. Enoplidae
3. *Porocoma*
4. *Monoposthia mirabilis*
5. *Mesacanthoides*
6. *Xyala*
7. *Sphaerolaimus*
8. *Anticoma*
9. *Halichoanolaimus*
10. *Microlaimus*
11. *Microlaimus kauri*
12. *Desmodora*
13. *Paracyatholaimus*
14. *Southernia*
15. *Viscosia*
16. *Didelta*
17. Epsilonematidae
18. *Ascolaimus*
19. *Monoposthia*
20. *Chromadora*
21. *Tricoma*
22. *Ceramonema*
23. *Desmoscolex*
24. Desmoscolecidae
25. *Latronema*
26. *Tricoma absidata*
27. *Rhynconema*
28. *Odontophora*
29. Unknown #3
30. *Paramonohystera*
31. *Oncholaimus*
32. *Sabatieria chitwoodi*
33. *Sabatieria* sp. 1
34. Unknown #1
35. *Choniolaimus*
36. *Theristus*
37. *Halalaimus*
38. *Tershellinga*
39. *Chromaspirina*
40. *Actinonema*
41. *Quadricoma*
42. Unknown #2
43. *Desmoscolex californicus*
44. *Tershellinga* sp. 1
45. *Biarmifer*

Table 7-9. Species identification list, Nematoda, Spring 1977.

1. Unknown #1
2. Epsilonematidaec
3. *Ascolaimus*
4. *Microlaimus kauri*
5. *Tricoma absidata*
6. *Halichoanolaimus*
7. *Anticoma*
8. *Desmoscolex californicus*
9. *Paracyatholaimus*
10. *Odontophora*
11. *Mesacanthion*
12. *Rhynconema*
13. *Southernia*
14. *Microlaimus*
15. *Theristus*
16. *Sphaerolaimus*
17. *Monoposthia*
18. *Paramonohystera*
19. *Ceramonema*
20. *Viscosia*
21. *Chromadora*
22. *Choniolaimus*
23. *Oncholaimus*
24. *Latronema*
25. *Tricoma pellucida*
26. *Quadricoma*
27. *Didelta*
28. *Araeolaimus*
29. *Desmoscolex*
30. *Halalaimus*
31. *Tershellinga*
32. *Sabatieria*
33. *Sabatieria chitwoodi*
34. *Euchromadora*

Table 7-10. Species distribution list, Nematoda, Summer 1977.

1. *Halichoanolaimus*
2. *Araeolaimus*
3. *Ceramonema*
4. *Gammanema*
5. *Ascolaimus*
6. *Actinonema*
7. *Halalaimus*
8. *Sabatieria chitwoodi*
9. *Sabatieria*
10. *Anticoma*
11. *Odontophora*
12. *Tershellinga*
13. *Theristus*
14. *Monoposthia*
15. *Latronema*
16. *Didelta*
17. *Hypodontolaimus*
18. *Mesacanthion*
19. *Desmoscolex*
20. *Choniolaimus*
21. *Viscosia*
22. *Tricoma pellucida*
23. Epsilonematidae
24. *Desmodora*
25. *Microlaimus*
26. *Euchromadora*
27. *Rhynconema*
28. *Tricoma*
29. *Cobbia*

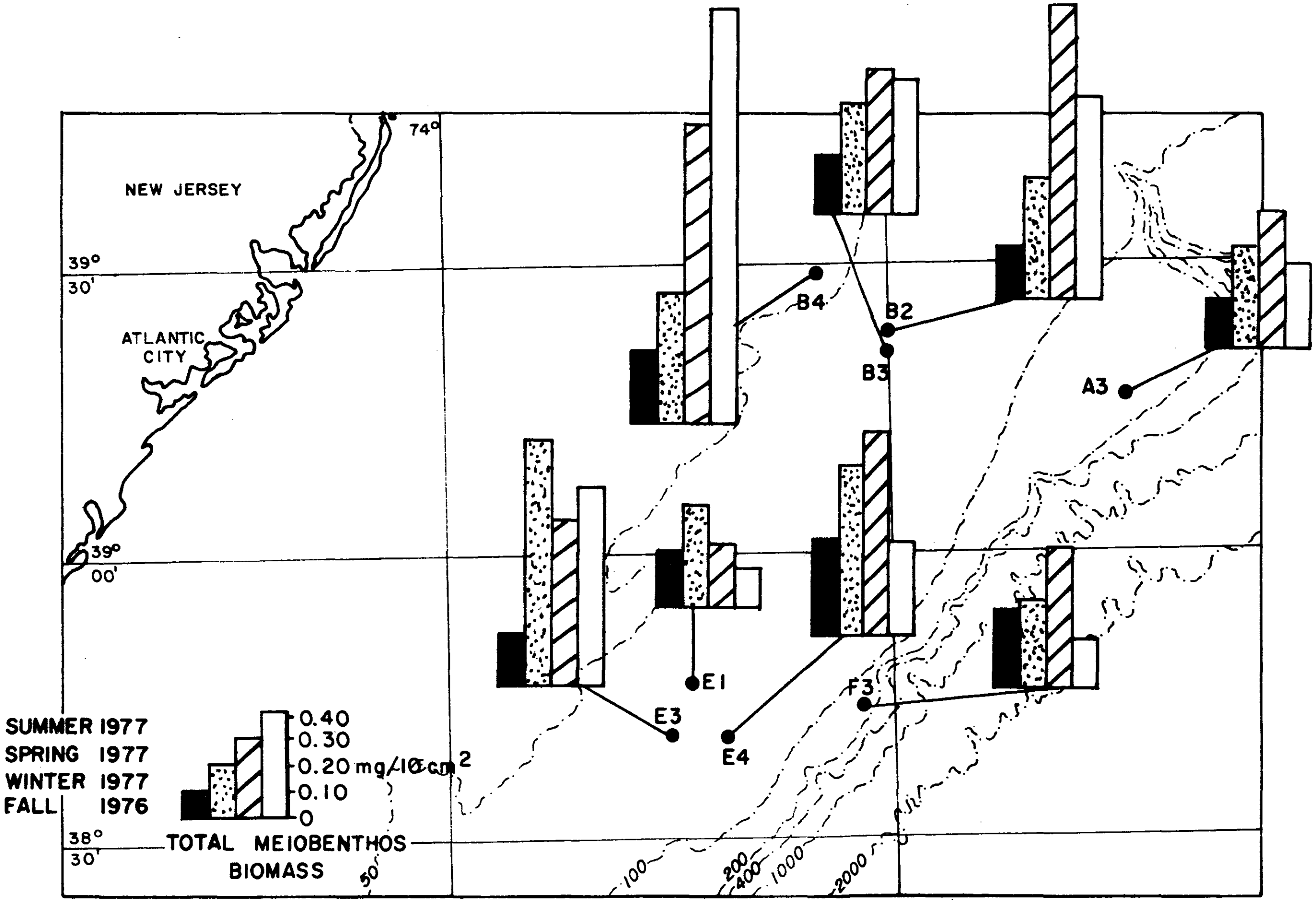

Figure 7-8. Estimated biomass of total meiobenthos.

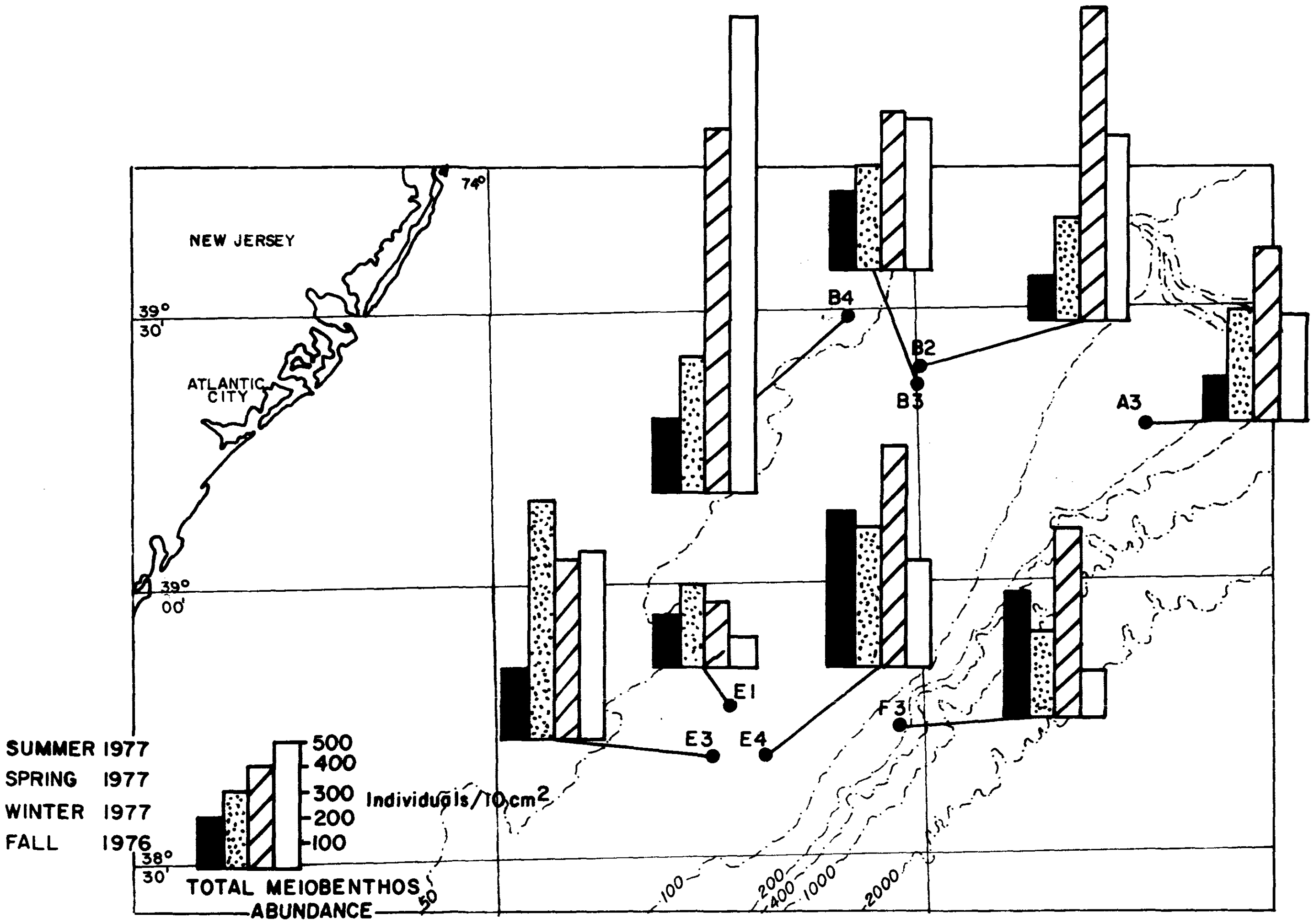

Figure 7-9. Estimated density of total meiobenthos.

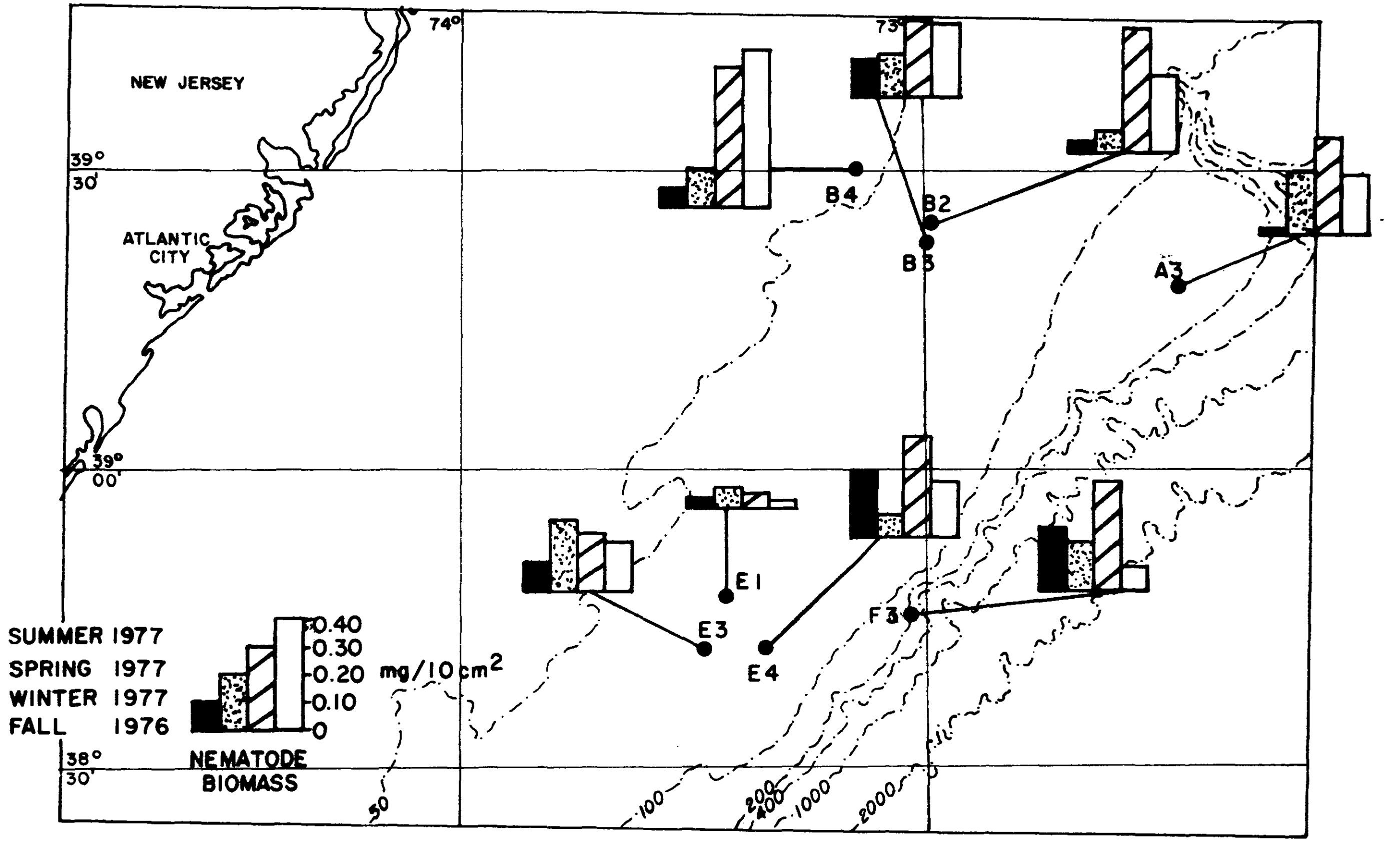

Figure 7-10. Estimated biomass of nematodes.

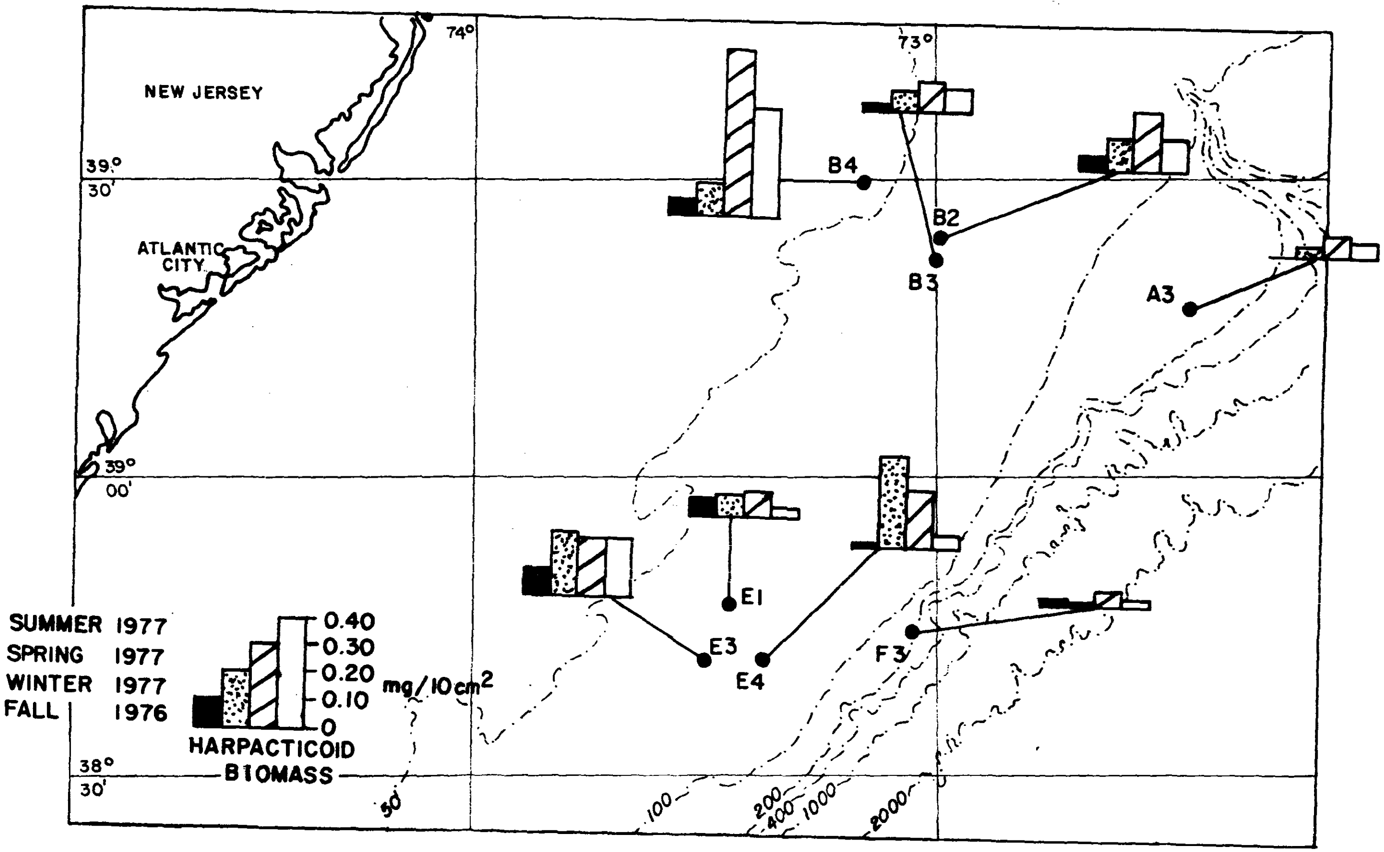

Figure 7-11. Estimated biomass of harpacticoid copepods.

biomass data for nematodes and harpacticoids respectively and Figures 7-12 and 7-13 summarize abundance data for these taxa.

In some samples such as at Station A3, fall 1976, polychaetes made up a significant proportion of the individuals in the collections. Juvenile polychaetes were usually much larger than the other organisms in these collections so that, where found in abundance, even if not dominant, polychaetes made up a disproportionately large part of the biomass value in these collections. Just the opposite was true of some less abundant meiofaunal taxa such as Gastrotricha, Tardigrada, and Kinorhyncha. These animals, even when found in abundance, did not make up a large portion of the total biomass because of their very small size.

Although it appears (Figures 7-8 and 7-9) that the highest density, and therefore the highest sample biomass, occurred in collections from the stations with coarser, more dynamic sediments (B2, B4, E3), statistically the samples from the whole range of stations could have been drawn from the same parent population. A series of Mann-Whitney comparisons was carried out by season to determine whether samples from collections at shelf ridge and terrace stations (B2, B4, E1, and E3) were drawn from the same overall population as samples from collections at the swale and shelf-break stations (A3, B3, E4, and F3). In all cases, with the exception of spring 1977, the test statistic does not allow rejection of the null hypothesis at the 95% confidence level, confirming that samples from all stations could have been drawn from the same parent population. The apparent differences in biomass and abundance, particularly in the spring 1977 collections, may be related to seasonal variation which will be discussed in a later section of this report.

Distributional Patterns of Total Meiofauna with Respect to Topography

The delineation and summarization of patterns of distribution was made difficult by large variations in abundance between seasons. For this reason, a number of approaches were used to determine distributional patterns. Numerical classification was carried out on the total abundance data summed at the phylum or class taxonomic level. The normal (station) classification was used to make a preliminary evaluation of site groups with respect to the entire data set. The inverse classification was not found to be useful because it was based on such high taxonomic groups. This classification was further confused by two other factors: 1) the classification was based in part on groups that were not members of the permanent meiofauna (e.g. juvenile polychaetes and ostracods) and which have different life histories and more variable abundance patterns than the permanent meiofauna, and 2) the classification was in part based on groups that occurred very rarely. This first constraint is critical for samples taken in fall 1976 because of the co-dominance of predaceous juvenile polychaetes with nematodes and harpacticoids. These constraints

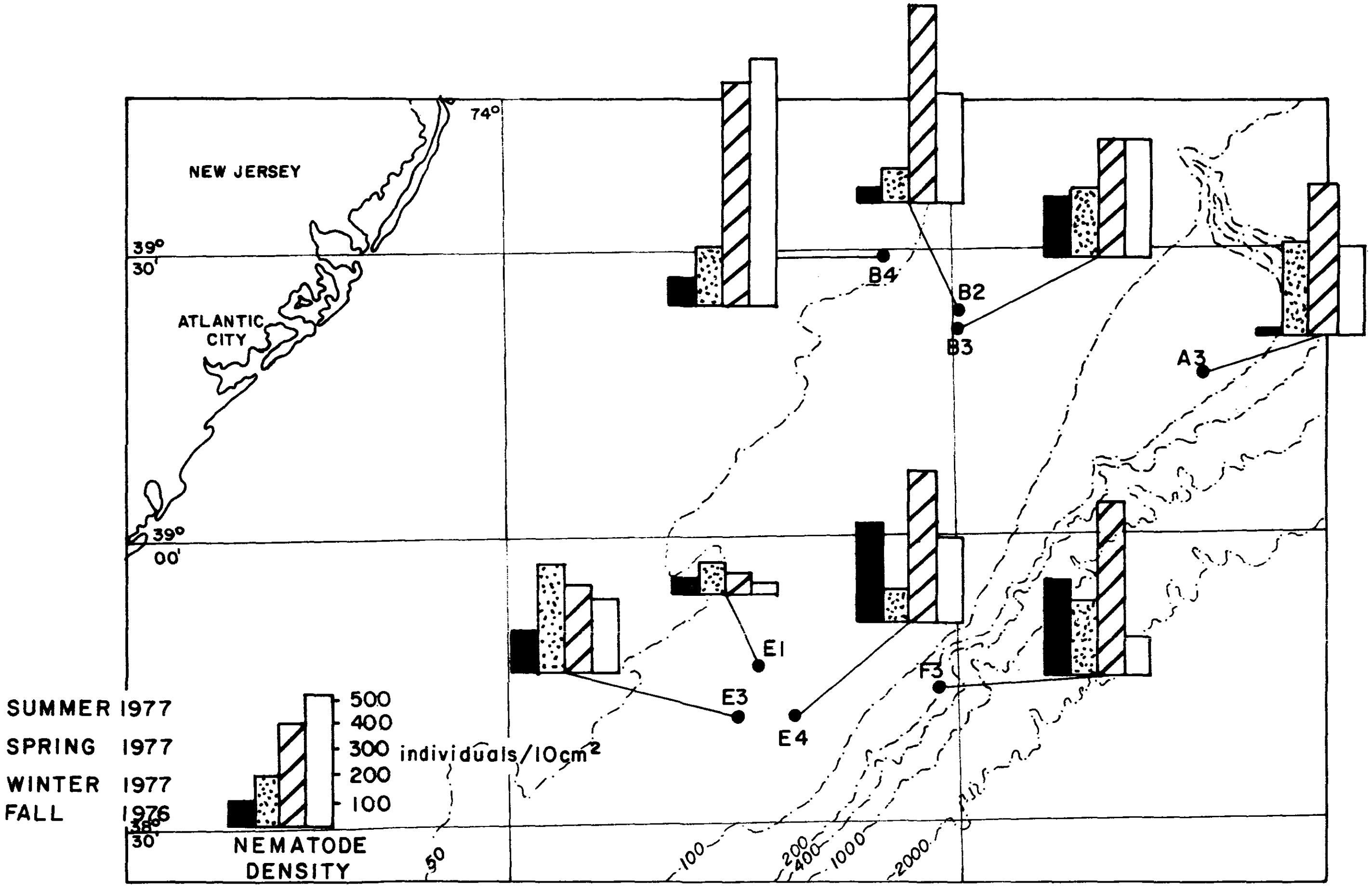

Figure 7-12. Estimated density of nematodes.

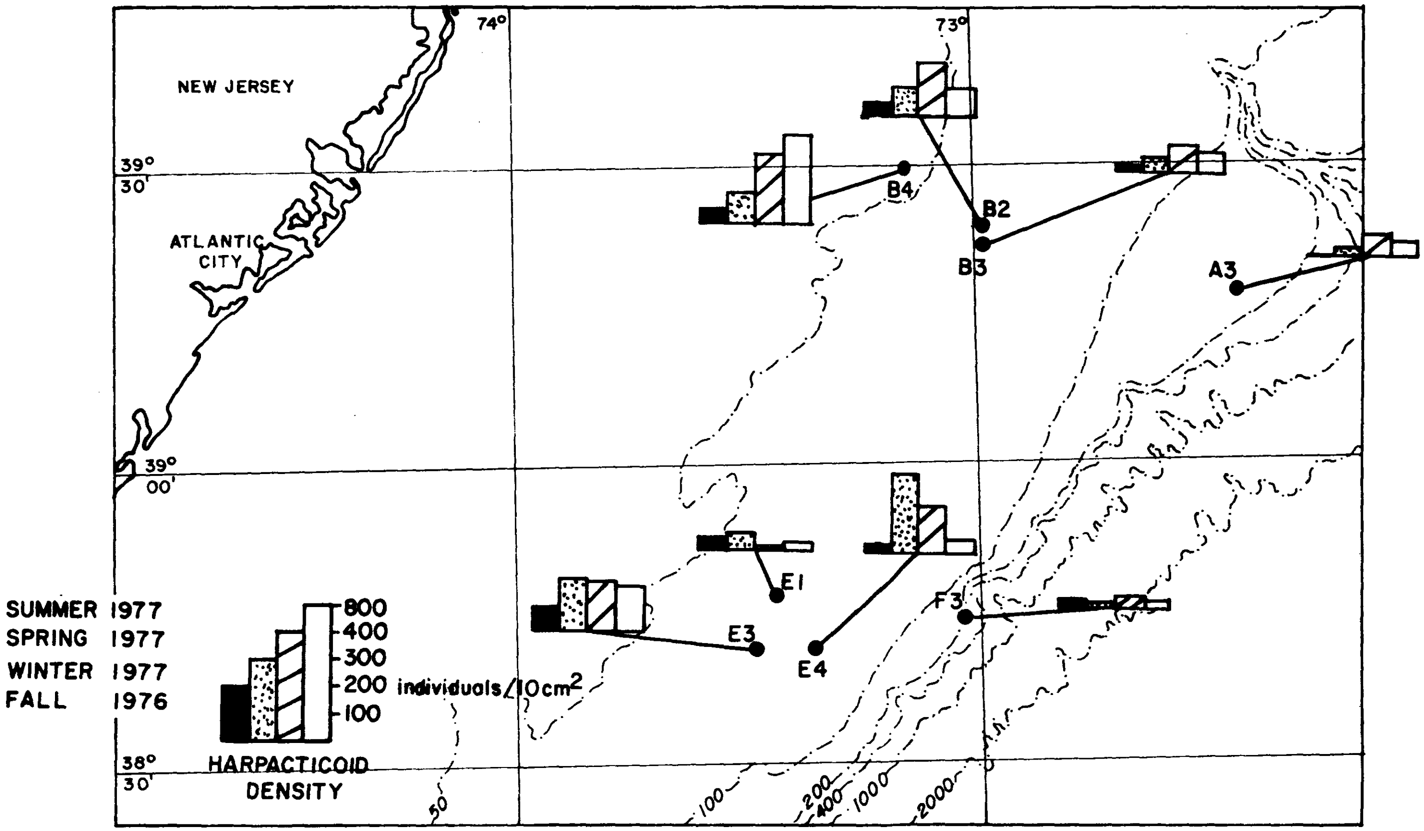

Figure 7-13. Estimated density of harpacticoid copepods.

definitely reduced the effectiveness of the numerical classification of the total data set with respect to the description of overall patterns; therefore, subsequent analyses of both distributional patterns and community structure concentrated on the genus and species level categorization of the dominant meiofaunal taxa, the Nematoda and Harpacticoida. These analyses were accomplished by reciprocal averaging ordination.

Figures 7-14 and 7-15 show the normal cluster analysis based on total meiofaunal occurrence for each seasonal sampling period and for all periods combined. Certain overall patterns were evident although somewhat obscured by the constraints already described. The shelf-break stations, A3 and F3, were more similar to each other than to any of the other stations. The outer shelf swale stations, B3 and E4, were more similar to each other than to any other stations but were also consistently related to the shelf break stations. Station E1, a ridge station, was either similar to the shelf-break and swale stations or was distinct. The remaining three stations, B2, B4, and E3, generally grouped together in the normal analysis. These are dynamic ridge and terrace stations with similar hydrographic and sedimentary conditions (Chapters 3 and 5). The dendrograms for fall 1976 and winter 1977 did not conform exactly to this pattern because these dendrograms were derived from collections which had significant occurrences of juvenile polychaetes and ostracods and also because these collections had a substantial proportion of occurrences of taxa which were found more rarely in later collections. The dendrogram for spring 1977 best represents the classification of stations with reference to the dominant meiofaunal taxa.

Figure 7-15 represents the normal classification of all collections of meiobenthos from 1976-1977. This dendrogram emphasizes the similarity, in terms of total meiobenthos, of the swale and shelf-break stations and also differentiates these stations from the outer shelf ridge and terrace stations. Anomalies in this pattern are attributable to the constraints already described and also to the large differences in total abundance between fall 1976 collections ($\bar{X} = 114$ individuals/core) and the other seasons ($\bar{X} = 544$,567 and 537 individuals/core). Site group I represents ridge and terrace stations from spring and summer 1977. This group is well defined with no anomalies. Site group II represents swale and shelf-break stations from spring and summer 1977. The inclusion of Station E1 from both seasons in this group is consistent with the separate seasonal classifications and indicates that during these two seasons collections from Station E1 were more similar, in terms of higher taxonomic composition, to those from the swale and shelf-break stations than they were to those from the other ridge and terrace stations. Site group III represents ridge and terrace stations from fall 1976 and winter 1977. Site group IV represents outer shelf swales from winter and spring 1977. Site groups IV and V both contain collections from Station E3 indicating that, in terms of higher taxonomic composition, the collections during these seasons were more

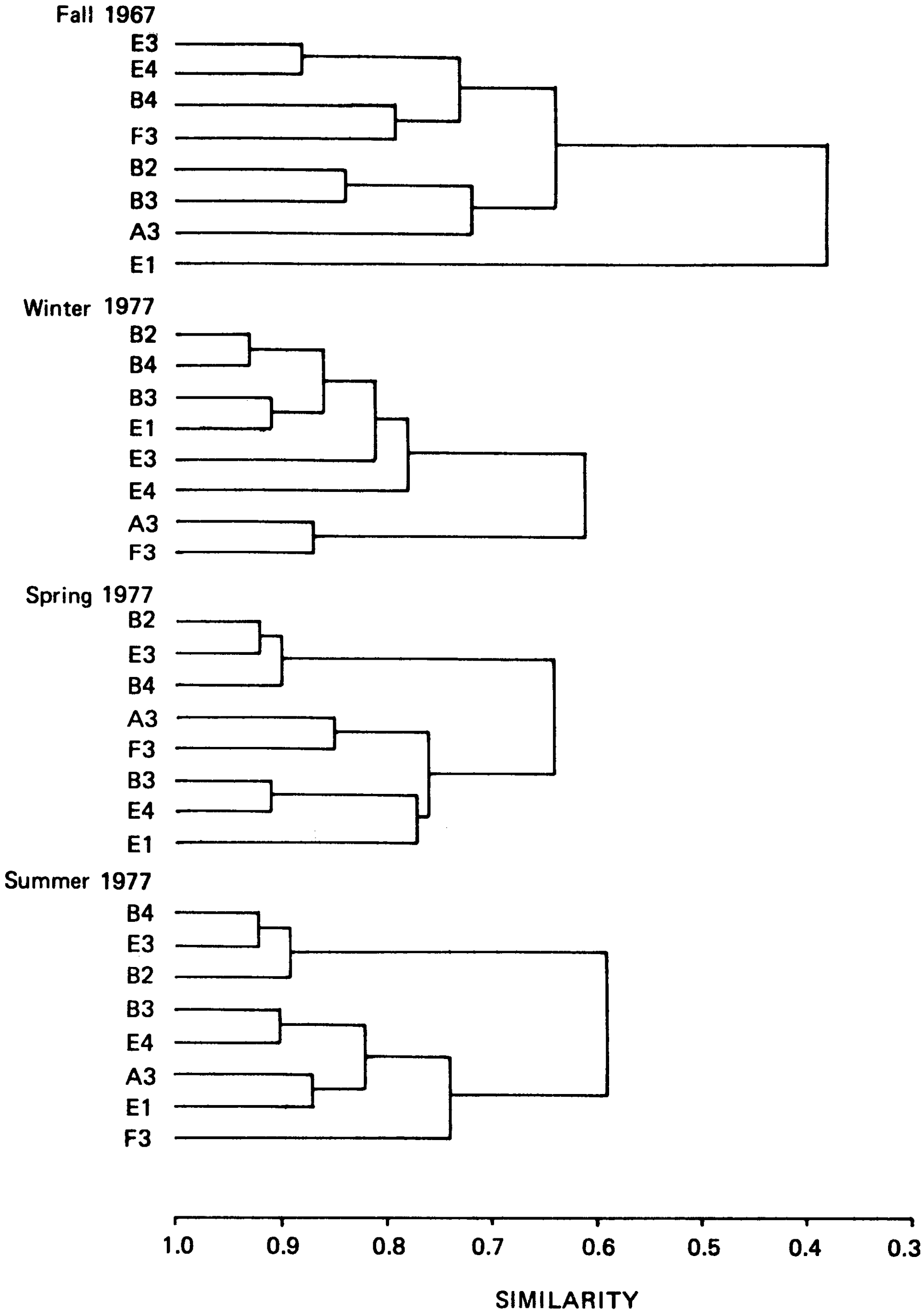

Figure 7-14. Dendrograms resulting from numerical classification of collections based on similarity of higher taxa, by season.

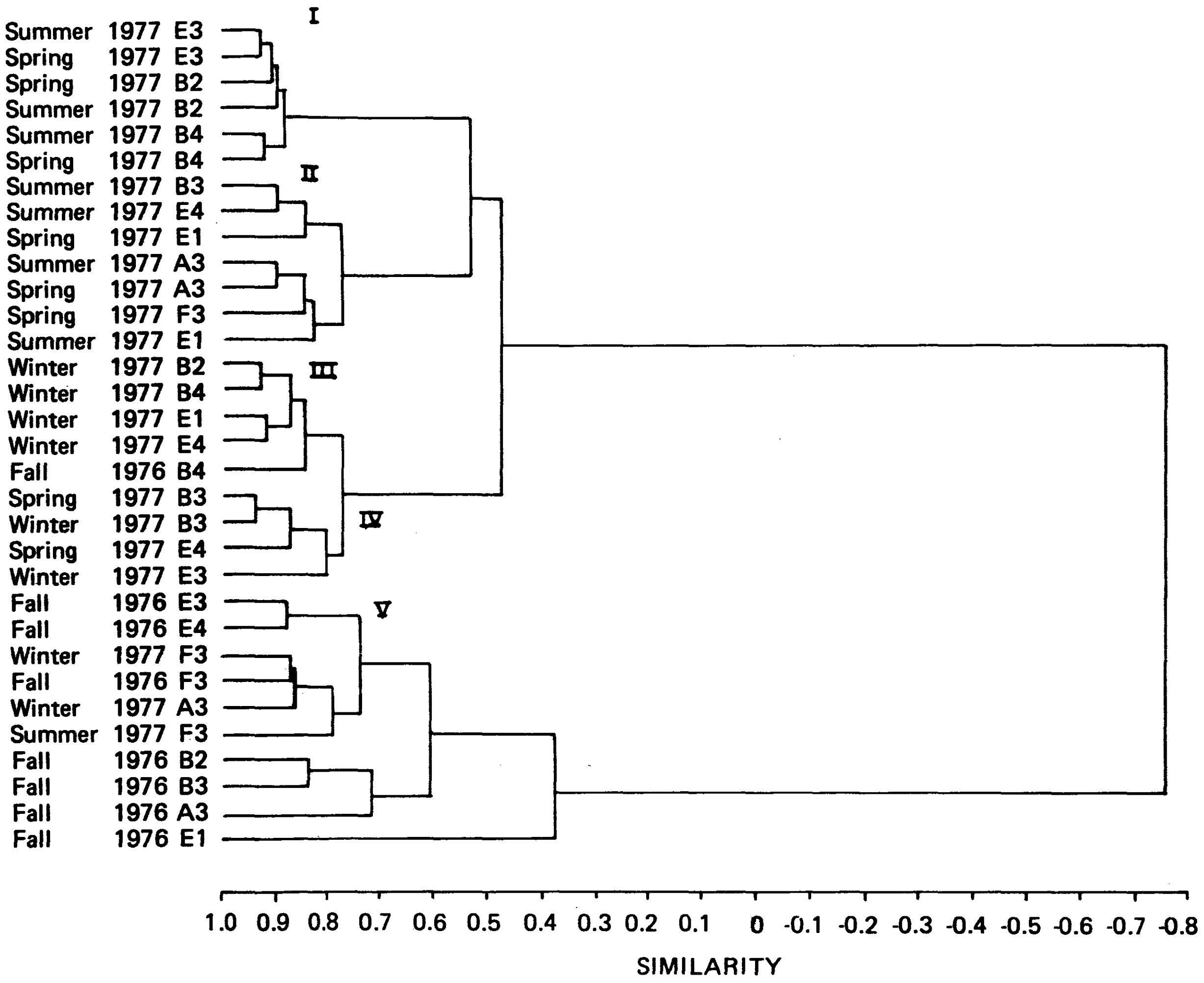

Figure 7-15. Dendrogram resulting from numerical classification of collections based on similarity of higher taxa, all collections.

similar to those from the swale and shelf-break stations than to those from the other shallower stations. Site group V also contains the fall 1976 collection at Station E1, which regularly was grouped with the swale and shelf-break stations.

Two trends were apparent from the classificatory analysis of total meiobenthos. First, there were two groups of stations which, with few exceptions (i.e. Station E1), corresponded to swale and shelf-break stations vs. ridge and terrace stations. Secondly, there were substantial differences in higher taxonomic composition between seasons, particularly between fall 1976 and winter 1977 vs. spring and summer 1977. Fall 1976 collections were characterized by low densities, the absence of Tardigrada and Gastrotricha, the rarity of Kinorhyncha and larvae, and relatively large numbers of juvenile amphipods. Winter 1977 collections resembled fall 1976 collections with low numbers of Tardigrada, Gastrotricha, and Kinorhyncha. Collections from both fall 1976 and winter 1977 contained large numbers of Turbellaria. Collections from spring and summer 1977 had high numbers of Tardigrada, Gastrotricha, Kinorhyncha, and Ostracoda and low numbers of Turbellaria. These different occurrence patterns account for much of the seasonal differentiation in classificatory analysis.

Distributional Patterns of Harpacticoida and Nematoda with Respect to Topography and Physico-chemical Factors

Harpacticoida

The preliminary trends already described were further investigated by reciprocal averaging ordination based on genus or species level identification of the dominant nematodes and harpacticoids. Figures 7-16 through 7-27 represent station and species ordinations for harpacticoid copepods for each season separately, while Figures 7-28, 7-29, and 7-30 represent station and species ordinations based on all harpacticoid collections combined.

The ordination along axes 1 and 2 accounted for 76% of the variance of fall 1976 data while the addition of axis 3 brought this figure to 91%. The ordination along axes 1 and 2 sufficiently describes patterns of copepod occurrence during fall 1976. The shelf-break station F3 is cast alone with a high score on axis 1 while the shelf-break station A3 and the swale stations B3 and E4 have low scores on axis 1 but increasingly high scores on axis 2. The remaining ridge and terrace stations are little differentiated by the first two axes having low scores on both.

Comparison with the species ordination for this season shows that several copepods occurred exclusively at specific stations, thus partially accounting for the station positions within the ordination space. _Mesochra pygmaea_ and _Halectinosoma_ sp. occurred exclusively at Station F3. _Robertgurneya rostrata_ and _Diarthrodes_ sp. occurred only

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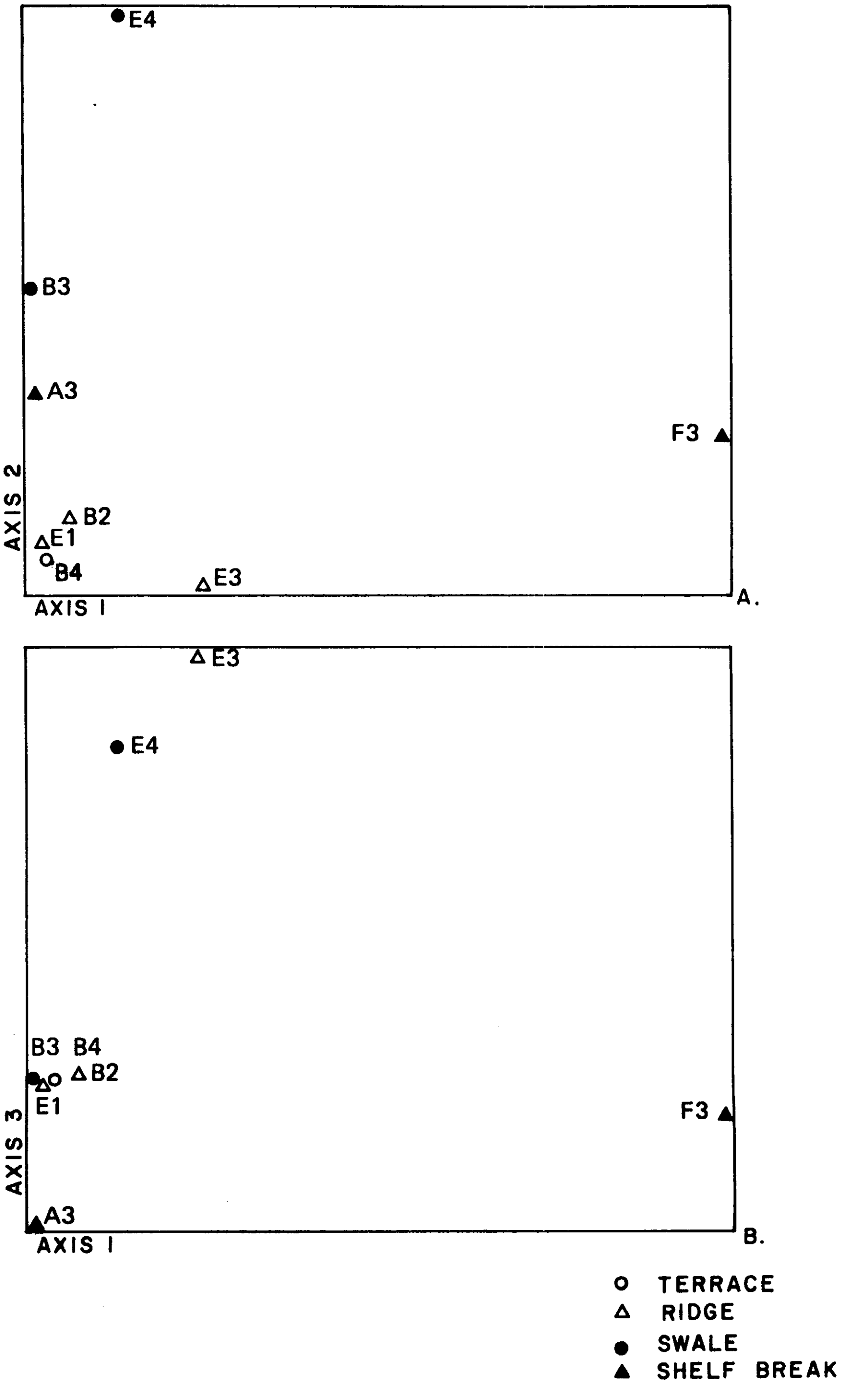

Figure 7-16. Reciprocal averaging ordination of collections of harpacticoid copepods, fall 1976.

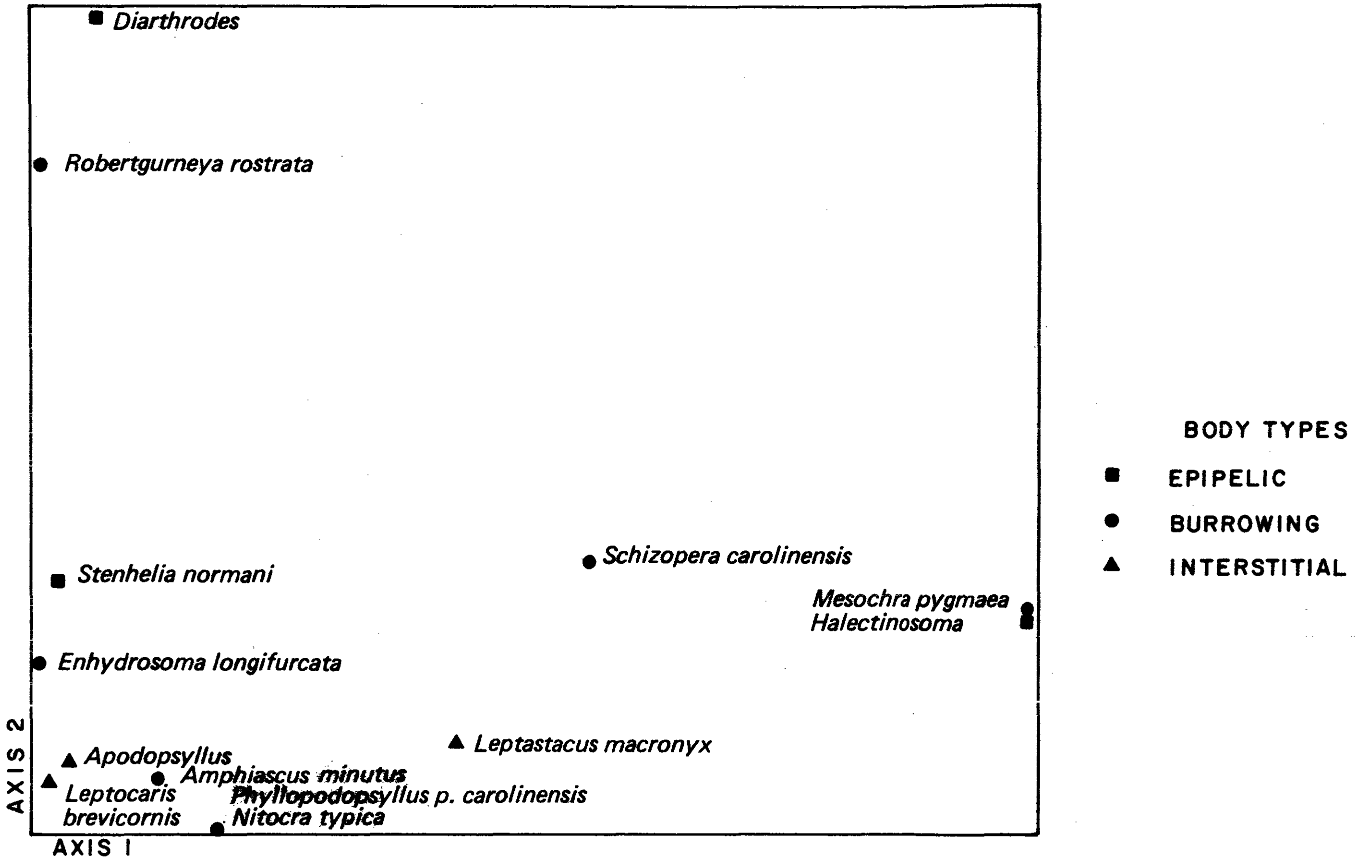

Figure 7-17. Reciprocal averaging ordination of harpacticoid species in collections from fall 1976.

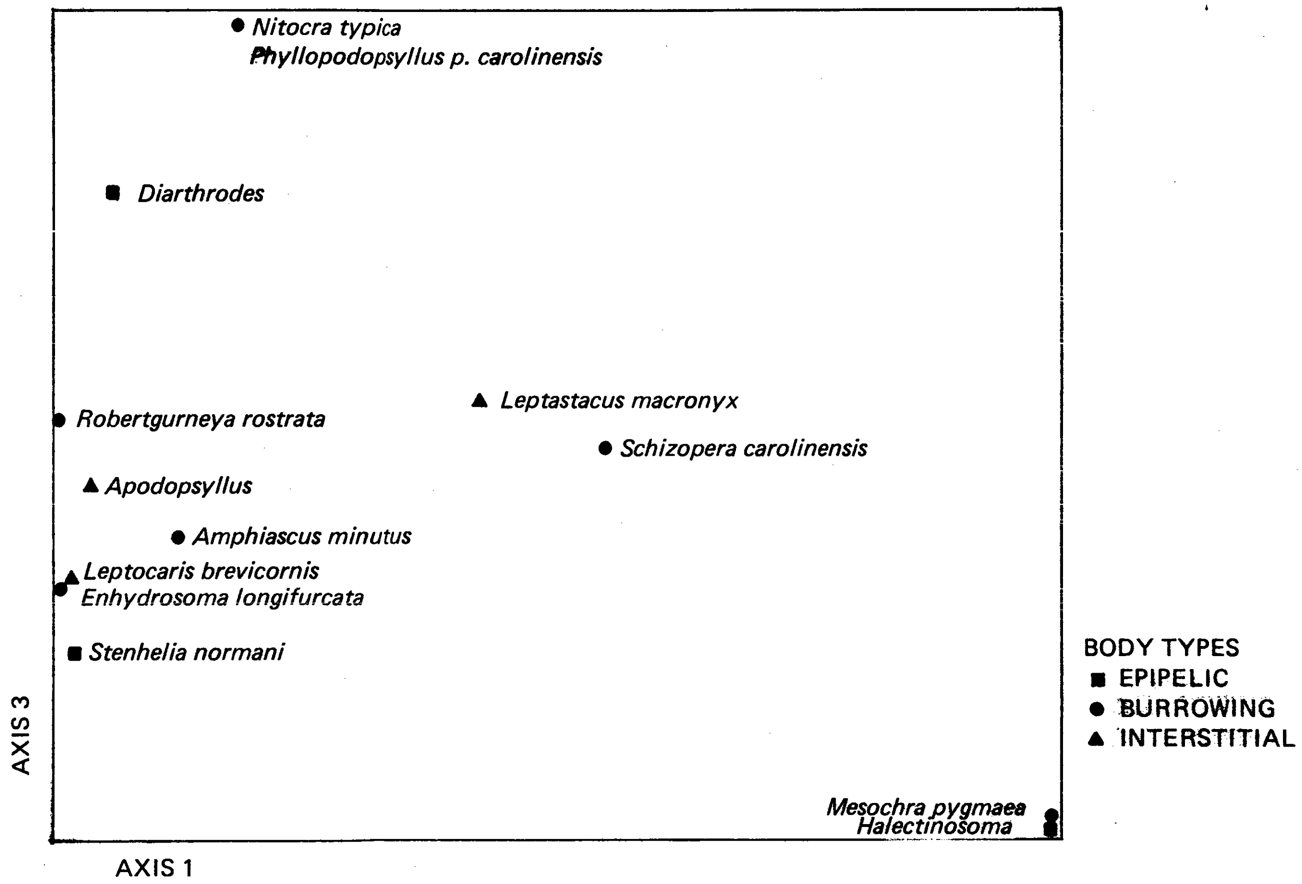

Figure 7-18. Reciprocal averaging ordination of harpacticoid species in collections from fall 1976.

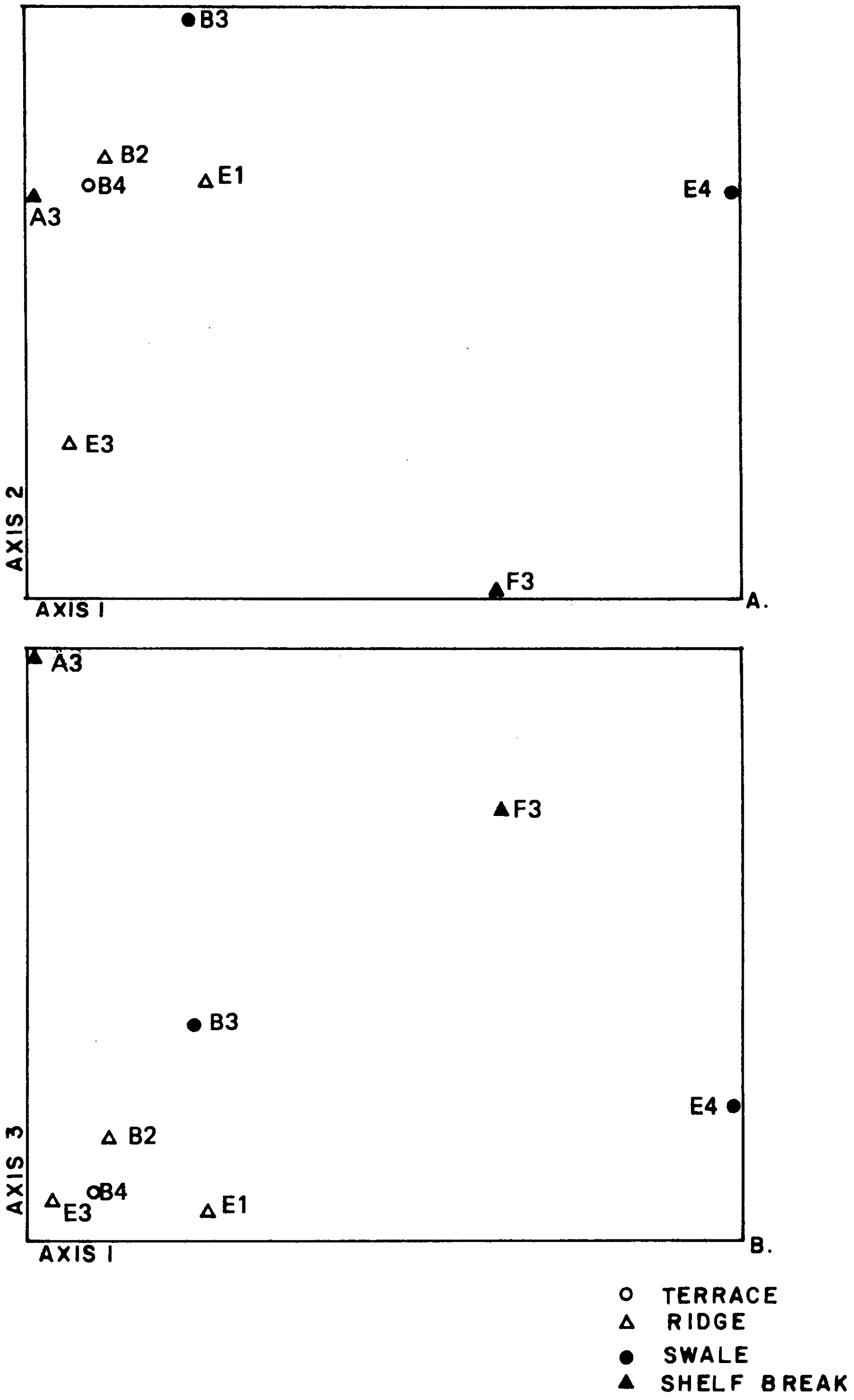

Figure 7-19. Reciprocal averaging ordination of collections of harpacticoid copepods, winter 1977.

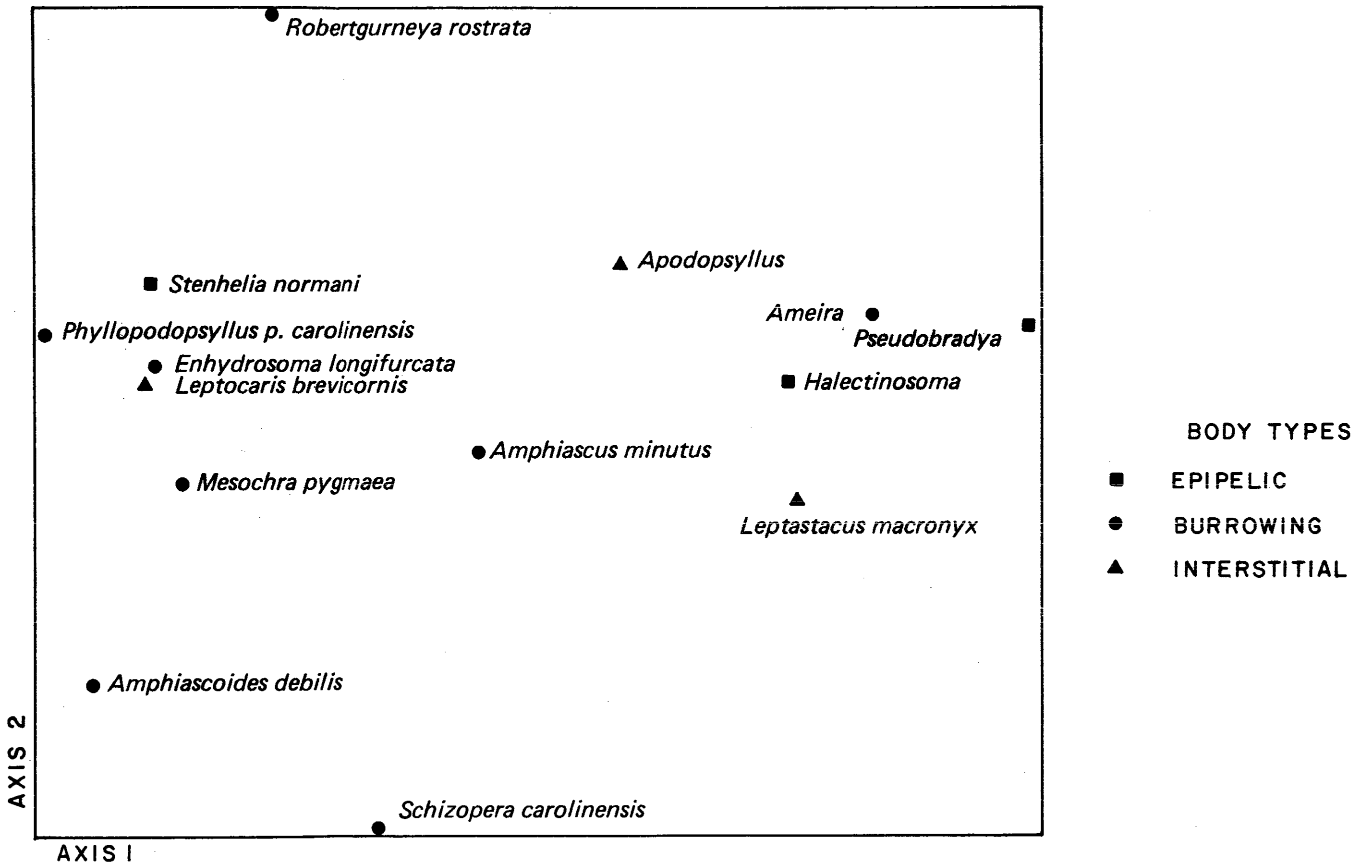

Figure 7-20. Reciprocal averaging ordination of harpacticoid species in collections from winter 1977.

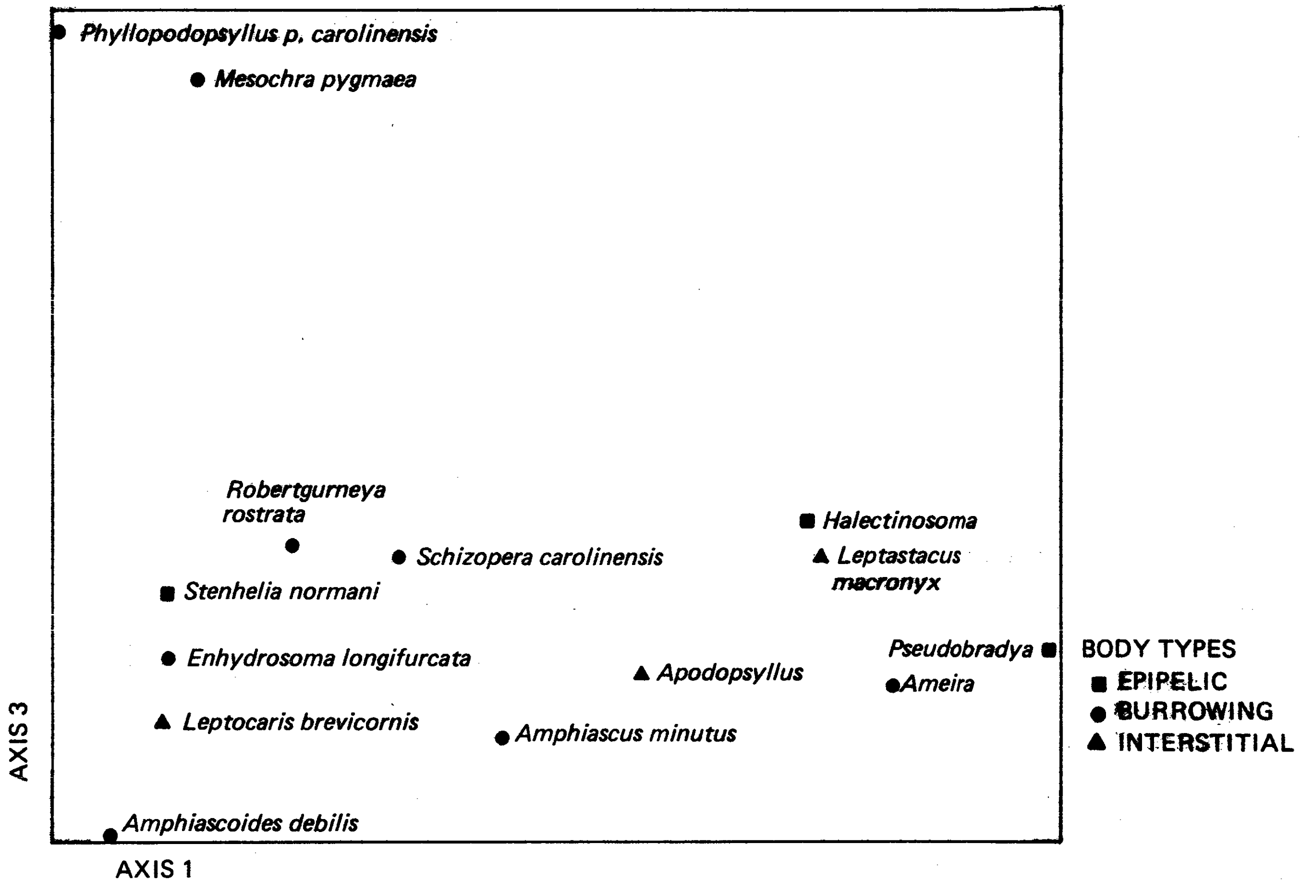

Figure 7-21. Reciprocal averaging ordination of harpacticoid species in collections from winter 1977.

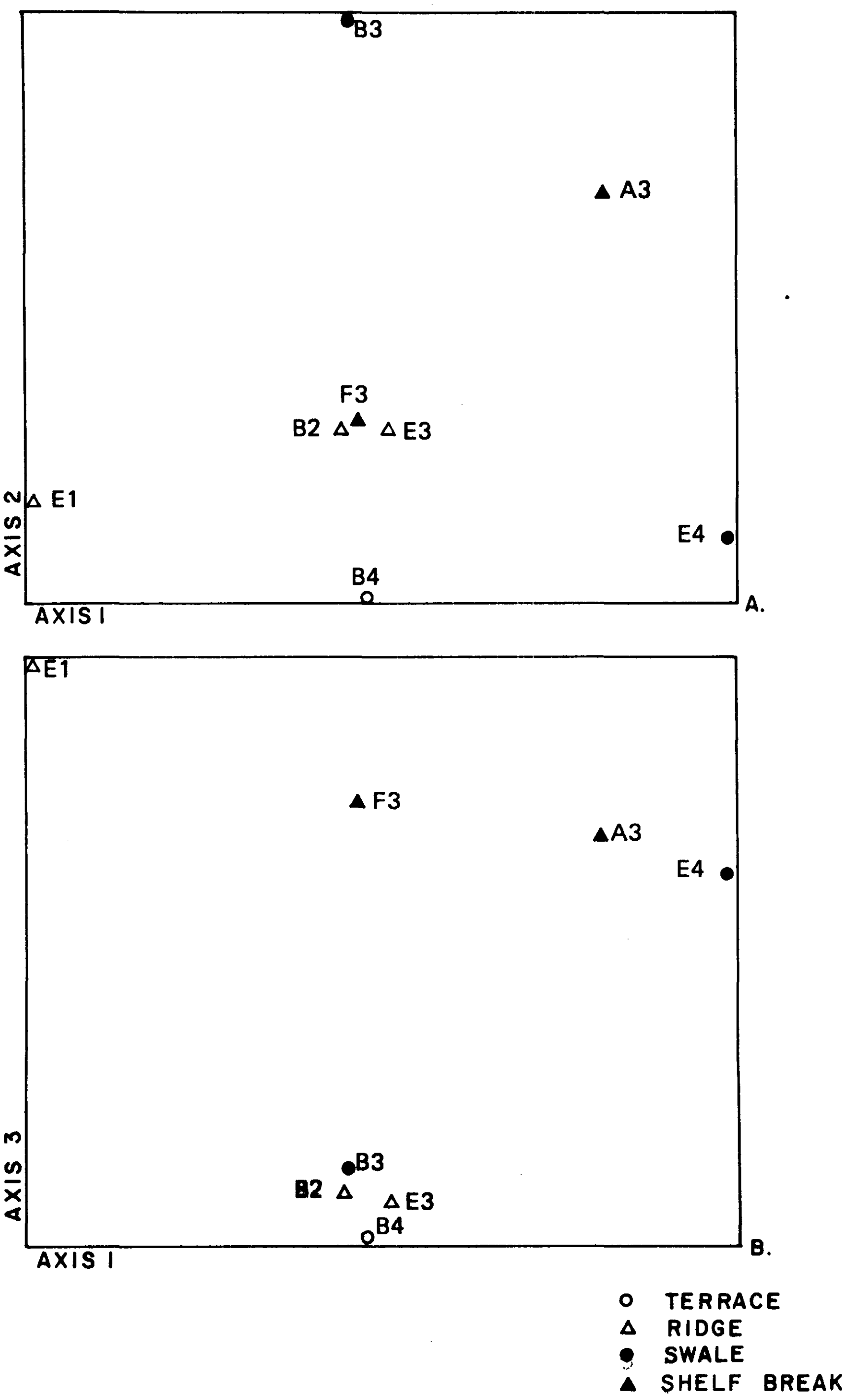

Figure 7-22. Reciprocal averaging ordination of collections of harpacticoid copepods, spring 1977.

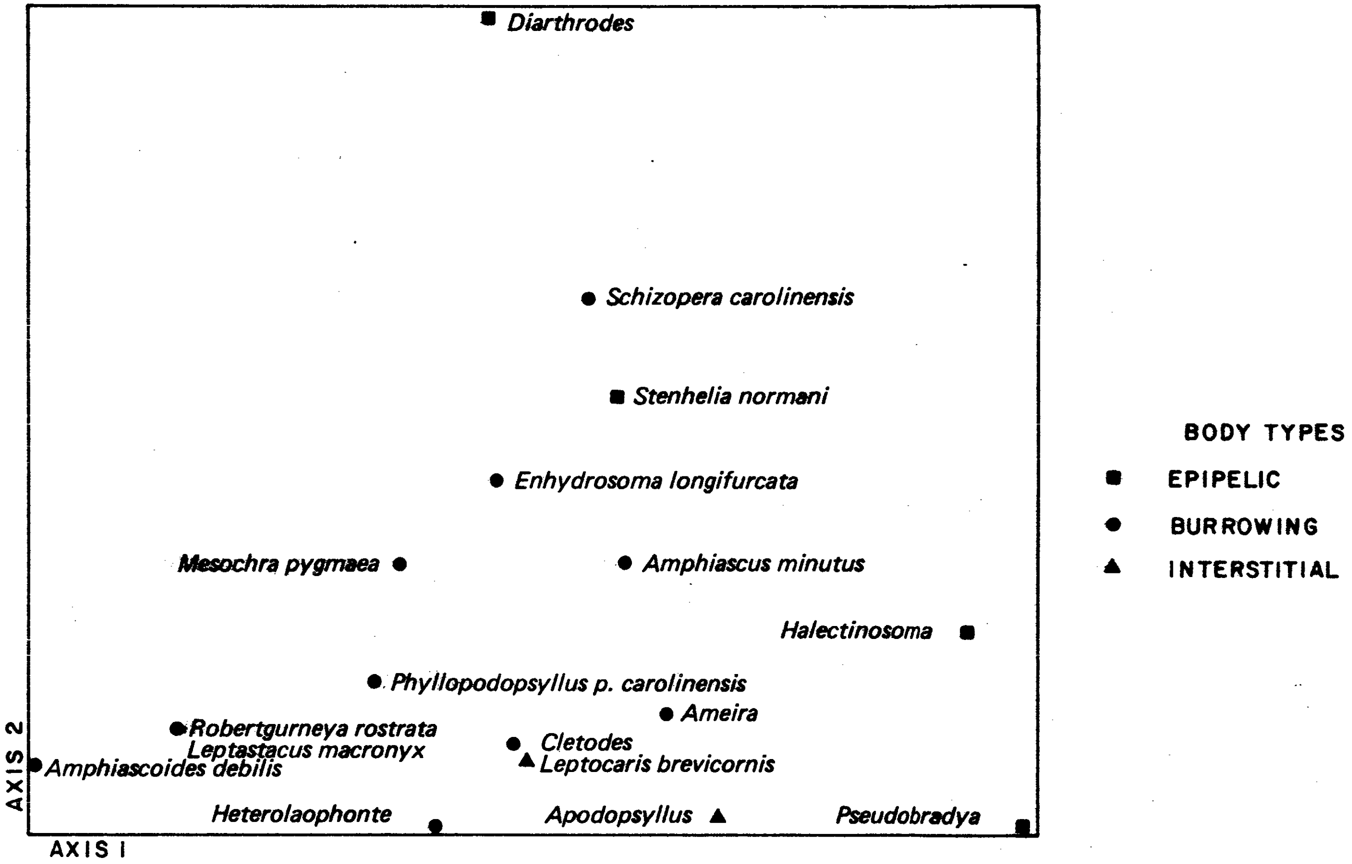

Figure 7-23. Reciprocal averaging ordination of harpacticoid species in collections from spring 1977.

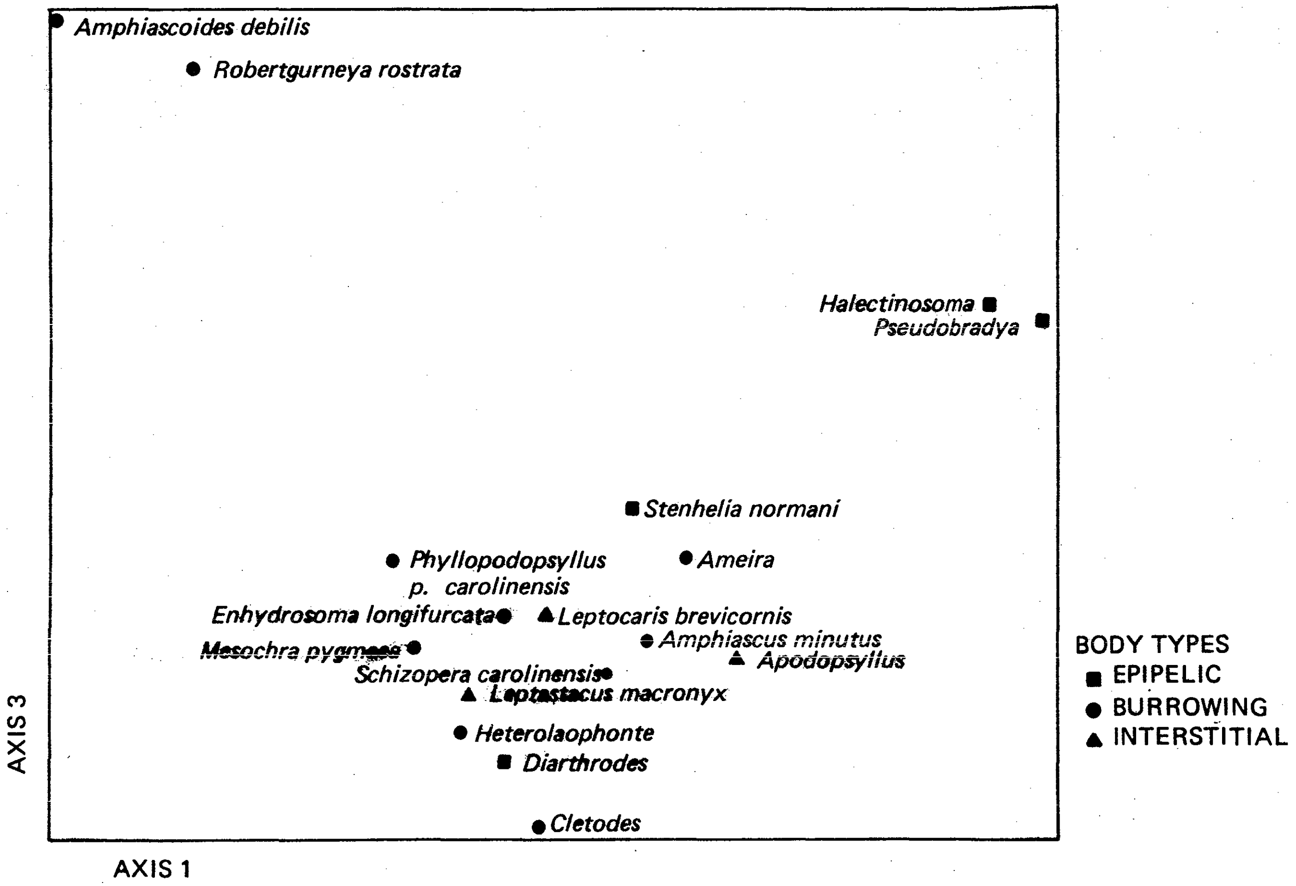

Figure 7-24. Reciprocal averaging ordination of harpacticoid species in collections from spring 1977.

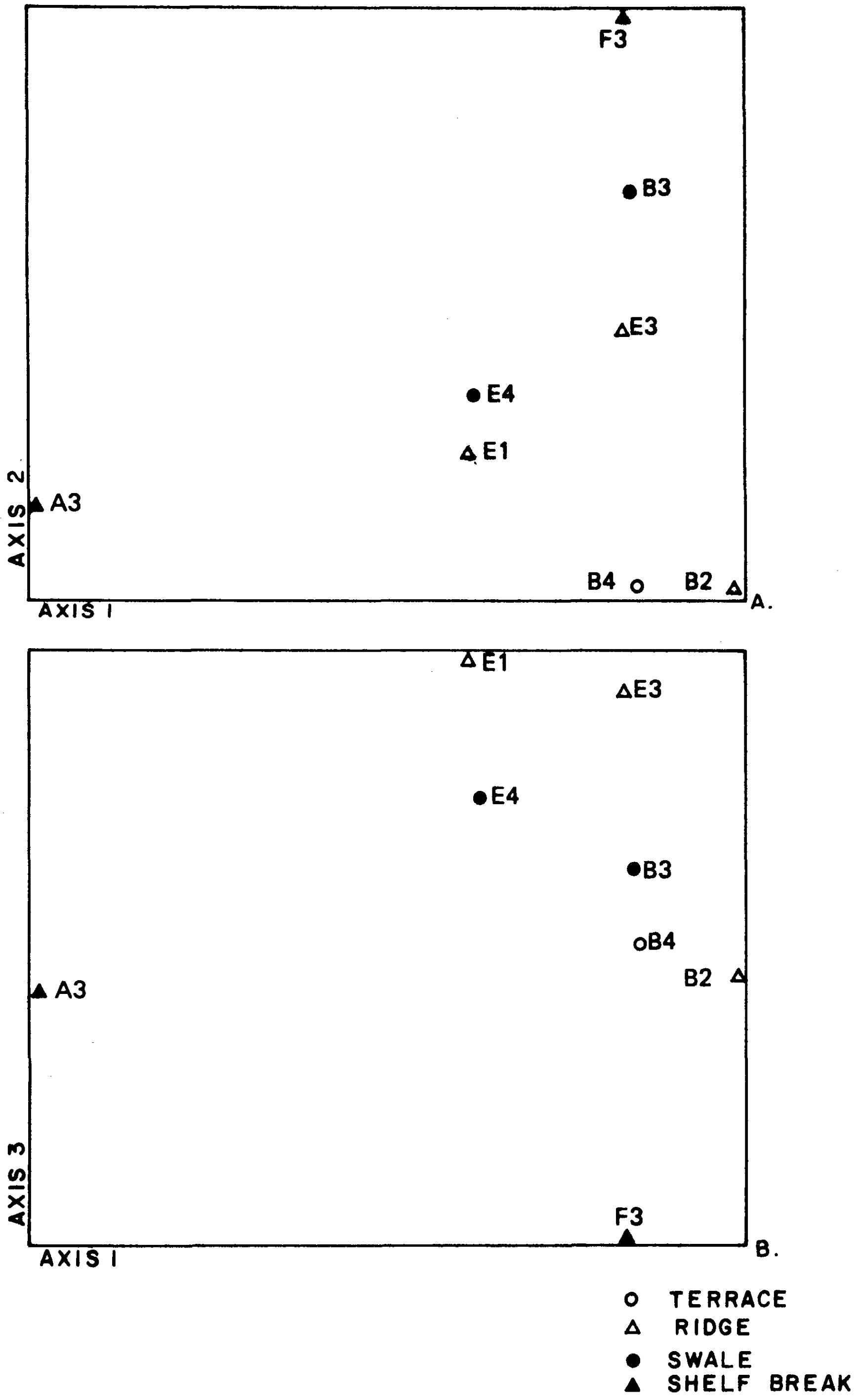

Figure 7-25. Reciprocal averaging ordination of collections of harpacticoid copepods, summer 1977.

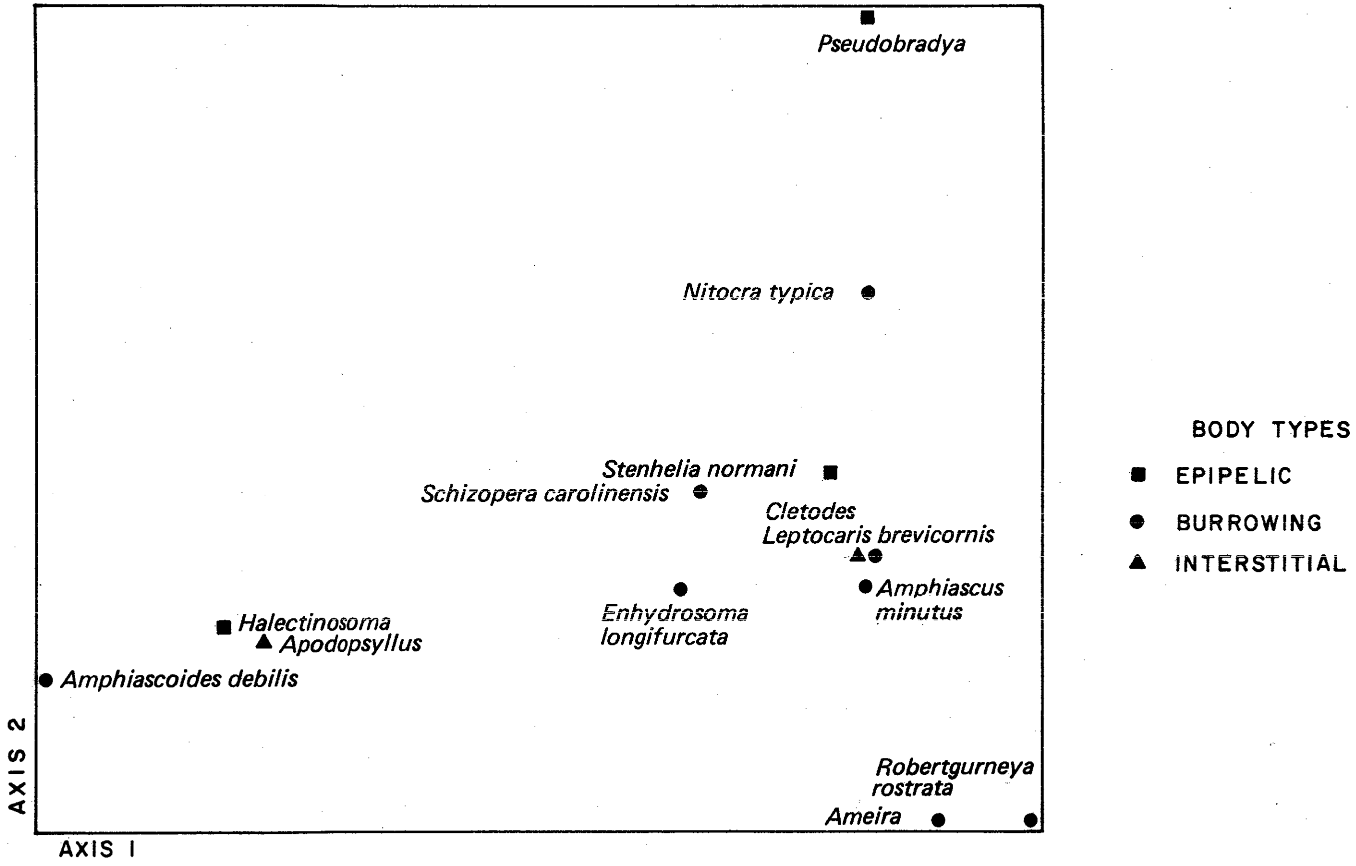

Figure 7-26. Reciprocal averaging ordination of harpacticoid species in collections from summer 1977.

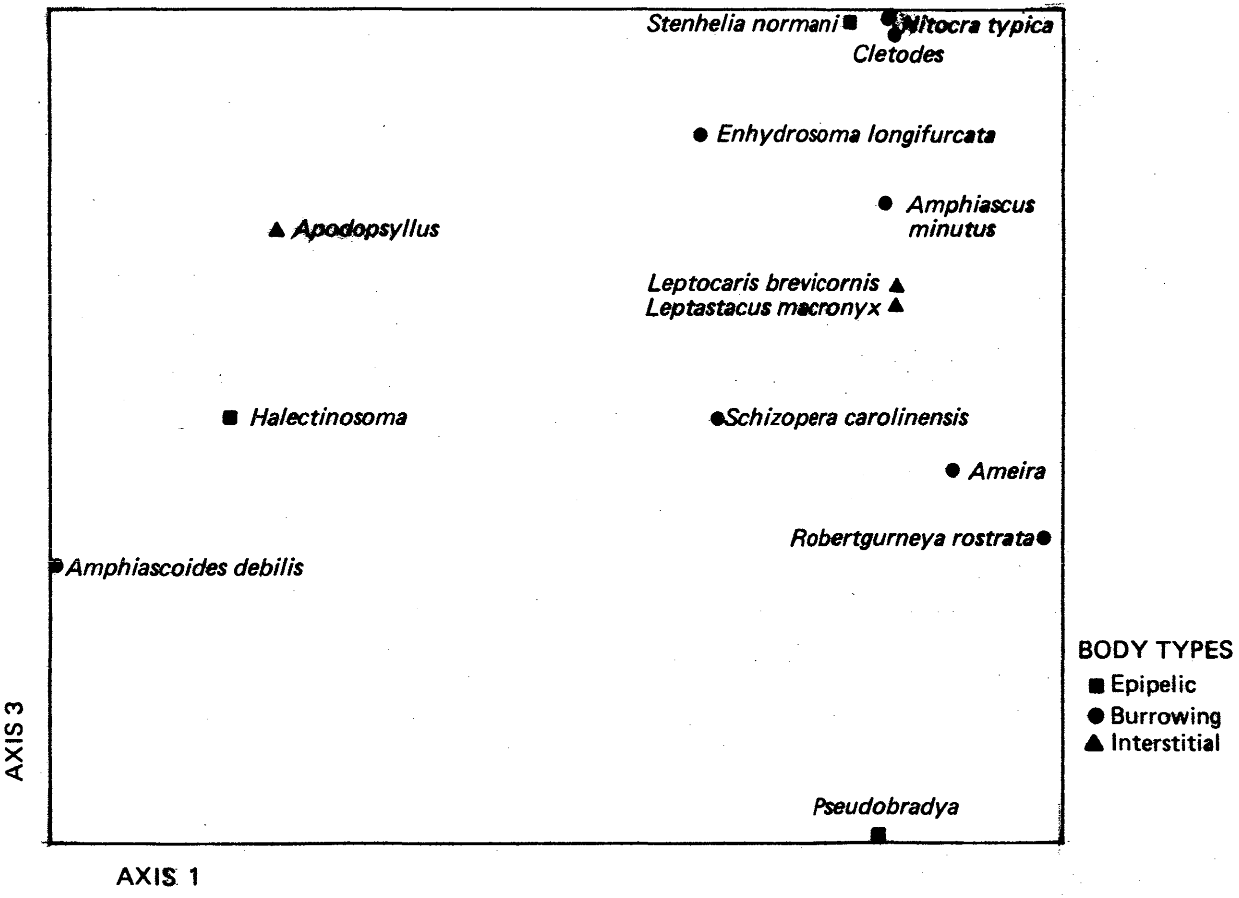

Figure 7-27. Reciprocal averaging ordination of harpacticoid species in collections from summer 1977.

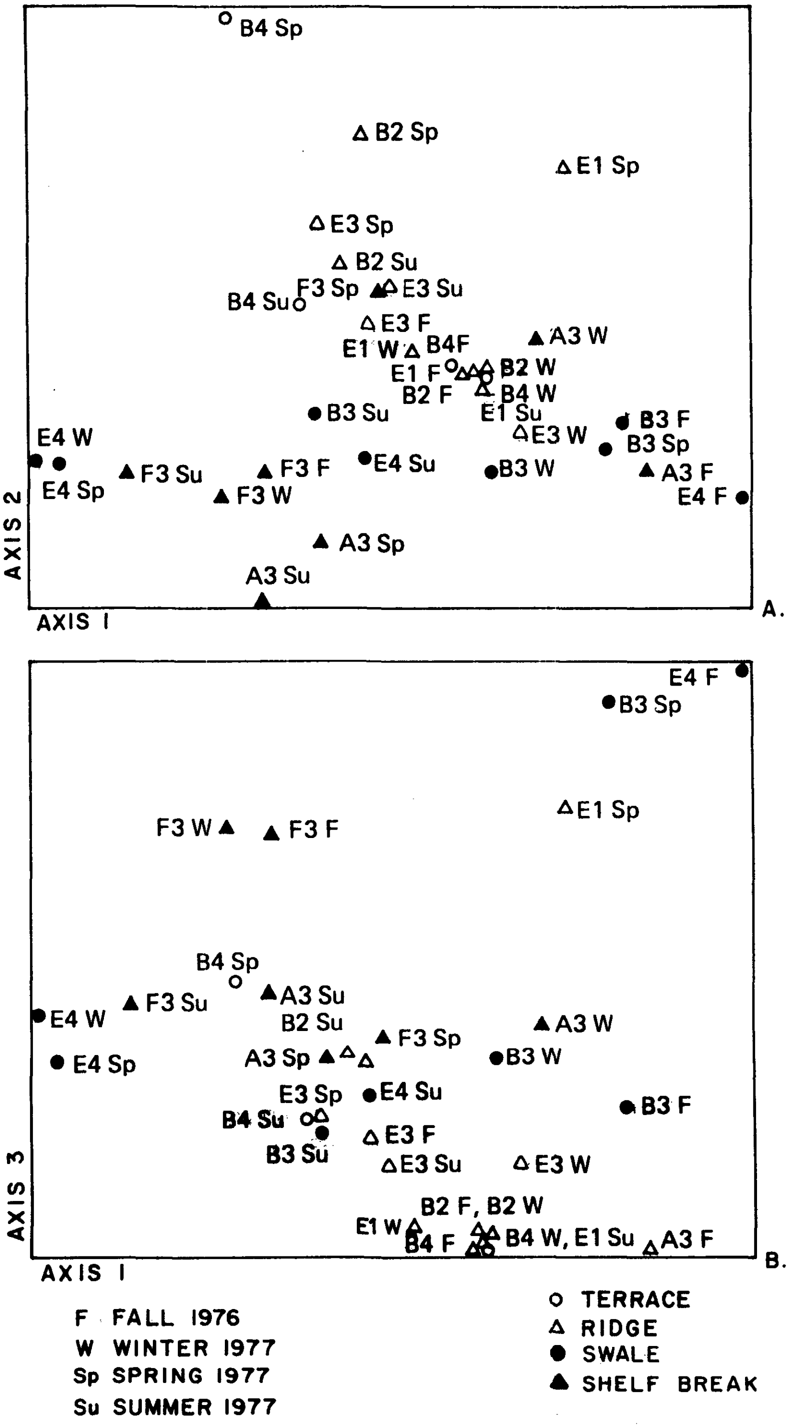

Figure 7-28. Reciprocal averaging ordination of all collections of harpacticoid copepods.

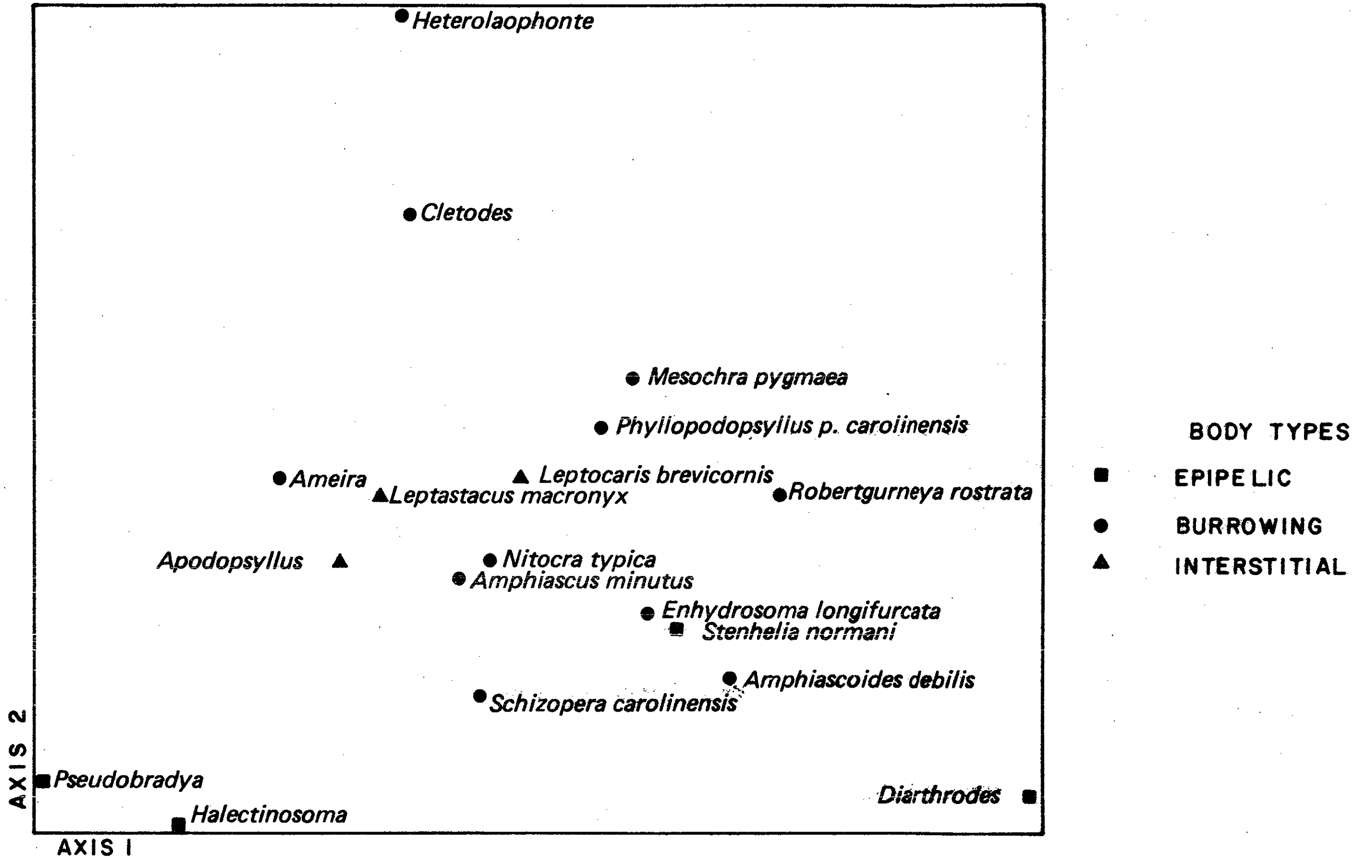

Figure 2-29. Reciprocal averaging ordination of harpacticoid species in all collections.

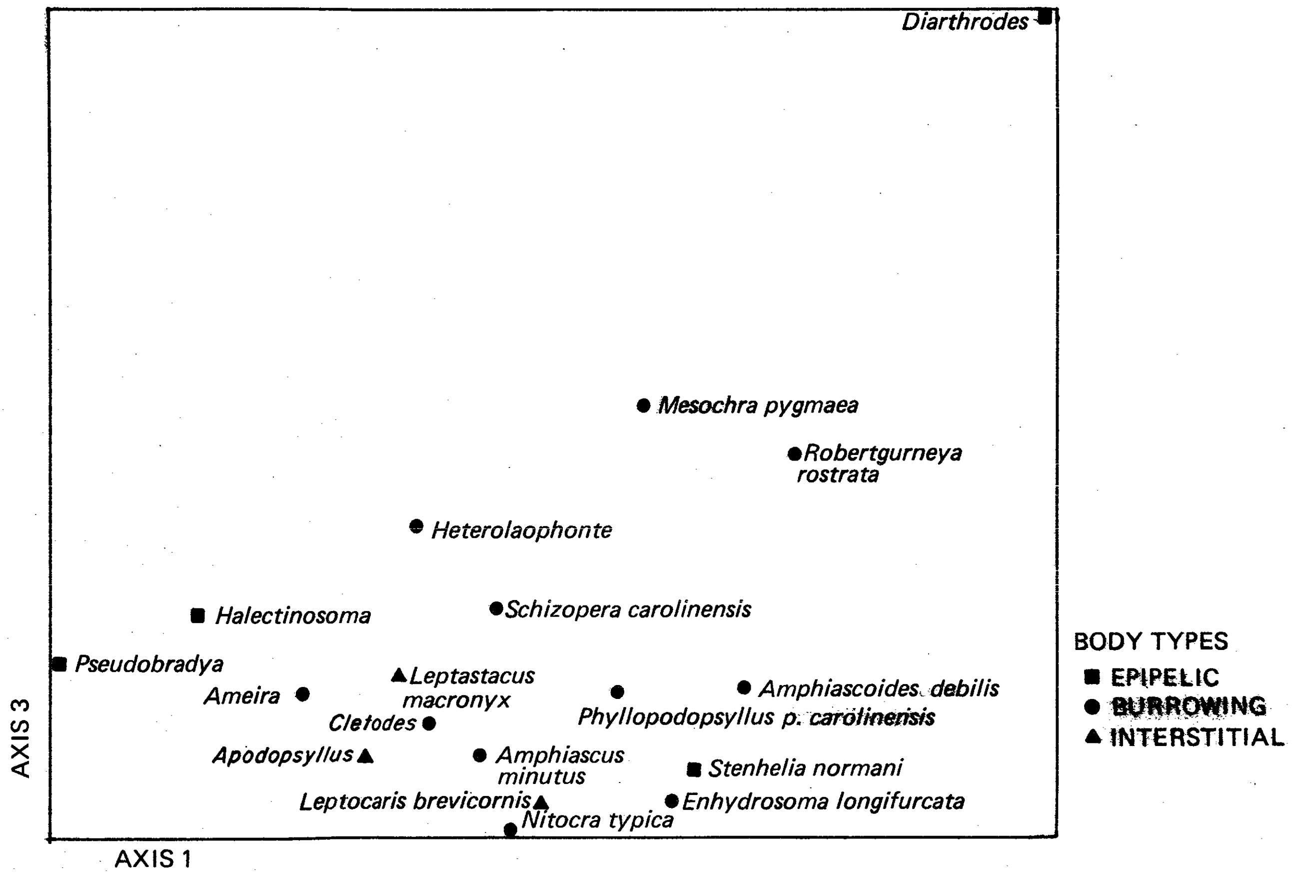

Figure 7-30. Reciprocal averaging ordination of harpacticoid species in all collections.

at B3 and E4, the two swale stations. Two strictly interstitial animals, Leptastacus macronyx and Leptocaris brevicornis, were dominant at the sandier stations B4, E1, and E3. The positions of the stations in the ordination space is somewhat confused because two species, Stenhelia normani and Enhydrosoma longifurcata, were dominant at almost all stations.

Figure 7-31 represents the proportional representation of harpacticoid copepods according to body type based on classifications by Noodt (1971) and Coull (1977): epipelic, interstitial, and burrowing. Copepods with dorsoventrally compressed body types are classed as epipelic (living at the sediment-water interface), while copepods with elongate, cylindrical bodies are classed as interstitial. Heavy bodied copepods with phyllopodus appendages are classed as burrowing. These categories are not absolute, but they do seem to relate to habitat selection. Swales and shelf-break stations had a large proportion of epipelic forms; S. normani and Diarthrodes sp., both epipels, were found in large numbers at these stations. Shelf break station F3 had large numbers of Halectinosoma sp. This organism, along with Pseudobradya sp. found in later collections, is a member of the family Ectinosomidae which have generally been considered to be burrowing forms. These are very large harpacticoids which feed by sweeping their antennae over the substratum and then cleaning the antennae with their mouth parts (Marcotte 1977a and b). This feeding method, combined with their very large size, indicates that these Ectinosomidae probably function as epipels feeding on surface detritus. Station F3 also showed large numbers of the interstitial form L. macronyx. The remaining coarser grained stations B2, B4, E1, and E3 had large numbers of the interstitial forms L. macronyx and L. brevicornis (Figure 7-31a).

The ordination of harpacticoid data for winter 1977 along axes 1 and 2 accounted for 60% of the variance in harpacticoid occurrence, while the addition of axis 3 brought this figure to 76%. Again Station F3 is rather distinct with a high score on axis 1 and a low score on axis 2 (Figure 7-19a). Station E4 scored highest on axis 1, and all the remaining stations had low scores on axis 1. The remaining shelf-break station A3 and the swale station B3 are separated from the ridge and terrace stations on axis 3 so that in three dimensions the swale and shelf-break stations are again separated from the stations with coarser sediments.

Station F3 was characterized by the epipel Halectinosoma sp. but also by the interstitial form L. macronyx, while swale station E4 was characterized by large numbers of Halectinosoma sp. and Ameira (Figure 7-20). The occurrence of Halectinosoma sp., M. pygmaea, and Phyllopodopsyllus parafurciger carolinensis differentiates Station A3, and the exclusive occurrence of R. rostrata separates Station B3. The remaining stations B2, B4, E1, and E3 were characterized by the interstitial forms L. macronyx and L. brevicornis, and also by large numbers of the burrowing form E. longifurcata. The proportion of

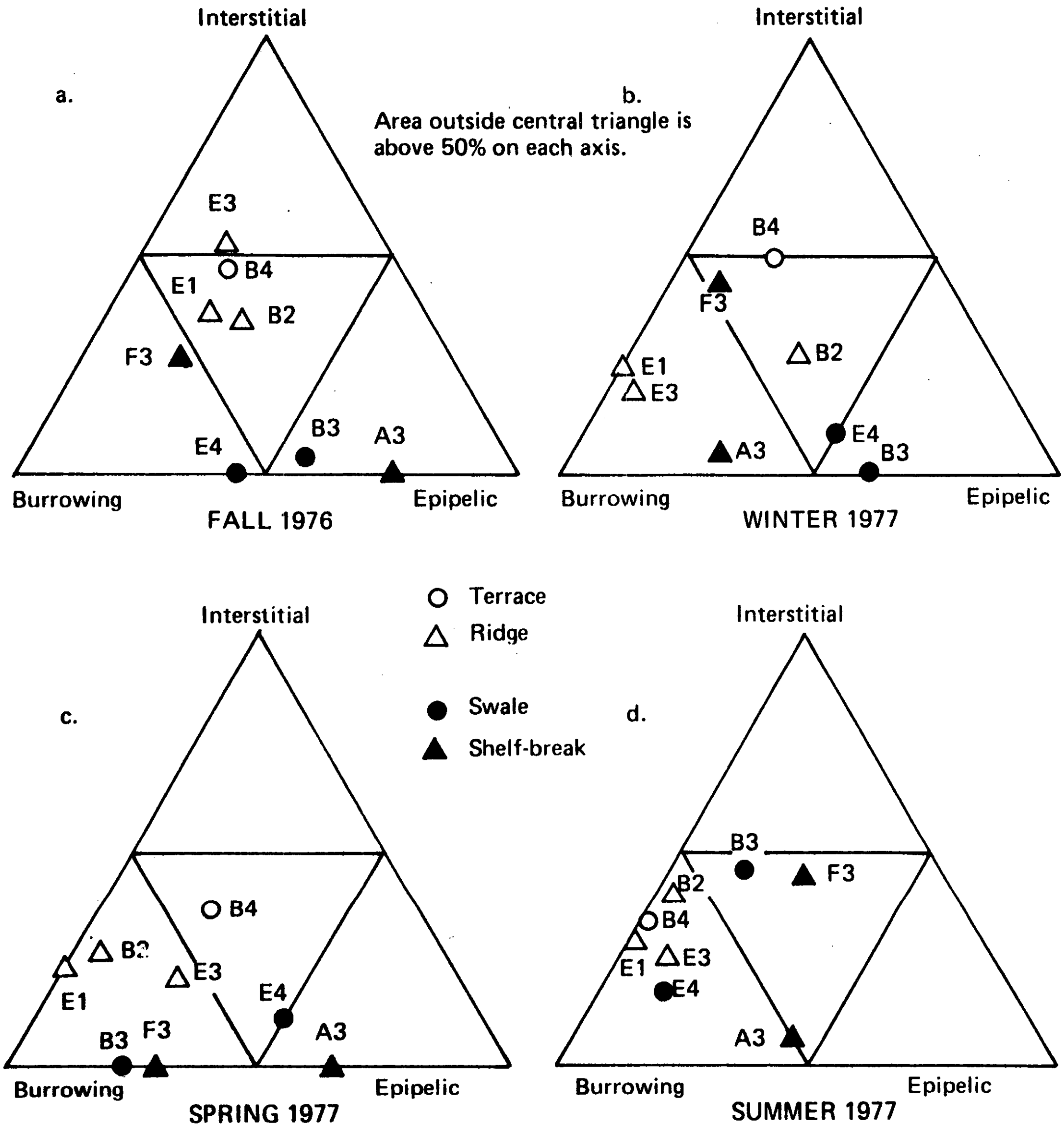

Figure 7-31. **Proportional representation of harpacticoid body types in collections by season.**

harpacticoid body types indicates that except for Station F3 the swale and shelf-break stations were differentiated from the ridge and terrace stations where interstitial and burrowing forms were dominant (Figure 7-31b).

The ordination along axes 1 and 2 of the spring 1977 harpacticoid data accounted for 55% of the variance in harpacticoid occurrence, while the addition of axis 3 brought this figure to 73%. Figure 7-22a shows Station B3 separated with a high score on axis 2 while shelf-break station A3 had a moderately high score on axis 2. The shelf-break stations A3 and F3 and the swale station E4 were separated from the stations with coarser sediments by their high scores on axis 3 (Figure 7-22b). The epipelic copepod Diarthrodes sp. occurred exclusively at swale station B3, and stations A3 and E4 were characterized by the robust epipels Halectinosoma sp. and Pseudobradya sp. (Figures 7-23 and 7-24). Station E1 was characterized by the exclusive occurrence of the minute burrower Amphiascoides debilis. The remaining ridge and terrace were again characterized by burrowing and interstitial forms (Figure 7-31c).

The ordination along axes 1 and 2 for summer 1977 harpacticoid data accounted for 61% of the variance in harpacticoid occurrence while the addition of axis 3 brought this figure to 77%. Shelf-break station A3 had low scores on both axes 1 and 2 while shelf-break station F3 and swale station B3 scored high on both axes (Figure 7-25). The ridge and terrace stations B2 and B4 are distinct in two dimensions, but the swale station E4 is poorly separated from either Station E1 or Station E3. Station A3 was characterized by large numbers of the epipel Halectinosoma sp. and the exclusive occurrence of the burrower A. debilis (Figures 7-26 and 7-27). Halectinosoma sp. also occurred at Station F3 while Station B3 was characterized exclusively by the very large epipelic form Pseudobradya sp. and also by the occurrence of the burrowing form Nitocra typica. Stations B2 and B4 were characterized by the occurrence of two burrowing forms, Ameira sp. and R. rostrata. The pattern of harpacticoid distribution was not as clear cut for summer 1977 as for the other seasons and this is reflected in the body form proportions (Figure 7-31d). Nonetheless, stations A3, B3, and F3 had larger proportions of epipelic forms than the other stations.

The ordination of the total set of harpacticoid collections along the first three axes (Figure 7-28) accounts for only 45% of the variance in the data so these ordinations will not be emphasized. The same constraints, i.e. inclusion of rare taxa and the seasonal change in dominant species at some stations, along with the overall dominance of two species S. normani and E. longifurcata, apply to this analysis as applied to the classificatory analysis of total meiofauna. Swale and shelf-break collections have low scores on axis 2 and high scores on axis 3, while ridge and terrace collections have mid-range scores on axis 1, high scores on axis 2, and low scores on axis 3. Axis 1 separates those swale and shelf-break stations with finer sediments

(B3, A3, and E4, fall 1976) from those with slightly coarser sediments (F3, E4, spring and summer 1977). The only overt exceptions to these patterns are Station A3 in winter 1977 and Station F3 in spring 1977. This Station A3 collection was overwhelmingly dominated by S. normani and E. longifurcata as were other collections from the coarser sediments during this season. This specific Station F3 collection had a large occurrence of Ameira sp. which was characteristic of the ridge and terrace stations during spring 1977.

The ordination of copepod species in the same sample space does, however, help the interpretation of the complex spatial representation of collections (Figures 7-29 and 7-30). Species which have low scores on axis 2 of the ordination space, such as Halectinosoma sp., Pseudobradya sp., Diarthrodes sp., Schizopera carolinensis, and A. debilis, occurred primarily at the swale and shelf-break stations. Those species which had mid-range scores on axis 1 and slightly higher scores on axis 2, such as S. normani and E. longifurcata, were broadly distributed over the stations, while most of the species which had high scores on axis 2 were characteristic of stations with coarser-grained, more dynamic sediments.

Nematoda

Patterns of nematode species distributions were delineated by reciprocal averaging ordination and by comparison of proportions of nematode feeding types. In addition, a partial non-parametric correlation model was used to try to identify the environmental parameters most closely related to the ordering of nematode collections along the three first ordination axis. The environmental parameters employed are tested in Table 7-11. This partial correlation model was designed to determine the strong association of a parameter with any of the three axes even if the axes themselves are closely related. This was accomplished by partially correlating each parameter with each axis while holding the effects of the other two axes constant.

The ordination along axes 1 and 2 for the fall 1976 nematode collections accounted for 52% of the variance in nematode occurrence, while the addition of axis 3 brought this figure to 66%. The swale and shelf-break stations in Figure 7-32a have low scores on axis 1. Axis 2 separates Station E4 from the other swale and shelf-break stations, while axis 3 separates the swale from the shelf-break stations. The coarser-grained stations B2, B4, E1, and E3 have high scores on axis 1 and intermediate scores on axes 2 and 3. Station E4 was characterized by the deposit feeding form Halalaimus sp. and the epigrowth feeders Choniolaimus sp. and Neotonchus sp. (Figures 7-33 and 7-34). It is clear that the other swale and shelf-break stations were characterized by deposit feeders such as Sabatieria chitwoodi, Sabatieria sp., Odontophora sp., and Tershellinga sp. The coarser

Table 7-11. Environmental parameters considered in partial correlation versus reciprocal averaging axes and symbolism used in Figures 7-35, 7-39, 7-43 and 7-47.

Parameter	Symbol
Median diameter of sediment particles (phi units)	Md_ϕ
Sorting coefficient of particle diameter (phi units)	σ
Percent gravel	% > 2mm
Percent sand	% sand
Percent silt and clay	% silt & clay
Depth	Depth
Bottom water temperature	Temp.
Bottom water salinity	Salinity
Bottom water dissolved oxygen	O_2
Bottom water nitrite	NO_2
Bottom water nitrate	NO_3
Bottom water orthophosphate	$O\text{-}PO_4$
Sediment organic carbon concentration	TOC

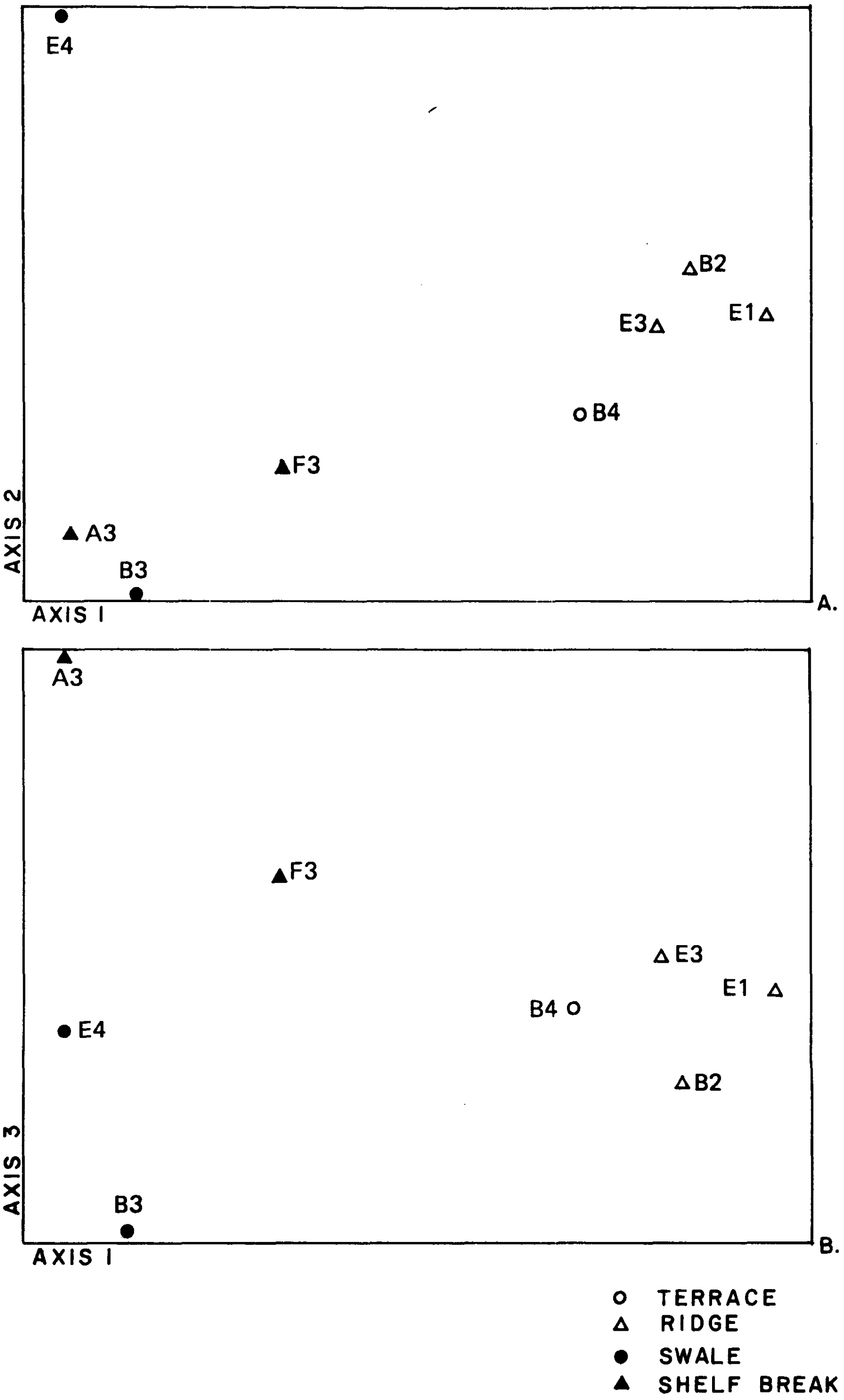

Figure 7-32. Reciprocal averaging ordination of collections of nematodes, fall 1976.

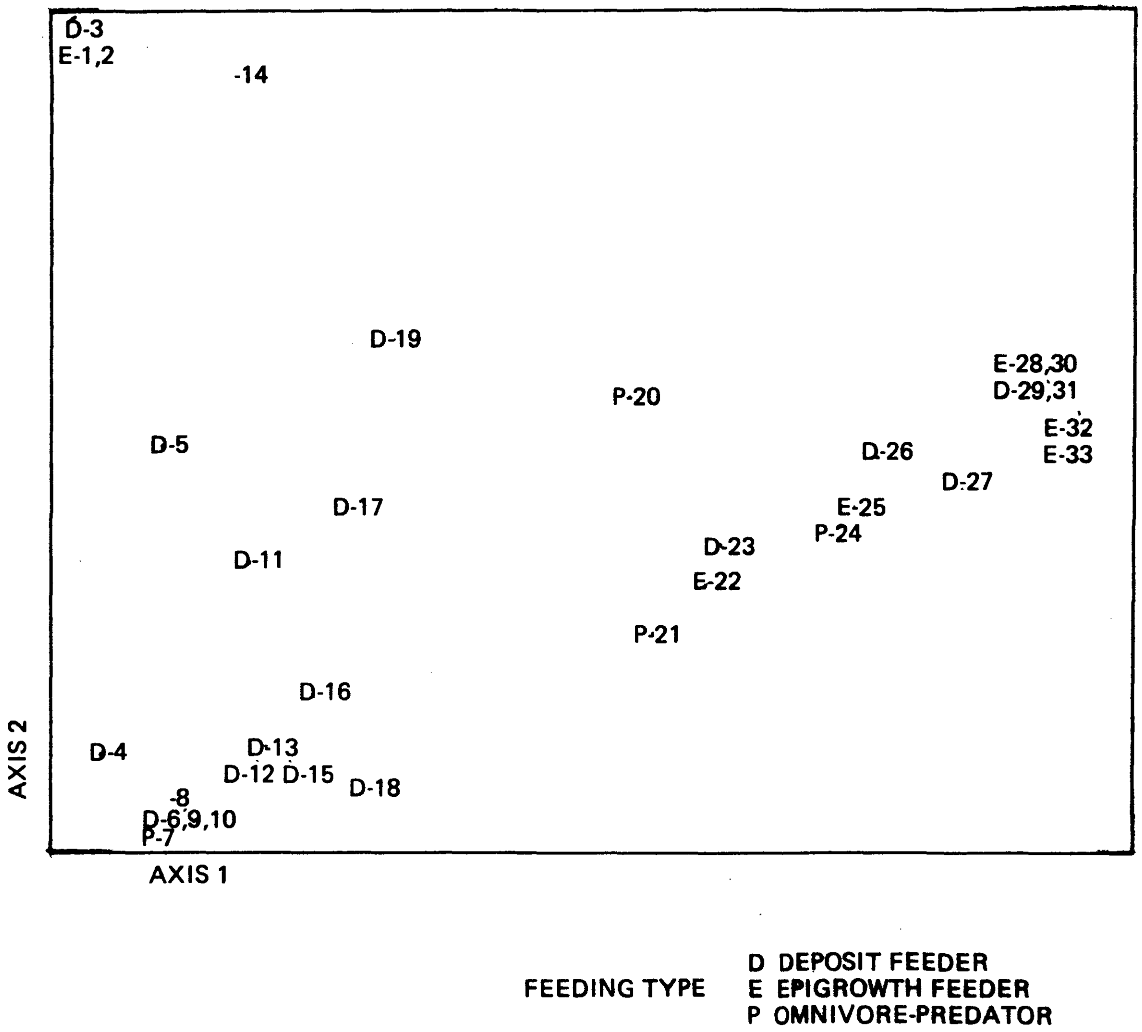

Figure 7-33. Reciprocal averaging ordination of nematode species in collections from fall 1976. Refer to Table 7-7 for species reference numbers.

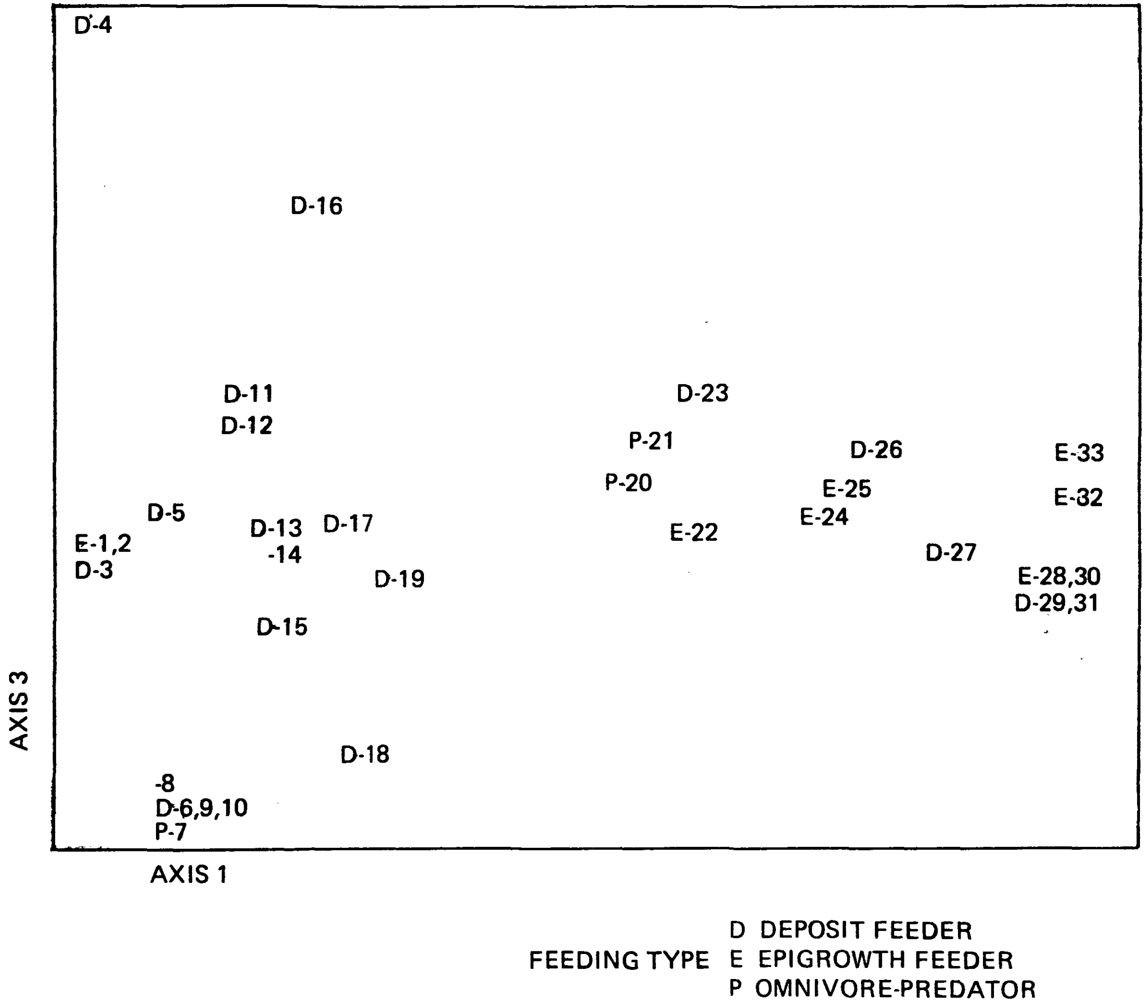

Figure 7-34. Reciprocal averaging ordination of nematode species in collections from fall 1976. Refer to Table 7-7 for species reference numbers.

sediment stations were characterized by epigrowth feeders such as *Microlaimus* sp. and *Desmodora* sp.

The pattern of trophic group dominance is further indicated in Figure 7-48a which shows that swale and shelf-break stations were very heavily dominated by deposit feeders and that the remaining stations were characterized by epigrowth feeders with the exception of Station B4 which had a substantial occurrence of the omnivore-predator *Oncholaimus* sp. Figure 7-35 presents the results of the partial non-parametric (Spearman's rho) correlation analysis of the relationship of environmental variables (Table 7-11) to the ordination axes for fall 1976 nematode collections. The analysis indicated a very strong association between sedimentary parameters, sorting, percent silt and clay, percent sand and total organic carbon, and the scores on axis 1. There was no strong association with the scores on axis 2, but temperature and percent gravel were strongly negatively associated with scores on axis 3 while bottom water ortho-phosphate was strongly positively associated with this axis. The analysis indicates that a suite of sedimentary factors related to depth paralleled the ordination along axis 1 and that a number of hydrographic factors (decreased temperature and increased orthophosphate) reflect the influence of slope water at the shelf break stations in the ordination along axis 3.

The ordination on axes 1 and 2 for the winter 1977 nematode data accounted for 46% of the variance in nematode occurrence, while the consideration of axis 3 brought this figure to 60%. The shelf-break stations have high scores on axis 1 while the swale stations have intermediate scores and the shelf stations with coarser sediments have low scores (Figure 7-36). Station E3 is positioned close to swale station E4 in the first three dimensions. The remaining shelf stations have low scores on axis 2. Axis 3 primarily separates Station B2 from the other stations.

The shelf-break stations were characterized by the deposit feeders *Tershellinga* sp. 1, *Quadricoma* sp., *Desmoscolex californicus*, and the epigrowth feeders *Chromaspirina* sp. and *Actinonema* sp. (Figures 7-37 and 7-38). The swale stations were characterized by the deposit feeders *Tricoma absidata*, *Rhynconema* sp., *Odontophora* sp., and *Paramonohystera* sp. Characteristic of both groups of stations were the deposit feeders *S. chitwoodi*, *Sabatieria* sp., *Theristus* sp., *Halalaimus* sp., and *Tershellinga* sp. Station B2 was characterized (on axis 3) by the exclusive occurrence of the deposit feeders *Paramonohystera ellipticus* and *Porocoma* sp. and the omnivore-predator *Enoplida* sp. The remaining shelf stations were characterized by the epigrowth feeders *Monoposthia mirabilis*, *Microlaimus* sp., *Desmodora* sp., and the omnivore-predators *Mesacanthoides* sp. and *Halachoniolaimus* sp.

This pattern was corroborated by the proportional representation of feeding types (Figure 7-48b). Stations A3, B3, and F3 show

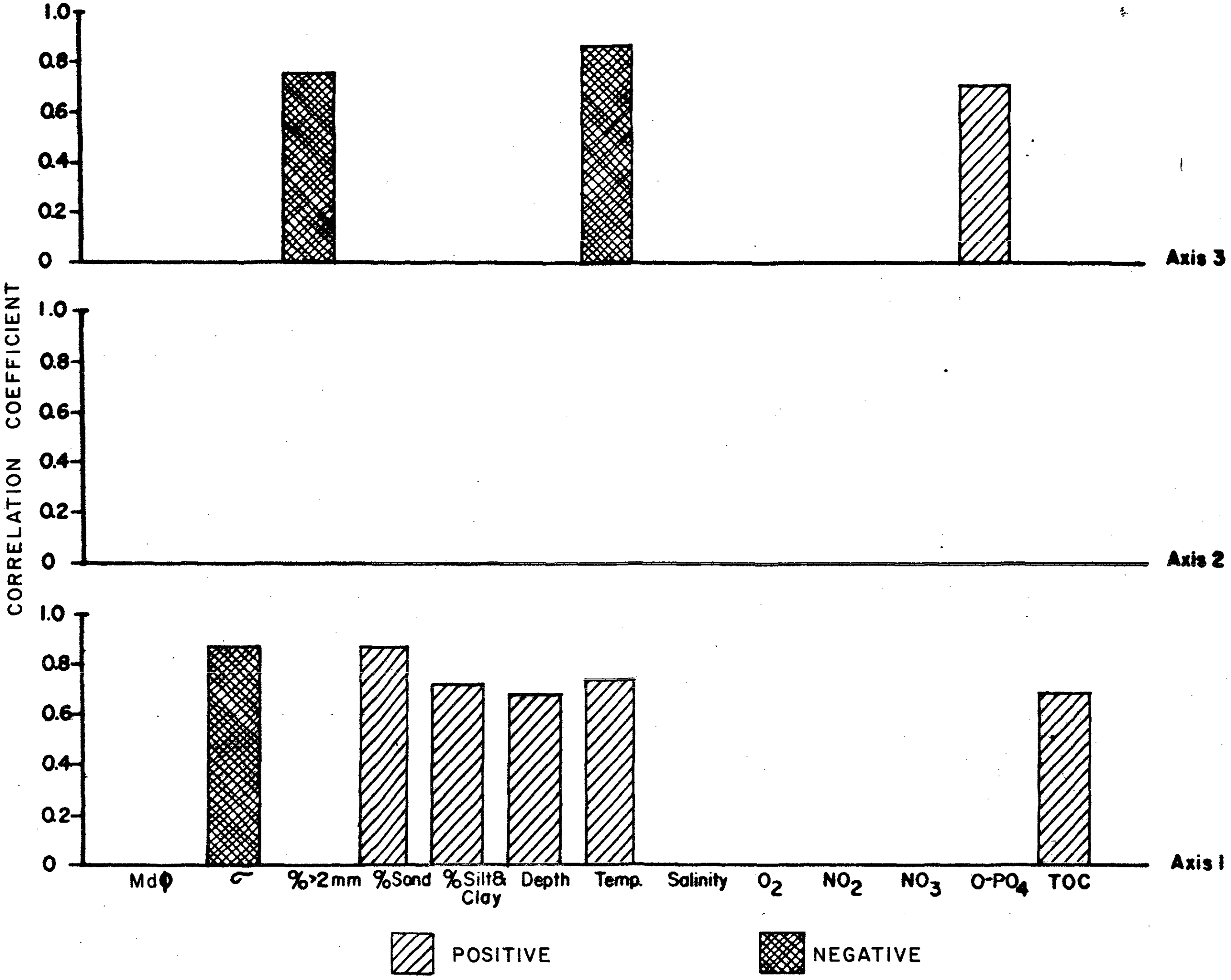

Figure 7-35. Partial correlation coefficients of axes resulting from reciprocal averaging ordination of fall 1976 nematode collections related to abiotic variables. Only those coefficients considerably different from zero are shown.

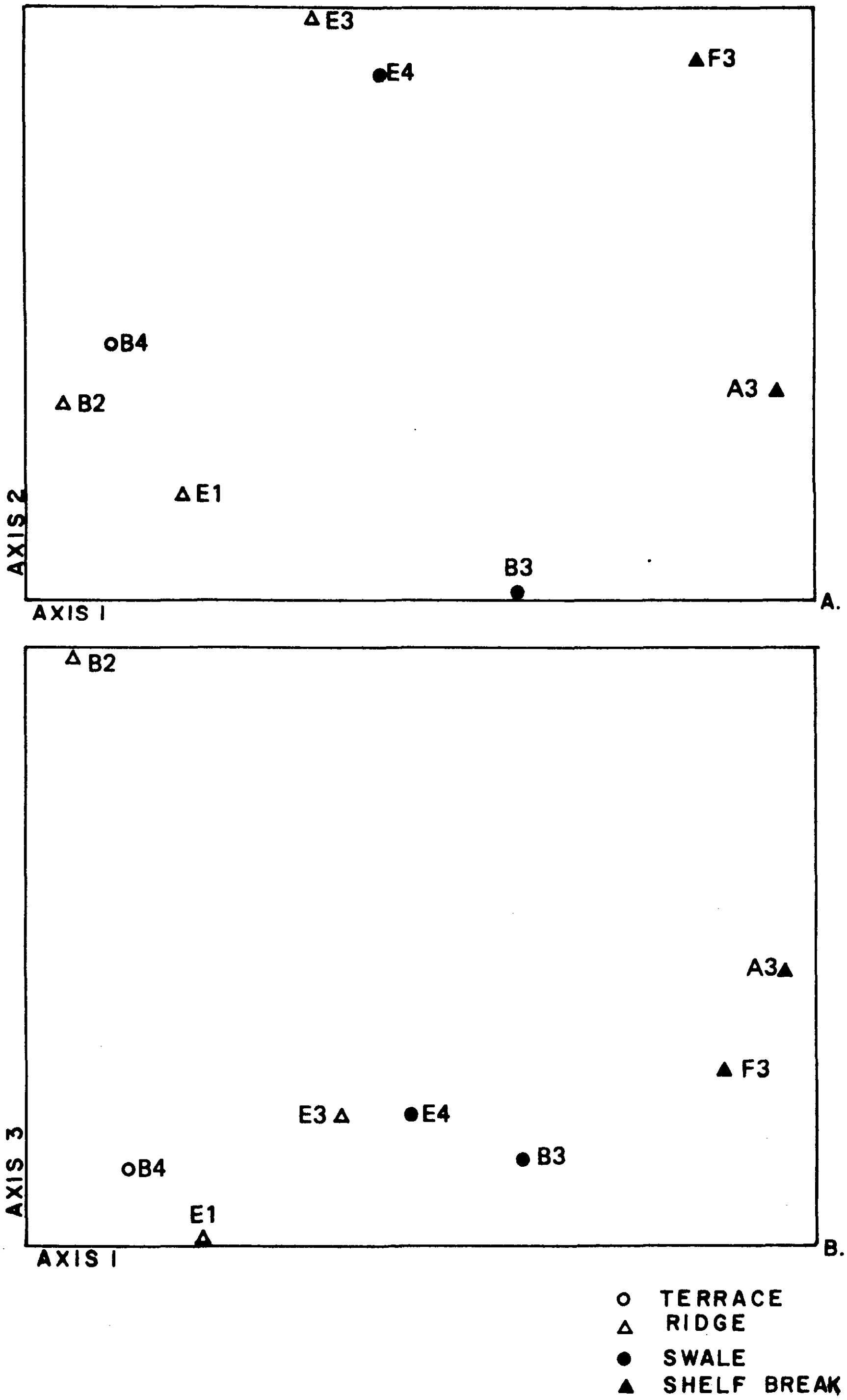

Figure 7-36. Reciprocal averaging ordination of collections of nematodes, winter 1977.

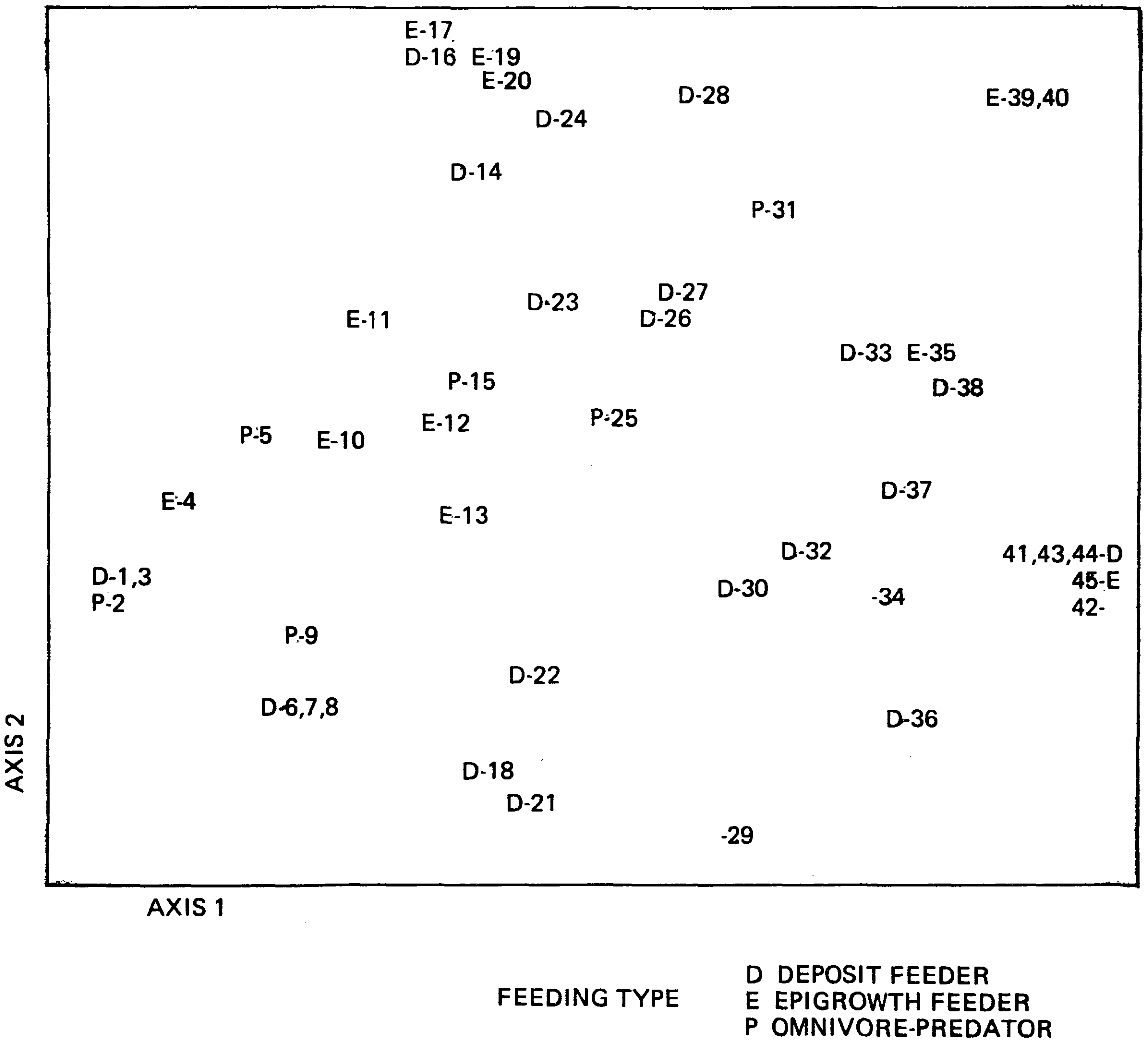

Figure 7-37. Reciprocal averaging ordination of nematode species in collections from winter 1977. Refer to Table 7-8 for species reference numbers.

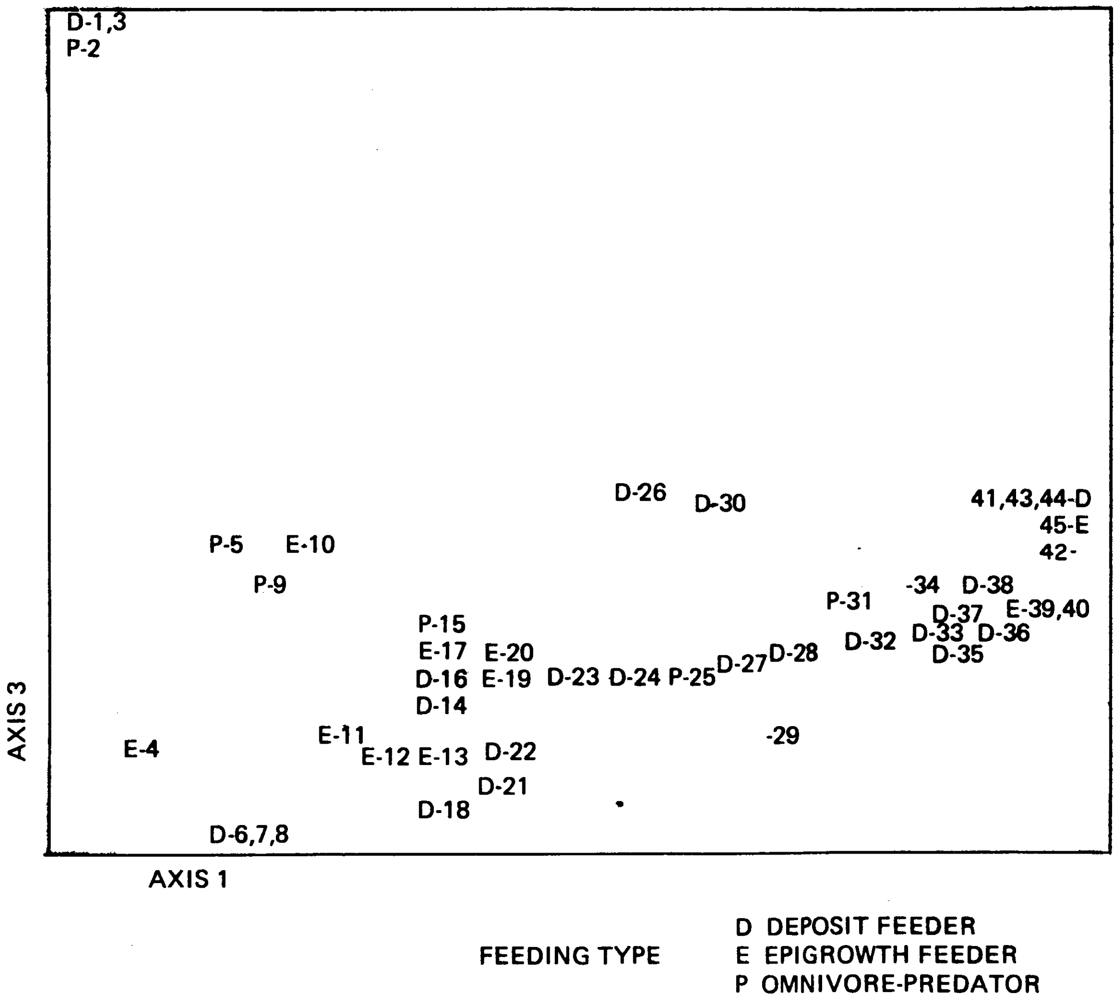

Figure 7-38. Reciprocal averaging ordination of nematode species in collections from winter 1977. Refer to Table 7-8 for species reference numbers.

overwhelmingly dominant numbers of deposit feeders with Station E4 inhabited by over 50% deposit feeders but with other types also represented. Station E1 was characterized by both deposit feeders and omnivore-predators, stations B2 and E3 by epigrowth feeders, and Station B4 again by omnivore-predators. Figure 7-39 presents the results of the partial correlation analysis of the ordination of nematode data from winter 1977 collections. A very strong association was indicated between axis 1 and the following: median grain size, percent silt and clay, depth, and total organic carbon. A strong negative association was indicated between salinity and percent silt and clay with axis 2. A strong negative association was indicated between percent gravel and concentration of nitrite and axis 3.

The ordination along axes 1 and 2 for the spring 1977 nematode data accounted for 49% of the variance while the addition of axis 3 brought this figure to 65%. The shelf-break and swale stations have low scores on axis 2 while axis 1 is difficult to interpret (Figure 7-40). Stations A3, B3, and F3 are closely positioned in three dimensional space, while swale station E4 has considerably different scores on axes 1 and 3. Axis 1 separated the coarser grained stations in area E from those in area B. Station A3 was characterized by the deposit feeding from *S. chitwoodi*; Station B3 was characterized by the deposit feeders *Halalaimus* sp., *Tershellinga* sp., and *Sabatieria* sp. Station E4 was characterized by the deposit feeder *D. californicus* and the epigrowth feeder *Paracyatholaimus* sp.; while Station F3 was characterized by deposit feeders *Tricoma pellucida* and *Quadricoma* sp. (Figures 7-41 and 7-42). Stations B2 and B4 were characterized by the deposit feeders *Didelta* sp. and *Arcolaimus* sp. and the omnivore-predators *Oncholaimus* sp. and *Latronema* sp., while stations E1 and E3 were characterized by the epigrowth feeders *Microlaimus kauri*, epsilonematids, and the deposit feeder *Ascolaimus* sp.

These patterns were confirmed by the proportional representation of trophic groups (Figure 7-48c). The swale and shelf-break stations were clearly dominated by deposit feeders while the ridge and terrace stations were characterized by epigrowth feeders and omnivore-predators. The partial correlation analysis for spring 1977 ordinations (Figure 7-43) indicated that several sedimentary factors were related to axis 1. These included percent sand (-), median grain size (-), and sorting (+). Dissolved oxygen also showed a strong correlation (-) with scores on axis 1. Depth (-), temperature (-) and oxygen (+) showed strong correlation with scores on axis 2, while temperature, salinity, and nitrate all showed strongly negative correlations with scores on axis 3.

The ordination along axes 1 and 2 for summer 1977 nematode collections accounted for 53% of the variance, while the addition of axis 3 brought this figure to 69%. Shelf-break and swale stations had low scores on axis 1 and the coarser sediment stations high scores. Axis 2 separated the swale stations from the shelf-break stations and

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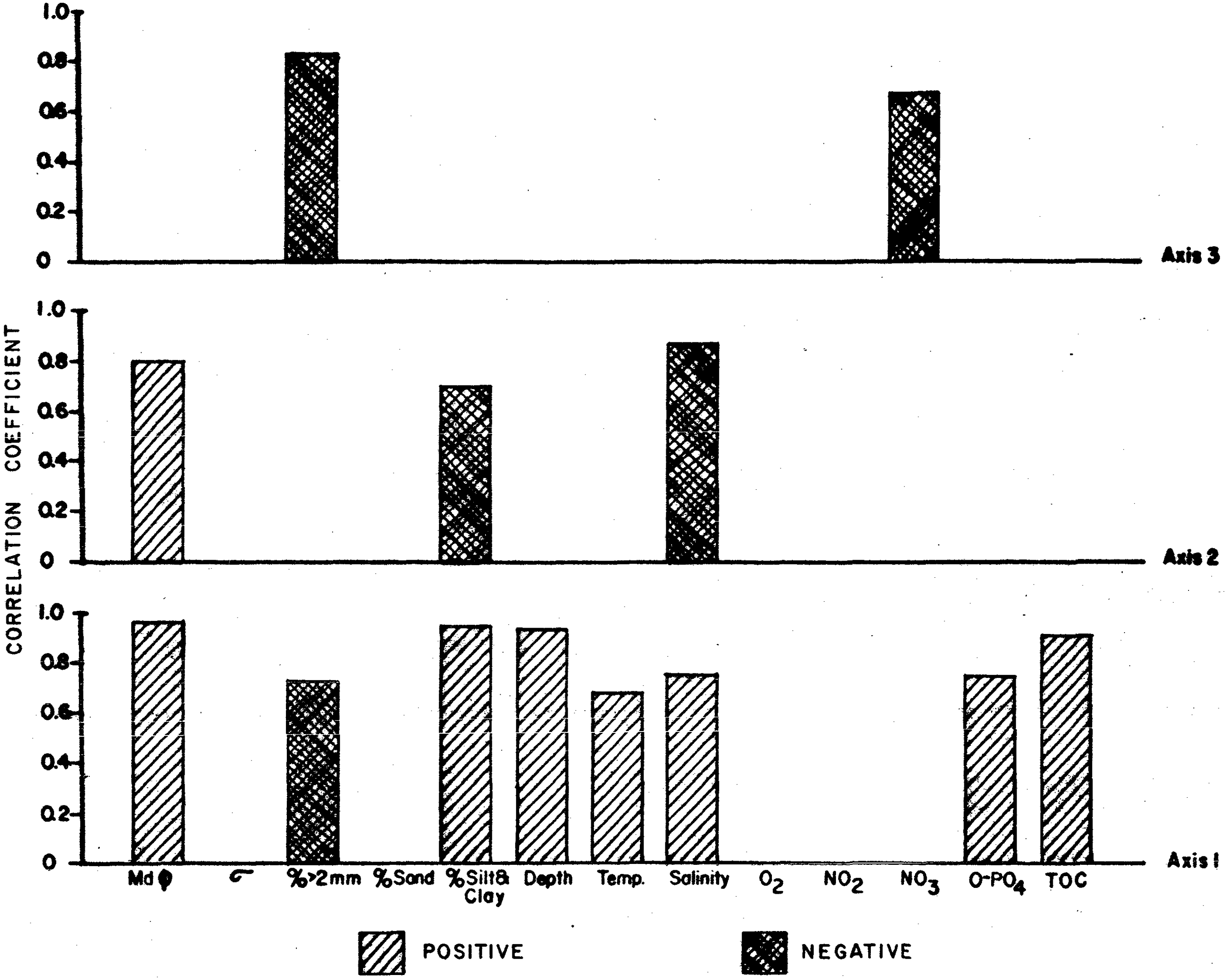

Figure 7-39. Partial correlation coefficients of axes resulting from reciprocal averaging ordination of winter 1977 nematode collections related to abiotic variables. Only those coefficents considerably different from zero are shown.

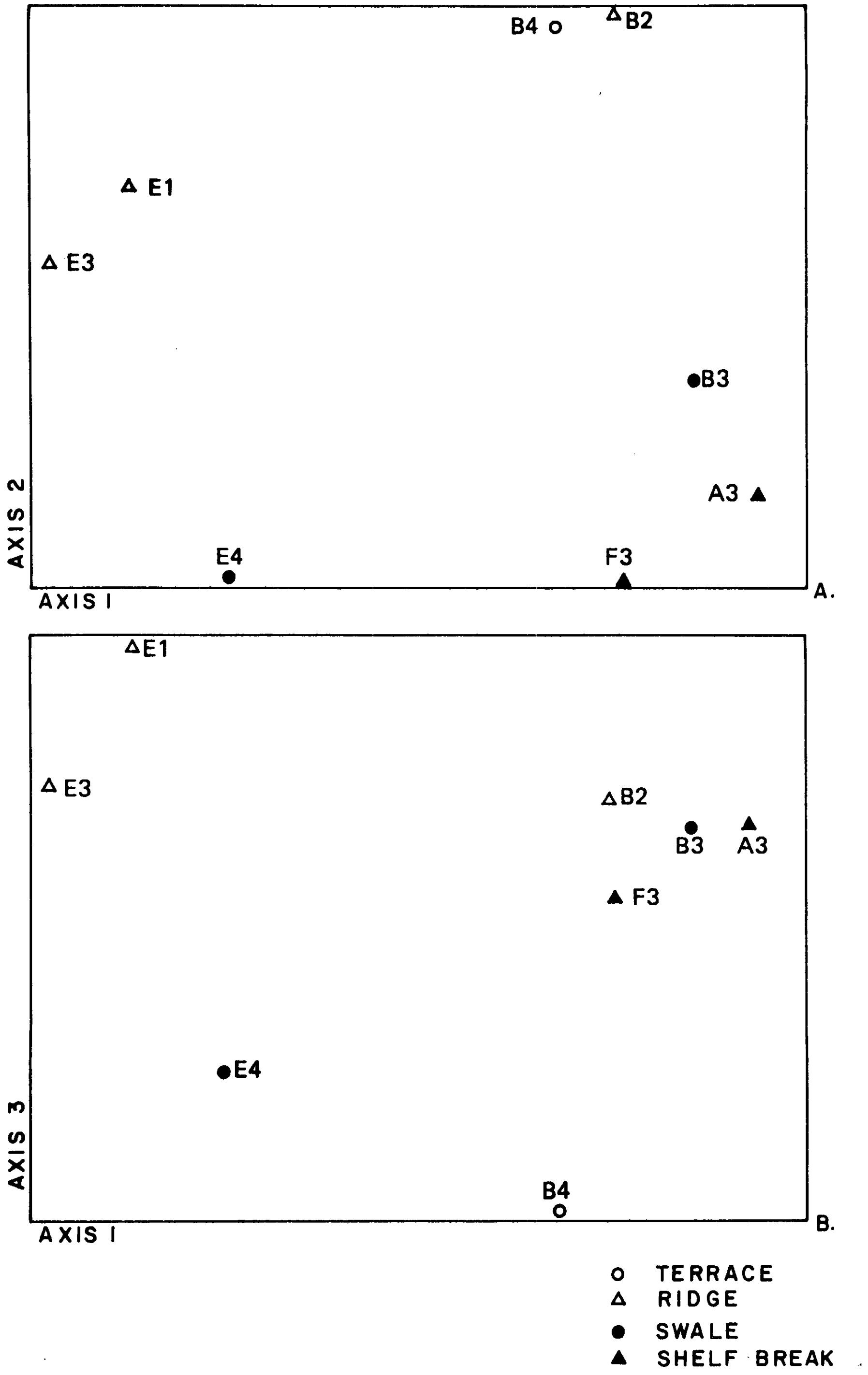

Figure 7-40. Reciprocal averaging ordination of collections of nematodes, spring 1977.

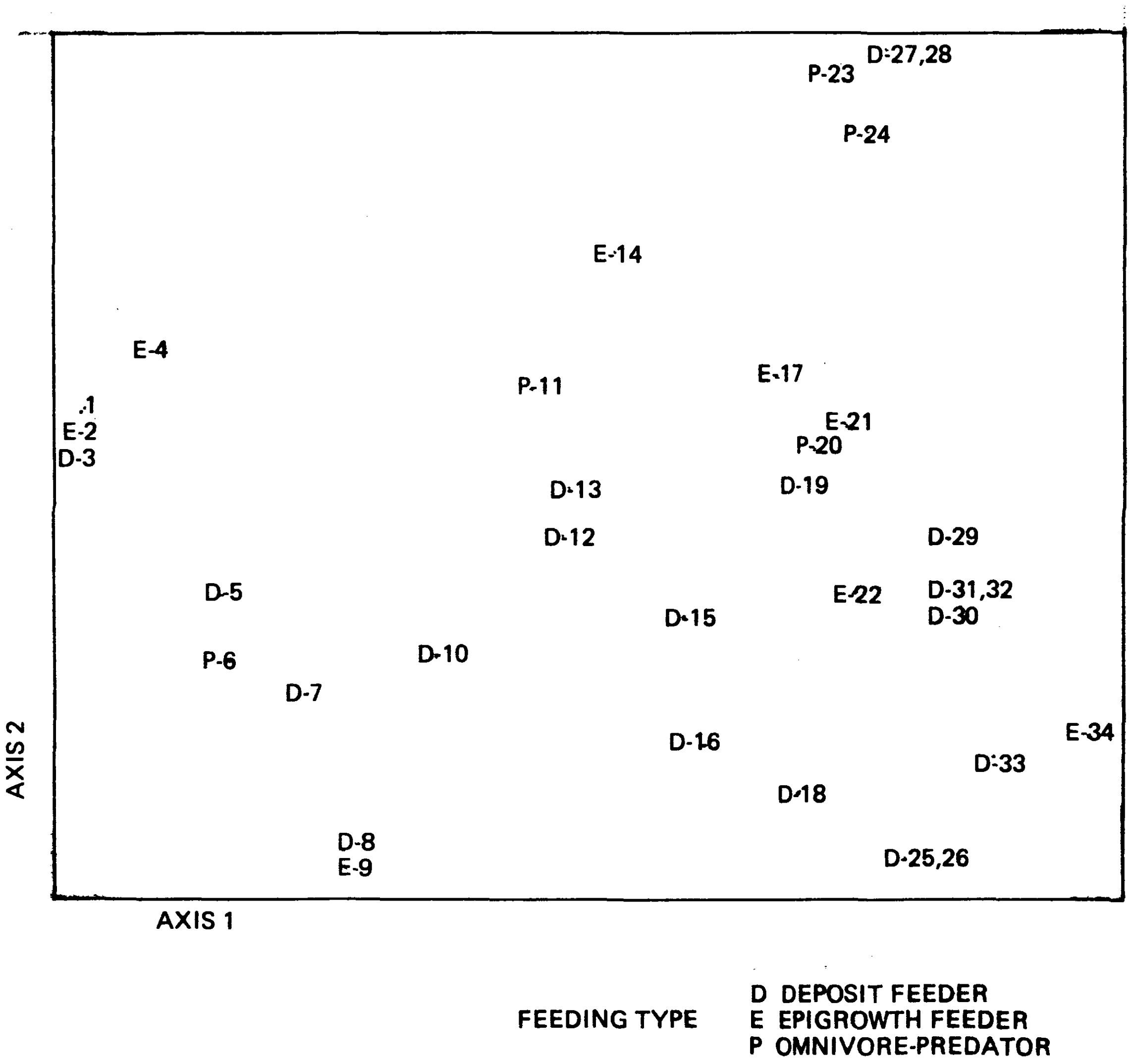

Figure 7-41. Reciprocal averaging ordination of nematode species in collections from spring 1977. Refer to Table 7-9 for species reference numbers.

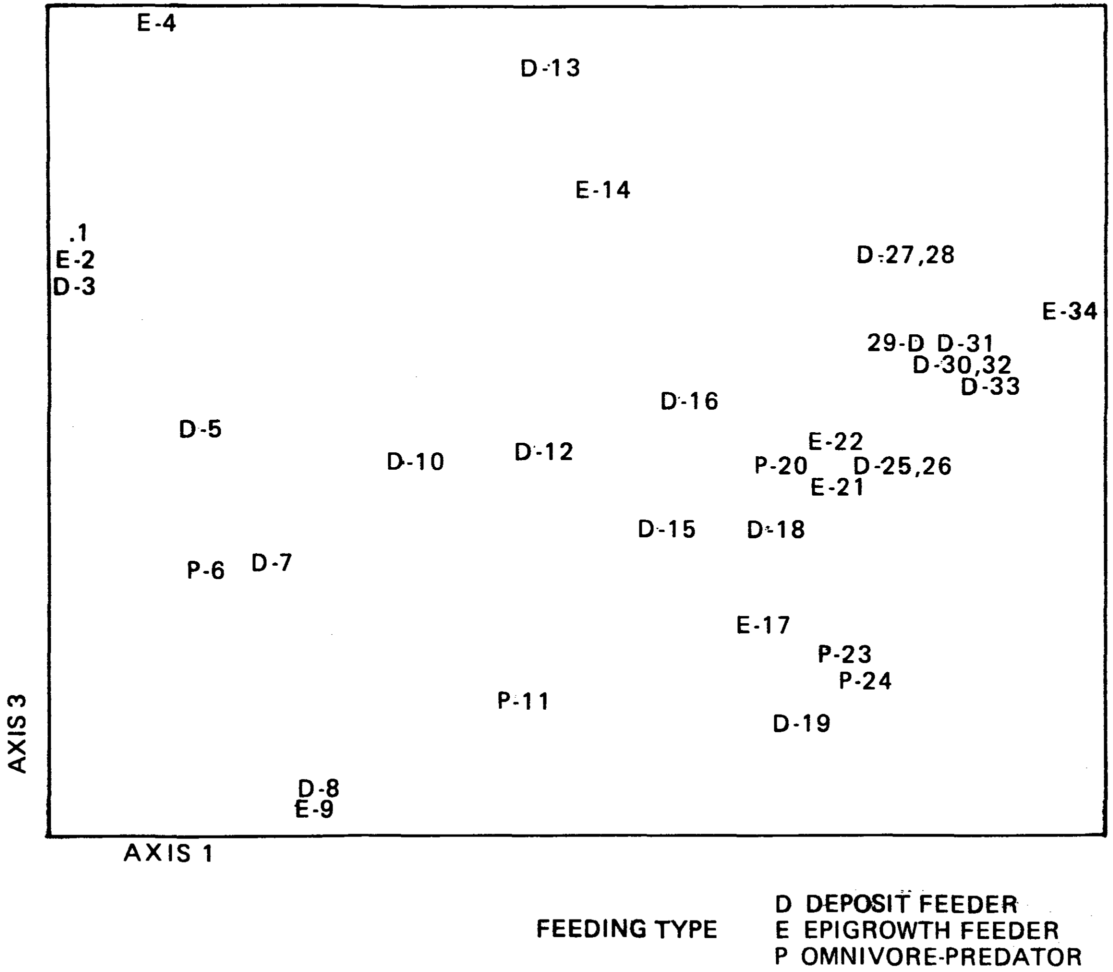

Figure 7-42. Reciprocal averaging ordination of nematode species in collections from spring 1977. Refer to Table 7-9 for species reference numbers.

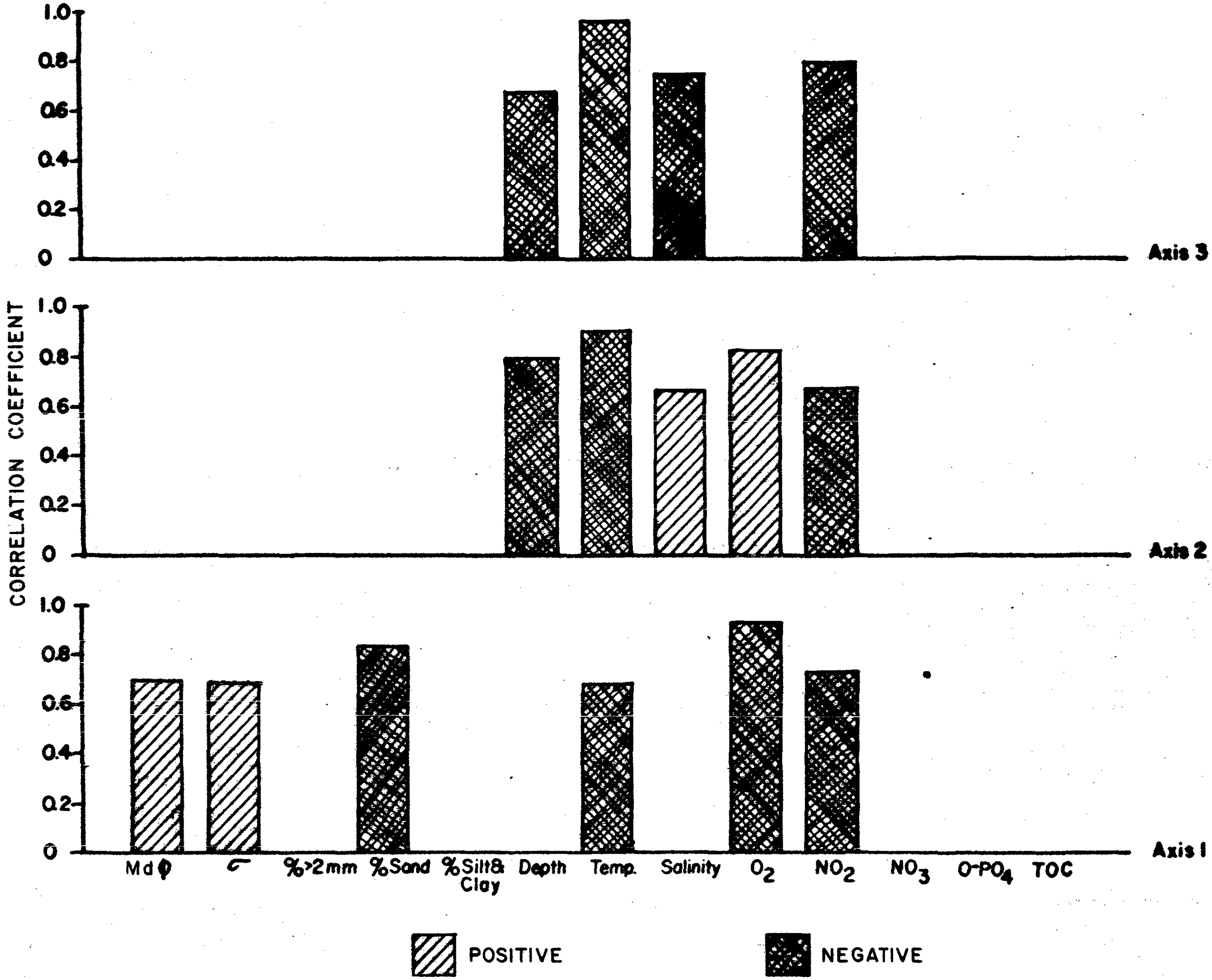

Figure 7-43. Partial correlation coefficients of axes resulting from reciprocal averaging ordination of spring 1977 nematode collections related to abiotic variables. Only those coefficients considerably different from zero are shown.

Station E3 from the other shelf stations. Axis 3 related differences between stations B3 and E4 and stations B2 and E1 (Figure 7-44).

The shelf-break stations were characterized by the occurrence of the deposit feeders *Halalaimus* sp., *Sabatieria* sp., *Odontophora* sp., *Tershellinga* sp., and *Theristus* sp. (Figures 7-45 and 7-46); while the swale stations were characterized by the deposit feeders *Areolaimus* sp., *Ceramonema* sp., *Ascolaimus* sp., *S. chitwoodi*, and *Anticoma* sp. and also the epigrowth feeder *Actinonema* sp. Stations B2 and E1 were characterized by the occurrence of the epigrowth feeders *Hypodontolaimus* sp., *Choniolaimus* sp., *Desmodora* sp., and *Microlaimus* sp. and the omnivore-predators *Mesacanthion* sp. and *Viscosia* sp. Station E1 was further delineated by the occurrence of the deposit feeder *T. pellucida*. Station B4 was characterized by the epigrowth feeders *Desmodora* sp., *Microlaimus* sp., and *Euchromodora* sp. and also the deposit feeder *Rhynconema* sp.; while Station E3 was characterized by the deposit feeder *Tricoma* sp.; and epigrowth feeders of the family Epsilonematidae. The trophic group proportions of the nematode taxocene (Figure 7-48d) confirmed that the swale and shelf-break stations were dominated by deposit feeders and that the ridge and terrace stations were dominated by epigrowth feeders.

The partial correlation analysis for the ordination of nematode occurrence data for summer 1977 collections (Figure 7-47) shows that a suite of sedimentary factors (median grain size, percent silt and clay, and total organic carbon) and also depth had strong negative correlations with scores on the first axis; nitrate had a strong negative correlation with scores on the second and depth had a strong negative correlation with scores on the third axis.

Certain patterns are evident from the species ordinations of nematode and harpacticoid abundance data. The organically richer, finer sediments in the swales and at the shelf break were dominated by deposit feeding nematodes such as *Tershellinga* sp., *Sabatieria* spp., *Paramonohystera* sp., and *Theristus* sp., by very robust harpacticoids such as *Halectinosoma* sp. and *Pseudobradya* sp. and also by clearly epipelic harpacticoid forms such as *Diarthrodes* sp. The outer shelf ridge and terrace stations, on the other hand, were characterized by epigrowth feeding nematodes such as *Microlaimus* spp., *Desmodora* sp., and *Monoposthia* spp. along with omnivore-predators such as *Mesacanthoides* sp. and *Latronema* sp. and by interstitial copepods such as *L. brevicornis* and *L. macronyx*.

Species Diversity and Harpacticoid/Nematode Ratio with Respect to Topography

Figure 7-49 presents H' species diversity values for Nematoda and Harpacticoida at each station for each season. Nematodes were more diverse than harpacticoids at all stations and in all seasons except for Station E1 fall 1976, Station B4 spring 1977, and Station B2

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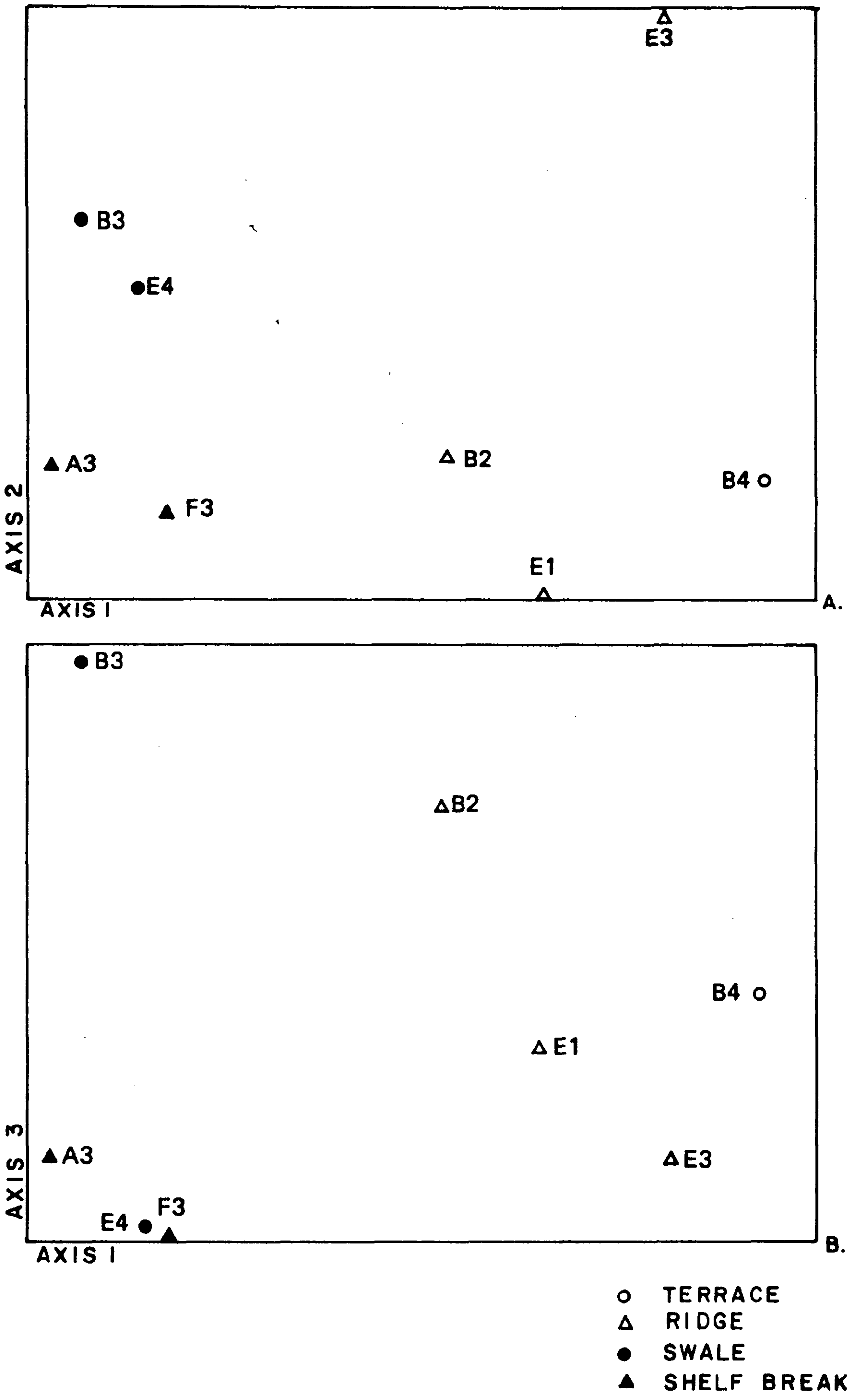


Figure 7-44. Reciprocal averaging ordination of collections of nematodes, summer 1977.

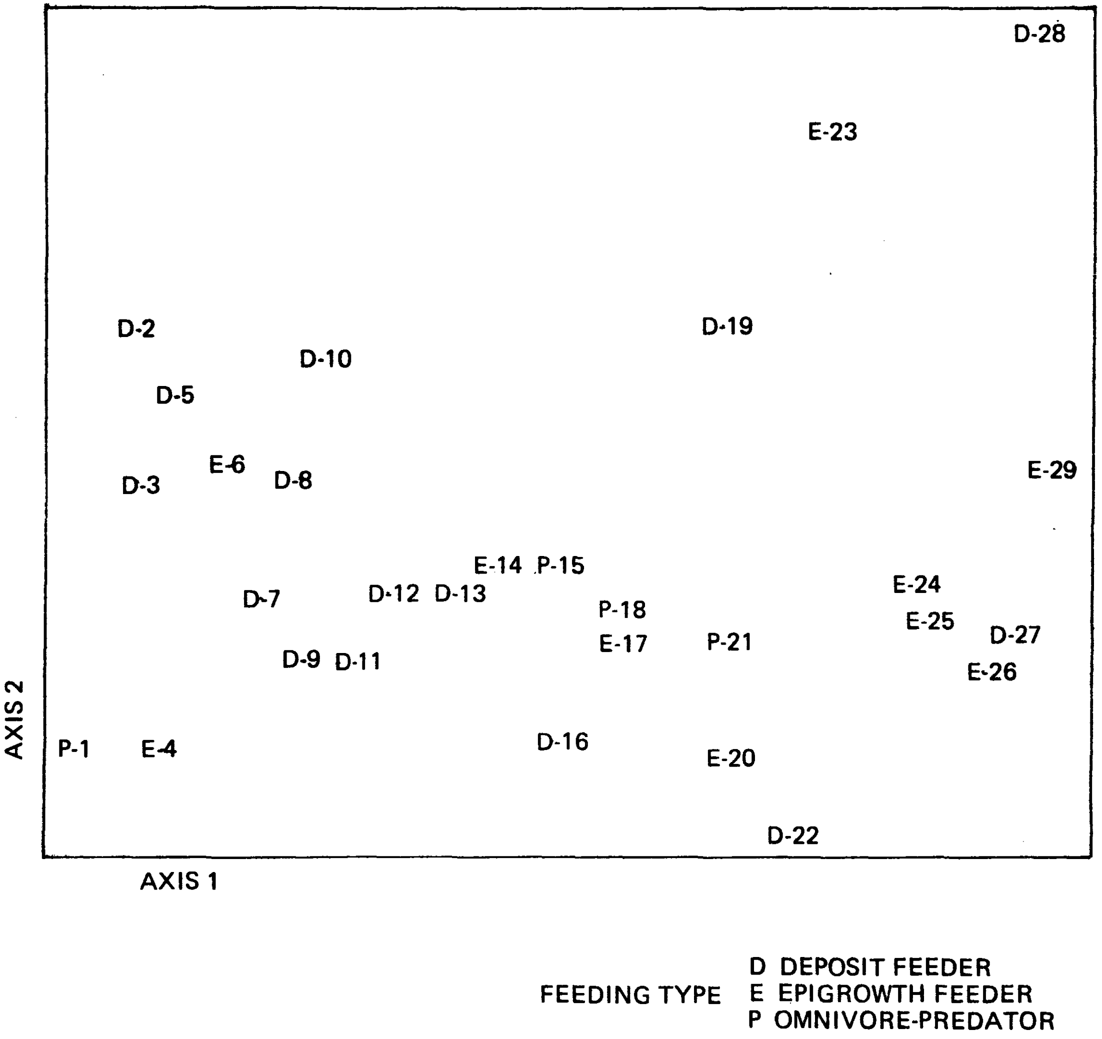


Figure 7-45. Reciprocal averaging ordination of nematode species in collections from summer 1977. Refer to Table 7-10 for species reference numbers.

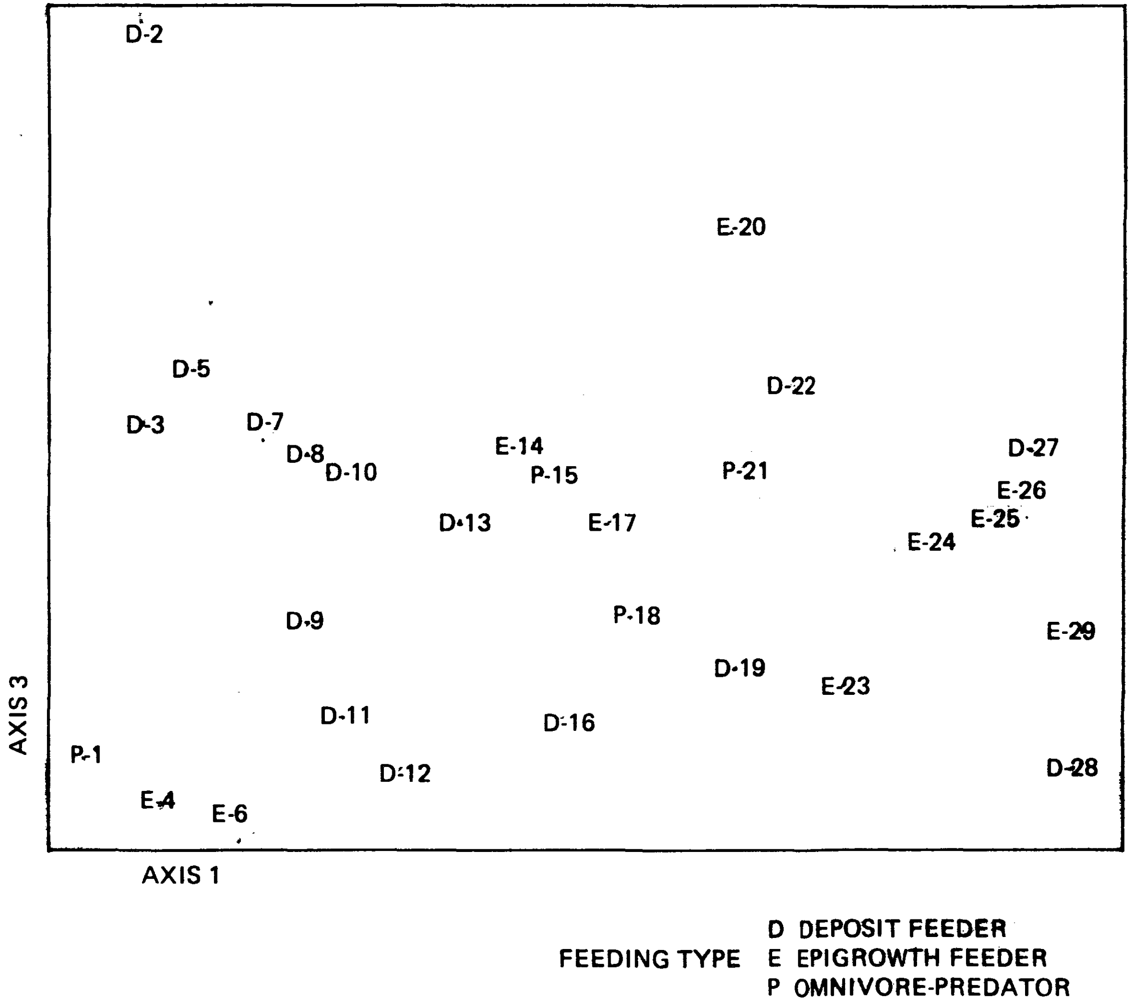


Figure 7-46. Reciprocal averaging ordination of nematode species in collections from summer 1977. Refer to Table 7-10 for species reference numbers.

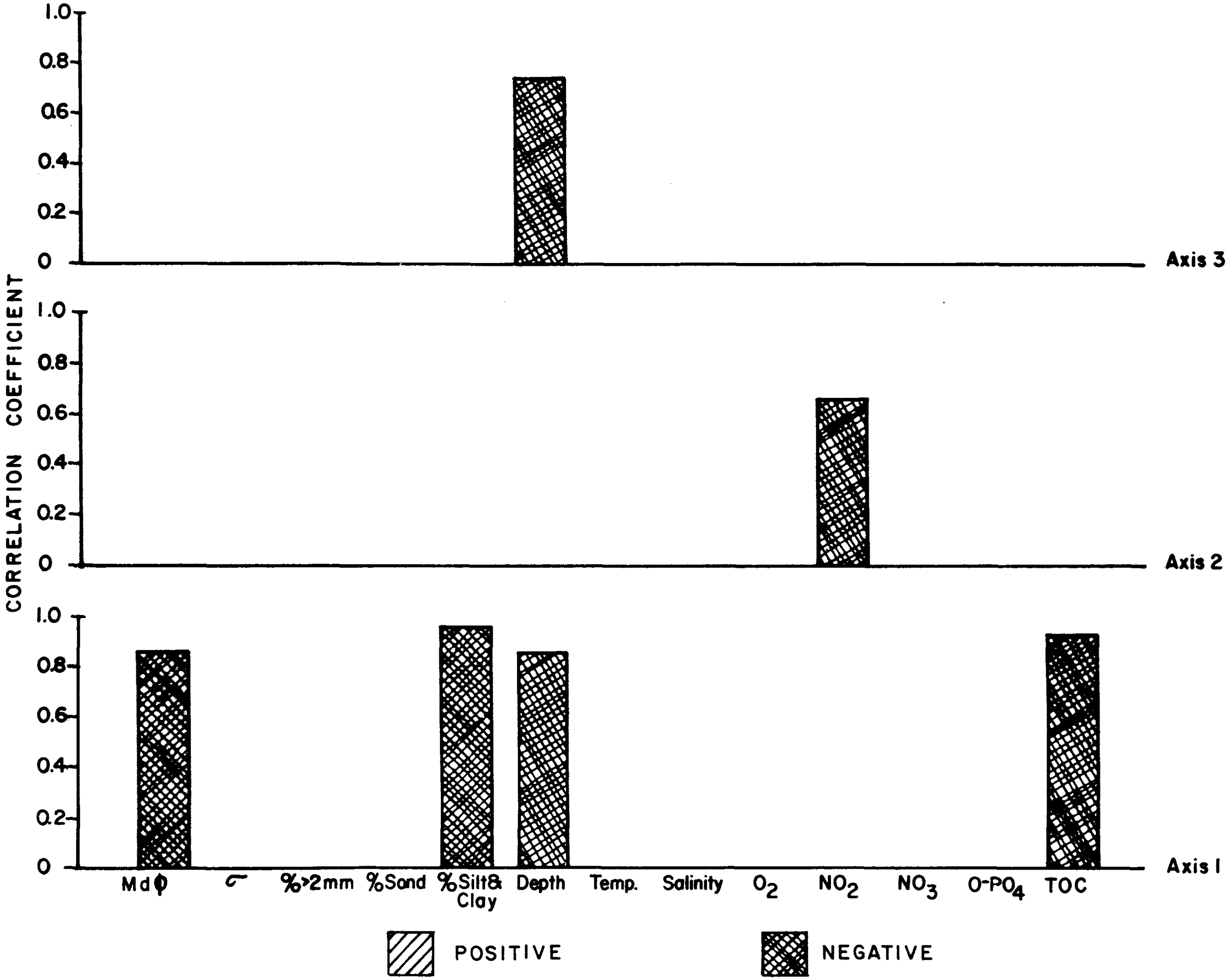


Figure 7-47. Partial correlation coefficients of axes resulting from reciprocal averaging ordination of summer 1977 nematode collections related to abiotic variables. Only those coefficients considerably different from zero are shown.

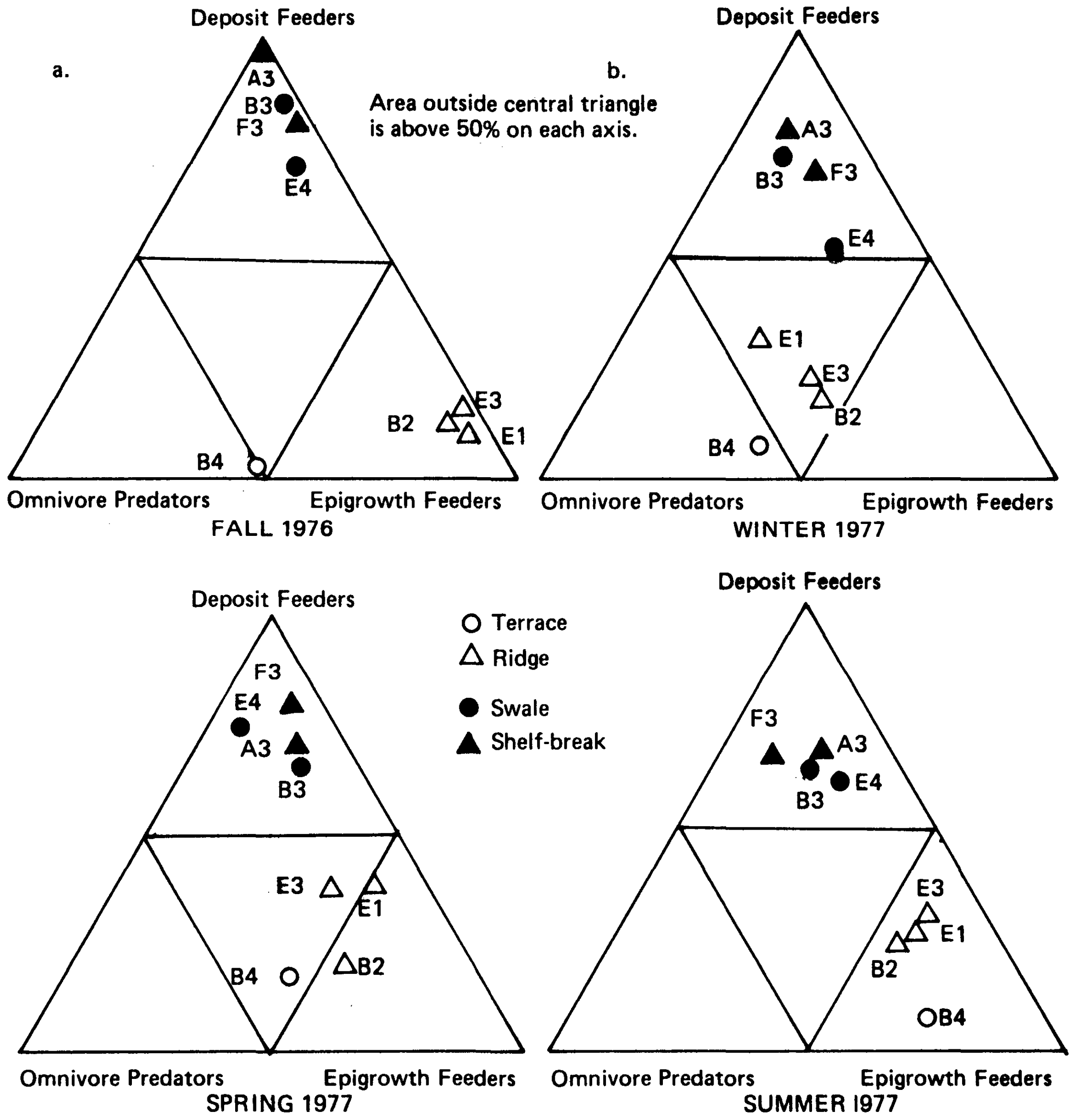


Figure 7-48. Proportional representation of nematode feeding types in collections by season.

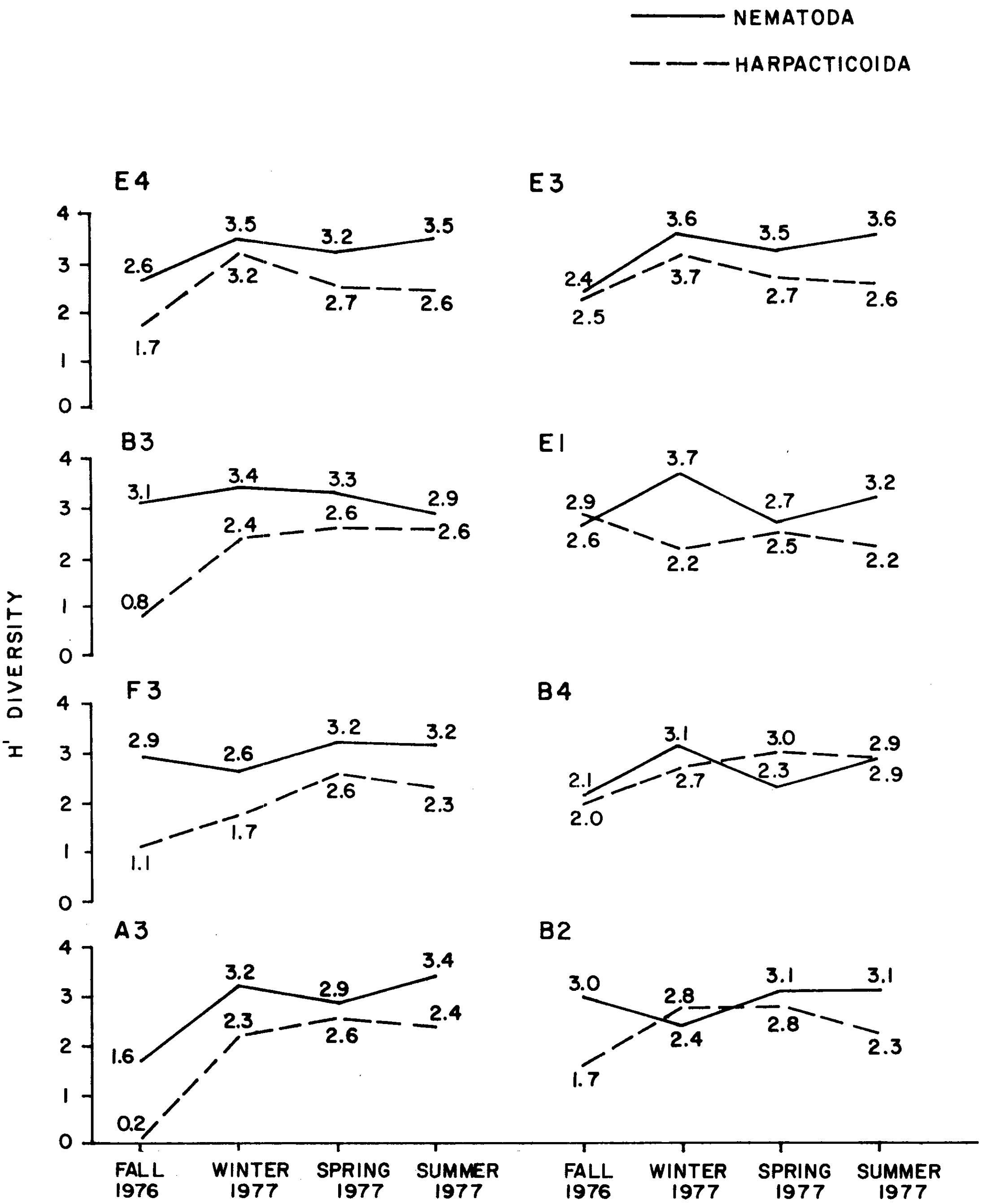


Figure 7-49. Shannon diversity (H^1) of nematode and harpacticoid collections by station and season.

winter 1977. All of these stations are in coarser, more dynamic sediments. In general diversity seemed to be low in fall 1976 collections and high in summer 1977. Many stations showed high diversity also in winter 1977, but generally not as high as in summer. A Mann-Whitney comparison showed no difference in nematode diversity between swale and shelf-break stations and ridge and terrace stations ($\alpha < 0.01$), but a similar comparison indicated that harpacticoid diversity was lower at the swale and shelf-break stations than at the ridge and terrace stations (T=66, range 67-189, $\alpha < 0.01$). The high diversities in the summer 1977 collections may be a reflection of the generally higher densities represented in these collections, but many stations exhibited higher densities in the spring 1977 collections when diversity was generally lower.

The ratio of harpacticoid to nematode abundance was used to delineate habitats that were similar in terms of the overall densities of these two taxa. There was an obvious difference in the H/N ratio computed for collections at the swale and shelf-break stations and those at the ridge and terrace stations (Table 7-12). The mean H/N value from the swale and shelf-break collections was 0.14 (SD=0.06) and the mean H/N value from the ridge and terrace collections was 0.54 (SD=0.12). This difference confirms that harpacticoid copepods were found in lower relative numbers in collections from the swale and shelf-break stations, and that nematodes were overwhelmingly dominant in these collections. It also indicates that harpacticoid copepods were found in higher relative numbers in collections from the ridge and terrace stations although nematodes were still dominant in these collections. A Mann-Whitney comparison showed that the H/N values were significantly lower at the swale and shelf-break stations as compared to the ridge and terrace stations (T=26, range 67-189, $\alpha < 0.01$).

The H/N value for swale station E4 winter 1977 was 2.36 indicating that harpacticoid copepods were more than twice as abundant as nematodes in this collections. The sediment composition of collections from Station E4 during winter 1977 was aberrant with a relatively large median grain size of 1.23ϕ as opposed to a median grain size of 2.09ϕ for other seasonal collections (Chapter 5). The larger winter 1977 median grain size was the result of the sediment consisting of 17.03% gravel (actually shell) as opposed to a mean gravel component of 3.92% in other seasons. This is another indication of the preference of harpacticoid copepods for larger grain size sediments.

Overall Correlation Analysis

Product-moment correlation coefficients were computed between total meiofuanal abundance, abundance of Nematoda and Harpacticoida, harpacticoid:nematode ratio, and sedimentary and physico-chemical

Table 7-12. Harpacticoid/Nematode ratio.

Station	Fall '76	Winter '77	Spring '77	Summer '77	Mean H/N	S.D.
A3	0.0215	0.0935	0.1018	0.1422	0.0898	0.0502
B2	0.5827	0.7887	0.2598	0.2405	0.4679	0.2653
B3	0.1100	0.2658	0.2063	0.1687	0.1877	0.0654
B4	0.4521	0.5542	0.3036	0.3646	0.4186	0.1090
E1	0.774	0.551	0.8202	0.6592	0.7011	0.1208
E3	0.5351	0.4663	0.7049	0.6228	0.5823	0.1039
E4	0.0480	2.36	0.3487	0.1334	0.7225	1.0990
F3	0.0651	0.0676	0.0763	0.1871	0.0990	0.0589

factors (Table 7-13). The constraints for this type of analysis were discussed in the Methods section.

Certain correlation trends appeared to be both consistent and meaningful. Harpacticoid abundance was significantly positively correlated with grain size, percent gravel, and oxygen level, and negatively correlated with total organic carbon, and percent silt and clay. Nematode abundance was positively correlated with percent silt and clay, total organic carbon, and salinity, and negatively correlated with grain size. High H/N values, indicating high relative numbers of harpacticoids, were generally related to the same factors as high harpacticoid abundance.

Small Scale Spatial Heterogeneity

The purpose of the three by three sampling matrix of square contiguous cores was to allow the larger sample (56.25 cm^2) to be partitioned into smaller subunits in order to determine small scale distributional patterns. A coefficient of dispersion (variance to mean ratio) was computed for total meiofaunal abundance, nematode abundance, and harpacticoid abundance at each station in each season. The coefficients of dispersion were in all cases greater than 1, indicating departure from random dispersion. Those for total meiobenthos ranged from 6.8 to 72.9, those for nematodes ranged from 1.6 to 86.9 and those for harpacticoids ranged from 1.2 to 34.4. This indicated that the distribution of total meiobenthos, Nematoda and Harpacticoid in the subsamples was in most cases contagious and often highly so. Appendix 7B presents microdistribution maps showing the distribution of abundance of harpacticoids and nematodes in each collection broken down by subsamples. This appendix also gives the H/N value associated with each collection.

Both of the dominant taxa showed highly contagious distributions, but it was not known if these distributions occurred as a result of some interaction or spatial requirement of either taxon. This possibility was tested as previously described by the technique of spatial autocorrelation (see Methods). The null hypothesis tested was that the standardized differences of nematode and harpacticoid abundances were distributed at random in the three by three sampling array and consequently that the abundance of one taxon did not affect the abundance of the other. This null hypothesis was rejected in only six of 32 collections (18.8%). For four of these collections (B2, winter 1977; B4, summer 1977; E4, fall 1976 and summer 1977) the null hypothesis was rejected because patchy standard difference distributions indicated that extreme abundance values of nematodes, relative to mean values, co-occurred with extreme abundance values of harpacticoids. For two collections (F3, fall 1976; and E3 spring 1977), the null hypothesis was rejected because similar or dissimilar nematode and harpacticoid abundances, regardless of their departure from the mean values, tended to co-occur. There was no apparent

Table 7-13. Animal - sediment and physico-chemical correlation analysis, 1976-1977.

	Season	Median Grain Size	Percent Gravel	Percent Sand	Percent Silt	Percent Clay	Total Organic Carbon
Total meiofaunal abundance	fall						
	winter						
	spring	-0.55	0.66			-0.66	
	summer	-0.52	0.57				
Harpacticoid abundance	fall	0.83*		0.78*	-0.69*	-0.73*	-0.73*
	winter	0.56	0.52				
	spring					-0.53	
	summer		0.50				
Nematode abundance	fall	-0.42					0.78*
	winter		-0.47			0.53	
	spring						
	summer						
H/N ratio	fall						
	winter						
	spring			0.66	-0.55	-0.83*	
	summer	0.73			-0.65		

* Values significant at α = 0.05

Table 7-13. (concluded)

	Season	Depth	Temperature	Salinity	Oxygen	Nitrate	Nitrite
Total meiofaunal abundance	fall				0.55		
	winter						
	spring	-0.55		-0.62			
	summer						
Harpacticoid abundance	fall			-0.62			
	winter	-0.48			0.88*		
	spring	-0.63		-0.56	0.51		
	summer	-0.57		-0.64			
Nematode abundance	fall			0.63		-0.70*	0.62
	winter						
	spring						
	summer						
H/N ratio	fall			-0.71*			
	winter						
	spring	-0.54	-0.52		0.71*		
	summer				0.71*		

pattern in the distribution of collections in which the null hypothesis of spatial autocorrelation was rejected.

A set of duplicate samples was taken during the summer 1977 sampling period at each of the B cluster stations sampled for meiobenthos. After these samples were processed in identical fashions, Mann-Whitney comparisons were computed to determine if the duplicate sample populations could have been drawn from the same parent population. It was assumed that since the duplicate samples were taken from separate Smith-McIntyre grab samples, that they represented spatially close, but not contiguous samples. Comparisons were made for total meiofauna, Nematoda, and Harpacticoida. In all cases the Mann-Whitney comparisons proved that the duplicate samples could all have been drawn from the same parent population ($\alpha > 0.05$). This result seems to confirm the conclusions of Coull et al. (1977) with regard to homogeneous meiofaunal distribution in larger areas despite high small scale variability.

Seasonal Variations

Seasonal variability in abundance of total meiobenthos, Nematoda, and Harpacticoida is depicted in Figures 7-50 through 7-52. These are logarithmic plots for ease of presentation which means that apparent additive differences are actually multiplicative. Total meiofaunal abundance was generally low in fall 1976, rose in winter and spring 1977, and dropped in summer 1977 (Figure 7-50). There were a number of exceptions to this pattern, namely Station B4 which rose steadily from fall 1976 to summer 1977, and stations F3 and E4 which had high meiofaunal densities in fall 1976 which dropped in winter 1977, reached a maximum in spring 1977, and dropped to a minimum in summer 1977. These different patterns were apparently the result of similar variations in nematode densities (Figure 7-51). Harpacticoid abundance rose to a maximum in summer 1977 but the patterns at stations F3 and E4 did not (Figure 7-52). Harpacticoid abundance at Station E4 followed more closely the general pattern described for total meiobenthos, and harpacticoid abundance at Station F3 did not show a large amount of seasonal variation.

It was not clear _a priori_ whether in situ seasonal variation would be present or could be detected if present in meiobenthos populations because of the highly dynamic nature of meiofaunal populations. This analysis indicates that concordant seasonal patterns appear to exist in meiofaunal populations on the Middle Atlantic outer continental shelf. This result was further confirmed by the evaluation of meiobenthos samples taken after the completion of this study in November 1977 at the B cluster stations. If collections from these samples were to follow the described seasonal pattern, population numbers should be much lower than the summer 1977 levels. This is the case for all collections made at this time.

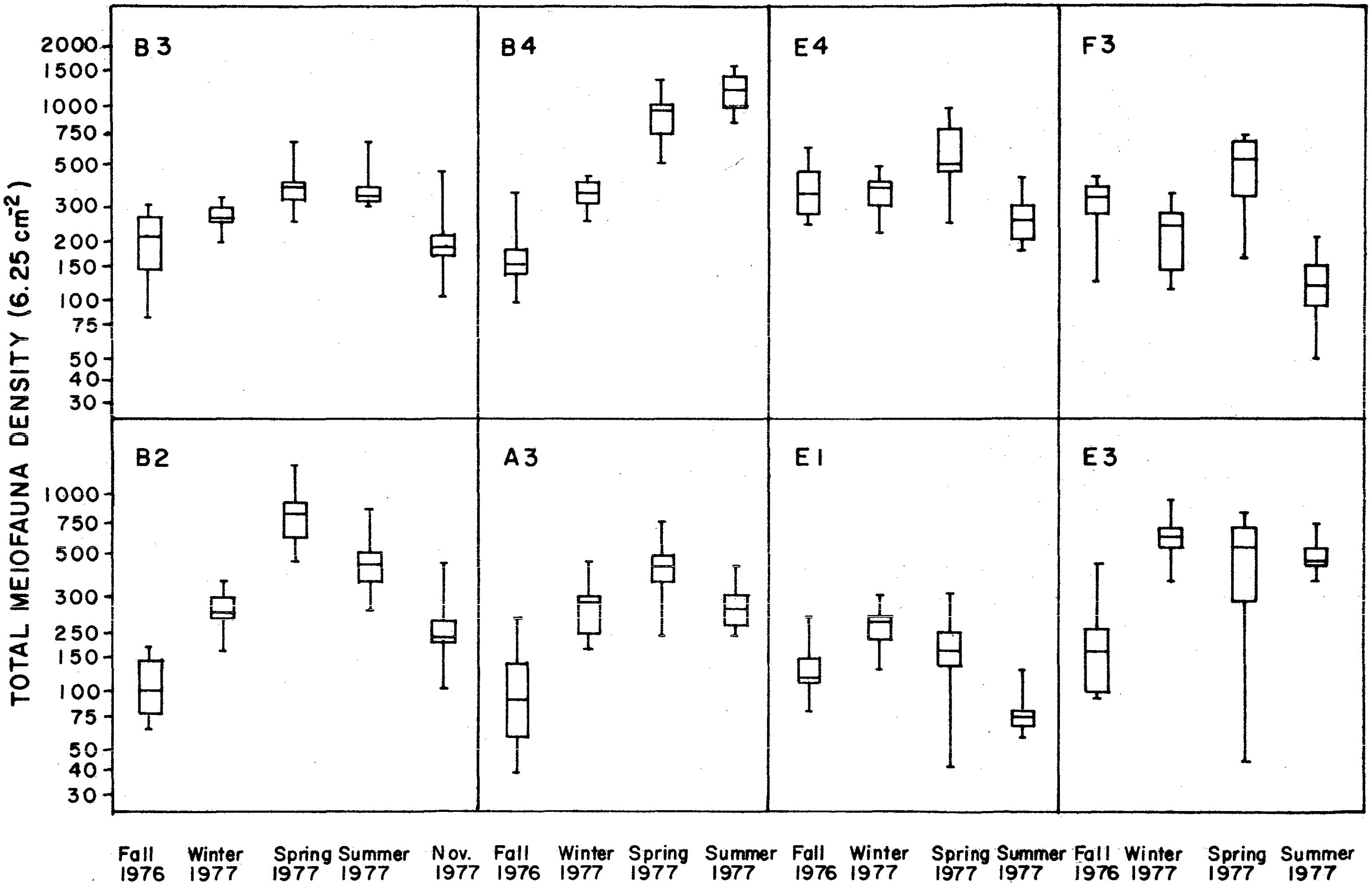


Figure 7-50. Seasonal variability of density of total meiobenthos. Vertical lines represent the range of 9 cores, bars represent the mid-range, and central horizontal lines the median.

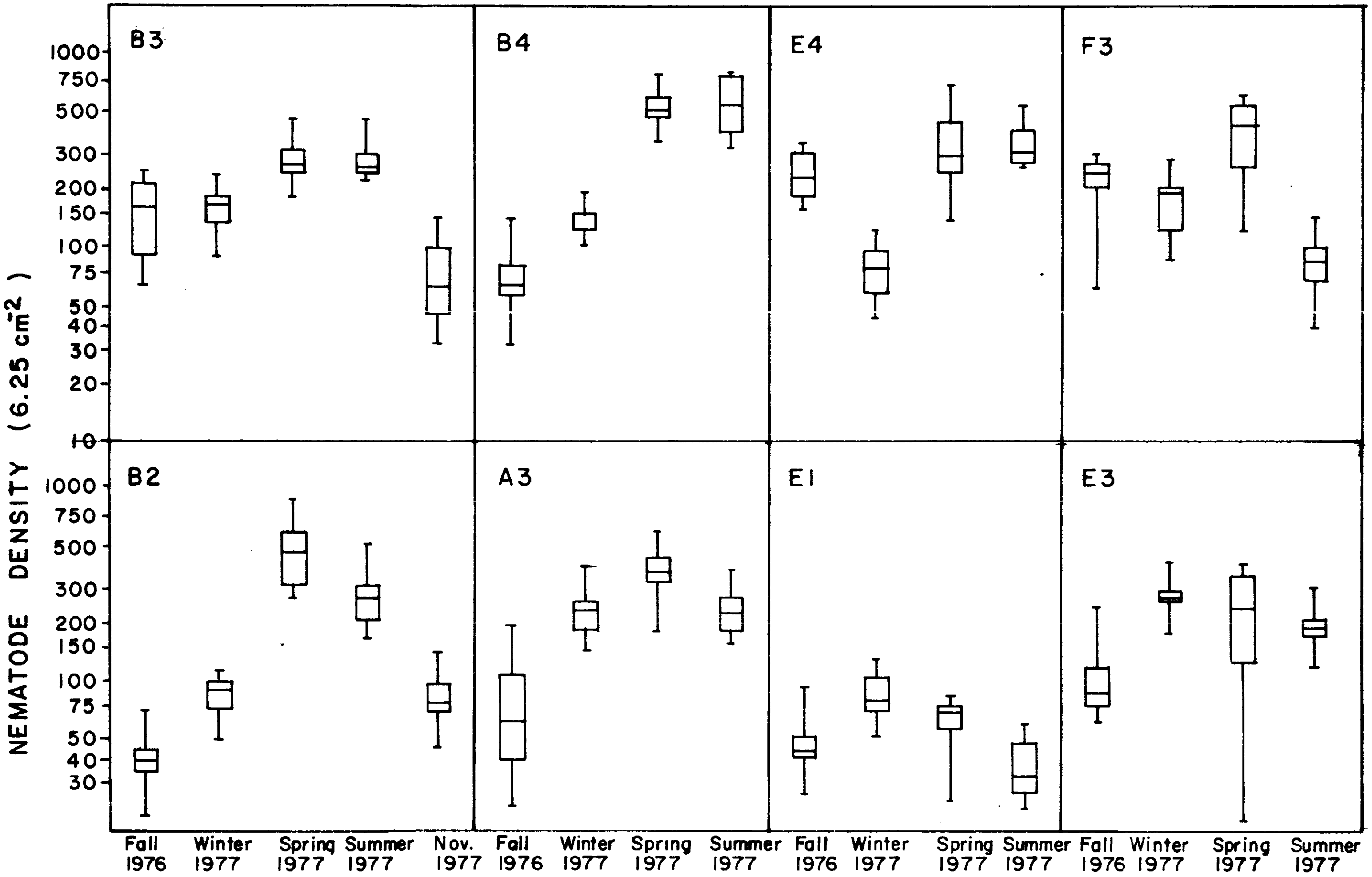


Figure 7-51. Seasonal variability of density of nematodes. Vertical lines represent the range of 9 cores, bars represent the mid-range, and central horizontal lines the median.

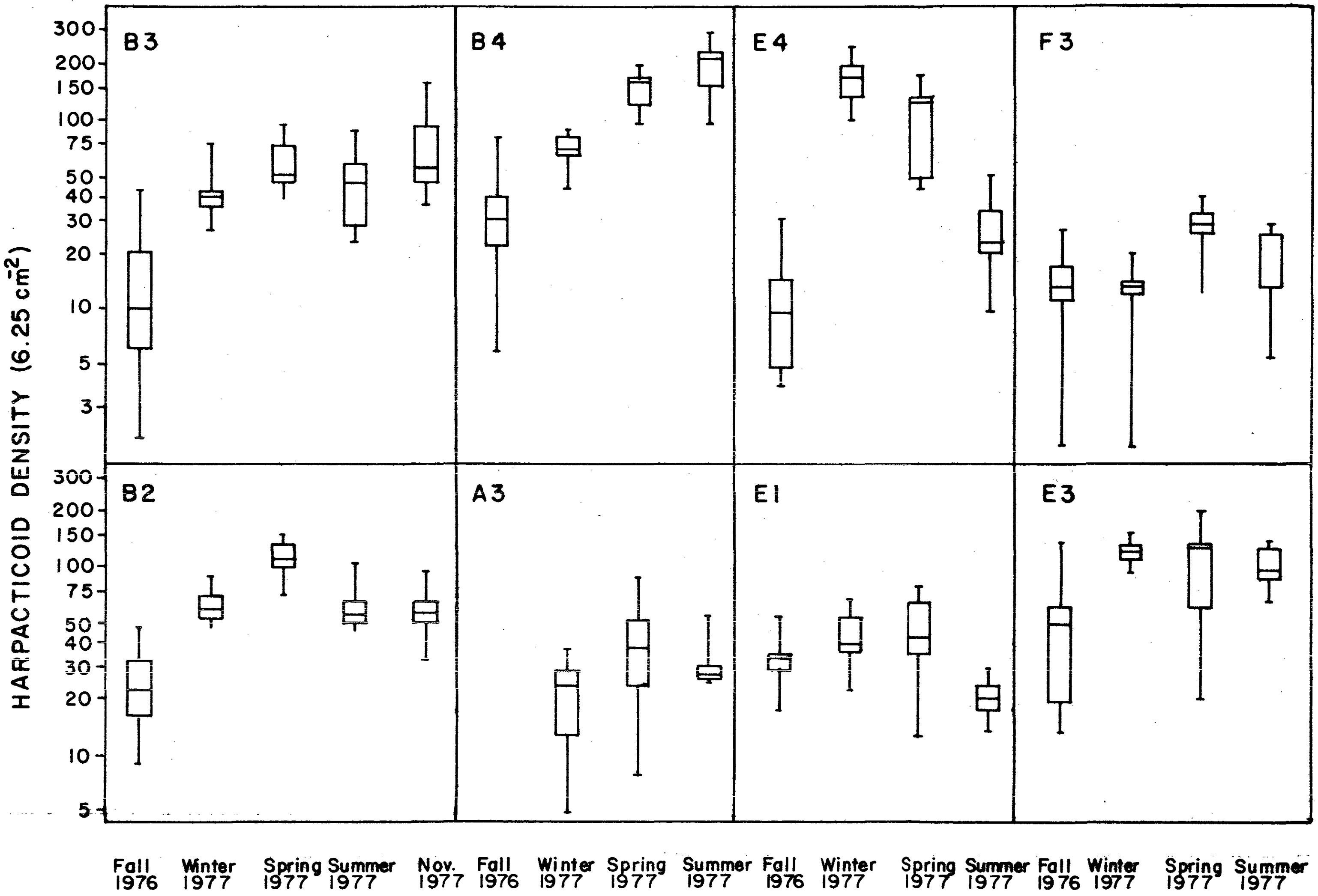


Figure 7-52. Seasonal variability of density of harpacticoid copepods. Vertical lines represent the range of 9 cores, the bars represent the mid-range, and central horizontal lines the median.

DISCUSSION

Delimitation of Major Biotopes

Little quantitative work has been done on the meiobenthos of the Middle Atlantic outer continental shelf, and no comparable work has been done with respect either to seasonal sampling or the effect of mesoscale topography on the meiobenthos. Several previous studies can be used to compare the delimitation of major biotopes (see Introduction). None of these studies provides the definition of the present work because none provides either a measure of small scale variation or of differences with respect to the typical ridge and swale topography of the outer continental shelf.

The distribution of major meiobenthic biotopes on the Middle Atlantic outer continental shelf is primarily a function of sediment composition which in turn is closely related to the ridge and swale topography and the sediment transition at the shelf break (Chapter 5). A number of different analyses indicated that meiobenthos found in topographic depressions was qualitatively and in some cases quantitatively different from that at nearby sites not located in such depressions. The patterns of meiobenthos composition and abundance were highly similar at the swale and shelf-break habitats as opposed to the outer shelf ridge and terrace habitats.

Normal cluster analysis (numerical classification) of total meiofaunal data summed at the phylum and class level showed high similarity values between collections from the outer shelf swale stations B3 and E4, and the shelf break stations A3 and F3. This analysis also showed high similarity values among collections from the coarser sediment ridge and terrace stations B2, B4 and E3, but generally showed collections from Station E1 to be more similar to those from the swale stations B3 and E4. The normal classification of all collections of total meiofauna combined for all seasons corroborates this separation of swale and shelf break collections from ridge and terrace collections. It also indicates that collections during fall 1976 and winter 1977 were highly similar while collections during spring 1977 and summer 1977 were also highly similar to each other but not to the fall and winter collections. Although numbers of organisms in the fall 1976 collections were low, the indicated differences in seasonal similarity were also qualitative. The occurrence of high numbers of Taridigrada, Gastrotricha, Kinorhyncha, and Ostracoda, and low numbers of Turbellaria in the spring and summer 1977 collections differentiate these samples from the fall 1976 and winter 1977 collections.

The patterns of distribution of both harpacticoid copepod species and body types reinforce this initial delimitation of meiobenthic biotopes. All collections were either dominated by or contained large percentages of two species, Stenhelia normani and Enhydrosoma longifurcata. Because of this, qualitative differences between collections were often indicated by the presence or absence of other species of copepods representing specific body or feeding types. The relationship between copepod body type, feeding type, and habitat preference is not clear cut except for the true interstitial forms. Organisms such as *Leptastacus macronyx* and *Leptocaris brevicornis* seem well adapted to navigate the interstitial lacunae and acquire food by scraping sand grains. These animals make up sizable proportions of the copepod fauna only in the ridge and terrace habitats where the larger size of the sand (medium to medium coarse) creates substantial interstitial spaces. Recent work by Marcotte (1977a, b) indicates that the feeding behavior of certain families of copepods important in this study may be inconsistent with their alleged habitat preferences on the basis of body morphology. Two genera of the family Ectinosomidae (*Halectinosoma* sp. and *Pseudobradya* sp.) were found exclusively at the swale and shelf-break stations which exhibited finer sediments and elevated total organic carbon levels.

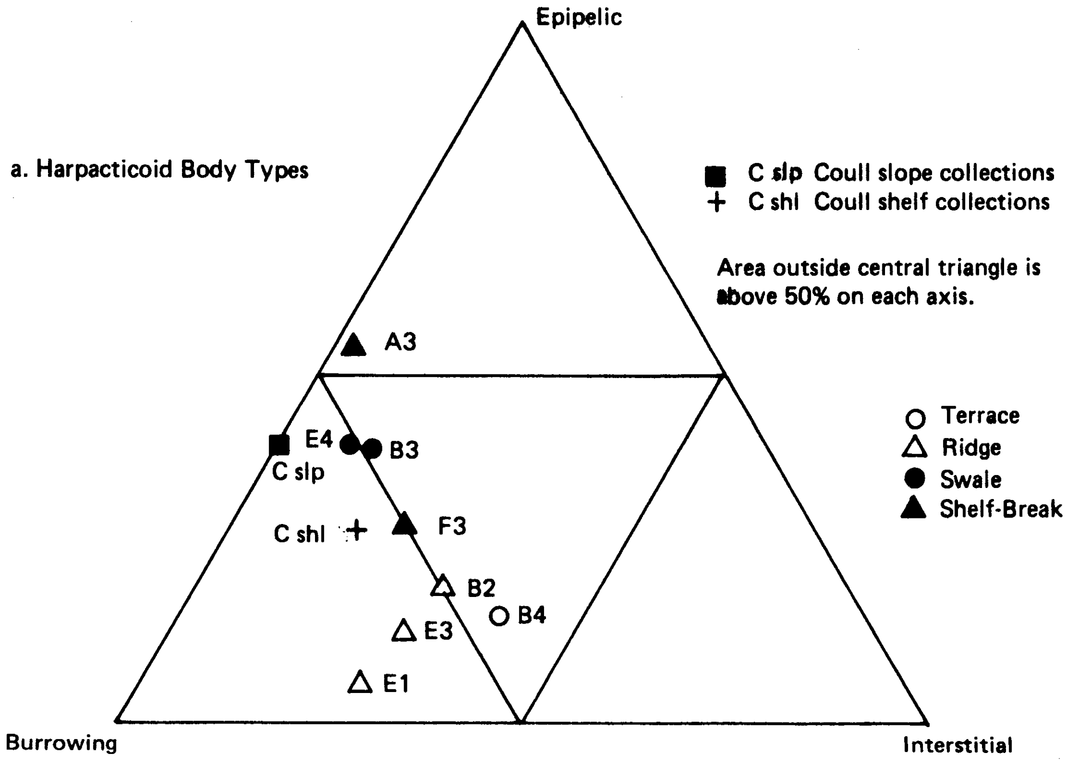
Both species are robust with a greatly expanded cephalo-thorax and have been thought to be strictly burrowing forms (Coull 1977), but Marcotte's work shows that ectinosomids feed by sweeping their antenna over the sediment water interface and then cleaning the antenna with their mouth parts. This feeding strategy is not consistent with a burrowing mode of existence; rather it suggests that these forms are epipelic at the relatively organic rich sediment surface of swale and shelf-break habitats. Diasaccids are small harpacticoid copepods which have also been thought to be burrowing forms; however Marcotte (1977a, b) has shown that they feed by turning balls of detritus in their oral cavity and probably selecting food material from this source. Two diasaccids, *Schizopera carolinensis* and *Amphiascoides debilis*, were characteristic of the swale and shelf-break collections, although other diasaccids were found throughout the collections. It appears as if certain copepods are successful in a variety of sedimentary regimes while others, such as the interstitial forms and the ectinosomids, are more stenotopic with regard to sediment conditions. These more stenotopic forms are responsible for the between habitat differences in harpacticoid assemblages. Interstitial forms are found mostly where the sediment grain size is larger and there is little organic material in the sediments (stations B2, B4, E1, and E3). On the other hand, epipelic forms are primarily found in swales and the shelf-break where sediments are finer and have higher organic content (stations A3, B3, and E4). Deviations from this pattern of species composition can be attributed to specific anomolies in sediment composition. Shelf-break station F3 had a higher overall percent occurrence of the interstitial form *Leptastacus macronyx* (28.25%) than would be expected from comparison with the other shelf-break and swale stations (overall percent occurrence of interstitial forms $\bar{x} = 7.9\%$), except in spring 1977 collections when no interstitial forms occurred at F3. Station F3 consistently had cleaner sands than the other swale and shelf-break stations and a large proportion of the sediment was comprised of medium sand, therefore providing a large amount of interstitial space. In spring

1977, the percent composition of the sediment collected at F3 changed to predominantly fine sand (Chapter 5) closing the interstitial spaces thus obviating the occurrence of interstitial copepods.

This basic pattern is consistent with the data of Coull (1972) on the North Carolina outer continental shelf. Figure 7-53a shows the proportion of harpacticoid body types at all stations from the present study (overall seasons) and from Coull's shelf and slope assemblages. Dominant forms in Coull's slope collections (silty sands, 500-1000 m) were characterized by 40% epipelic and 60% burrowing forms with no interstitial organisms. Coull's shelf collections (medium sands, 20-100 m) were characterized by 27% epipelic, 56% burrowing and 17% interstitial copepods. Coull did not relate differences attributable to shelf topography which is probably less important to animal distribution south of Cape Hatteras but the overall percent composition of harpacticoid body types in his samples is consistent with the patterns shown by the present study.

The examination of the patterns of distribution of both nematode species and feeding types further reinforces the delimitation of meiobenthic biotopes with respect to mesoscale topography. The feeding type classification used in this study is modified from Wieser (1953) as follows: nematodes with no buccal armament were classed as deposit feeders, nematodes with small teeth or buccal projections were classed as epigrowth feeders and nematodes with large teeth were classed as omnivore-predators. Tietjen (1977) has shown, that deposit feeders, which feed only by the sucking power of the esophagus, selectively bacteria over algae. On the other hand, epigrowth feeders, which feed either by 1) scraping food material from larger particles or 2) piercing food objects and ingesting the cell liquid by means of the sucking power of the esophagus, selectively ingested algae over bacteria. Deposit feeders comprised between 65 and 81 percent of all nematodes at the swale and shelf-break stations, while epigrowth feeders comprised 51 to 59 percent of all nematodes at the sandy ridge and terrace stations (Figure 7-53b).

Tietjen (1971, 1976) studied the meiobenthos of the North Carolina outer continental shelf with particular emphasis on the nematode fauna. Proportions of feeding types in his collections are compared to those from the present study in Figure 7-53b. Dominant nematodes in Tietjen's collections from sand were characterized by 54 percent epigrowth feeders, 33 percent deposit feeders and 13 percent omnivore-predators, while nematode collections from his silt-clay stations were characterized by 67 percent deposit feeders, 5 percent epigrowth feeders and 28 percent omnivore-predators. Nematode collections from Tietjen's sandy-silt stations were characterized by 80 percent deposit feeders and 20 percent omnivore-predators. These percentages from Tietjen's collections parallel the pattern of nematode occurrence established in the present study, i.e. that deposit feeding forms dominate in the finer, organically richer sediments of the swale and shelf-break stations while epigrowth



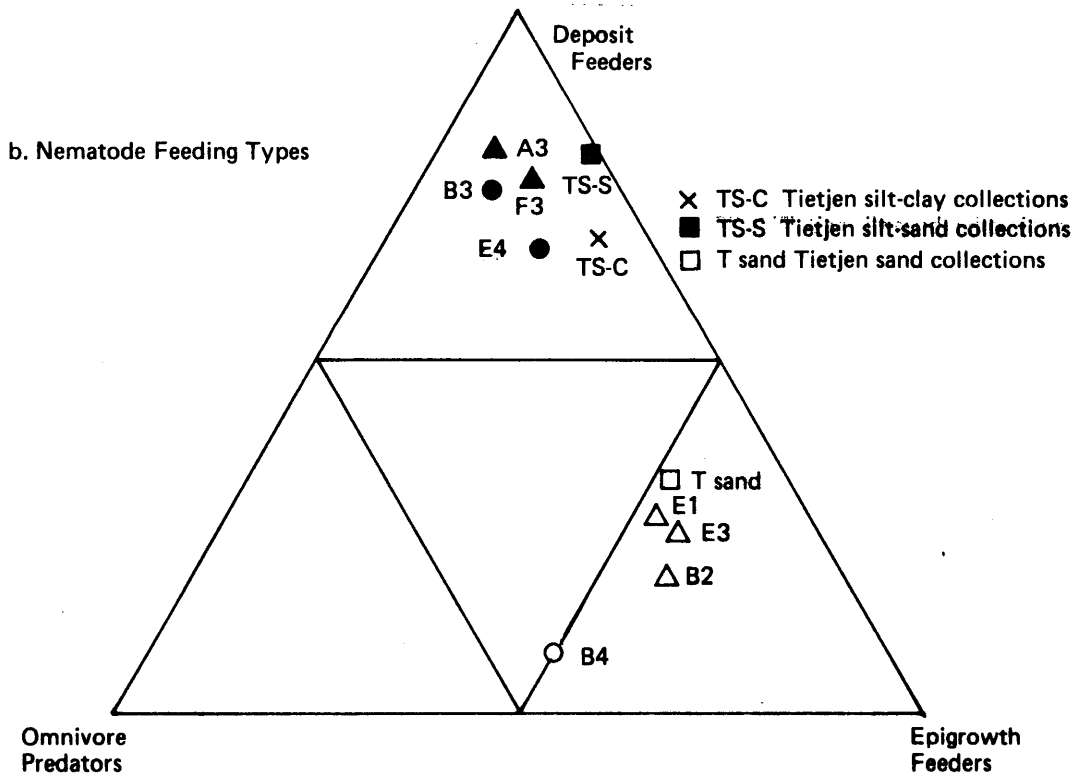


Figure 7-53. Proportional representation of harpacticoid body types and nematode feeding types at stations based on combined seasonal collections.

feeding forms along with omnivore-predators dominate the more dynamic, coarser grained sediments of the ridge and terrace stations.

Partial non-parametric correlation analysis was employed to determine the most important factors in ordering the nematode data from this study along each ordination axis. It was not meant to delineate causal relationships but to preliminarily identify those factors which might be of importance to the nematode fauna. This statistic has not been sufficiently characterized to establish levels of significance at different sample sizes; therefore these values cannot be used to test hypotheses but must simply be taken as indicators of association between independent variables. It seemed clear that the most effective factors relative to the ordination of nematode data along the first axes were factors related to sediment composition. In all cases either median grain size or sorting and either percent sand or percent silt-clay were strongly associated with the first axis. The relationship of abiotic factors to the other axes was less clear. The ordination of spring 1977 collections along both axis 2 and axis 3 seemed to be related to a suite of physico-chemical factors such as temperature, salinity, oxygen, and nitrate. There were few strong associations along these axes in other seasonal collections. There were a number of instances where axes 2 and 3 were expended in separating organisms which occurred exclusively at a specific station. It may be that these instances reflect biological habitat preferences which are not indicated in the partial correlation analysis.

Spatial and Temporal Variability

Arlt (1973) determined patch size of various meiofaunal taxa including nematodes and harpacticoids from samples taken in the very shallow, sandy Greifswalder Bodden (Baltic Sea). Arlt sampled a 40 x 40 cm sampling grid (1600 cm^2) from which he removed 64 one-cm^2 samples. His description of small scale spatial variability was based on only a 4% coverage of the initial grid with non-contiguous samples. This makes his estimates of patch size somewhat suspect. Arlt's data suggest that the typical nematode patch size was about 90 cm^2 and the harpacticoid copepod patch size was about 56 cm^2.

Data from this study indicate that nematode patch size varied between 18.75 cm^2 and 37.5 cm^2 ($\bar{x}$ = 26.3 cm^2) and that harpacticoid patch size varied between 18.75 cm^2 and 31.25 cm^2 ($\bar{x}$ = 26.1 cm^2). Neither taxon showed apparent differences in patch size related to mesoscale topography.

Coull et al. (1977) reported on quantitative estimates of meiofauna from deep sea samples (400-4000 m). On the basis of an analysis of variance of within versus between-sample variation, they concluded that within habitat meiofaunal density was constant over large areas but that small scale variation (patchiness) is expressed at the level of small subsamples (10 cm^2). Data from the present study also suggest that distributional patterns of nematodes and harpacticoids are highly contagious at the level of the 6.25 cm^2 subsamples, but that densities of these taxa over larger areas are more homogeneous.

Juario (1975) studied the nematode fauna of the German Bight (near the mouths of the Elbe and Weser rivers) for a 13 month period during 1972-1973. The habitat was sampled in 35 m of water and was characterized by fine sand with a silt-clay content of about 25 percent. Juario could demonstrate no statistically significant seasonal differences in nematode abundance, although his data appeared to show peaks in April and August. There was an evident shift of dominant species between the April and August "peaks", but this shift was between species in the same dominant genera. Warwick and Buchanan (1971) also failed to find significant seasonal variation in the nematode population off the Northumberland coast (U.K.).

Data from the present study indicate that total meiofauna and nematode density generally increased from fall 1976 to reach a peak in spring 1977 and fell off slightly in summer 1977. Limited data available for fall 1977 showed a large drop in the density of total meiofauna and nematodes from the summer levels. This seasonal variation was generally statistically significant (i.e. between sample variability was less than between season variability). Subtidal samples from Banyuls-sur-Mer (Mediterranean) indicated that nematode densities were 2.5 times higher in the summer (or autumn) than in winter (Soyer 1971), and shallow subtidal samples from the Baltic also indicated a summer peak in nematode density 2.5 times higher than winter levels (Elmgren 1973).

Information from previous work is ambiguous with regard to meiofaunal temporal variation. Some studies in shallow water showed significant seasonal variation while others in similar areas did not. It appears that significantly concordant seasonal patterns exist in meiofaunal densities on the Middle Atlantic outer continental shelf and that these seasonal patterns are characterized by shifts both quantitatively in densities and also qualitatively in the make-up of dominant fauna from collections during each season. This is in marked contrast to the macrobenthos which shows an amazing lack of seasonality (Chapter 6). This may be related to seasonal supply of food to the benthos and differences in the feeding biology and life history characteristics between macrobenthos and meiobenthos. The main source of organic matter in the Middle Atlantic Bight is phytoplankton production on which all the benthos essentially depends. Phytoplankton production is seasonally variable with a maximum in spring (Ryther and Yensch 1958). A portion of this production sinks to the bottom where it sustains bacterial production, which in turn supports deposit feeding animals. This bacterial response to enrichment is probably fairly rapid and the meiobenthos which has shorter generation times may be able to respond to this enrichment with population increases until the resources are depleted or the meiofaunal populations are limited by predation by the fall season. The macrobenthos must rely on longer generation times and more complicated life histories many of which include planktonic development. Thus, the macrobenthos cannot respond with population increase within this seasonal time frame. Rather, the macrobenthos populations may be continuously regulated by predation and competition (Chapter 6).

Community Structure

Community structure is here taken to be reflected by the suite of indices and ratios, such as diversity and faunal ratios, that are used to characterize collections of organisms for comparative purposes. Tietjen (1971, 1975) computed Shannon-Weaver diversity (H') for assemblages of nematodes from the North Carolina outer continental shelf and delineated four sedimentary environments along a depth gradient of 50 to 2500 m, of which the sand zone (50 to 500 m) corresponds most closely to the habitats sampled from the present study. Diversity of nematodes in Tietjen's sand zone ranged from 2.88 (500 m) to 3.48 (50 m) bits/individual with J' evenness values of 0.95 and 0.91, respectively. Diversity decreased along the depth gradient which Tietjen attributed to the fewer number of microhabitats at the deeper stations, although environmental predictability also seemed to be a factor. Diversity of nematodes from this study ranged from 2.47 to 3.65 bits/individual with J' evenness values of 0.78 and 0.89, respectively. No difference in diversity values could be demonstrated between swale and shelf-break stations as opposed to ridge and terrace stations. It is difficult to interpret this finding in light of Tietjen's conclusions because 1) Tietjen did not take mesoscale topography into account and 2) Tietjen's material was taken from unreplicated samples at a small number of stations. Diversity values from the two studies are similar although Tietjen's samples had higher evenness. Species richness (S-1/ln N, where S is the number of species and N the number of individuals) in Tietjen's samples ranged from 5.59 (500 m) to 9.47 (50 m) while in the present study this index ranged from 1.3 to 2.5. Clearly, Tietjen's samples contained higher numbers of species and had a more even composition between species and individuals than the samples from the Middle Atlantic outer continental shelf. This difference in species richness was largely due to the more complete identification of all nematode species by Tietjen, while just dominant species were determined in this study, mostly just to genus. The Middle Atlantic outer continental shelf samples, however, demonstrated higher meiofaunal densities ranging from 56 to 859 nematodes/10 cm^2 as opposed to 0.6 to 10.4 nematodes/10 cm^2 from Tietjen's samples.

Coull (1972) computed H' species diversity for samples of harpacticoid copepods from the North Carolina shelf and slope. His stations were located in medium sands at depths of 20 to 100 m. No allowance was made for mesoscale topographic variation. Diversity values in Coull's collections range from 1.19 (J = 0.42) to 3.47 bits/individual (J = 0.76). Diversity values for harpacticoids in the present study ranged from 0.2 (J' = 0.13) to 3.2 (J' = 0.96) for swale and shelf-break collections and 1.7 (J' = 0.85) to 3.7 (J' = 0.99) for ridge and terrace collections. Harpacticoid diversity in this study was significantly lower in the swale and shelf-break stations, but except for two collections with very low diversity values (A3, fall 1976, and B3, fall 1976), values from both studies seemed to be equivalent.

Coull's values show an increase in diversity with depth which he attributes to the greater environmental predictability of deeper habitats. Data from this study indicate that even though sediments at the swale and shelf-break stations are more similar to the deeper stations in Coull's work, harpacticoid diversity is significantly lower than at Coull's deeper stations. This seems to indicate that topography and sediment dynamics are important influences on harpacticoid diversity on the outer shelf while stability and predictibility may be more influential in deeper habitats.

Harpacticoid/nematode ratios were computed from data taken from several other studies of meiobenthos on the Middle Atlantic continental shelf (Table 7-14). These ratios show that harpacticoids copepods occur in relatively large numbers in coarse sediments but that in fine sediments nematodes may have densities of one order of magnitude or more greater than that of harpacticoids.

Relationship of Meiobenthos to Environmental Factors

Sediment composition was clearly the most important measured environmental factor in influencing patterns of occurrence of meiobenthos. Many previous studies have reached the same conclusion. Gerlach (1953, 1958) concluded that the species composition of nematodes in the Baltic sea was dependent on sediment grain size, stability of the habitat and the amount of organic material available. Warwick and Buchanan (1970) and Tietjen (1971, 1976) have reached the same conclusions for nematode populations in the North Sea and the South Atlantic continental shelf. Coull (1972) has characterized meiobenthic copepod populations with the same criteria from the South Atlantic OCS.

In the present study, changes in sediment composition could often explain anomalies in the described patterns of distribution. For example, the dominance of harpacticoid copepods in the winter 1977 samples at swale station E4 coincided with a very high percentage of gravel in the sediment during that season; also the absence of interstitial harpacticoids at shelf-break station F3 during spring 1977 coincided with an atypically high percentage of fine sand which filled the interstitial spaces. The partial correlation analysis of

Table 7-14. Harpacticoid/Nematode ratios of collections from the Middle Atlantic continental shelf.

Collection	Gravel	Sand	Ridge & Terrace	Shelf-break Swale	Silt/Clay
Wigley & MacIntyre (1964)	0.09	0.1			0.003
Tietjen (1971)		0.22			
		0.19			0.04
Present Study			0.54	0.14	

environmental factors with respect to the ordination of nematode collections again indicated that sediment composition was consistently and strongly related to the distribution of nematode species.

Relationships of the meiobenthos with factors other than those related to sediments is less clear. Jansson (1967a and 1967b) evaluated the importance of temperature, salinity, and oxygen for the interstitial fauna of sandy beaches and concluded that oxygen was a limiting factor while temperature and salinity seemed less influential. Little work has been done to pinpoint the importance of non-sedimentary factors for meiofaunal distribution in subtidal populations. Tietjen (1977) studied nematode populations in Long Island Sound with respect to highly "impacted" areas near New York City and concluded that there was no demonstrable relationship between nematode density or species diversity and sediment with heavy metal or organic carbon concentrations. His data indicated, however, that nematode density was significantly higher (Mann-Whitney test $\alpha > 0.01$, T = 77, range = 14-66) in areas with high heavy metal concentrations so it is not clear that his conclusion can be supported.

Data from the present study indicate that the distribution of meiofauna and particularly harpacticoid copepods somewhat correlated with the distribution of salinity and dissolved oxygen in bottom water. Harpacticoid occurrence showed a correlation of 0.61 with salinity and a correlation of 0.58 with dissolved oxygen over the course of the sampling period. This apparent relationship is a result of the harpacticoids being relatively more abundant in the shallower areas with coarser sediments, rather than any direct effect of salinity or dissolved oxygen.

Relationship of Meiobenthos to Other Benthos

It is clear that the meiobenthos does not exist in a vacuum, but must be viewed in the larger context of the benthos as a whole. To this end a series of analyses was carried out to try to determine interrelationships between the meiofauna and both microbial (bacteria and foraminifera) and macrofaunal elements of the benthos. A partial correlation analysis was carried out between density of meiobenthos and density of bacteria determined by indirect counts (Figures 7-54 and 7-55). This analysis indicated that total density of meiobenthos was positively associated with density of heterotrophic bacteria. Nematode density was most strongly correlated to heterotroph density (range -0.31-0.86, $\bar{x} = 0.43$). This is consistent with the high dominance of deposit feeding nematodes in fine sediments which also support greater bacterial numbers. Tietjen and Lee (1977) have shown that bacteria make up an important portion of the food of deposit feeding nematodes as opposed to epigrowth feeding forms.

Density of meiobenthos was, on the other hand, somewhat negatively correlated with density of hydrocarbonoclastic bacteria.

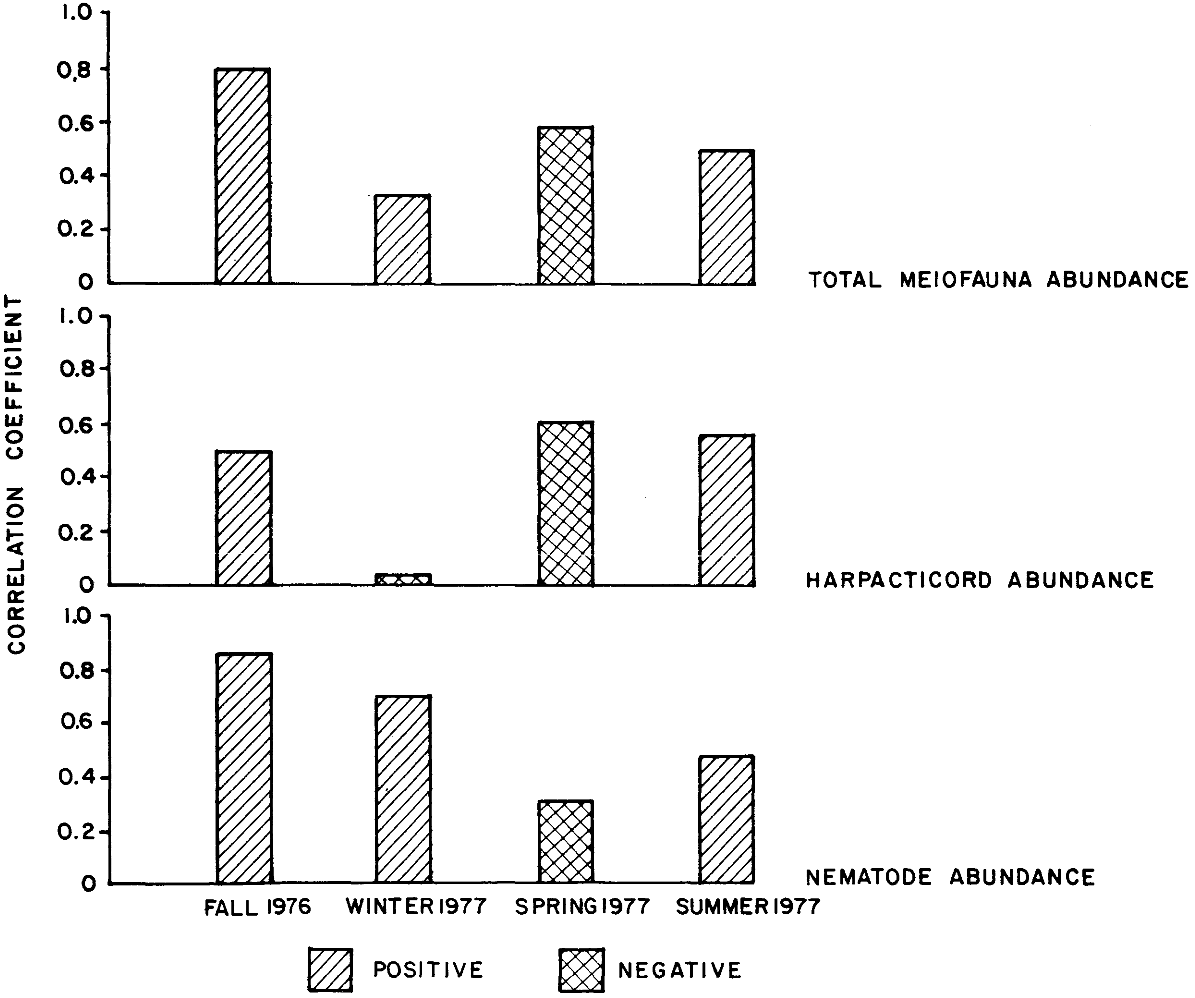


Figure 7-54. Partial correlation coefficients of density of meiobenthos related to abundance of total heterotrophic bacteria.

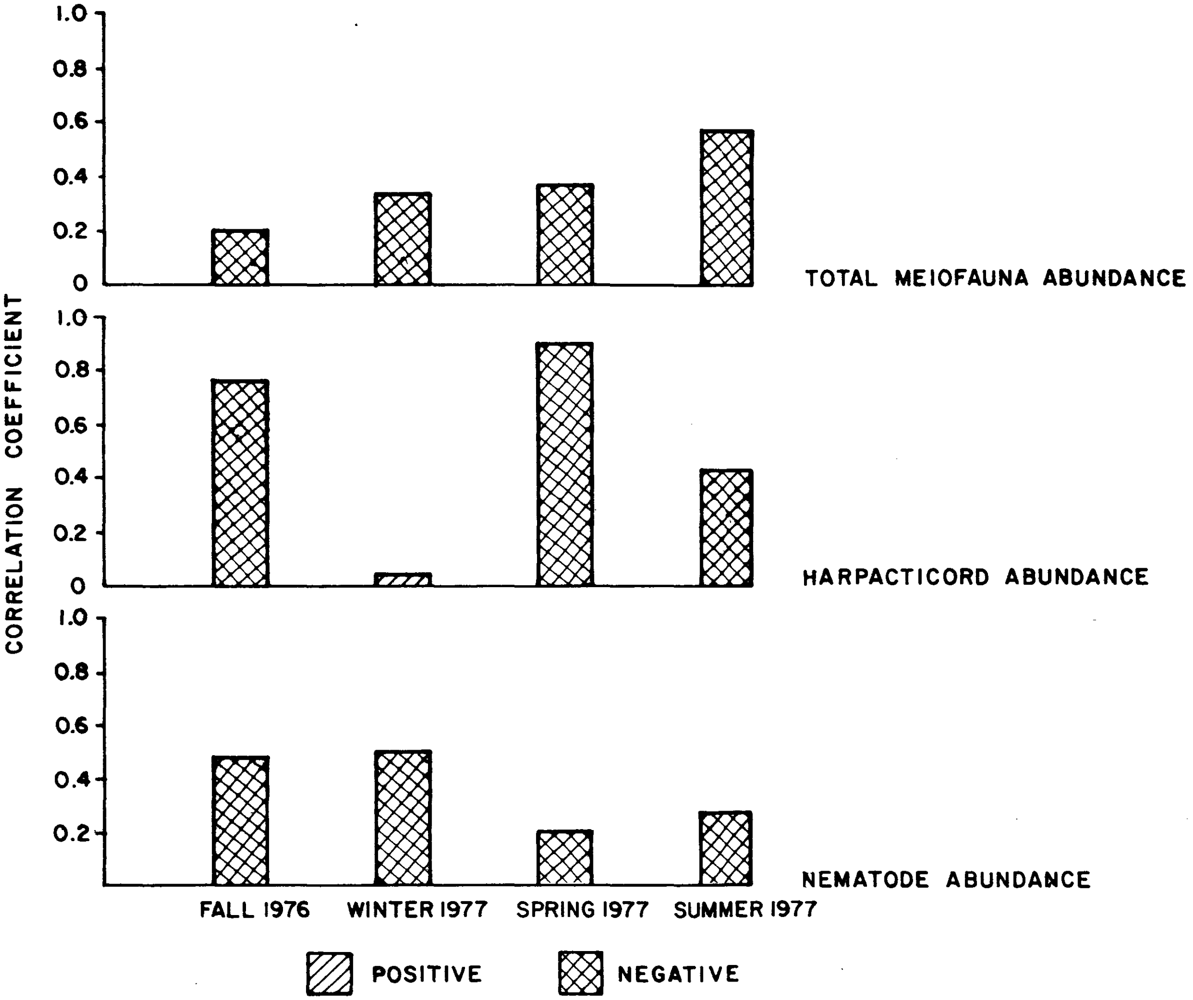


Figure 7-55. Partial correlation coefficients of density of meiobenthos related to abundance of hydrocarbonoclastic bacteria.

Harpacticoid copepod density was most negatively correlated with hydrocarbonoclastic bacterial density (range 0.04 to -0.09, $\bar{x} = -0.51$ <0.01).

Buchanan and Hedley (1960) have shown that the large foraminiferan *Astrorhiza limicola* is an active predator on meiofauna, specifically nematodes and harpacticoid copepods. *Astrorhiza limicola* occurs abundantly in the study area, but this large arenaceous form was sampled only by the small biological trawl and anchor dredge used in the study of megabenthos (Chapter 6). This made it very difficult to compare the density of this foraminiferan with the density of meiobenthos, however a partial correlation analysis was carried out between density of meiobenthos and the density of total foraminifera and the density of *Rheophax* spp., another dominant agglutinate species. There were few consistent correlations indicated by this analysis, and those that were more basically related to sediment composition, e.g. harpacticoids were negatively correlated with *Rheophax* density (range -0.025 to -0.76, $\bar{x} = 0.16$) but *Reophax* had its highest densities in swales and finer sediments where the harpacticoids occurred in low relative densities.

The relationship of the meiobenthos to the macrobenthos is poorly documented. Until this time it has been unclear whether these two size categories are generally interrelated by trophic and energy dynamics and whether they respond to common-environmental factors or whether they operate independently (Coull 1973). It is clear from the present study that species distributions of both meio- and macrobenthos were greatly influenced by variations in mesoscale topography of the Middle Atlantic outer continental shelf (Chapter 6). Interstitial macrofaunal feeders, such as the small polychaetes *Goniadella gracilis* and *Lumbrinerides acuta*, occur in the more dynamic coarser sediment habitats of the ridge and terrace stations. These are the only areas where true interstitial meiofauna occur. The swales and shelf-break areas are dominated by surface and deeper deposit feeding macrofauna, and these are the only areas that epipelic meiofauna occur in large numbers. Although it has not been shown that a trophic relationship exists between meio- and macrobenthos on the Middle Atlantic outer continental shelf, both groups appear to react to similar factors in terms of sediment composition. Although this correspondence primarily reflects concommitant adaptation to the nature of resources and sediment microhabitats, the trends do suggest trophic interaction among meiobenthos and macrobenthos.

Usefulness of Meiobenthos in Impact Assessment

The distribution and abundance of meiobenthos on the Middle Atlantic outer continental shelf show distinct patterns with respect to mesoscale topography, sediment composition, and physico-chemical factors related to depth such as salinity and dissolved oxygen concentration. Meiobenthic community structure also shows characteristic patterns with respect to these same factors. Many of these patterns were statistically significant and consistent. Anomalies in these patterns can often be correlated to anomalies of sedimentary or physico-chemical factors. This indicates that there is a causal relationship on some level between these factors and the meiobenthos. Further it suggests that small changes in the sedimentary and environmental factors due to environmental impact will be reflected by changes in the community structure of the meiobenthos.

Pequegnat (1975) has suggested that meiofauna, because of their relatively fast generation times, general absence of pelagic larvae, and potential competitive advantage over macrofauna, would respond more quickly than macrofauna to environmental perturbations. Furthermore, the consistent differences in the composition and structure of the meiobenthos communities between habitats demonstrated here lends confidence in one's ability to detect changes in these communities. Although compromised by the sampling problems caused by the relationship of meiofauna distribution to microhabitats and the probably greater resilience of meiofauna than macrofauna following perturbation, we believe that the meiobenthos may serve as useful indicators of the impacts of man's activities on the continental shelf sea bed.

In particular, it seems important to continue to monitor those depositional areas (swales) in the area of offshore oil exploration and production. These swale habitats would probably be affected by impacts from offshore activities most directly because they would be the repository of sediment accumulated pollutants. Thus, it is suggested that monitoring of meiobenthos in these swale habitats would give an early indication of impact from offshore exploration and production activities.

Significant Findings

1. The distribution, abundance, and community structure of meiobenthos was highly related to the characteristic mesoscale topography of the Middle Atlantic outer continental shelf.

2. Deposit feeding nematodes dominated the finer, more organically rich sediments of swales and the shelf-break while epigrowth feeding nematodes dominated the sandier, more dynamic sediments of ridges and terraces.

3. Epipelic harpacticoid copepods were an important component of the meiofauna in swales and the shelf-break, while interstitial harpacticoid copepods were important on ridges and terraces.

4. Concordant seasonal fluctuations were observed in abundance at most stations. Meiofaunal density increased to a peak in spring 1977 and dropped slightly in summer 1977. The pattern of low fall

densities was further corroborated by samples taken in November 1977.

5. All components of the meiofauna had contagious distributions at the level of the 56.25 cm^2 and 6.25 cm^2 subsamples, but density seemed constant over larger areas within similar habitats.

6. Sediment composition was the most important environmental factor in establishing the relationships of nematode assemblages.

7. The distribution and abundance of copepods were related to sediment composition and to depth related factors.

8. Meiobenthos of depositional (swale) habitats should be more susceptible to environmental impact due to petroleum exploration and production activities than that of the more dynamic ridge habitats. This conclusion may be drawn based on the inferred greater frequency of disturbance and thus higher resilience of the fauna in ridge habitats and in the greater probability of deposition of fine sediments in swales. These swale habitats should be monitored for any early indication of impact.

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Many investigators of meiofauna made suggestions during the course of this work which were incorporated into this report. They include Drs. Rheinhard Rieger and Edward Ruppert, University of North Carolina, Chapel Hill, NC; Dr. Bruce Coull, Belle Baruch Institute, University of South Carolina, Columbia, SC; Dr. Lee Pollock, Drew University, Madison, NJ; and Dr. William Hummon, Ohio University, Athens, OH.

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APPENDIX 7-A

Numbers of Individuals of Meiobenthic Taxa Collected in Nine 6.25 cm^2 (56.25 cm^2) Cores by Station and Season

Table 7A-1. Fall 1976

Taxon	Stations A3	B2	B3	B4	E1	E3	E4	F3
Nematoda								
Odontophora	16		33					51
Tershellinga	67		330				758	136
Paramonohystera	24		291					218
Theristus	41							145
Sabatieria sp.1	474		264			17	419	859
Sabatieria chitwoodi	61							
Biarmifer	4	22	10	51				
Oncholaimus	3		4	176				18
Leptolaimus		21						
Rhynconema		9				57		99
Xyala		11	3	9	39			
Microlaimus		166	7	185	75	341		247
Desmodora		49	34	17	58	271		42
Ceramonema		11						
Actinonema		19			52	36		
Paracyatholaimus		12						
Tricoma		11			121	120	3	56
Tricoma absidata		17						
Anticoma		9	36				47	131
Mesacanthion		18	2	115	17	33	168	49
unknown #1		12					198	
Araeolaimus			35					
Diplopeltis			13					
Disconema			23					
Sabatieria sp. 2			64					31
Ascolaimus			9					
Latronema			129					
Porocoma			14			25	49	
unknown #2			39					
Epsilonamatidae					40	41		
Neotonchus							262	
Choniolaimus							139	
Halalaimus							49	
Harpacticoida								

Table 7A-1. (concluded)

Taxon	Station A3	B2	B3	B4	E1	E3	E4	F3
Stenhelia normani	3	61	83	56	64	14	30	4
Enhydrosoma longifurcata	1	85	45	75	113	91	19	
Robertgurneya rostrata			15				31	
Leptastacus macronyx		8				91		37
Leptocaris brevicornis		58		122	95	87		
Phyllopodosyllus (p.) carolinensis						65		
Apodopsyllus		10	4	25	17	78		
Amphiascus minutus				32	22	36		3
Schizopera carolinensis						26	10	58
Diarthrodes							17	
Nitocra typica						3		
Halectinosoma								16
								24
Others								
Ostracoda		50	9	101		3	8	9
Mollusca	3	9	3	36		6	6	3
Turbellaria	2	3	14	81		20	10	
Amphipoda	1	1	31	1		35	6	
Kinorhyncha	1		2			7	7	
Polychaeta	153	157	120			60	50	324
Oligochaeta	2					1		2
Decapod larvae		46	13	62			13	44
Other	62	109	138	217	458	96	1053	217
Eggs	74							
Cumacea			4					
Sipuncula			1					
Tardigrada			1					
Archiannelida				3			3	
Isopoda								1

Table 7A-2. Winter 1977.

Taxon	Stations							
	A3	B2	B3	B4	E1	E3	E4	F3
Nematoda								
Sabatieria	236		245			65	34	789
Sabatieria chitwoodi	59		127				57	
Theristus	229		371					
Oncholaimus	55					148		32
Tershellinga	730		20			33	29	185
Tershellinga sp. 1	15							
Halalaimus	81		74				11	43
unknown #1	57				7			
Biarmifer	103							
Tricoma absidata	101	95				135		
Desmoscolex	22				29	168		
Paramonohystera	83	19	54				12	
Latronema	197		73	145	60	176	88	28
Rhynconema	20				32	89		40
Desmoscolex californicus	37							
Quadricoma	8							
Ceramonema	4		99	73				
unknown #2	14							
Choniolaimus	13				6			41
Microlaimus		329	42	164	73	197	73	
Viscosia		76	159	335	72	425	39	128
Mesacanthoides		108		100	51	116		
Paramonohystera ellipticus		15						
Halichoanolaimus		85	41	73	128			
Enoplidae		13						
Porocoma		23						
Ascolaimus			50		85			
Tricoma			79		59		34	55
Paracyatholaimus			37	16	14	31		
unknown #3			11					
Monoposthia mirabilis				111				
Microlaimus kauri				114	57	148	50	
Southernia				24		31	174	
Desmodora				37	24		5	13
Xyala					14			

Table 7A-2. (continued)

Taxon	Station							
	A3	B2	B3	B4	E1	E3	E4	F3
Sphaerolaimus					11			
Anticoma					8			
Monoposthia						468	72	
Odontophora						26	32	82
Epsilonematidae						35		
Chromadora						61	26	
Didelta						10		
Desmoscolecidae							6	
Chromaspirina								146
Actinonema								58
Harpacticoida								
Stenhelia normani	122	164	174	149	27	53		
Enhydrosoma longifurcata	132	220	91	190	184	529		
Phyllopodopsyllus (p.) carolinensis	23							
Leptocaris brevicornis	21	150		169	96	188		
Mesochra pygmaea	72							6
Halectinosoma	8		23				431	23
Apodopsyllus		25	38	17	17		353	
Leptastacus macronyx		15					186	35
Robertgurneya rostrata			43					
Amphiascus minutus				61	31	129	194	4
Ameira					34		415	
Schizopera carolinensis						83		66
Amphiascoides debilis						121		
Psuedobradya							61	
Others								
Mollusca	5	14	12	16	12	11	31	2
Ostracoda	20	299	106	207	214	683	205	8
Kinorhyncha	20	12	19	5		76	2	3
Turbellaria	2	112	27	218	34	99	32	
Gastrotricha		4	1	1	4	61	4	3
Polychaeta	91	162	105	69	148	248	117	107
Larvae	58	304	213	419	243	654	364	56
Tardigrada		12		17		5	6	

Table 7A-2. (concluded)

Taxon	Stations A3	 B2	 B3	 B4	 E1	 E3	 E4	 F3
Other	30	45	36	38	119	104	43	34
Cnidaria		1						1
Arachnida	1					1		
Isopoda							1	
							11	

Table 7A-3. Spring 1977

Taxon	Stations A3	B2	B3	B4	E1	E3	E4	F3
Nematoda								
Chromadora	241	626	361	460	7		7	446
Theristus	101	60	207	184	44	119	933	1087
Paramonohystera	247		129				516	547
Halalaimus	9	17	32					62
Tershellinga	298	166	381			2		418
Desmoscolex	36	98	170				2	68
Viscosia	100	271	144	106	4	13	52	62
Ceramonema	114		83	680		4	92	83
Sabatieria chitwoodi	224		98					331
Choniolaimus	72	49					29	30
Monoposthia	373	273	43	1672	19	80	67	108
Sabateira	1383	177	687				65	
Southernia	36				76			
Euchromadora	52							
Rhynconema		154				140	135	133
Mesacanthion		48		909	37	245	390	34
Microlaimus		1517	193	97	167	452		
Latronema		559	67	783				
Didelta		111						
Araeolaimus		117						
Oncholaimus		52		36				
Odontophora			41		12	192	311	47
Anticoma					5		29	
Tricoma absidata					50	228	292	
Microlaimus kauri					43	13		
Halichoanolaimus						70	112	
Sphaerolaimus						20		175
Ascolaimus						9		
unknown #1						19		
Epsilonematidae						219		
Paracyatholaimus						58	79	
Desmoscolex californicus							149	
Tricoma pellucida								47
Quadricoma								42

Table 7A-3. (concluded)

Taxon	Station A3	B2	B3	B4	E1	E3	E4	F3
Harpacticoida								
Stenhelia normani	170	45	73			15		56
Enhydrosoma longifurcata	56	174	73		35	125		
Leptocaris brevicornis		227		270	63	152		29
Mesochra pygmaea		79	108	94	61			
Amphiascus minutus		136	77			137	114	16
Leptastacus macronyx		62		134	22	84	82	5
Ameira	49	77		244		53	212	120
Cletodes		187		206		244		
Heterolaophonte		27		200	12			
Schizopera carolinensis	25		99			77		
Diarthrodes			67					
Halectinosoma	92						254	
Apodopsyllus				287		113	262	
Phyllopodopsyllus (p.) carolinensis					12	56		
Robertgurneya rostrata					171			34
Amphiascoides					17			
Pseudobradya							43	
Others								
Ostracoda	21	419	84	626	85	314	178	12
Tardigrada		30		22	1	14		
Kinorhyncha	13	10	11	6	1	49	32	4
Polychaeta	50	222	109	127	40	85	124	52
Mollusca	2	40	16	17	10	22	19	
Larvae	130	918	153	772	212	520	254	91
Cnidaria		4						
Gastrotricha	3	177	7	389	30	182	21	11
Turbellaria		1	4	18	10	2		1
Other	5	90	39	117	10	29	48	71
Eggs	11	187		5338	79	788	32	543
Arachnida		8	1	4		1	2	2
Archiannelida		4				1		
Amphipoda			1					

Table 7A-4. Summer 1977

Taxon	Stations							
	A3	B2	B3	B4	E1	E3	E4	F3
Nematoda								
Desmodora	36	119	13	1374	10	244	39	
Viscosia	65	323	175	848	15	87	5	66
Theristus	268	437	464	97	12	57	427	126
Monoposthia	129	850	332	28	17	92	168	27
Sabatieria chitwoodi	295	61	894			70	137	36
Hypodontolaimus	232	178	134	557	11	19	185	12
Sabatieria	432	25	83		12	20	7	263
Latronema	45	51	177	65	5	39	11	40
Halalaimus	65	26	44				9	
Odontophora	100	29			21		335	21
Gammanema	42						3	22
Tershellinga	296			21		51	138	99
Halichoanolaimus	60							
Microlaimus	13	193	13	1405	67	394		49
Mesacanthion	9	49	17	138	21	50	181	43
Anticoma	8		157			25	91	
Didelta	12			45	29		66	46
Ceramonema	7		19				4	
Choniolaimus		27						
Euchromadora		100		411	81	65	7	
Rhynconema		47		89		11		
Desmoscolex		29				103	52	
Tricoma pellucida		32			14	167		
Ascolaimus			26				15	
Araeolaimus			44					
Epsilonemotidae			8			276	11	
Cobbia				198		92	5	
Tricoma				17				
Actinonema				48			111	
Harpacticoida								
Enhydrosoma longifurcata	57		6	214	94	113	82	
Schizopera carolinensis	80		41	232		44	32	
Apodopsyllus	35				12			
Halectinosoma	91						17	

Table 7A-4. (concluded)

Taxon	Station A3	B2	B3	B4	E1	E3	E4	F3
Amphiascoides debilis	8							
Stenhelia normani		33	36		43	166	19	
Leptocaris brevicornis		222	72	605	50	254	12	
Robtgurneya rostrata		72						
Amphiascus minutes		89	45	188	5	133	50	
Leptastacus macronyx		86	36			172	34	
Ameira		239		753				
Pseudobradya			18					
Nitocra typica			23			28		
Cletodes				28		79		
Others								
Ostracoda	7	288	128	819	12	337	42	16
Tardigrada		11		35	1	34	1	2
Kinorhyncha	5	5	16	23	4	39	4	1
Polychaeta	35	259	114	240	58	219	66	55
Mollusca		22	22	7		4	8	1
Larvae	58	304	99	297	76	665	143	10
Gastrotricha	3	173	25	281	54	327	30	9
Other	17	86	40	41		17	24	2
Eggs	37	200	72	799	16	270	51	
Arachnida		1				1	2	
Archiannelida						1		
Amphipoda		1						1
Turbellaria						1		
Cnidaria						1		

APPENDIX 7-B

Microdistribution Maps of Harpacticoid and Nematode Abundances

Fall 1976

A3

0/106	2/106	0/186
0/38	0/38	0/53
10/22	1/89	1/61

0.02

B2

16/32	9/20	33/44
22/34	33/64	16/35
19/39	45/69	29/44

0.57

B3

44/180	20/237	7/121
10/89	17/209	4/79
38/209	6/159	2/62

0.10

B4

31/62	6/32	22/57
30/77	20/45	41/64
37/107	42/81	83/143

0.44

E1

35/41	36/39	35/42
29/50	19/32	55/88
28/25	38/55	35/47

0.77

E3

20/59	58/84	34/84
14/68	65/112	61/114
16/71	74/124	142/229

0.47

E4

4/169	5/288	5/233
12/223	15/311	10/349
13/185	18/163	25/307

0.05

F3

14/208	13/248	21/256
12/282	28/248	18/331
2/64	12/166	18/317

0.06

14	– Harpacticoid Abundance
208	– Nematode Abundance

0.07 Harpacticoid/Nematode Ratio

Winter 1977

A3

13/140	24/252	29/234
31/208	5/174	38/380
17/298	13/142	25/242

0.09

B2

60/81	54/96	62/109
47/53	65/73	72/110
54/49	74/91	28/100

0.79

B3

35/89	21/185	35/231
58/167	29/131	41/199
41/190	5/26	61/122

0.26

B4

72/105	47/142	66/197
84/152	79/152	63/191
90/127		85/105

0.53

E1

27/72	23/49	40/85
32/72	42/57	68/116
40/104	55/102	64/76

0.55

E3

115/265	135/381	147/256
133/244	158/364	128/287
88/171	118/243	81/198

0.47

E4

139/44	114/48	178/128
261/51	260/117	208/74
123/96	150/102	123/81

2.36

F3

15/292	14/209	20/242
1/120	20/199	10/212
1/110	14/89	15/176

0.07

15/292	- Harpacticoid Abundance - Nematode Abundance

0.05 Harpacticoid/Nematode Ratio

Spring 1977

A3

$\frac{72}{330}$	$\frac{23}{236}$	$\frac{8}{176}$
$\frac{54}{416}$	$\frac{31}{346}$	$\frac{39}{317}$
$\frac{92}{570}$	$\frac{53}{536}$	$\frac{24}{383}$

0.11

B2

$\frac{112}{300}$	$\frac{138}{587}$	$\frac{144}{861}$
$\frac{74}{308}$	$\frac{108}{601}$	$\frac{104}{503}$
$\frac{86}{266}$	$\frac{148}{429}$	$\frac{110}{410}$

0.26

B3

$\frac{97}{461}$	$\frac{90}{247}$	$\frac{51}{237}$
$\frac{72}{344}$	$\frac{63}{261}$	$\frac{47}{279}$
$\frac{39}{247}$	$\frac{45}{192}$	$\frac{50}{312}$

0.22

B4

$\frac{104}{361}$	$\frac{124}{609}$	$\frac{172}{402}$
$\frac{173}{777}$	$\frac{128}{477}$	$\frac{157}{549}$
$\frac{188}{589}$	$\frac{202}{646}$	$\frac{175}{475}$

0.30

E1

	$\frac{82}{72}$	$\frac{81}{79}$
$\frac{36}{37}$	$\frac{51}{66}$	$\frac{68}{54}$
$\frac{13}{24}$	$\frac{19}{68}$	$\frac{40}{70}$

0.82

E3

$\frac{82}{117}$	$\frac{140}{156}$	$\frac{144}{369}$
$\frac{31}{38}$	$\frac{64}{333}$	$\frac{139}{284}$
$\frac{21}{12}$	$\frac{149}{227}$	$\frac{213}{387}$

0.72

E4

$\frac{52}{280}$	$\frac{66}{572}$	$\frac{53}{405}$
$\frac{180}{249}$	$\frac{133}{300}$	$\frac{140}{700}$
$\frac{139}{237}$	$\frac{47}{137}$	$\frac{187}{455}$

0.35

F3

$\frac{40}{273}$	$\frac{30}{439}$	$\frac{27}{569}$
$\frac{34}{587}$	$\frac{37}{518}$	$\frac{32}{626}$
$\frac{13}{128}$	$\frac{17}{247}$	$\frac{29}{395}$

0.08

$\frac{40}{273}$

– Harpacticoid Abundance
– Nematode Abundance

0.15 Harpacticoid/Nematode Ratio

Summer 1977

A3

$\frac{28}{218}$	$\frac{29}{223}$	$\frac{25}{181}$
$\frac{29}{153}$	$\frac{26}{175}$	$\frac{27}{180}$
$\frac{55}{360}$	$\frac{28}{268}$	$\frac{36}{261}$

0.14

B2

$\frac{78}{261}$	$\frac{67}{221}$	$\frac{107}{505}$
$\frac{56}{461}$	$\frac{66}{204}$	$\frac{48}{162}$
$\frac{47}{207}$	$\frac{51}{266}$	$\frac{57}{300}$

0.24

B3

$\frac{89}{450}$	$\frac{67}{225}$	$\frac{55}{242}$
$\frac{59}{312}$	$\frac{22}{247}$	$\frac{28}{263}$
$\frac{47}{260}$	$\frac{33}{229}$	$\frac{22}{300}$

0.17

B4

$\frac{220}{363}$	$\frac{139}{405}$	$\frac{111}{341}$
$\frac{271}{544}$	$\frac{307}{738}$	$\frac{220}{808}$
$\frac{161}{539}$	$\frac{242}{818}$	$\frac{183}{814}$

0.36

E1

$\frac{25}{28}$	$\frac{30}{46}$	$\frac{14}{36}$
$\frac{28}{34}$	$\frac{21}{37}$	$\frac{17}{31}$
$\frac{21}{42}$	$\frac{19}{25}$	$\frac{20}{25}$

0.66

E3

$\frac{102}{163}$	$\frac{138}{205}$	$\frac{740}{779}$
$\frac{130}{290}$	$\frac{135}{178}$	$\frac{103}{199}$
$\frac{93}{111}$	$\frac{70}{135}$	$\frac{87}{196}$

0.64

E4

$\frac{11}{158}$	$\frac{23}{158}$	$\frac{25}{159}$
$\frac{54}{279}$	$\frac{21}{228}$	$\frac{35}{308}$
$\frac{20}{157}$	$\frac{24}{233}$	$\frac{36}{181}$

0.13

F3

$\frac{13}{97}$	$\frac{27}{98}$	$\frac{30}{149}$
$\frac{6}{41}$	$\frac{27}{107}$	$\frac{23}{117}$
$\frac{10}{74}$	$\frac{13}{61}$	$\frac{13}{100}$

0.19

$\frac{13}{97}$

- Harpacticoid Abundance
- Nematode Abundance

0.13 Harpacticoid/Nematode Ratio

APPENDIX 7-C

Density and Estimated Biomass of Meiobenthos

For Each Station by Collection Period.

	DENSITY			ESTIMATED BIOMASS		
	No./10 cm^2			mg/10 cm^2		
Station/Season	Nematodes	Harpacticoids	Total Meiobenthos	Nematodes	Harpacticoids	Total Meiobenthos
A3/Fall 76	123	1	176	0.074	0.001	0.091
Winter 77	367	67	474	0.220	0.081	0.392
Spring 77	584	70	696	0.351	0.084	0.600
Summer 77	376	48	453	0.225	0.058	0.370
B2/Fall 76	69	39	175	0.041	0.047	0.248
Winter 77	135	102	409	0.081	0.122	0.510
Spring 77	764	180	1319	0.458	0.216	1.280
Summer 77	458	132	830	0.275	0.158	0.890
B3/Fall 76	238	26	324	0.143	0.031	0.272
Winter 77	263	66	421	0.158	0.079	0.491
Spring 77	469	88	633	0.281	0.106	0.630
Summer 77	462	49	603	0.277	0.059	0.594
B4/Fall 76	98	55	242	0.059	0.066	0.322
Winter 77	212	104	492	0.127	0.125	0.562
Spring 77	876	255	1504	0.526	0.306	1.320
Summer 77	950	359	1761	0.570	0.431	1.810
E1/Fall 76	71	55	208	0.043	0.066	0.253
Winter 77	130	69	337	0.078	0.083	0.421
Spring 77	82	70	237	0.049	0.084	0.280
Summer 77	56	36	132	0.034	0.044	0.182
E3/Fall 76	167	87	295	0.100	0.105	0.234
Winter 77	420	196	961	0.252	0.235	1.090
Spring 77	335	188	879	0.201	0.225	0.732
Summer 77	331	176	847	0.199	0.211	0.870

APPENDIX 7-C. (concluded)

	DENSITY			ESTIMATED BIOMASS		
	No./10 cm^2		Total	mg/10 cm^2		Total
Station/Season	Nematodes	Harpacticoids	Meiobenthos	Nematodes	Harpacticoids	Meiobenthos
E4/Fall 76	372	19	596	0.223	0.023	0.427
Winter 77	132	292	568	0.079	0.350	0.753
Spring 77	532	172	829	0.319	0.206	0.901
Summer 77	357	44	466	0.214	0.052	0.404
F3/Fall 76	370	25	502	0.222	0.030	0.363
Winter 77	292	24	353	0.175	0.029	0.401
Spring 77	661	46	847	0.397	0.055	0.607
Summer 77	151	29	197	0.091	0.035	0.209

CHAPTER 8

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CHAPTER 8

BENTHIC ECOLOGICAL STUDIES: FORAMINIFERA

Robert L. Ellison

INTRODUCTION

Foraminifera have been shown to be useful in evaluating ecological conditions in a wide variety of marine environments (see Murray 1973, for a comprehensive survey). For this reason, and because these micro-organisms are sensitive to environmental change, delineating the distribution of assemblages of foraminiferal species is a valuable component of ecological surveys of benthic invertebrates. Because of their relatively short life-span and rapid turnover, foraminifera respond quickly to environmental modification. On the other hand, because of their small size and large numbers, foraminifera tend to be distributed heterogeneously over small areas.

The present study represents the second in a two-year investigation of the distribution of living benthic foraminifera on the continental shelf of the Middle Atlantic Bight and the correlation of these distributions with measured environmental parameters.

METHODS AND MATERIALS

With slight modifications, the methods and materials employed during 1976-1977 were the same as those used during 1975-1976 (Ellison 1977). On the last cruise (Summer 1977), all of the 3-cm samples collected on the "K-transect" were split into a top 1 cm portion and a bottom 2-cm portion. These fractions were prepared and studied separately to assess the vertical distribution of foraminifera. However, for the purpose of this report these fractional data have been combined.

On-Board Processing

Two plastic coring cylinders, 5 cm in diameter, were inserted into one grab at each benthic station. After the sediment cores were withdrawn from the grab, the top 3 cm of sediment was cut off and preserved in labeled glass jars of sea water and buffered formalin, shaken, and stored on deck in storage boxes.

Laboratory Processing

Upon delivery to the laboratory, the samples were refrigerated until sieved. In all cases, the samples were sieved within two weeks of delivery to the lab. Before sieving, the samples were stained overnight in rose Bengal, and immediately before sieving, the sample volume in the jar was measured and recorded. Sieving was done through a nest of two sieves (one 0.5 mm and one 0.063 mm), using flowing tap water. In order to remove excess stain, most samples were allowed to soak in water for several hours, then sieved a second time.

The stained and sieved samples were then oven-dried at low heat (28°C) and floated in a mixture of 38 parts acetone (S.G. 0.7851) and 100 parts bromoform (S.G. 2.8899). The specific gravity of the resulting liquid (2.30) is such that foraminiferal tests (and little else) float, and the remainder (mostly grains of quartz) sink. The floated material, along with the heavy liquid, was poured through #4 Whatman filter paper and washed 5-10 times with acetone to remove excess bromoform. After drying, this floated material was placed in labeled vials, and catalogued for later study. The residual sediment was bagged and archived. All of the floating was done in a fume hood especially modified for working with fumes from heavy liquids.

Before removing the living (stained) foraminifera, one must decide whether or not to split the dried, floated sample. Many samples, particularly those from the outer shelf (e.g. cluster areas A and F) were large, composed almost solely of tests of planktonic foraminifera. These samples were split as many as six times (into 64ths) before a manageable fraction (enough material to completely cover the bottom of the glass dish no more than one layer deep) was obtained. The sample to be sorted was spread as evenly as possible over a 100-square grid in a glass Petri dish. The sample was moistened with just enough water to wet the specimens, making it simpler to determine whether or not a specimen was stained. Working with a binocular microscope (X50 to X100), all (up to 300) live foraminifera were picked from the sample (or sample fraction) with a 000 sable brush. These were transferred onto a cardboard micropaleontology slide that had been covered with water-soluble glue, gum tragacantha. Because of the several splits required for some samples, it was not possible in those few cases to sort the entire sample even though 300 specimens were not obtained. A workable number of splits to be sorted was three. The data, therefore, are based on either: 1) approximately 300 living specimens picked from part of a sample in which living specimens were abundant, 2) fewer than 300 specimens from small samples in which there were less than 300 living foraminifers, or 3) fewer than 300 specimens from at least three fractions of samples which were so large, owing to the abundance of tests of planktonic foraminifera, that several splits were necessary. After the living specimens were picked and mounted, and the fractional volume of picked sediment was recorded, the empty tests were counted and recorded.

Although rose Bengal does stain protoplasm, it is somewhat ambiguous. Specimens with fungi inside a foram chamber will also stain. In specimens where rose Bengal is faint, the tests should have other signs of having been alive when collected, namely: 1) a lustrous sheen, 2) no broken chambers, except, perhaps, the last or next-to-last, 3) no holes in the chambers, and 4) no debris filling the chambers. Species of Reophax are particularly ambiguous because the mucilaginous or chitinous cement of empty tests may pick up the stain.

Taxonomic identification was done by the principal investigator utilizing type specimens and figured specimens on deposit in the Cushman Laboratory at the U.S. National Museum in Washington, D.C. Many species remain unresolved and are, therefore, referred to as "sp. A", "sp. B", or other letter designations.

Identification and counts were recorded on data sheets. From these, data were transferred to coding forms and subsequently to punched cards. Data analyses (see Chapter 6 for details) were performed at the Virginia Institute of Marine Science, and included: 1) data listing by stations, 2) calculation of diversity measures (species numbers, Shannon's H', and "evenness"), 3) cluster analysis (Bray-Curtis similarity measure on log-transformations of species abundance; clusters were subsequently grouped by visual examination of print-outs) of A-F stations for the year, and all stations for one cruise, and 4) correlation ("r" correlation coefficients) of foraminiferal and physico-chemical data.

RESULTS

As was true for the first year, the data for the second year show considerable variation in population size over small areas. Replicate cores from a single grab often yielded quite different values. Table 8-1 shows the mean and standard deviation for total densities at several stations representative of shelf environments (as classified in the 1975-76 report), as determined from data for spring, 1976 and 1977. Although the ratios of the standard deviation to the mean were large in both years, the ratios for the second year were smaller. The relatively larger variance in the data from the shelf break (F2, F3, and F4) is attributable, partly, to sample splitting and the multiplication of error that follows the extrapolation of sample values from data based on a small fraction of that sample.

By the end of the second year, 212 species has been tabulated. Most of the unidentified species are very small and difficult to classify, and they may simply be miniature individuals of other species or morphological variants. Additional taxonomic study would likely reduce the total number of species to 200 or fewer.

Table 8-1. Sample mean and standard deviation of densities of living populations in numbers per 20 cm^3 (two replicates for several stations in spring, 1976 and 1977).

		Inner Shelf	Outer Shelf			Shelf Break			
Date		C2	B1	B2	B3	F2	F3	F4	Mean
	$\bar{X}_1$	48.0	31.0	82.5	285.5	70.0	42.5	99.0	
1976	σ_1	35.36	9.90	36.06	178.9	42.43	19.09	39.6	
	$\sigma_1/\bar{X}$	0.74	0.32	0.44	0.63	0.61	0.45	0.39	0.47
	$\bar{X}_2$	135.0	498.5	263.0	1023.5	548.0	121.0	104.5	
1977	σ_2	43.84	166.17	31.11	447.6	504.87	55.15	26.16	
	$\sigma_2/\bar{X}$	0.32	0.33	0.19	0.44	0.92	0.46	0.25	0.42

Density of Living Populations

Sample estimates of population size in numbers per 20 cm^3 range from two (D2 in fall, 1976) to 3,757 (A2 in spring, 1977), and average 324. The data for stations in each biotope (established on the basis of macrobenthic data) are presented in Table 8-2 and summarized in Table 8-3 for purposes of comparison with results from the first year.

Populations in the second year were from two, to nearly five times larger than those in the first year. Based on data from cluster stations (A through F), the central shelf biotope had the sparsest populations of living foraminifera (two-year mean = 32 living forams per 20 cm^3), but the inner shelf had populations that were only slightly denser (54 per 20 cm^3). Offshore, the average population density on the outer shelf was 151 per 20 cm^3, and increased to a maximum average of 409 per 20 cm^3 at the shelf break. The largest values obtained were in cluster area A during the second year; the average population density for stations A2, A3, and A4 in the shelf-break biotope was 613 per 20 cm^3 during the second year. Superimposed on this bathymetric coenocline is the effect of local bottom topography, especially the swale habitats. Swales on the inner, central, and outer shelf are habitats that invariably have foraminiferal populations larger than those areas adjacent to the swales. Populations in swales on the inner and central shelf average 281 living forams per 20 cm^3 (for two years) while those on the outer shelf have average populations of 334 specimens per 20 cm^3. These may be compared to densities of 53 and 153 specimens per 20 cm^3 for non-depression habitats in these respective shelf regions.

Over the two-year period, foraminiferal populations in each of the biotopes increased from 1976-1977 (see Tables 8-2 and 8-3). This was least apparent in the central shelf where the average population size remained smaller than 100 per 20 cm^3 from the fall of 1975 to the summer of 1977. No systematic changes in population density of macrobenthos (Chapter 6) or in sediment characteristics (Chapter 5) were observed paralleling the yearly variation of foraminifera. Although bottom water temperatures at the shelf break were not different among years, the outer shelf experienced substantially higher bottom temperatures during fall 1976 (Chapter 3). No obvious seasonality is seen in data from either of the two years; the smallest populations of 1975-1976 were in the summer of 1976, and the smallest populations of 1976-1977 were in the fall of 1976. This summer-fall minimum was followed by an increase in population density in the winter and spring of 1977. Although this is not a demonstrably cyclical pattern, it could represent an annual, or longer term rhythm.

To isolate which species were the most important contributors to these fluctuations in population size, average population densities of *Reophax atlantica* were plotted for all cruises in each of the biotopes (Figure 8-1). This species is the principal foraminiferal component of the outer shelf and in topographic depressions. Population

Table 8-2. Number of living foraminifera per 20 cm^3 of sediment. Each value is an average of two replicates at that station.

Biotopes/	1975-76					1976-77				
Stations	F	W	S	Su	Mean	F	W	S	Su	Mean
Inner Shelf										
C1	8	9	104	105		-	-	-	-	
C2	33	29	48	24		33	29	135	228	
C3	13	17	22	22		-	-	-	-	
Mean	18	18	58	50	36	33	29	135	228	106
Central Shelf										
B4	14	31	7	43		11	16	29	69	
D1	12	61	16	48		12	28	66	126	
D2	2	3	24	15		-	-	-	-	
D3	25	20	85	8		+	-	-	-	
Mean	13	29	33	29	26	12	22	48	98	45
Inner & Central Shelf Swales										
C4	43	-	78	64		162	428	314	114	
D4	28	63	986	63		62	929	534	271	
Mean	36	63	532	64	174	112	679	424	193	352
Outer Shelf										
A1	207	688	122	61		152	102	288	116	
B1	36	131	31	91		58	165	499	113	
B2	42	25	82	31		19	128	263	110	
E1	87	51	104	75		34	56	152	142	
E2	87	175	331	-		1,180	-	-	-	
E3	31	73	19	64		113	146	79	150	
F1	130	155	79	70		82	196	174	351	
Mean	89	185	110	66	113	234	132	243	164	193
Outer Shelf Swales										
B3	168	171	285	116		280	1,172	1,024	565	
B5	-	-	-	-		-	272	390	186	
E2	-	-	-	105		-	457	403	738	
E4	185	200	63	37		157	184	311	597	
Mean	177	186	174	86	156	219	521	532	522	449
Shelf Break										
A2	395	-	111	122		77	424	3,757	1,586	
A3	334	67	35	75		198	350	2,195	528	
A4	79	195	180	128		313	662	762	1,542	
F2	171	220	70	39		173	353	548	934	
F3	176	77	67	39		58	42	122	157	
F4	638	83	99	159		158	436	105	234	
Mean	299	128	94	94	154	163	378	1,248	830	655

Table 8-3. Mean density (individuals per 20 cc of wet sample) of living populations of foraminifera in each of the biotopes.

	1975–1976					1976–1977				
Shelf	Fall	Winter	Spring	Summer	Mean	Fall	Winter	Spring	Summer	Mean
inner	18	18	58	50	36	33	29	135	228	106
central	13	29	33	29	26	12	22	48	98	45
outer	89	185	110	66	113	234	132	243	164	193
break	299	128	94	94	154	163	378	1248	830	655
Swales										
inner	36	63	532	64	174	112	679	424	193	352
outer	177	186	174	86	156	219	521	532	522	449
Mean	123	120	127	67	110	167	325	588	433	324

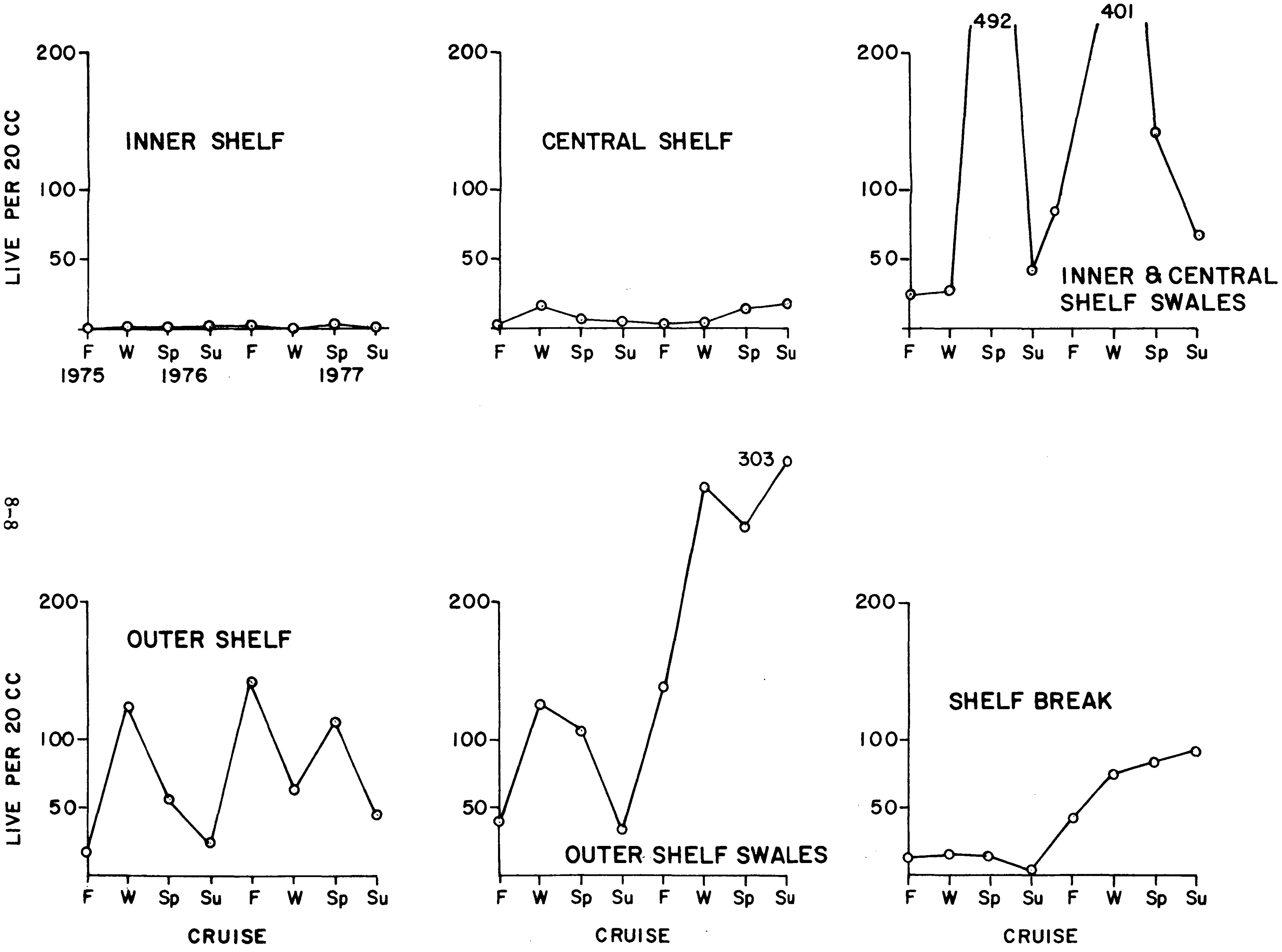

Figure 8-1. Living populations of <u>Reophax</u> <u>atlantica</u> (number of living specimens per 20 cm^3) for all eight cruises, summarized for each of the biotopes.

densities of this species show no well-defined seasonality except in swales where the densities were, in general, highest in winter-spring, and lowest in summer-fall (with the exception of summer, 1977, on the outer shelf). Outside the swales, populations of *R. atlantica* were also generally, sparsest in the summer-fall. However, there were many exceptions to the rule.

Species other than *R. atlantica* also were important contributors to foraminiferal faunas of some biotopes. Figure 8-2 shows changes in population size of *R. atlantica* and three other numerically dominant species (*Elphidium excavatum clavatum*, *Eggerella advena*, and *Cibicides lobatulus*) for the swales of the inner and central shelf through all eight cruises. None of these species was as important as *R. atlantica* in influencing the population fluctuations of total living foraminifera. Except for *C. lobatulus*, these other species also showed a winter-spring maximum in 1977, but not in 1976. Sediments sampled at both swale stations C2 and D4 were finer and contained more organic carbon and silt and clay in winter and spring 1977 than in those periods of 1976.

Agglutinate Foraminifera

Agglutinate foraminifera construct tests by assembling and cementing sedimentary particles together, rather than by secreting tests of calcium carbonate. The proportion of specimens of agglutinate species was largest (greater that 50%) at intermediate depths on the shelf--between 30 and 100 m for 1975-1976, and from about 60 to 100 m for 1976-1977. A somewhat smaller fraction (less than 50%) was found at depths less than 60 m and greater than 100 m. These data for spring, 1977 are summarized in Table 8-4. Table 8-4 also shows the percentages of the total number of species that are agglutinate. In depths shallower than about 60 m, 41% of the species was agglutinate, but in intermediate depths of 60-100 m, and also in depths greater than 100 m, the proportion was 34-35%. Despite the relatively smaller numbers of agglutinate individuals at shallower depths, the agglutinate species were relatively more diverse than they were at greater depths.

Densities of Empty Tests

Empty tests in surface sediment represent the accumulation of dead foraminifera over various periods of time, depending on the rate of production of tests and processes which remove tests. If the average generation time is 0.1 to 1.0 years, and if the average living population density is 300 per 20 cm^3, then 300 to 3,000 tests should be deposited annually on a 20 cm^2 area (by 1 cm deep). At that rate, from 6-60 years would be required to accumulate 17,000 empty tests--approximately the average density of empty tests found in the study area. However, from the first to the second year, our data show

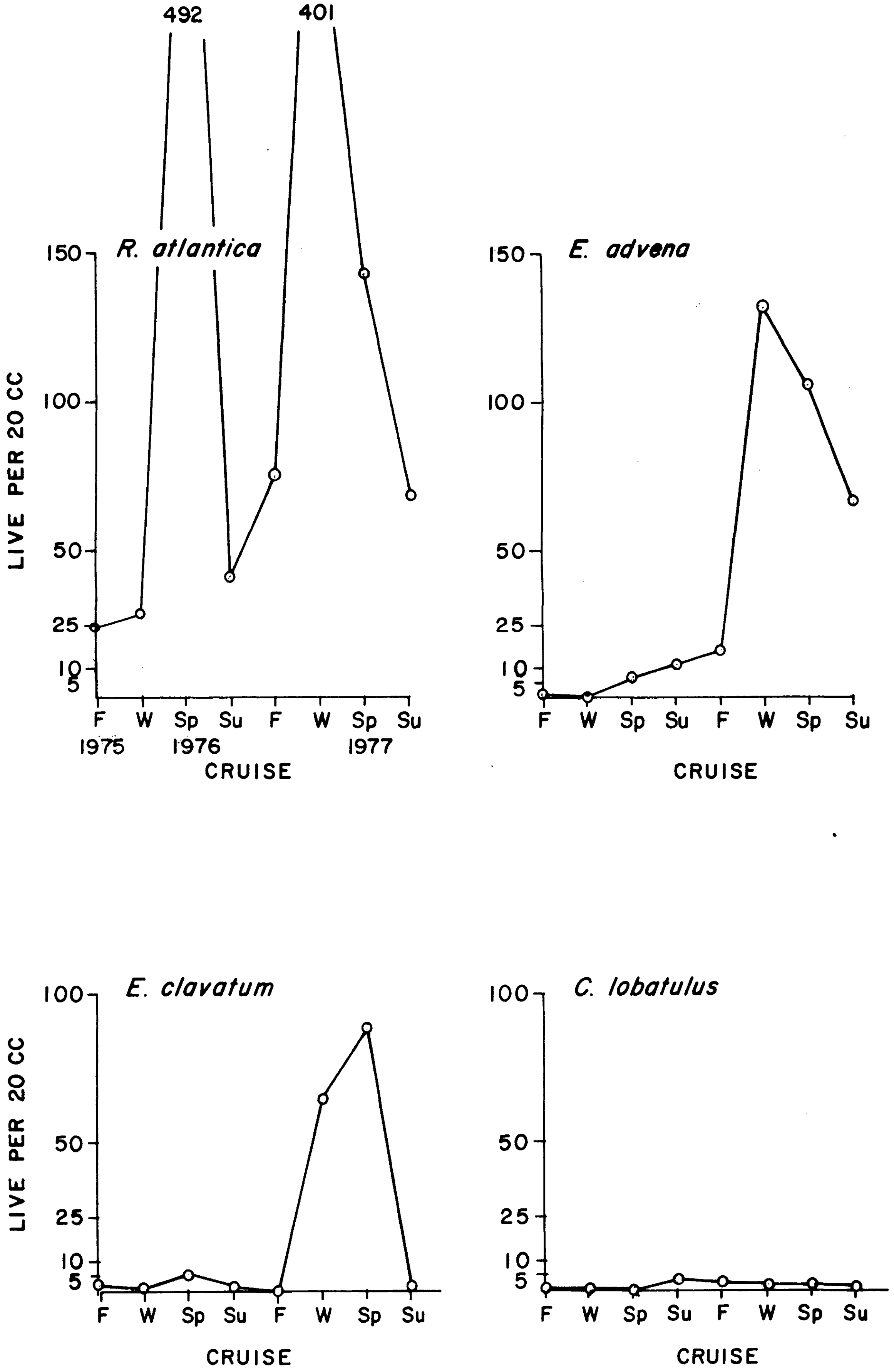

Figure 8-2. Numbers of living Reophax atlantica, Cibicides lobatulus, Eggerella advena, and Elphidium excavatum clavatum per 20 cm^3 for all eight cruises, summarized for the swale biotope of the inner and central shelf (selected because in Figure 8-1 this biotope shows pronounced seasonal change.)

Table 8-4. Percentage of agglutinate forams vs. depth for spring, 1977, cruise.

Station	Depth (m)	Percentage of specimens that are agglutinate	Percentage of species that are agglutinate
C2	26	26	42
D1	31	87	38
C4*	34	47	50
B4	42	46	38
D4*	51	83	43
B2	61	34	33
E3	64	64	32
B1	65	86	40
E1	68	75	33
E2*	73	68	31
B3*	74	65	33
E4*	80	64	22
F1	85	75	43
A1	91	62	38
F2	113	21	38
A2	132	8	25
A3	139	37	40
F3	153	10	19
F4	184	52	48
A4	198	47	40

*Swale Stations

that the average densities of empty tests increased from about 8,000 to about 17,000 per 20 cm^3, or more than double. The increase in productivity of living foraminifera (Table 8-2) did not increase by that amount in the same amount of time, so the explanation must be found elsewhere. It may be partly the result of laboratory methods of foraminferal concentration being refined through experience, or it could be a function of reworking of bottom sediments by waves and currents. Periodic resuspension of the sediments would tend to concentrate the lighter sediment, including foraminiferal tests, at the surface.

Table 8-5 shows the density of empty tests per 20 cm^3 for the biotopes for both years. As with data for living foraminifera, these data are highly variable, ranging from fewer than 50 to more than 50,000. The shelf break (stations A2-4 and F2-4) had by far, the greatest density of empty tests, and in this area, where sediment reworking may be lowest and the rate of test removal may be low, the period of production represented by the top few centimeters may indeed be tens of years.

Live-Empty Test Ratios

If one can assume that turnover rates of foraminifera are uniform over the study area, i.e. that numbers of generations of foraminifera per year are constant, and if empty tests were not destroyed or removed by physical or chemical processes, then the ratio of live forams to empty tests in a volume of sediment is a function of the rate of deposition of sediment. A large L/E ratio would indicate a more rapid rate of sedimentation, or dilution of foraminifera, than would a small ratio. By comparison of ratios, one would be able to determine areas of relatively rapid or slow deposition. However, patterns of sedimentation on the continental shelf are complex, with little net sedimentation but with local redistribution of relict sediments (Swift et al. 1972). Furthermore, considerable differences in the rate of test removal (through destruction or transportation) probably exists, depending on the proportion of agglutinate tests and on physical disturbances of the bottom sediments. Consequently, L/E ratios are difficult to interpret in terms of sedimentation rates. The L/E ratios for the first and second year are summarized in Table 8-6. Although the values for the second year are smaller than those for the first, the inner and central shelf remain a region of high L/E's, possibly reflecting a more rapid rate of test removal, whereas the shelf break is a region having L/E's on order of magnitude smaller, suggesting greater survival of tests and less sediment redistribution. On the inner and central shelf, L/E ratios show a tendency to be larger in the winter and summer than in the fall and spring. Comparison of data from Tables 8-2, 8-5, and 8-6 suggests that this is chiefly the result of relatively fewer empty tests in winter and summer.

Table 8-5. Numbers of empty tests per 20 cm^3, for cluster stations.

Biotopes/ Stations	1975-76					1976-77				
	F	W	S	Su	Mean	F	W	S	Su	Mean
Inner Shelf										
C1	20	37	344	998		-	-	-	-	
C2	94	60	205	103		306	74	789	270	
C3	13	17	49	99		-	-	-	-	
Mean	42	38	199	400	170	306	74	789	270	360
Central Shelf										
B4	22	78	25	42		86	57	224	74	
D1	14	849	120	87		61	34	595	114	
D2	5	3	5	40		-	-	-	-	
D3	40	70	68	38		-	-	-	-	
Mean	20	250	55	52	94	74	46	410	94	156
Inner & Central Shelf Swales										
C4	45	-	2,828	432		834	761	1,300	1,427	
D4	137	711	2,715	293		121	2,980	3,365	1,751	
Mean	91	711	2,772	363	984	478	1,871	2,333	1,589	1,568
Outer Shelf										
A1	2,835	46,242	5,909	7,657		5,036	6,496	7,312	5,801	
B1	110	194	180	144		371	488	1,328	708	
B2	82	709	484	57		491	392	623	369	
E1	179	784	354	922		711	101	686	1,490	
E2	925	7,283	1,878	-		3,469	-	-	-	
E3	92	178	468	210		568	207	7,314	339	
F1	1,211	1,250	1,470	2,948		1,207	4,602	2,024	3,577	
Mean	776	8,085	1,535	1,990	3,097	1,693	2,048	3,215	2,047	2,251
Outer Shelf Swales										
B3	1,397	7,003	3,543	1,919		3,429	3,374	5,450	6,357	
B5	-	-	-	-		-	651	1,194	2,402	
E2	-	-	-	2,584		-	15,790	6,491	21,201	
E4	2,937	4,928	4,564	2,904		13,235	5,092	13,299	4,407	
Mean	2,167	5,966	4,054	2,252	3,610	8,332	6,332	6,609	8,592	7,440

Table 8-5. Continued.

Biotopes/	1975-1976					1976-1977				
Stations	F	W	S	Su	Mean	F	W	S	Su	Mean
Shelf Break										
A2	6,577	-	65,934	19,312		21,753	20,020	116,830	55,250	
A3	12,721	29,668	39,433	18,259		22,938	34,212	41,814	60,863	
A4	11,472	36,170	70,277	74,512		35,440	19,833	65,015	84,419	
F2	4,277	8,982	9,562	16,118		32,858	23,802	28,774	12,762	
F3	4,980	20,623	17,933	20,442		8,895	129,535	41,567	25,593	
F4	12,228	16,201	21,017	64,170		21,374	64,913	31,120	37,267	
Mean	8,709	18,607	37,359	35,469	25,036	18,470	48,719	54,187	46,026	41,851

Table 8-6. Live/empty test ratios, derived from cluster station data.

Biotope	1975-76	1976-77				
		F	W	S	S	$\bar{x}$
Inner Shelf	0.21	0.11	0.39	0.17	0.84	0.29
Central Shelf	0.28	0.16	0.48	0.12	1.04	0.29
Inner-Central Shelf Swales	0.18	0.23	0.36	0.18	0.12	0.22
Outer Shelf	0.04	0.14	0.06	0.08	0.08	0.09
Outer Shelf Swales	0.04	0.03	0.08	0.08	0.06	0.06
Shelf Break	0.01	0.01	0.01	0.02	0.02	0.02

Species Composition and Distribution

Diversity

Over 200 species have been recorded during the two-year study of shelf foraminifera, but the average number per sample was about 20. In any single sample, as few as one, or more than 40 species have been counted. Table 8-7 summarizes data (averaged for each biotope) for the number of species of living forams in each aggregate of samples. From this table, it can be seen that greatest diversity as expressed by the number of different species occurred during spring-summer, 1977. Furthermore, swales on the outer shelf had a particularly diverse fauna (22-31 species per 20 cm^3); the outer shelf and shelf break supported a moderately diverse fauna (14-30 species per 20 cm^3); and the inner and central shelf had the least diverse fauna (9-17 species per 20 cm^3).

Diversity also can be expressed in terms of Shannon diversity (H') which is a function of the number of species and the evenness of equitability of numbers of individuals in each species. These values for the six biotopes are summarized in Table 8-8 in which each value is the mean H' value for the two replicates taken at that station. The shelf break stations represent the most diverse area (3.14), and the stations in the swales on the inner and central shelf (2.04) were least diverse. Temporally, the assemblages on the inner shelf appeared to be more diverse in fall-winter, whereas the outer shelf and shelf-break were most diverse in summer. The data, however, are suggestive and not conclusive. The values for the various stations generally show little systematic change throughout the year, and the differences are small.

Using Spearman rank correlation, the areal species richness values from Table 8-7 show no correlation with H'-diversity values from Table 8-8. This indicates that evenness is an important aspect of Shannon diversity on the shelf. Swales (both inner and outer shelf) had low H'-diversity values but relatively large numbers of species as a result of an uneven distribution of species (i.e. an unusually large number of one species, e.g., *Reophax atlantica*).

Foraminiferal Faunas

Foraminifera are classified into three suborders - Miliolina, Rotaliina, and Textulariina (Loeblich and Tappan 1964). Murray (1969-1973) used the proportions of these three taxa to classify assemblages from different environments. Data are presented on ternary diagrams so that gross taxonomic differences between different biotopes can be seen clearly.

Table 8-7. Mean number of species in a single core (20 cm^3) for each biotope, based on data from cluster stations.

	1976-1977				
Biotope	Fall	Winter	Spring	Summer	Mean
Inner Shelf	14.5	13.5	15.0	17.0	15.0
Central Shelf	9.0	9.3	13.0	17.0	12.1
Inner & Central Shelf Swales	14.8	14.0	17.8	16.3	15.7
Outer Shelf	16.2	25.1	28.3	25.3	23.7
Outer Shelf Swales	21.5	26.9	29.6	30.5	27.1
Shelf Break	13.8	21.3	30.3	25.3	22.7

Table 8-8. Diversity (H') for stations in cluster areas in 1976-77.

Biotope	Station	Fall	Winter	Spring	Summer	Mean
Inner Shelf	C2	3.24	2.74	2.52	2.41	2.73
Central Shelf	B4	2.95	2.36	3.28	2.41	2.75
	D1	2.01	2.49	2.00	2.36	2.21
Inner & Central Shelf Swales	C4	1.80	2.04	1.83	2.20	1.97
	D4	1.70	1.59	2.50	2.62	2.10
Outer Shelf	A1	2.52	1.98	3.39	3.04	2.73
	B1	1.16	1.92	1.89	2.19	1.79
	B2	2.11	2.78	3.24	3.04	2.80
	E1	2.27	4.14	2.52	4.03	3.24
	E2	2.41	-	-	-	2.41
	E3	2.75	3.08	2.79	3.61	3.06
	F1	1.70	2.91	3.63	2.98	2.81
Outer Shelf Swales	B3	2.40	3.05	2.69	2.76	2.72
	B5	-	2.59	3.03	3.06	2.89
	E2	-	2.41	3.39	2.88	2.89
	E4	1.97	2.87	2.67	3.42	2.73
Shelf Break	A2	3.30	4.09	1.46	3.06	2.98
	A3	3.62	3.48	3.57	3.38	3.51
	A4	4.02	4.25	4.01	4.28	4.14
	F2	2.33	2.24	2.78	3.09	2.61
	F3	2.19	2.00	1.87	4.01	2.52
	F4	3.01	3.68	2.83	2.93	3.11

$\overline{X}_G = 2.68$

Following Murray's example, the data for spring 1977 were plotted and boundaries were delineated between three of the shelf environments (Figure 8-3). Although such a figure is not a rigorous test of any classification scheme, it does provide a means for visualizing the general taxonomic gradient that accompanies changing position on the shelf. Foraminiferal faunas on the shelf are, for the most part, composed of species belonging to the suborders Textulariina and Rotaliina. Only a few are miliolids. Furthermore, from the central shelf, across the outer shelf to the shelf break, the faunas become increasingly rotaline and decreasingly textularine (some samples fall outside this simple picture- C2, B4, and E3). This would appear to be consistent with the fact that marshes are chiefly textularine (Figure 8-3), and the Middle Atlantic coast is, in large part, marshland.

At the species level, a more detailed picture of foraminiferal assocations is provided by cluster analysis. This analytical procedure was performed on the data, yielding two classifications: 1) stations grouped on the basis of similarity of species composition, and 2) species grouped on the basis of similarity of station occurrences. The station groups are summarized in Table 8-9, and a list of the species groups is presented in Table 8-10.

The two largest station groups are groups 1 and 2, and these also are the groups in which the member stations remain most closely associated with one another throughout the year (e.g. station A2-4 and F4 remain in station group 2 from fall 1976 to summer 1977). Station group 1 includes the inner and central shelf biotopes, but also includes several outer shelf stations in summer 1977. Station group 2 represents the shelf break and, as would be expected for a deeper water habitat, exhibits little seasonal change in station composition.

Station groups 3, 4, and 5 are less well delineated. Group 3 includes swale and outer shelf stations; and group 4 represents the outer shelf biotope, including outer shelf swales. The inconsistent classification of seasonal samples from several stations indicates either population changes in response to environmental seasonality or sampling variation due to imprecision of station relocation (Chapter 5) or small-scale spatial heterogeneity.

Species assocations (Table 8-10) can be correlated with station groupings by means of nodal (constancy) analysis (see Figure 8-4). Species group 1, including *Reophax atlantica*, *Eggerella advena*, and *Fursenkoina fusiformis*, is found nearly everywhere, and is composed of eurytopic species. Species groups 6-10 show little, if any, direct correlation with the station groups, except for species group 8 which, along with species groups 2, 3, and 5, seems to be associated principally with station group 2, at the shelf break. These species groups compose a fauna characterized by *Gyroidina soldanii* and *Cassidulina neocarinata* (Group 2); *Stainforthia compressa* and *Haplophragmoides canariensis* (Group 3); *Islandiella subglobosa* and *Lenticulina stephensoni* (Group 5); and *Hoglundina elegans* and *Plectina*

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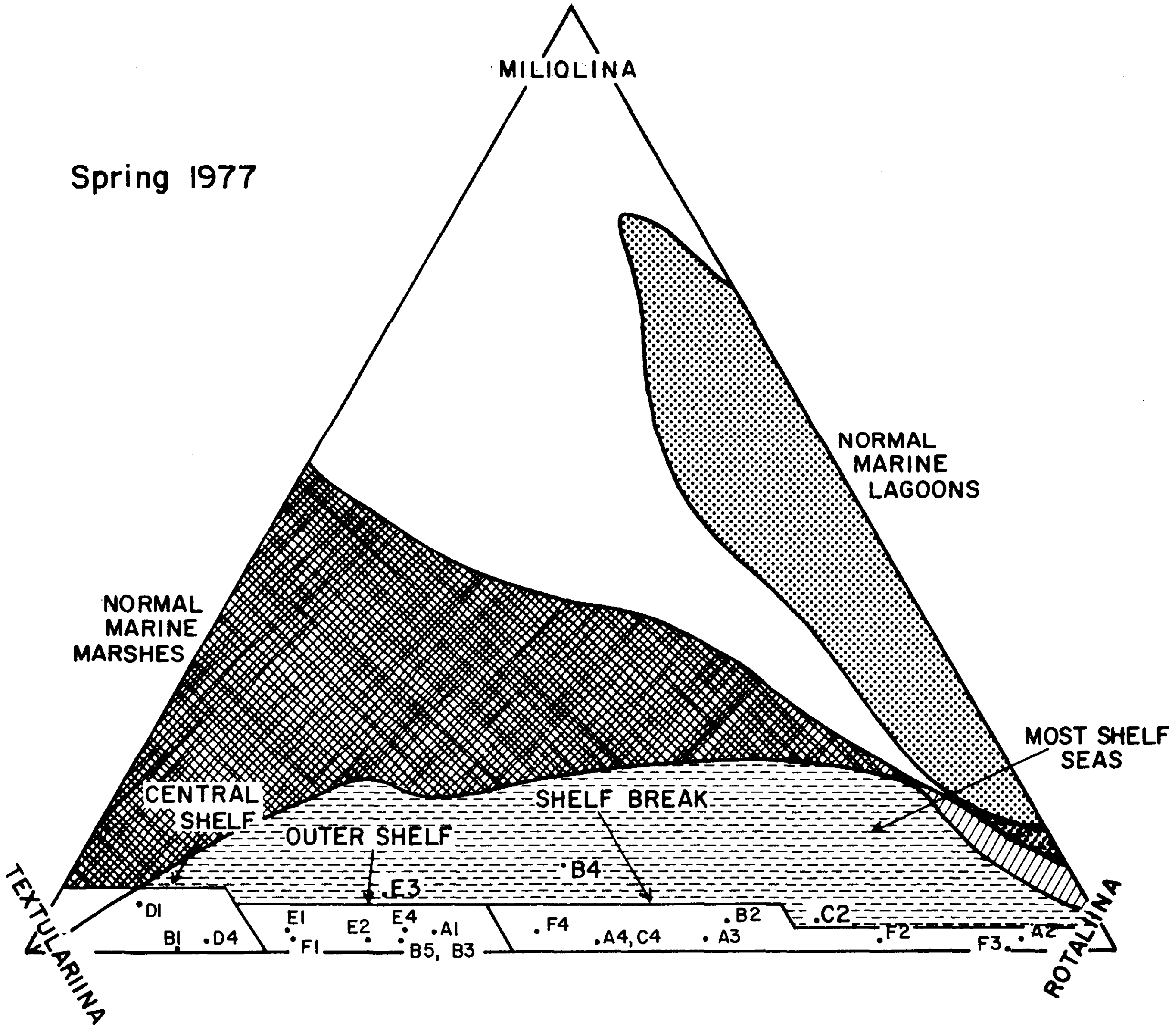

Figure 8-3. Diagram showing proportions of the three foraminiferal suborders (Textulariina, Rotaliina, and Miliolina) represented by samples collected during the spring cruise, 1977 (chosen because of the especially large populations persisting at that time). Boundaries for various environments taken from Murray (1973).

Table 8-9. Station groups obtained by cluster analysis of samples collected during second year from areas A-F.

	Cruise Season (number)			
Station Group	Fall (5)	Winter (6)	Spring (7)	Summer (8)
1 (inner to central shelf, plus ridges)				A1
				B1
	B2			B2
	B4	B4	B4	B4
	C2	C2	C2	C2
				C4
	D1	D1	D1	D1
	E1	E1		E1
				E3
		F3		
3 (central to outer shelf, plus swales)			B1	
		B3	B3	B3
		D4	D4	
	E2	E2		E2
				E4
4 (outer shelf)	A1	A1		
	B1			
		B2	B2	
				B5
	D4			
	E3	E3	E3	
	F1		F1	
5 (outer shelf, plus swales)			A1	
		B1		
	B3			
		B5	B5	
	C4	C4	C4	
				D4
			E1	
			E2	
	E4	E4	E4	
		F1		F1
	F2	F2		
2 (shelf break and upper slope)	A2	A2	A2	A2
	A3	A3	A3	A3
	A4	A4	A4	A4
			F2	F2
	F3		F3	F3
	F4	F4	F4	F4

Table 8-10. Species groups, based on 1976-1977 data.

Species Group 1

Reophax curtus
Bulimina marginata
Cibicides lobatulus
Eggerella advena
Reophax atlantica
Fursenkoina fusiformis

Species Group 2

Bucella sp. B
Trochammina sp. A
Valvulina conica
Cassidulina subcarinata
Cf. *Reophax*
Gyroidina soldanii
Cibicides pseudungerianus
Cassidulina laevigata
Cassidulina neocarinata
Bolivina spathulata

Species Group 3

Haplophragmoides canariensis
Reophax sp. A (irregular)
Stainforthia compressa
Eponides tumidulus
Trochammina advena
Nonion grateloupi

Species Group 4

Elphidium incertum
Elphidium subarcticum
Trochammina lobata
Elphidium excavatum clavatum
Pseudopolymorphina novangliae
Webbinella concava
Eponides sp. D
Hemisphaerammina sp. A
Quinqueloculina seminula
Trochammina ochrecea
Ammodiscus sp. A

Species Group 5

Trifarina angulosa
Discorbis sp. A
Ammodiscus catinus
Lenticulina stephensoni
Nonionella atlantica
Guttulina lactea

Species Group 5 (cont)

Reophax sp. C
Islandiella subglobosa
Bolivina pseudoplicata
Fissurina lucida
Marginulina bachei
Bolivina sp. B
Textularia conica

Species Group 6

Lagena acuticosta
Elphidium sp. C
Quinqueloculina jugosa
Ammobaculites sp. C
Pyrgo sarsi
Trilogulina sp. B
Cancris sagra

Species Group 7

Quinqueloculina poeyanum
Reophax scottii
Nodosaria catesbyi
Trochammina squamata
Valvulineria laevigata
and others

Species Group 8

Textularia sp. A
Cassidella sp. A
Chilostomella oolina
Bolivina lanceolata
Nonion sp. B
Plectina sp. A
Quinqueloculina sp. A
Ammobaculites sp. B
Haplophragmcides glomeratum
Planulina mera
Bolivina subaenariensts mexicana
Höglundina elegans
Sphaeroidina bulloides
Globobulimina turgida
Bolivina subaenariensis
Haplophragmoides sp. A
Glomospira gordialis

Table 8-10. Continued.

Species Group 9

Discorbinella
Planulina arminensis
Textularia sp. B
Marginulopsis
Rosalina candeiana
Siphotextularia rolshauseni

Species Group 10

Dentalina communis
Psammosphaera fusca
Rosalina floridana
Eponides repandus
Trochamiona sp. B
Sigmoilina tenuis
Textularia candeiana

Species Group 11

Triloculina sp. C
Lagena laevis
Rosalina floridensis
Elphidium advena
Lagena tenuis
Cassidulinoides bradyi
Bulimina sp. C

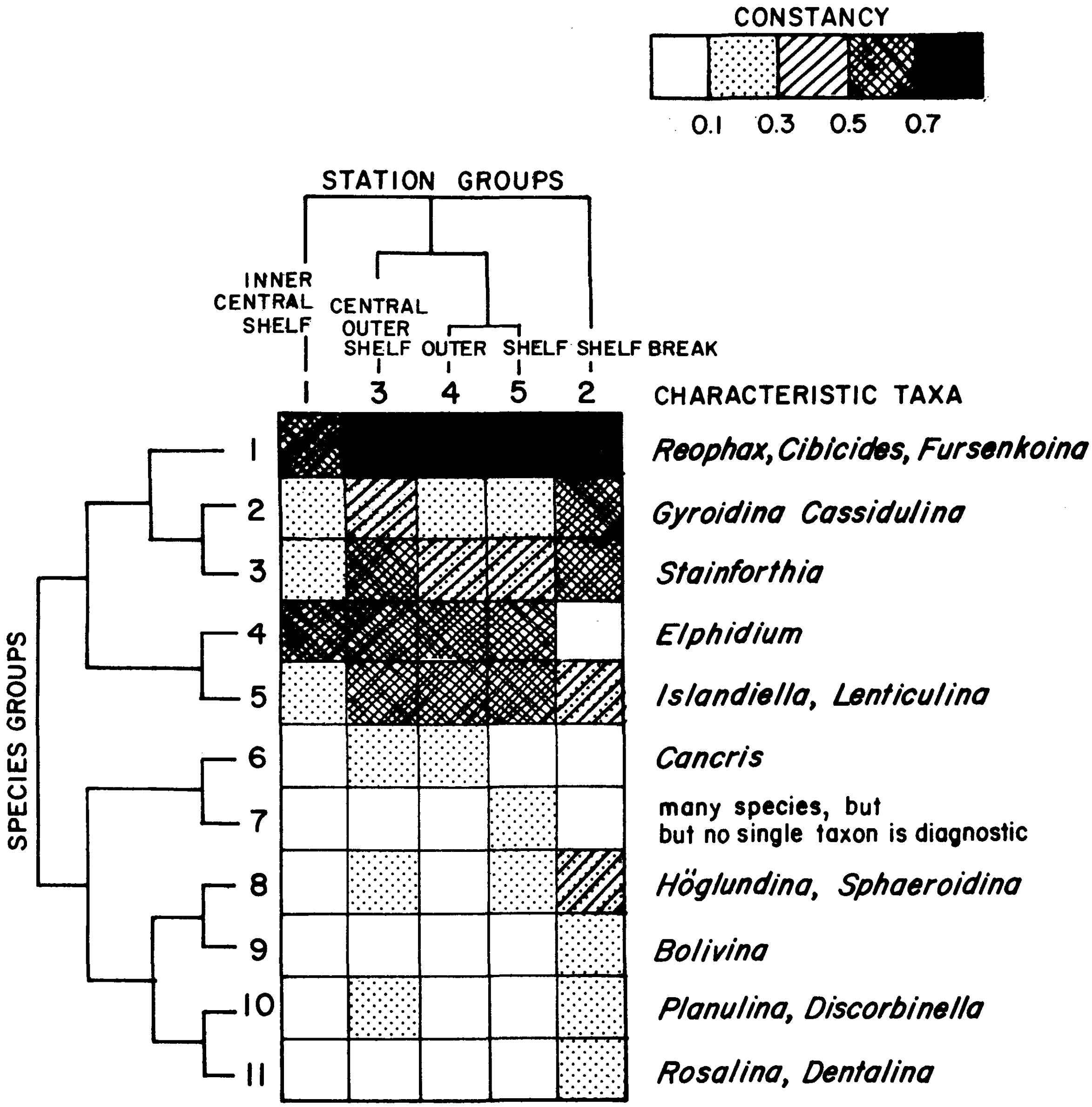

Figure 8-4. Normal and inverse classification hierarchies and nodal constancy for stations-species group coincidence based on data from Cruises 5-8 for cluster areas A-F.

sp. (Group 8). Although cluster analysis was not performed on foraminiferal data from stations H-L, these same species that characterize the shelf break also prevail on the upper and middle slope.

Relationships Between Environmental Factors and the Distribution of Living Foraminifera

In shallow coastal waters, estuaries, and marshes, the distribution of foraminifera is influenced by those environmental parameters that fluctuate widely with seasonal, climatic change. Salinity, temperature, fresh-water input, along with nutrient input, all experience seasonal maxima and minima that, in turn, produce measurable changes in numbers and species of forams (Ellison 1976; Buzas 1977).

On the continental shelf, however, the environmental factors are less variable and their influence on foraminiferal communities is less well known. In general, researchers have found a relationship between foraminiferal communities and depth or distance offshore (Parker 1948; Schnitker 1971; Sen Gupta and Kilbourne 1976).

Several approaches were used to assess relationships between foraminiferal distributions and environmental parameters. Depth, for example was examined in three ways. Plots of density across the three transects (G, K, and L) for both years of study (Figure 8-5) show no recognizable relationship between population size and depth. Furthermore, correlation coefficients (Table 8-11) indicate that no statistically significant association exists between depth and foraminiferal densities. On the other hand, cluster station classified bathymetrically as in Table 8-12 do show an apparent increase in foraminiferal numbers with depths.

Correlation coefficients between other environmental factors and some foraminiferal measures also were calculated from spring 1977 cruise data (Table 8-11). With one exception, foraminifera appeared to be independent of depth and temperature. The exception was "percent Textulariina" which is the percentage of the fauna composed of agglutinate forams. Smaller percentages of agglutinate forams were found in deep water than in shallow water, but this relationship is significant only at the 5% level. Of much greater importance, and statistically more convincing, are the relationships between total organic carbon (T.O.C.), percent silt/clay, and several different foraminiferal measures (ln live, percent Textulariina, percent *Reophax*). Most significant are the correlations betwen percent silt/clay and density of living foraminifera. Larger populations of living forams were associated with higher concentrations of T.O.C. and silt/clay. This does not prove a causal relationship, but may indicate that some processes may be responsible for the distribution

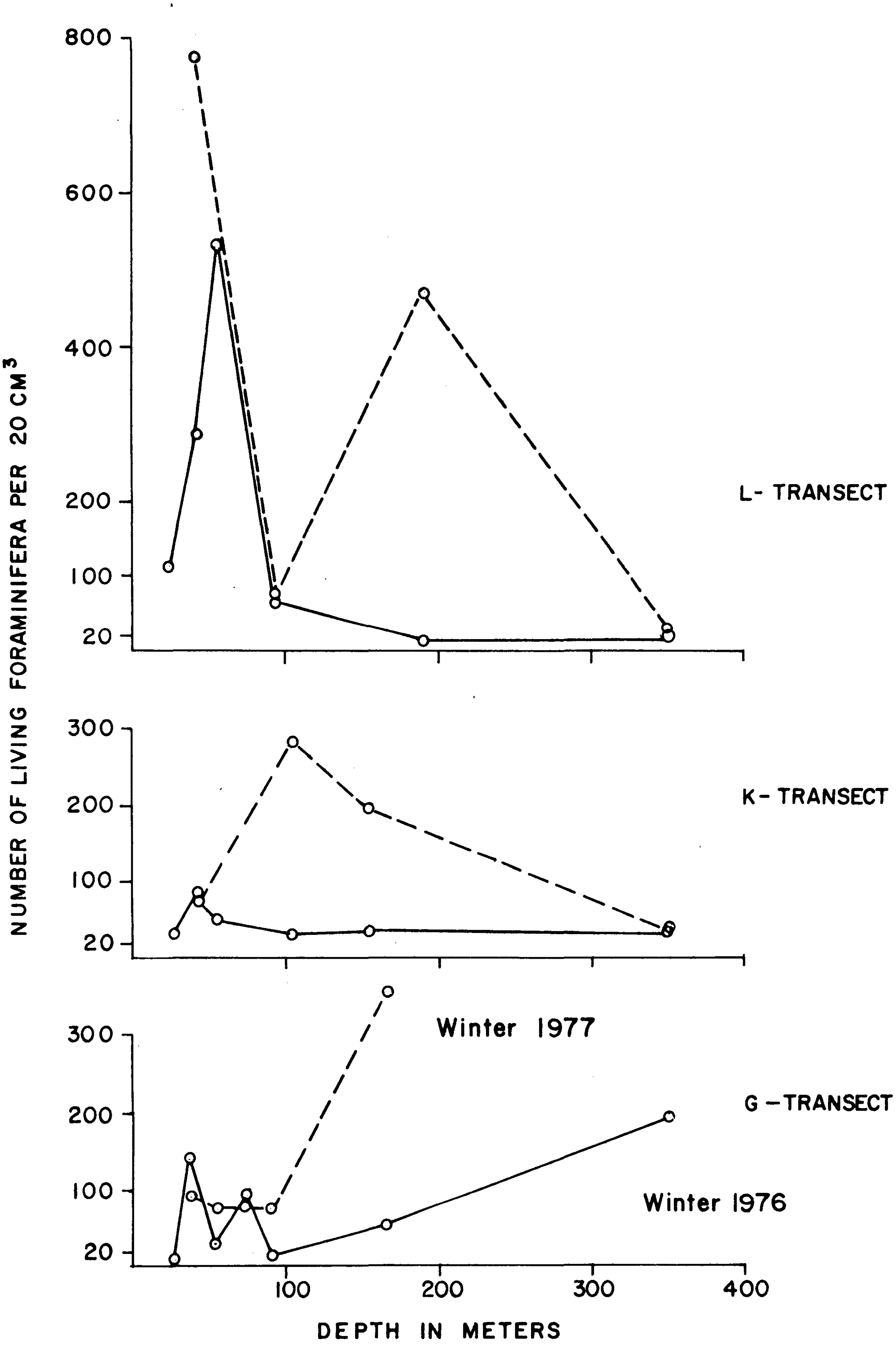

Figure 8-5. Density (number of foraminifera per 20 cm^3) of living foraminifera along transects G, K, and L for both years (Cruises 2 and 6) of study plotted against depth in meters.

Table 8-11. Correlation coefficients determined from data for all cluster stations on Cruise 7, Spring 1977. Results are believed to be representative for other cruises.

	ln LIVE per 20 cm^3	Percent Textulariina	Percent *Reophax*	Diversity (Evenness)
Depth	0.28	-0.41*	-0.30	0.32
T.O.C.	0.57**	-0.43*	-0.42*	-0.1
Percent silt/clay	0.69**	-0.44*	-0.38	-0.1
T^oC	0.04	-0.29	-0.11	0.18

*significant at 5% level
**significant at 2% level

Table 8-12. Mean number of living foraminifera per 20 cm^3 of wet sediment for 1976-1977, compared with averages for 1975-1976.

Bathymetric Stratum (Stations)	Number live/20 cm^3 Fall	Winter	Spring	Summer	Overall 1976-77	Overall 1975-76
25-49 cm (B4, C2, C4, D1, D4)	58	286	216	161	180	61*
59-99 m (A1, B1-B3, E1-E4, F1)	231	290	355	316	298	92
100-199 m (A2-A4, F2-F4)	162	377	1,248	830	654	154

*also includes C2, C3, D2, D3

of silt/clay and T.O.C., and for the distribution of living foraminifera.

Lastly, percent Reophax spp. was inversely correlated with total organic carbon, a relationship that is slightly puzzling. It indicates that an increase in T.O.C. is in some way more favorable for many genera than for Reophax.

The "evenness" measure of diversity showed no correlation with the four environmental factors.

Although foraminiferal distributions overall were not directly correlated with depth, another bathymetric parameter, namely submarine topography, does influence foraminiferal numbers. Samples collected from "ridge" stations (B2, C2, D1, and E1) invariably had smaller populations than those collected from "swale" stations (B3, C4, D4, and E4). Table 8-13 shows the averages for each year of the study as well as the averages for the two-year period. Using the t-test, the difference in population size between ridges and swales was statistically significant at the 1% level. The same is true for empty test data; the average number of tests on the ridges was 386 per 20 cm^3, and the average in the swales was 3,599 per 20 cm^3. This, too, is statistically significant, at the 2% level. Unquestionably, living and empty test populations were larger in the swales than on the ridges. Three explanations seem possible: 1) living conditions in the swales are more favorable than on the ridges for foraminifera; 2) forams are being swept by currents from ridges into swales, where they collect; or 3) foraminiferal tests are destroyed more rapidly in ridges than in swales. All three of these explanations probably apply, but the latter two certainly are important because empty tests of planktonic forams also are more numerous in the swales, and planktonic species, of course, are not influenced by benthic environmental conditions.

Ratios of numbers of living forams to numbers of empty tests may be used to indicate relative rates of sedimentation, but these ratios also may reflect differences in rates of removal by destruction or transportation of empty tests. With rapid deposition, the empty tests are diluted with more sediment than with low deposition. For a given volume of sediment and number of living forams, regions of rapid deposition will have fewer empty tests (denominator in the ratio) and the L/E ratios, therefore, will be larger. However, the same result could be obtained if foraminifera were differentially removed from the sediment. If empty tests were destroyed or winnowed from the sediment more readily that living specimens, the L/E ratio would be increased. Sandifer (1969, unpublished ms) has demonstrated that dead specimens of Elphidium clavatum and Ammonia tepida settle in standing water at about the same rate as fine to very fine sand. Little, if any, fine sand is found on the submarine ridges. It is suggested that winnowing and test destruction may account for the fact that the average L/E ratios are larger for all ridge stations than for all swale stations.

Table 8-13. Comparison of number of live foraminifera per 20 cm^3 on ridges and in swales. Sediment data from second year only.

	Cluster Station	Mean No. live/20 cm^3 1975-1976	1976-1977	Two-year mean	Sediment Silt/Clay %	T.O.C. mg/g
RIDGE	B2	45	130	88	0.57	0.49
	C2	34	106	70	0.32	0.43
	D1	34	58	46	0.41	0.46
	E1	79	96	88	0.54	0.54
			AVERAGE	73	0.46	0.48
SWALE	B3	185	760	473	6.54	2.34
	C4	62	255	159	13.25	2.76
	D4	285	449	367	5.34	1.54
	E4	121	312	217	4.68	1.98
			AVERAGE	304	7.45	2.16

Living foraminifera probably are not so readily winnowed because they are loosely joined to the substrate, either temporarily or permanently. The existence of larger number of living foraminifera in swales than elsewhere would, therefore, indicate that swales are a preferred habitat. The differences in numbers of empty tests, however, is complicated by the "transportation/destruction" factor. One would expect the lighter components of the substrate (foraminiferal tests, silt/clay, organic debris) to be physically winnowed from the topographically elevated regions (ridges) and deposited, or "enriched" in the intervening swales. Furthermore, differential destruction of tests on the ridges (as compared with the swales) also may produce a relative enrichment of tests in the swales. The "enrichment factor" for empty tests of benthic forams is about 15 (that is, for every empty test found on the ridges, 15 are found in the swales); for tests of planktonic forams, it is about 12; and for silt/clay it is about 15. For benthic forams this "enrichment" is, perhaps more importantly, a function of the difference in the sizes of living populations between swales and ridges.

DISCUSSION

Living populations of foraminifera during the second year of study were larger and more diverse than those of the first year. As seen from Table 8-3, second-year populations were nearly three times as large as first-year populations. Consistent with results from the first year, the shelf break continued to support the largest populations, with densities averaging 655, and as large as 5,500 per 20 cm^3 (about 2.8×10^6 per m^2); and the central shelf supported the smallest populations, with densities averaging less that 50 per 20 cm^3. Standing crops (densities of living populations) do not differ much from standing crops in some bays and on continental shelves elsewhere, as may be seen by comparing "I" with "D", "E" and "F" in Figure 8-6 (densities expressed in numbers of living forams per 10 cm^3). These data (from Phleger 1976) suggest that foraminiferal faunas from the nearshore turbulent zone of the west coast, from the Gulf of Panama, and from Todos Santos Bay are similar to those found on the shelf in this study. Most of the samples contained fewer than 100 living specimens per 10 cm^3, while a few yielded much larger populations. With two years of data one can see little in the temporal changes in population size that is convincingly seasonal. Some species, and consequently total living populations too, reached their maximum densities in spring 1977, when most species occurred in larger numbers than at any other time during the two-year period. The factors (physical-chemical changes, biotic interactions, algal blooms) influencing this population increase have not been established. In the first-year set of samples, average total numbers were nearly unchanged until the summer of 1976 when population sizes dropped appreciably.

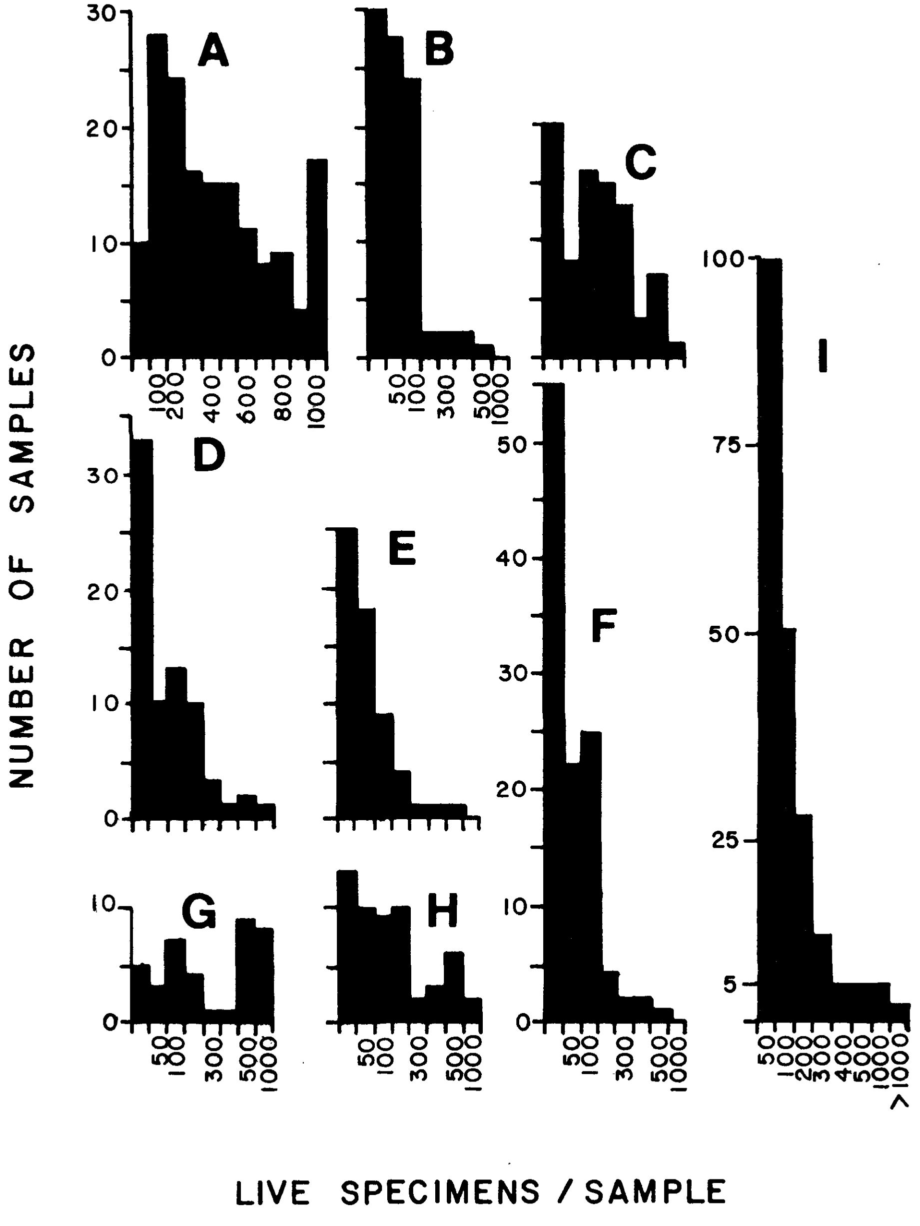

Figure 8-6. Frequencies of standing crops of benthic foraminifera (numbers of living forams per 10 cm^3) on some continental shelf areas (A-H from Phleger 1976). (A) Off San Diego (Uchio 1960). (B) Off central Texas (Phleger 1956). (C) Off central Oregon (Boettcher 1967). (D) Nearshore turbulent zone, western North America (Lankford and Phleger 1973). (E) Gulf of Panama (Golik 1965). (F) Todos Santos Bay, Mexico (Walton 1955). (G) Eastern Mississippi Delta (Lankford 1959). (H) Eastern Gulf of California (Phleger 1965). (I) New Jersey-Maryland (present study).

A large fraction of the foraminifera was agglutinate (more than 34%); and this fraction was greatest at depths of 50-100 m. Because *Reophax* was such a widespread agglutinate genus on the shelf, the proportions of *Reophax* in the various biotopes are summarized and averaged in Table 8-14. With regard to the biotopes, *Reophax* was most important in the swales and least important on the inner shelf and at the shelf break for both years. The proportion of the total population that is composed of *Reophax atlantica* (by far the most dominant of the *Reophax* spp.) changed relatively little through the year, although it seemed to favor the winter.

Foraminiferal faunas were moderately diverse, with an average of about 20 species per sample; but diversity as expressed in numbers of species, Shannon's H', or "evenness" showed no consistent trend with environmental factors. Areas at the outer shelf-shelf break contained the most diverse faunas, and those in the inner and central shelf had the least diverse faunas. Species belonged principally to the suborders Textulariina and Rotaliina and form several assemblages (as defined by cluster analysis). The most widespread and, therefore, the least diagnostic ecologically, was species group 1 consisting of six of the most abundant and ubiquitous foraminifera--*Reophax atlantica*, *R. curtus*, *Eggerella advena*, *Cibicides lobatulus*, *Bulimina marginata*, and *Fursenkoina fusiformis*. Other species groups or assemblages were more confined geographically on the shelf, and, therefore, may be more useful in habitat delineation.

Correlations were found between two environmental parameters (amount of organic carbon and percent silt/clay) and two foraminiferal measures (population size and percentage of agglutinate specimens). These results relate to those obtained from the ridges and swales: swales are sites of larger populations of foraminifers (as compared with ridges) and also are sites of accumulation or greater amounts of organic carbon and silt/clay.

Summary of Significant Findings

1. Size and composition of the foraminiferal fauna ranged from fewer than 10 per 20 cm^3 (in the upper 3 cm of substrate) to over 5,500, averaging approximately 200 cm^3; the average number of species per sample was about 20.

2. *Reophax atlantica* was, by far, the most abundant and ubiquitous foram, and its fluctuations strongly influenced numerical fluctuations of the foraminiferal community as a whole. Other very abundant species included *Cibicides lobatulus*, *Eggerella advena*, *Elphidium excavatum clavatum*, and *Fursenkoina fusiformis*.

3. Foraminiferal faunas can be classified into three bathymetric zones that correspond with the six biotopes that were recognized on the basis of macrobenthic data: 1) an inner zone including

Table 8-14. Percentages of *Reophax* spp. for biotopes.

	Fall	Winter	Spring	Summer	$\bar{X}$
Inner Shelf					
1975-1976	0	1	1	1	1
1976-1977	3	0	1	0	1
Central Shelf					
1975-1976	10	57	27	21	29
1976-1977	26	22	28	19	24
Inner & Central Shelf Swales					
1975-1976	69	46	93	65	68
1976-1977	67	59	33	35	49
Outer Shelf					
1975-1976	20	66	51	35	43
1976-1977	61	47	46	26	45
Outer Shelf Swales					
1975-1976	23	68	62	40	48
1976-1977	64	55	48	58	56
Shelf Break					
1975-1976	5	15	19	5	11
1976-1977	26	21	7	11	16
$\bar{X}$					
1975-1976	21	42	42	28	33
1976-1977	41	34	27	25	32

the inner and central shelf biotopes characterized by *Elphidium* spp.; 2) an outer shelf zone, or outer shelf biotope characterized by *Reophax atlantica*, *R. curtus*, *Bulimina marginata*, and *Cibicides lobatulus*; and 3) a shelf break zone or biotope characterized by a more rotaliid fauna with such species as *Gyroidina soldanii*, *Hoglundina elegans*, and *Stainforthia compressa*. In addition, the faunas of the swales were different in many respects from those in other biotopes, principally in their greater numbers of *R. atlantica*.

4. Fluctuations in the sizes of populations comprising the foraminiferal community were not obviously seasonal.

5. Live/empty test ratios were larger on the inner to central-shelf areas, suggesting more rapid deposition there than toward the shelf break where ratios are smallest. The utility of these ratios as sedimentation rate indicators may be severely compromised by test removal through destruction and transportation.

6. Statistically significant differences existed between foraminiferal faunas on the ridges and those in the swales. Both living individuals and empty tests were more numerous in the swales, probably as a combined result of environmental preference, transportation, and selective destruction of tests or ridges.

7. Numbers of living foraminifera and percentages of agglutinate forams both correlated significantly with percent silt/clay and amount of organic matter (T.O.C.) in the sediment, but only percentages of agglutinates was related to depth.

8. Periods of greatest susceptibility to environmental disruption were late summer to early fall (August-November), when populations were smallest, and late winter to early spring (February-April), when populations were largest.

9. Regions of greatest susceptibility to environmental disturbance were swales, where finer or lighter materials accumulate.

10. Taxa most susceptible to environmental disturbance are agglutinate forminifera because: 1) they are more abundant in the swales and the central shelf near the lease areas; and 2) their ability to construct tests from sediment could be hampered by sediment contamination.

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