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Macrobenthos–sediment relationships on the continental shelf off Cape Hatteras, North Carolina

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Abstract—The complex current regime associated with Cape Hatteras, North Carolina results in an unusually broad range of sediment textures for open shelf areas of comparable spatial extent. The median grain size ranged from coarse to very fine sand, while the percentage of silt and clay ranged from 0 to 27%. Four assemblages of macrobenthic species were recognized, separable on the basis of sediment characteristics: (1) a muddy, very fine sand assemblage dominated by the polychaetous annelid *Lumbrineris impatiens*; (2) a fine to medium sand assemblage dominated by the archiannelid *Polygordius* sp.; (3) a well-sorted, fine sand assemblage dominated by the amphipod *Protohaustorius* cf. *deichmannae*; and (4) a medium to coarse sand assemblage characterized by the polychaetes *Hemipodus roseus* and *Hesionura elongata*. Multiple discriminant analysis and detrended correspondence analysis, a linear ordination technique, were used to identify which of eight sediment parameters were most useful in interpreting faunal patterns. Sediment sorting, as reflective of sediment mobility, was important in determining the dominance of fossorial species. The percentage of very fine sand and the combined percentage of silt and clay were found to be of greatest value in differentiating biotic assemblages. This conclusion is supported by similar results from previous estuarine studies, and is probably a result of surface area-related control of the type and quantity of food resources for deposit feeders.

INTRODUCTION

THE importance of sediment in structuring macroinvertebrate communities has often been demonstrated, but mainly in estuaries (MCNULTY *et al.*, 1962; NICHOLS, 1970; BLOOM *et al.*, 1972) or shallow marine embayments (SANDERS, 1958; YOUNG and RHOADS, 1971; FRANZ, 1976; BIERNBAUM, 1979). This emphasis is largely a result of both the accessibility of these environments and the wide diversity of sediment types present in relatively close proximity. Animal–sediment relationships on open continental shelves have received considerably less attention. Some investigators of shelf habitats in Europe (GLÉMAREC, 1973; BUCHANAN *et al.*, 1978), Asia (RHOADS *et al.*, 1985) and North America (FLINT, 1981; BOESCH, in press) have successfully differentiated macrobenthic communities on the basis of sedimentary parameters, although other studies have found little influence of sediment type on animal distribution (BUCHANAN, 1963; DAY *et al.*, 1971). The potential role of sediments in structuring benthic communities is unquestionable, but in some shelf environments sediment-related effects are often masked by considerably greater variation in other, often depth-related, environmental parameters.

The continental shelf off Cape Hatteras, North Carolina has a number of unique features which make it especially suitable for investigations of animal–sediment

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relationships. Diamond Shoals, extending seaward across two-thirds of the shelf off Cape Hatteras, is characterized by water depths of less than 10 m. The complex current regime associated with Diamond Shoals results in an unusually broad range of sediment textures for open shelf areas of comparable extent. For example, in the Middle Atlantic Bight immediately to the north, the percentage of silt and clay of shelf sediments is generally less than 10% ((BOESCH and BOWEN, in press). In contrast, shelf sediments in the Cape Hatteras region range from near 0 to in excess of 27% silt and clay.

Additionally, the sedimentary environment of the Cape Hatteras area may have important zoogeographic implications. The Cape Hatteras area acts as an effective zoogeographic barrier for a wide variety of faunal groups (BRIGGS, 1974; CERAME-VIVAS and GRAY, 1966; WESTON, 1983). Temperature limitations are undoubtedly of major importance in the termination of many species distributions in this area, but factors other than temperature appear to be involved for some species (VERNBERG and VERNBERG, 1970). HERBST *et al.* (1978) speculated that substrate characteristics in the Cape Hatteras area may limit the distribution of decapod crustaceans. HARRINGTON (1981) suggested that the unstable sands of the Diamond Shoals area limit the distribution of those echinoderm species not having a sufficiently long pelagic larval life to survive passage over the Shoals.

The principal objective of this study is to describe the sedimentary environment of the Cape Hatteras area and its relationship to the macrobenthic communities. Secondly, the value of alternative sediment grain size parameters as predictors of the observed faunal distributions is assessed. In doing so, the utility of several multivariate statistical techniques in investigating animal–sediment relationships is evaluated.

This study is one component of a larger investigation conducted by the University of Wisconson–Madison of physical and biological processes associated with a thermal front on the continental shelf north of Cape Hatteras. Related reports can be found in HERBST *et al.* (1978, 1979), HARRINGTON (1981), MAGNUSON *et al.* (1981), and WESTON (1979, 1983).

METHODS

Field sampling

Collections were made during four quarterly cruises of the R.V. *Eastward* from mid-1977 to early 1978. The sampling area (Fig. 1) was subdivided into three strata, Hatteras:North, Hatteras:Mid and Hatteras:South, located to the north, east and south of Diamond Shoals, respectively. The water depth at the sampling sites ranged from 23 to 54 m. On each cruise sampling locations were chosen randomly within each stratum with equalized sampling effort among strata. A total of 76 samples was collected for biological and sediment analyses over the four cruises.

At each sampling site bottom water temperature and salinity were measured using a shallow-water mechanical bathythermograph (BT) and Beckman induction salinometer. Measurements were also taken periodically with a reversing thermometer and Hytech salinometer, and the BT and Beckman salinometer readings corrected accordingly.

Macrofauna was collected using a 0.1-m^2 Smith–McIntyre grab. Most organisms were separated from the sediment by elutriation through a 0.5-mm mesh Nitex screen, with the material remaining in the container washed through a 1.0-mm mesh screen. Both the 0.5- and 1.0-mm fractions were placed in $MgCl_2$ to anesthetize the organisms, and then transferred to 10% buffered formalin stained with Rose Bengal.

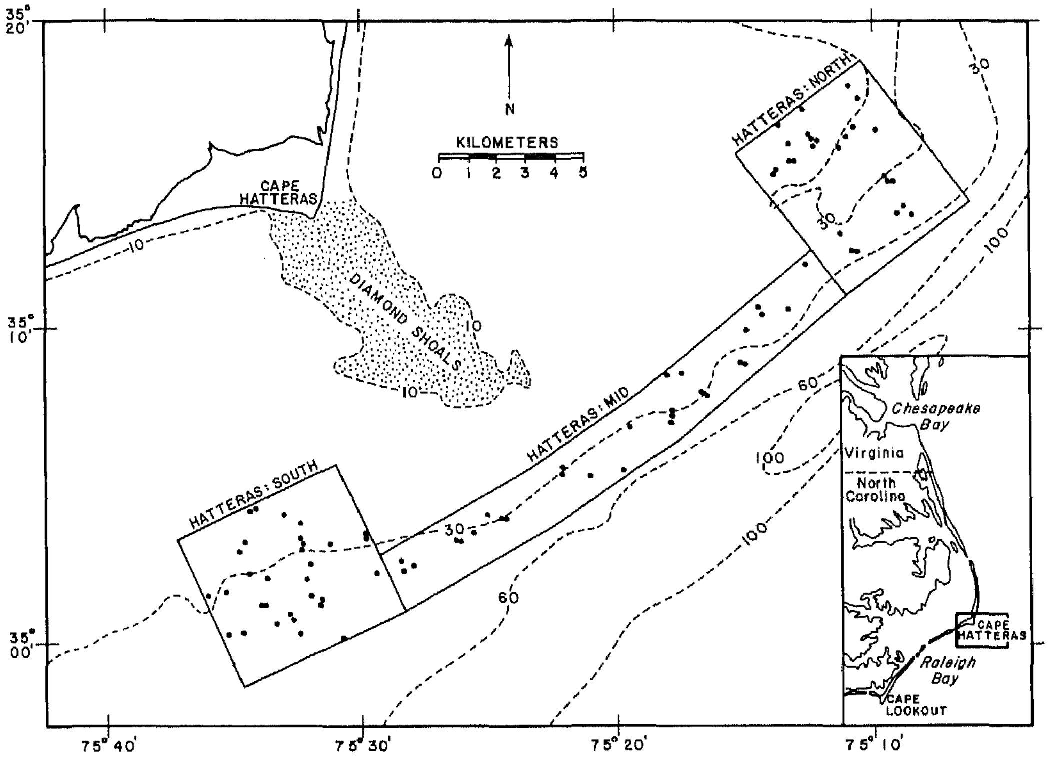

Fig. 1. Location of the three sampling strata with the collection sites indicated. Depth contours in meters.

Sediment samples collected from each grab were dried at 100°C and 100-g aliquots obtained by use of a sediment cutter. The material was sieved through a series of Standard Sieves with silts and clays combined as pan weight. Sediment parameters were determined using Inman measures (Inman, 1952).

Statistical analyses

In order to delimit zones of faunal similarity, cluster analysis was performed, deleting those species which occurred in three or fewer samples. Algorithms used included log-transformation of species abundances, the Bray–Curtis similarity measure (Bray and Curtis, 1957), and flexible sorting with β set at –0.25 (Clifford and Stephenson, 1975).

Multiple discriminant analysis (Nie *et al.*, 1975) was used to evaluate the group separation derived by cluster analysis, and to interpret this separation in light of a variety of sedimentary variables. Sediment percentages used in the analysis were transformed by arcsin $\sqrt{p}$ to induce normality. The sorting coefficient was left untransformed as it was already in logarithmic phi units.

Ordination was performed using detrended correspondence analysis (DCA). DCA is a modification of reciprocal averaging ordination, and was originally developed to avoid many of the perceived problems inherent in the unmodified technique (Hill, 1979; Hill and Gauch, 1980). Specifically, DCA eliminates the compression of ordination distances at the ends of the axes, and the "arch" or "horseshoe" effect which may be apparent on the second and higher axes. These modifications have been applauded by some investigators (GAUCH *et al.*, 1981; GAUCH, 1982), while others suggest that the modifications have made DCA no better and perhaps worse than reciprocal averaging (WARTENBERG *et al.*, 1987).

RESULTS

Temperature and salinity

The Cape Hatteras region is marked by abrupt temperature and salinity fronts between widely divergent water masses (HERBST *et al.*, 1979; MAGNUSON *et al.*, 1981). The three Hatteras sampling strata, however, were all exposed to similar conditions of temperature and salinity because of their proximity to one another (Table 1). The greatest differences observed in mean temperature and salinity among strata during any cruise were 2.5°C and 1.1‰ during the fall sampling period, a time when the Hatteras:North stratum was influenced by a thermal front (HARRINGTON, 1981).

The temperature of bottom water varied seasonally from 16°C during the winter cruise to 27°C during the summer sampling period. Bottom salinity ranged from 32‰, indicative of Virginia shelf water, to 36‰, representative of Gulf Stream water. It is noteworthy that the lowest salinities measured were during the fall and winter cruises, indicating intrusion of Virginia shelf water into the study area during this period. This intrusion has been attributed to prolonged periods of strong northeasterly winds which may force Virginia shelf water over Diamond Shoals and into Raleigh Bay (WELLS and GRAY, 1960; GRAY and CERAME-VIVAS, 1963; HUNT *et al.*, 1977).

Table 1. Temperature (°C) and salinity (‰) observations (mean and range) of bottom water in the three strata during the four sampling periods (from physical-chemical data base, J. Magnuson, University of Wisconsin–Madison)

Season	Strata Hatteras:North	Hatteras:Mid	Hatteras:South
Spring (June 1977)			
Temperature	24.4 (23.8–25.2)	23.9 (22.5–24.9)	24.1 (23.2–24.7)
Salinity	35.03 (34.32–35.94)	34.70 (34.20–35.00)	34.82 (33.91–35.60)
Summer (August 1977)			
Temperature	26.9 (26.3–27.5)	25.5 (23.5–26.2)	25.4 25.1–25.9)
Salinity	35.09 (34.65–35.57)	35.22 (34.69–35.58)	35.35 (34.74–36.25)
Fall (October 1977)			
Temperature	20.3 (16.4–26.7)	22.8 (19.4–26.3)	21.3 (19.6–25.6)
Salinity	33.00 (31.68–35.71)	34.08 (32.92–35.72)	34.11 (33.23–35.50)
Winter (January 1978)			
Temperature	17.3 (15.4–19.2)	17.3 (15.8–18.6)	15.8 (14.8–16.7)
Salinity	35.68 (32.64–36.29)	36.00 (35.10–36.30)	35.57 (33.28–35.98)

Sediments

The surficial sediments of the study area showed considerable spatial variation as a result of both the bathymetry of the Diamond Shoals area and the complex current regime. Median grain size ranged from 0.11ϕ (coarse sand) to 3.41ϕ (very fine sand) (Fig. 2a). The coarsest sand occurred in portions of the Hatteras:North stratum. The finest sand was in an area of the Hatteras:South stratum which probably receives fine sediments winnowed from Diamond Shoals (Hunt *et al.*, 1977).

The percentage of silt and clay was generally low (Fig. 2b). The majority of the surficial sediments of the study area had less than 5% silt and clay, although portions of the Hatteras:Mid and Hatteras:South strata had as much as 27%.

Numerical classification

Cluster analysis was performed to group the stations according to faunal similarity. Four discrete groups resulted with the second group sub-divided into three smaller station groupings (Fig. 3). It is important to note that temporal changes were of no significance at the similarity level at which groups were defined. Seasonal faunal differences were not responsible for the major grouping, although they were quite apparent as sub-groups within each major cluster.

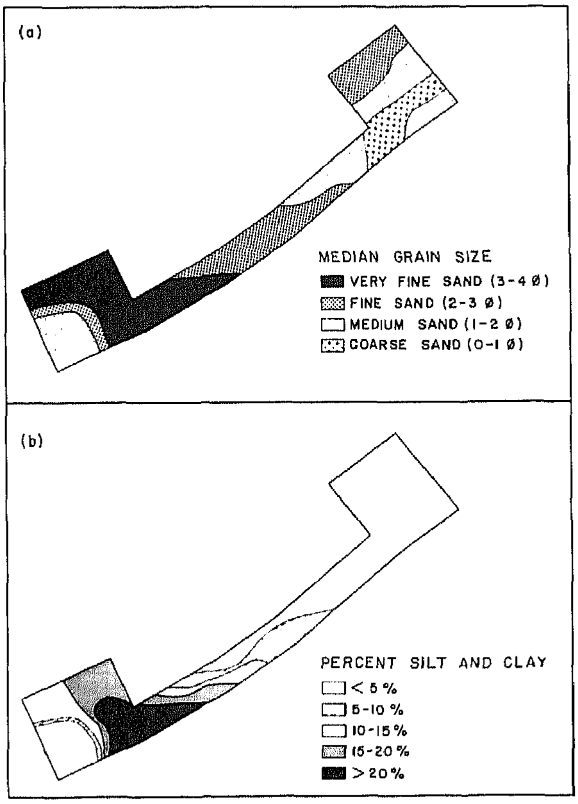

Fig. 2. Grain size parameters of surficial sediments in the study area: (a) median grain size; (b) percentage of silt and clay.

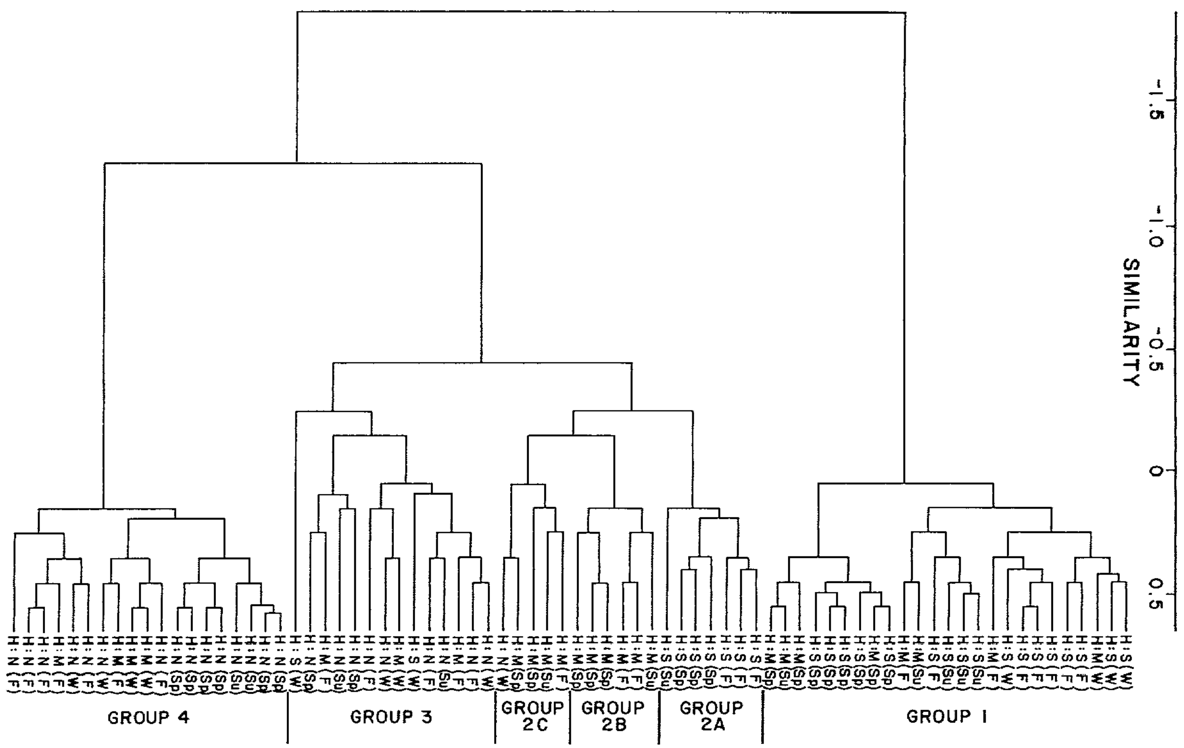

Fig. 3. Dendogram illustrating numerical classification of all macrobenthic sampling sites. Strata: H:N, Hatteras:North; H:M, Hatteras:Mid; H:S, Hatteras:South. Season: Sp, spring; Su, summer; F, fall; W, winter.

It is clear that station groupings can be interpreted largely by sedimentary parameters such as median grain size (Fig. 4). The faunal dissimilarity of Groups 2 and 4 is surprising given their similar median particle size; however, the sediments of Group 4 were generally better sorted.

Group 1 was comprised of the fine and very fine sands of Hatteras:South and the southern portion of Hatteras:Mid. The percentage of silt and clay was greatest in this group, ranging from 10 to 27% and averaging 16.5%. Group 1 stations were the most speciose of all groups, containing 275 of the 368 species collected during the investigations. Species with a high fidelity to Group 1 stations are illustrated in Fig. 5. *Lumbrineris impatiens* was the numerically dominant species in the fine and very fine sands, attaining densities of 100–1000 individuals m^{-2}. Other species not illustrated but with affinity to Group 1 stations included *Mediomastus californiensis* and *Prionospio cristata*.

Group 2 was composed of medium and fine sand stations located throughout the study area. Groups 2A and 2B included stations with coarser and finer substrates, respectively. Characteristic species included the polychaetous annelids *Magelona* cf. *pettiboneae*, *Glycera oxycephala* and *Polygordius* sp. (Fig. 5).

Stations of Group 3 were the coarsest grained in the study area, with the percentage of silt and clay less than 1%. This group was comprised of stations primarily in the Hatteras:North area, but included some sites in both Hatteras:Mid and Hatteras:South. *Spisula solidissima similis* was the only species abundant in Group 3 stations, although it was not faithful to stations of this group. Those species showing a high fidelity to Group 3

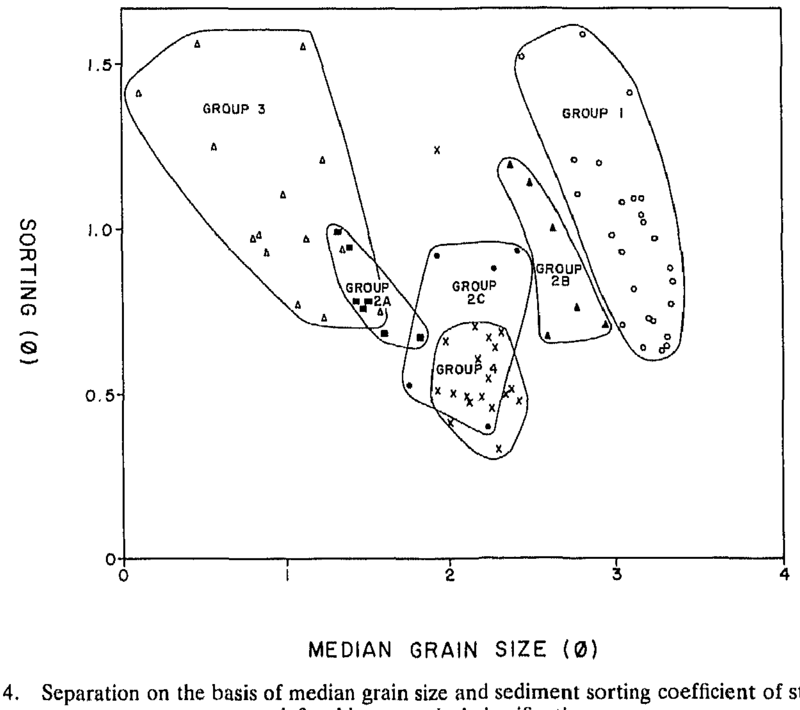

Fig. 4. Separation on the basis of median grain size and sediment sorting coefficient of station groups defined by numerical classification.

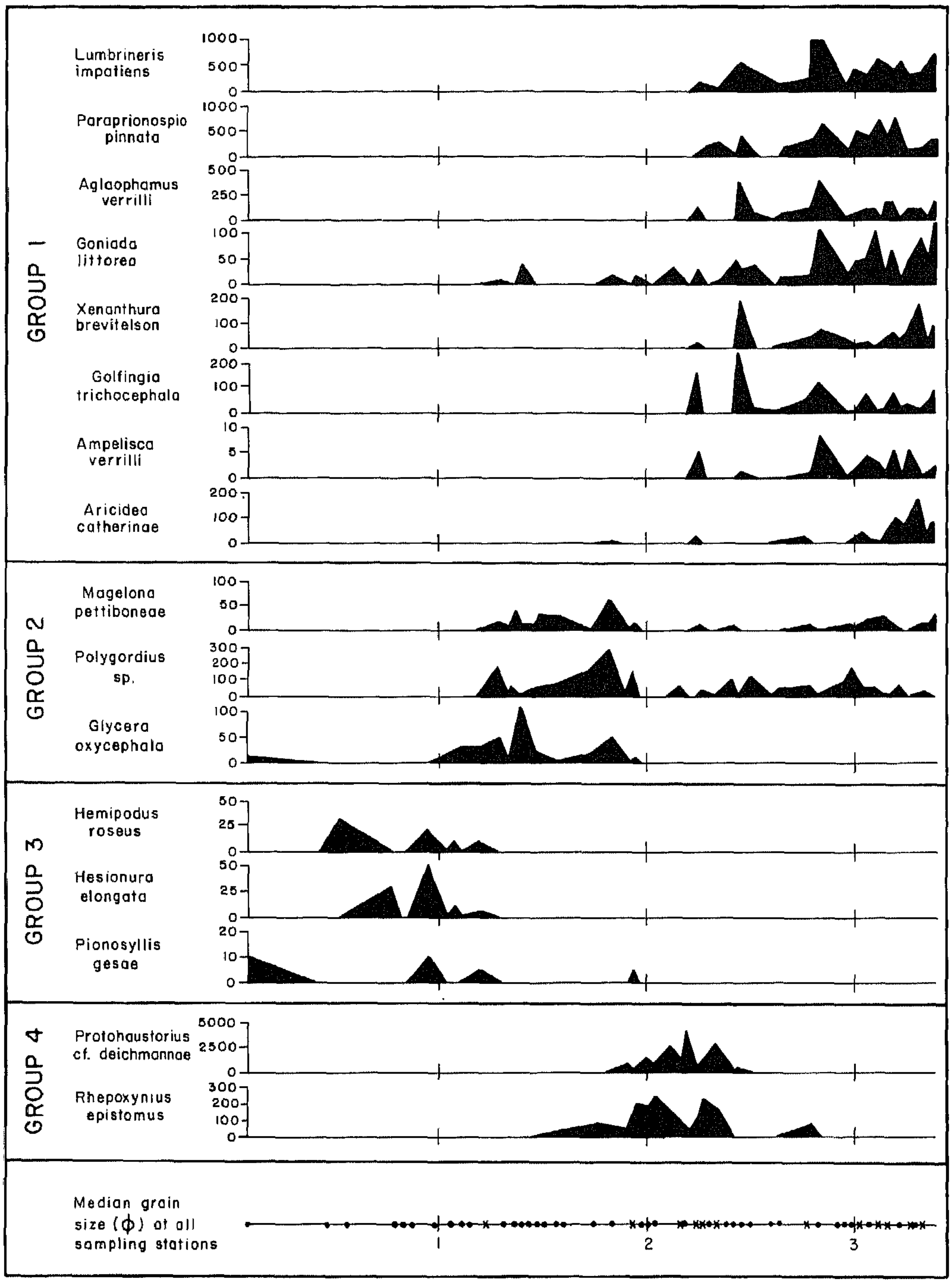

Fig. 5. Species characteristic of each station group and their abundances (individuals m^{-2}) as a function of median grain size (ϕ). In order to differentiate between grain size intervals which were not sampled and those in which no individuals were collected, the median grain size of all sampling sites is shown beneath the figure. Asterisks indicate multiple stations having approximately the same median grain size.

stations were small, interstitial burrowers such as *Hemipodus roseus, Hesionura elongata* and *Pionosyllis gesae* (Fig. 5). They were all collected in low numbers, possibly as a result of loss through the 0.5-mm sieve used.

Group 4 stations occupied a relatively small geographic area in Hatteras:North and Hatteras:Mid. Median grain size at these stations ranged from 1.9 to 2.4ϕ (fine sand) with less than 1% silt and clay. With the exception of one outlier, sediments of Group 4 stations were the best sorted of any in the study area, with a standard deviation around the mean grain size of about 0.5ϕ. Three fossorial amphipods, *Protohaustorius* cf. *deichmannae*, *Rhepoxynius epistomus* and *Bathyporeia parkeri* were characteristic of Group 4 stations (Fig. 5).

Discriminant analysis

Multiple discriminant analysis was performed to identify the sediment variable(s) which would best account for the station groupings created by numerical classification. These groups were discriminated on the basis of eight sediment variables including the sediment sorting coefficient and the percentages of shell and gravel, very coarse sand, coarse sand, medium sand, fine sand, very fine sand, and silt and clay (Table 2). Phi size intervals were as defined by WENTWORTH (1922). Intercorrelations among all variables were less than 0.90 as recommended by MATTSON *et al.* (1977) with the exception of the percentages of very fine sand and the combined percentages of silt and clay (r = 0.94). It should be recognized throughout this discussion that since the sediment sorting coefficient is calculated as a measure of deviation from the mean grain size, a high sorting coefficient is indicative of poor particle sorting while low coefficient values are representative of well-sorted sediments.

The overall chi-squared test of among-group differences was highly significant (χ^2 = 422.94, d.f. = 40) as were the χ^2 tests of the first two functions (function 1 χ^2 = 206.45, d.f. = 28; function 2 χ^2 = 52.92, d.f. = 18). The first and second functions accounted for 70.40 and 26.47% of the total group separation, respectively. Only these functions were considered further in the interpretation.

The standardized discriminant function coefficients (SDFC) (Table 3) indicate the relative contribution of the variables in calculating the discriminant scores on each function, and are commonly used as a measure of the relative importance of the variables in discriminating among the groups (GREEN, 1971; GREEN and VASCOTTO, 1978). On

Table 2. Untransformed mean values of sediment parameters used in the discriminant analysis

Group	Number of stations in group	Sorting (ϕ)	Percent shell and gravel	Percent very coarse sand	Percent coarse sand	Percent medium sand	Percent fine sand	Percent very fine sand	Percent silt and clay
1	25	0.97	0.50	1.80	4.48	5.22	12.89	57.78	16.53
2A	7	0.80	1.26	3.62	8.95	56.46	27.13	2.12	0.58
2B	6	0.92	0.29	2.15	4.29	4.15	45.05	36.79	6.96
2C	5	0.73	0.77	1.59	2.80	16.59	67.81	8.81	1.67
3	14	1.08	7.00	8.54	22.77	49.76	11.54	0.51	0.15
4	19	0.58	0.49	0.62	2.01	9.44	82.27	4.64	0.32

Table 3. Standardized discriminant function coefficients and total structure coefficients showing relative importance of all variables on the first two discriminant functions (DF). Those considered most important are underlined

	Standardized discriminant function coefficients		Total structure coefficients	
Variable	DF 1	DF 2	DF 1	DF 2
Sorting	1.011	0.569	0.312	-0.540
% Shell and gravel	-0.529	-0.003	-0.339	-0.611
% Very coarse sand	-0.346	-0.640	-0.208	-0.732
% Coarse sand	0.020	-0.026	-0.251	-0.822
% Medium sand	-0.240	-0.426	-0.574	-0.738
% Fine sand	-0.354	0.698	-0.541	0.832
% Very fine sand	0.491	0.188	0.970	0.179
% Silt and clay	0.356	-0.135	0.984	0.049

discriminant function 1 the sediment sorting coefficient had, by far, the greatest SDFC (1.011). The sorting coefficient was also important on discriminant function 2 (SDFC = 0.569) as were the percentages of very coarse (SDFC = -0.640) and fine (SDFC = 0.698) sand.

An alternative method of identifying those variables of greatest importance in discriminating groups is to calculate total structure coefficient (TSC) (KLECKA, 1980). These coefficients are the Pearson product-moment correlations between the variables and the discriminant scores on each function (Table 3). They can be represented graphically, following the procedure of JOHNSON (1977), as vectors in two-factor discriminant space (Fig. 6). Using this procedure, discriminant function 1 was largely representative of the percentage of very fine sand and the combined percentage of silt and clay (TSC = 0.970 and 0.984, respectively). The function clearly discriminated between the finer sediments of Groups 1 and 2B and the coarser sediments in the remainder of the study area. Discriminant function 2, with about one-third the discriminating power of the first function, was more difficult to interpret. Several of the variables had high total structure coefficients on this function, although the percentages of fine sand and coarse sand were the most highly correlated (TSC = 0.832 and -0.822, respectively). The function generally serves to differentiate Groups 2A and 3, the coarsest-grained station groups in the study area.

Ordination

Detrended correspondence analysis, in which the groups defined by numerical classification were plotted in ordination space, was performed (Fig. 7). Only the first (eigenvalue 0.642) and the second (eigenvalue 0.364) axes are presented. Neither the third nor fourth axes (eigenvalues 0.279 and 0.217, respectively) are considered further in the analysis.

The groups defined by numerical classification generally showed clear spatial separation in the ordination, largely on axis 1. The very fine sand stations of Hatteras:South (Group 1) showed a high degree of faunal similarity, forming a tightly clustered group scoring low on axis 1. The coarser sands of Hatteras:North (Group 3) formed a diffuse grouping scattered over much of axis 2. The segregation of Group 2C in the numerical

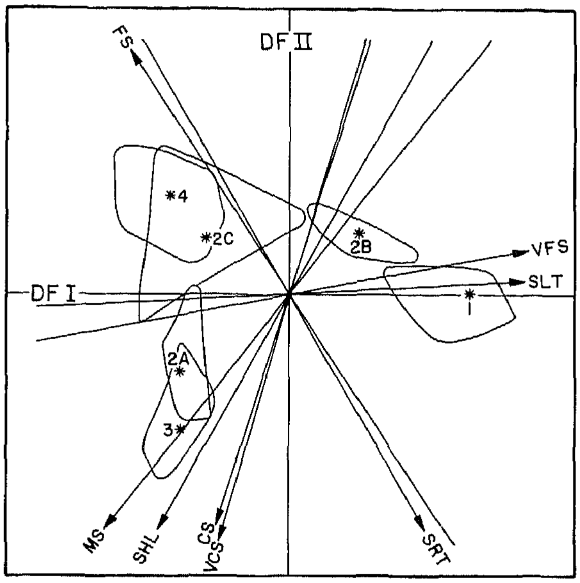

Fig. 6. Centroids (indicated by asterisks) and limits of station groups in two-factor discriminant space. Vectors are determined from the total structure coefficients and indicate the relative orientation of the environmental variables; arrows point toward increasing values. SRT, sediment sorting coefficient; SHL, percentage of shell and gravel; VCS, percentage of very coarse sand; CS, percentage of coarse sand; MS, percentage of medium sand; FS, percentage of fine sand; VFS, percentage of very fine sand; SLT, combined percentage of silt and clay.

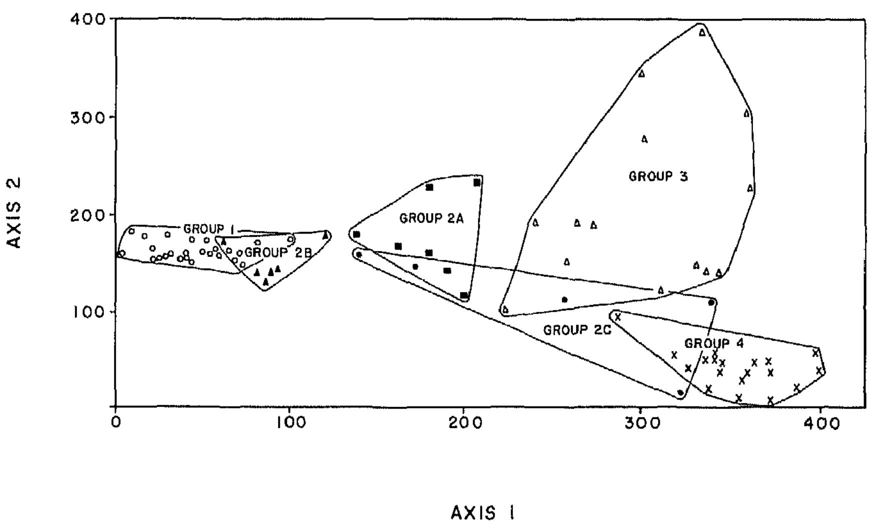

Fig. 7. Location of station groups in ordination space. Lengths of axes are scaled in proportion to the eigenvalues.

Table 4. Spearman rank correlation coefficients between sediment parameters and sample scores on the first two DCA axes. (= significant at overall α ≤ 0.05 when multiple testing accounted for using Bonferoni's inequality)*

Sorting	−0.428*	0.633*
% Shell and gravel	0.221	0.326*
% Very coarse sand	0.008	0.506*
% Coarse sand	−0.080	0.483*
% Medium sand	0.362*	0.130
% Fine sand	0.541*	−0.755*
% Very fine sand	−0.678*	0.070
% Silt and clay	−0.775*	0.211

classification was not reflected in the ordination, with the positions of stations in that group overlapping those of Groups 2A, 3 and 4.

Although ordination axes are not necessarily a reflection of any specific environmental parameter, the axes can frequently be correlated with one or more physical variables. Spearman rank correlation coefficients (SIEGEL, 1956) were calculated between the station scores on the first two ordination axes and the same sediment variables used in the discriminant analysis (Table 4). Axis 1 was most highly correlated with the percentage of medium and fine sands and secondarily with the percentage of very fine sand. Sorting and the percentage of medium and fine sands had smaller but statistically significant r_s values. Axis 2 showed the greatest correlation with the percentage of fine sand. Sorting and the percentages of very coarse sand and shell and gravel showed progressively lesser but still statistically significant correlations.

DISCUSSION

Evaluation of multivariate techniques

Ordination techniques unconstrained by linearity (catenations, NOY-MEIR, 1974) are available, but all have serious drawbacks (NOY-MEIR and WHITTAKER, 1977). Detrended correspondence analysis, like most ordination techniques, assumes a linear relationship between the axes and species abundance. With even a moderate degree of environmental variation among the samples (beta diversity), species distribution curves are curvilinear and non-monotonic, and any ordinations based on assumptions of linearity can produce misleading results (GAUCH and WHITTAKER, 1972; GAUCH *et al.*, 1977). The DCA procedure does, however, attempt to correct for the effects of curvilinearity, most notably by modifying reciprocal averaging ordination so as to eliminate the "horseshoe" or "arch" of ordination scores often apparent on the second or higher axes when using reciprocal averaging or many other ordination techniques. Tests with simulated coenoclines have shown DCA induces little distortion even with high beta diversity, and DCA has been rated highly in comparative tests with other ordination procedures (HILL and GAUCH, 1980; GAUCH *et al.*, 1981), leading some investigators to acclaim it as a near-optimal ordination method (GAUCH, 1982). Although DCA has not been used extensively in benthic ecology, the procedure has proven to be popular among terrestial ecologists, and has been used successfully in analyses of plant and avian gradients (SABO, 1980; CHRISTENSEN and PEET, 1981; WESTMAN, 1983; CARLETON, 1984; LIEFFERS, 1984).

DCA has, however, come under recent criticism, with some investigators claiming that the modifications made to reciprocal averaging ordination in the development DCA actually make it no better and perhaps worse than the unmodified technique (WARTENBERG *et al.*, 1987). It is argued that the "arch effect" is not an unwanted artifact as maintained by the developers of DCA (HILL, 1979; HILL and GAUCH 1980), but rather an accurate representation of the data inherent in succession-replacement of species along an environmental gradient. By eliminating the arch, DCA may mask real biological patterns (WARTENBERG *et al.*, 1987). Furthermore, rescaling of the axes in DCA to eliminate the compression of ordination distances at the ends of the axes implicitly assumes species appear and disappear at a constant rate along an environmental gradient. WARTENBERG *et al.* (1987) argue that this assumption has not been substantiated, and that any universally applied rescaling of the data is arbitrary.

DCA was used in the present study to identify sedimentary factors associated with community differences by correlation of station ordination scores with measured grain size parameters. Despite the recent criticism of the technique, it appears to have performed satisfactorily. The most severe criticism of DCA pertains to its derivation of the second and higher axes. As the conclusions drawn from the test in my study were based largely on group separation on the first axis, the potential problems with the second and higher axes would not affect the validity of the results. The ordering of stations on the first axes of DCA is very similar to that obtained when using its parent technique, reciprocal averaging ordination (WARTENBERG *et al.*, 1987). At most, DCA may have masked biological information on the higher axes, but the conclusions drawn from the first axis remain supportable. The ecological credibility of the results obtained in this study, and the general agreement of these results with those of discriminant analysis, support the validity of the approach.

Multiple discriminant analysis (RAO, 1952) has been used extensively in fields such as the social sciences (COOLEY and LOHNES, 1962) and terrestial ecology (M'CLOSKEY, 1976; DUESER and SHUGART, 1978, 1979), and is being increasingly utilized in marine ecological investigations. Discriminant analysis has been used in benthic ecological studies to identify mechanisms of resource partitioning among polychaetes (FLINT and RABALAIS, 1980) and amphipods (SCHAFFNER and BOESCH, 1982) and to relate station groups to physical variables (BERNSTEIN *et al.*, 1978; FLINT, 1981; SHIN, 1982). The second approach is used herein, in an attempt to identify environmental factors (or unmeasured correlates) responsible for faunal differences among stations.

Standardized discriminant function coefficients are usually considered measures of each variable's importance in discriminating among groups. Use of this approach in the present study led to the conclusion that the sediment sorting coefficient was considerably more important than any other variable in discriminating between groups. This conclusion, however, does not seem intuitively correct, and it is likely that this finding results from correlations among the other variables. Grain size percentages of adjacent phi size intervals (e.g. coarse sand and very coarse sand) may be correlated; thus, the discriminating information they carry may be similar. Their standardized discriminant function coefficients may be small even though their joint contribution is very important. Similar difficulties arise with grain size percentages that are widely separated on the phi size spectrum (e.g. coarse sand and very fine sand), for they are likely to have an inverse correlation. The sorting coefficient had a high standardized discriminant function coefficient probably because it was the only variable used which is not inherently correlated with any other variable.

Interpretation of the discriminant functions in terms of total structure coefficients leads to the more credible conclusion that the percentages of silt and clay and very fine sand are the most important sedimentary variables in discriminating among groups. Total structure coefficients have been used successfully as alternative measures of a variable's importance (DUESER and SHUGART, 1978, 1979; FLINT and RABALAIS, 1980). They may be more valid than standardized discriminant function coefficients in cases of high variable colinearity (JOHNSON, 1977; KLECKA, 1980). They are calculated only as correlations between independent variables, and the discriminant scores are therefore unaffected by correlations among the variables. Total structure coefficients can also be used to present the variables as vectors in a two-function discriminant plot (OVERALL and KLETT, 1972; JOHNSON, 1977).

Significance of sediment parameters

Benthic communities and their member organisms are distributed in a continuum along environmental gradients (MILLS, 1969). Nonetheless, it remains common practice to recognize discrete faunal assemblages with the realization that their junctures are often not as discrete as might be implied. Assemblages of benthic species have often been designated on the basis of substrate association (FRANZ, 1976 and numerous others), and the same appears possible on the North Carolina continental shelf. Recognizable assemblages include: (1) a muddy, very fine sand assemblage (Group 1) dominated by *Lumbrineris impatiens*; (2) a fine to medium sand assemblage (Group 2) dominated by *Polygordius* sp.; (3) a well-sorted, fine sand assemblage (Group 4) dominated by *Protohaustorius* cf. *deichmannae*; and (4) a medium to coarse sand assemblage (Group 3) characterized by *Hemipodus roseus* and *Hesionura elongata*.

A goal of this study is to identify the grain size parameters which best explain the observed community patterns. The recognized faunal assemblages listed above have been designated by reference to the median grain size of the sediments in which they are found. However, median grain size *per se* is probably not the factor to which the organisms are responding. Median grain size alone is not responsive to differences in the grain size distribution which could have profound biological consequences, yet be unexpressed by any measure of central tendency. Efforts to determine what physical properties are of greatest importance in structuring communities have frequently been frustrated by high correlation among the environmental variables. Community changes have often been correlated to depth (NICHOLS, 1970; LIE, 1978; FLINT and RABALAIS, 1980), but in shallow marine environments sedimentary or other physical variables which vary with depth are more likely to be the controlling factors than depth itself.

In most benthic studies the degree of sediment sorting has been of minimal use in interpreting community differences. There are, however, some notable exceptions. NICHOLS (1970) found similarity among polychaete assemblages to be best correlated with sorting, although he suggested that sorting was only a manifestation of the clay content. FLINT (1981) reported sorting to be one of four environmental variables (with depth, sand:mud ratio and percent silt) that were useful in differentiating among macrobenthic assemblages on the Texas continental shelf. GRAY (1974) argued that sorting, as a measure of structural complexity, may be a determinant of species diversity. Greater species diversity should be found on those sediments which are more poorly sorted, since a wider variety of particle types would be available for utilization by the benthos. A similar argument has been advanced relating deposit-feeding species diversity to food particle and total particle diversity (WHITLATCH, 1981). In the Cape Hatteras area no relationship was found between sorting and number of species (Spearman rank correlation, $\alpha > 0.05$), but it should be noted that number of species is not necessarily correlated with species diversity, which contains an evenness component as well.

In the present study the degree of particle sorting was of greatest importance in differentiating Group 4 stations from the remainder of the station groups. Although the median particle sizes of Group 4 sediments were similar to those of Group 2, the Group 4 sediments were better sorted and characterized by a dramatically different fauna. The importance of particle sorting was probably due to its correlation with sediment mobility; a property more difficult to quantify. The well-sorted sands of Group 4 are indicative of a dynamic hydraulic regime with a high degree of sediment mobility. Bedforms at the Group 4 stations are characterized by megaripples superimposed upon sand waves with heights of 2–8 m (HUNT *et al.*, 1977). These bedforms are responses to modern flow, and are maintained by suspensive transport of fine sand. Tubiculous and non-fossorial species would be rapidly washed out of the sediment in such an environment. Only fossorial species, such as the haustoriid and phoxocephalid amphipods characteristic of these stations, are able to burrow rapidly enough in order to maintain purchase.

The percentage of gravel has been identified as an important factor in differentiating between benthic assemblages and, in some instances, has been found to be the most important environmental factor in determining the distribution of species, feeding types and life styles of benthic amphipods (BIERNBAUM, 1979). The percentage of shell and gravel was of no detectable biological significance in the Cape Hatteras area, but this finding is believed to be a result of the small range of shell and gravel content encountered (up to 23% but generally less than 1%).

The percentage of fine sand was found to be the most important variable on the second axis of the ordination and the second discriminant function. Differences in the fine sand component were most important in distinguishing the interstitial burrowers of Group 3 stations. The importance of fine sand has been noted for both certain amphipod species (SCHAFFNER and BOESCH, 1982) and the whole macrobenthic community (BOESCH, in press; BOESCH and BOWEN, in press) in the Middle Atlantic Bight, although it should be noted that in these studies fine sand was considered to be the aggregate of both the fine and very fine sand size classes used here. BOESCH (in press) speculated that the exclusion of interstitial species with increasing proportions of fine sand is due to the occlusion of the interstitial spaces. The fact that many species of Group 3 were interstitial burrowers probably reflects the low proportion of fine sand particles in stations of this group.

The sediment variables found most useful for interpreting faunal distributions were the percentage of very fine sand and the combined percentage of silt and clay. Both percentages scored highly in the discriminant analysis and ordination. The percentage of silt and clay appeared slightly more important than very fine sand in both analyses, but, because both percentages were highly correlated, it is difficult to determine their independent contributions. These results are generally consistent with those from studies on the Texas continental shelf where discriminant analysis of nine sedimentary texture measurements identified percent silt and the sand: mud ratio as two of the three (the third being sorting) most important sedimentary variables in differentiating macrobenthic assemblages (FLINT, 1981).

The importance of the very fine sand and silt and clay components is, in part, a reflection of their roles in determining sediment permeability. Sediment permeability is diminished as the proportion of finer particles in the sediment increases and sorting decreases (Webb, 1958). Dissolved oxygen is unable to penetrate as deeply in sediments containing a high proportion of fine particles, and, thus, deep-burrowing species are restricted to those species which can maintain contact with the sediment–water interface (e.g. by elongate siphons or burrow irrigation) or which have physiological adaptations to anaerobic conditions.

A second reason that finer particles were found to be so important in structuring benthic communities is probably related to their crucial role in determining the type and abundance of food resources. The importance of very fine sand and silts and clay particles observed in the present field studies is supported by a considerable body of evidence from other work indicating that finer particles have a proportionately greater organic content per unit volume, deposit-feeders utilize this organic coating as a food resource, and many organisms actively select for these food-rich, finer particles. The greater surface area:volume ratio provided by small particles permits adherence of a proportionately greater amount of organic matter, including both the living and non-living components. The direct relationship between microorganism abundance and the surface area available for attachment has been demonstrated repeatedly by both direct counts of bacteria (ZoBell, 1938; Fenchell, 1970; Tsernoglou and Anthony, 1971; Dale, 1974; DeFlaun and Mayer, 1983) and by measurements of microbial activity (Newell, 1965; Fenchell, 1970; Hargrave, 1972; Hargrave and Phillips, 1977). Deposit-feeding macroinvertebrates utilize this particle-associated organic matter as a food source, efficiently assimilating microbial epigrowth and mucopolysaccharide exudates (Newell, 1965; Fenchell, 1970; Kristensen, 1972; Yingst, 1976; Hobbie and Lee, 1980). As reviewed by Taghon (1982), most deposit-feeders have been shown to preferentially ingest smaller particles, and are able to discriminate between particles with and without organic coatings. The value of using very fine sand or silt and clay content as discriminators among North Carolina shelf macrobenthic communities probably lies in their surface area-related correlation with the type and quantity of food resources.

Sanders (1958) found the distribution of many deposit-feeding macrobenthos to be correlated with the percentage of silt and clay. He speculated that the amount of clay was the more important variable since clay particles have the greatest surface:volume ratio, allowing adherence of relatively more organic matter. This study did not differentiate between clay and silt particles; however, there is preliminary evidence from other work (DeFlaun and Mayer, 1983) that sediment organic content (and thus, food value to deposit-feeders) may be more dependent upon the abundance of silt particles than of clays. Bacteria tend not to attach to particles smaller than 10 μm, but rather these particles tend to accumulate in the mucus coatings surrounding bacterial colonies. Thus, the abundance of bacteria may control the clay content of the sediments, rather than vice versa.

The proportion of silt and clay (generally combined) has been found to be the most important sediment parameter in differentiating benthic communities in several studies (Sanders, 1958; Nichols, 1970; Kiørboe, 1979). Although these studies were done in estuarine or coastal areas where percentages of silt and clay ranged as high as 50–90%, it appears that silt and clay are of equal biological significance at the considerably lower concentrations found on the North Carolina shelf. Even modest changes in silt and clay content in the range observed (0–27%) correlate with profound changes in the macrobenthic community.

CONCLUSIONS

The North Carolina continental shelf in the vicinity of Cape Hatteras is characterized by an unusually wide diversity of surficial sediment types in comparison to most shelf areas of comparable spatial extent. Sediments range from coarse to very fine sands, with the proportion of silts and clays ranging from near 0 to 27%.

Multivariate analytical techniques were found to be a valuable tool in recognition of station groupings and in the identification of environmental gradients correlating with these groupings, although some precautions should be noted to avoid misinterpretation of results. Total structure coefficients appear to be preferable to standardized discriminant function coefficients when employing discriminant analysis with a high degree of correlation among the variables. Detrended correspondence analysis performed well in the present investigation, yet recent work indicates potential problems with the technique when interpreting the second or higher axes.

Four macrobenthic assemblages, separable largely on the basis of sediment characteristics, were recognized within the study area. Temporal changes in macrobenthic assemblages were apparent, but they were of secondary importance to spatial changes related to differences in sediment texture.

The utility of substrate characteristics in discriminating among macroinvertebrate communities appears to be as great in continental shelf habitats as in the more often studied estuarine areas. Most past work demonstrating correlations between macrobenthic communities and sediment characteristics has been conducted in areas where the silt and clay content covered an extremely broad range, often attaining 50–80%. This study, however, documented dramatic community changes over a much smaller range of 0–27%.

Sediment sorting, as representive of a dynamic hydraulic regime, was found to be a useful parameter in differentiating a station group characterized by fossorial haustoriid and phoxocephalid amphipods.

The sediment variables most useful in differentiating among macrobenthic assemblages were the percentage of very fine sand and the combined proportion of silt and clay. The biological importance of these variables is probably related to their role in determining sediment permeability and in controlling the type and quantity of food resources for deposit feeders.

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