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Distribution of macrobenthic mollusca and amphipoda in relation to a sharp thermal front: Cape Hatteras region, North Carolina

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DISTRIBUTION OF MACROBENTHIC MOLLUSCA AND AMPHIPODA IN RELATION TO A SHARP THERMAL FRONT: CAPE HATTERAS REGION, NORTH CAROLINA

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

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

by
Donald P. Weston
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APPROVAL SHEET

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ABSTRACT

Investigations were conducted on the North Carolina continental shelf in depths of 29 to 54 m during the period May 31 - June 14, 1977. Sampling areas were established within three thermal regimes: 1) a stable warm area in Raleigh Bay, 2) a stable cool region north of Oregon Inlet and 3) a highly dynamic thermal front northeast of Cape Hatteras. This front was found to migrate frequently and rapidly, exposing the benthos to daily rapid and unpredictable temperature changes.

A total of 106 0.1 m^2 Smith-McIntyre grab samples were taken in the study area, and identifications were made of all macrofaunal Mollusca (94 spp.; 8,291 individuals) and Amphipoda (53 spp.; 3,682 individuals). Analysis of species distributions indicates strong sediment specificity in both groups, at times masking any thermal response. Other factors implicated in delimiting distributions of some species include biotic interactions, planktonic dispersal of larvae and adults and concommitant temperature-salinity variation. Temperature exerts a dominant influence on the distributions of most species, especially those of southern affinity which have their northern distribution limit off North Carolina.

Assessment of the effectiveness of several possible zoogeographic barriers indicates the existence of partially effective barriers at Cape Hatteras and the observed position of thermal front, though both of these are overshadowed by the faunal changes which occur in Raleigh Bay, between Cape Lookout and Cape Hatteras. This faunal change seems to be in response to seasonal incursions of cool Virginian water around Cape Hatteras and into the northern and inshore portions of Raleigh Bay. This phenomenon is of greatest importance in establishing a northern limit for southern species. The northern species are generally eurythermal and are not restricted by a thermal discontinuity in the Cape Hatteras region.

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INTRODUCTION

The geographical range of any given species is determined by a wide variety of evolutionary, physical and biotic factors, but often the most important among these is temperature. Kinne (1963) stated, "Temperature and salinity are two of the most potent physical factors in the life of marine and brackish water organisms." Gunter (1957) declared that "temperature is the most important single factor governing the occurrence and behaviour of life."

Since temperature is so critical in determining occurrence of a species, it follows that where a temperature change occurs, a corresponding change in species composition should also be found. A good example of this correlation can be found in the shelf waters of the continental shelf waters off North Carolina. Here one finds the Gulf Stream closer to the coast than any point north of Cape Canaveral. In close proximity lies the Virginian coastal water, which can reach temperatures as low as 4°C at shelf depths off North Carolina (Walford and Wicklund, 1968). Paralleling the change in water type, a rapid latitudinal change of fauna in the North Carolina area has been recognized for over a century. First described by Dana (1853) and further substantiated by numerous other authors, North Carolina, and Cape Hatteras in particular, has become a classic example of a biogeographic barrier (Ekman, 1953; Briggs, 1974).

With few exceptions, nearly all distributional studies of the marine fauna of the eastern United States have demonstrated a distributional discontinuity at Cape Hatteras. Molluscs, a group often used in biogeographic studies, have frequently been shown to have a strong response to Cape Hatteras as a faunal barrier. Warmke and Abbott (1961) considered Cape Hatteras to be the northern limit of the Caribbean molluscan fauna, while Bousfield (1960) recognized it as the southern boundary of the boreal molluscan province. Coomans (1962) also considered it as a major molluscan barrier as did investigators working on specific molluscan groups such as scaphopods (Henderson, 1920) and opisthobranchs (Franz, 1970).

Polychaetous annelids frequently have the widest distributions among macrobenthic invertebrates (Thorson, 1950) and consequently many species have been shown to have distributions which transcend Cape Hatteras (Wells and Gray, 1964). Even so, a significant portion of the species are limited at North Carolina (49% according to Wells and Gray, 1964 and 26% according to Gardiner, 1976).

Among the Crustacea, calanoid copepods of the mid-shelf have been found to be limited at Cape Hatteras (Bowman, 1971). Amphipods collected in the estuaries of North Carolina (Fox and Bynum, 1975) are largely wide-ranging species with few (17%) showing distributional limits in North Carolina waters. However, as Fox and Bynum pointed out, the dispersal opportunities provided by shipping, the connections between estuaries formed by the Intracoastal Waterway and the inherent eurytopy of estuarine animals are *a priori* reasons for expecting few effective distributional barriers for estuarine amphipods. In contrast, decapods from North Carolina estuarine and shelf waters respond strongly to a North Carolinian faunal barrier, particularly in the case of southern species (Williams, 1965). Williams found Cape Lookout to be a more effective barrier than Cape Hatteras, a fact which he postulated to be an artifact of inadequate sampling. However, further work in this area, based largely on collections made in conjunction with the present study, has supported Williams' initial observations (Herbst et al., 1979b).

Other studies citing Cape Hatteras or the North Carolina region as a significant faunal barrier include those on benthic algae (Taylor, 1957), foraminifera (Cushman, 1918), sponges (Wells et al., 1960), chaetognaths (Pierce, 1953) and sipunculans (Cutler, 1975).

Despite the frequent reference to a Carolinian faunal barrier, surprisingly little work has been done in the North Carolina region with the specific intent of testing the reality and effectiveness of this barrier or the mechanisms involved in its establishment. Work by Cerame-Vivas and Gray (1966) provides the most notable exception. In particular, few collections of invertebrates in the vicinity of Cape Hatteras have been made, with most of the sampling effort concentrated near Cape Lookout because of its proximity to several marine laboratories. It is the intent of this study and ongoing investigations to fill these gaps in our knowledge of the shelf fauna off North Carolina. Five specific goals are outlined:

1. Describe the physical and geological regimes of the Cape Hatteras shelf region and their roles in determining the macrobenthic faunal composition;
2. Determine the location and effectiveness of faunal barriers for the benthic Amphipoda and Mollusca in North Carolina waters;
3. Describe the local distribution patterns of some representative species in both taxa;
4. Examine the benthic community structure at the juncture of two water masses, an area where the benthos is exposed to rapid and unpredictable temperature fluctuations; and
5. Compare the distribution and diversity patterns of the Amphipoda and Mollusca, as related to their evolutionary histories and modes of reproduction.

Characteristics of North Carolina Offshore Waters

Physical Environment

The hydrography of the North Carolina shelf region is quite complex because of the cape-associated shoals which extend far out from the coast and to the close proximity of several water masses. Much attention has been devoted to the area, largely in connection with studies of the shoreward margin of the nearby Gulf Stream.

Originating in the Gulf of Mexico, the Gulf Stream passes through the Straits of Florida and moves northward, parallel to the coast of the southeast United States. The Gulf Stream is also known as the Florida Current in this region. The main body of the water mass overlies the continental slope and the Blake Plateau, though meanders may result in interaction with mid-shelf waters. As the shelf narrows to the north, the Gulf Stream moves closer to the coast to a point where its inner edge lies approximately 40 km off Cape Lookout and only 37 km off Cape Hatteras (Stefansson and Atkinson, 1967), at times crossing Diamond Shoals in as little as five meters of water (Parr, 1933). North of Cape Hatteras, the Gulf Stream turns to the east, moving away from the coast.

The most readily recognizable characteristics of Gulf Stream water are the high salinity and high temperature of surface waters. Salinity is generally 36 ^{o}/oo or greater (Stefansson and Atkinson, 1967). Surface temperature is high throughout the year with little seasonal variation, ranging from 20 to 23°C in winter and 25 to 29°C in late summer off the North Carolina coast (Steffansson and Atkinson, 1967).

Interaction of Gulf Stream and shelf water is accomplished by two mechanisms. Gray and Cerame-Vivas (1963) postulated back eddies of Gulf Stream water in both Onslow and Raleigh Bay, due to deflection of a portion of the water mass by the shoals off the capes. This hypothesis was substantiated in work by Stefansson and

Atkinson (1967) who found these back eddies consistently throughout the year.

A second mechanism for interaction of Gulf Stream and shelf water in the North Carolina region is frequent meanders of the Gulf Stream over broad areas of the shelf, particularly in Raleigh Bay (Bumpus, 1955). South of Cape Hatteras, meanders of varying magnitude have been observed by numerous investigators (Bumpus and Pierce, 1955; Webster, 1961; Blanton, 1971; Stefansson et al., 1971). The position and movement of these meanders are regularly photographed and tracked as part of the Experimental Ocean Frontal Analysis Program of the United States Naval Oceanographic Office.

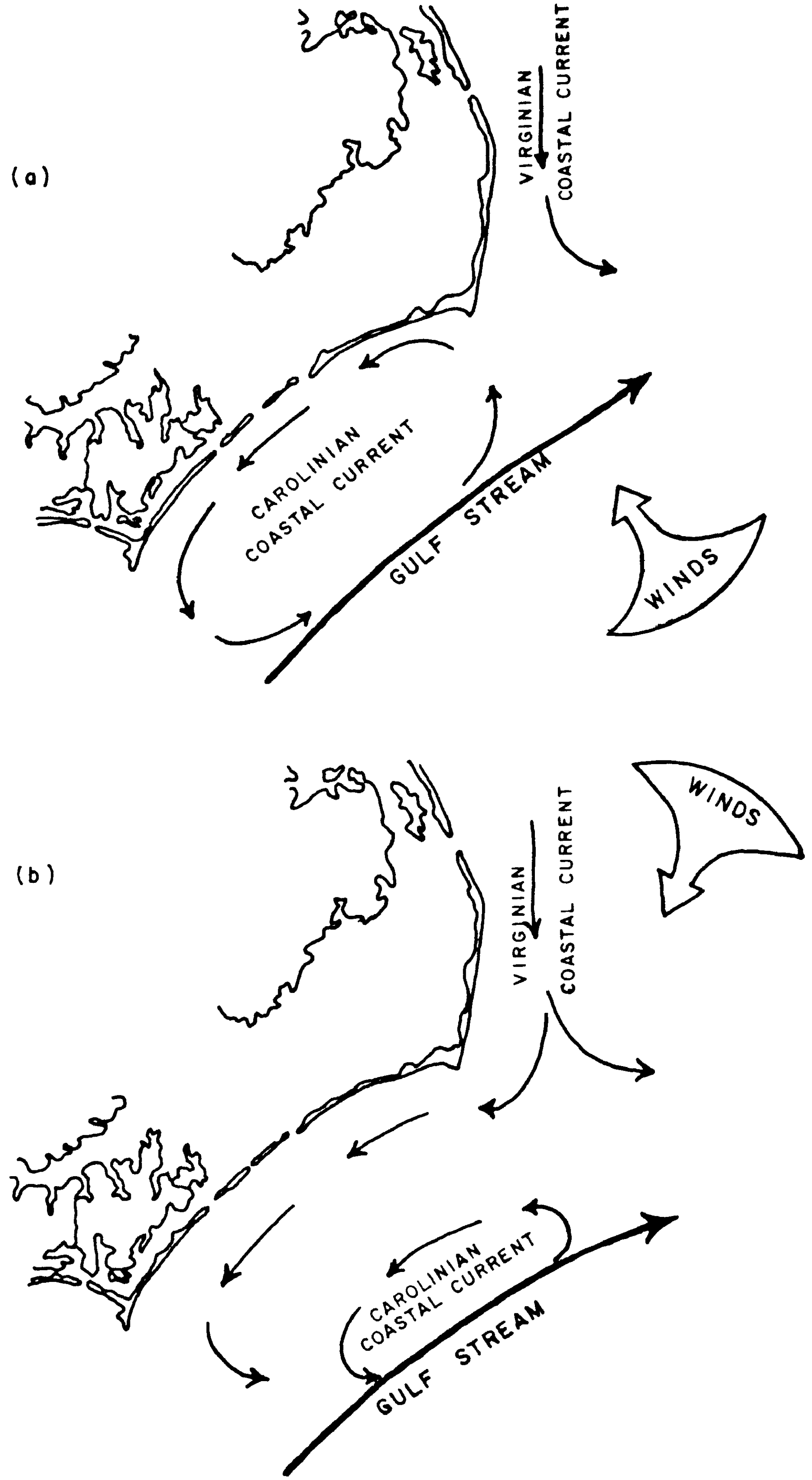
North of Cape Hatteras, the shelf is occupied by the Virginian Coastal Current. In contrast to the Gulf Stream, salinities never exceed 35 $^{o}/oo$ and the annual temperature range is much broader, varying between 4 and 24°C for both surface and bottom waters off North Carolina (Cerame-Vivas and Gray, 1966; Stefansson and Atkinson, 1967).

Flowing south from New England, the Virginian Coastal Current occupies most of the shelf off the Middle Atlantic Bight. Upon reaching the Cape Hatteras region, much of the water mass turns seaward and is entrained along the north wall of the Gulf Stream (Ford et al., 1952; Fisher, 1972; Bumpus, 1973). Depending on prevailing wind conditions however, some may flow over Diamond Shoals and into Raleigh Bay or even into Onslow Bay. This flow is enhanced by moderate to strong northeasterly winds (Wells and Gray, 1960; Gray and Cerame-Vivas, 1963; Hunt et al., 1977).

The continental shelf south of Cape Hatteras is overlain by the Cardinian Coastal Current. This water mass is of Gulf Stream origin, later modified by runoff from the sounds of the North Carolina coast. The relative contribution of the later source determines the salinity of the Carolinian shelf water, which may vary from 30 to 36 $^{0}/oo$ (Stefansson and Atkinson, 1967). Temperature of the Carolinian coastal water is strongly related to depth; however at 30 m, a low temperature of 16°C in January and a high temperature of 26°C in August were recorded (pers. observation). Inshore temperatures can reach a low of 10°C (Stefansson and Atkinson, 1967).

The direction of flow of the Carolinian shelf water, a subject of some debate, seems to be variable over time. Bumpus (1955), on the basis of theoretical considerations and surface drift bottle returns, postulated a northward flow over most of the shelf, interrupted only infrequently by reversals caused by northeast storms with unusually high runoff. On the other hand, Gray and Cerame-Vivas (1963), working only on the inner shelf, found a southward flow by the use of surface drift bottles released both in April and August, 1962. They postulated that the southward flow was much more prevalent than originally believed and that only moderate northeast winds were necessary to force Virginian water over Diamond Shoals. The surface currents suggested by Gray and Cerame-Vivas for Raleigh Bay and for much of the North Carolina shelf are shown in Figure 1.

Figure 1. Surface currents postulated for shelf waters of the Cape Hatteras region, North Carolina. (a) southerly and southeasterly winds prevailing, (b) northerly and northeasterly winds prevailing. (from Gray and Cerame-Vivas, 1963).



(a)
VIRGINIAN COASTAL CURRENT
CAROLINIAN COASTAL CURRENT
GULF STREAM
WINDS
(b)
VIRGINIAN COASTAL CURRENT
WINDS
CAROLINIAN COASTAL CURRENT
GULF STREAM

Bottom waters over much of Raleigh Bay and the area north of Cape Hatteras have been found to have primarily an onshore flow though there is much variation over time (Schumacher, 1974).

The Gulf Stream is the fastest ocean current, whereas both the Virginian and Carolinian Coastal Currents are comparatively sluggish. Owing to the shear induced by these different velocities, the juncture of Gulf Stream and shelf waters is characterized by an abrupt and highly dynamic thermal front. In Onslow Bay, Menzies et al. (1966) observed a sharp thermal gradient in the surface waters of 10°C in 0.2 km. The dynamic nature of this front was indicated by its absence on a thermistor trace taken ten days later in the same area. Blanton (1971), working in the same region years later, found a surface front to move 11.3 km/day and the corresponding bottom water front to migrate 10.6 km/day.

North of Hatteras, the Virginian water - Gulf Stream front is equally as dynamic. Its movements have been recorded to be as rapid as 4.6 km/day (Cook and Kosmark, 1977), 18.3 km/day (Cook et al., 1977) and 26 km/day (J. Magnuson, pers. comm.). The most detailed information on the structure of the front in this area was gathered in 1975 and 1977 by Magnuson (pers. comm.). Bottom temperatures were found to change up to 12°C over a distance of less than one kilometer, with an accompanying change in salinity of 4 to 5 $^{o}/oo$. Little evidence of the front was found in the surface isotherms as it was obscured by a lens of cool, brackish water originating in the sounds along the Carolina coast.

Biological Environment

Just as the physical environment of North Carolina shelf waters is complex, and partially as a result of this complexity, the biological environment too is quite variable. Even at a constant depth, shelf sediments can range from very fine sands, often with anaerobic conditions within less than one centimeter of the sediment surface, to hard reef-like substrates of Trent Marl encrusted by a variety of small corals, encrusting algae, and calcareous annelid tubes (Pearse and Williams, 1951). Each substrate type provides a habitat for a particular faunal assemblage. The temperatures encountered in the various water masses of the region provide thermal regimes suitable for both sub-tropical species (Warmke and Abbott, 1961) and cold water species (Cerame-Vivas and Gray, 1966).

The warm water fauna of Onslow and Raleigh Bay has received the most attention in the past, little collecting being done on the North Carolina shelf north of Cape Hatteras. One of the earliest attempts to describe the offshore fauna was by Pearse and Williams (1951) who examined the fauna associated with Trent Marl reefs in Onslow Bay. Carolinian coastal water can be assumed to be the dominant if not the sole influence on the hydrography of the area, since they were all in less than 17 m of water, and within 11 km of the coast. It was found that most species (47%) were of southern affinity, ranging only southward from North Carolina. The next highest percentage (32%) was composed of widespread species. (These percentages should be viewed with caution for Pearse and Williams (1951) have numerous internal inconsistencies in their geographic distribution data, as Wells et al. (1964) pointed out.)

Further offshore, Menzies et al. (1966) examined another hard substrate habitat formed by Lithothamnion, a reef-building calcareous alga. The Gulf Stream was found to overlie this structure, located 70 km offshore at 80 to 100 m depth. Southern species made up 91% of the fauna, 4% were northern and the remainder were widely distributed in the western North Atlantic.

Partially because of its economic importance, the calico scallop, Argopecten gibbus, has been the subject of several studies in the Onslow Bay area. It provides a hard substrate for attachment in an otherwise sandy environment, thus its valves are encrusted with a surprising array of invertebrate species. In examining the community living on the scallop valves, Wells et al. (1964) found 112 species, many of which were tropical or sub-tropical, and absent from inshore waters. 49% were distributed from North Carolina southward, and another 31% were widespread along the western Atlantic coast. Only 3.6% of the species were classified as of northern affinity.

A basic ecological concept, and one of great importance to the present study, is that of increased species diversity in habitats having the greatest environmental constancy. This relationship has been demonstrated in two studies conducted off the North Carolina coast. Grassle (1967), in a comparison of soft-bottom habitats of the continental shelf and slope, noted an increased diversity at the deeper stations. He attributed this to the environmental constancy of the deeper areas as compared to the shelf stations which are exposed to greater variation in temperature and other physical variables.

Day et al. (1971) undertook seasonal sampling of a transect trending southeast off Cape Lookout at depths of 0 to 205 m. On the basis of the macrobenthos, they were able to group the stations into four biotic zones: the open sandy beach, the turbulent zone (0-20 m), the outer shelf (40-120 m) and the upper slope. These zones were arranged on a physical stress gradient as well, since the shallower stations were subjected to greater wave action and daily and seasonal variation in temperature. The environmental constancy-stability relationship was found to hold in this instance as well.

Cerame-Vivas and Gray (1966) were the first to examine the benthos of the North Carolina shelf with the intent of delineating zoogeographic barriers. They established three biogeographic areas on the shelf, roughly corresponding to the location of the three water types discussed earlier. On the inner shelf, Cape Hatteras served as a formidable barrier between the northern and southern fauna. The outer shelf, the area primarily under direct and constant influence of the Gulf Stream, showed no faunal barrier at Cape Hatteras, but retained a uniform faunal assemblage to near Oregon Inlet where the Gulf Stream leaves the shelf. Their conclusions will be examined later to illustrate certain parallels between the present study and their work.

As preliminary work to the current research, Magnuson (pers. comm.) conducted trawling over much of the northern North Carolina shelf. As this early work was not so broad in scope as ongoing investigations, decapod crustaceans were the only invertebrate taxon closely examined. This group did not show any abrupt distributional response to the Gulf Stream - Virginian water front previously discussed. No pronounced faunal barrier at either Cape Hatteras or the thermal front 35 km north of the Cape was observed. Rather, a gradual faunal change was evident, extending over a broad region from Cape Hatteras to off of Oregon Inlet.

METHODS

Sampling Area

Samples were collected during the period May 31 - June 14, 1977 on board the R/V Eastward, a 118 ft. side trawler operated by the Duke University Marine Laboratory, Beaufort, North Carolina. The sampling area, illustrated in Figure 2, extended for 165 km along the North Carolina coast from Cape Lookout to slightly north of Oregon Inlet. Sampling areas were all established near the 30 m depth contour to minimize the effects of bathymetric faunal variation. Since sediment type may vary with depth on the continental shelf (Newton et al., 1971), the narrow depth range also reduced sediment variability. However, the effect of local bottom topography on sediment distribution remains an important factor.

The South area was located in Raleigh Bay in an area predominantly influenced by the Carolinian coastal water, though the Gulf Stream may periodically inundate the region. The Hatteras stations were subdivided into three strata located to the south, east and north of Diamond Shoals. This area may be influenced by any of the three water types at different times of the year. During June, 1975 it was found to be a mixing zone of Carolinian and Gulf Stream water (J. Magnuson, pers. comm.). Virginian water may also invade

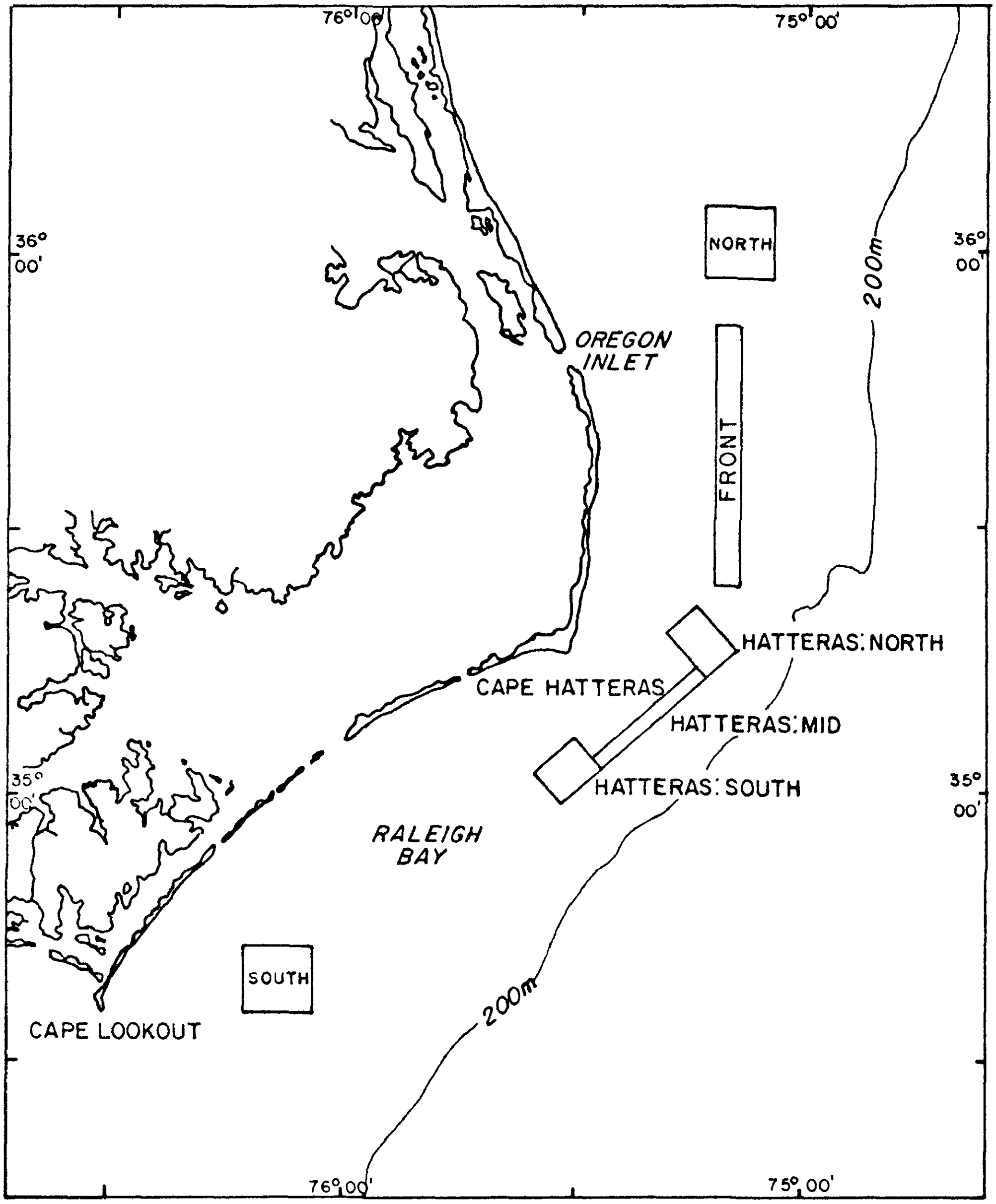


Figure 2. Location of sampling sites on the North Carolina continental shelf. All sites located in 30 - 42 m water depth.

the Hatteras strata, particularly during the winter months (pers. observation). The North area, located 83 km north of Cape Hatteras, is occupied by Virginian water throughout the year.

The thermal front was sampled by systematic collection along a transect extending from slightly north of Cape Hatteras to a point east of Oregon Inlet. Unlike the other areas, the location of which had been established prior to the cruise, the location of the frontal transect was determined only after much time had been spent studying the structure and migrations of the front. During the early portion of the cruise, the location of the front was found to oscillate six kilometers to the north and south of latitude 35°39.0'N. The frontal transect extended 29 km to the south and 23 km to the north of 35°39.0'N latitude along longitude 75°13.0'W. Twenty stations were established along this transect, spaced 1.8 to 3.7 km apart. Each station is designated by minutes latitude north of 35°00.5'N (e.g. Front:27').

Biological Sampling Procedure

Macrofaunal sampling was done using a 0.1 m^2 Smith-McIntyre grab. Eight grab samples were taken at random within each area other than the front. Three grab samples were taken at each of the twenty front stations with the exception of the station at 35°39.5'N which was visited three times during the cruise resulting in nine grabs taken at this point.

After retrieval of a sample, maximum depth of penetration, sediment temperature, and depth and appearance of the reduction potential discontinuity (RPD) were measured. Depth of penetration was between 5 and 12 cm. Any samples obtained with less than 5 cm were discarded. A core sample was taken from the grab for sediment grain size analysis, and the remaining material saved for biological analysis. The biological sample was placed in an elutriation apparatus and washed with seawater while constantly being stirred, until no more organisms could be seen overflowing the container. The sea water in the container was periodically decanted to facilitate removal of macrofauna, as many tended to remain at the sediment-water interface. Organisms from the overflow were collected on a removable 0.5 mm mesh Nitex screen mounted in the bottom of the apparatus, which was then placed in a cloth bag and submerged in 6.5 % $MgCl_2$ for approximately 30 minutes to anesthetize the organisms. The remaining sediment was then washed on a 1.0 mm mesh screen. This 1 mm fraction was similarly relaxed in $MgCl_2$ and then both fractions were transferred to 10% formalin buffered with borax. Rose Bengal, a vital stain, was later added to the formalin to aid in the sorting process.

In the laboratory, the macrofauna was removed from the elutriated portion by examination under a dissecting microscope. The 1.0 mm sieved fraction, usually composed of very coarse sediment and heavy organisms such as large molluscs, was again elutriated in the laboratory and the remaining material sorted by eye. The double washing procedure (i.e. elutriation through a 0.5 mm mesh followed by sieving through a 1.0 mm mesh) is highly efficient in that all sediment finer than coarse sand is lost, yet there is near total recovery of the macrofauna. Most organisms are removed during elutriation with only the heavier organisms, which are generally larger than 1.0 mm, retained on the coarser screen.

Statistical Analysis

Several indices of community structure were employed in data analysis of the biological collections. Diversity was measured using Shannon's formula (Pielou, 1966):

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

where p_i are the proportion of the i-th species and s equals the number of species in the sample. This index is dependent on both the number of species in the sample as well as their relative dominance. To examine these two parameters independently, species richness (S.R.) and evenness (J) were computed separately using the formulae:

$$S.R. = \frac{s-1}{\ln N} \qquad J = \frac{H'}{\log_2 s}$$

where N equals the total number of individuals. These indices, when calculated for an area, are based on the number of species and their cumulative abundances in all eight grabs taken. Likewise for the frontal stations, they represent the totals of all three grab samples taken at each station (nine grabs taken at 35°39.5'N).

In order to present the large data set in an interpretable form, as well as determine zones of rapid faunal change, numerical classification techniques were employed. Clustering was performed using the VIMS program COMPAH (Combinatorial Polythetic Agglomerative Hierarchical Program). Log transformation (log X-1) and the Bray-Curtis similarity measure (Bray and Curtis, 1957) were employed in the clustering. This similarity measure can be expressed as:

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

where, in normal clustering, S_{jk} equals the similarity between stations j and k, and X_{ji} and X_{ki} equal the abundances of species i in station j and k respectively. In inverse (species) clustering, the roles of the stations and species are reversed and S_{jk} becomes the similarity between species j and k.

The clustering hierarchy is in part determined by the sorting strategy chosen and its inherent degree of space dilation. Space-contracting strategies (e.g. nearest neighbor) tend to cause excessive chaining, in which, as a cluster grows, new entities are added to a few existing nuclear groups instead of forming new groups. The resulting dendogram is difficult to interpret as most entities must be treated as individuals. A space-dilating strategy (e.g. farthest neighbor) favors the opposite effect, in that, as new entities are joined to the cluster, they are more likely to form new groups. Space dilation causes intense clustering with minimal chaining.

With the small number of entities used for the normal cluster, a group average sorting strategy was employed because of its space-conserving properties (Sneath and Sokal, 1973, as "unweighted pair-group method using unweighted arithmetic averages"). Having characteristics intermediate between the contracting and dilating strategies discussed earlier, it induces a minimum of space distortion in the dendogram. However, in the larger data set of the inverse cluster, a space-dilating technique was found necessary in order to eliminate excessive chaining. Flexible sorting (Lance and Williams, 1967), with β established at -0.25, was used in the inverse cluster. This value of β, widely used in ecological research, induces a slight space dilation with moderately intense clustering.

To supplement the cluster analysis, the ordination technique of reciprocal averaging (Hill, 1973) was performed using the ORDIFLEX program (Gauch, 1977) with square root transformation of abundances. Reciprocal averaging was chosen over other forms of ordination as recent studies (Gauch et al., 1977) have demonstrated it causes less distortion in the ordination of simulated coenoclines. It also permits both species and station ordinations to be performed in the same space, a feature assisting in interpretation.

While cluster analysis is beneficial in delineating zones of similarity along a wide environmental gradient, ordination is advantageous in other respects. Ordination may be more desirable for establishing relationships among stations within a relatively homogeneous area. The multi-dimensional character of ordination allows a better appreciation of the inter-entity relationships than does the single axis of the cluster analysis. Interfacing the two techniques, such as by plotting the species groups derived from the cluster analysis in ordination space, may in some cases give added insight into biological relationships.

Physical and Geological Sampling

A wide variety of instruments was used in measuring the physical parameters of the waters in the study area, including a mercury thermometer, reversing thermometers, shallow water bathythermograph (BT), Hytech salinometer and Beckman salinometer. Temperature-salinity profiling was usually done using a CSDT (Conductivity-salinity-depth-temperature meter), though if this was inoperable, the Beckman salinometer was attached to the BT and lowered by intervals. In addition, surface temperature, as measured by a thermistor, was graphically recorded continuously throughout the cruise.

Sediment samples were taken by extracting a 3.5 cm diameter core from the sample obtained in the Smith-McIntyre grab. Cores were immediately frozen and remained so during transport to the University of Wisconsin where particle size distribution was determined. Samples were dried at 100°C and 100 gram aliquots obtained by using a sediment cutter. The material was sieved through a series of Standard Sieves (-6 to 4.0 ϕ at 1 ϕ intervals) with silts and clays combined as pan weight. Mean and median phi size, skewness, kurtosis and modes were determined using modified Inman measures (Inman, 1952).

Other parameters measured during the cruise but either unanalyzed at present or not discussed in this report include air temperature, barometric pressure, sea state, wind direction and velocity, dissolved and particulate organic carbon, dissolved O_2 and vertical light penetration.

RESULTS

Physical Results

The general temperature and salinity structure of the sampling area in early June, 1977 is illustrated in Table 1. (It should be noted that as intercalibration of instruments has not yet been completed, values of temperature and salinity are not yet considered final.) The North area was exceptional in its low salinity and temperature (31.46 $^{o}/oo$ and 12.8°C respectively for bottom waters). All other areas were more homogeneous in these respects, though the South region showed a warming of surface water and a slight cooling of bottom water. This was due primarily to local climatic conditions as no evidence of Gulf Stream intrusion into Raleigh Bay and over the South area was found at this time.

Vertical stratification was particularly well developed in the North area, with a 8.1°C difference in temperature between surface and bottom. The South area showed a 2.6°C vertical difference. All Hatteras strata showed little vertical stratification, never exceeding 1°C. This can be attributed to the turbulent mixing associated with Diamond Shoals. These shoals form a ridge in less than ten meters of water which extends halfway across the shelf off Cape Hatteras, creating turbulent mixing and surf action. Under

Table 1. Salinity and temperature (mean and range) of surface and bottom waters off North Carolina in June, 1977. Mean values are determined from 14-21 observations.

Area	Temperature (°C)		Salinity (^{o}/oo)	
	Surface	Bottom	Surface	Bottom
South	25.2 (24.7 - 25.8)	22.6 (21.9 - 23.6)	34.61 (33.32 - 35.88)	34.57 (33.95 - 35.55)
Hatteras:South	23.8 (22.6 - 25.0)	23.6 (22.4 - 24.4)	35.04 (33.51 - 36.05)	34.74 (33.90 - 35.56)
Hatteras:Mid	24.4 (21.7 - 25.5)	23.5 (22.1 - 24.7)	34.43 (34.41 - 35.86)	34.71 (33.28 - 35.38)
Hatteras:North	23.8 (22.6 - 25.1)	23.9 (23.2 - 24.9)	34.79 (32.20 - 35.70)	35.14 (34.32 - 35.94)
North	20.9 (19.7 - 22.0)	12.8 (10.5 - 14.6)	30.71 (27.36 - 31.41)	31.46 (30.58 - 32.13)

these conditions, little opportunity exists for development of vertical stratification.

The thermal front found in 1975 (J. Magnuson, pers. comm.) was relocated in the same general area, oriented primarily on a northeast - southwest axis. The temperature and salinity isoclines are shown in Figures 3-6 for two CSDT frontal transects made on longitude 75°13.0'W. The front happened to be near the same point on these two occasions though its vertical structure had changed somewhat and the isotherms were more vertical on June 8. A ten degree bottom water gradient was established across the front, temperatures varying from 14° to 24°C. Accompanying the thermal gradient was a salinity difference of 3 ^{o}/oo across the front (33 ^{o}/oo to 36 ^{o}/oo). Evident in the June 4 profiles is a surface lens of brackish water presumably originating from estuarine discharges as was the case in 1975 (J. Magnuson, pers. comm.).

The dynamic nature of the front is indicated in Figure 7, in which bottom temperature measurements made during five periods of frontal observation are shown. As the front moved somewhat during each observation period, the lines shown represent an average position of the front in the time interval indicated. Migrations over a 13 km latitudinal distance, with wide temperature fluctuations at any given point, are shown in the figure. For example the front station at 35°39.5'N had a bottom temperature of 20°C during the June 2-3 interval, had risen to 21°C by June 6-8, dropped to 16°C during June 8-9, and finally was 17°C on June 11-13.

Figures 3 - 6. Isotherms and isohalines found across the front on two transects along longitude 75°13.0'W. Solid dots indicate location of observations.

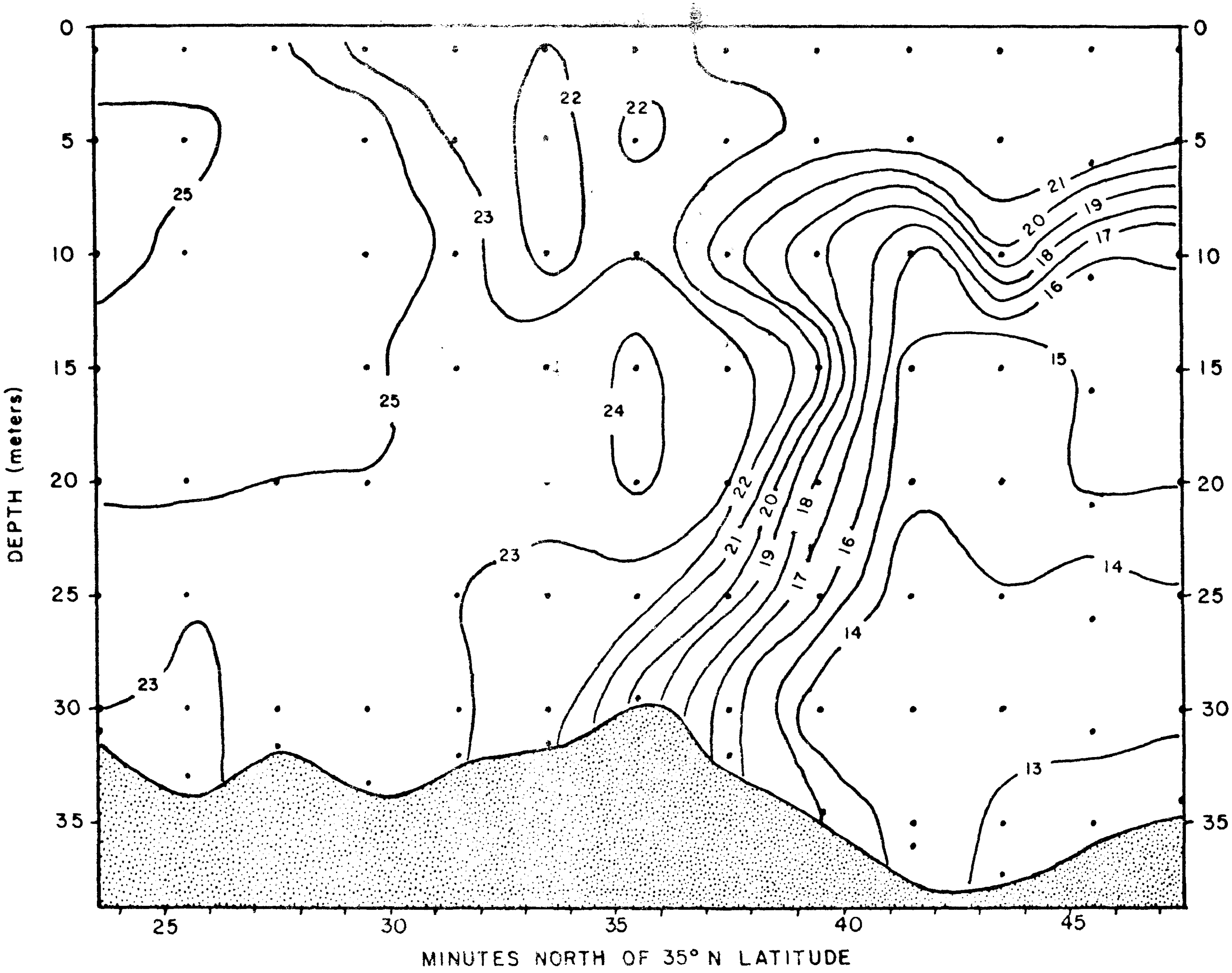


Figure 3. Isotherms observed June 4, 1977.

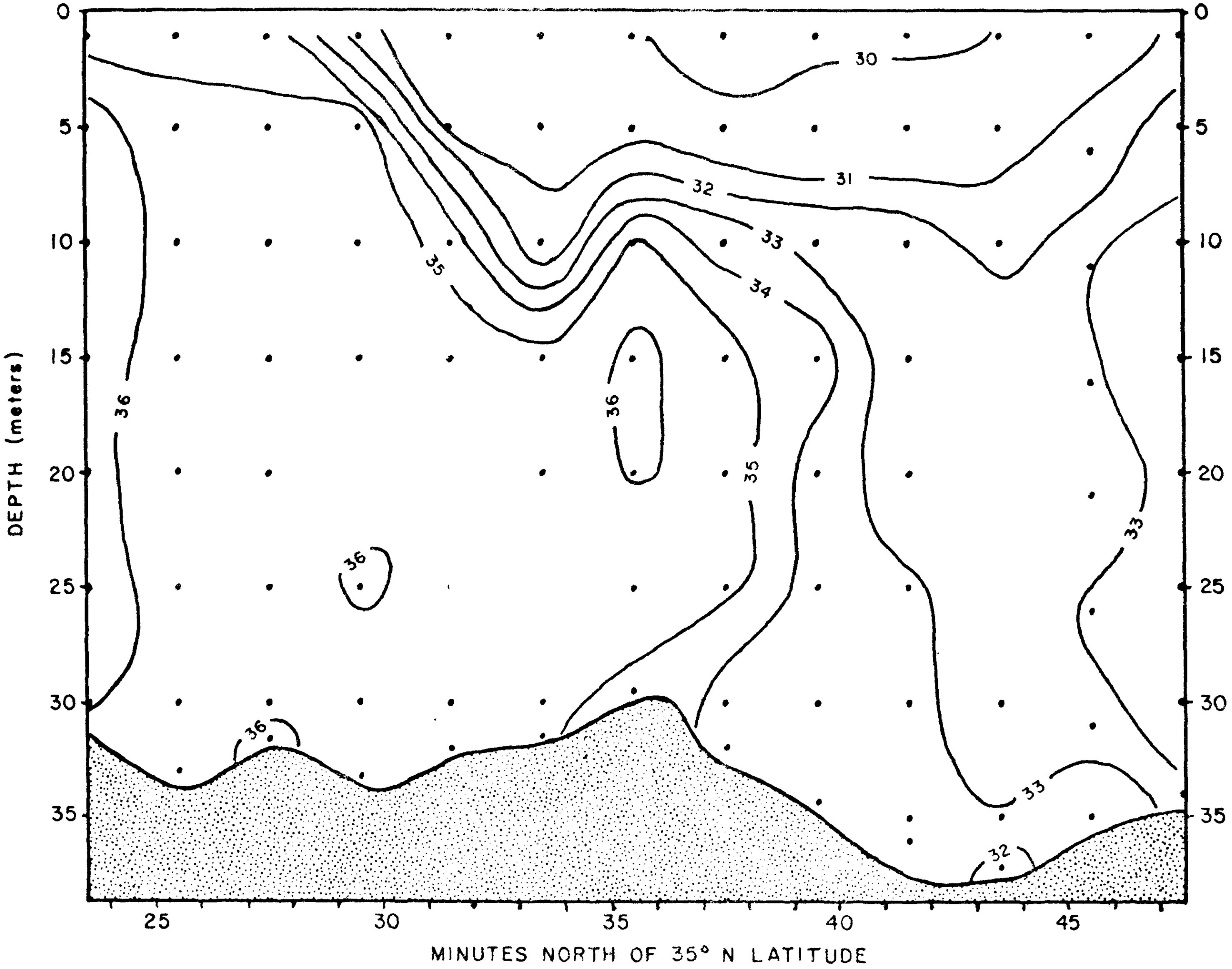


Figure 4. Isohalines observed June 4, 1977.

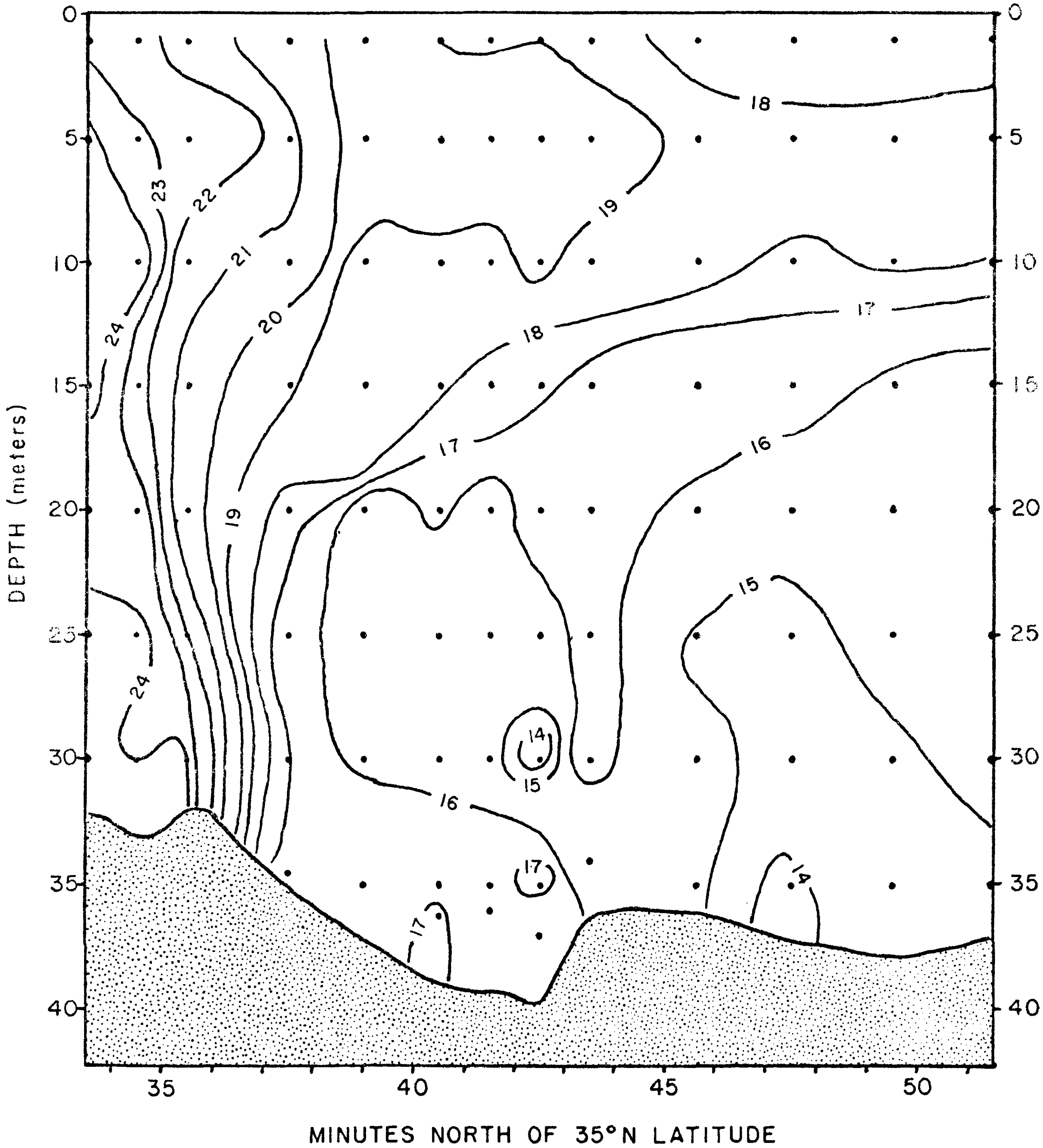


Figure 5. Isotherms observed June 8, 1977.

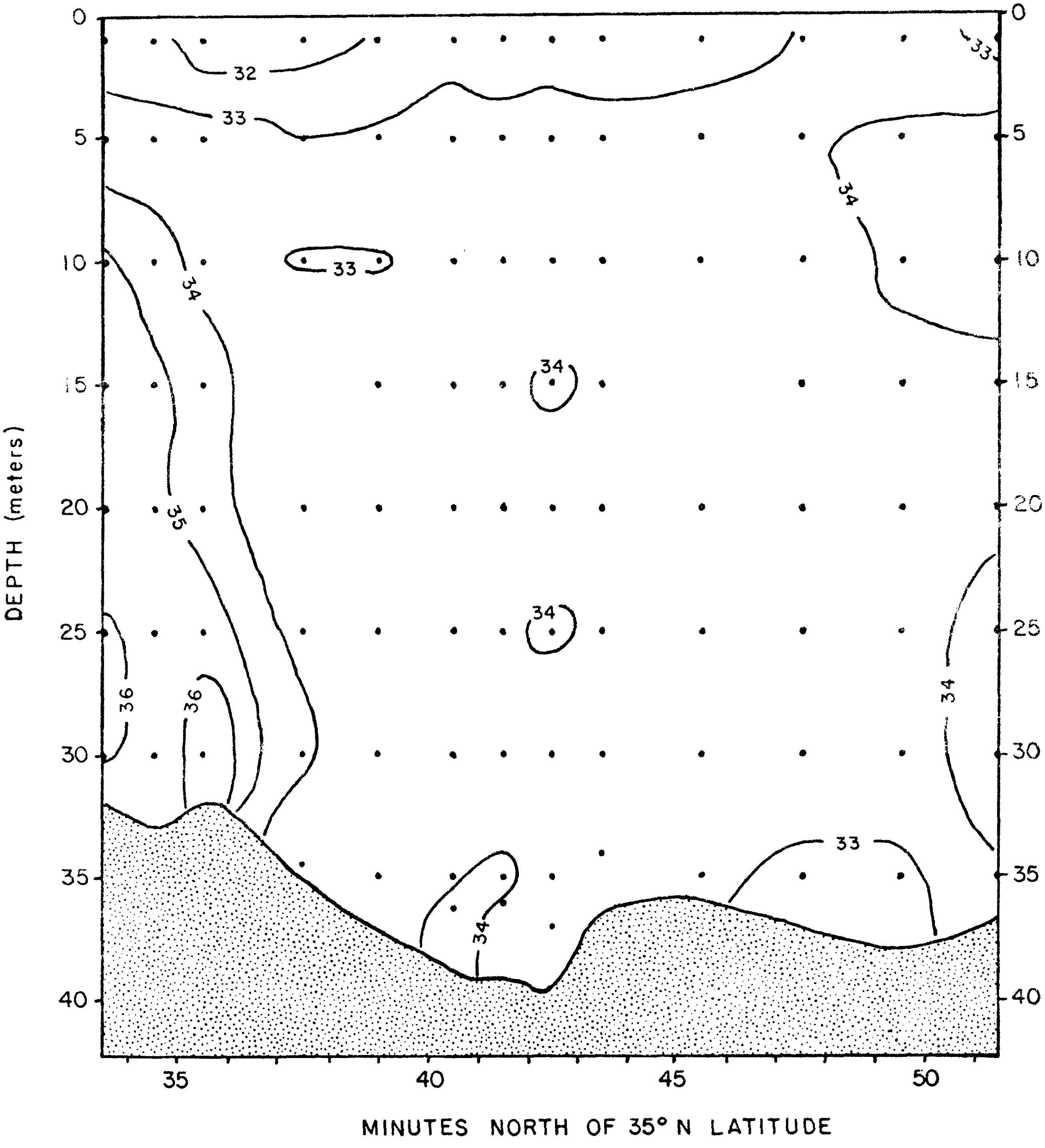


Figure 6. Isohalines observed June 8, 1977.

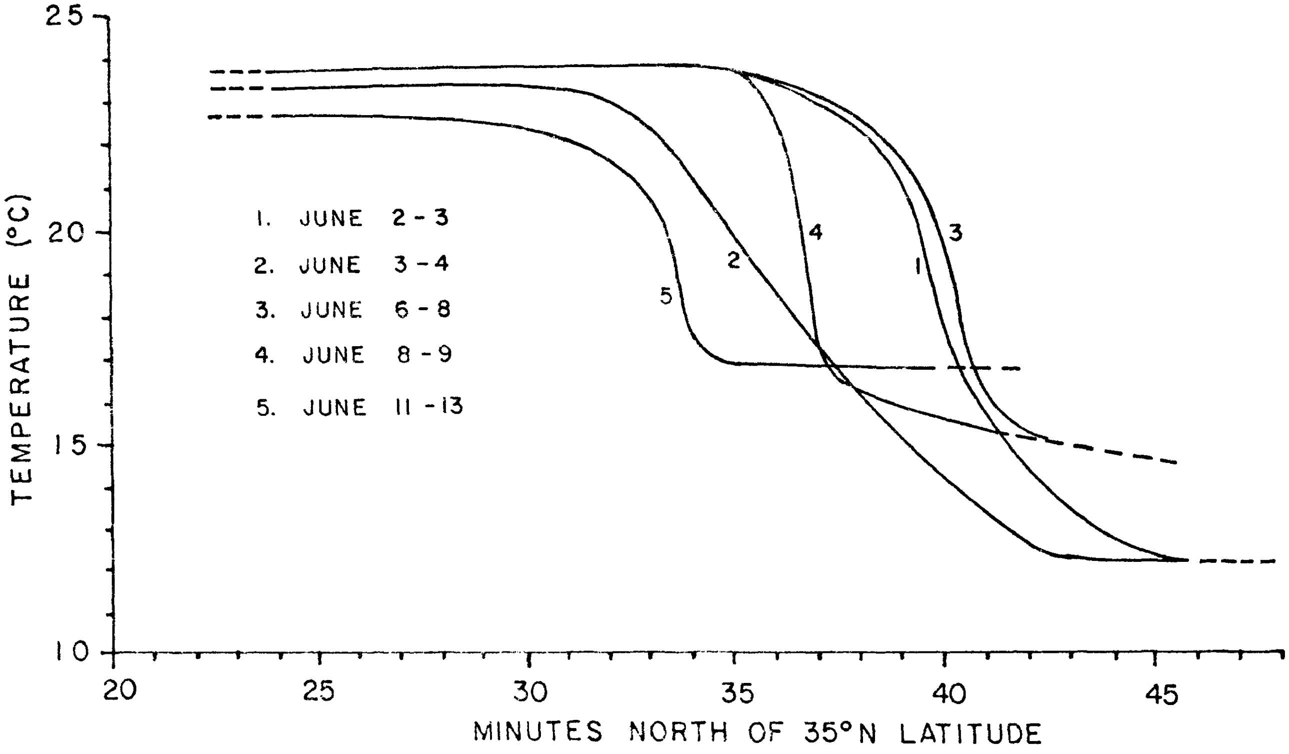


Figure 7. Bottom water temperatures in the frontal region as derived from a composite of temperature data collected over 2-3 day intervals. Each line fit by eye based on more than 25 observations (from Herbst et al., 1979a).

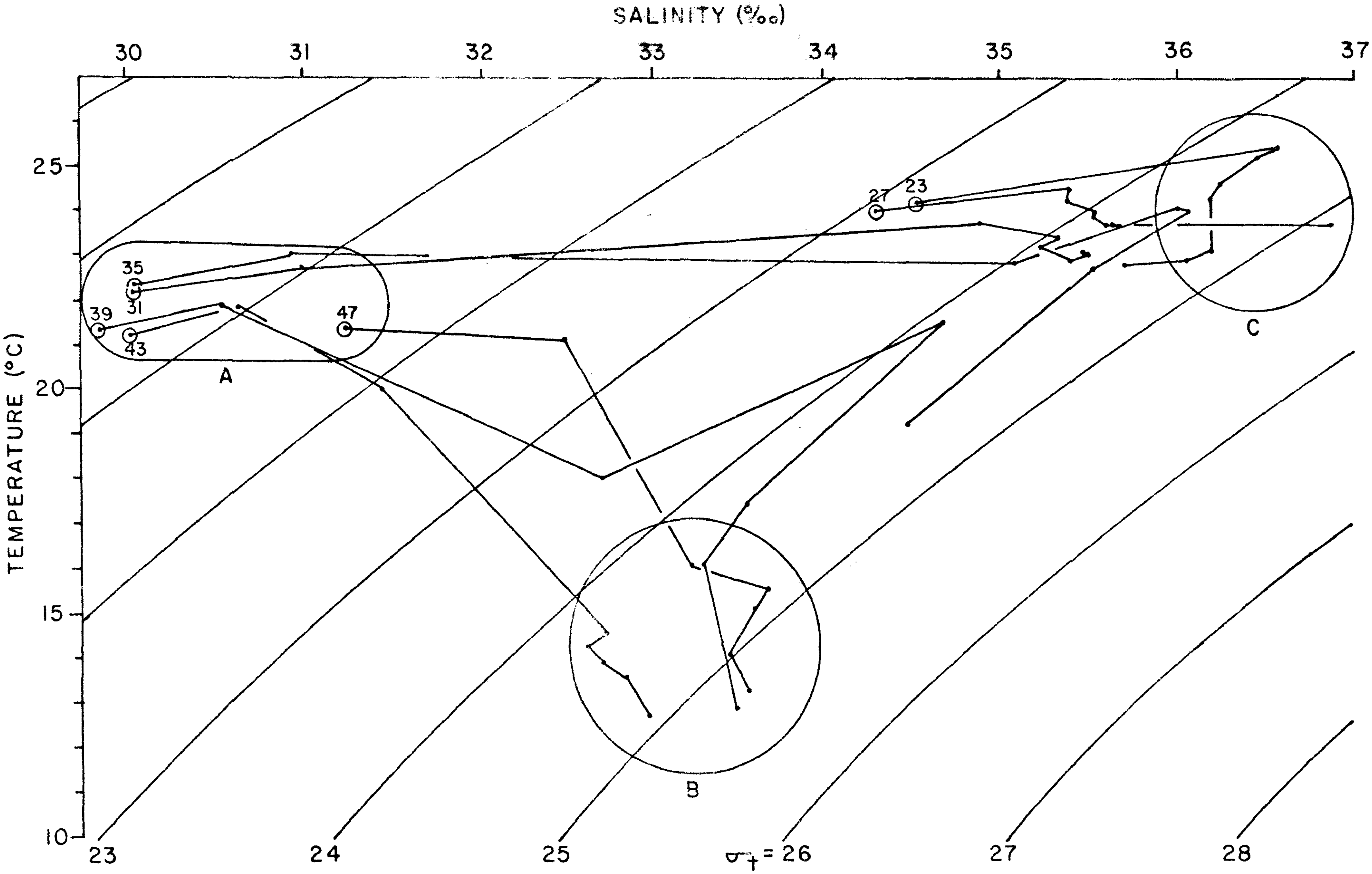
In an effort to establish the identity of the water masses involved in formation of the front and the structure of their juncture, a temperature-salinity plot (Figure 8) was made using seven vertical profiles from Figures 3 and 4. Profiles were selected at 4' intervals between 35°23'N and 35°47'N, with measurements on each vertical profile made at 5 m depth intervals.

The pronounced vertical stratification of northern water is again evident. Surface water of the northern front (type A) and bottom water at the same latitude (type B) showed clear differences in both salinity and temperature. All measurements taken in the northern vertical profiles (43' and 47') can largely be accounted for by mixing between surface and bottom water in varying proportions.

Profiles taken farther south (39', 35', and 31') showed evidence of warmer, more saline water mass (type C) intruding at mid-depths. The profile at 23' showed this warm, saline water to occupy much of the water column in the southernmost portion of the frontal zone. As the salinity of type C water exceeded 36 ^{o}/oo, it may be classified as of Gulf Stream origin, following the convention of earlier workers (Bumpus and Pierce, 1955; Stefansson and Atkinson, 1967; Stefansson et al., 1971; Atkinson et al., 1978). It is not certain, however, that this water parcel was continuous with the main body of the Gulf Stream. In fact, it seems unlikely that the north wall of the Gulf Stream would be found so far on the continental shelf.

It should also be noted that the 47' profile is exceptional, in

Figure 8. Temperature-salinity plot of seven vertical CSDT profiles made at equal latitudinal intervals across front. Observations were made June 4, 1977. Circled values indicate near-surface conditions; other measurements were taken at 5 m. depth intervals. Location of profile, expressed as minutes north of 35°00.5'N latitude, given by number adjacent to near-surface value. Letters A-C indicate water mass or type (see text).


SALINITY (‰)
30
31
32
33
34
35
36
37
TEMPERATURE (°C)
25
20
15
10
23
24
25
σ_t = 26
27
28
A
B
C
35
31
39
43
47
27
23

that, it is out of sequence with the trend towards warmer, more saline water at lower latitudes. On the TS diagram, it is displaced to the right of the 43' profile, whereas all other profiles are in sequence from lower left to upper right. This illustrates the three-dimensionality of the frontal structure. The front was not simply the two-dimensional structure seen in the contours of Figures 3-6, but rather there was folding at an angle to the main axis of the front.

Sediments

Data on station location and sediment characteristics are contained in Table 2. Except in the region of Diamond Shoals, the North Carolina shelf at 30 m depth was generally characterized by medium and fine sands with the RPD usually deeper than three centimeters. Percentage of silt-clay varied from 0 to 6.5%. These conditions were found to exist in the South, Front and North areas, though coarse sand was found in two samples taken in the later region. With few exceptions, the particle size distribution was skewed towards the coarser sizes and the high kurtosis indicates a very low peakedness relative to the normal curve.

Around Cape Hatteras, the modification of current patterns by Diamond Shoals results in the formation of a variety of sedimentary regimes. In the Hatteras:South area and the most southern portions of Hatteras:Mid, the protection afforded by the Shoals allows deposition of finer materials, resulting in a very fine sand bottom

Table 2. Station location, depth and sediment parameters for all Smith-McIntyre grab samples. Sediment parameters represent mean values where multiple replicates were taken.

Area	Replicates	North Latitude	West Longitude	Depth (m)	RPD (depth-cm)	Median Diameter (ϕ)	Sorting (σ_ϕ)	Skewness (ϕ)	Kurtosis (ϕ)	Percent silt-clay	Classification (sand)
South	1	34°34.5'	76°13.1'	38	Absent	1.33	0.81	-0.209	4.208	0.61	medium
South	1	34°33.2'	76°11.0'	42	Indistinct (4)	2.74	1.18	-2.260	10.677	3.26	fine
South	1	34°37.9'	76°09.6'	38	Absent	1.92	0.63	-0.770	5.747	0.29	medium
South	1	34°36.6'	76°06.3'	39	Absent	1.58	0.70	-0.873	8.001	0.13	medium
South	1	34°34.9'	76°07.9'	41	Absent	2.17	0.75	-1.193	6.114	0.44	fine
South	1	34°37.9'	76°08.0'	40	Absent	1.09	0.89	-1.394	9.547	0.23	medium
South	1	34°39.5'	76°09.6'	36	Absent	1.16	0.82	-0.670	4.976	0.15	medium
South	1	34°40.0'	76°06.0'	36	Absent	1.90	1.34	-2.226	9.949	1.26	medium
Hatteras:South	1	35°03.5'	75°29.8'	32	Distinct(<1)	3.04	.93	-1.459	5.138	13.04	very fine
Hatteras:South	1	35°02.0'	75°32.2'	38	Distinct(<1)	2.81	1.59	-0.801	2.431	10.43	fine
Hatteras:South	1	35°03.2'	75°32.4'	29	Distinct(<1)	3.16	1.09	-1.882	6.433	17.45	very fine
Hatteras:South	1	35°04.2'	75°34.4'	30	Distinct(<1)	3.09	1.41	-2.160	8.639	12.96	very fine
Hatteras:South	1	35°01.1'	75°34.0'	33	Absent	1.50	0.78	-1.179	6.772	0.41	medium
Hatteras:South	1	35°00.5'	75°33.5'	40	Absent	1.42	0.78	-0.539	8.482	1.09	medium
Hatteras:South	1	35°01.2'	75°35.5'	38	Distinct(<1)	2.44	1.52	-0.414	1.968	10.85	fine
Hatteras:South	1	35°00.1'	75°35.5'	37	Absent	1.60	0.68	-2.360	18.214	0.24	medium
Hatteras:Mid	1	35°03.2'	75°26.3'	44	Distinct (1)	3.04	1.08	-1.353	4.431	17.81	very fine
Hatteras:Mid	1	35°04.0'	75°24.5'	44	Distinct(<1)	2.98	0.98	-1.217	4.324	15.66	fine
Hatteras:Mid	1	35°05.4'	75°21.0'	54	Distinct (1)	2.76	1.21	-1.128	2.666	11.28	fine
Hatteras:Mid	1	35°06.1'	75°19.6'	42	Distinct (1)	2.63	1.00	-1.082	4.162	4.77	fine
Hatteras:Mid	1	35°07.3'	75°17.7'	52	Indistinct (1)	2.50	1.14	-0.992	3.754	8.43	fine
Hatteras:Mid	1	35°08.0'	75°16.5'	51	Distinct (2)	2.38	1.19	-1.950	9.566	6.06	fine

Table 2. (continued)

Area	Repli-cates	North Latitude	West Longitude	Depth (m)	RPD (depth-cm)	Median Diameter (ϕ)	Sorting (σ_ϕ)	Skewness (ϕ)	Kurtosis (ϕ)	Percent silt-clay	Classification (sand)
Hatteras:Mid	1	35°09.0'	75°15.0'	52	Indistinct (4)	2.28	0.88	-1.336	6.351	2.85	fine
Hatteras:Mid	1	35°10.7'	75°13.2'	41	Absent	1.75	0.53	-3.351	35.199	0.02	medium
Hatteras:North	1	35°16.1'	75°13.1'	32	Absent	2.36	0.51	-2.697	19.782	0.04	medium
Hatteras:North	1	35°16.2'	75°12.0'	32	Absent	2.19	0.49	-2.824	19.714	0.01	medium
Hatteras:North	1	35°16.3'	75°10.8'	35	Absent	2.03	0.50	-1.848	11.383	0.03	medium
Hatteras:North	1	35°15.1'	75°13.6'	34	Absent	2.17	0.60	-2.316	11.871	0.03	medium
Hatteras:North	1	35°14.8'	75°09.0'	32	Absent	0.11	1.41	-0.876	3.776	0.00	coarse
Hatteras:North	1	35°16.5'	75°09.5'	40	Absent	1.93	0.51	-2.849	26.094	0.04	medium
Hatteras:North	1	35°17.6'	75°10.2'	40	Absent	2.01	0.42	-3.694	48.202	0.11	fine
Hatteras:North	1	35°12.6'	75°10.2'	37	Absent	0.84	0.98	-2.396	11.898	0.01	coarse
Front:23'	3	35°23.5'	75°13.0'	35	Absent	2.94	0.50	-1.764	13.147	3.66	fine
Front:25'	3	35°25.6'	75°13.0'	37	Absent	2.97	0.61	-1.968	11.418	4.72	fine
Front:27'	3	35°27.5'	75°12.9'	37	Variable (3)	2.96	0.60	-2.238	12.996	4.35	fine
Front:29'	3	35°29.6'	75°13.0'	38	Indistinct (3)	2.80	0.81	-1.807	7.982	3.66	fine
Front:31'	3	35°31.5'	75°13.0'	38	Indistinct (3)	2.73	0.75	-1.287	6.550	6.51	fine
Front:33'	3	35°33.5'	75°13.0'	35	Distinct (3)	2.57	0.74	-1.607	8.913	4.59	fine
Front:34'	3	35°34.5'	75°13.0'	35	Indistinct (5)	2.51	0.77	-1.315	7.118	3.06	fine
Front:35'	3	35°35.5'	75°13.0'	34	Absent	1.93	0.59	-0.628	7.955	0.56	medium
Front:36'	3	35°36.5'	75°13.4'	35	Absent	1.53	0.70	0.050	9.776	1.30	medium
Front:37'	3	35°37.5'	75°13.0'	36	Absent	1.66	0.76	0.068	7.641	1.81	medium
Front:38'	3	35°38.5'	75°13.0'	33	Absent	1.60	0.85	-1.058	9.741	0.67	medium
Front:39'	3	35°39.5'	75°13.0'	38	Absent	2.42	1.20	-2.499	13.477	3.05	fine
Front:39'	3	35°39.5'	75°13.0'	34	Absent	1.37	0.90	-2.196	16.793	0.64	medium

Table 2. (concluded)

Area	Repli-cates	North Latitude	West Longitude	Depth (m)	RPD (depth-cm)	Median Diameter (ϕ)	Sorting (σ_ϕ)	Skewness (ϕ)	Kurtosis (ϕ)	Percent silt-clay	Classification (sand)
Front:39'	3	35°39.5	75°13.0	37	Distinct (4)	1.62	1.05	-1.678	12.334	2.38	medium
Front:40'	3	35°40.5'	75°13.0'	42	Variable (3)	2.02	1.35	-1.704	9.046	4.14	fine
Front:41'	3	35°41.5'	75°13.0'	42	Distinct (2)	2.16	0.99	-1.719	10.793	3.01	fine
Front:42'	3	35°42.5'	75°13.0'	43	Variable (2)	1.89	1.79	-1.762	6.794	2.57	medium
Front:43'	3	35°43.5	75°13.0	39	Absent	1.13	1.05	-1.482	10.963	0.68	medium
Front:45'	3	35°45.4'	75°12.9'	39	Absent	1.12	1.17	-2.177	12.368	0.68	medium
Front:47'	3	35°47.5'	75°13.0'	40	Variable (2)	2.39	0.64	-1.540	8.908	0.94	fine
Front:49'	3	35°49.5'	75°13.0'	41	Variable (3)	2.40	0.65	-2.056	13.287	0.87	fine
Front:51'	3	35°51.5'	75°13.0'	40	Absent	2.24	0.55	-0.169	8.201	0.44	fine
North	1	36°03.3'	75°11.4'	34	Indistinct (3)	1.91	0.44	-0.526	8.103	0.06	medium
North	1	36°02.2'	75°09.0'	41	Absent	1.50	1.01	-1.627	8.104	0.07	medium
North	1	36°00.6'	75°10.6'	33	Absent	1.14	1.57	-1.714	6.142	0.31	medium
North	1	35°56.8'	75°11.2'	39	Absent	0.97	1.16	-2.400	10.459	0.02	coarse
North	1	35°58.6'	75°08.0'	40	Absent	2.03	0.55	-3.322	30.933	0.03	fine
North	1	36°00.0'	75°10.4'	32	Absent	1.31	1.58	-2.339	7.830	0.03	medium
North	1	35°59.3'	75°14.2'	36	Absent	0.45	1.75	-1.198	4.027	0.33	coarse
North	1	36°01.7'	75°12.7'	30	Absent	1.58	0.57	-1.434	7.690	0.30	medium

type and a higher percentage of silt and clay particles. Frequently only a thin oxidized surface layer was found.

In the Hatteras:North area, on the outer portion of Diamond Shoals, current velocities are greater, creating a region of medium to coarse sands. Values for skewness and dispersion from this region showed the greatest skewness towards larger particle sizes and the best sorting encountered. Only in this region was difficulty encountered in sieving some biological samples, for much material remained after sieving through the 1.0 mm screen.

Biological Results

The 106 grab samples analyzed during this study yielded 11,973 individuals apportioned among 147 amphipod and mollusc species. Molluscs were both more diverse and numerous than the amphipods, and represented 64% (94) of the species and 69% (8,291) of the total individuals. The number of species and individuals for each of the areas are shown in Table 3. These results are included primarily for completeness, but a high degree of caution is necessary in their interpretation. High numbers of individuals frequently reflect the contribution of only a few abundant species. For example, the extremely high number of amphipods in the Hatteras:South area was due almost entirely to the contribution of *Protohaustorius* cf *deichmannae*. Likewise, the increased abundance of molluscs in the southern portion of the front can be attributed to only a few

Table 3. Number of species and individuals obtained within each area or station. Density per meter^2 provided for comparison as sampling intensity was variable.

Mollusca				Amphipoda		
No. of Species	No. of Indiv.	No. of Indiv. Scaled to #/m^2	Station or Area (south to north)	No. of Species	No. of Indiv.	No. of Indiv. Scaled to #/m^2
46	333	416	South	37	755	944
52	1634	2043	Hatteras:South	19	126	158
26	373	466	Hatteras:Mid	16	59	74
8	86	108	Hatteras:North	7	1533	1916
16	703	2343	Front(23')	5	64	213
19	669	2230	Front(25')	4	64	213
20	408	1360	Front(27')	6	113	377
24	552	1840	Front(29')	8	50	167
30	742	2473	Front(31')	7	24	80
23	456	1520	Front(33')	2	49	163
24	392	1307	Front(34')	5	31	103
16	107	357	Front(35')	7	86	287
3	31	103	Front(36')	4	7	23
19	184	613	Front(37')	6	43	143
15	96	320	Front(38')	6	27	90
29	320	356	Front(39')	13	28	31
22	169	563	Front(40')	8	29	97
17	194	647	Front(41')	4	9	30
15	143	477	Front(42')	7	18	60
12	97	323	Front(43')	11	42	140
10	24	80	Front(45')	7	24	80
13	204	680	Front(47')	7	10	33
10	95	317	Front(49')	3	14	47
4	17	57	Front(51')	5	30	100
24	262	328	North	14	447	559

species, notably Lucinidae (juvenile) and *Spisula solidissima similis*. Paramaters such as diversity, evenness and species richness are more informative than either number of species or individuals.

Species collected in the grab samples and their distributions as recorded in the literature are listed in Appendices 1 and 2. Nomenclature used is largely that of Abbott (1974) and Bousfield (1973) for the molluscs and amphipods respectively. Among the Amphipods, genera are grouped according to the scheme of Barnard (1969, 1973). Some organisms have been identified only to the generic level for several reasons. Among the molluscs, this is largely due to the fact that many of the species obtained were represented by recently metamorphosed individuals, the shells of which were insufficiently developed for accurate identification. Though juvenile specimens created some difficulty in the amphipods, a greater difficulty was found to be insufficient taxonomic literature, particularly in the case of the southern species on which little work has been done. A great need exists for a comprehensive treatment of the amphipod fauna of the southeastern United States, since existing literature is sparse, out-dated or habitat-specific.

Many species encountered represent significant range extensions, largely northern extensions of southern species. These may represent reproductive populations of the species or fortuitous introductions brought into the area by the Gulf Stream. As juvenile mollusc specimens were frequently encountered, their occurrence does not necessarily denote the range of the parent population, particularly for those molluscs with pelagic larvae.

One mature specimen of the polyplacophoran *Acanthochitona pygmaea* was obtained in the Hatteras:South area. This species had previously been known only from the west coast of Florida and the West Indies (Abbott, 1974). Only one other congener has been found in North Carolina waters. Pearse and Williams (1951) obtained one specimen of *A. spiculosa* near Cape Lookout. Less significant extensions are those of *Cryoturris citronella*, *Diplodonta punctata* and *Pitar fluminatus*, all of which were not previously known to occur north of Cape Hatteras (Porter, 1974), but were encountered in the front or North areas during the present study.

Records are more numerous among the Amphipoda because of the paucity of work in this regions. *Ampelisca cristoides*, a species previously known from the Caribbean and Eastern Pacific Ocean (Mills, 1967), was frequently found throughout the study area. Of particular interest is the specimen of *Jerbarnia* sp. A obtained in Hatteras: South. Until recently, the genus was known only from the type locality of Eniwetok Atoll (Croker, 1971). Specimens of this genus have recently been collected off New Jersey (M. Bowen, pers. comm.), Florida and the Gulf of Mexico (L. Watling, pers. comm.). Both *Lembos unicornis* and *Microdeutopus myersi* were obtained in the South stratum, but were previously known only from the type localities in North Carolina estuaries (Bynum and Fox, 1977). *M. myersi* has since also been found off Georgia by Bowen (pers. comm.). *Argissa* hamatipes and Byblis serata are northern species which have only recently been found south of Virginia (Bowen et al., 1979). Kris Thoemke of the University of South Florida is presently describing a new Argissa from Florida and comparison is necessary. Southern records of Siphonoectes smithianus and Parametopella inquilinus were established by this study as they were not known to occur south of Chesapeake Bay (E. L. Bousfield, unpub. data) or Delaware Bay (Watling, 1976), respectively.

Cumulative Diversity

In order to make statements concerning the structure of a community, one must have some assurance that the degree of sampling effort is adequate to provide a reasonable representation of the community as a whole. Determination of needed sampling effort is often impossible to make beforehand, as it requires knowledge of population density and the physical and biological heterogeneity of the environment. Often the final sampling effort employed becomes a trade-off between biological adequacy and the limitations imposed by time and funding.

A cumulative diversity test can be used as one criterion in demonstrating adequacy of sampling. Using this technique, samples are successively summed and the diversity is determined as if the species abundances were for a single sample (Pielou, 1966). When after a certain number of samples, the cumulative diversity curve nears an asymptote, it can be concluded that further sampling of the habitat would produce no change in diversity aside from random variation.

Cumulative diversity graphs are illustrated in Figures 9a and b using a random summation of the eight grabs taken at the North and South areas. For the most part, eight grab samples were more than adequate in providing a true representation of the community diversity. Only in the case of the Amphipoda from the North area, was the diversity potentially underestimated. It seems probable from the curves shown that the three grab samples taken at the front stations were adequate as well. Again with the exception of the amphipods from the North area, three grab samples provided greater than 90% of the asymptotic diversity.

Species Diversity, Richness and Evenness

Figure 10 illustrates the trends in Shannon diversity, species richness and evenness across the study area. For both the Amphipoda and the Mollusca, the South area clearly showed the highest values of the Shannon diversity index. Some reduction in diversity occurred to the north in the Cape Hatteras region, though the species diversity of both the Hatteras:South and Hatteras:Mid areas remained relatively high. A pronounced reduction in diversity was observed in the Hatteras:North area where the lowest values of the Shannon diversity were found. No obvious trend in diversity across the frontal area was observed, for values fluctuated greatly even between adjacent stations. This indicates that factors other than latitude

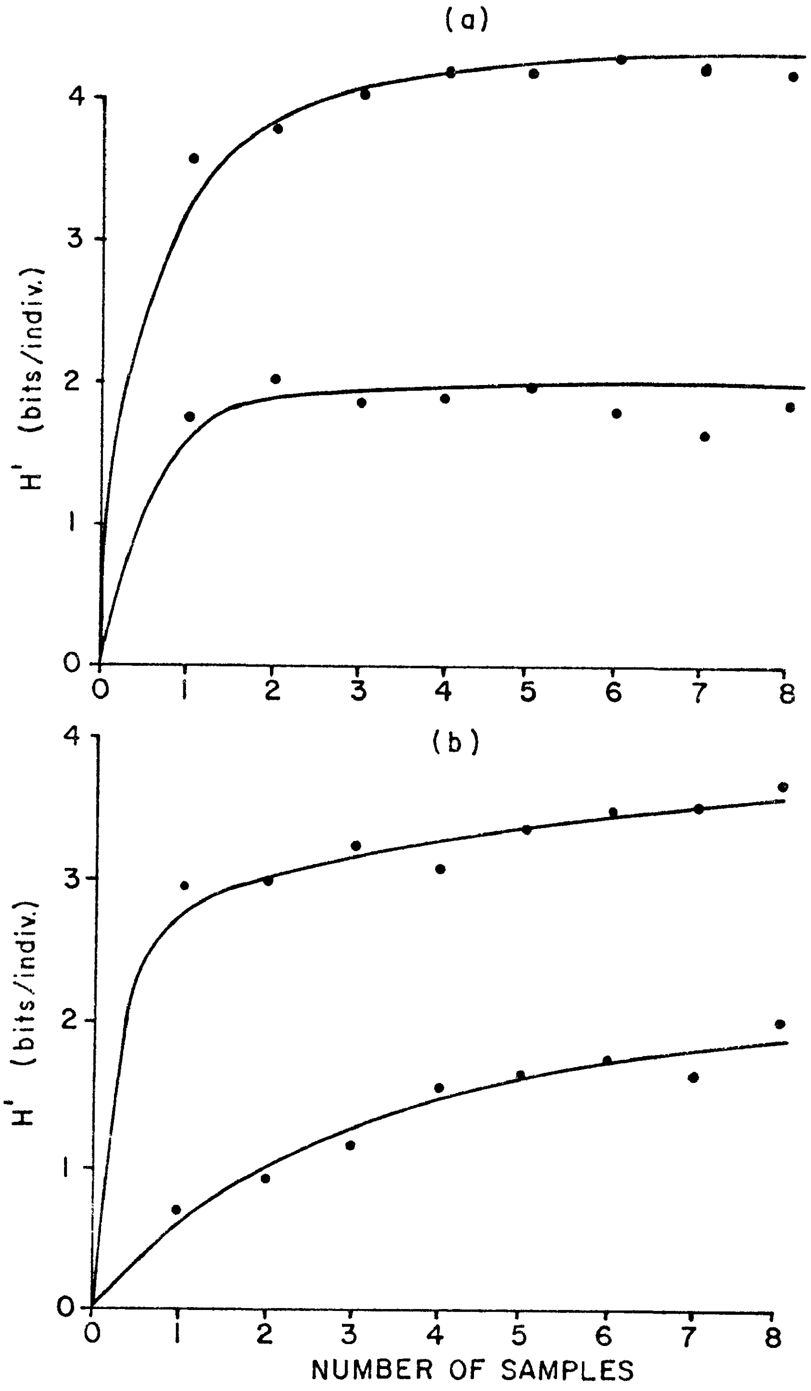
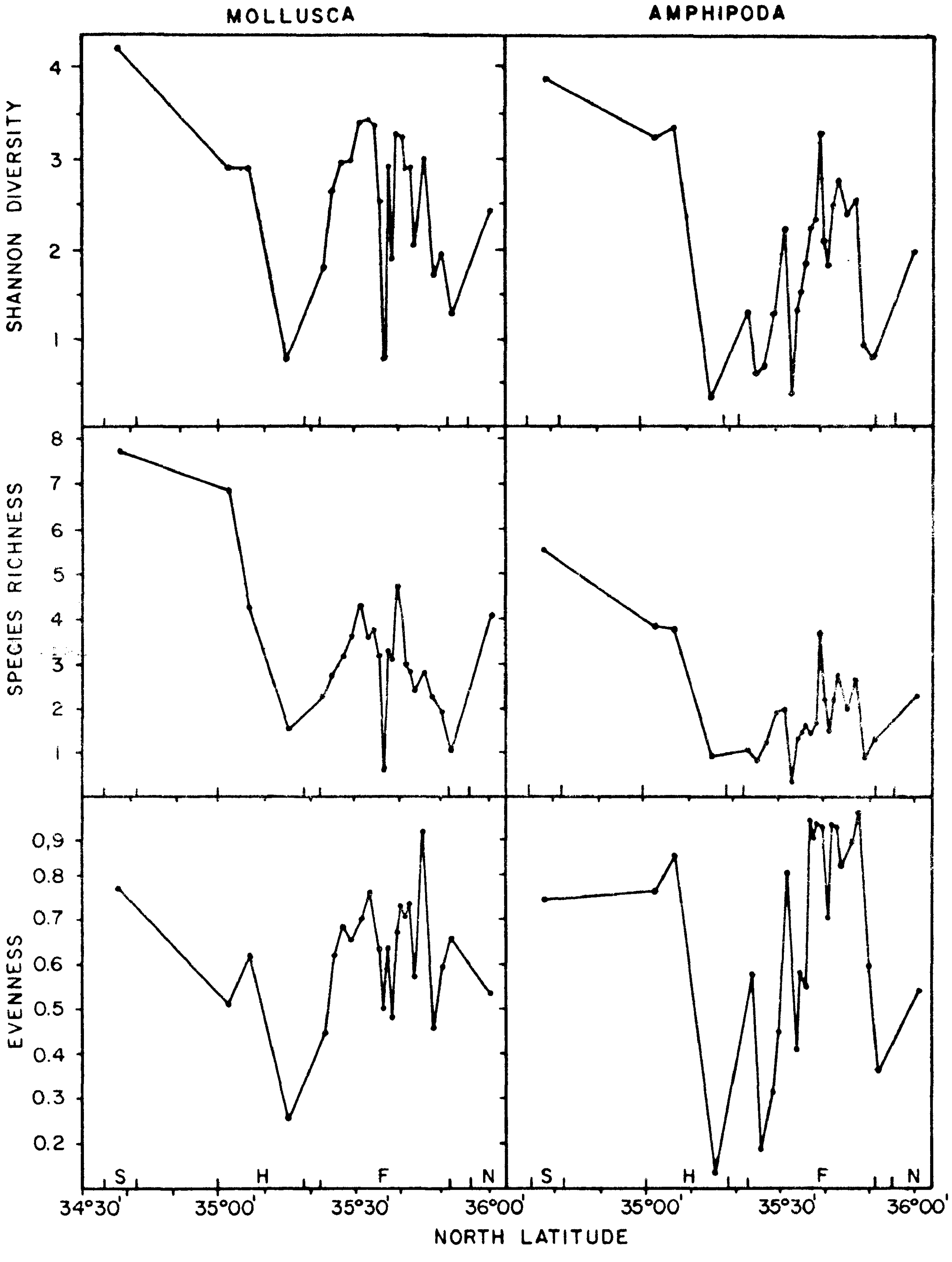


Figure 9. Cumulative diversity graphs in which samples are successively summed, and the diversity calculated as if species abundances were for a single sample. When the curve approaches an asymptote, it can be assumed that no increase in diversity would occur with further sampling, (a) Mollusca, (b) Amphipoda.

Figure 10. Shannon diversity, species richness and evenness of the Mollusca and Amphipoda in all sampling areas. Diversity expressed in the units of bits/individual. Areas: S = South, H = Hatteras, F = Front, N = North.



MOLLUSCA
AMPHIPODA
SHANNON DIVERSITY
4
3
2
1
SPECIES RICHNESS
8
7
6
5
4
3
2
1
EVENNESS
0,9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
S
H
F
N
S
H
F
N
34°30'
35°00'
35°30'
36°00'
35°00'
35°30'
36°00'
NORTH LATITUDE

(temperature) play a significant role. The diversity in the North area was approximately intermediate in the range of values encountered in the front.

The species richness component was closely correlated with the Shannon diversity. Front:39' showed a peak in species richness for both taxa, which was in part due to the greater number of grab samples taken there.

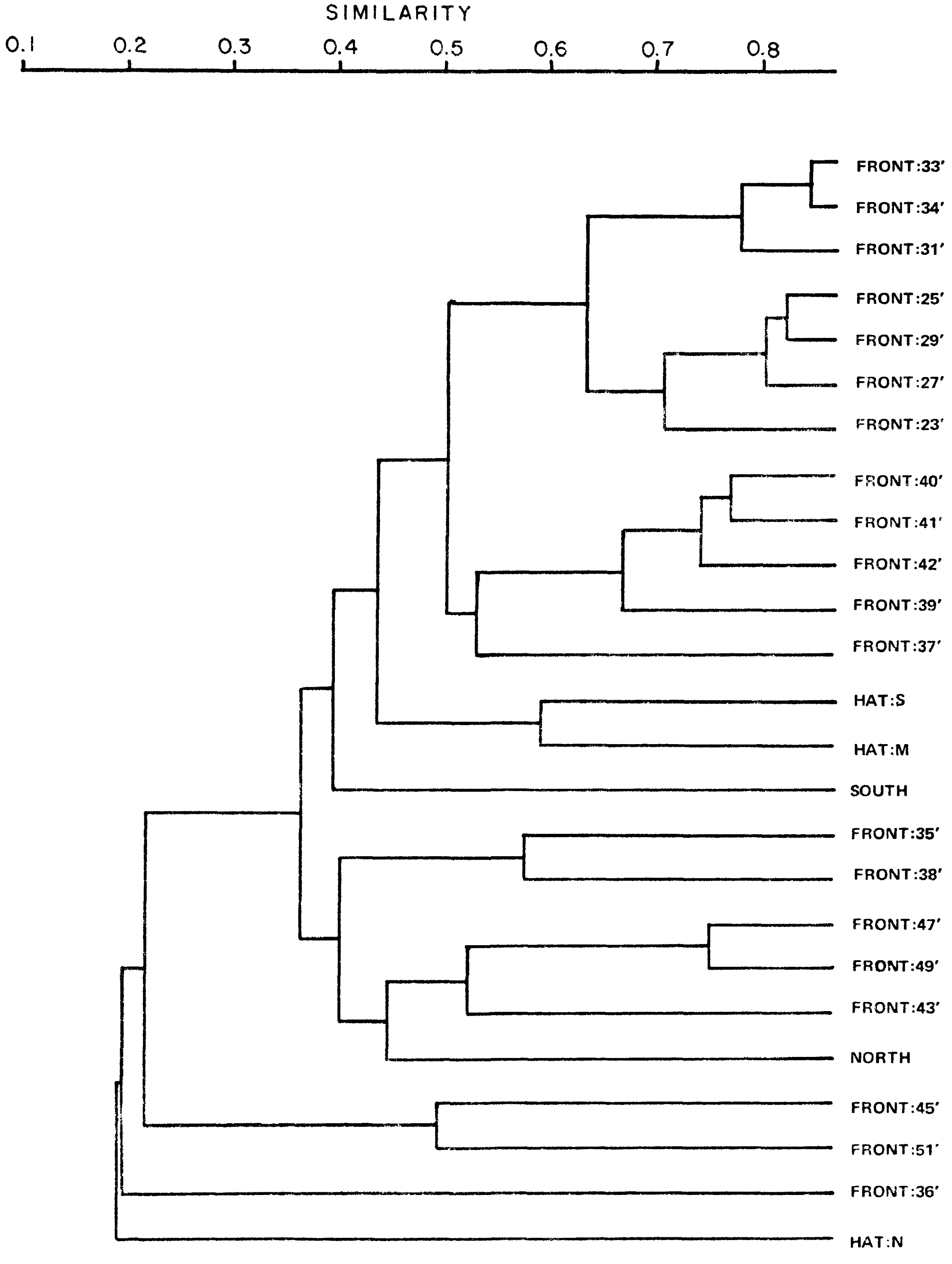
Evenness is the only index calculated which did not reach the maximum value in the South area. The amphipods showed higher evenness in Hatteras:South, Hatteras:Mid and ten front stations. For the molluscs, evenness was greater at Front:45' than in the South area.

Comparison of the amphipods and molluscs reveals a high similarity of all three indices between the taxa, excluding the variability in the frontal region. The only clear differnece in species diversity between the taxa was a slight higher diversity of the molluscs in the fine sands of the southern front. The molluscs consistently scored higher in species richness in all sampling areas, though the amphipods showed a higher evenness in the Hatteras region and much of the frontal region.

Cluster Analysis

The dendogram formed by normal analysis of the mollusc data is illustrated in Figure 11. Front stations 36', 45', 51' and the

Figure 11. Station dendogram based on mollusc data. Fusion higher position in the cluster hierarchy reflects a decreased similarity between station groups.

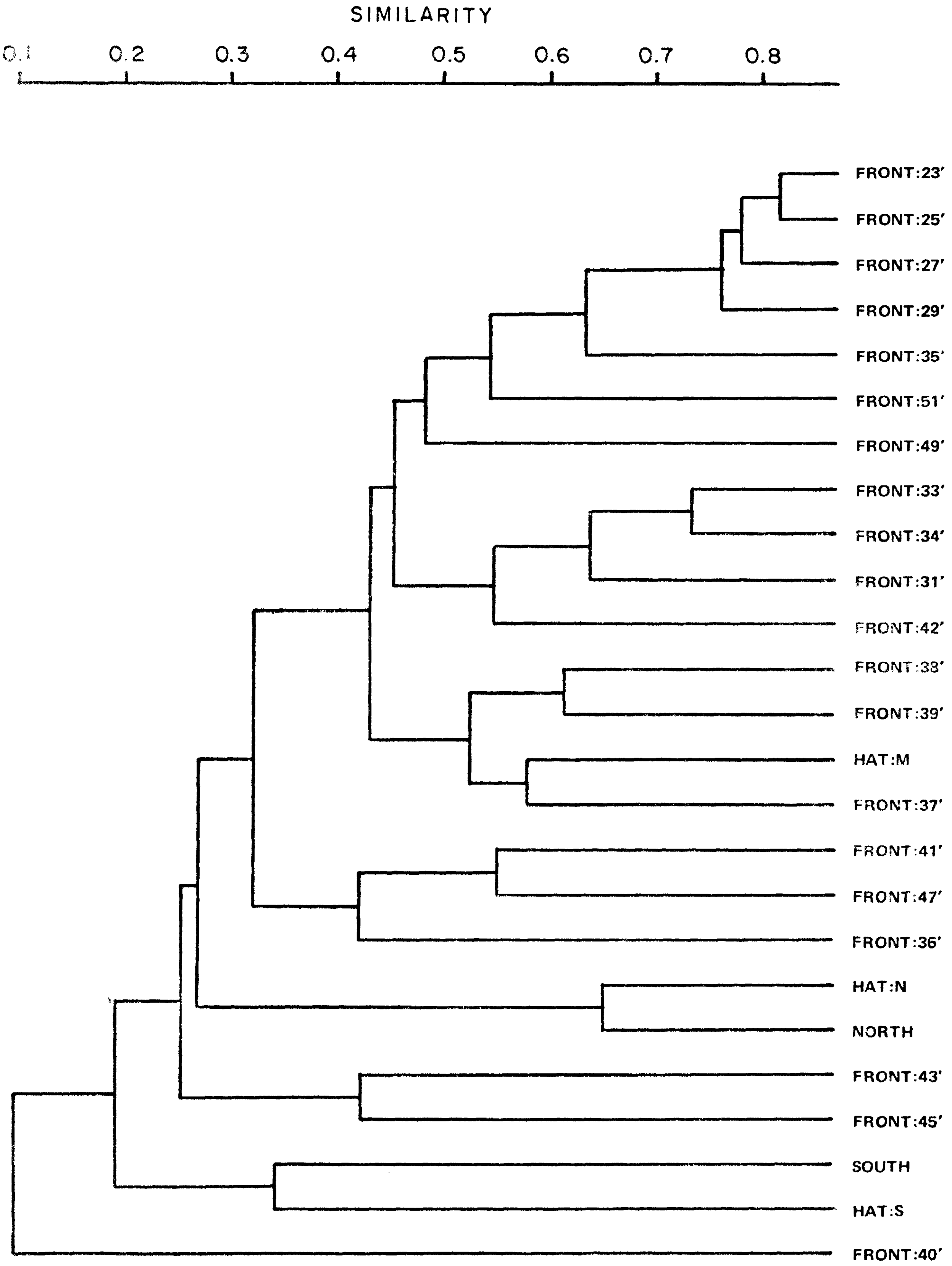

SIMILARITY
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
FRONT:33'
FRONT:34'
FRONT:31'
FRONT:25'
FRONT:29'
FRONT:27'
FRONT:23'
FRONT:40'
FRONT:41'
FRONT:42'
FRONT:39'
FRONT:37'
HAT:S
HAT:M
SOUTH
FRONT:35'
FRONT:38'
FRONT:47'
FRONT:49'
FRONT:43'
NORTH
FRONT:45'
FRONT:51'
FRONT:36'
HAT:N

Hatteras:North area joined the cluster hierarchy at a very low similarity level. Collections from these four stations contained the fewest number of individuals, thus their position in the cluster is likely to be an artifact of insufficient densities.

Groupings of stations based on the mollusc data were primarily reflective of substrate type. The front was subdivided into northern, middle and southern subgroups reflecting differences in sediment median diameter and percentage of silt-clay. Sediments of the southern front stations 23' - 34' were characterized by fine sands with 3.1 - 6.5% silt-clay. The mid-front stations of 37' - 42', exclusive of 35' and 38', had coarser sand and a lower percentage of silt-clay (0.6 - 4.1%). The cluster of northern front stations (43' - 47', with 35' and 38') reflects similarity of fauna inhabiting sediments of very low silt-clay content, for percentage of silt-clay did not exceed 0.9% in these areas. The inclusion of the North area in this group was due to both its close proximity and similarity of sediment type.

The fusion of the Hatteras and South areas with the southern front/mid-front complex can not be explained by substrate similarities alone. On the basis of median diameter and percent silt-clay, the South area might be expected to group with the northern front or North area. Other factors, possibly thermal, were responsible for the similarity of the molluscs of the southern portion of the study area.

Figure 12. Station dendogram based on amphipod data. Fusion at a higher position in the cluster hierarchy reflects a decreased similarity between station groups.

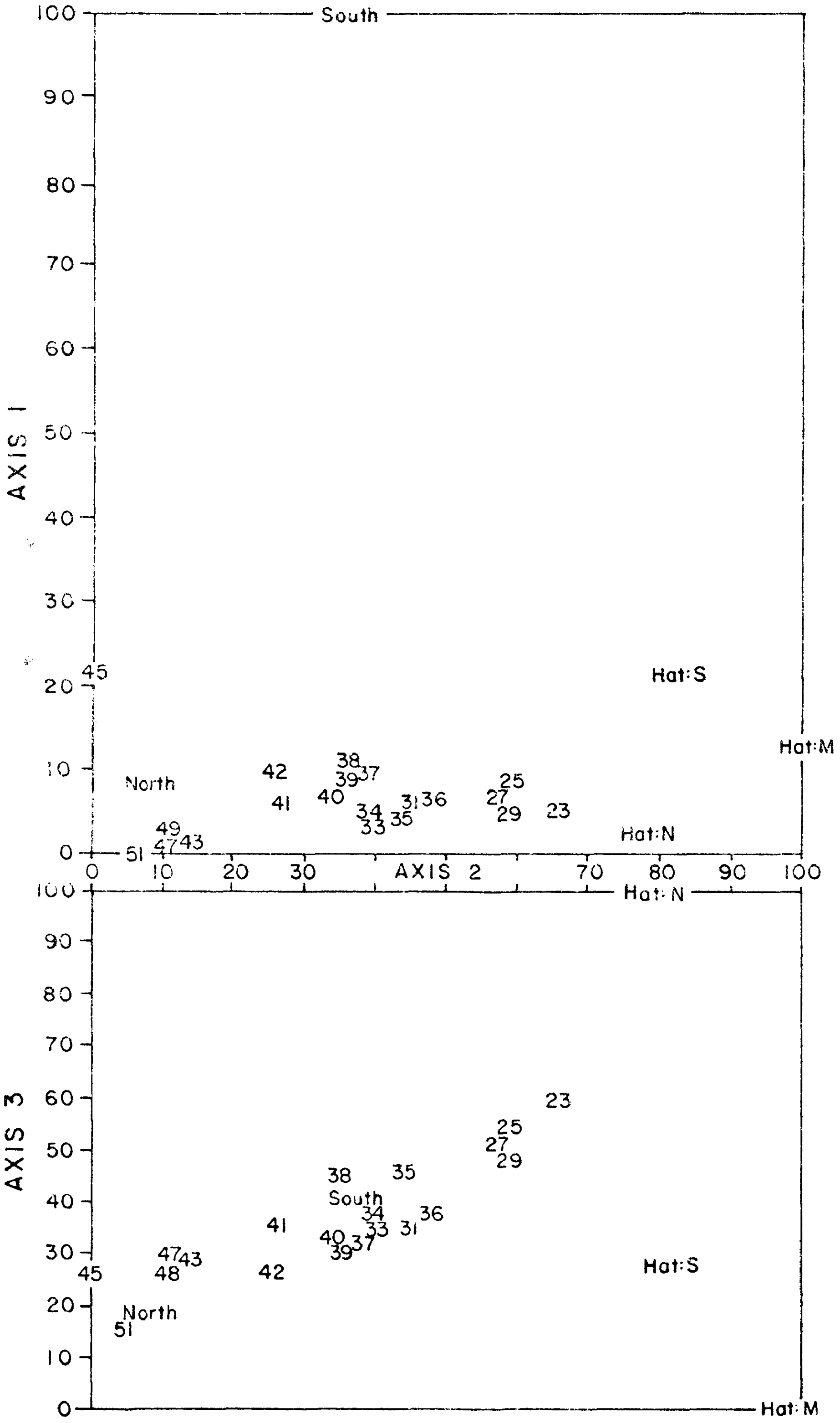

SIMILARITY
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
FRONT:23'
FRONT:25'
FRONT:27'
FRONT:29'
FRONT:35'
FRONT:51'
FRONT:49'
FRONT:33'
FRONT:34'
FRONT:31'
FRONT:42'
FRONT:38'
FRONT:39'
HAT:M
FRONT:37'
FRONT:41'
FRONT:47'
FRONT:36'
HAT:N
NORTH
FRONT:43'
FRONT:45'
SOUTH
HAT:S
FRONT:40'

Groupings of stations based on the amphipod data (Figure 12) was not as discrete as for the molluscs, due in part to the lower densities of the amphipod assemblages. As with the molluscs, the fauna of some of the southern front stations showed the greatest homogeneity. Many of the remaining front stations and other sampling areas joined the cluster hierarchy in an uninterpretable manner. The similarity of the fauna of Hatteras:North and North areas, without the inclusion of any front stations which fall in between, may have been due to the well-sorted medium to coarse sands which are in common to both areas, rather than their respective thermal regimes. Some indication of a faunal break at Cape Hatteras may be inferred by the clustering of the South and Hatteras:South areas, however the weakness of this link is shown by the low similarity level at which they cluster.

Ordination

Reciprocal averaging ordination of stations based on the mollusc data is shown in Figure 13. Nearly all of the resolution of axis 1, accounting for 17.3% of the toal variation, was used in separating the South area from the remainder of the stations. Stations were arranged on Axis 2, explaining 14.3% of the variation, according to latitudinal position. With the exception of the South area, all other stations were distributed along axis 2 in near perfect correlation with their latitudinal position (Figure 14). Axis 3, accounting for 10.6% of total variation, also in part illustrated a latitudinal gradient, but its greatest importance lay in the

Figure 13. Reciprocal averaging ordination of stations based on mollusc data. Front stations are indicated by number denoting their latitudinal position in minutes north of 35°00.5'N latitude. Length of axis is proportional to the percentage of variation explained (17.3, 14.3 and 10.6% for axes 1, 2 and 3 respectively).


South
AXIS 1
North
Hat:S
Hat:M
Hat:N
45
42
41
38
39
37
40
34
33
31
36
35
25
27
29
23
49
47
43
51
AXIS 2
AXIS 3
Hat: N
South
North
48
Hat:S
Hat: M
0
10
20
30
40
50
60
70
80
90
100

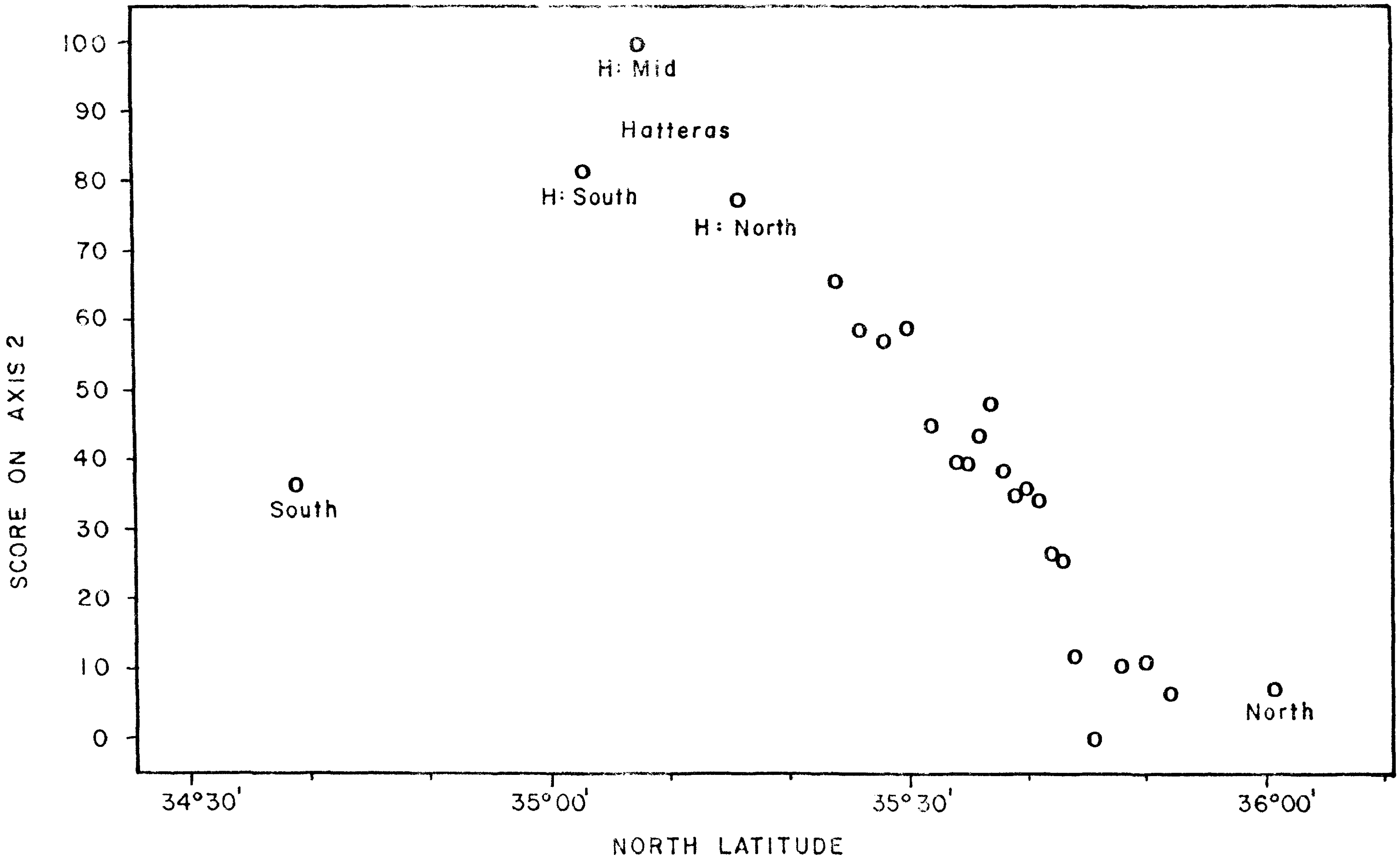


Figure 14. Score on axis 2 for each station of the mollusc ordination as plotted against latitudinal position of the station.

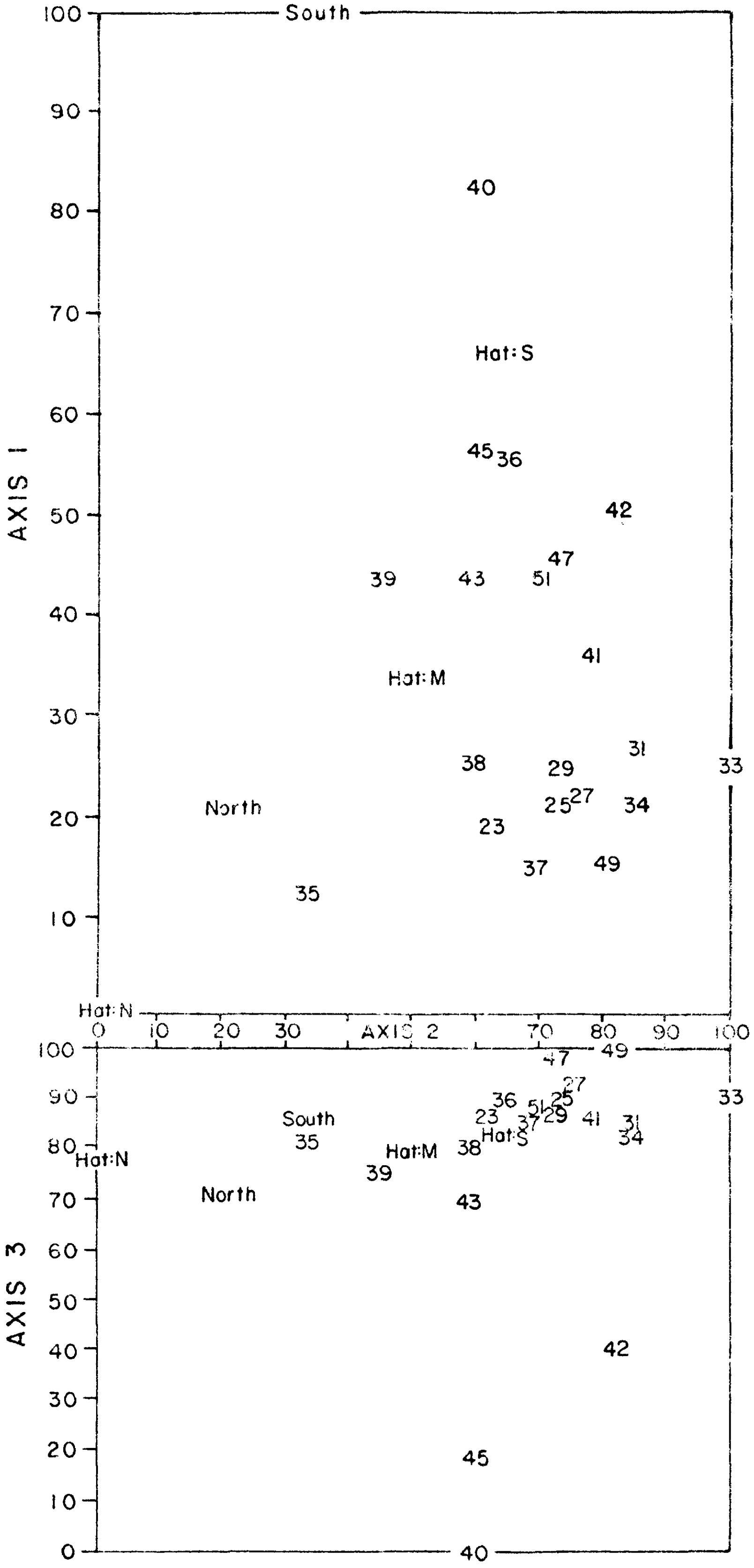
separation of the Hatteras complex. Hatteras:North was particularly distinct from Hatteras:Mid and Hatteras:South.

Ordination of the amphipod collection (Figure 15), as with the amphipod cluster analysis, was much less straightforward than that obtained from the molluscs. Axis 1, describing 20.0% of the total variation, again served to isolate the South area from the other stations, though its distinctiveness was not as clear as with the molluscs. Axes 2 and 3 accounted for much lower amounts of the total variation, explaining 12.5 and 9.9% respectively. No correlation exists between latitude, percent silt-clay or median grain size and scores on any of the first three axes.

Inverse Analysis

Just as normal classification groups stations on the basis of shared species, inverse analysis forms species groups on the basis of similarity of distribution, as determined by the similarity of the set of stations in which they occur. As rare species are often collected on a random basis, without a demonstrable affinity to any particular site, it is often the practice in inverse classification to establish an arbitrary abundance value below which species are not considered in the classification. Such an *a priori* cut-off value was not deemed desirable in this case, since it is the great number of rare species which imparts much of the uniqueness to the South area. As an alternative, largely subjective criteria were used after clustering to discard many rare species which did not readily join

Figure 15. Reciprocal averaging ordination of stations based on amphipod data. Front stations are indicated by number denoting their latitudinal position in minutes north of 35°00.5'N latitude. Length of axis is proportional to the percentage of variation explained (20.0, 12.5 and 9.9% for axes 1, 2 and 3 respectively).

AXIS 1
South
North
Hat:S
Hat:M
Hat:N
40
45
36
42
47
39
43
51
41
38
29
31
33
25
27
34
23
37
49
35
AXIS 2
0
10
20
30
70
80
90
100
AXIS 3
South
North
Hat:N
Hat:M
Hat:S
47
49
27
36
25
51
29
23
37
41
31
34
35
38
39
43
42
45
40
33
0
10
20
30
40
50
60
70
80
90
100

species groups and remained as single entities to relatively low similarity levels. The resulting species groups shown in Tables 4 and 5 comprise 57 and 64% of the molluscs and amphipods respectively. For simplicity of presentation, discussion of inverse analysis is based largely on the results obtained by the cluster analysis. The inverse ordination is in general agreement.

The eight recognizable groups of molluscs (Table 4, Figure 16a) can be differentiated primarily on the basis of latitude and sediment type. Group 1 species are those found exclusively in the North area. The number of specimens obtained (shown in parentheses) indicate that all these species were represented by only one or two individuals. Thus consideration of these as representative of a northern species suite is unwarranted and in fact all of these species have distributions extending to at least Florida and the Gulf of Mexico (excepting the unidentified Nudibranchia sp A).

Group 2 species were very abundant in the northern portions of the study area. All showed a disappearance or drastically reduced abundance south of Front:31'. Such a distribution might be expected since these species are known to range from Canada to Florida or only to North Carolina in the case of <u>Cerastoderma pinnulatum</u>.

Group 3 species were found exclusively in the frontal region (Front:25'-41') though low abundances makes their classification as "front species" somewhat tenuous.

Species of Groups 4 and 5 showed a strong response to the

Table 4. Species groups of molluscs formed by inverse classification. Number in parentheses following each species name indicates total number of individuals collected.

Group 1

Nudibranchia sp. A (1)
Doridella obscura (1)
Calliostoma pulchrum (1)
Pitar fulminatus (2)

Group 2

Ensis directus (811)
Solemya velum (226)
Cerastoderma pinnulatum (80)

Group 3

Nassarius trivittatus (8)
Pleurobranchaea hedgpethi (8)
Armina tigrina (9)

Group 4

Acteon punctostriatus (201)
Cyclichnella bidentata (226)
Caecum pulchellum (80)
Tellina versicolor (1190)
Lucinidae (juvenile) (906)
Abra aequalis (614)
Lyonsia hyalina (495)
Varicorbula operculata (815)
Spisula solidissima similis (1634)

Group 5

Nuculana acuta (58)
Corbula sp. A (28)
Corbula barrattiana (199)

Group 6

Vitrinellidae sp. A (1)
Gastropoda sp. C (1)
Lucina nassula (1)
Epitonium sp. A (1)
Nassarius albus (1)
Cardiomya costellata (2)
Mercenaria mercenaria (2)
Musculus lateralis (2)
Modiolus modiolus squamosus (2)

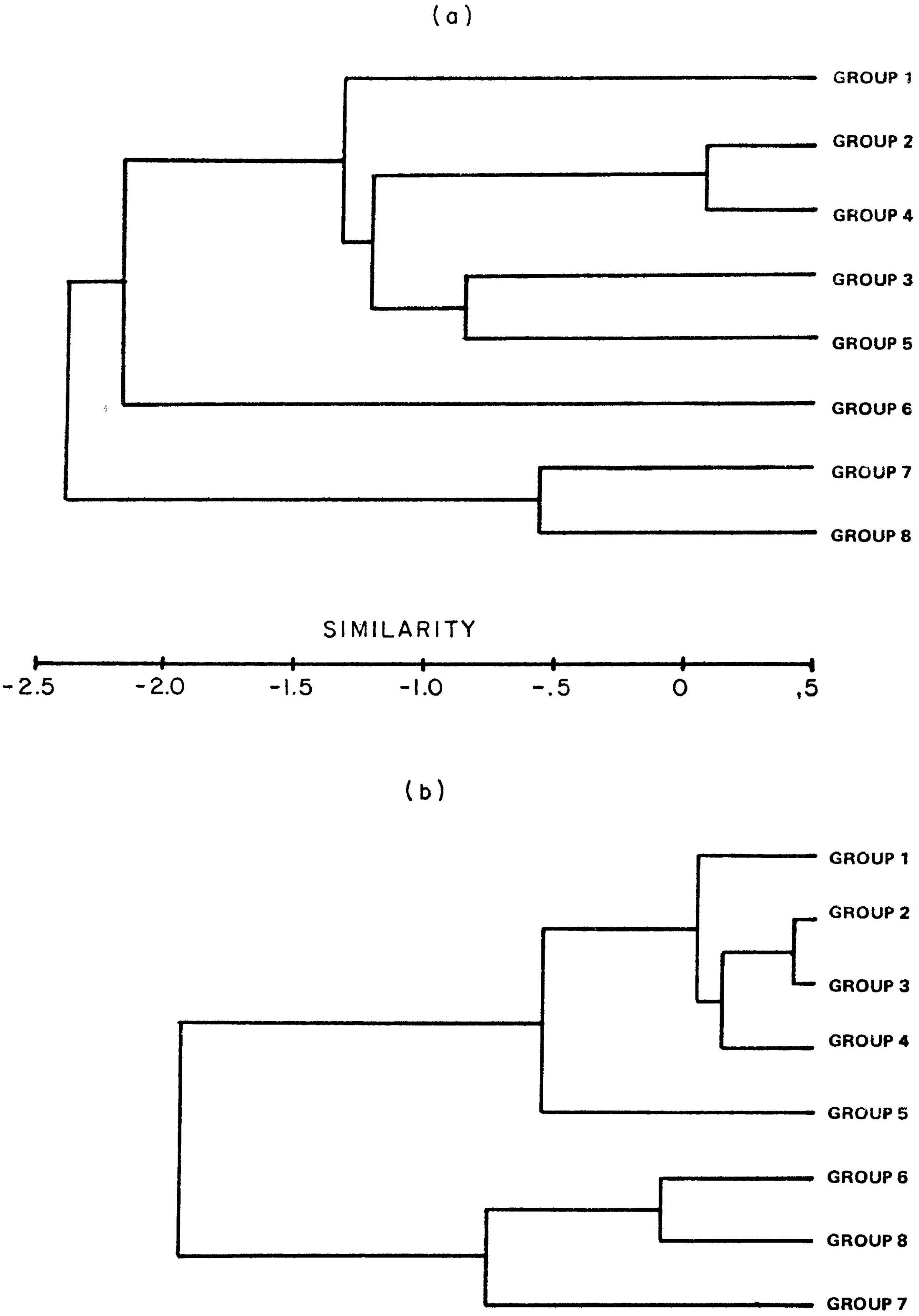
Group 7

Chaetopleura apiculata (6)
Chione grus (3)
Laevicardium laevigatum (2)
Palliolum sp. A (3)
Macoma tenta (3)
Laevicardium pictum (12)
Crenella divaricata (17)
Thyasira trisinuata (29)
Caecum johnsoni (16)
Nucula proxima (21)
Argopecten gibbus (5)
Lima pellucida (3)
Chione cancellata (5)

Group 8

Atrina seminuda (1)
Cyclopecten nanus (1)
Acanthochitona pygmaea (1)
Cryoturris elata (1)
Dentalium eboreum (1)
Chama macerophylla (1)
Lucinidae sp. A (1)
Codakia orbicularis (1)

Figure 16. Classification hierarchies of species groups. Negative similarity values result from the use of a flexible sorting strategy. (a) Mollusca, (b) Amphipoda.


(a)
GROUP 1
GROUP 2
GROUP 4
GROUP 3
GROUP 5
GROUP 6
GROUP 7
GROUP 8
SIMILARITY
-2.5
-2.0
-1.5
-1.0
-.5
0
,5
(b)
GROUP 1
GROUP 2
GROUP 3
GROUP 4
GROUP 5
GROUP 6
GROUP 8
GROUP 7

sedimentary regime. Group 4 species were found to reach high abundance in Hatteras:South and the southern front, areas in which the percent silt-clay varied from 3-18% (Table 2). These species all were only rarely found in areas with less than 2% silt-clay. Species in this group were among the most abundant encountered, ranging from 80 individuals of *Caecum pulchellum* to 1634 *Spisula solidissima similis*.

Group 5 species frequently occurred with those of Group 4 but the habitat requirements of the former were more stringent. These species were only found in areas with 10-18% silt-clay, conditions met only in Hatteras:South and a limited portion of Hatteras:Mid. Two *Corbula* species and *Nuculana acuta* were placed in this group. These are filter-feeding and deposit feeding bivalves respectively, known for their abundance in muddy environments (Stanley, 1970).

Group 6 species are those characteristic of the Hatteras:South area. All are found exclusively in this area though at low abundances. They are all of southern affinity, for with the exception of *Mercenaria mercenaria*, they are at their northern limit in North Carolina.

Species of Groups 7 and 8 are those either restricted to or reaching peak abundance in the South area. The two groups differ only in the number of individuals collected. In contrast to the Group 1 species of the North area, many of the South area species are at their distributional limit. Nine are at their extreme northern limit (*Chione grus*, *Crenella divaricata*, *Lima pellucida*, *Atrina seminuda*, *Acanthochitona pygmaea*, *Cryoturris elata*, *Dentalium eboreum*, *Chama macerophylla*, *Codakia orbicularis*). Five more range only as far north as Virginia (*Laevicardium pictum*, *Laevicardium laevigatum*, *Argopecten gibbus*, *Chione cancellata*, *Cyclopecten nanus*). The remainder are widespread species, though *Caecum johnsoni* is primarily a northern species.

The inverse analysis of the amphipod species (Table 5, Figure 16b) is interpretable at the eight group level. Group 1 is comprised of those species which had their peak abundance in the North area, although they occurred throughout the study area. *Lembos websteri* and *Trichophoxus floridanus* fall into this category though inclusion of the later is perplexing as it is of southern affinity and reaches its northern limit in North Carolina.

Group 2 species, *Trichophoxus epistomus* and *Protohaustorius* cf *deichmannae*, were among the most abundant amphipod species and are characterized by a pronounced sediment specificity independent of latitude. Both species showed extremely high abundances in the Hatteras:North and, to a lesser degree, the North areas. These species seem to prefer the dynamic, well-sorted sands characteristic of these areas.

Group 3 contains the ubiquitous *Synchelidium americanum*. With only two exceptions, it was found at all sampling sites in the study area in moderately high abundance. In addition, its abundance was

Table 5. Species groups of amphipods formed by inverse classification. Number in parentheses following each species name indicates total number of individuals collected.

Group 1

Trichophoxus floridanus (97)
Lembos websteri (73)

Group 2

Trichophoxus epistomus (210)
Protohaustorius cf *deichmannae* (1774)

Group 3

Synchelidium americanum (501)

Group 4

Ampelisca verrilli (40)

Group 5

Tiron tropakis (11)
Elasmopus sp. A (7)

Group 6

Unicola serrata (89)
Liljeborgia sp. A (15)
Siphonoectes smithianus (11)

Group 6 (cont)

Ampelisca agassizi (8)
Lembos smithi (34)
Microdeutopus sp. A (21)
Erichthonius brasiliensis (47)
Photis pugnator (189)
Ampelisca cristoides (32)

Group 7

Garosyrrhoe sp. A (1)
Melitidae sp. A (1)
Photidae sp. A (1)
Cerapus tubularis (2)
Lembos unicornis (2)
Melita appendiculata (3)
Listriella sp. A (3)
Amphipoda sp. C (1)
Stenopleustes gracilis (5)

Group 8

Microdeutopus sp. C (9)
Podocerus brasiliensis (8)
Microdeutopus myersi (10)
Gammaropsis sp. A (10)
Unciola sp. A (12)
Amphipoda sp. B (17)
Ampelisca vadorum (20)
Corophiidae sp. A (23)

---

correlated with the median diameter of the sediments, reaching a peak in the fine sands of the southern front.

Ampelisca verrilli is the only species contained in Group 4. It reached peak abundance in the Hatteras:South and Hatteras:Mid areas, with only scattered occurrences throughout the front, and, as with the Group 5 molluscs, seemed to be responding to the high percentage of silt-clay in these areas. Though Mills (1967) states *A. verrilli* reaches greatest abundance in coarse sands, in the Cape Hatteras region it was found only in fine and very fine sands having between 10.4 and 17.5% silt-clay. The apparent discrepancy may in part be due to taxonomic uncertainties for Mills (1967) points out that the North Carolina specimens of *A. verrilli* have small morphological differences from the northern populations.

Group 5 species were not abundant in the Hatteras:South area, and in this regard are comparable to the Group 6 molluscs. *Tiron tropakis* exhibited an additional lower abundance peak in the South area.

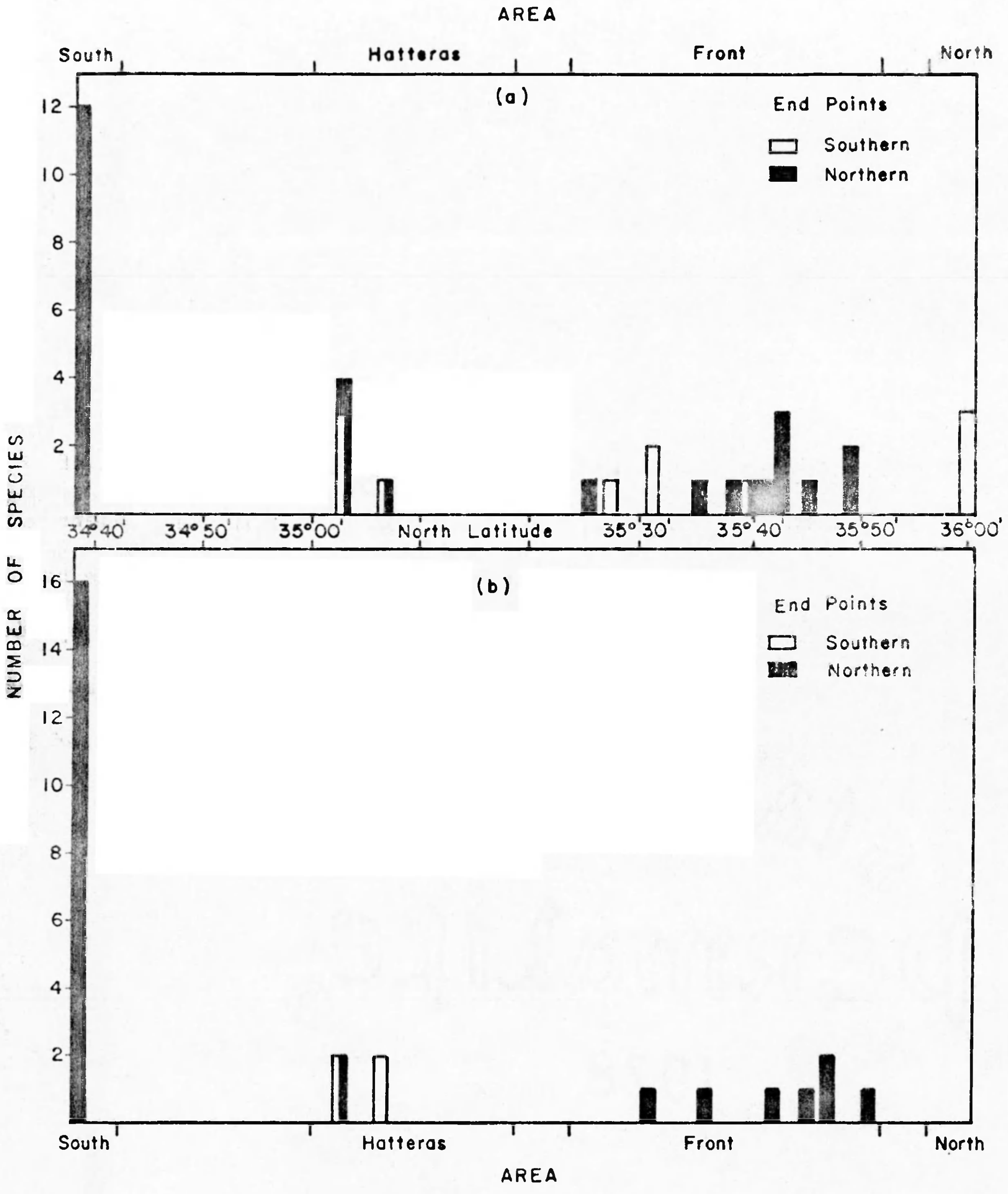
Groups 6, 7 and 8 which are so clearly separated by the species group hierarchy of Figure 17b, were all representative of the South area, differing only in their abundance and fidelity. Species of Group 6 were most abundant in the South, though scattered collections were also made in the front and Hatteras strata. Most of the species in this group are of southern affinity, though they generally range north to Cape Cod. Only Ampelisca cristoides is at its northern limit in North Carolina.

With the exception of Ampelisca vadorum, one individual of which was found in the front, species of Groups 7 and 8 were all restricted to the South area. Separation of these groups is on the basis of abundance alone, for 8 or more individuals of Group 8 species were obtained, while Group 7 species were represented by 5 or less individuals. Determining biogeographic affinity of these species is difficult because of the high proportion of these species identifiable only to genus. However, the shallow-water temperate Amphipoda are fairly well known, and it would seem more likely that these undescribed species are of subtropical or tropical affinity, where much less work has been done.

Range End Point Analysis

Location of biogeographic barriers can often be determined simply by establishing points of termination of the ranges of many species (Horn and Allen, 1978). This has been done in Figure 17, where the end points of the ranges of 15 northern and 54 southern species have been plotted. In determining northern end points, the species collected in the South area were established as the initial group, and the northernmost appearance of these species was taken as their end point. A similar procedure was followed in determining southern end points. These end points are not to be interpreted as absolute, beyond which the species has never been recorded, but

Figure 17. Location of range end points in the study area of both northern and southern species suites. Where both northern and southern endpoints occur, the bar is divided vertically. (a) Mollusca. Initial species groups consist of 39 southern and 21 northern species. (b) Amphipoda. Initial species groups consist of 34 southern and 13 northern species.


AREA
South
Hatteras
Front
North
(a)
End Points
Southern
Northern
12
10
8
6
4
2
34°40'
34°50'
35°00'
North Latitude
35°30'
35°40'
35°50'
36°00'
NUMBER OF SPECIES
(b)
End Points
Southern
Northern
16
14
12
10
8
6
4
2
South
Hatteras
Front
North
AREA

rather only as the northernmost or southernmost collections made in this study. This approach was followed for two reasons; 1) this study covers only a narrow depth range and is not concerned with the extension of a species range by a change in habitat (e.g. submergence), 2) it is impossible to determine the total range of the numerous unidentified and/or undescribed amphipods.

Perhaps even more clearly than the cluster analysis or ordination, end point analysis illustrates the uniqueness of the South area. Of the 73 species collected there, 28 species (38%) were found no where else. This is especially true in the amphipods in which nearly half of the South area species were unique to the area.

Apart from the concentration of northern end points in the South area, frequency of end points reached a second peak at Hatteras:South. This was the case in both taxa, though slightly more prominent in the Mollusca.

The mid to north front also showed a significant loss of southern species, for 12 mollusc and 7 amphipod species reached a northern end point in this area. In the case of six of the species (Acteocina candei, Kurtziella limonitella, Cadulus carolinensis, Varicorbula operculata, Philine sagra, Ampelisca cristoides), the front represents an absolute range limit as well, with no known occurrences north of this region.

It is readily apparent that southern end points are much less numerous than northern end points. Only 52% of the northern molluscs and 31% of the northern amphipods had southern end points in the study area, whereas 74% of the southern species of both taxa had northern end points.

The regions with the highest frequency of southern end points were the Hatteras:South and Hatteras:Mid areas. In the amphipods, southern end points were found exclusively at these locations. It is certainly of significance that of the four amphipods with southern end points near Cape Hatteras, three are in the family Haustoriidae, a group with predominantly cold-temperate affinities (Bousfield, 1965).

DISCUSSION

Factors Limiting Faunal Distribution

Although temperature is an important factor in determining distribution of species, it alone does not account for all distributional patterns observed or the type of community encountered at any given point. Numerous other factors such as sedimentary factors, inter- and intraspecific interactions, dispersal and salinity may also play a role. Though not the primary focus of this investigation, some discussion of these factors is warranted.

Hard Substrate

Not only is the South area unique in its warm, stable thermal regime, but it also is the only area sampled containing any appreciable hard substrate (excluding mollusc shells and other similar microhabitats). Pearse and Williams (1951) and Menzies et al. (1966) have examined the reefs off North Carolina and described a predominantly southern faunal assemblage. As the South area fauna shows a high similarity to that reported by these earlier studies, and has an unusually high diversity, it may be postulated that this is in part due to the contribution of the hard substrate fauna. For the decapods of the South area the hard substrate has been held partially responsible for the high diversity (Herbst et al., 1979a). Decapod species specifically adapted to a hard substrate environment such as *Pylopagurus corallinus* and *Glyptoxanthus erosus* were frequently obtained in the South area collections by Herbst et al.

This however does not seem to be the case for the molluscs and amphipods. In contrast to the decapods, they were obtained by grab rather than trawl. The Smith-McIntyre grab is not suitable for sampling of hard substrate and the few grabs obtained containing rubble were discarded because of insufficient penetration. Further evidence of the minimal contribution of the hard substrate environment is seen in the absence of species typical of such habitat (*Plicatula*, *Chama*, *Echinochama*, *Crepidula*). Of these genera only one *Chama macerophylla* was found (on a *Limulus* shell), and three *Crepidula fornicata* were found attached to shell fragments in the frontal region. Thus, the hard substrate of the Raleigh Bay area does not seem to play a significant role in determining the faunal distributions observed in the present study.

Sediment

Sanders (1958), McNulty et al. (1962), Young and Rhoads (1971), Gray (1974) and many other investigators have discussed the importance of animal-sediment relationships. As noted earlier, many species collected respond closely to the sedimentary environment independently of or in some cases concurrently with the thermal environment. In areas where the percentage of silt-clay exceeded

10%, species such as *Nuculana acuta*, *Corbula barrattiana*, *Corbula swiftiana* and *Ampelisca verrilli* peaked in abundance. Overlapping this environment, but also found in slightly coarser sands with as little as 2% silt-clay, *Lyonsia hyalina*, *Abra aequalis*, *Varicorbula operculata*, *Cylichnella bidentata* and *Acteon punctostriatus* were found. In dynamic environments with < 1% silt-clay, fossorial species such as *Protohaustorius* cf *deichmannae* and *Trichophoxus epistomus* proliferated.

The specificity of sediment preference is dramatic at times, as evidenced by the haustoriid amphipod, *Protohaustorius* cf *deichmannae*; abundant only in restricted regions of the Hatteras:North and North areas. Field studies (Sameoto, 1969a) have shown that *P. deichmannae* is rare in coarse sands, its abundance increasing as the median grain size decreases. Laboratory studies of sediment preference (Sameoto, 1969b) showed equal preference for sediments with a median grain size of 1.5 ϕ and 1.8 ϕ and an avoidance of coarser sediments. No finer sediments were offered in the preference test, though a slightly smaller grain size seemed preferred in the present study. Sameoto (1969b) suggested that as this species burrows by passing sand grains between the peraeopods, the optimal sediment is that containing the major portion of grains small enough to pass between the peraeopods. If this were the case, then a difference in size distribution between the Massachusetts population examined by Sameoto, and the North Carolina population may account for the slight difference in preferred grain size.

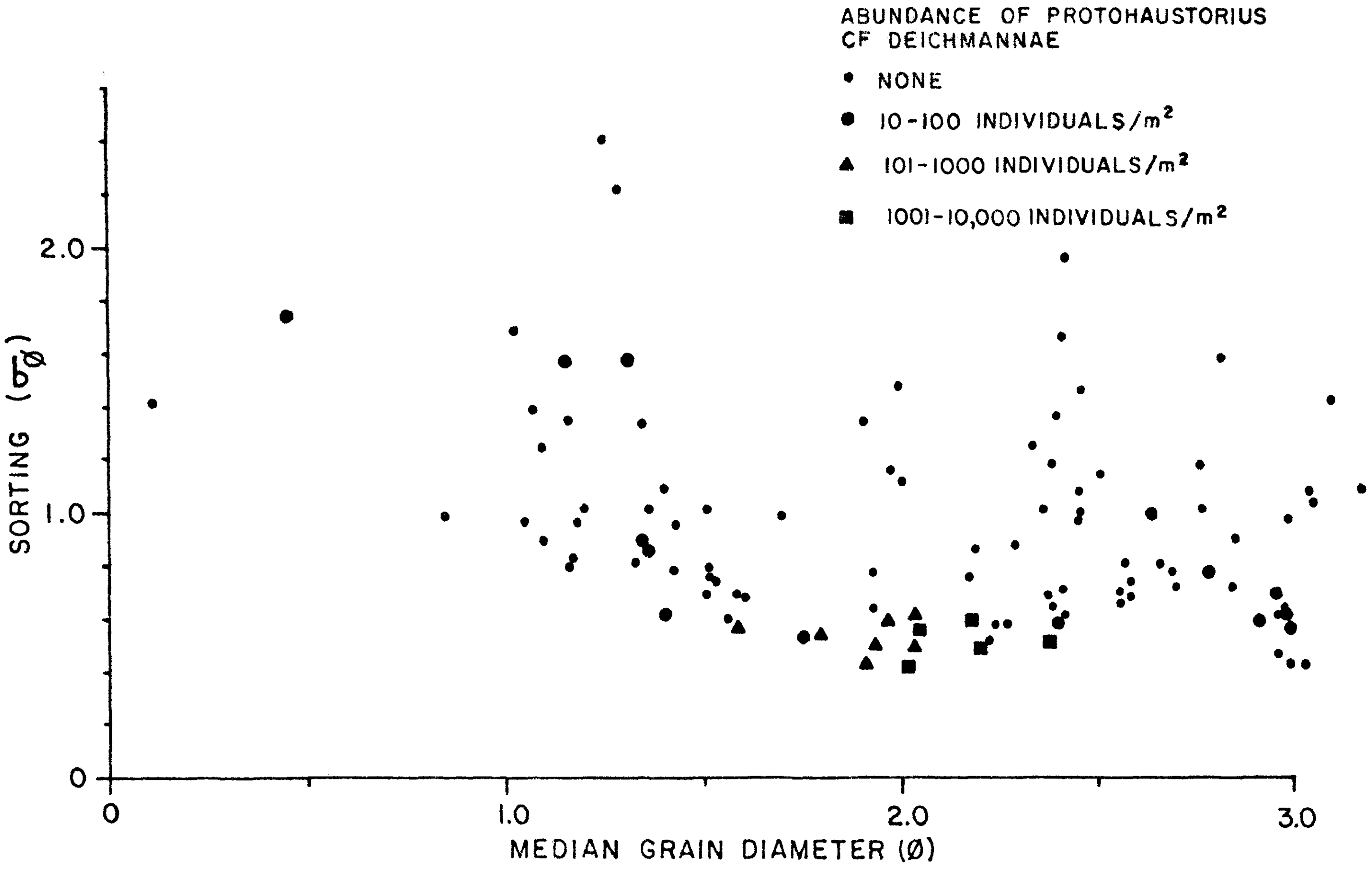


Figure 18. Abundance of the haustoriid amphipod *Protohaustorius* cf. *deichmannae* in all grab samples as a function of both median grain size diameter (ϕ) and degree of sorting ($\sigma\phi$).

The narrow range of sediment found suitable for Protohaustorius cf deichmannae in the present study is illustrated in Figure 18 in which abundance is plotted as a function of both sorting ($\sigma\phi$) and median grain size. P. cf deichmannae was found in high abundance ($> 1000\ m^{-2}$) only in areas having a median grain diameter between 2.0 ϕ and 2.4 ϕ and a dispersion of less than 0.6 ϕ. Both factors were important and abundance dropped rapidly if either criterion was not met.

A significant correlation ($r = 0.847$; $p < .01$) was found to exist between the density of molluscs in the frontal region and the percentage of silt-clay at these stations (Figure 19). To determine the cause of this correlation, the abundance of the ten most abundant species in the frontal area, representing 88% of the total number of individuals, were separately correlated with the percentage of silt-clay (Table 6). Eight of these species are responsible for the original correlation observed. All species which show significance, except Solemya velum, are members of the Group 4 molluscs obtained by inverse classifiction. Solemya velum had not been included in the group because of peak abundances in the northern front, whereas the others were most abundant in the southern front.

A second correlation observed was that between Shannon diversity of the molluscan population across the front and the percentage of silt-clay ($r = 0.519$; $p < .05$). Separating diversity into its components of evenness and species richness, reveals that the richness component is responsible for the correlation.

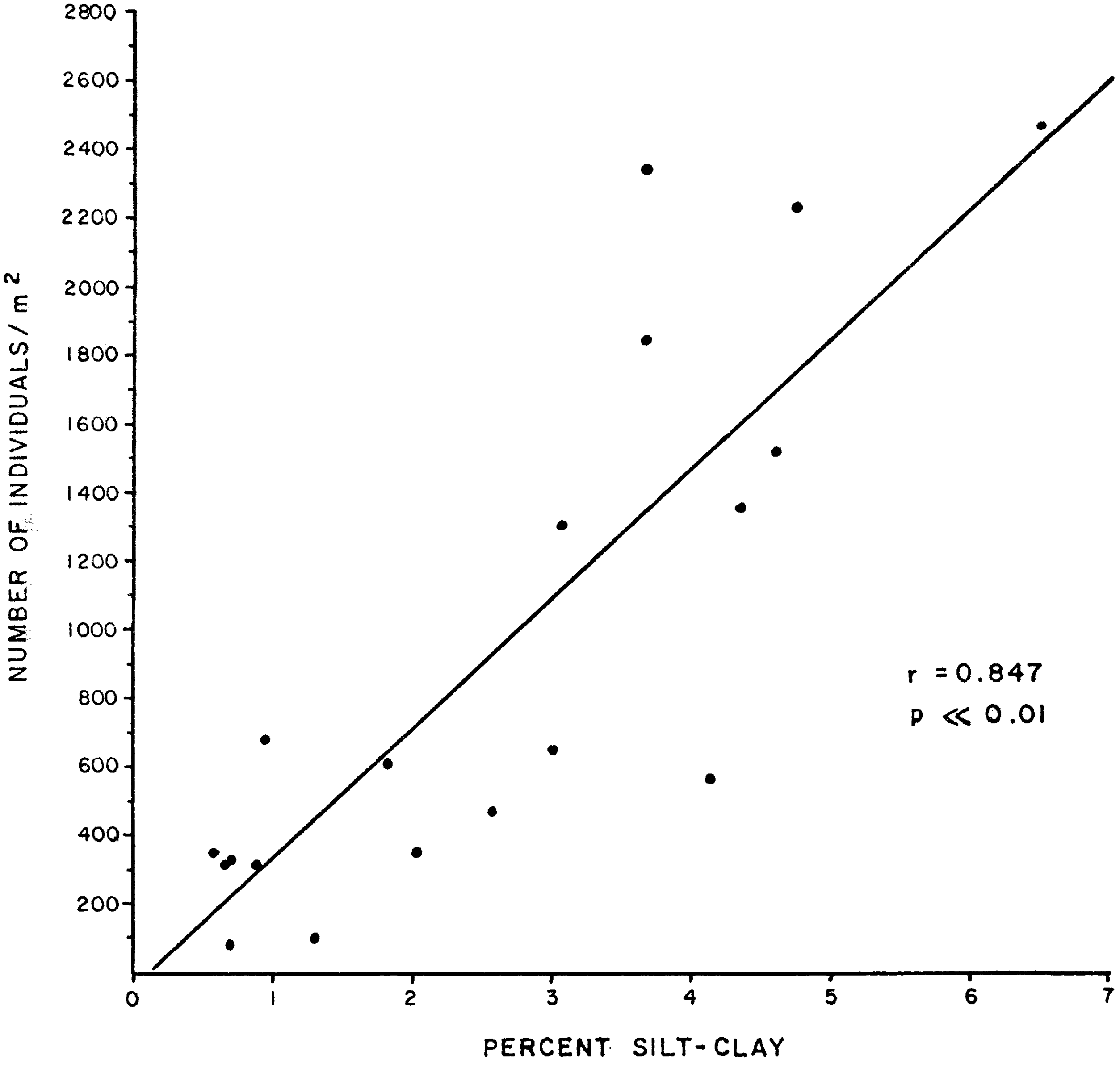


Figure 19. Least squares regression of mollusc density in the frontal region against the percentage of silt-clay in the sediments.

Table 6. Correlation coefficient (product-moment) of abundance and percentage of silt-clay for the ten most abundant mollusc species in the frontal region. The ten most common species comprise 88% of the total number of individuals in the frontal area.

Species	No. of Individuals Obtained in Front	Correlation Coef. (r)
Spisula solidissima similis	1039	0.391
Tellina versicolor	807	0.537*
Lucinidae (juvenile)	774	0.735**
Ensis directus	637	-0.162
Abra aequalis	509	0.702**
Lyonsia hyalina	307	0.599**
Varicorbula operculata	233	0.769**
Cylichnella bidentata	225	0.706**
Solemya velum	222	0.553*
Acteon punctostriatus	160	0.836**

* $p < 0.05$
** $p < 0.01$

Other authors have remarked on a diversity/silt-clay correlation, but contrary to these results, it has been reported as a negative correlation. Sanders (1968) found the sand bottom fauna of Buzzards Bay to be more diverse than the mud bottom fauna. He presumed this to be the result of the greater variety of microhabitats available in a sandy environment. Boesch (1972) found a similar trend in Hampton Roads, and remarked that the species richness component was primarily responsible. Franz (1976), working with the molluscan fauna of Long Island Sound, found few significant correlations between diversity and its components and various sediment parameters. Regarding species richness, Franz found only the percentage of gravel to show a significant correlation and this was only deemed significant in coarse and very coarse sands.

The discrepancy between the positive correlation of species and percentage of silt-clay observed in the present study, and the negative correlation frequently observed by others, is largely a result of scale. The concept was developed in environments having as much as 91% silt-slay (Sanders, 1960) and the pattern observed in the present study represents only an aberration in the 0.4 to 6.5% range. Slight expansion of this range might be possible by including non-front areas (i.e. Hatteras:South and Hatteras:Mid) but this might be somewhat tenuous because of possibly differing zoogeographic affinities.

Salinity

Salinity is an important factor in determining faunal distribution in some habitats, such as estuaries (Carriker, 1967), although in the open ocean, marine organisms do not generally encounter marked salinity variation. Nevertheless, as some change in salinity occurs across the study area, an attempt should be made to assess the importance of this change in determining species distributions. A 3 $^{o}/oo$ difference (31.46 - 34.57 $^{o}/oo$) exists between the North and South areas and a salinity change of up to 4 $^{o}/oo$ (32.78 - 36.85 $^{o}/oo$) accompanies the thermal gradient across the front. As no direct assessment of the importance of changes of this magnitude can be made from the data, an examination of literature sources is necessary.

Wells (1961) examined the salinity tolerance of twenty species associated with the oyster beds in North Carolina estuaries. Of the species he studies, five of the molluscs (_Urosalpinx cinerea_, _Busycon carica_, _Fasciolaria lilium hunteri_, _Pagurus longicarpus_) and three echinoderms (_Asterias forbesi_, _Arbacia punctulata_, _Lytechnius variegatus_) are known to occur in the offshore study area (pers. observation). The salinity death points for these 10 species average 13 $^{o}/oo$ and all are below 23 $^{o}/oo$. These lethal salinities are well below those encountered in this study. Admittedly, a reduction of viability may occur at higher salinities, and species adapted to estuarine conditions are inherently more euryhaline. However, the difference between observed salinities and those considered by Wells to be lethal is so great that variation in the range and of the magnitude encountered in the study area is considered biologically unimportant. Other studies confirming this include those on *Ophiothrix angulata* (Stancyk and Shaffer, 1977), *Protohaustorius deichmannae* and *Acanthohaustorius millsi* (Sameoto, 1969b), *Bathyporeia* spp. (McGrorty, 1971) and larvae of several decapod species (Vernberg and Vernberg, 1970a).

In the frontal region, the change in salinity is coupled with a large temperature fluctuation. Simultaneous change of these two parameters can modify the biological effect of variation of either parameter taken separately (Kinne, 1964). Even so, as the maximum change of 4 °/oo across the front occurs in a salinity range that is not generally deleterious to marine organisms, it is thought that the biological effect of this salinity change on most organisms of the front will be little modified by the concurrent thermal variation. This view is supported by work on simultaneous temperature/salinity variation on the harpactacoid copepod, *Tigriopus fulvus* (Ranade, 1957) and the American lobster, *Homarus americanus* (McLeese, 1956).

However, for sub-tropical species that are already stressed by a drastic temperature decrease, the concurrent salinity decrease could prove deleterious. Such is the case for the brachyuran, *Sesarma cinereum*, the larvae of which were studied by Costlow et al. (1960). This species is found from Mexico to the Chesapeake Bay and therefore is near its thermal limit off North Carolina. Though the first three zoeal stages could tolerate temperature/salinity changes of the magnitude encountered in the front, the fourth zoeal and megalops stages showed a significant increase in mortality resulting from a synergistic interaction between temperature and salinity.

Biotic Interactions

The importance of biotic interactions in benthic communities is well documented in the literature (Dayton and Hessler, 1972; Sutherland, 1977; Woodin, 1974, 1976). However, it is much more difficult to measure competition or predation pressures than it is to measure temperature, sediment type or other distribution-limiting factors. Nevertheless, in the present study, biotic control of distribution seems possible in some instances.

Biotic exclusion is suspected in the case of many of the species encountered in the frontal and North areas, but absent from the South area, despite adequate thermal tolerance. Nearly all of the northern species absent from the South stratum are found in coastal and estuarine waters throughout the southeast, a habitat reaching temperatures even greater than the South area. Examples of this can be found in the collections of Fox and Bynum (1975) in the estuaries near Beaufort, North Carolina (e.g. Unciola irrorata, Bathyporeia parkeri) and those of Heard and Heard (1971) in Georgia estuaries (e.g. Unciola serrata and Trichophoxus epistomus). Although these estuarine waters reach summer temperatures (> 30°C) even higher than offshore waters, they are similar to the waters north of Hatteras in that they experience wide annual temperature variation, making them uninhabitable by the warm water, stenothermal species characterisitc of the offshore habitat. Where these stenothermal species are able to survive, as in the South area, the northern species are out-competed (or preyed upon).

The exclusion of species of physically-controlled environments (Sanders, 1968) such as the front and inshore waters, from thermally-stable biologically accommodated environments, such as the South area has been suggested before as a natural extension of Sanders' stability-time hypothesis (Slobodkin and Sanders, 1969; Grassle, 1972). Species of unpredictable environments are, by necessity, generalists. They are capable of exploiting a wide variety of resources. In contrast, species adapted to stable, predominantly biologically accommodated environments are confined to a smaller niche size. They are highly specialized in terms of the resource type utilized and the microhabitat occupied. Thus, they can frequently out-compete species invading from physically controlled areas. Though the biological barriers separating these faunal types do not seem insurmountable for all northern species in this instance, those northern species which are excluded from the South area in spite of adequate thermal tolerance, may in part be controlled by this biotic mechanism.

Other biotic interactions might be expected on the basis of knowledge of behaviour and life history of the species encountered. Foremost among these is predation, particularly in the Mollusca. As many of the species are carnivorous, their abundance is in part determined by the availability of prey species. This would be the case for families such as the Naticidae, Columbellidae, Marginellidae, Olividae, Turridae and Terebridae (Taylor and Taylor, 1977).

Conversely, the distribution or at least the abundance, of prey species would depend on the abundance of predators. This may be of special significance in the front, which has been shown to be a region of dense aggregations of bottom-feeding fishes such as spot (Leistomus xanthurus), croaker (Micropogon undulatus) and scup (Stenotomus chrysops) (J. Magnuson, pers. comm.)

Symbioses can also be expected to play a role in the distribution of some of the species encountered during the study. Such would be the case for the Leptonacea, commensal or parasitic on a wide variety of marine organisms. Included in this group is Pythinella cuneata which is associated with sipunculids inhabiting empty gastropod shells (Abbott, 1974). Epitonium sp. A is parasitic and/or forages on benthic coelenterates (Salo, 1977; Perron, 1978). Turbonilla interrupta and Odostomia sp. A both belong to the family Pyramidellidae, a group containing many ectoparasitic species. Known hosts of Turbonilla are polychaetes, coelenterates or molluscs, although Sanders (1960) found it in such great abundance that he suggested that it is only a facultative parasite, capable of deposit-feeding in certain environments.

The Nudibranchia often prey on a wide variety of epibenthos, and the species collected during this study are no exception. Armina tigrina feeds on sea pansies (Abbott, 1974) and its distribution corresponds to that of Renilla reiniformis which is found northward only to the mid-frontal region. Doridella obscura is known to feed on the encrusting bryozoan, Membranipora (Abbott, 1974).

Dispersal

As important as substrate type, biotic interactions and physical conditions are in determining a species distribution, they are only of secondary importance in that there must first exist mechanisms for transport of the species into an area. For species with planktonic larvae, their distributional opportunities are determined by the movement of the water mass in which the larvae are carried. This passive transport allows dispersal over very great distances for larvae with long planktonic lives (Scheltema, 1966). Undoubtedly the occurrence of many of the tropical and sub-tropical species of the South area results from northward transport of larvae from southern populations by the Gulf Stream. In some cases, a continual input of larvae from tropical areas is necessary to maintain the North Carolina population, for reproduction may be possible only at lower latitudes (H. Porter, pers. comm.).

Differences in the species present within each sampling area may in part be a result of differences in the planktonic species pool to which the areas are exposed. For example, while both the South and Hatteras areas are influenced by Carolinian and Gulf Stream water most of the year, the Hatteras area is also exposed to Virginian water during the winter months, while the South area is not. This may permit the establishment of populations of northern species in the Cape Hatteras region though not in the South area. The capacity for southern transport of Mytilus edulis larvae by winter intrusions of Virginian water has been demonstrated (Wells and Gray, 1960).

Because of the current patterns of the region, the frontal area is likely to act as an effective barrier to north-south transport of planktonic larvae. In the frontal region both the southward flowing Virginian water and the northward flowing Gulf Stream turn to the northeast and move off the continental shelf. Larvae of shallow-water benthic species are thereby prohibited from further dispersal to the north and south along the Atlantic seaboard. Opportunities for breaching this barrier are few and infrequent. The seasonal movement of Virginian water around Cape Hatteras allows limited southward transport. Northward transport of larvae beyond the front can be accomplished only by entrainment of larvae in warm-core Gulf Stream eddies which break off the north wall of the Gulf Stream and subsequently move on to the continental shelf in the Middle Atlantic Bight (Bowen et al., 1979)

End point analysis did provide some evidence of a northern range limit in the front for some southern species, which may be a result of the effect of the hydrographic conditions on planktonic larval transport. This discontinuity was not of sufficient magnitude to clearly show in the cluster analysis and ordinations. In view of the effect of current patterns on planktonic dispersal, it is surprising that a greater faunal discontinuity does not exist at the front. Three explanations are apparent for this: 1) periodic breaching of the barrier as discussed, 2) confounding of dispersal-induced distribution patterns by sedimentary, thermal and other factors and 3) the limited number of species studied which have planktonic larval stages. Amphipods brood their young and thus do not depend on movements of water masses for larval dispersal. While most of the molluscs have planktonic larval stages, some of these too have a brooding reproductive strategy (e.g. many Neogastropoda, Pulmonata).

Thermal Factors

The great differences in temperature of offshore water masses in the North Carolina region strongly suggests the existence of thermally-induced faunal boundaries. As discussed earlier, Virginian bottom water north of Cape Hatteras can vary seasonally from 4°C to 24°C. South of Hatteras, bottom temperature is higher and there is considerably less seasonal variation (16°C to 26°C in South area).

The importance of temperature in determining faunal distributions in the North Carolina region has been shown (e.g. Wells and Gray, 1960). The studies most applicable to current investigations are those of Vernberg and Vernberg (1970a, 1970b). These studies are particularly valuable in that they relate laboratory physiological results to the ecology and distribution of the organisms in the field. Determinations were made on the lethal maximum and minimum temperatures (Vernberg and Vernberg, 1970a) and the thermal-dependence of metabolic rates (Vernberg and Vernberg, 1970b) of selected crustaceans, echinoderms and molluscs collected from the North Carolina shelf. Collecting sites roughly corresponded to the South and mid-frontal areas, though the existence of a sharp thermal front in the area was not known at the time of this study, and the frontal region was assumed to be constantly cold.

Based on the laboratory results, Vernberg and Vernberg found that species collected from near our South area were unable to survive the cold temperatures typical of inshore waters (10°C) and the area north of Cape Hatteras (4°C). Species of northern affinity collected in the frontal region were unable to survive abnormally high temperatures as well as the southern species and showed a depression of metabolic rate above 20-25°C. Species of southern affinity found in the frontal region and those with widespread distributions were largely unaffected by temperatures encountered in the North Carolina region.

As related to the present study the most effective thermal barrier may be that preventing many of the South stratum species from inhabiting the Hatteras strata or any area north of the Cape. Many of the South stratum species are warm stenothermal species widely distributed throughout the Caribbean, but reaching a northern limit in North Carolina (e.g. *Laevicardium pictum*, *Codakia orbicularis*, *Podocerus brasiliensis*, *Ampelisca cristoides*).

As shown by the limited number of southern range limits of the end point analysis, few of the northern species are unable to tolerate temperatures of the South area. As discussed, many are able to tolerate even the higher temperatures of estuaries of the southeastern states. Of the 147 species collected, only one, the deep-sea scallop *Placopecten magellanicus*, is not known to occur south of Cape Hatteras (though it was found in the Hatteras:South area).

A boreal faunal component, restricted to cold water, seems to be absent from collections made in this study. This in in contrast to Cerame-Vivas and Gray (1966) who found several northern species in the same general area as the frontal and North areas (e.g. *Astarte borealis*, *A. castenae*, *A. undata*, *Solemya borealis*, *Yoldia limatula*, *Aeginina longicornis*, *Leptocheiras pinguis*, *Pontogenia inermis*). Three explanations are readily apparent for this.

Cooler temperatures may have existed in the frontal area at the time of the study by Cerame-Vivas and Gray. Given satisfactory thermal conditions, establishment of a cold-water fauna would be possible as the Virginian Coastal Current provides a mechanism for transport of larvae of adults from northern waters. However, the likelihood of such a climate change is somewhat diminished by the fact that the front was found to span a similar temperature range in 1971, 1975, 1977 and 1978 (J. Magnuson, pers. comm.; pers observation).

A second explanation is that these cold water species were obtained in deeper, cooler waters though at similar latitudes to the present study sites, Cerame-Vivas and Gray (1966) do not give the depth and location of all collecting sites and the sites at which the various species were collected.

Thirdly, a seasonal factor may be involved for this study describes only the situation existing in late spring. Cerame-Vivas and Gray are vague as to the time of sampling, describing it only as "seasonal". It is possible that a cold water fauna could be more prevalent at certain times of the year and investigations of such seasonality are currently underway.

Assessment of Faunal Barriers

Cape Hatteras

Intensive sampling in a relatively small geographic area, as this project entails, allows assessment of Cape Hatteras itself as a zoogeographic barrier. Though adequate evidence exists in this and other investigations demonstrating the importance of the North Carolina region as a whole as a faunal barrier, some authors (Cerame-Vivas and Gray, 1966) have been quite specific in locating this barrier precisely at Cape Hatteras.

The three applicable analyses, ordination, cluster analysis and end point analysis, allow examination of the effectiveness of separation of northern and southern fauna at Cape Hatteras. Were this the case, the Hatteras:South area would be most similar to the South area and show pronounced dissimilarity to Hatteras:North, which would in turn, tend to show similarity to the frontal and North areas.

Such a pattern is not apparent for the Mollusca, but is evident, to a limited extend, for the amphipods. In the amphipod cluster analysis, the South and Hatteras:South areas do cluster together, though at a low similarity. Axis 1 of the amphipod ordination also gives some indication of a faunal discontinuity at Cape Hatteras, for both the South and Hatteras:South areas have high scores on this axis (with the anomolous inclusion of Front:40').

End point analysis (Figure 17) does provide some evidence of a faunal barrier located precisely at Cape Hatteras, particularly for the northern amphipod species, and to a lesser degree, for the other faunal groups. The importance of this barrier is, however, overshadowed by the species loss occurring in the northern frontal area and Raleigh Bay.

Thermal Front

The frontal area has been cited as being of greater importance than Hatteras itself as a zoogeographic barrier for fishes and decapods (J. Magnuson, pers. comm.; Herbst et al., 1979a). Both these groups are generally more mobile than the macrobenthos examined in this study, in which a gradual, rather than an abrupt faunal change is evident. This is seen in the end point analysis, in which all faunal groups but the northern amphipods, show a gradual species attrition across the frontal area. This is seen most dramatically in the plot of score on axis 2 vs. latitude for the mollusc ordination (Figure 14), in which there is a gradual faunal change from the Hatteras strata to the North area.

Within the frontal region, most species seem to be sufficiently eurythermal so that their distribution is more dependent on sedimentary parameters than on the thermal fluctuations. This is evident in the cluster analysis for both taxa in which the sub-divisions within the front were made on the basis of median grain size and percent silt-clay. This is especially true for the most abundant species, for as shown earlier, eight of the ten most abundant mollusc species in the front and the three most abundant amphipods were highly substrate dependent.

It seems that rather than demonstrating strong response to the short-term thermal fluctuations within the frontal region, the two groups of macrobenthos examined are more responsive to the long-term (annual) fluctuations. Though the Hatteras strata were covered by warm water at the time of sampling, it is known that northeasterly winds can drive the cold Virginian water over these strata and along the inshore portions of Raleigh, and in some cases, Onslow Bay (Wells and Gray, 1960; Gray and Cerame-Vivas, 1963; Stephansson and Atkinson, 1967). The faunal similarity of the Hatteras and frontal stations and the uniqueness of the South area seem to be in response to these annual fluctuations.

The absence of a strictly northern fauna in the North area and the lack of a pronounced faunal dissimilarity from the front stations, raises the question of whether the North area too may lie within the effective frontal region as the Hatteras area does. Though the possibility cannot be categorically dismissed, it is unlikely for several reasons: 1) four seasonal cruises throughout 1977 and 1978 did not detect warm, high salinity water in the area, 2) weekly charts of sea surface temperature published by the U. S. Naval Oceanographic Office do not show the Gulf Stream any less than 20 km from the North area and generally further away and 3) little difference in fish and decapod fauna exists between the North area and an area at similar depths off Cape Henry, Virginia (J. Magnuson, pers. comm.).

Frontal Community Ecology

Patterns of diversity and its components are regularly used by community ecologists to examine the response of a community to various types of perturbations such as pollution (Littler and Murray, 1975), temperature extremes (Warriner and Brehmer, 1966; Ward, 1976), fire (Loucks, 1962) and predation (Harper, 1969). Similar analysis was applied in the present study to evaluate the impact of the thermal fluctuations of the front on the benthic macroinvertebrate community.

Front as a Physically Controlled Environment

Because of the rapid and unpredictable thermal fluctuations to which the frontal macrobenthos are exposed, it would seem reasonable to categorize the front region as a predominantly physically controlled environment (Sanders, 1968). Environments such as this are typically characterized by low diversity (Sanders 1968, 1969; Woodwell, 1970), as reflected in decreases in both species richness (Cairns et al., 1972) and evenness (Grassle, 1972; Littler and Murray, 1975).

Surprisingly, the diversity observed in the frontal region does not show an obvious depression relative to the more thermally constant North area, and is depressed relative to the Hatteras strata only for the Amphipoda. Three explanations can be presented to account for this.

First, the frontal region differs from many other physically variable environments in that it is not surrounded by a relatively homogenous species pool, but is partially bounded by a very diverse and speciose habitat (South area). The northward flowing Gulf Stream provides a transport mechanism whereby adults or larvae from this large species pool could easily be transported into the frontal region. It has been shown that the size of the species pool potentially able to invade an area has a great effect on the number of species actually found in the community (Patrick et al., 1967; Cairns and Ruthven, 1970). It may be that invasion by eurythermal species of the South area is able to sufficiently raise the diversity so that no depression is evident relative to the North area.

Secondly, systems already subjected to energy-requiring forces are more likely to resist future perturbations than those adapted to stable environmental conditions (Copeland, 1970). As an example, Copeland examined a tropical and a temperate bay, both subjected to a disturbance of similar magnitude. Whereas the tropical area showed drastic biotic alteration as a result (Cerame-Vivas et al., 1967), the temperate bay showed no change detectable by normal sampling procedures (Jeffries, 1962). A similar situation may exist in the front, for it lies at a latitude having great seasonal fluctuation in climate. Though the thermal regime of the front is characterized by rapid temperature fluctuation, it is only stressful in a temporal sense. The magnitude of the changes is near that normally encountered on a seasonal basis by the North area organisms. While a thermal front may have a profound effect on diversity in other regions of the world, the thermal conditions of the area may be well within the tolerance range of most temperate amphipod and mollusc species.

Thirdly, a remarkably high evenness is evident in the front, at certain stations even exceeding that of the South area. Such a pattern may result from non-selective predation. As noted earlier, large schools of bottom-feeding fishes congregate in the frontal area. Furthermore, it may be that the frequent thermal fluctuations cause behavioural changes increasing the susceptibility of the benthos to predation. Since the degree of predation on a species is in part dependent upon its density, non-selective predatory pressures would tend to decrease the relative dominance of species in the habitat. In a stable environment, species richness would also increase because of reduction of competitive exclusion (Dayton and Hessler, 1972), but colonization of additional species may be prohibited by intolerance of the thermal stress.

Comparisons Between Taxa

Evolutionary History: Center of Origin

When this study was initially undertaken it was thought that the Amphipoda and Mollusca would provide an ideal comparison for several reasons, including widely differing evolutionary histories. Amphipods have a boreal center of origin and have undergone their greatest generic diversification at higher latitudes (Barnard, 1969). Barnard noted that the warm-temperate region south of Cape Hatteras contains only 39% of the genera found in the boreal zone north of the Cape. In contrast, molluscs are primarily tropical in origin and show the greatest diversification at low latitudes (Stanley, 1970; Jackson, 1974). With such divergent centers of origin and evolutionary dispersal histories, one might expect their patterns of diversity across the study area to show strong differences.

Surprisingly, an extremely close correlation exists between the Shannon diversity (H') values of both taxa ($r = 0.920$; $p << .01$; frontal area taken as a unit). Ecological (e.g. substrate) rather than evolutionary (e.g. center of origin) factors seem to be the primary determinant of diversity in this study. This is probably a result of the relatively narrow latitudinal range encompassed in the present investigation. The high boreal diversity of the amphipods is not evident since even the northernmost stations contained few cold-water species. Likewise, the diversity of the molluscs, even in the South area, is below that reached in more tropical area. It is felt that a broader latitudinal range than that covered by the present study is necessary to provide a true test of the role of evolutionary factors in determining species diversity.

Reproduction and Dispersal

Amphipods are anomalous not only in their high degree of boreal diversification, but also in their mode of reproduction and dispersal. Amphipods, like all peracaridans, brood their young and have no pelagic larval dispersal stage. Brooding of young occurs in some groups of molluscs as well, but a large portion of the phyla have free-swimming trochophore and veliger larvae which may remain in the plankton for up to several months. This pelagic dispersal stage would seem to increase the likelihood of a species having the ability to penetrate zoogeographic barriers. Examples of this would include the transport of *Mytilus edulis* larvae around Cape Hatteras (Wells and Gray, 1960) and the entrainment of tropical decapod larvae in warm-core Gulf Stream eddies occurring in the Middle Atlantic Bight (Bowen et al., 1979). Similarly, the limited larval dispersal capabilities inherent in brood protection would seem to lead towards narrow distributional ranges and a high degree of endemism.

Surprisingly, it is the amphipods rather than the molluscs which seem less restricted by faunal barriers. This is evident in the end point analysis (Figure 17) in which 31% of the northern species of amphipods are lost across the study area, whereas 52% of the northern molluscs show a corresponding loss (loss of southern species is roughly comparable). It is also evident in Appendices 1 and 2 in which the amphipods include a much larger proportion of widespread species. It is this absence of a close attuning to faunal barriers by the amphipods and a corresponding wide distribution, which best differentiates the distributional responses of amphipods and molluscs.

Data from other workers in the North Carolina region shows similar results. The shallow water reefs off the Carolinas contain an amphipod assemblage including 44% widespread species, whereas the molluscan fauna of the same habitat contains only 35% widespread species (Pearse and Williams, 1951). An examination of the estuarine amphipod fauna around Beaufort (Fox and Bynum, 1975) revealed that few species (7.2%) had a northward distribution terminated at Cape Hatteras, while the molluscan fauna of Beaufort (Hackney, 1944; analysis by Coomans, 1962) showed 58.2% of this taxa to be restricted to south of Cape Hatteras.

The wide distribution of amphipod species is surprising, considering their brooding reproductive mode. It seems that rafting of adults on detached marine plants, debris and logs functions as an effective dispersal mechanism, at least for epifaunal forms (McCain, 1968; Barnard, 1970). Such dispersal has been shown to be sufficient to allow colonization of remote island groups without the benefit of insular stepping stones. For example, nearly 30 Hawaiian species (25% of the fauna) have travelled more than 2.000 miles from adjacent continents to reach the Hawaiian archipelago (Barnard, 1970). similar explanations have been employed to explain the wide dispersal of caprellid amphipods (McCain, 1968) and the faunal similarity between Californian warm-temperate regions and the Galapagos Islands (Barnard, 1970) and between Australia and New Zealand (Barnard, 1972a).

A rafting dispersal mechanism seems applicable only for epifaunal amphipods. Infaunal forms, such as ampeliscids and corophiids, are not likely to be transported in this manner. However, many infaunal species may move into the plankton for breeding or other purposes (Williams and Bynum, 1972). It is possible that they may be transported limited distances during this period.

Comparative eurytopy

The postulate of a decreased response to zoogeographic barriers in amphipods in relation to the molluscs implies a greater capacity for eurytopy in the Amphipoda. However, information in this respect is limited and only three examples of immediate consequence were found. In examination of the physiological adaptations of high-intertidal organisms, Vermeij (1972) remarked that, "eurytopy is more often encountered among high-level Crustacea than among gastropods in the same habitat". Bousfield (1973) noted that in the intertidal region, amphipods are better adapted to harsh physical conditions than other Crustacea, outnumbering both the isopods and decapods. The euryhalinity of Crustacea in general, which usually exceeds that of the molluscs, has been noted by several investigators (Pearse, 1936; Topping and Fuller, 1942; Wells, 1961). Therefore, while the evidence is not conclusive, there is some indication that Crustacea, and amphipods in particular, may generally be more tolerant of adverse physical conditions than are the molluscs.

SUMMARY

1. A sharp thermal front between Gulf Stream water and the Virginian Coastal Current was found in June, 1977, approximately 50 km northeast of Cape Hatteras, North Carolina. Bottom temperatures indicated a gradient of 14-24°C across the front, most of this change occurring over less than three kilometers.

2. The front was found to be highly dynamic, rapidly migrating over large distances, resulting in rapid and unpredictable temperature fluctuations at any given point.

3. Sedimentary parameters proved to be as important or more so than thermal conditions in determining the distribution of many species.

4. The data suggest that biotic interactions, rather than intolerable thermal conditions, are responsible for the absence of some northern species from the warm, thermally-stable waters off Cape Lookout.

5. Many southern species have a northern distributional limit in Raleigh Bay, between Cape Lookout and Cape Hatteras. This barrier is thermally-induced, and maintained by seasonal incursions of Virginian water over Diamond Shoals and into the northern and inshore portions of Raleigh Bay.

6. Most northern species collected are not limited in their southward distribution in the North Carolina regions, but are usually found south to at least Florida.

7. Few strictly cold water species were found indicating that the boreal fauna, previously suggested to extend south to Cape Hatteras, is lost at higher latitudes or at least is displaced into deeper water than the area examined.

8. Despite the thermal fluctuations, no evidence of a depression in diversity is found in the front. This may be due to the proximity of a diverse species pool, the eurytopic nature of temperate fauna or a high degree of non-selective predation.

9. Amphipods seem less restricted by zoogeographic barriers than are the molluscs. Though the reasons for this are not completely clear, it may in part be due to more effective adult dispersal, and possibly an inherently greater degree of eurytopy in the Amphipoda.

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APPENDICES

APPENDIX 1

Mollusc Species Collected and Their Distributional Limits

(Numbers in table indicate source of data. Dash indicates assumed intermediate occurrence)

	Caribbean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Polyplacophora												
Acanthochitonidae												
Acanthochitona pygmaea	7	-	-	-	1							
Chaetopleuridae												
Chaetopleura apiculata	7	2	2	1	-	-	-	1	-	9	2	
Scaphopoda												
Dentaliidae												
Dentalium eboreum	7	2	2	1	-	-	-	6				
Siphodentaliidae												
Cadulus carolinensis	2	2	2	1	1	1	-	1	-	6		
Gastropoda												
Acteocinidae												
Acteocina candei	2	2	2	1	-	-	-	1				
Acteonidae												
Acteon punctostriatus	7	2	2	1	1	1	-	1	1	9	2	
Aplysiidae												
Aplysia sp.												
Caecidae												
Caecum cooperi	8	2	2	-	-	-	-	1	-	2	5	

Appendix 1. (continued)

	Caribbean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Caecum johnsoni			*	1	1	1	-	-	-	2	2	
Caecum pulchellum	8	2	2	-	1	1	-	1	-	9	2	2
Columbellidae												
Anachis lafresnayi		2	2	-	-	-	-	1	-	9	2	2
Mitrella lunata		2	4	1	-	-	-	1	-	9	2	
Crepidulidae												
Crepidula fornicata	7	2	3	-	-	1	-	1	-	9	2	2
Cylichnidae												
Cylichnella bidentata	7	2	2	-	1	-	-	1				
Epitoniidae												
Epitonium sp. A												
Marginellidae												
Marginella roscida			2	-	-	-	-	1	1	2	2	
Melanellidae												
Niso aeglees	7	2	2	1	1	-	-	1	1			
Strombiformis auricinctus	2	2	2	-	1	-	-	1				
Nassariidae												
Nassarius albus	8	2	2	-	1	-	-	6				
Nassarius trivittatus		2	2	-	-	-	-	1	-	9	2	2
Naticidae												
Polinices duplicatus	7	2	3	-	1	1	-	1	-	2	2	
Sigatica carolinensis	2	2	2	-	1	1	-	1				
Sinum perspectivum	7	2	2	-	1	1	-	1	-	9		
Olividae												
Olivellinae sp. C												

Appendix 1. (continued)

	Caribbean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Philinidae												
Philine sagra	2	2	2	1	-	-	-	1				
Pleurobranchidae												
Pleurobranchea hedgpethi	2	2	2	-	-	-	-	1				
Pyramidellidae												
Odostomia sp. A												
Turbonilla interrupta	8	2	3	-	-	-	-	1	1	9	2	2
Retusidae												
Haminoea solitaria			*	-	1	-	-	1	-	9	2	
Pyrunculus caelatus	2	2	2	-	1	1						
Volvulella persimilis	2	2	2	-	1	1						
Terebridae												
Terebra concava	7	2	2	-	-	-	-	1	-	6		
Terebra dislocata	8	2	3	-	1	-	-	1	-	9		
Trochidae												
Calliostoma pulchrum	7	2	2	-	-	-	-	-	1			
Turridae												
Cryoturris citronella	2	2	-	-	-	-	-	1				
Cryoturris elata	2	2	2	1								
Kurtziella limonitella	2	2	2	1	-	-	-	1				
Kurtziella rubella	2	2	2	-	-	-	-	1				
Vitrinellidae												
Cyclostremiscus pentagonus	8	2	2	-	-	1						
Vitrinellidae sp. A												

Appendix 1. (continued)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Unidentified												
Gastropoda sp. C												
Nudibranchia												
Arminidae												
Armina tigrina	2	2	2	-	-	-	-	1				
Corambidae												
Doridella obscura	2	2	2	-	-	-	-	-	1	9		
Unidentified												
Nudibranchia sp. A												
Pelecypoda												
Cardiidae												
Cerastoderma pinnulatum								1	1	2	2	2
Laevicardium laevigatum	8	2	2	1	-	-	-	-	-	6		
Laevicardium pictum	8	2	2	1	-	-	-	-	-	6		
Chamidae												
Chama macerophylla	8	2	2	1								
Corbulidae												
Corbula barrattiana	2	2	2	-	1	1	-	1	1			
Corbula swiftiana	7	2	3	-	1	1	-	1	1	2	2	
Corbula sp. A												
Varicorbula operculata	8	2	2	1	1	1	-	1	-	6		
Crassatellidae												
Crassinella lunulata	7	2	2	1	1	-	-	1	-	2	2	

Appendix 1. (continued)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Cuspidariidae												
Cardiomya costellata	8	2	2	-	1							
Leptonacea												
Leptonacea sp. A												
Limidae												
Lima pellucida	8	2	2	1	1							
Lucinidae												
Codakia orbicularis	8	2	2	1								
Divaricella quadrisulcata	8	2	3	-	1	-	1	1	-	2	2	
Lucina nassula	7	2	2	-	1	-	-	6				
Lucinidae sp. A												
Lucinidae sp. B												
Parvilucina multilineata	7	2	3	-	1	1	-	1	-	9		
Lyonsiidae												
Lyonsia hyalina			3	1	1	1	-	1	1	9	2	2
Mactridae												
Spisula solidissima similis	7	2	3	1	1	1	1	1	1	2	2	
Mytilidae												
Crenella divaricata	8	2	2	1	1							
Modiolus modiolus squamosus	2	2	2	-	1							
Musculus lateralis	8	2	2	-	1							
Nuculanidae												
Nuculana acuta	7	2	2	-	1	1	-	1	-	2	2	
Nuculidae												
Nucula proxima	7	2	3	1	1	-	-	1	1	9	2	2

Appendix 1. (continued)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Pandoridae												
Pandora inflata	2	2	2	1	1	1	1	1	-	9		
Pinnidae												
Atrina seminuda	8	2	2	1								
Pectinidae												
Argopecten gibbus	8	2	2	1	1	-	-	-	-	2		
Cyclopecten nanus	2	2	2	1	-	-	-	-	-	2		
Palliolum sp. A												
Placopecten magellanicus					1	-	-	1	1	2	2	2
Semelidae												
Abra aequalis	7	2	3	1	1	1	-	1	1	9		
Solemyacidae												
Solemya velum		2	2	-	-	-	-	1	1	9	2	2
Solenidae												
Ensis directus			3	1	-	-	-	1	1	9	2	2
Tellinidae												
Macoma tenta	7	2	2	1	-	-	-	-	1	9	2	
Strigilla cf *mirabilis*	8	2	3	-	1	1	1	1				
Tellina versicolor	7	2	3	1	1	1	1	1	-	2	2	
Tellina sp. B												
Tellina sp. C												
Thraciidae												
Thraciidae sp. A												
Thyasiridae												
Thyasira trisinuata	8	2	2	1	-	-	-	-	-	2	2	2

Appendix 1. (concluded)

	Caribbean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Ungulinidae												
<u>Diplodonta</u> <u>punctata</u>	8	2	2	1	1	-	-	-	1			
Veneridae												
<u>Chione</u> <u>cancellata</u>	7	2	2	1	-	-	-	-	6			
<u>Chione</u> <u>grus</u>	7	2	2	1	-	-	-	1				
<u>Chione</u> <u>latilirata</u>	8	2	2	1	-	-	-					

* Found south of Cape Lookout (Porter, 1974).

Data sources: 1, present study; 2, Abbott (1974); 3, Dorjes and Howard (1975); 4, Howard and Frey (1975); 5, Johnson (1934); 6, Merrill et al. (1978); 7, Perry (1940); 8, Warmke and Abbott (1961); 9, Wass (1972).

APPENDIX 2

Amphipod Species Collected and Their Distributional Limits

(Numbers in table indicate source of data. Dash indicates assumed intermediate occurrence)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Caprellidea												
Caprellidae												
Caprella equilibra	11	11	11	-	-	1	-	-	-	11	11	
Luconacia incerta	11	11	11	-	-	-	-	1	-	11	11	
Phtisca marina	11	11	11	-	-	-	-	1				
Gammaridea												
Ampeliscidae												
Ampelisca agassizi	13	13	13	1	1	-	-	-	-	13	13	
Ampelisca cristoides	2	-	6	1	-	-	-	1				
Ampelisca vadorum	12	4	10	1	-	-	-	1	-	16	4	12
Ampelisca verrilli	9	-	-	-	1	1	-	1	-	16	13	
Ampelisca sp. A												
Ampelisca sp. B												
Byblis serrata			6	-	-	-	-	1	-	4	4	
Aoridae												
Lembos smithi	9	4	9	1	1	-	-	1	-	16	4	
Lembos unicornis			*	1								
Lembos websteri		5	10	1	-	-	-	-	-	-	4	

Appendix 2. (continued)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Natteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
<u>Microdeutopus</u> <u>myersi</u>			6	1								
<u>Microdeutopus</u> sp. A												
<u>Microdeutopus</u> sp. C												
Argissidae												
<u>Argissa</u> <u>hamatipes</u>		6	-	1	1	-	-	1	1	-	4	4
Corophiidae												
<u>Cerapus</u> <u>tubularis</u>	9	4	10	1	-	-	-	-	-	16	4	
<u>Corophiidae</u> sp. A												
<u>Erichthonius</u> <u>brasiliensis</u>	4	9	10	1	1	-	-	1	-	16	4	
<u>Erichthonius</u> sp. A												
<u>Siphonoecetes</u> <u>smithianus</u>				1	1	-	-	-	-	8	5	
<u>Unciola</u> <u>irrorata</u>			*	-	-	-	-	1	-	8	4	4
<u>Unciola</u> <u>serrata</u>		4	10	1	-	-	-	1	1	16	4	
<u>Unciola</u> sp. A												
Gammaridae												
<u>Elasmopus</u> sp. A												
<u>Gammaridae</u> sp. A												
<u>Jerbarnia</u> sp. A												
<u>Melita</u> <u>appendiculata</u>	9	9	10	1	-	-	-	-	-	16		
Haustoriidae												
<u>Acanthohaustorius</u> <u>intermedius</u>		4	10	1	-	1	1	1	1	16	4	
<u>Acanthohaustorius</u> <u>millsi</u>		4	9	-	1	1	1	1	1	-	4	4
<u>Bathyporeia</u> <u>parkeri</u>		4	9	-	1	1	1	1	1	-	4	

Appendix 2. (continued)

	Caribbean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Haustoriidae cf *Platyischnopus*												
Protohaustorius cf *deichmannae*		4	4	-	-	1	1	1	1	4	4	4
Isaeidae												
Gammaropsis sp. A												
Gammaropsis sp. C												
Photis pugnator	15	5	-	1	1	1	-	1	-	15		
Isaeidae sp. A												
Liljeborgiidae												
Listriella barnardi	9	4	10	-	-	1	-	1	-	16	4	
Listriella sp. A												
Liljeborgia sp. A												
Oedicerotidae												
Synchelidium americanum		5	4	1	1	1	-	1	1	-	4	4
Phoxocephalidae												
Trichophoxus epistomus			10	-	1	1	1	1	1	16	4	4
Trichophoxus floridanus	14	5	14	1	1	1	1	1	1			
Pleustidae												
Stenopleustes gracilis			5	1	-	-	-	-	-	4	4	
Podoceridae												
Podocerus brasiliensis	9	9	9	1								
Stenothoidae												
Parametopella cypris		4	9	-	1	-	-	1	-	16	4	
Parametopella inquilinus								1	-	5		

Appendix 2. (concluded)

	Carribean or Gulf of Mexico	Cape Canaveral Florida	Georgia	South area	Hatteras:South	Hatteras:Mid	Hatteras:North	Front	North area	Virginia	Cape Cod Massachusetts	North of Cape Cod
Stenothoe georgiana	7	7	7	-	-	-	-	1	-	7		
Synopiidae												
Garosyrrhoe sp. A												
Tiron tropakis		5	-	1	1	-	-	-	1	3		
Unidentified												
Amphipoda sp. B												
Amphipoda sp. C												

* Found near Beaufort, North Carolina by Fox and Bynum (1975)

Data sources: 1, present study; 2, Barnard (1954); 3, Barnard (1972b); 4, Bousfield (1973); 5, Bousfield (unpublished data); 6, M. Bowen (personal communication); 7, Bynum and Fox (1977); 8, Feeley and Wass (1971); 9, Fox and Bynum (1975); 10, Heard and Heard (1971); 11, McCain (1968); 12, Mills (1963); 13, Mills (1967); 14, Shoemaker (1933); 15, Shoemaker (1945); 16, Wass (1972)

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