

Gulf of Mexico Outer Continental Shelf Benthos: Macroinfaunal-Environmental Relationships*

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Abstract Subtropical outer continental shelf macroinfauna off the south Texas coast were studied seasonally over a two-year period. Ordination of the original 25 study sites distinguished five major groupings of stations with respect to infaunal assemblages and a group of stations representing a transition zone between mid-shelf and deep-water communities. Based upon frequency of occurrence for infaunal species that comprised greater than 1% abundance for any sample, six species groups were identified for the station groupings. Multiple discriminant analysis was used to test the biological model (species/station groupings), with environmental parameters measured during the study. The results suggested that the null hypothesis of no environmental difference between infaunal station groups should be rejected. Several environmental variables were identified that may be influencing the distribution of macroinfauna. These variables included water depth and the sediment characteristics of sand/mud ratio, percent silt, and grain size deviation. The results of this investigation indicated that sediment structure played a major role in structuring the benthos. Superimposed upon the sediment dynamics, however, were factors representing a food source to the benthos as well as factors

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involved in producing variability of the bottom hydrologic environment such as temperature.

Since Petersen (1913, 1918), investigators have delineated benthic communities in relation to environmental parameters such as hydrological variables (Molander, 1928), physical properties of the bottom sediments (Jones, 1950), and biological adaptation derived from species interactions in relatively stable environments (Sanders, 1968). Community distributions have been examined in a number of different aquatic environments in recent years, including temperate marine, tropical marine, and temperate freshwater (e.g., Lie and Kelley, 1970; Johnson, 1970; Field, 1971; Boesch, 1973; Flint and Merckel, 1978). These studies and others have found that the benthos varies considerably in space due to the general heterogeneity of aquatic systems and the tendency toward patchiness in the benthic fauna.

A large multidisciplinary research program in the subtropical Gulf of Mexico off south Texas provided the opportunity to contrast benthic community structure and influencing factors with other shelf regions. The south Texas shelf is comprised of siltier and less stable sediments than other areas such as the middle Atlantic region, which is characterized by sandier sediments (Boesch, 1979) to greater depths on the shelf. The outer Texas shelf can also be considered a true soft-bottom environment, because unlike other shelves of the eastern Gulf, south Atlantic, or Pacific, there are very few reef areas or extensive banks with their influential biogeographic effects, i.e., "islands in a sea of mud." Additionally, with pressure of extensive energy exploitation slated for the near future on the south Texas shelf, it is imperative to document the benthic species assemblages in a pristine habitat, but one which would probably be most directly impacted should a major environmental disturbance occur (e.g., oil well blowout, etc.). This area is also a direct supportive element to many of the regional fisheries such as shrimp.

Methods

Twenty-five stations located on four transects on the outer continental shelf of the Gulf of Mexico (Figure 1), their depths ranging from 10 m to 134 m, were sampled on six cruises between the winter of 1976 and fall of 1977. These cruises covered the seasons of winter (January–

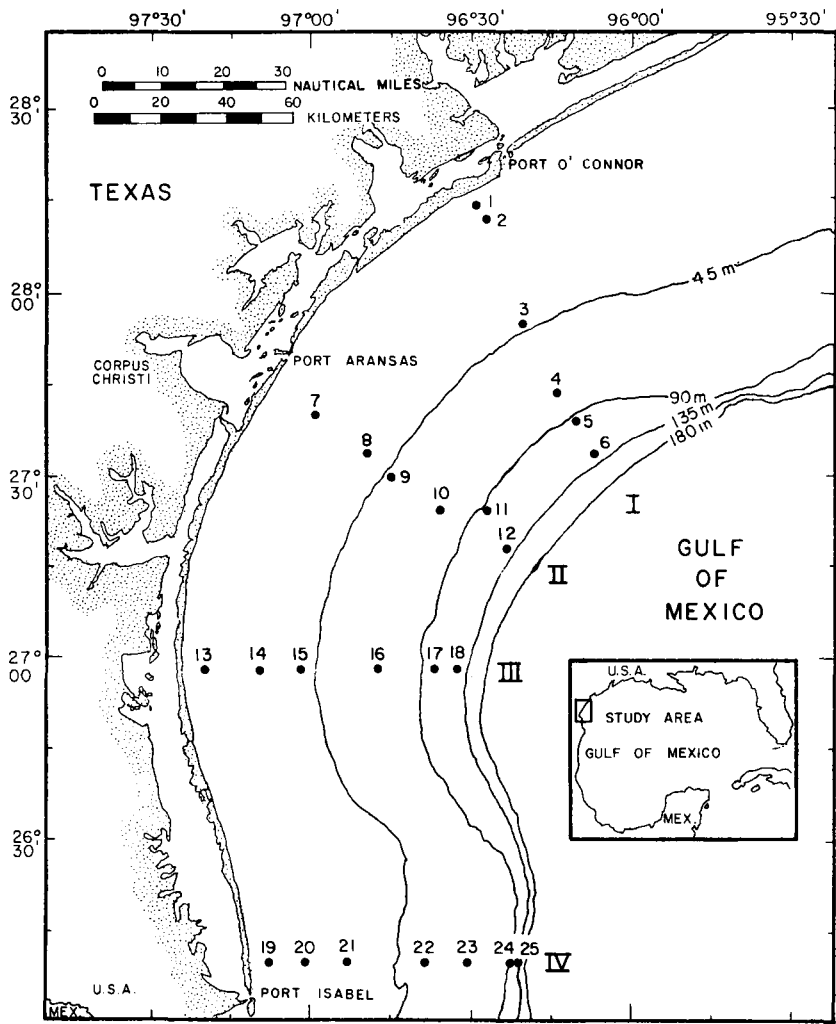


FIGURE 1. Location of sampling sites along four transects (I–IV) running perpendicular to shore in the Gulf of Mexico. Insert illustrates the study area with respect to the Texas coastline.

February), early summer (May–June), and fall (September–October) of each year, corresponding to seasonal shifts in shelf circulation patterns (Smith, 1979).

Six replicate samples at each station were made with a Smith-McIntyre bottom grab (0.1 m²). A small portion of the sediment for textural analysis was removed from each grab with a 5-cm diameter core. The remainder was washed through a 0.5-mm mesh, and the remains were relaxed in a saturated magnesium sulfate solution and preserved with 10% seawater-formalin containing Rose Bengal as a vital stain. Bottom water salinity and temperature were measured.

Sediment texture was analyzed by the rapid sediment analyzer (Schlee, 1966) for the sand-sized fraction and by the pipette method (Folk, 1974) for the mud fraction. Interpretations for the proportion of sand were done graphically at each 0.25 phi (ϕ) interval and used to calculate moment and graphic grain size parameters by standard methods (McBride, 1971). Percent total organic carbon was measured by combustion.

In the laboratory, fauna were sorted into major groups. Organisms were identified to species or lowest possible taxon and counted. The measure of species diversity for each station and sampling interval was estimated by a modification of the Shannon-Wiener diversity index (Pielou, 1966), using \log_{10} :

$$H'' = \sum (n_i/N) \log_{10} (n_i/N)$$

and the measure of equitability after Lloyd and Ghelardi (1964);

$$E = \frac{s'}{s}$$

where s equals the measured number of species and s' equals the expected number of species from MacArthur's model of diversity.

Species compositions of individual stations were compared with simple community ordination, using the similarity measure and axis construction method introduced by Bray and Curtis (1957). After comparing several transformations including the log and fourth root, the square root transformation of species abundances was chosen for analysis to decrease the effects of a few abundant species. Although a relatively weak transformation, this procedure accomplished the objectives of the analysis by emphasizing the more abundant species (> 1%

total density) at each site while lessening the effect on the Bray-Curtis index of the few dominant fauna. The ordination results were compared with results from cluster analysis of the same data (Canberra-Metric dissimilarity measure and flexible sorting strategy) and found to be very similar. Ordination results are presented here because of their ease of graphical display.

Correlations that existed between the ordination-produced infaunal classification groups and environmental parameters were studied with multiple discriminant analysis (Poole, 1974). This analysis provided a means of testing the goodness of fit of the infaunal station groupings evaluated for their environmental information. Green (1971, 1974, 1977), Knight (1974), Bernstein *et al.* (1978), and Flint and Rabalais (1980) used this analysis in ecological studies with good success. The Wilk's stepwise method of analysis was employed (Nie *et al.*, 1970, p. 434). The environmental variables chosen for study included nine sediment texture measures, bottom water temperature and salinity, water depth, and sediment total organic carbon. The objective was to maximize the ratio of among-group to within-group separation (Flint and Rabalais, 1980). The axes defined by the discriminant functions were assumed to be independent and to correlate with the variables potentially important in group separation (Green, 1971). The number of functions evaluated depended upon the amount of variation each explained and the chi-square significance ($p < 0.05$).

Results

Community Patterns

Ordination analysis of the infaunal species composition for each collection site indicated that 73% of the total variation among sites was accounted for by the first and second coordinates. The third coordinate only accounted for an additional 4% variation and showed no meaningful trends. Therefore, all emphasis was placed on the first two coordinates (X and Y axes).

In order to define objectively community differences, the station scores from community ordination were evaluated by the LSD multiple range test (Sokal and Rohlf, 1969). Both coordinate mean scores of the

six collection periods were compared for each station. The first ordination coordinate was able to significantly delineate ($P < 0.05$) four station groupings, Groups I, II, III, and V (Figure 2). Station Group I consisted of sites 1 and 20, while Group II was characterized by sites 13 and 19 of Figure 1. Station Group III (Figure 2) was defined by the largest number of collection sites and included Stations 2, 3, 7, 8, 9, 14, 15, and 21. According to the LSD results for the second ordination coordinate, Stations 22, 23, and 24 significantly ($P < 0.05$) differed from the other sites in Station Group III and were considered a group within themselves (Station Group IV). Station Group V was comprised of five stations showing consistently low scores for both the first and second ordination coordinates (Figure 2) and included Stations 6, 12, 17, 18, and 25, the deepest sites in the study area (Figure 1).

A group of five stations, including 4, 5, 10, 11, and 16, did not show a significant difference from most sites in Station Groups III or V according to first coordinate means and were not further differentiated by the second coordinate. Therefore, these stations were defined as a transition zone between the mid-shelf communities (Station Group III) and the deep-water communities (Station Group V).

The community variables of species number, infauna density, species diversity, and equitability exhibited trends (Figure 3) that were consistent with the community ordination results for the station groups. The number of species (Figure 3) was consistently the highest at the shallow stations (Groups I and II), with a significant drop for Group III sites. Density was also greatest for the shallowest sites, with decreases in deeper waters. High species numbers and infaunal densities resulted in high species diversity measures for the shallow stations (Groups I and II). The highest diversities, however, were measured for Station Group IV. Equitability increased in the offshore direction, indicating that although the shallow stations were high in numbers of species and densities, they were characterized by a few dominant fauna, in contrast to more evenly distributed population densities for the offshore stations (Groups IV and V). Results of one-way ANOVA indicated there was a general significant difference ($P < 0.01$) between station groups for all four community measures, further verifying the separation of stations from ordination procedures. LSD range tests showed, however, no difference between the transition zone and at least one of the station groups (III or V) bordering this zone for each of the four variables presented in Figure 3, emphasizing the transitional nature of this fauna.

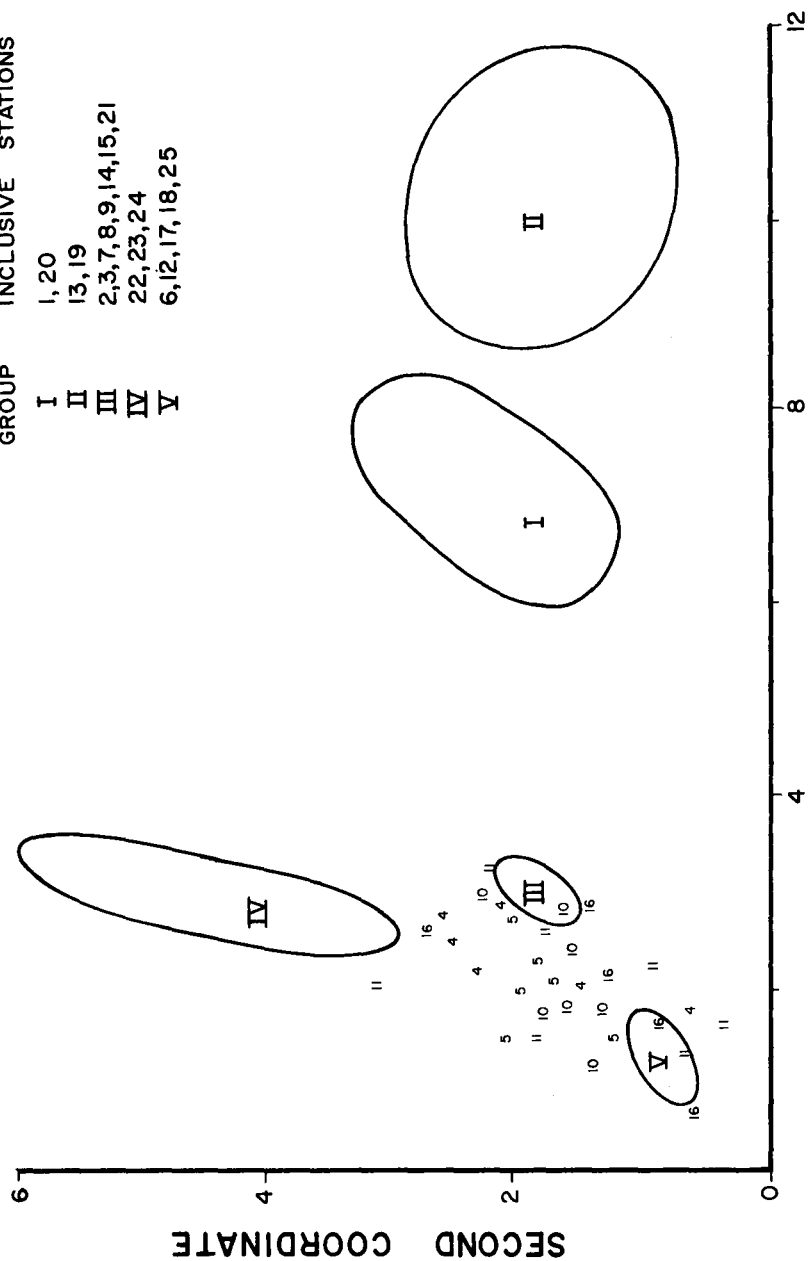


FIGURE 2. Ninety-five percent confidence ellipses for the mean first and second coordinates for each station group defined from community ordination. The stations included in each group are defined in the key. The transition station coordinates are plotted independent of group classification. Confidence regions were computed from bivariate means, variances, and covariances, using the principal axis technique of Sokal and Rohlf (1969).

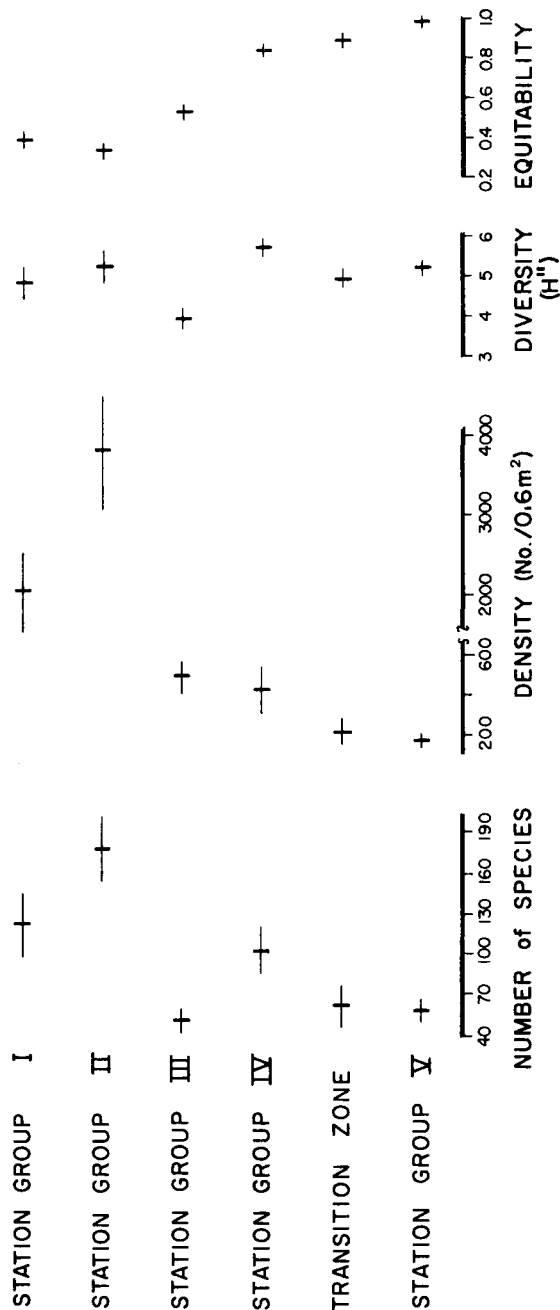


FIGURE 3. The mean and 95% confidence intervals (bars) of the community variables measured in this study for each station group defined in Figure 2.

Inverse community ordination (R mode), identifying the species characteristic of collection sites, aided in the interpretation of infaunal assemblages that described the station groups highlighted above. Fifty-eight species that showed a minimum of at least 1% abundance at a station over the study period were identified by this ordination analysis (Figure 4). They comprised six groups coincident with one or more of the station groups. Species Group I represented shallow water fauna, while Species Groups II and III consisted of infauna showing shallow to mid-shelf distributions. Species Group IV was comprised almost exclusively of deep-water infauna. Groups V and VI were composed of infaunal species relatively ubiquitous over the south Texas shelf. Most major taxonomic classes (i.e., polychaetes, molluscs, crustaceans) were represented by these faunal groupings, but polychaetes were by far the dominant taxa of the shelf benthos.

The transition stations shared species characteristic of both mid-shelf and deep-water stations (Figure 4). The frequency of species occurrences at stations in Group IV suggested that this area may be unique within the study area. These sites supported infauna characteristic of shallow stations (e.g., *Prionospio steenstrupi* and *Ceratocephale oculata*), as well as infauna representative of deeper water. Figure 4 further illustrates two points stressed in Figure 3. First, the occurrence of more species in Station Group IV showed why this grouping had the highest species diversity on the shelf. Secondly, the proportionately more species with higher frequencies of occurrence at the shallower stations hinted to the dominance of some of these organisms in the shallower shelf waters (i.e., *Magelona phyllisae*, *Paraprionospio pinata*, and *Lumbrineris verrilli*).

Environmental-Infaunal Relationships

Assemblages of organisms are rarely present as discrete groups with clearcut boundaries as evidenced by the transition community in the observations presented above. Therefore, in confirming community boundaries, interactions between the fauna and their environment must also be considered. Multivariate discriminant analysis was used to aid in identifying discriminating environmental variables for the infaunal station groupings and also to test the null hypothesis that there was no

FIGURE 4. The frequency of occurrences of infaunal species that represent greater than 1% total faunal abundance at any collection site during the study. The station groups from Figure 2 are listed and those species groups coincident with the station groups identified by roman numerals.

difference environmentally between these groups, similar to the methods employed by Flint and Rabalais (1980).

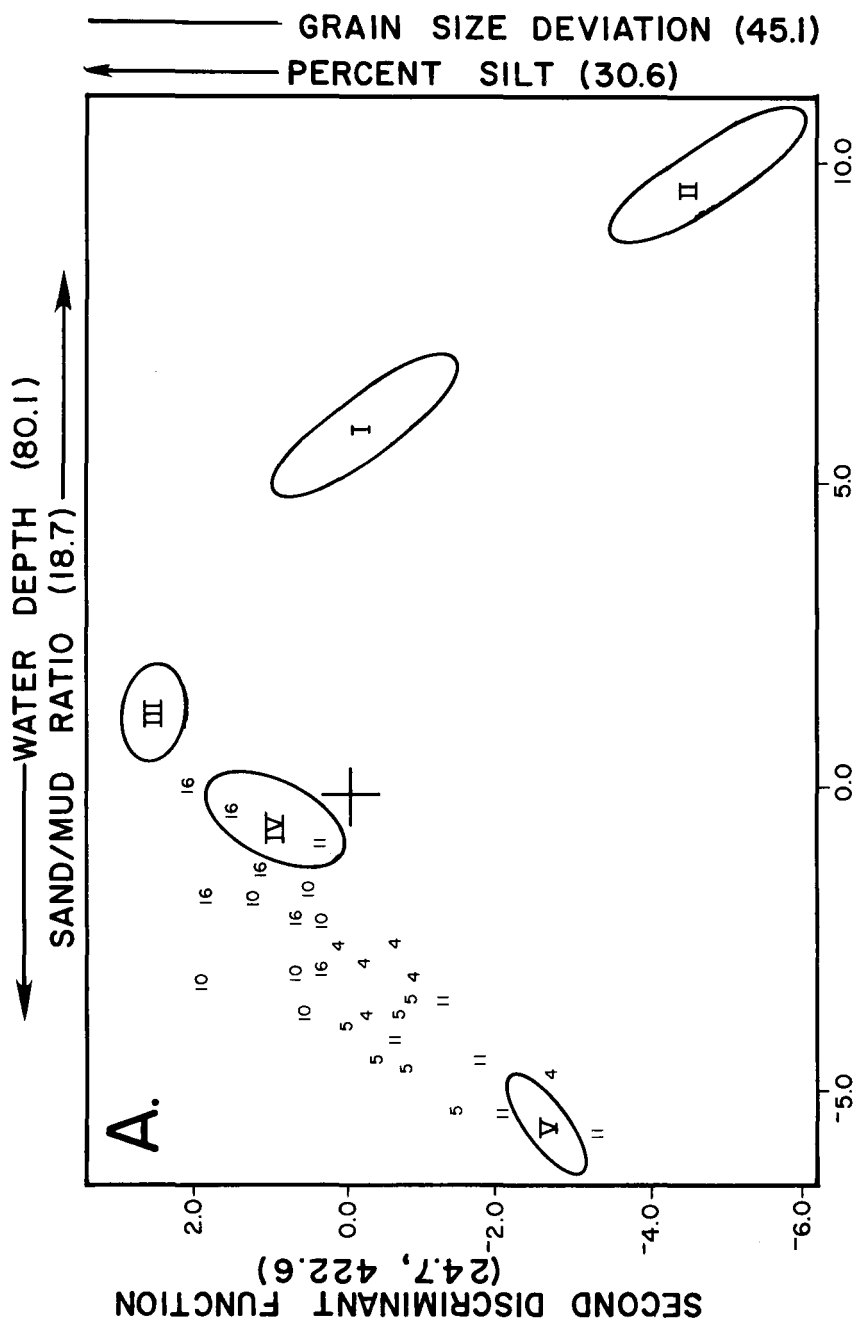
Figure 5 illustrates the position of station group mean discriminant function scores in a two-dimensional space defined by the first and second functions (Figure 5A) and the first and third functions (Figure 5B). Also indicated on each plot are the individual transition station scores for each collection period. From a suite of 13 original environmental variables, none of which were significantly correlated with one another as described elsewhere (Flint and Rabalais, 1980), four variables proved to be good discriminators of the infaunal station groupings (Figure 6).

The first and second discriminant functions accounted for 94.7% of the variation between station groups, and were both significant ($P < 0.01$) in discriminating between groups as indicated by their chi-square values (Figure 5A). Approximately 80% of the variation in the first function was accounted for by water depth. Sand/mud ratio accounted for an additional 18.7%. Water depth differentiated the shallow stations (Groups I and II) from the mid-shelf stations (Groups III and IV) and the mid-shelf stations from the deep-water stations (Group V) (Figure 6). The sand/mud ratio differentiated Station Group I from Group II.

On the second discriminant function (Figure 5A), grain size deviation of the sediments further distinguished differences between Groups I and II (Figure 6), as well as showing a more subtle but significant split between Groups III and IV. The sediment variable, percent silt, however, showed the strongest differentiation between the latter groups.

The third discriminant function (Figure 5B) was also significant ($P < 0.05$) and accounted for an additional 4% in variation between station groups. This function further illustrated the discriminating power of percent silt in not only differentiating Groups III and IV but also Group IV from the transition stations, which were in the same general depth range (Figure 6).

The overall chi-square ($P < 0.001$) derived from the general Mahalanobis distance squared was 640.9 for the discriminant analysis of station groups according to environmental variables and suggested that the null hypothesis of no environmental difference between groups be rejected. It was assumed, therefore, that there was very little probability the station groups could have been formed by chance, and the separation



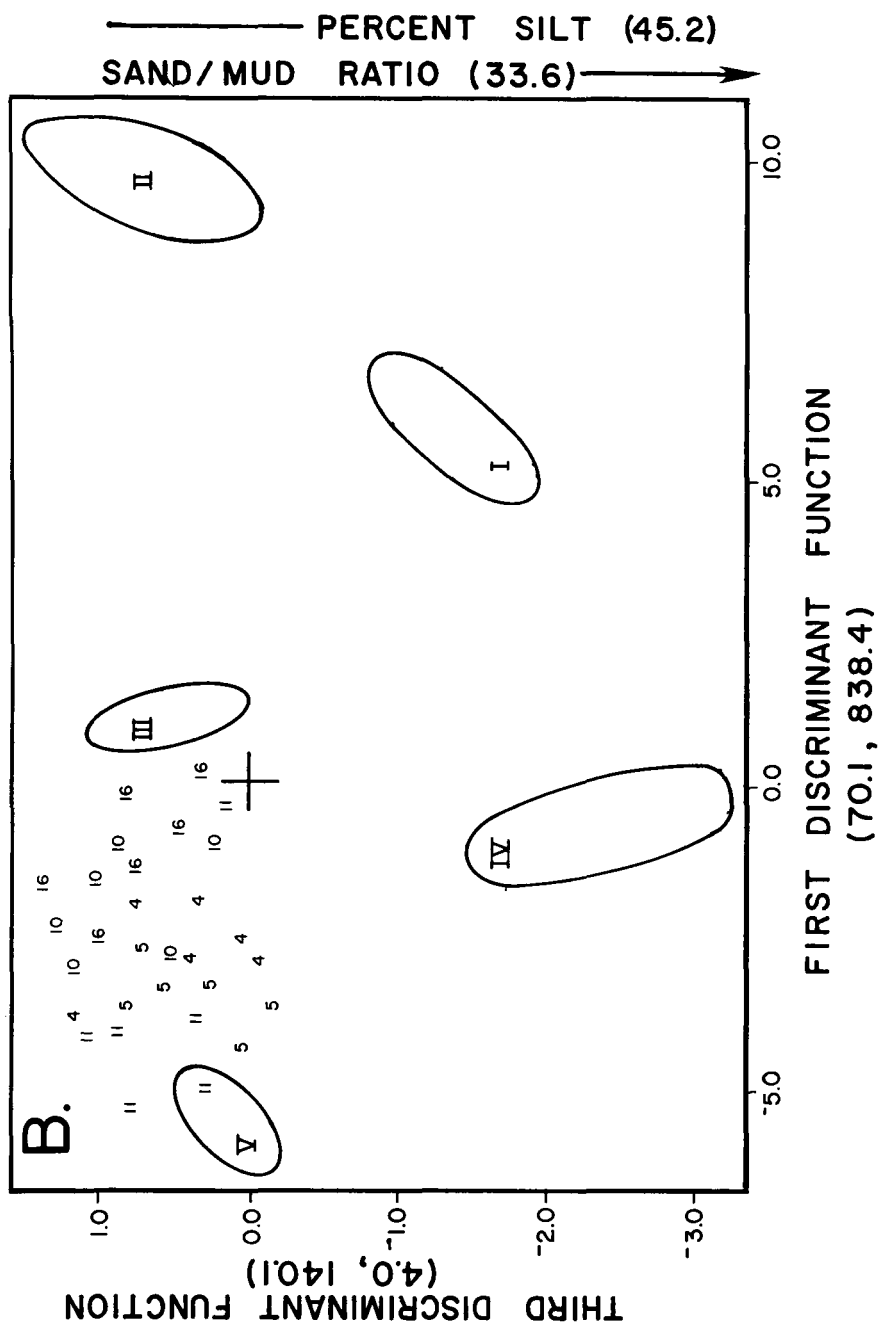


FIGURE 5. Ninety-five percent confidence ellipses for the mean first and second discriminant scores (A) and first and third discriminant scores (B) for each station group defined from Figure 2 according to analyses of environmental variables. The variables contributing most to axis construction are shown with their percent explained variation and direction of score correlation. The percent between group variation accounted for by each function and the chi-square value of that function are shown under the respective axis label. Confidence regions were

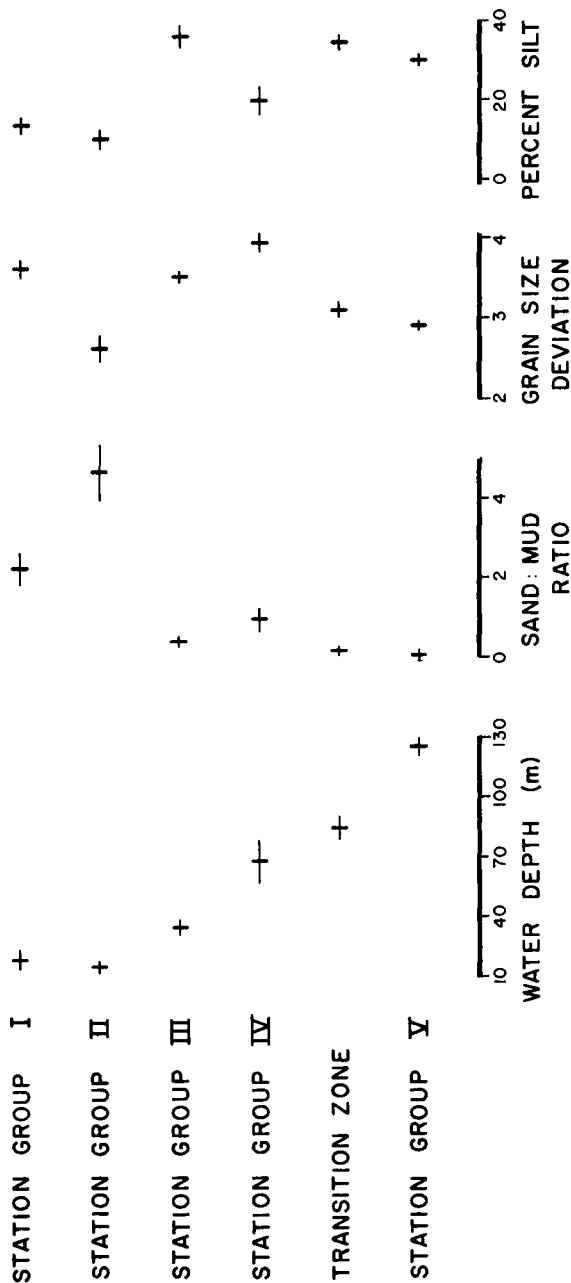


FIGURE 6. The mean and 95% confidence intervals (bars) of the environmental variables judged best in discriminating the station groups according to Figure 5.

between them was real. These results confirmed the biological model and suggested some of the variables potentially influential in structuring the infaunal communities.

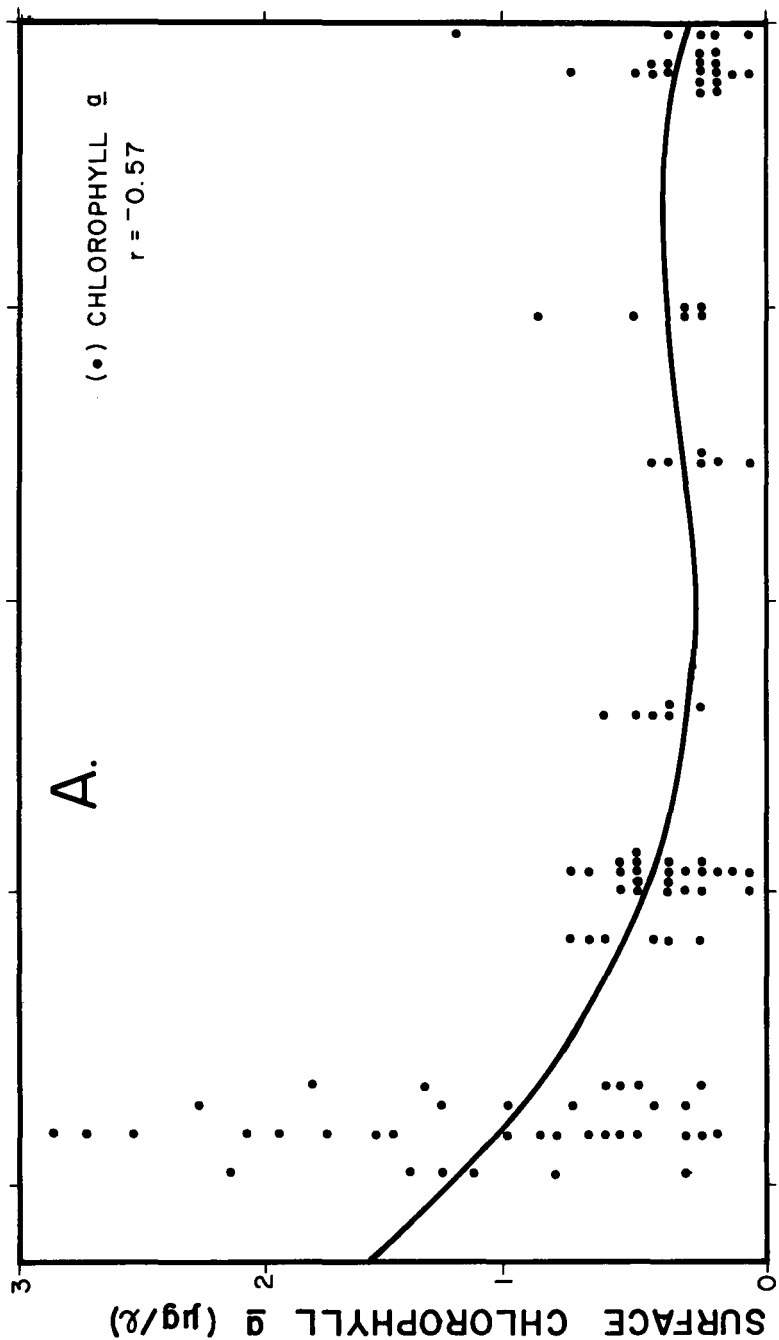
Sediment properties appeared to be relatively important in structuring community patterns. Although these properties are mildly correlated with water depth, the most powerful discriminating variable observed, there are other factors related to water depth that must be considered in the interpretation of the results. These factors include the degree of food availability to the benthos and bottom water environmental variability along the depth gradient as characterized by surface chlorophyll *a* concentrations and the standard deviation measure of temperature and salinity.

Figure 7 illustrates the changes associated with these factors as water depth increased on the shelf. Chlorophyll *a* concentrations (Figure 7A) were highest and also most variable in shallower waters where highest densities of infauna were observed. Lower concentrations of primary producers, whose abundances were less variable throughout the study interval, were associated with lower densities of infauna but progressively more evenly distributed population numbers within these assemblages at deeper stations (Figure 3).

Temperature and salinity were both most variable at the shallower collection sites, with decreasing variability as water depth increased (Figure 7). This implied that the shallower benthic habitat was much more variable and less predictable in environmental change. This variability of the shallow shelf could be further magnified by the fluctuations of chlorophyll *a* affecting the detrital pool food source to the benthos. Therefore, besides the influential effects of certain sediment characteristics on benthos community structure, it is felt that gradational features of a food source to the benthos and variability in the bottom water environment are also suspect in potentially causing the different faunal patterns observed.

Discussion

Other benthic marine systems investigated have been shown to be typically gradational in space with respect to sediment and other environmental variables (e.g. Day *et al.*, 1971; Field, 1971; Boesch, 1973; Glemarec, 1973). Closely correlated with these environmental changes



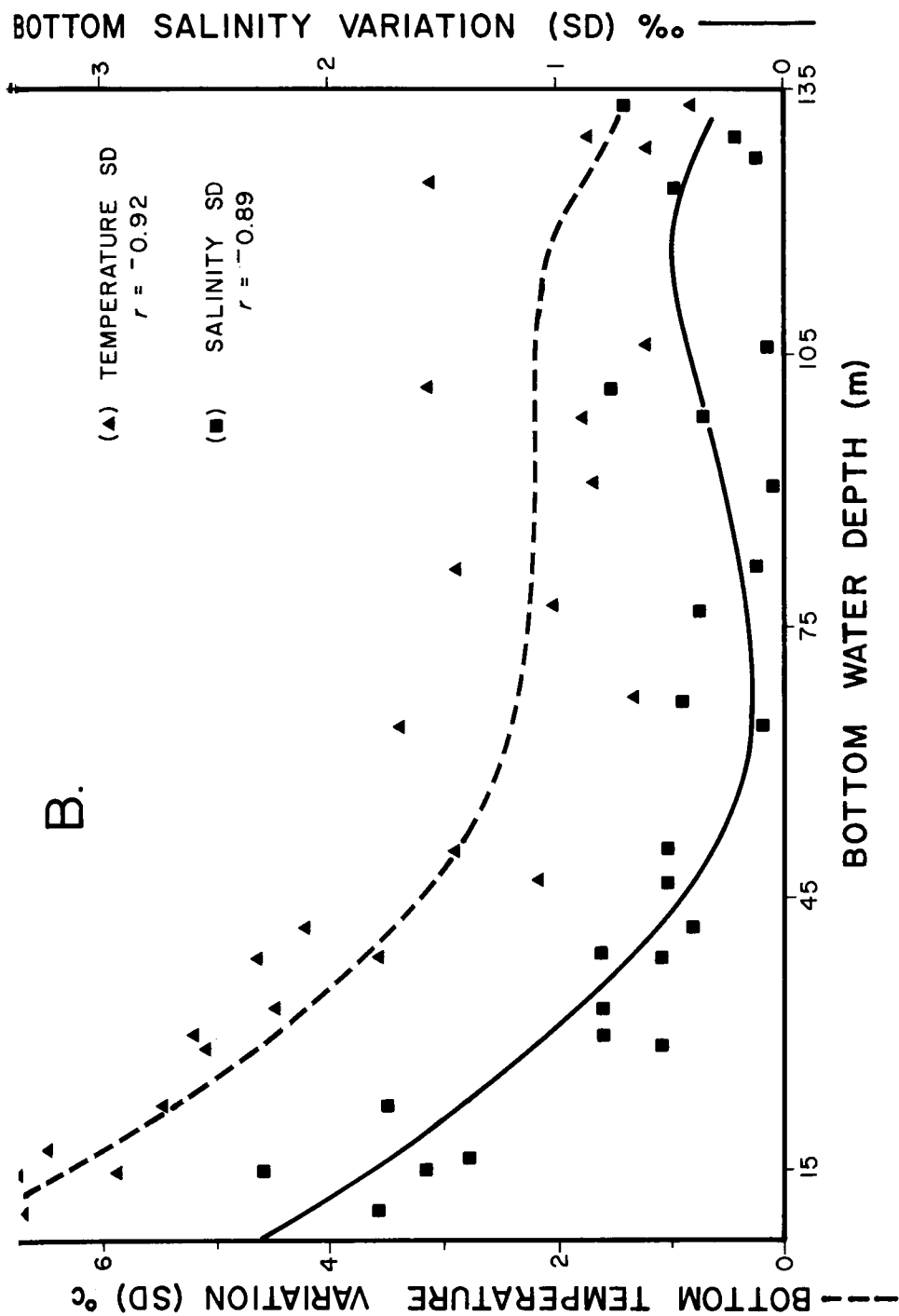


FIGURE 7. Total chlorophyll *a* (A) and the standard deviation (B) of temperature and salinity observed during the study period plotted against water depth on the shelf. The simple correlation coefficients (*r*) are indicated on each plot.

are changes in macroinfaunal communities. According to the observations presented above, sediment structure plays an important role in structuring the benthos. Superimposed on the mechanics that the substrata pose on the benthic infauna, however, are factors involved in producing variability both to a food source of the benthos and the overlying hydrologic environment. These environmental aspects couple together to produce a very complex association between the Gulf of Mexico benthos and the habitat in which they live.

According to Glemarec (1973), nature of the sediments is of prime importance for the settlement of most invertebrate larvae and the resultant composition of communities. He extends his definition of spatial stages of the benthos, however, to include the effects of variations in bottom water temperature and cites examples from Jones (1950) and Lie (1967). Glemarec concludes that the environmental properties that permit a distinction between faunal assemblages are different depending upon whether the assemblages are in shallow or deep water.

Therefore, significant variability in the shallow waters combines with coarse, ill-sorted sediments to provide an unstable habitat. This habitat is characterized by many different fauna, with a small number exhibiting dominant abundances (low evenness). In contrast, another habitat also with coarse sediments (Station Group IV) exhibits the most diverse fauna observed during the study period. These sites, in addition to having a very heterogeneous sediment structure, are characterized by very stable hydrologic variables as well as a more predictable food source (Figure 7).

There was a variable sand/silt/clay mid-shelf mixture observed at most stations between water depths of 20 and 50 m (Station Group III), with silt representing the dominant component (Figure 6). These stations generally showed a sand/mud ratio of 0.3 to 0.5, much lower than the shallow stations. Percent silt was also a major discriminating variable separating Station Groups III and IV in Figure 5. Group III exhibited the lowest number of infaunal species on the shelf while supporting population densities second only to the shallow stations (Figure 3). Associated with these community parameters were low measures for both species diversity and equitability, suggesting that these species assemblages were dominated by a few species at high densities.

Siltier sediments present a difficult environment to which fewer species can adapt. Not only are the niches decreased by a more

homogeneous substrata (Ward, 1975), but the stability of particle sizes to bottom water currents is less, as illustrated by the sediment resuspension associated with nepheloid layer dynamics that occur frequently during the year (Kamykowski *et al.*, 1977) on this shelf. This can produce a relatively unstable substrate for the existence of infauna.

Polychaetes were the dominant taxa observed in this study. The majority of their feeding strategies, according to comparisons with the fauna discussed by Fauchald and Jumars (1979), involves deposit feeding. These strategies are much more conducive to silty, unstable bottom habitats (Sanders, 1960; Salla, 1976). In contrast, the dominant fauna observed on the Middle Atlantic shelf were amphipods (Boesch, 1979). This shelf is characterized by sandier sediments than the Texas shelf. Amphipods derive their nutrition primarily by suspension feeding which, according to Sanders (1960) and Levinton (1972), is a more appropriate feeding strategy for sandier, more stable sediments.

The subtropical Texas shelf showed infaunal patterns consistent with other shelf ecosystems in terms of environmental gradation (Day *et al.*, 1971) and shallow water variability as found in temperate marine systems (Sanders, 1968). The Texas shelf differed, however, from at least one other shelf extensively studied (Boesch, 1979) in that different taxa dominated the infauna, and this difference was possibly related to the sediment structure differences of the mid-shelf habitat.

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