

A NUMERICAL ANALYSIS OF THE DISTRIBUTION OF
THE BENTHIC INFAUNA
OF THE SOUTHEASTERN BERING SEA SHELF

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A
THESIS

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ABSTRACT

The continental shelf region of the southeastern Bering Sea may be classified into five provinces (station groups) based on infaunal distribution. Three large station groups lie in adjacent bands extending from the Alaskan coast to the shelf break, roughly paralleling the bathymetry. Two smaller groups occupying positions at the head of Bristol Bay and off Nunivak Island were identified. Stations in the northwestern section of the study area (near the Pribilof Islands) show no strong affinity to the major station groups.

Fourteen major biocoenoses identified on the basis of species distribution show strong correlation with the spatial positioning of station groups. Spatial patterning of these species groups is described on the basis of their representation at station groups. Characteristic differences in trophic structure between station groups are attributed to the effects of storm-induced turbulence in nearshore environments and periodic intensive input of organic carbon in the midshelf region.

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INTRODUCTION

Initial surveys of the benthic macrofauna of the southeastern Bering Sea have been carried out by both Russian and American scientists as part of several expeditions to the area, dating back to 1932 (Alton 1974). This work has resulted in a basic knowledge of the organisms present and an overview of standing stocks (Nieman 1963; Semenov 1968; Stoker 1973, 1978). Much of the work either cannot be considered quantitative (in the sense that only one sample was taken at each station), or is based on a sampling interval too large to be valid for community studies. The work of Stoker (1973, 1978) was of sufficient intensity to facilitate community description but was concentrated in the northern shelf areas.

The purpose of the present study was to delineate provinces on the basis of the distribution and abundance of major infaunal species found on the southeastern Bering Sea shelf. In addition, an attempt has been made to distinguish species assemblages also defined on the basis of distribution and abundance information.

A traditional manner of approaching benthic community studies has been to search for groups of organisms sharing coincident ranges and to find groups of stations

characterized by a similar fauna. Such approaches have often considered only dominant species (Petersen 1913; Thorson 1957; Neiman 1963; Semenov 1964) simply because difficulties in handling large sets of data prohibited the inclusion of less common forms in ecological studies. Numerical approaches to the problem of community delineation have been developed with the advent of high speed computers. These approaches are now useful in situations requiring the digest of large numbers of observations, a situation generated by studies such as this in which many rare species are considered.

Statistical methods designed to resolve problems in classification are now commonly used by benthic ecologists (Field 1970; Lie and Kisker 1970; Stephenson, Williams, and Lance 1970; Stephenson 1973; Williams and Stephenson 1973). Of these methods, cluster and discriminant analysis deal directly with the problem of classification. "Ordination" techniques such as principal coordinates and principal components analysis are also useful in this capacity. Other multivariate statistical methods, primarily variants of factor analysis, are often used in addressing both the problems of classification and the exposition of underlying sources of variation.

Detailed studies of both species groups (assemblages) and station groups (provinces) may be employed as checks on postulated group boundaries. If such groups are valid, then evidence supporting the hypothesis of their existence should be forthcoming in the form of contrasting biotic and/or abiotic properties associated with the groups. In this study, examinations of such properties have been confined to those associated with station groups, with an emphasis on substrate types, diversity, and trophic structure found within groups.

The definition of station groups via the techniques mentioned is formally independent of the definition of species groups and vice-versa. A third area of study--that of the correlation between species and station groups--relates the two. Such a study has been approached informally here in the course of drawing both species and station group boundaries, although a rigorous mathematical approach to the problem of station group-species group relations was not undertaken.

STUDY AREA

The study area encompasses the southeastern Bering Sea continental shelf from St. Matthew Island south to the Alaska Peninsula. The station grid occupied during three cruises (NOAA Ship *Discoverer*, spring 1975; NOAA Ship *Miller Freeman*, fall 1975; NOAA Ship *Miller Freeman*, spring 1976) is presented in Figure 1. Station positions and associated water depths are listed in Appendix I. Station locations extend from shallow areas near the Kuskokwim River and the head of Bristol Bay to the shelf slope, with a maximum depth of 1,500 m.

The shelf topography is remarkable for its width (450-500 km in the study area), shallowness (generally <150 m), and gentle slope (average slope = 0.0024%). The bottom sediments of the southeastern Bering Sea shelf have been described by Sharma (1974, 1975), Sharma et al (1972), and Hoskin (1978). Two major depositional environments are evident on the basis of particle size analysis--an inner and an outer continental shelf area. The inner shelf region is characterized by a preponderance of fine to coarse sands and gravel while the outer shelf sediments are a clay, silt, and sand mixture. The apparent trend is one of decreasing mean size with increasing water depth. To

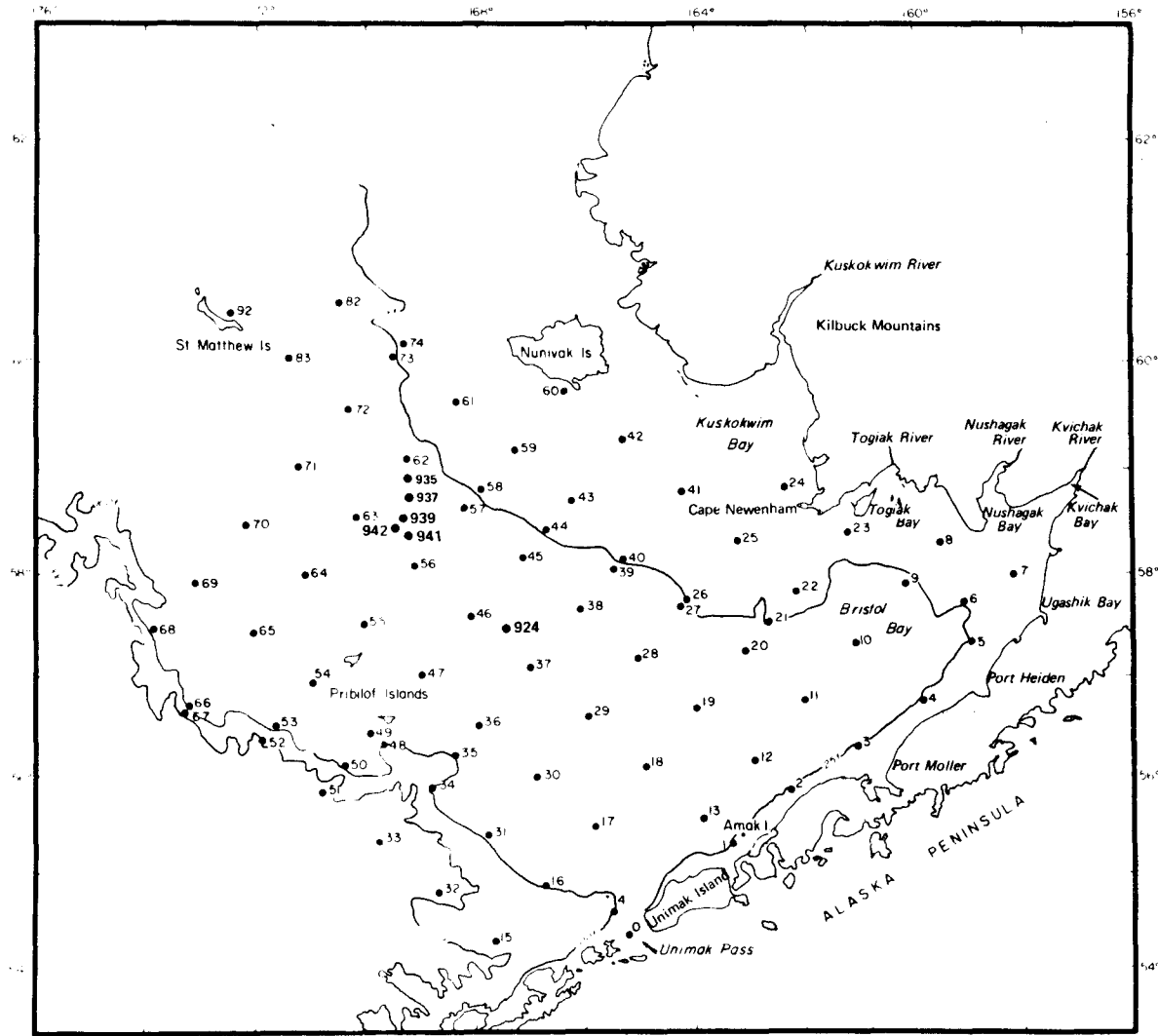


Figure 1. Study area used in Bering Sea infaunal studies.

account for this trend, Sharma (1971) postulates a suspension of bottom sediments resulting from long wave action, an effect that would decrease with increasing water depth. The decreasing long wave action is then thought to be reflected in the increased deposition of fine-grained sediments in the deeper areas.

Much of the shelf is ice-covered during the winter and an intensive bloom is associated with the retreat of the ice in the spring (McRoy and Goering 1972, Alexander 1978). Further input of organic carbon to the shelf-based marine system is supplied by several rivers draining into the area (especially the Kvichak, Nushagak, and Kuskokwim rivers) and from seagrass beds located in several large estuaries along the Alaska Peninsula.

The physical oceanography of the Bristol Bay area has been reviewed by Coachman and Charnell (1977). Three water masses are discernible: (a) a warm (3° to 4°C at its coldest) and saline (32 to $33^{\circ}/\text{oo}$) Bering Sea source water with origins in the deep Bering Sea and the Alaskan Stream via Unimak Pass; (b) a colder (-1° to $+2^{\circ}\text{C}$ in June) and slightly less saline mass of resident shelf water exhibiting little salinity stratification but usually markedly stratified with respect to temperature in summer; and (c) a nearshore water mass with a low salinity attributable

to coastal runoff and often stratified with respect to both temperature and salinity in the deeper layers.

Circulation over the shelf has been described by Takenouti and Ohtani (1974) and generally verified by the work of Coachman and Charnell (1977). Deep Bering Sea or Alaskan Stream water tends to move onto the shelf in central and southern Bristol Bay and then towards the head of the bay paralleling the Alaska Peninsula. Currents over the main shelf are to the northwest, or roughly parallel to the bathymetry. T-S diagrams presented by Coachman and Charnell (1977) suggest that Bering Sea source water interacts with resident shelf water along a front extending 100 to 150 km inshore from the shelf break. Evidence of penetration of this water further inshore is obscured by the relatively small volumes of source water involved.

METHODS

COLLECTION AND TREATMENT OF SAMPLES

Six replicate bottom samples were collected at most stations using a 0.1 m² van Veen grab. The performance of the grab was highly dependent on substrate, being least satisfactory in the inshore areas with coarse sand bottoms. Station averages for grab volumes ranged from 1 to 14 l (Table 1).

The grab contents were washed over a 1 mm screen and all invertebrates left on the screen were preserved in a 10% buffered formalin solution. Samples were taken to the Marine Sorting Center at the University of Alaska, Fairbanks, for identification and weighing.

DATA ANALYSIS

Type and Quality of Available Data

The raw data included both the numbers of individuals of all taxa found and their wet weights. These figures were standardized to the square meter and from this information station totals and means were derived. An example

Table 1. Average grab volumes (in liters) from Bering Sea benthic stations.

Station	Average Volume	Station	Average Volume	Station	Average Volume	Station	Average Volume
1	6	17	14	38	2	65	9
2	10	18	7	39	3	924	5
3	4	19	6	40	3	935	5
4	2	20	4	41	8	937	9
5	8	22	5	42	1	939	11
6	4	23	5	43	7	941	12
7	8	24	3	45	8	942	12
8	4	25	5	49	8	47	3
9	7	27	6	57	5	55	3
10	5	28	8	59	7	70	12
11	3	29	9	60	6	71	10
12	3	30	12	61	4	72	9
13	5	31	7	62	3	73	7
14	5	35	6	63	12	82	12
15	11	36	10	64	14	82	9
16	11	37	2				

of the results of this procedure is shown for Station 7 in Appendix II.

Four hundred and sixty-four (464) distinct species were identified; in addition, as only fragments of organisms were commonly encountered, many identifications were necessarily made to taxonomic levels more general than that of species. To use the multivariate techniques mentioned earlier, a significant reduction in the number of species to be considered was necessary, hence only those occurring at five or more stations were included in the numerical analysis. One hundred and eighty (180) such species were found. Representation by phyla of both these 180 species and the original 464 species is given in Table 2. A listing of the names of the 180 species may be found in Appendix III.

The data base consisted of the mean number of individuals of each particular species and the corresponding mean wet weight, each mean being that calculated for a particular station. Although these mean figures were subsequently regarded as fixed values, they are obviously estimates and have an associated sampling variance. A review of the data presented in Appendix II illustrates the sort of between-sample (grab) variance encountered. This source of variance is generally ignored in benthic

Table 2. Number of species collected and number used
in analysis.

Phyla	Number of Species Found	Number of Species Used in Numerical Analysis
Cnidaria	2	0
Annelida	194	80
Mollusca	117	41
Arthropoda	119	45
Echiuroidea	1	0
Sipunculida	4	2
Ectoprocta	4	0
Priapulida	1	1
Brachiopoda	1	1
Echinodermata	17	8
Urochordata	4	2

community studies. Feder et al. (1978) have performed a nested ANOVA based on station groups divided into stations and then samples (as randomly chosen subgroups), using diversity, total numbers of individuals per m^2 , and total wet weight per m^2 as sample variables for several different runs. Their results suggest that while the largest single source of variation is the between-sample variance, the between-station and between-station-group differences are still significant.

This approach does not directly address the problem of between-sample variation, for only a single variable was chosen to represent each sample while the actual number of variables equals the number of species. A multivariate analysis-of-variance would seem a more appropriate solution, but problems arise from both the large number of variables and the presence of many zeroes in the data set. For these reasons no attempt has been made to incorporate such an analysis in this study.

Cluster Analysis and the Delineation of Station Groups

Several different numerical methods were used to define station groups: an agglomerative, polythetic cluster analysis, principal coordinates analysis, and

principal components analysis. These methods are described below; summaries appear in an appendix of numerical methods, Appendix IV.

Clear introductions to the techniques of cluster analysis may be found in the works of Pielou (1977), Williams and Lance (1977), and others. More extensive discussions of the subject are presented in Gower (1969), Blackith and Reyment (1971), Anderberg (1973), Clifford and Stephenson (1975), and Hartigan (1975). In the present study, fusion procedures were used with a stored similarity matrix approach. The Czekanowski and Canberra metric dissimilarity coefficients were chosen to act as complementary distance measures. Their formulas are:

$$\begin{aligned} \text{Czekanowski coefficient} \quad d_{jk} &= \frac{\sum_{i=1}^n |x_{ij} - x_{ik}|}{\sum_{i=1}^n (x_{ij} + x_{ik})} \\ \text{Canberra metric coefficient} \quad d_{jk} &= \frac{1}{n} \sum_{i=1}^n \frac{|x_{ij} - x_{ik}|}{(x_{ij} + x_{ik})} \end{aligned}$$

where x_{ij} represents the value for the i th species at the j th station.

A separate clustering effort was undertaken for each of the similarity measures. The advantage to clustering

several times using differing distance measures is that different measures admit varying degrees of influence on the part of the dominant species. Since, in the computation of the Canberra metric measure, a dominant species affects but one of a series of fractions, the Canberra metric-based interpretation is less influenced by the dominant species than is an interpretation based on the Czekanowski coefficient. Another means of reducing the effect of dominance is the transformation of raw data. Many investigators in this field have found that logarithmic or square root transformations are necessary to produce useful results. In the present study all techniques were run with data that had been transformed to the natural logarithm, as preliminary results proved the need for transformations to produce interpretable results.

A general model for updating a stored distance matrix after each stage in the cluster analysis has been given by Lance and Williams (1977) as:

$$d_{hk} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} + \gamma |d_{hi} - d_{hj}|$$

where d_{hi} and d_{hj} represent the appropriate calculated distances between the two entities that have been fused (the i th and j th) and the third (h th) entity. The entity formed by the fusion of the i th and j th entities is denoted

by the subscript k . The parameters α_i , α_j , β , and γ determine the nature of the strategy (space-dilating, space-conserving, or space-contracting).

The nearest-neighbor [$\alpha_i = \alpha_j = +0.5$, $\beta = 0$, $\gamma = -0.5$], group-average [$\alpha_i = n_i/n_k$, $\alpha_j = n_j/n_k$, $\beta = \gamma = 0$ where n_z is the number of items in the z th cluster], and flexible [$\alpha_i + \alpha_j + \beta = 1$, $\alpha_i = \alpha_j$, $\beta < 1$, $\gamma = 0$] sorting strategies were used to construct several different cluster interpretations. The nearest-neighbor strategy is intensely space-contracting, tending to cause large clusters to be formed. The group-average is space-conserving, incorporating little artificial sharpening of the cluster boundaries. The flexible strategy ranges from space-contracting to space-dilating as the value of β becomes negative. A commonly used β value for this strategy is -0.25 (Lance and Williams 1977). This value proved overly space-dilating and a value of -0.05 was found to better separate groups of stations at high similarity levels.

Cluster Analysis and the Delineation of Species Groups

A clustering technique was also used to delineate species groups. The species themselves became the clustered entities while their abundances at given stations

were the variables. This procedure is generally termed "inverse analysis," the station clustering being a "normal analysis." Williams and Lambert (1961) have developed some theoretical and practical aspects of this usage employing a correlation coefficient matrix. Field (1970) has also commented on the appropriateness of using various similarities in an inverse analysis and advocates the use of a presence/absence-based coefficient (as in McConnaughey 1964) for the reason that consideration of differences in abundance may mask a real association between species with similar areal distribution (one being present in constantly lower numbers). However, it seems that differences in abundance are at least as important as the simple coincidence in the spatial distribution of species and for this reason the standard Czekanowski coefficient which does recognize abundance differences was used.

The problems associated with abundance effects in a species group analysis are also mitigated by a logarithmic transformation. Thus, the only species grouping effort that will be used in this report is based on the Czekanowski coefficient calculated for natural logarithm of the variate values, clustered according to the group-average algorithm.

Principal Components Analysis and the
Delineation of Station Groups

The technique of principal components analysis has found many applications in ecological work. Development of the technique may be traced to Pearson (1901) and Hotelling (1933). Excellent summaries of the extensive body of literature concerning the use of principal components analysis may be found in Gower (1967), Blackith and Reyment (1971), Morrison (1975), and Pielou (1977). The usual results of a principal components analysis are: (a) a set of projections of the entities onto a space of lower dimension than the original variate space; (b) a set of basis vectors for this space that are uncorrelated linear combinations of the original variates and used to explain the trends represented by the projections; and (c) a summary of the amount of variance accounted for by the projections onto the principal axes.

In this analysis only projections of the stations on the component axes were desired as it seemed that the 180 coefficients of the factors would be both too difficult to interpret and unnecessarily expensive to produce. Orloci (1966) has illustrated a "Q" technique for the method of principal components that bypasses the factor interpretation

of the classical "R" technique but yields the desired projections.

The computation of solutions for both the R and Q techniques may be succinctly described. For the Q technique, given the matrix X , where the n columns represent the station counts for the m rows of species, the matrix A is formed by centering the rows of the X matrix. The projection vector y_i is then found as $y_i = \beta_i$, where β_i is the i th latent vector of the matrix $Q = A'A$ (A' denotes the transpose of the matrix A). The relation between R and Q techniques is that $y_i = A'\alpha_i$, where α_i is the i th latent vector of the matrix $R = AA'$. The proof of the duality of the two techniques depends on the equality of eigenvalues of the R and Q matrices. A formal development of this proof may be found in Gower (1966) and Orloci (1967). Finally, the total system variance equals the sum of the individual eigenvalues; hence, the proportion of variance associated with each principal component may be found as $\alpha_i / \sum_{i=1}^n \alpha_i$, where α_i is the eigenvalue associated with the i th eigenvector and n is the rank of the matrix A .

The Q technique may make much smaller demands of the computer than the R technique since it necessitates the extraction of the latent vectors of the smaller matrix when the number of variates (species) exceeds the number of

cases (station). A salient point, however, is that its use bypasses the generation of the vector α , which is normally the subject of study in a classical principal components analysis. Since in the present study the number of variables far exceeds the number of cases, use of the Q technique was highly favored and was chosen for use over the R technique.

Principal component results from both the variance-covariance and the correlation matrices were obtained. To accomplish this the matrix X was alternately centered by row and then centered and standardized by row as follows (see Orloci 1966):

$$\begin{array}{ll} \text{Variance-covariance} & a_{ij} = \frac{x_{ij} - \bar{x}_i}{\sqrt{n-1}} \\ \\ \text{Correlation} & a_{ij} = \frac{x_{ij} - \bar{x}_i}{\sqrt{\sum_{k=1}^n (x_{ik} - \bar{x}_i)^2}} \end{array}$$

where x_{ij} is the number of individuals of the i th species found at the j th station, \bar{x}_i is the mean value for the i th species taken over all stations (the row mean), and n is the number of observations (stations). By this method, two different analyses are performed yielding

station projections exactly equal to those produced by the principal components analysis of the covariance and correlation matrices respectively. Mathematical operations involved in this technique are summarized in Appendix IV.

Principal Coordinate Analysis and the Delineation of Station Groups

The method of principal coordinates analysis was developed by Gower (1966) and is so similar to principal components analysis that the two have been lumped along with several other techniques into the general category of "inertial methods" by Chardy, Glemarec, and Laurec (1976). The results of a principal coordinates analysis are again projections of stations onto principal axes, but the model on which these projections are based differs from that of principal components analysis. Original interpoint distances are defined by an appropriate similarity or distance measure (the Czekanowski or the Canberra metric, for example). S is an $n \times n$ similarity matrix similar to that calculated at the initial stage of a cluster analysis. Coordinates of the point Q_i (the i th point or station) constitute the i th component of each of the latent vectors of the S matrix.

A principal components analysis, using as variables the latent vectors of this Q matrix, yields a centered representation of the original points in a multidimensional space. The procedure may then be described as: (a) a co-ordinatization of the association matrix and (b) the subsequent principal components analysis of these coordinates to produce a least squares projection onto as many axes as are desired. As in principal components analysis, the proportional variance associated with each individual component is based on the eigenvalue corresponding to that component (% variance = $\alpha_i / \sum_{i=1}^n \alpha_i$).

The process described above requires the extraction of latent vectors of two matrices whose dimensions are determined by the number of stations under analysis (i.e., S is $n \times n$). The method requires extraction of the eigenvectors of only one matrix if the original association matrix (S) is first transformed according to the formula:

$$q_{ij} = s_{ij} - \bar{s}_i - \bar{s}_j + \bar{s},$$

where q_{ij} and s_{ij} are the corresponding i th row, j th column elements of matrices Q and S respectively. The projection vector y_i may again be found as $y_i = \beta_i$, where β_i is the i th latent vector of the Q matrix scaled such

that $\beta_i' \beta_i = \gamma_i$, where γ_i is the i th latent root. Gower (1967) has shown that this method will be valid (i.e., result in a real configuration of points) for a wide variety of association matrices. In the current study, both the Czekanowski and Canberra metric coefficients were used as distance functions in the principal coordinates analysis. The mathematical operations used in this technique are also summarized in Appendix IV.

Differences between Principal Coordinates and Principal Components Analysis

While the formal results of the principal coordinates analysis and the principal components analysis (based on a Q technique) are similar (i.e., a projection of stations onto a low dimensional space--typically, that defined by the first three component axes), the underlying model is different. An understanding of these differences is essential to the complete utilization of these methods.

Principal components analyses are based on variance covariance or correlation matrices. The correlation measure may be thought of as a standardization of the raw data to terms of standard deviations and results in a mitigation of the effects of large departures of the variates from their respective means.

Principal coordinates analysis is based on an association matrix for which the definition of distance is rooted in ecological considerations. These distances ultimately determine the relative positions of stations and should be based on a desired weighting for the variables. The significant implication for this work is that the principal coordinates analysis based on the Canberra metric coefficient will be less influenced by dominant species than will that of the Czekanowski coefficient.

Finally, if an R technique is used to arrive at the principal components projection, the factor interpretation can be an integral part of the principal components analysis. Analysis of component coefficients affords us a direct knowledge of the roles of all variables in producing the projections. Such capabilities are not a part of the principal coordinates analysis.

Measurement of Diversity

The Shannon and Brillouin measures of diversity and the Simpson index of dominance were calculated from the data on numbers of individuals per square meter. Their formulas, according to Pielou (1977) are as follows:

$$\text{Brillouin index } H = \frac{1}{N} \log \frac{N!}{N_1! N_2! \dots N_s!},$$

where s equals the number of species, and N_j equals the number of individuals of the j th species and $N = \sum_{j=1}^s N_j$.

$$\text{Shannon index } H' = c \sum_j p_j \log p_j$$

where c is a positive constant, p_j is the proportion of individuals from the population that are of the j th species ($p_j = N_j/N$). In addition, species richness has been calculated after the development of Margalef (1957) as:

$$D = (s-1)/\ln N,$$

where s equals the number of species and N the number of individuals. A discussion of the theory behind these measures and the attendant implications of their use may also be found in Pielou (1977). General difficulties involved in using diversity indices are related to inequalities in both the numbers of species found and the number of individuals found in the different sampled sites. An increase in either tends to increase the value of the index and, though the increase may be small, the end result is that it is usually difficult to draw comparisons in diversity between sampled areas. As the number of species and the number of individuals found in the areas to be compared become closer, comparisons become more

meaningful. Unfortunately, such equality or near equality is rarely encountered in surveys of the marine benthos. Sanders (1968) has formulated a method to circumvent the above mentioned difficulties but his approach was beyond the scope of this study.

The Shannon index is used to estimate diversity of a large population from a sample and has an associated sampling error. Some use of this index will be made in a later section of the thesis, although no attempt has been made to estimate the sampling variance of this estimate. The Brillouin index is used to measure the diversity of a population or collection that is assessed in entirety and is therefore free of sampling error. The Simpson index is used here as a dominance measure, although it may be easily transformed to a diversity measure with characteristics inferior to the other two diversity indices mentioned above (Pielou 1977).

The Simpson dominance and Brillouin diversity indices can be used to examine both the diversity of the grab contents and the effects of dominance on the results of various clustering alternatives. The collection of organisms to be assessed must then differ. In studies of the entire community, the entire array of organisms captured by the grab should be considered. When examining the effects

of dominance on cluster or ordination analysis, the appropriate set is composed only of those organisms used in the analysis.

RESULTS AND DISCUSSION

STATION CLUSTERING

All clustering programs were written by University of Alaska personnel or adapted from Anderberg (1973). The dendrograms resulting from the cluster analyses are shown in Figures 2 through 5. The most useful results were obtained using the group average and flexible ($\beta = -0.05$) sorting strategies; therefore, only dendrograms originating from these strategies have been included. Clusters were initially determined by drawing a line across the dendrogram at approximately the .30 similarity level; groupings formed to this point were then evaluated as clusters. Subsequent cluster redefinitions were achieved by examining both the next larger and next smaller clusters corresponding to the next lower and higher similarity levels indicated on the dendrogram. The station groupings selected by this reexamination are shown in Figures 6 through 9.

Table 3 lists stations that have been designated core groups on the basis of their consistent conjoint appearance in clusters. It is apparent from Figures 6 through 9 and Table 3 that: (1) certain stations repeatedly group together by different analyses and (2) the composition

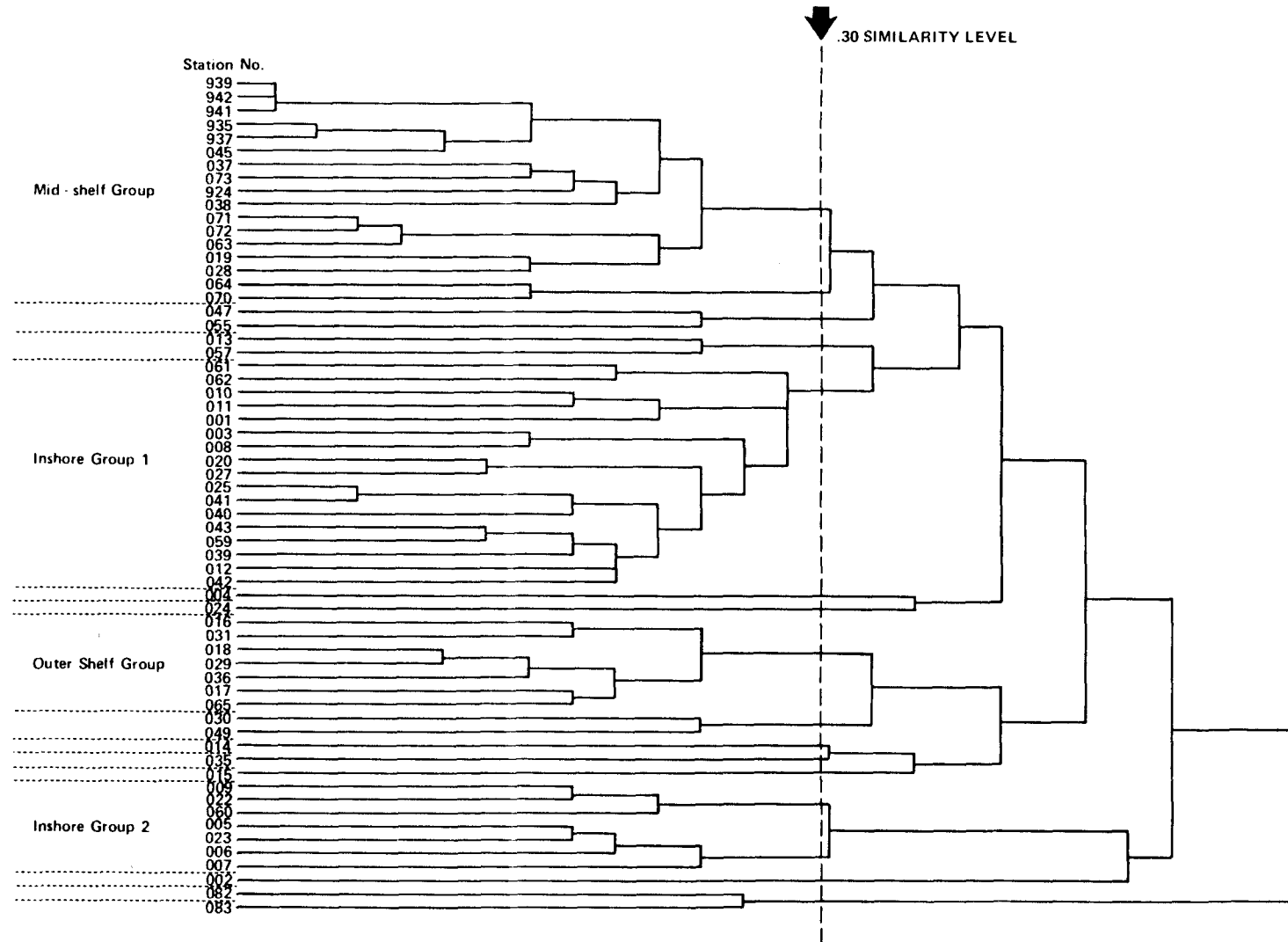


Figure 2. Dendrogram resulting from the clustering of stations using the Czekanowski distance measure and a flexible sorting strategy.

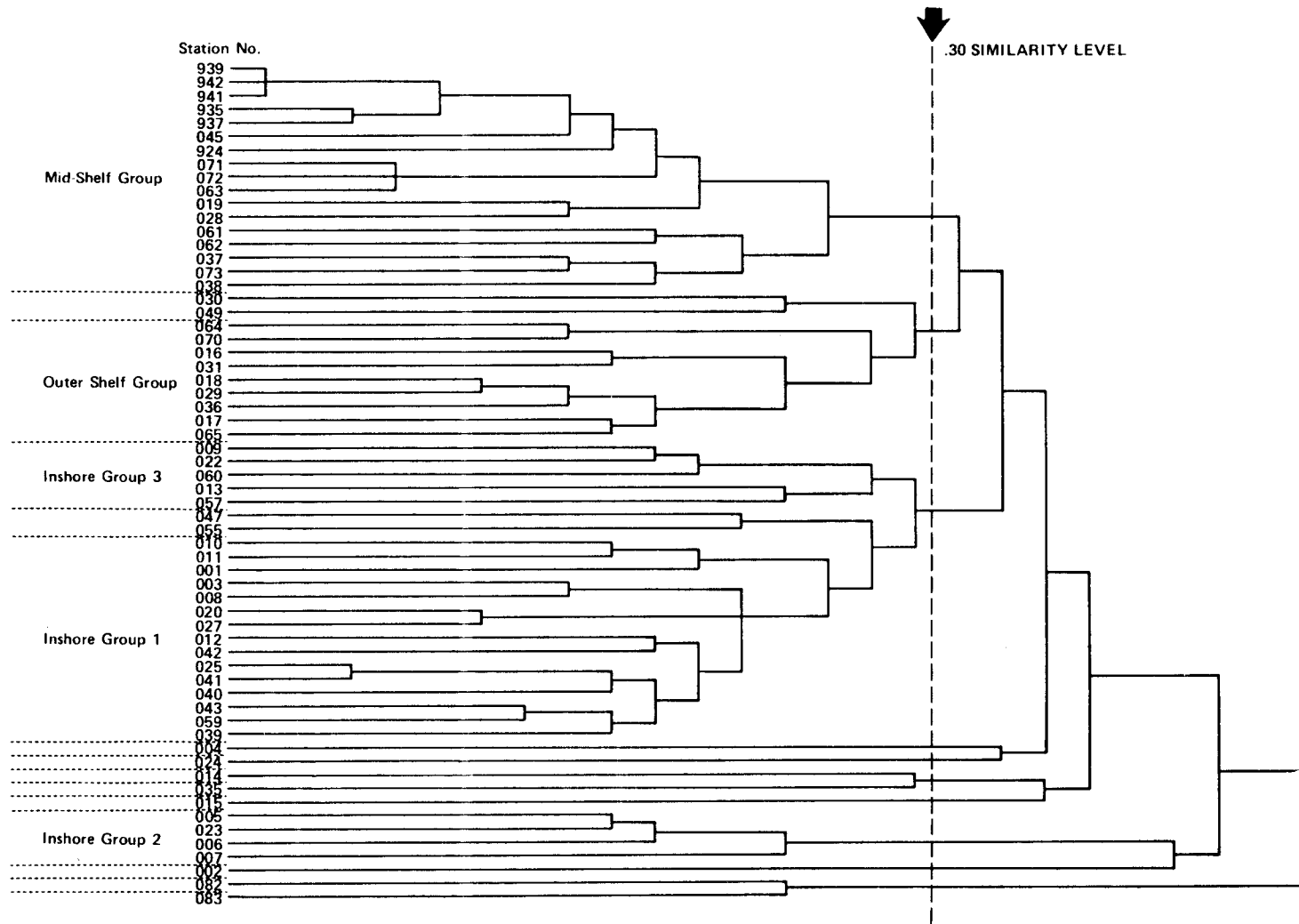


Figure 3. Dendrogram resulting from the clustering of stations using the Czekanowski distance measure and a group-average sorting strategy.

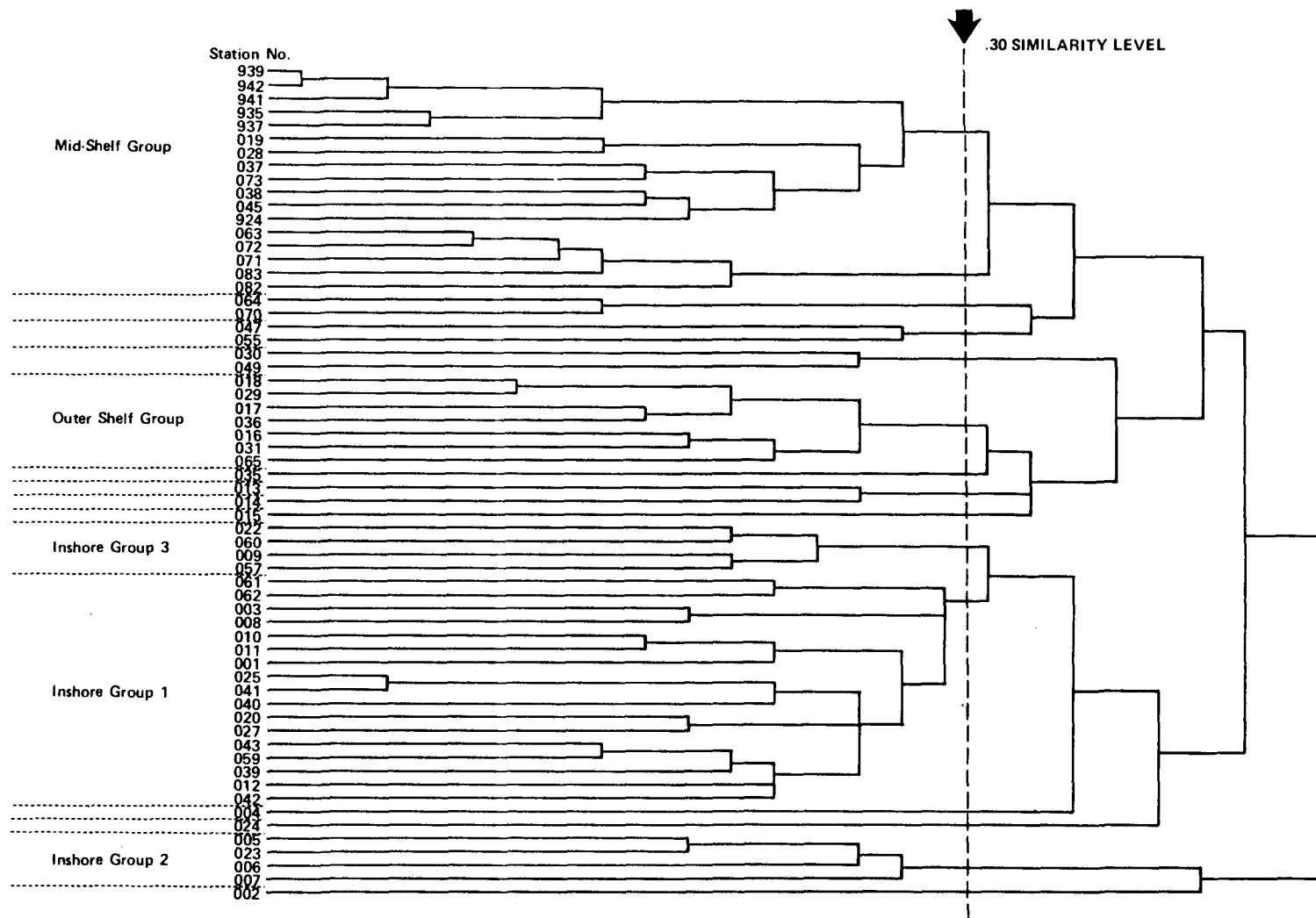


Figure 4. Dendrogram resulting from the clustering of stations using the Czekanowski distance measure and a flexible sorting strategy.

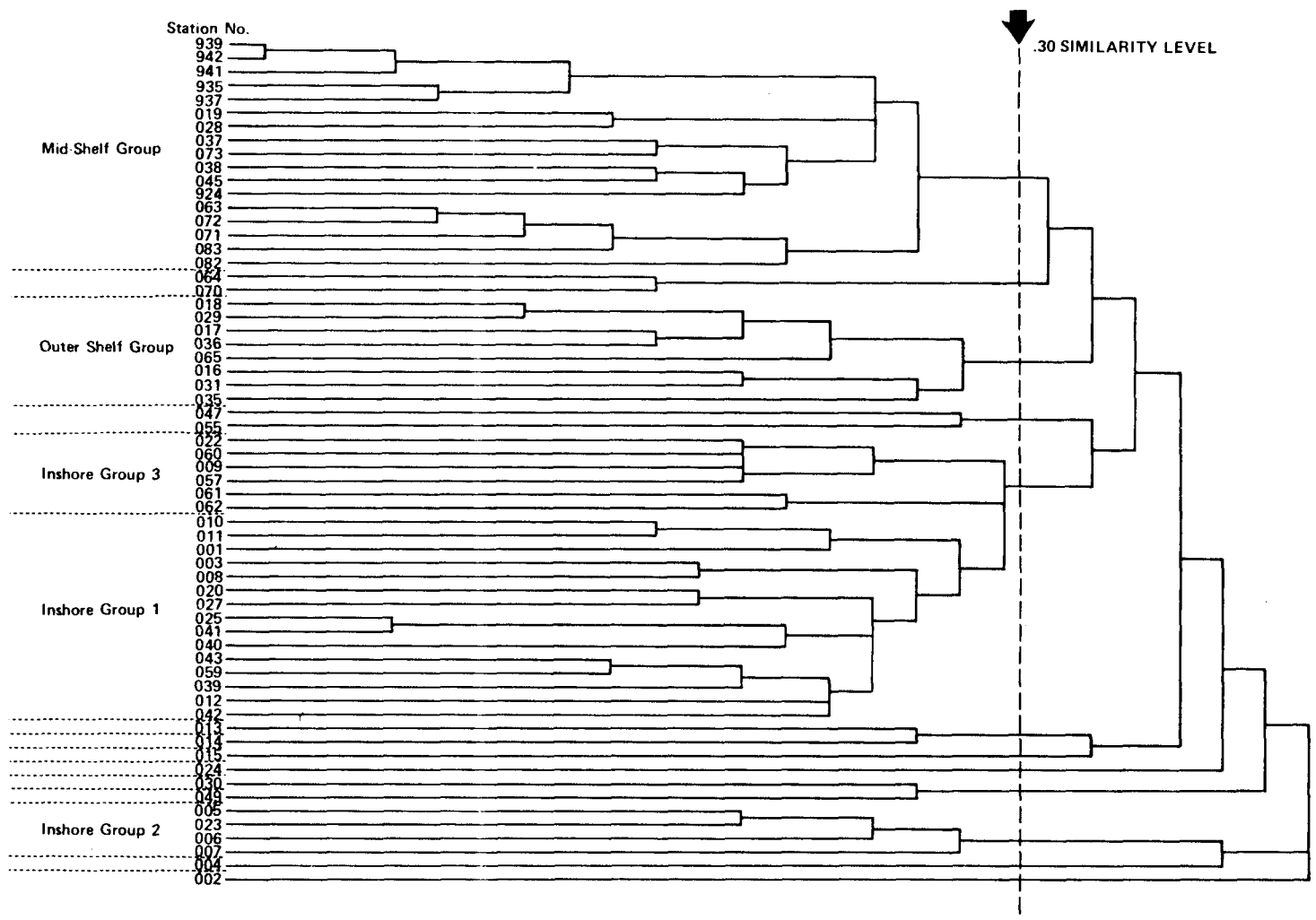


Figure 5. Dendrogram resulting from the clustering of stations using the Canberra-metric distance measure and a group-average sorting strategy.

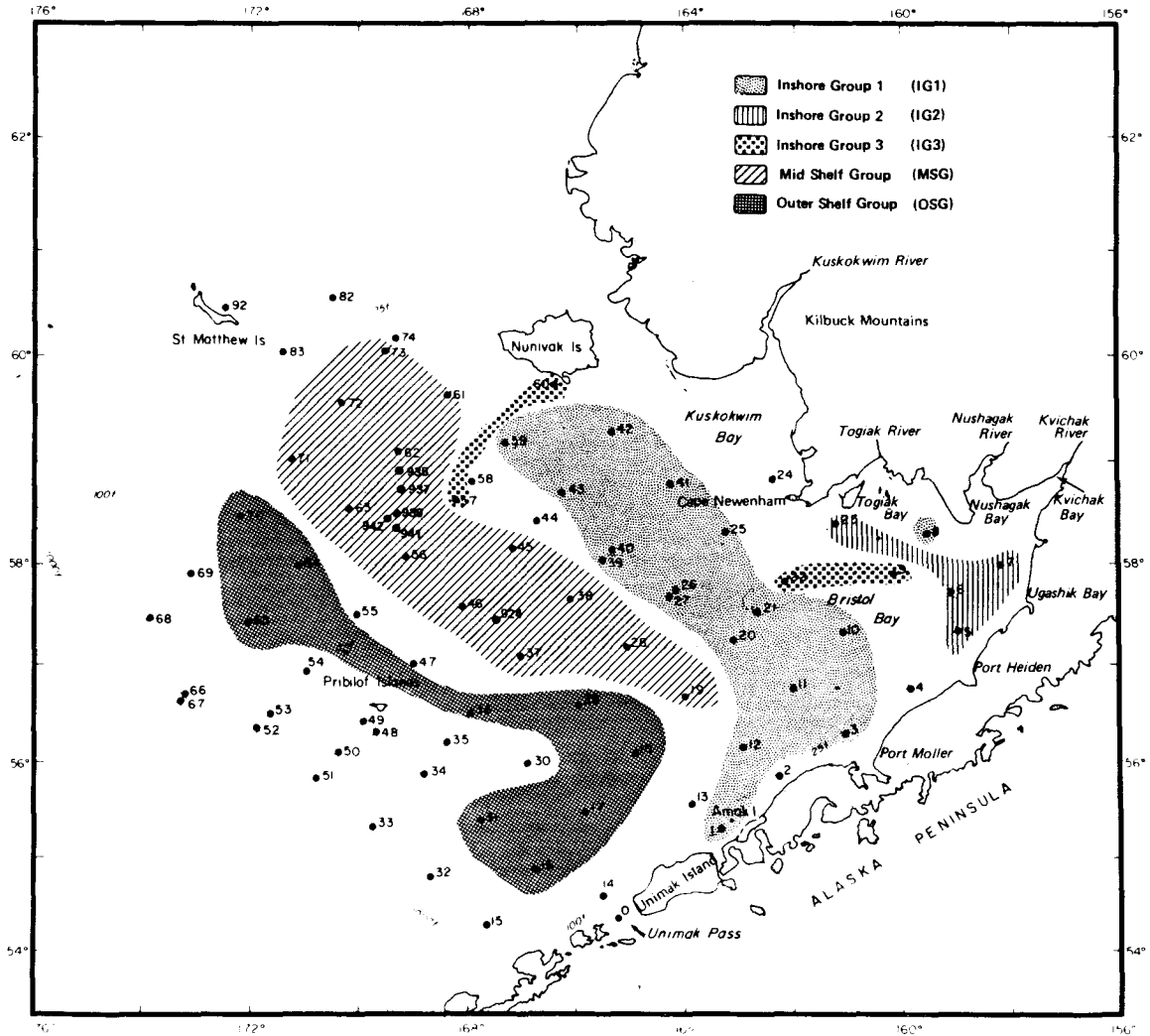


Figure 6. Station groups indicated by the results of a cluster analysis based on the Czekanowski dissimilarity measure and using a group average sorting strategy.

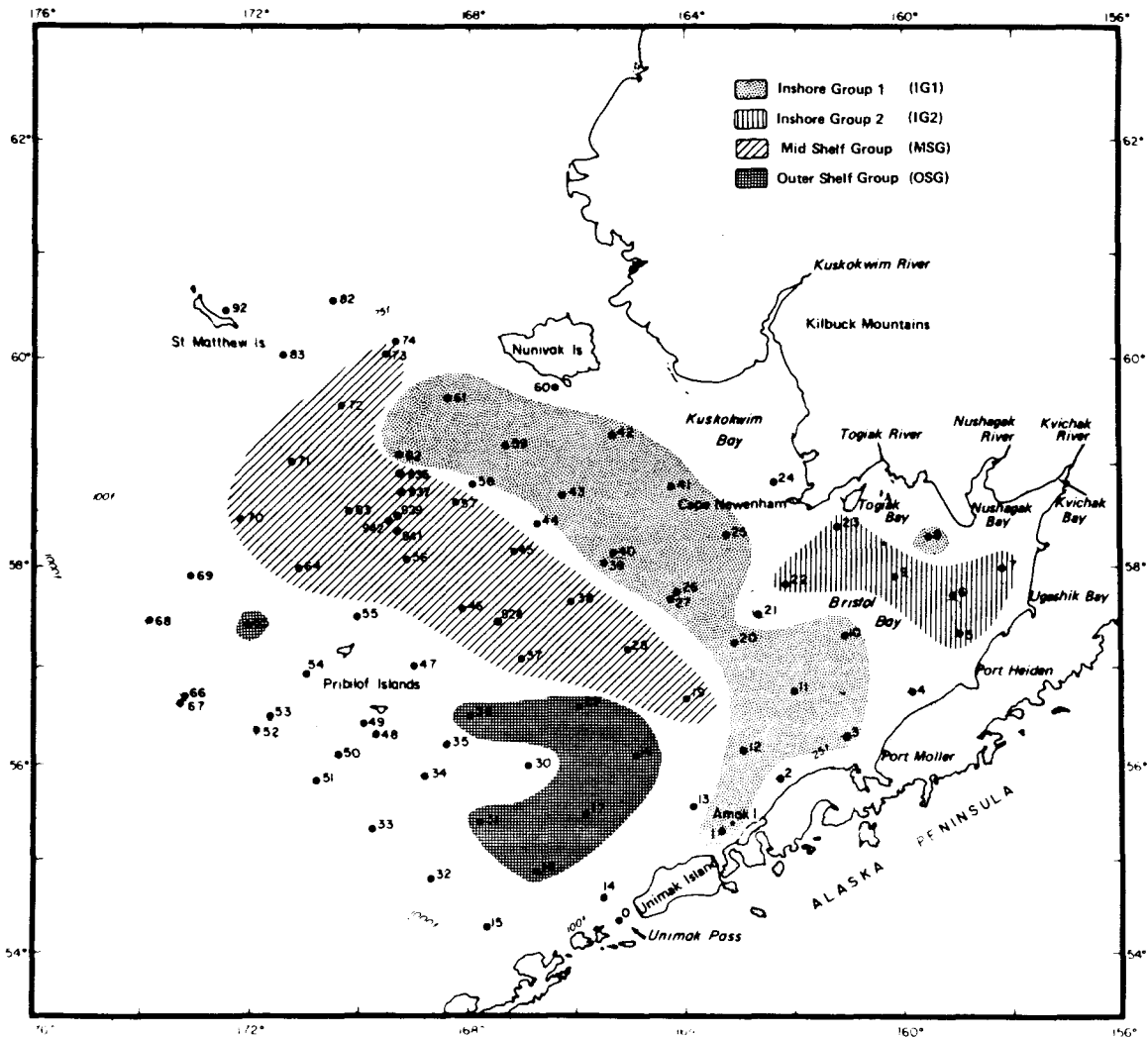


Figure 7. Station groups indicated by the results of a cluster analysis based on the Czekanowski dissimilarity measure and using a flexible-sorting strategy ($\beta = -0.05$).

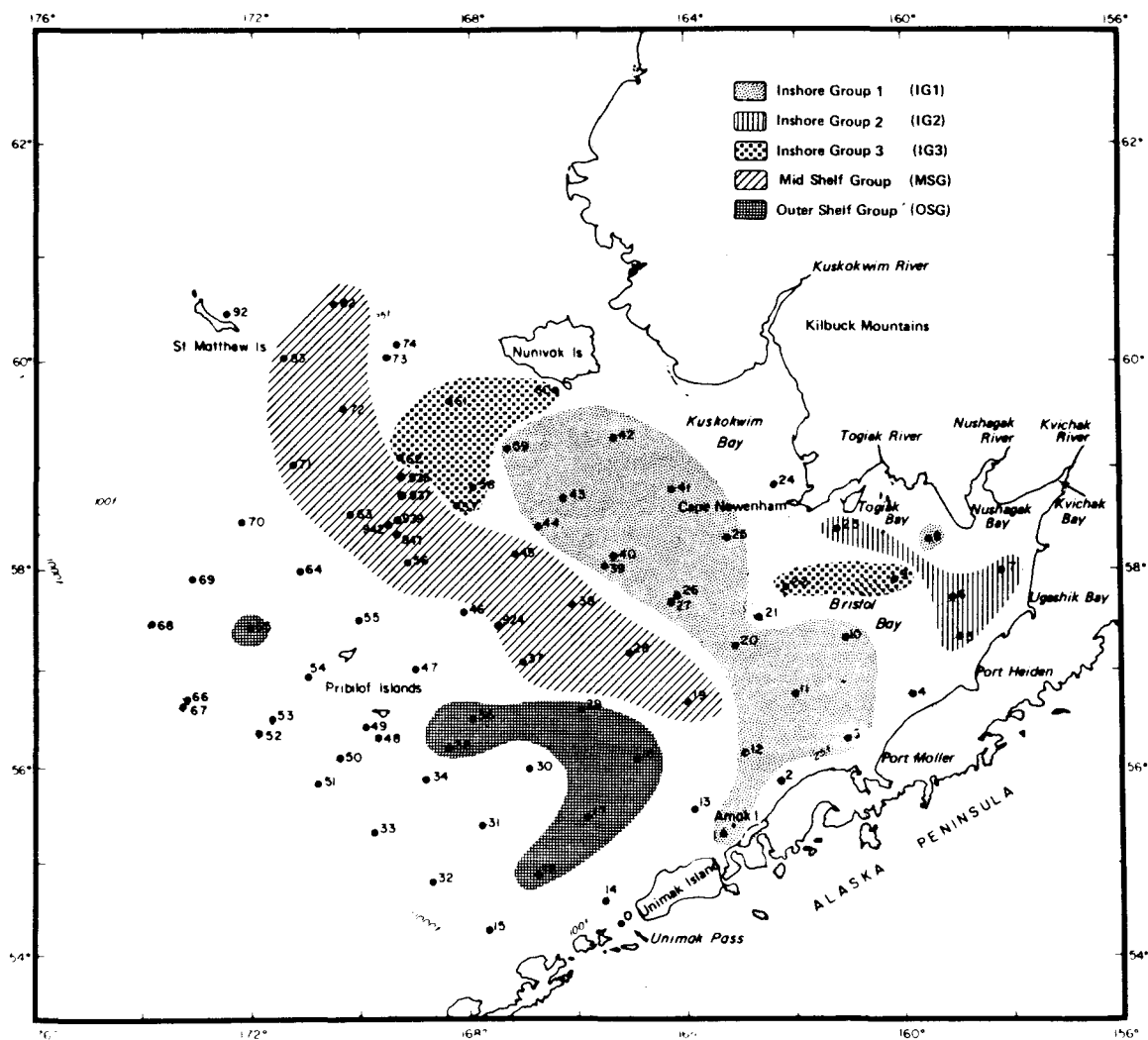


Figure 8. Station groups indicated by a cluster analysis based on the Canberra-metric distance measure and using a group-average sorting strategy.

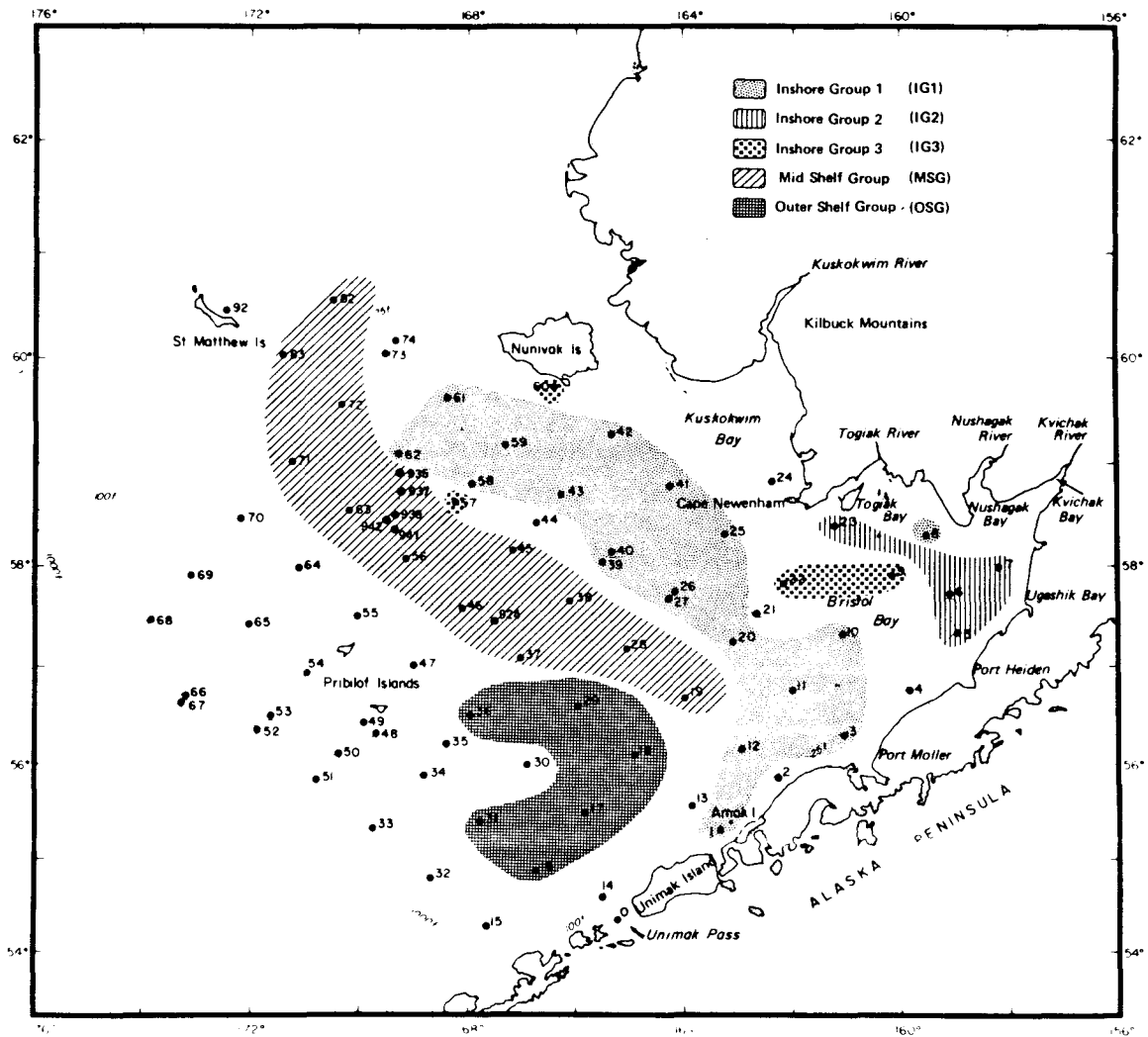


Figure 9. Station groups indicated by a cluster analysis based on the Canberra-metric distance measure and using a flexible sorting strategy ($\beta = -0.05$).

Table 3. Bering Sea infaunal study: station groups identified by cluster analysis at .30 similarity level.

Stations	Group	Clustering Strategy
1,3,8,10,11,12,20,25,27, 39,40,41,42,43,59	IG1	Czekanowski--group average
As above with 61 and 62		Czekanowski--flexible ($\beta = -0.05$)
As above with 61 and 62		Canberra metric--flexible ($\beta = -0.05$)
As above without 61 and 62		Canberra metric--group average
5,6,7,23	IG2	Czekanowski--group average
5,6,7,9,22,23,60		Czekanowski--flexible ($\beta = -0.05$)
5,6,7,23		Canberra metric--flexible ($\beta = -0.05$)
5,6,7,23		Canberra metric--group average
9,13,22,57,60	IG3	Czekanowski--group average
nonexistent--merges with IG2		Czekanowski--flexible ($\beta = -0.05$)
9,22,57,60		Canberra metric--flexible ($\beta = -0.05$)
9,22,57,60,61,62		Canberra metric--group average
19,28,37,38,45,63,71,72,73, 924,935,937,939,941	MSG	Czekanowski--group average
As above with 64 and 70		Czekanowski--flexible ($\beta = -0.05$)
As above with 82 and 83		Canberra metric--flexible ($\beta = -0.05$)
As above with 82 and 83		Canberra metric--group average

Table 3. continued

Stations	Group	Clustering strategy
16,17,18,29,31,36,64,65,70	OSG	Czekanowski--group average
16,17,18,29,31,36,65		Czekanowski--flexible ($\beta = -0.05$)
16,17,18,29,31,36,65		Canberra metric--flexible ($\beta = -0.05$)
16,17,18,29,31,35,36,65		Canberra metric--group average
2,4,15,19,24,35; 30,49; 47,55; 82,83	Singles and small groups	Czekanowski--group average
2,4,15,24;47,55;82,83		Czekanowski--flexible ($\beta = -0.05$)
2,4,24;30,49;64,70;47,55		Canberra metric--flexible ($\beta = -0.05$)
2,4,15,24;30,49;13,14,47,55		Canberra metric--group average

of most clusters, while generally verified by several procedures, is inherently variable. The differences between the interpretations is at least as interesting as the similarities, and stem from the basic options (i.e., similarity measure and sorting strategy) discussed in the preceding section. This topic will be dealt with after the results have been described.

The core station groups may be characterized as follows (see Figures 6 through 9):

IG1 -- (Inshore Group 1) This large group is comprised of stations which lie, for the most part, under waters of less than 50 m depth, with several stations (10, 11, 12, and 20) lying in slightly deeper water (maximum is 83 m). Most members lie at least 60 km from land, with stations 1, 3, and 8 anomalous in that they lie just off (~20 km) the Alaska Peninsula (stations 1 and 3) or the Bristol Bay coast (station 8).

IG2 -- (Inshore Group 2) This group is a consistent four station group found along the coast in Bristol Bay. Under the flexible strategy using Czekanowski's coefficient, it merges with IG3; otherwise it stands alone.

- IG3 -- (Inshore Group 3) This small group (stations 9, 22, 60, and 57) includes station 13 under the group average Czekanowski similarity classification and station 61 and 62 under the group-average Canberra metric distance scheme. The only geographical continuity apparent in this cluster is that all stations are relatively close to the mainland but not, with the exception of station 60 (lying just off Nunivak Island), directly offshore.
- MSG -- (Mid-Shelf Group) This is a large group occupying a band roughly parallel to the 50 m bottom depth contour and extending seaward to stations in locations of about 80 m water depth. The southern end of the group, station 19, is displaced slightly to the west and lies in water of 77 m depth. The northern boundary of the group is variable; it includes the northernmost stations (82 and 83) under the Canberra metric classification, but usually terminates with the station string 71, 72, and 73.
- OSG -- (Outer Shelf Group) This mid- to outer shelf group does not allow a consistent marked geographical pattern. All group members are outer

shelf to shelf edge in position and, with the exception of station 65, are found in the southwestern corner of the study area. Station 35 occasionally links with this cluster. Station 30, adjacent to OSG, invariably remains separate.

Outliers--These are stations or pairs of stations that form no strong associations with the core groups.

Under different analyses some of these stations may link with some of the groups outlined above, however stations 2, 4, 15, and 24 are always single. The relations of individual outlying stations and pairs of outlying stations to other outliers and to the main station groups will be dealt with in a later section.

ORDINATION METHODS--THE CLASSIFICATION OF STATIONS

As mentioned earlier (see Methods, page 22) the models underlying the development of the various ordination techniques need be understood to facilitate the interpretation of the results of these procedures. It should be emphasized that both principal coordinates and principal components analysis are sensitive to the presence of extreme values in the input data. In principal

coordinates analysis, reduction of the effect of these extreme values may be accomplished by the use of a distance measure (e.g. the Canberra metric measure) that mitigates the effect of dominance. In principal coordinates analysis a similar function is performed by initially standardizing the variates (i.e., by finding the principal components of the correlation matrix rather than the covariance matrix).

The foregoing considerations carry several implications concerning the relation of ordination results to the outcome of a cluster analysis. The principal coordinates analysis based on a specific similarity or distance measure will obviously parallel the results of a cluster analysis based on the same measure. The outcome of a principal components analysis based on the correlation matrix will be similar to the results of both the cluster analysis and the principal coordinates analysis that are derived from a distance matrix for which the effect of dominance has been reduced.

The ordination methods used resulted in plots of station projections on principal axes; they are shown in Figures 10 through 21. Several plots are presented for each ordination procedure, the difference between plots of any given ordination output being that individual stations or groups of stations have been removed to clarify specific relationships. Also, the station group memberships suggested

by cluster analysis results have been indicated to give some idea of the agreement between these techniques. An interpretation of these figures follows.

PRINCIPAL COORDINATES ANALYSIS

Analysis Based on the Czekanowski Coefficient

A plot of the projections of all stations, produced by use of this coefficient, is shown in Figure 10. Immediately apparent is the good separation between MSG, IG1, IG2, and IG3 and the relatively poor resolution of OSG. The relationship of outliers to the main groups is more easily seen in Figure 11, which has had the stations of IG2, IG3, and OSG removed. It is apparent that stations 61 and 62 are among the stations of IG1, and 82 and 83 with MSG. It also seems that station 8 might be displaced towards IG3. Figure 12 shows the close association between IG1 and IG3. The proportions of variance accounted for by the first three axes are 7.8%, 6.1%, and 3.2% for components one, two, and three, respectively.

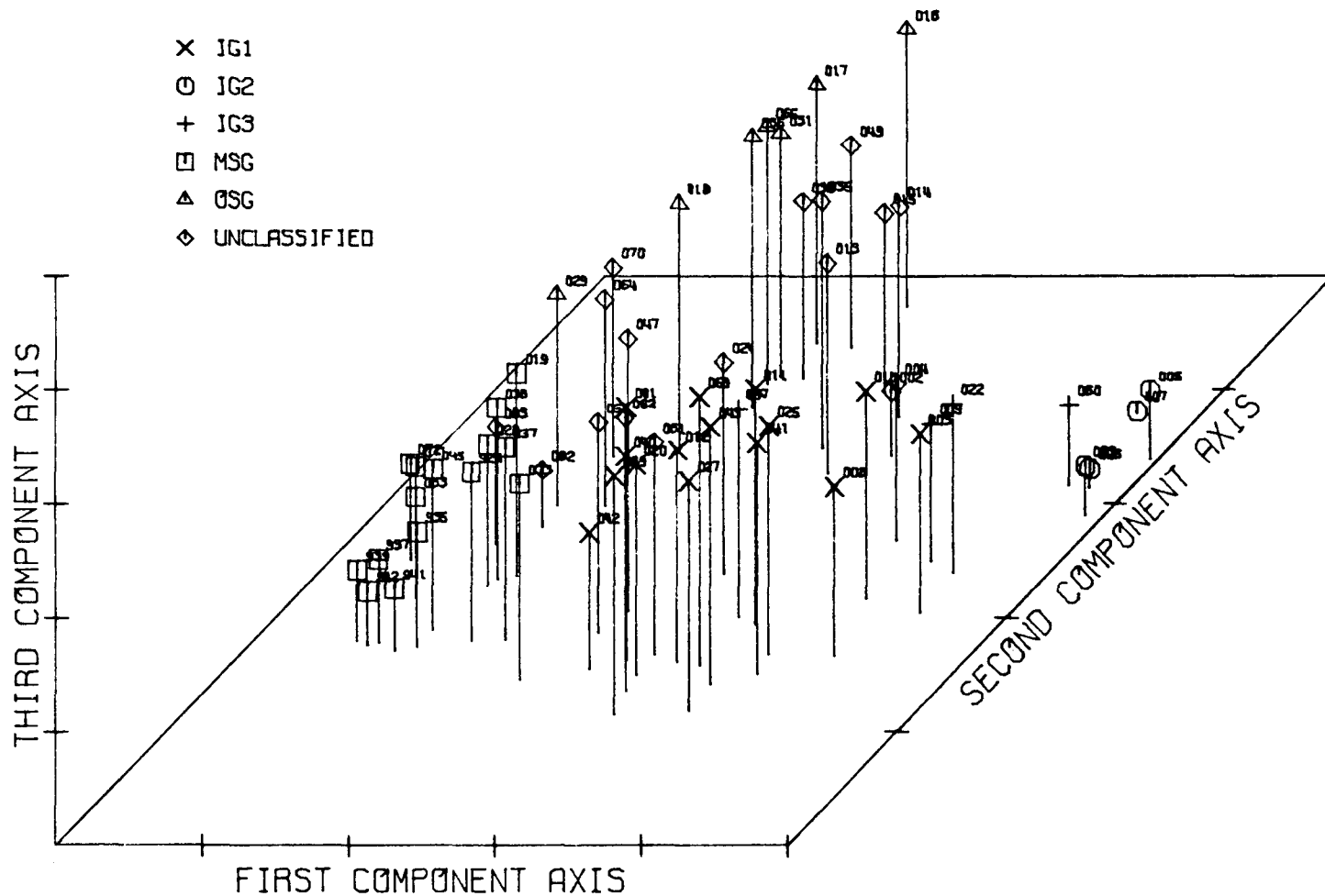


Figure 10. Projections of all Bering Sea infaunal stations onto the first three axes derived from a principal coordinates analysis based on Czekanowski dissimilarity measure.

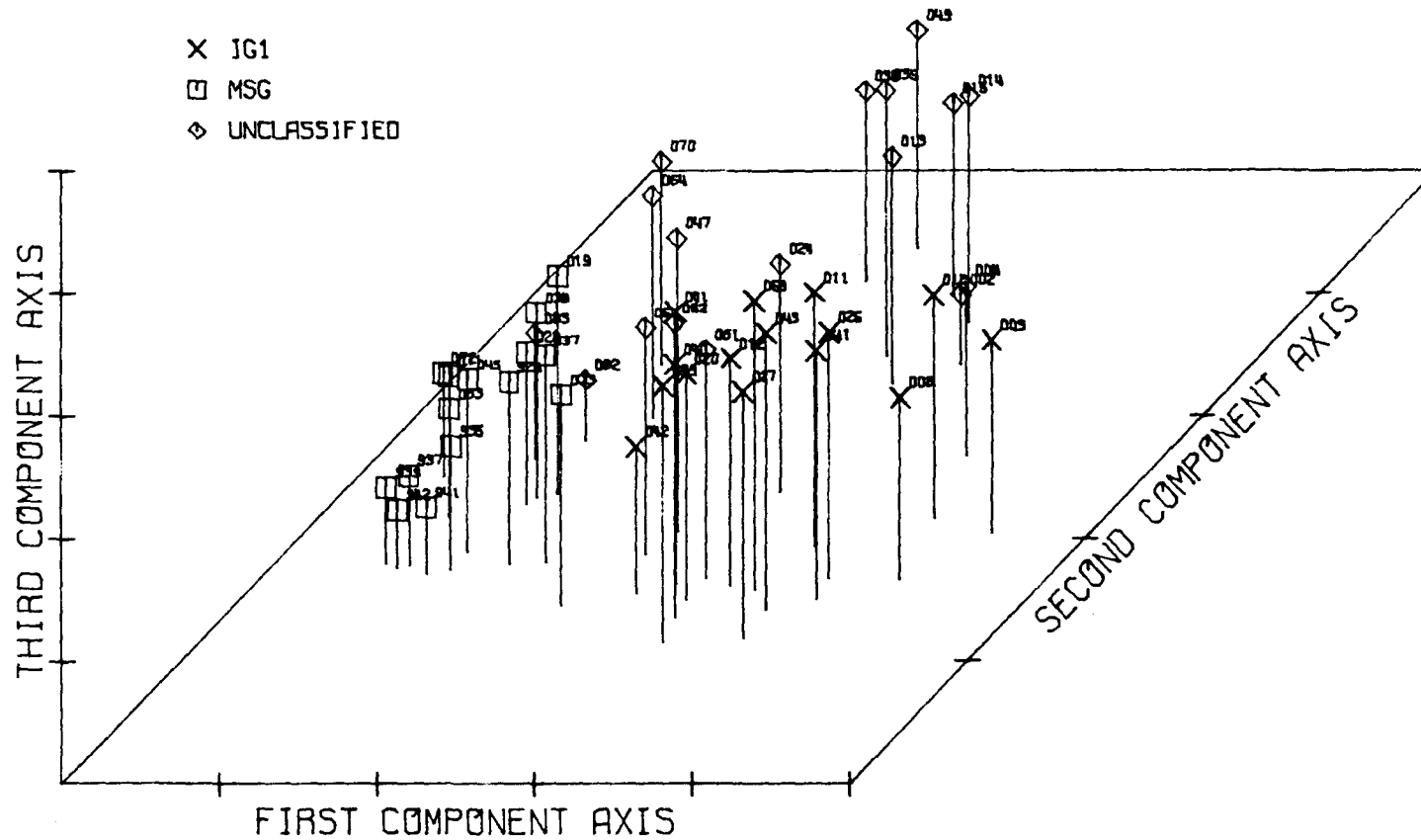


Figure 11. Projections of stations onto principal axes (principal coordinates analysis, Czekanowski distance) as in Figure 10, but with groups IG2, IG3, and OSG omitted.

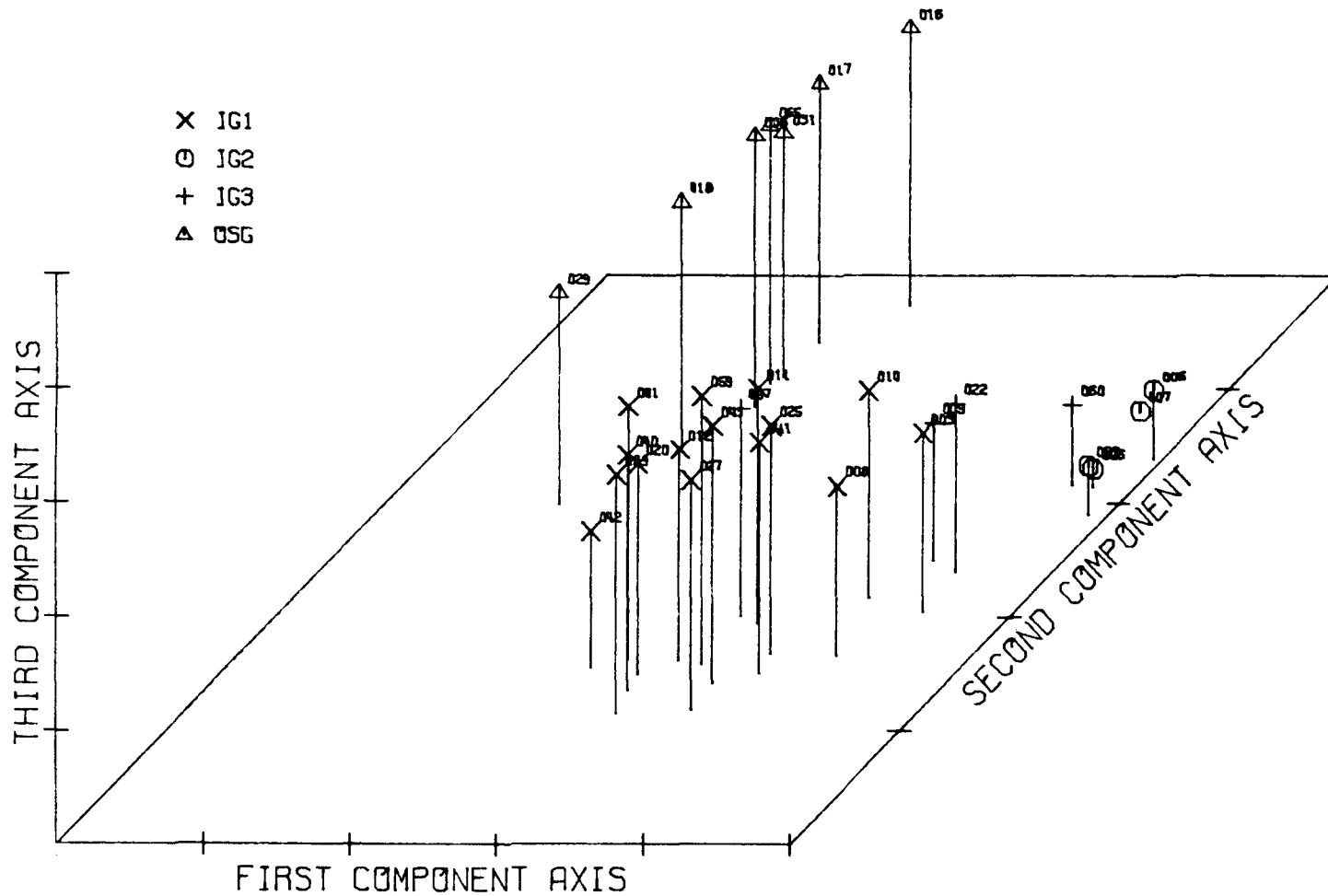


Figure 12. Projections of stations onto principal axes (principal coordinates analysis, Czekanowski distance) as in Figure 10, but with MSG and unclassified stations omitted.

Analysis Based on the Canberra Metric Measure

Figure 13 (all stations included) shows an excellent discrimination between MSG and IG1. This difference is most evident on the first principal axis and probably results in the corresponding scatter in the remaining groups on that axis. The outlier relationships to IG1 and MSG indicated by the Czekanowski-based analysis are little changed by the Canberra-metric-based analysis, as illustrated by Figure 14 (IG2, IG3, and OSG removed). Stations 82 and 83 are closely tied to MSG although their relative positions are reversed when compared to those derived from analysis based on the Czekanowski coefficient. Station 61 falls out near IG1, although stations 57 and 4 are also found in the general area. Figure 15 illustrates the sort of confusion that outliers bring into this type of study. It is very difficult to draw station group boundaries between OSG and IG3 when many unclassified stations appear to be transitional between the two. The proportions of variance removed by the first three components was 6.8%, 5.0%, and 3.8%.

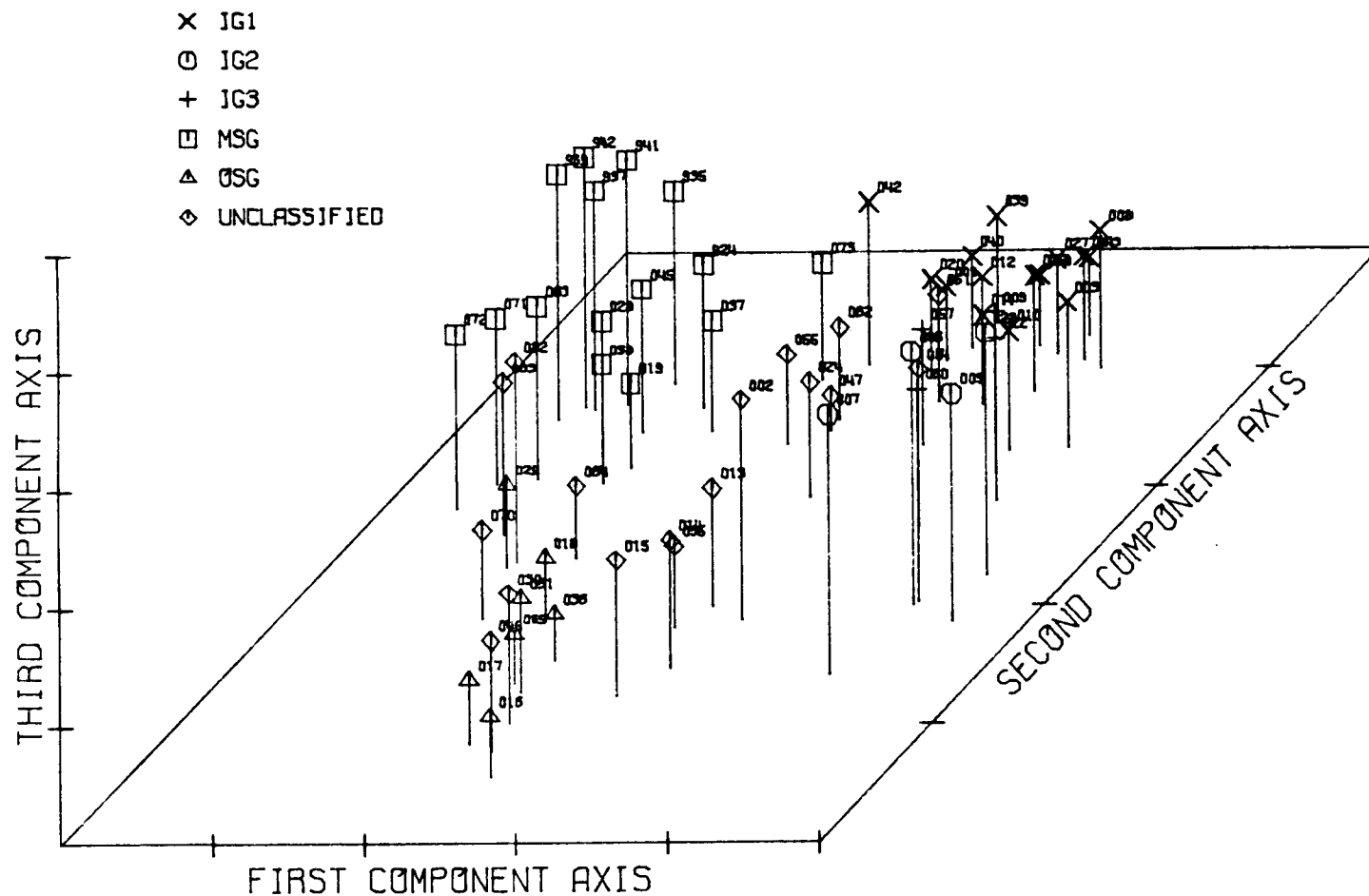


Figure 13. Projections of all Bering Sea infaunal stations onto principal axes defined by a principal coordinates analysis based on the Canberra-metric dissimilarity measure.

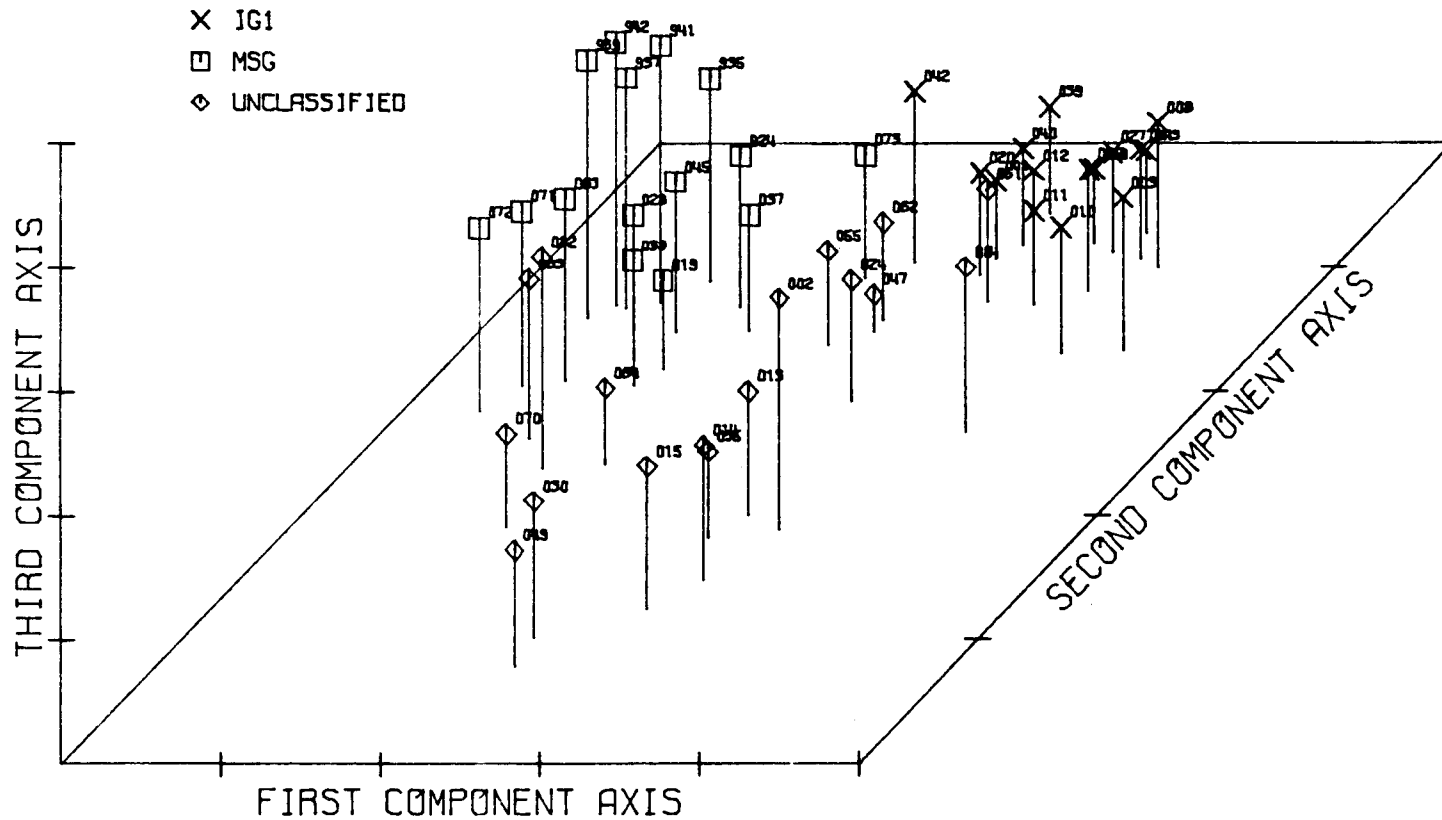


Figure 14. Projections of stations onto principal axes (principal coordinate analysis, Canberra-metric distance) as in Figure 13, but with groups IG2, IG3 and OSG removed.

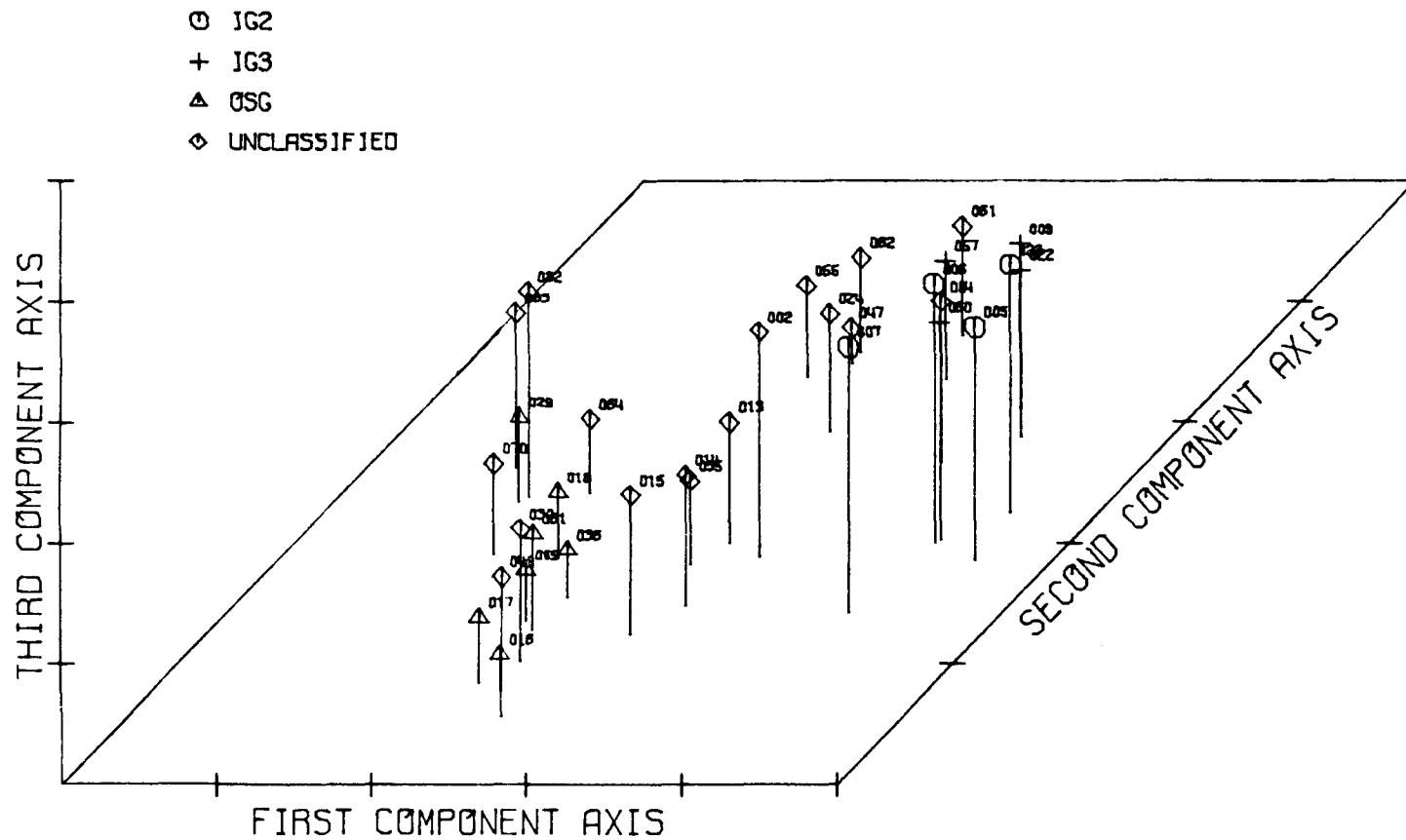


Figure 15. Projections of stations onto principal axes (principal coordinates analysis, Canberra metric distance) as in Figure 13, but with groups IG1 and MSG removed.

PRINCIPAL COMPONENTS ANALYSIS

Analysis of the Covariance Matrix

Figure 16 shows the station projections (i.e., scores on the principal axes) derived from the principal components analysis of the covariance matrix. Station groups MSG and IG1 are rather poorly separated while IG2 and IG3 are better resolved. Figure 17 (IG2, IG3, and OSG removed) shows the difficulties in the classification of MSG and IG1. In particular, stations 37, 38, 73, and 924 seem to be almost as close to IG1 as they are to their normal group, MSG. Station 83 is closely allied to MSG while the affiliation of station 82 remains ambiguous. The positions of 61 and 62 indicate their typical affinity with IG1. Figure 18 shows a diffuse OSG with one member (station 29) being markedly displaced towards MSG (as it was in the principal coordinates analysis using Czekanowski coefficient). IG3 is fairly well removed from IG1 and this time station 10 appears to be better classified as a member of IG1. Again, station 8 exists on the periphery of IG1. The proportions of variances removed by the first three components was 16.8%, 10.6%, and 7.2%.

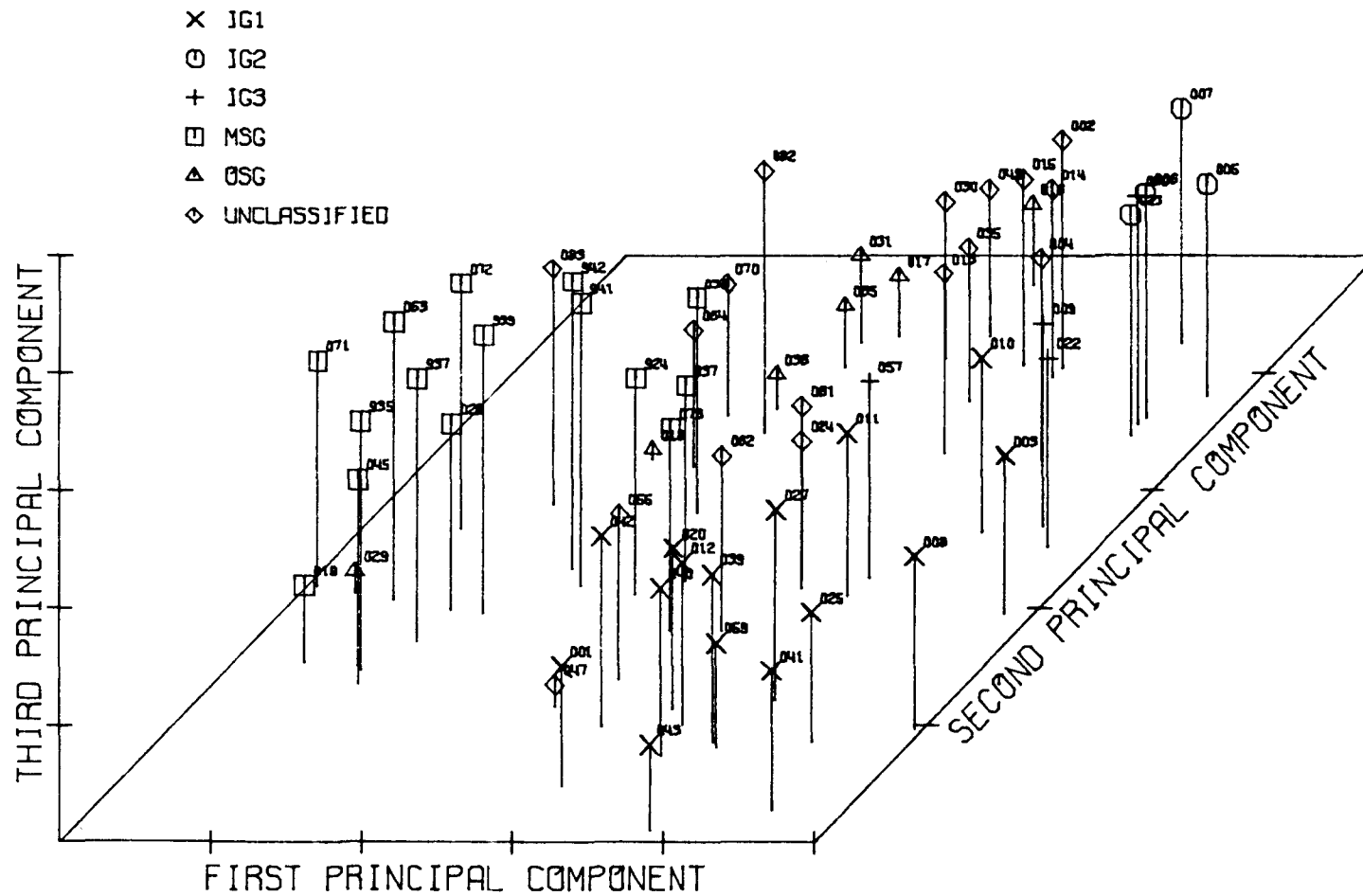


Figure 16. Projections of all Bering Sea infaunal stations onto the first three axes defined by a covariance-based principal components analysis.

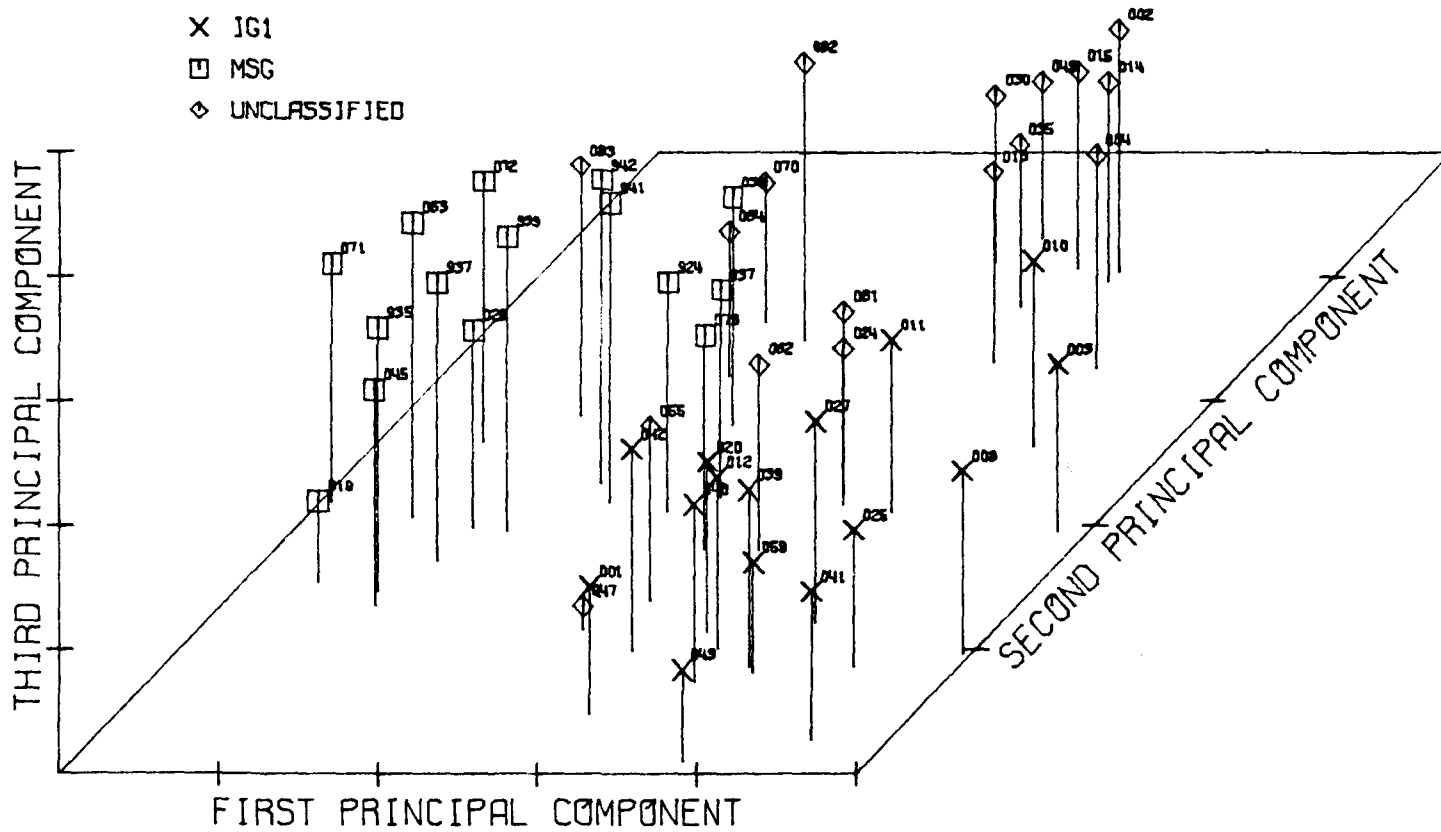


Figure 17. Projections of stations onto principal axes (principal components analysis, covariance matrix) as in Figure 16, but with groups IG2, IG3, and OSG removed.

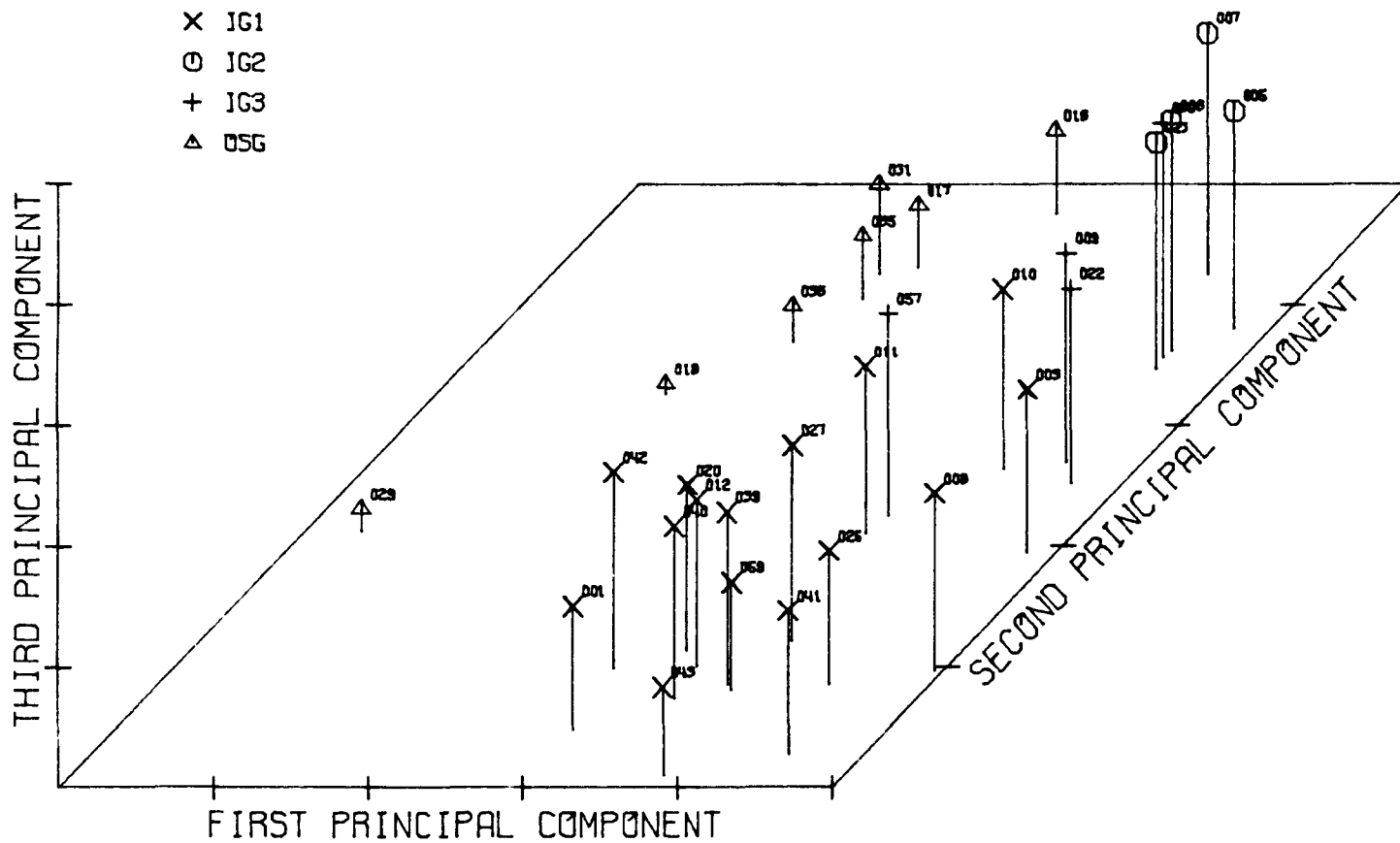


Figure 18. Projections of stations onto principal axes (principal components analysis, covariance matrix) as in Figure 16, but with MSG and unclassified stations removed.

Analysis of the Correlation Matrix

The projection of all stations onto principal axes derived from the correlation matrix is presented in Figure 19. It is surprising in that it is practically unipolar on the second axis, with only several members of OSG and several outliers being positioned near the lower end. Figure 20 (IGL and MSG removed) confirms the usual trend of stations 82 and 83 being positioned close to MSG and stations 62 and 63 near IGL. Another addition to MSG under this analysis is the pair of possible transition members, stations 64 and 70. From Figure 21 it appears that stations 3, 8, and 10 may again be as closely linked with IG3 as they are with IGL, although divisions between these groups are perhaps somewhat arbitrary in the first place. The proportions of variance accounted for by the first three components was 15.2%, 8.7%, and 6.9%.

INVERSE ANALYSIS--THE CLUSTERING OF SPECIES

The results of the clustering of variables to form species groups is shown in Table 4, which gives the composition of 56 species groups suggested by the analysis and the feeding type and mobility of the group members, if

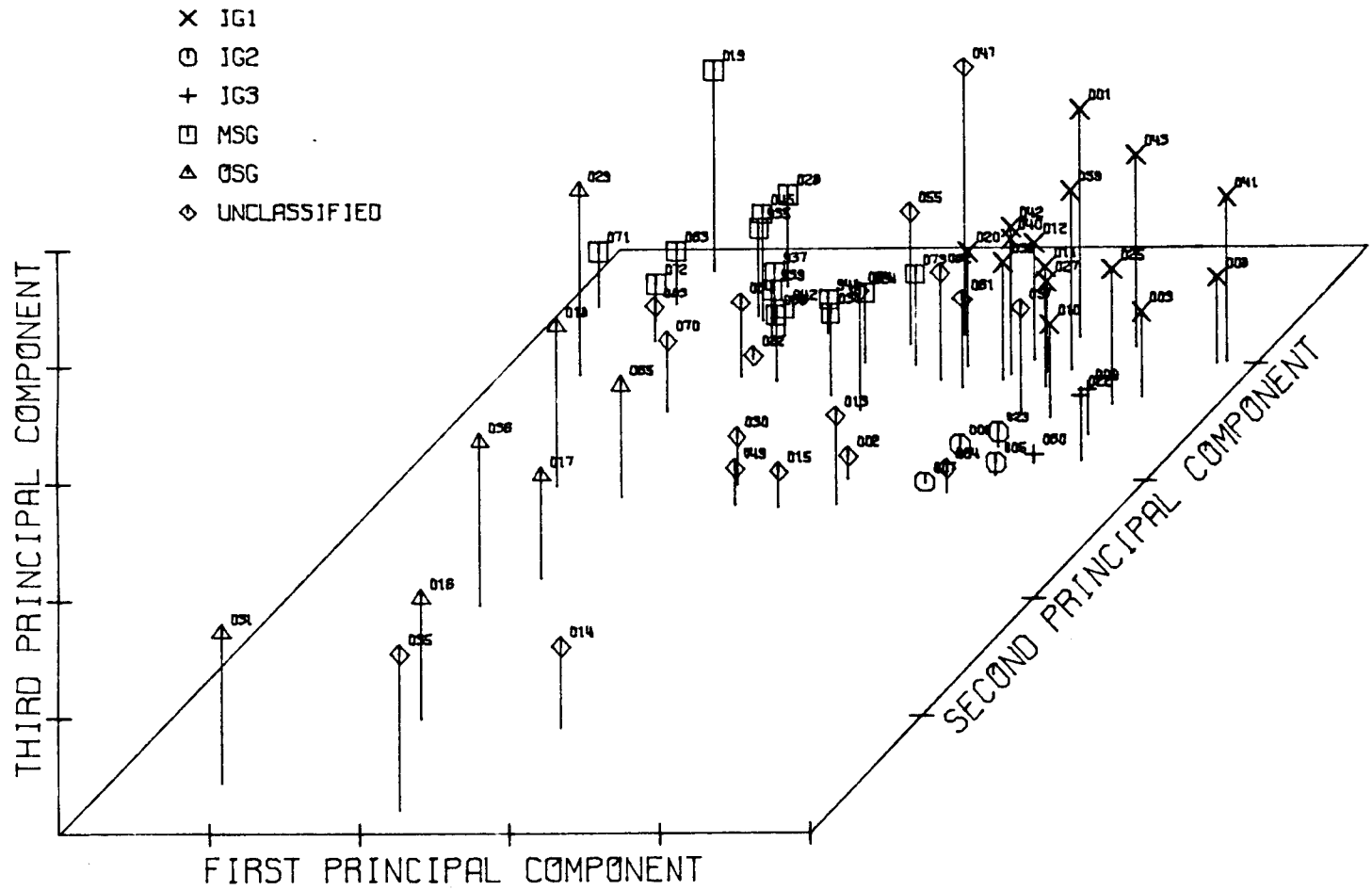


Figure 19. Projections of all Bering Sea infaunal stations onto the first three principal axes defined by a correlation-based principal components analysis.

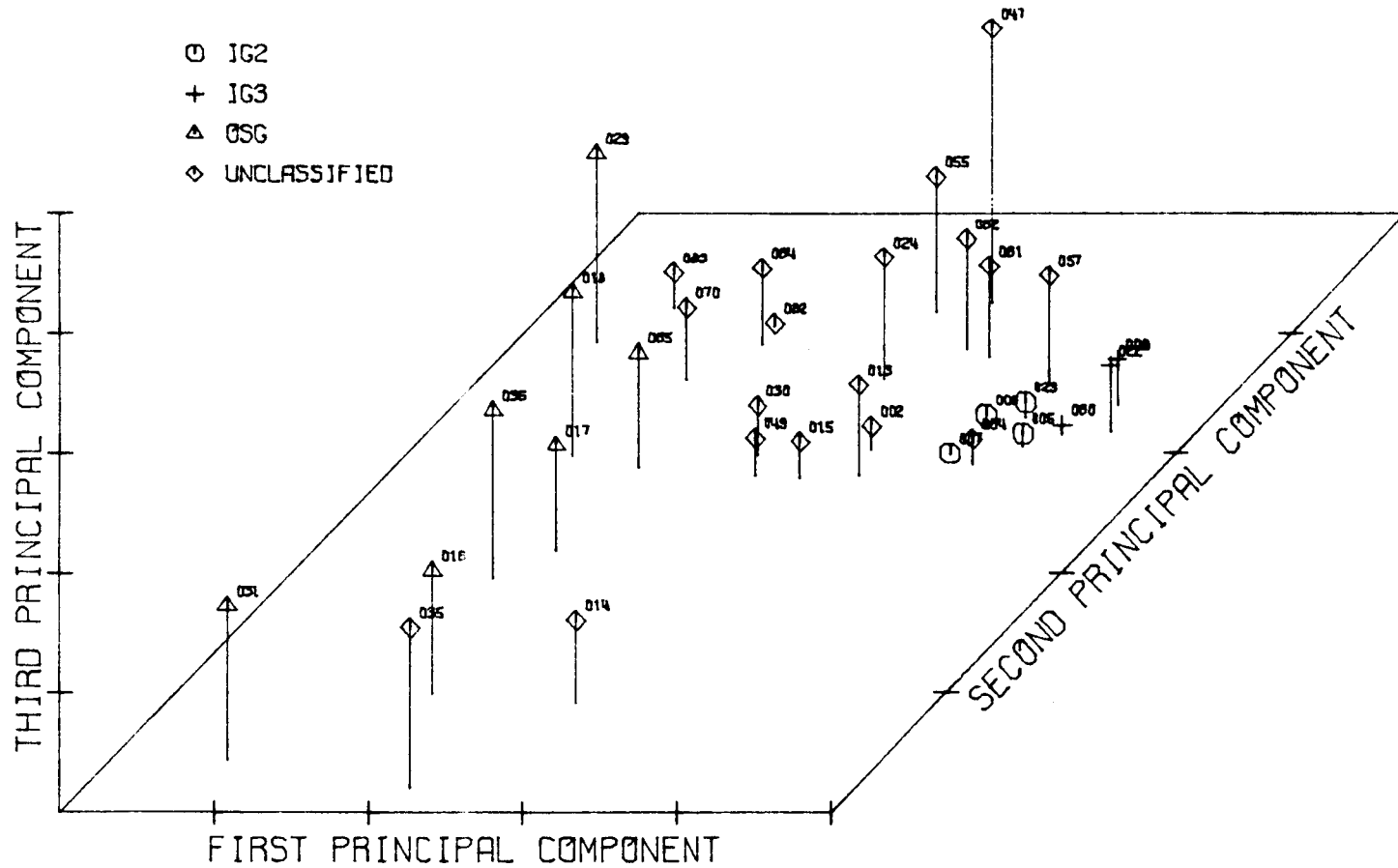


Figure 20. Projections of stations onto principal axes (principal components analysis, correlation matrix) as in Figure 19, but with groups IG1 and MSG removed.

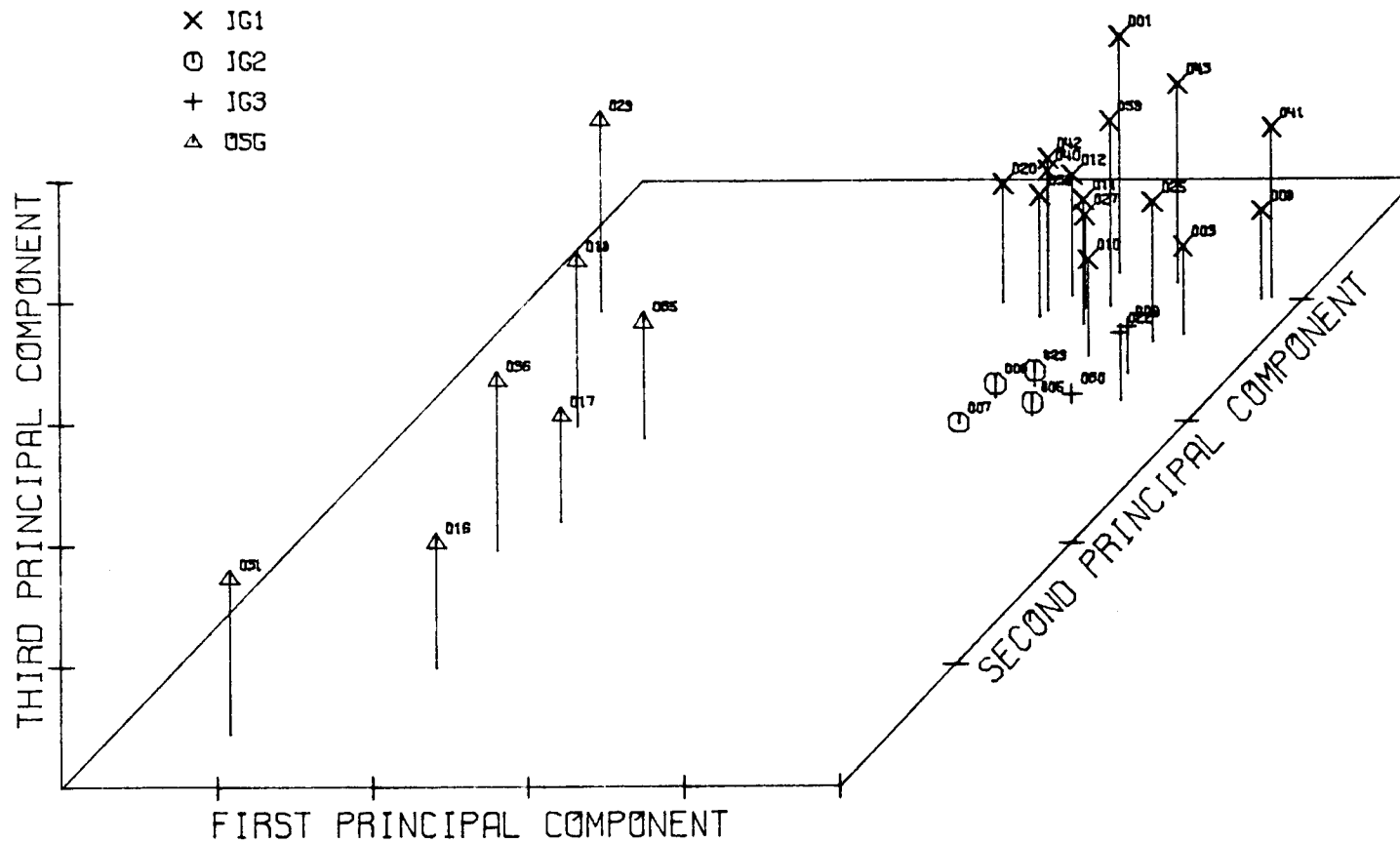


Figure 21. Projections of stations onto principal axes (principal components analysis, correlation matrix) as in Figure 19, but with unclassified stations and MSG removed.

Table 4. Species group membership as indicated by cluster analysis. Feeding type and mobility from Feder and Matheke (1978).

Group Number	Species Name	Feeding Type ¹	Mobility Type ²
1	<i>Eteone spitsbergensis</i>	-	S
	<i>Psolus phantapus</i>	DF	S
	<i>Onuphis geophiliformis</i>	S	DM
	<i>Eunice valens</i>	DF	M
2	<i>Lysippe labiata</i>	DF	S
	<i>Psephidia lordi</i>	SF/S	DM
3	<i>Nicomache personata</i>	DF	S
	<i>Astarte esquimalti</i>	SF	DM
	<i>Harmothoe imbricata</i>	S	M
4	<i>Travisia brevis</i>	DF	M
	<i>Paraphoxus obtusidens</i>	DF	M
	<i>Haploscoloplos panamensis</i>		
	<i>Protomedea grandimana</i>	DF	-
5	<i>Anaitides mucosa</i>	P/DF	M
	<i>Anonyx nugax</i>	S	M
6	<i>Chone cincta</i>	SF	DM
7	<i>Cyclocardia crassidens</i>	SF	S
8	<i>Glycera capitata</i>	P/DF	M
	<i>Aricidea suecica</i>	DF	M
	<i>Ampeliscida escherichti</i>	SF	S/DM
	<i>Ampeliscida furcigera</i>	SF	S/DM
	<i>Polydora socialis</i>	DF	DM
	<i>Phascolion strombi</i>	DF	S

¹Feeding types: P = predator, S = scavenger, DF = detrital feeder, SF = suspension feeder.

²Mobility types: M = motile, DM = discreetly motile, S = sessile.

Table 4. continued

Group Number	Species Name	Feeding Type	Mobility Type
8	<i>Laonice cirrata</i>	DF	DM
	<i>Urothoe denticulata</i>	SF	S/DM
	<i>Odontogena borealis</i>	SF	-
	<i>Ninoe gemmea</i>	DF	M
9	<i>Terebratalia crossei</i>	SF	S
	<i>Modiolus modiolus</i>		
10	<i>Peisidice aspera</i>	S	M
	<i>Notoproctus pacifica</i>	DF	S
	<i>Ampeliscida birulai</i>	SF	S
	<i>Golfingia margaritacea</i>	DF	S
	<i>Pista cristata</i>	DF	S
11	<i>Spiophanes kroyeri</i>	DF	DM
	<i>Laphanis boeckii</i>		DF
	<i>Thysanoessa baschii</i>	DF	M
12	<i>Diastylis</i> Cf. <i>D. tetradon</i>	S	M
13	<i>Orchomene nugax</i>	S	M
14	<i>Nephtys rickettsi</i>	P	M
	<i>Cucumaria calcigera</i>	S	S
15	<i>Maldane glebiflex</i>	DF	S
16	<i>Aricidea uschakovi</i>	DF	M
	<i>Lyonsia norvegica</i>	SF	S
17	<i>Margarites olivaceous</i>	DF	M
18	<i>Chone gracilis</i>	SF	DM
	<i>Admete couthouyi</i>	SF	M
19	<i>Macoma lana</i>	DF	S
	<i>Asterias ameurensis</i>	P/S	M
	<i>Cyclocardia ventricosa</i>	SF	S
20	<i>Cistenides hyperborea</i>	DF	M
	<i>Proclea emmi</i>	DF	M

Table 4. continued

Group Number	Species Name	Feeding Type	Mobility Type
21	<i>Serripes groenlandicus</i>	SF	S
22	<i>Cossura longicirrata</i>	-	-
23	<i>Gattyana treadwelli</i>	S	M
	<i>Polinices pallida</i>	P	M
24	<i>Polynoe canadensis</i>	S	M
	<i>Yoldia hyperborea</i>	SD	M
	<i>Artacama proboscidea</i>	DF	DM
25	<i>Sternaspis scutata</i>	DF	M
	<i>Eudorella pacifica</i>	DF/S	M
	<i>Brada villosa</i>	DF	DM
	<i>Eteone longa</i>	P	M
	<i>Magelona pacifica</i>	DF	DM
	<i>Spio filicornis</i>	DF	DM
	<i>Phloe minuta</i>	S	M
	<i>Tharyx</i> sp.	DF	S/DM
	<i>Praxillella praetermissa</i>	DF	S
	<i>Capitella capitata</i>	DF	M
	<i>Harpinia gurjanovae</i>	SF	M
	<i>Nephtys ciliata</i>	DF/P	M
	<i>Macoma moesta alaskana</i>	DF	S
	<i>Axinopsida serricata</i>	SF	S
<i>Praxillella gracilis</i>	DF	-	
26	<i>Nephtys punctata</i>	P	M
	<i>Eudorella emarginata</i>	DF/S	M
	<i>Yoldia amygdalaea</i>	SF	M
	<i>Bathymedon nanseni</i>	DF/S	M
	<i>Heteromastus filiformis</i>	DF	M
27	<i>Aglaophamus rubilla anops</i>	DF/P	M
	<i>Melita formosa</i>	DF/S	M
	<i>Priapulid caudatus</i>	P	M
	<i>Prionospio malmgreni</i>	DF	DM
	<i>Melita dentata</i>	DF/S	M
	<i>Ammotrypane aulogaster</i>	DF	M
<i>Paraonis gracilis</i>	DF	M	

Table 4. continued

Group Number	Species Name	Feeding Type	Mobility Type
28	<i>Eudorellopsis integra</i>	DF/S	M
	<i>Pontoporeia femorata</i>	SF	S/DM
	<i>Scalibregma inflatum</i>	DF	M
	<i>Byblis gaimardi</i>	SF	S
	<i>Haploscoloplos elongatus</i>	DF	M
	<i>Chaetozone setosa</i>	DF	DM
	<i>Macoma calcarea</i>	DF	S
	<i>Retusa obtusa</i>	P	M
	<i>Nucula tenuis</i>	S	M
29	<i>Yoldia secunda</i>	DF	M
	<i>Dacrydium pacificum</i>	SF	S
30	<i>Drilonereis falcata minor</i>	DF	M
	<i>Paraphoxus simplex</i>	SF	M
	<i>Ophiura sarsi</i>	DF/P	M
	<i>Lumbrinereis zonata</i>	DF	M
	<i>Harpinia tarasovi</i>	SF	M
	<i>Terebellides stroemi</i>	DF	S
	<i>Lumbrinereis similabris</i>	DF	M
	<i>Clinocardium ciliatum</i>	SF	S
	<i>Nuculana permula</i>	DF	M
	<i>Diamphiodia craterodermeta</i>	-	DF
	<i>Thyasira flexuosa</i>	-	SF
	<i>Maldana sarsi</i>	DF	M
	<i>Cistenides granulata</i>	DF	M
	<i>Solariella varicosa</i>	S/P	M
31	<i>Photis spasskii</i>	DF	M
	<i>Photis ninogradovi</i>	DF	M
	<i>Protomedea fasciatoides</i>	DF	M
32	<i>Ampharete acutifrons</i>	DF	S
	<i>Yoldia scissurata</i>	DF	M
	<i>Leucon nasica</i>	DF/S	M
33	<i>Diastylis bidentala</i>	DF	S
34	<i>Polydora concharum</i>	DF/S	M
	<i>Owenia fusiformis</i>	SF/DF	-

Table 4. continued

Group Number	Species Name	Feeding Type	Mobility Type
35	<i>Chone infundibuliformis</i>	SF/DF	M
	<i>Chone dumeri</i>	SF	DM
36	<i>Anaitides groenlandica</i>	P/DF	M
	<i>Magelona japonica</i>	DF	DM
	<i>Euchone analis</i>	SF	DM
37	<i>Anaitides maculata</i>	DF	M
	<i>Glycinda armigera</i>	P	M
	<i>Mysella aleutica</i>	SF/DF	-
	<i>Paraphoxus milleri</i>	SF	M
38	<i>Cylichna oculata</i>	DF	M
	<i>Protomedea chaelata</i>	DF	M
	<i>Mysella tumida</i>	SF/DF	-
39	<i>Tachyrhynchus erosus</i>	S/P	M
	<i>Westwoodilla coecula</i>	DF/S	M
	<i>Rhodine loveni</i>	DF	S
	<i>Nephtys caeca</i>	P	M
	<i>Diastylis alaskensis</i>	DF/S	M
	<i>Orchomene lapidula</i>	S	M
40	<i>Cyclocardia crebricostata</i>	SF	S
	<i>Polinices nanus</i>	P	M
	<i>Spiophanes bombyx</i>	DF	DM
	<i>Haustorius eous</i>	SF	S/DM
	<i>Ophelia limacina</i>	DF	M
	<i>Echinarachnius parma</i>	DF	M
	<i>Tellina lutea alternidentata</i>	DF	M
	<i>Travisia forbesii</i>	DF	DM
	<i>Glycinde picta</i>	P	M
	<i>Scoloplos armigera</i>	DF	DM
	<i>Nephtys longasetosa</i>	P	M
	<i>Solariella obscura</i>	S/P	M
	<i>Eudorellopsis deformis</i>	DF/S	M
	<i>Ampelisca macrocephala</i>	SF	S
	<i>Hippomedon kurilious</i>	S/DF	M
	<i>Cylichna alba</i>	P	M
	<i>Ampharete arctica</i>	DF	S
<i>Myriochele heeri</i>	DF	S	
<i>Corophium crassicorne</i>	SF	S	

Group 4. continued

Group Number	Species Name	Feeding Type	Mobility Type
41	<i>Spisula polynyma</i>	SF	M
42	<i>Protomedia fascata</i>	DF	M
43	<i>Spiophanes cirrata</i>	DF	DM
	<i>Acila castrensis</i>	SF/DF	M
44	<i>Cistenides brevicoma</i>	DF	-
	<i>Amphipholis pugetana</i>	DF	M
45	<i>Balanus crenatus</i>	SF	S
	<i>Euhaustorius eous</i>	SF	S/DM
46	<i>Macoma brota</i>	DF	S
	<i>Harpinia kobjakovae</i>	SF	M
47	<i>Pista maculata</i>	DF	S
48	<i>Argissa hamatipes</i>	-	-
49	<i>Boltenia ovifera</i>	SF	S
	<i>Boltenia villosa</i>	SF	S
	<i>Psuedopotamilla rentiformis</i>	SF	S
	<i>Erichthonius hunteri</i>	SF	DM
50	<i>Astarte polaris</i>	SF	S
51	<i>Monoculodes zernovi</i>	DF/S	M
52	<i>Neptunea ventricosa</i>	S/DF	M
53	<i>Balanus hesperius</i>	SF	S
54	<i>Dendraster excentricus</i>	DF	M
55	<i>Neptunea heros</i>	S/DF	M
56	<i>Balanus rostratus</i>	SF	S

known, based on Jumars and Fauchald (1977) and Feder et al. (1978). Again, the size of the clusters (species groups) is arbitrary but tends to be as large as possible while still defining an assemblage of organisms whose station occurrences tend to coincide. To this end the two-way table of abundances of species (arranged according to potential cluster membership) at the different stations (arranged according to station-group membership) was used to define the species-cluster boundaries.

A summary of the standard two-way table is shown in Appendix V. The entries are termed cell densities and are defined as

$$D = \frac{\sum_{i=1}^n \sum_{j=1}^s x_{ij}}{ns}$$

where n is the number of species in the cell, s is the number of stations in the cell, and x_{ij} is the number of the i th cell species found at the j th cell station. These entries directly indicate the concentration of a single species group for a single station group.

Statements concerning spatial patterning found among species groups are generally less satisfactory than those concerning station groups. One reason is that the geographic distribution of a species group must be a

synthesis of the varying ranges of the constituent species which in themselves are not limited to single locations (as are the numbers of station groups). Secondly, the higher number (14) of major species groups leads to confusing results in the production of a conglomerate distribution map similar to those constructed for station groups. However, given the coherent spatial patterning characteristic of all station groups other than IG3, some generalizations concerning species group ranges may be made on the basis of the two-way table by using station group positions as indicators.

A condensed version of the cell density table is presented in Table 5, in which the densities of species groups with over four members are listed for the five major station groups. This table is used to describe briefly the areas in which the species groups are found. Stations not classified as part of the major station groups have been incorporated into this discussion when significant concentrations of a species group were noted.

Group 1 -- Found mainly in the shelf break area with a slight representation in the nearshore stations of IG3.

Table 5. Cell densities of major species groups for major station groups identified by cluster analysis of Bering Sea infaunal data.

Species Group	No. of Species in Group	Station Group				
		IG1	IG2	IG3	MSG	OSG
1	4	0	0	.1	0	.4
4	4	1.2	1.5	33.7	.6	.1
8	10	.1	0	.1	.1	6.2
10	5	0	0	.2	0	.3
24	3	.8	0	.2	10.2	10.1
25	15	26.0	.3	4.3	40.1	14.6
26	5	2.2	0	.6	11.6	5.2
27	7	.3	.3	.2	3.9	.6
28	9	10.9	.1	2.7	45.5	26.0
30	14	.3	0	.3	6.3	42.7
37	4	1.9	0	1.2	.2	.6
39	9	29.1	8.0	3.3	20.2	.3
40	16	30.4	12.3	13.3	2.8	7.4
49	4	0	0	0	0	.1

- Group 4 -- High numbers in the nearshore/Bristol Bay stations of IG3.
- Group 8 -- The only significant concentrations are in the shelf edge group OSG.
- Group 10 -- Found predominantly offshore and in the scattered nearshore/Bristol Bay stations of IG3. By far the most important concentration is at station 35 (density at this station is 70 individuals per square meter).
- Group 24 -- Richest in the midshelf area with concentrations decreasing gradually seaward and much more rapidly shoreward. There is also an appreciable occurrence in the pair of stations 82 and 83.
- Group 25 -- Richest in the midshelf regions with generally lower numbers shoreward and seaward. Nearshore abundances are distinctly higher than those from shelf break stations.
- Group 26 -- As in 24 with highest density values for the pair of stations 64 and 70 located north of the Pribilof Islands.
- Group 27 -- The only distinct concentrations are in the shelf edge group (OSG) and the northeast pair of stations, 82 and 83.

- Group 28 -- Similar to 26 with high densities in station pairs 82 and 83, 64 and 70, and 30 and 49, in order of decreasing density.
- Group 30 -- Richest near the shelf break with decreasing concentrations over the shelf. High densities are also seen at the pair of stations 64 and 70 and, to a lesser degree, at the pair of stations 47 and 55.
- Group 37 -- Mainly found in water of depths less than 50 m, but the overall distribution is not clearly defined.
- Group 39 -- Largely nearshore and includes Bristol Bay, with some representation in the midshelf area (MSG) and in the pair of stations 47 and 55, near the Pribilof Islands.
- Group 40 -- Ubiquitous, with lower numbers in the midshelf and shelf break areas and medium densities in the station pair 47 and 55.
- Group 49 -- Predominantly shelf break with extremely high densities (32 individuals per square meter) at the unclassified station 4 near the Alaska Peninsula.

TRENDS IN ABUNDANCE AND DIVERSITY

Station count and wet weight profiles are found in Table 6. The number of individuals per square meter ranged from 420 to 4,680. Station wet weights were generally low, ranging from 9.3 to 2,420.1 gm/m², with values of over 200 gm/m² occurring at only 14 stations.

Very high wet weight figures are usually attributable to: (1) the sampling of dense aggregates of pelecypods, or (2) the sampling of one or more large echinoderms. Ideally, wet weights should reflect biomass, but in both the situations just mentioned, the high weights result from the inclusion of either shell material or exoskeleton in the weight. The high wet weights associated with stations 5, 6, and 7 of IG2 and the generally high figures from IG2 ($\bar{x} = 517$ gm/m²) coupled with the very low figures for the number of individuals per m² ($\bar{x} = 506$) are an example of this problem. At station 5, most of the weight was associated with eighteen (18) individuals of the pelecypod *Tellina lutea altermidentata*. The high wet weight of station 6 is chiefly due to one large asteroid, *Asterias ameurensis* and the high station 7 weight resulted from a large haul (78 in seven grabs) of the sand dollar, *Echinarachnius parma*.

Table 6. Total numbers of individuals and taxa, total wet weight, dominance, and diversity indices calculated for Bering Sea benthic stations.

Station Group & Station	Total Numbers m ²	Total Wet Weight gm/m ²	Simpson Dominance Index*	Shannon Diversity Index*	Brillouin Diversity Index*	Number of Taxa
IG1 1	3570/3396	726.0	.073/.080	3.28/3.11	3.23/3.06	106/ 84
3	1130/ 938	40.5	.045/.057	3.62/3.37	3.48/3.24	87/ 66
8	3924/3864	32.5	.063/.086	2.91/2.85	2.87/2.81	71/ 61
10	762/ 682	167.0	.053/.064	3.43/3.19	3.28/3.06	66/ 52
11	1044/ 922	28.2	.038/.048	3.91/3.68	3.74/3.52	104/ 86
12	2254/2162	33.3	.085/.093	3.14/2.99	3.07/2.93	86/ 71
20	2622/2540	111.8	.092/.098	3.04/2.92	2.98/2.86	87/ 73
25	2056/1967	82.5	.083/.091	3.11/2.96	3.04/2.90	83/ 67
27	2152/2096	84.0	.131/.138	2.64/2.53	2.59/2.48	61/ 51
39	1964/1806	9.3	.111/.130	2.90/2.67	2.83/2.61	73/ 57
40	2478/2385	17.2	.101/.109	2.85/2.70	2.80/2.65	81/ 63
41	4464/4221	168.7	.201/.224	2.54/2.37	2.51/2.34	88/ 70
42	1134/1086	111.0	.053/.057	3.52/3.39	3.39/3.28	82/ 71
43	3022/2770	137.5	.074/.087	3.24/3.05	3.18/3.00	89/ 74
59	2428/2260	144.5	.097/.111	3.17/2.99	3.19/2.93	73/ 60

*Double entries represent values derived from consideration of all organisms identified to phylum and, secondly, all taxa identified to genus.

Table 6. continued

Station Group & Station	Total Numbers m ²	Total Wet Weight gm/m ²	Simpson Dominance Index*	Shannon Diversity Index*	Brillouin Diversity Index*	Number of Taxa
IG2 5	690/ 630	714.5	.098/.116	2.70/2.48	2.62/2.40	28/ 22
6	690/ 546	925.3	.118/.178	2.71/2.21	2.60/2.12	43/ 30
7	227/ 217	264.9	.269/.295	1.98/1.81	.83/1.68	25/ 19
23	420/ 392	164.3	.085/.097	2.85/2.66	2.72/2.54	35/ 27
IG3 9	1294/1054	202.9	.123/.155	2.94/2.76	2.83/2.65	89/ 73
22	709/ 590	121.9	.044/.053	3.65/3.45	3.45/3.26	98/ 77
57	2504/1793	40.5	.129/.181	2.52/2.28	2.47/2.22	77/ 65
60	531/ 474	139.5	.108/.133	2.99/2.71	2.80/2.54	71/ 57
MSG 19	4166/4044	268.9	.081/.086	3.19/3.07	3.13/3.02	116/100
28	4394/4326	2420.1	.479/.494	1.77/1.68	.73/1.64	91/ 75
37	652/ 628	33.4	.114/.123	3.01/2.88	2.88/2.76	54/ 45
38	612/ 588	639.5	.195/.211	2.65/2.51	2.51/2.37	55/ 48
45	2606/2454	95.0	.099/.112	2.89/2.72	2.84/2.67	77/ 65
63	2574/2462	156.7	.084/.091	3.02/2.91	2.97/2.86	65/ 56
71	2708/2626	175.9	.091/.097	2.94/2.83	2.89/2.79	64/ 53
72	1592/1490	122.4	.067/.075	3.21/3.06	3.13/2.99	63/ 52
73	734/ 658	14.2	.062/.076	3.33/3.10	3.19/2.97	59/ 48

Table 6. continued

Station Group & Station	Total Numbers m ²	Total Wet Weight gm/m ²	Simpson Dominance Index*
MSG 924	644/ 598	283.6	.082/.094
935	2406/2328	98.8	.090/.095
937	1566/1512	76.4	.097/.104
939	1250/1170	192.9	.091/.102
941	836/ 794	187.6	.077/.085
942	820/ 793	207.5	.067/.071
OSG 16	674/ 630	23.1	.077/.087
17	872/ 818	30.5	.051/.057
18	1632/1586	83.7	.081/.085
29	4454/4344	334.2	.149/.157
31	1035/ 927	20.9	.033/.040
36	1178/1034	44.9	.048/.053
65	960/ 940	34.0	.100/.104
2	2877/2120	983.5	.458/.784
4	1167/ 960	671.4	.043/.058
13	547/ 482	36.0	.031/.038

Shannon Diversity Index*	Brillouin Diversity Index*	Number of Taxa
3.10/2.96	2.95/2.84	54/ 48
2.99/2.89	2.94/2.85	59/ 51
2.87/2.74	2.80/2.68	55/ 43
2.80/2.62	2.74/2.57	44/ 33
2.94/2.80	2.84/2.71	43/ 36
2.95/2.85	2.88/2.76	39/ 33
3.27/3.10	3.11/2.95	66/ 55
3.45/3.29	3.30/3.15	74/ 63
3.33/3.23	3.72/3.13	100/ 89
2.79/2.68	2.75/2.64	90/ 76
3.96/3.73	3.77/3.56	130/108
3.65/3.57	3.51/3.43	92/ 82
3.17/3.10	3.05/2.98	69/ 63
1.35/0.66	1.32/0.64	34/ 23
3.73/3.36	3.59/3.25	82/ 59
3.91/3.72	3.66/3.98	86/ 74

Table 6. continued

Station Group & Station	Total Numbers m ²	Total Wet Weight gm/m ²	Simpson Dominance Index I	Shannon Diversity Index*	Brillouin Diversity Index*	Number of Taxa
14	1516/ 494	32.5	.171/.034	2.92/3.75	2.82/3.52	96/ 71
15	588/ 332	42.3	.153/.141	2.76/2.81	2.61/2.62	55/ 42
24	1973/1825	578.8	.117/.136	2.94/2.66	2.86/2.60	78/ 55
35	1260/1004	81.9	.036/.047	3.90/3.65	3.75/3.50	115/ 90
30	626/ 598	31.3	.221/.242	2.20/2.04	2.12/1.96	33/ 26
49	577/ 515	19.2	.091/.113	3.01/2.73	3.89/2.61	48/ 36
47	4680/4336	100.0	.040/.046	3.63/3.44	3.58/3.40	103/ 80
55	3330/3030	106.0	.162/.194	2.94/2.67	2.88/2.63	97/ 76
61	622/ 584	30.5	.083/.094	3.13/2.95	2.98/2.82	56/ 46
62	1724/1668	52.2	.281/.300	2.34/2.19	2.27/2.13	65/ 54
64	1757/	196.2	.165/	2.50/	2.45/	56/
70	1914/ 967	110.3	.173/.070	2.68/3.03	2.61/2.94	54/ 39
82	1120/ 774	116.7	.105/.141	2.84/2.65	3.58/3.40	49/ 38
83	2282/2076	106.2	.087/.103	3.04/2.83	2.88/2.63	67/ 52

While formation of shell and skeletal material does represent an energy requirement of the benthos, such material should not be confused with biomass, which carries an attendant respiratory requirement. Thus, a simple extension of wet weights to benthic biomass or productivity may not be made without some attempt to evaluate the magnitude of interference from non-organic materials. It should also be realized that sampling of aggregations and large individuals is a rare event and may not be considered to be representative.

Abundance and wet weight data for the five main groups are summarized in Table 7. The lower wet weight per square meter figures for MSG, OSG, and IG1 reflect the removal of a single station with extremely high wet weight values (three to four times higher than the next highest value). IG1 and OSG are areas of low wet weight while IG3 and MSC are progressively higher. IG2 is difficult to classify since wet weights from three of the four stations are completely dominated by non-organic material.

A listing of station abundance and diversity profiles is also presented in Table 6. Diversities have been calculated twice, initially using data representing all individuals identified to phylum level and then data that include only individuals identified to at least genus

Table 7. Average abundance, wet weight, and number of taxa for major station groups identified in Bering Sea infaunal studies.

Station Group	Average Number* of Individuals/m ²	Average* Wet Weight gm/m ²	Average Number of taxa per station
IG1	2333	126.3/83.46 ¹	67.1
IG2	506	517.3	24.5
IG3	1259	126.2	68.0
MSG	1837	331.4/182.3 ²	52.4
OSG	1543	81.6/39.5 ³	76.6

¹Lower figure omits high value for station 1.

²Lower figure omits high value for station 28.

³Lower figure omits high value for station 29.

*Based on all organisms identified to phylum level.

level. One may expect the former scheme to include the same taxa under different levels of classification and so overestimate diversity by including too many species. The latter method would produce an error in the opposite direction.

The following remarks are directed towards comparisons of estimated community diversity and are therefore oriented around the Shannon index (see section on diversity in Methods). Average values of the Shannon diversity for the five station groups are listed in Table 8. The species richness results are also included in this table. It is apparent that the diversity of IG2 is quite low, that of OSG the highest, and those of IG1, IG2, and MSG practically the same. In fact, given the lack of information on variance, the latter three cannot be safely separated on the basis of diversity.

TROPHIC STRUCTURE

Results from investigations into the trophic structure of the main station groups are shown in Table 9, which lists both numbers of species in different trophic categories and the average numbers of individuals per station in the assigned classes, for the five major station

Table 8. Average species richness and diversity for station groups identified by Bering Sea infaunal studies.

Station Group	Total Number* of Species	Average Number* of Individuals/m ²	Average Diversity (Shannon Index)	Species Richness
IG1	116	1408.1	2.98	5.92
IG2	32	299.9	2.29	2.56
IG3	90	756.6	2.80	7.08
MSG	126	1625.8	2.70	5.27
OSG	132	651.9	3.24	7.35

*Based only on organisms used as variables in numerical analysis.

Table 9. Total numbers of species¹ found in groups and number of individuals/m²/station in groups, by feeding² and mobility³ type.⁴

Station Group	S, P M		DF M		DF DM	
	No of Species	Individuals/m ² /station	No of Species	Individuals/m ² /station	No of Species	Individuals/m ² /station
IG1	36	285.9	41	460.0	10	243.6
IG2	15	41.9	10	158.9	3	54.1
IG3	27	137.8	26	335.4	7	67.9
MSG	34	218.6	35	650.7	10	56.3
OSG	34	90.5	41	378.4	10	18.5

¹Based on 180 species used in numerical analysis.

²Feeding types: P = predator, S = scavenger, DF = detrital feeder, SF = suspension feeder.

³Mobility types: M = motile, DM = discretely motile, S = sessile.

⁴Feeding type and mobility type after Feder et al. (1978).

Table 9. continued

Station Group	DF S		SF M		SF DM	
	No of Species	Individuals/ m ² /station	No of Species	Individuals/ m ² /station	No of Species	Individuals/ m ² /station
IG1	14	201.9	4	41.3	11	76.2
IG2	3	35.4	0	0	0	0
IG3	11	59.8	3	59.4	7	15.1
MSG	17	197.5	4	98.3	9	76.6
OSG	18	43.2	7	15.9	8	14.3

Station Group	SF S	
	No of Species	Individuals/ m ² /station
IG1	10	99.9
IG2	1	8.7
IG3	9	81.1
MSG	7	387.8
OSG	14	91.1

groups. Table 10 is derived from Table 9 and illustrates the differing ratios in which suspension feeding organisms are found in the different station groups. Emphasis has been placed on the occurrence of suspension feeders as their distributions have often been linked to substrate changes and changes in diversity.

Several interesting contrasts between groups are apparent: (a) IG2 possesses relatively few suspension feeding organisms, both in terms of the number of species and number of individuals found; (b) OSG is host to the greatest number of suspension feeding species although they are not numerically abundant; and (c) MSG, which is represented by a fairly high number of suspension feeding species is most obvious for the extremely high fraction of both suspension feeding individuals and sessile individuals present.

SEDIMENT ANALYSIS

Table 11 summarizes particle size data for the five major station groups (Hoskin, pers. comm.; data submitted to NOAA under OCSEAP program, RU #291/292). Not all stations are included as data were unavailable for some. An overview of the particle size distribution is shown in

Table 10. Proportions of suspension-feeding (SF) individuals found in station groups.*

Station Group	Total Number of Species	SF Species	SF Species / Other Types	Individuals/ m ² /station	SF Individuals/ m ² /station	Mean SF Individuals / Mean Other Types
IG1	126	25	.198	1408.1	217.4	.183
IG2	32	1	.031	299.9	8.7	.031
IG3	90	19	.268	756.5	155.6	.259
MSG	116	20	.208	1625.8	502.7	.448
OSG	132	29	.282	651.9	121.3	.229

*Based only on organisms used in numerical analysis.

Table 11. Average mean and standard deviation for sediment parameters characterizing station groups.

Station Group	Gravel/Sand		Silt		Clay	
	Mean %	Standard Deviation	Mean %	Standard Deviation	Mean %	Standard Deviation
IG1	85.25	8.77	7.76	6.20	6.97	4.81
IG2	98.86	1.19	0.26	0.239	0.877	0.96
IG3	91.45	8.05	4.07	5.82	2.87	3.29
MSG	62.45	16.0	29.12	14.67	7.91	1.55
OSG	59.96	14.56	31.26	12.40	9.27	2.63

Figure 10 (from Sharma, in prep.). A complete listing of sediment data for the major station groups is presented in Table 12.

Sediment types were found to vary between the major station groups. Since information on the variance of this data is unavailable, no attempt was made to separate these station groups on a statistical basis. Thus, a simple description of the sediment types for the major station groups follows. Unless otherwise noted, sand/gravel fractions are composed primarily of the sand fraction as the occurrence of non-zero gravel percentages in the sampled stations was rare.

IG1 -- A high percentage of gravel is found in these stations, indicating an intermediate position between groups MSG/OSG and IG2/IG3. The low standard deviation for this group may be a sampling artifact as the sample size for this group is the largest (n = 16, stations 61 and 62 included).

IG2 -- The most obvious attribute of this group is the high percentage of sand and gravel ($\bar{x} = 98.86\%$) found at all stations. Stations 5 and 7 registered 77.03% and 18.49% of their respective totals as actual gravel. IG2 is probably

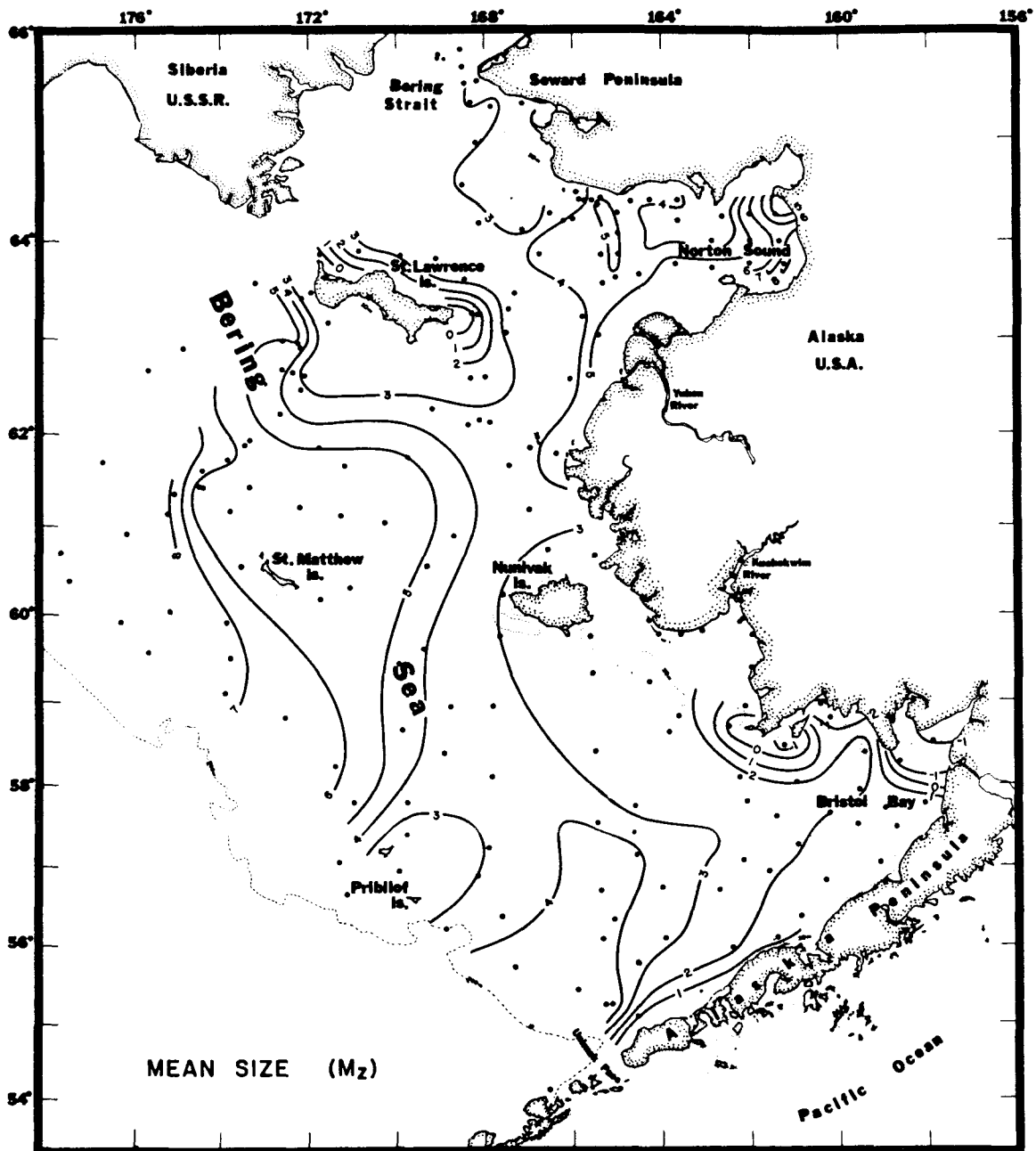


Figure 22. Mean particle size (ϕ units) of sediments of the eastern Bering Sea shelf (from Sharma, in prep.).

Table 12. Sediment data for Bering Sea stations classified into station groups by cluster analysis.*

Station Group	Station	% Gravel/Sand	% Silt	% Clay
IG1	1	72.61	19.57	7.82
	8	99.85	.15	0.0
	10	80.90	8.68	10.42
	11	84.67	5.66	9.67
	20	85.79	6.41	7.80
	25	99.44	.26	.30
	27	84.77	8.25	6.98
	39	76.75	15.37	7.90
	40	84.04	7.65	8.30
	41	96.91	.63	2.46
	42	97.51	1.26	1.22
	43	85.00	7.47	7.26
	57	80.81	12.47	6.72
	59	83.18	9.18	7.64
	61	77.08	2.66	20.26
62	74.72	18.45	6.84	
IG2	5	99.86	.10	.04
	6	97.61	.61	1.78
	7	99.90	.11	0.0
	23	98.08	.23	1.69

*Data after Hoskin (pers. comm.) submitted to NOAA under OCSEAP Program, 1976.

Table 12. continued

Station Group	Station	% Gravel/Sand	% Silt	% Clay
IG3	9	99.97	.02	0.0
	22	90.70	2.80	6.50
	60	94.31	3.52	2.28
	57	80.81	12.47	6.72
MSG	19	59.27	33.28	7.45
	28	53.42	36.85	9.74
	37	65.63	25.70	8.66
	38	47.07	44.28	8.65
	45	59.40	34.29	6.31
	71	69.01	22.95	8.04
	72	46.05	45.06	8.89
	82	88.17	5.20	6.63
	83	50.82	39.43	9.75
	935	90.74	4.17	4.99
OSG	16	62.34	28.01	9.65
	17	36.44	49.92	13.64
	29	62.05	30.99	6.96
	31	76.90	15.27	7.83
	65	59.59	32.13	8.28

separable from the other station groups on this parameter alone.

- IG3 -- Stations from this group show the nearshore trait of high sand and gravel content (\bar{x} = 91.45% sand/gravel and 8.05% for silt). These figures indicate a resemblance to IG1, albeit with a significant increase of sand/gravel content.
- MSG -- Sediments from this group show a high value for silt and clay fractions. The high variance suggests a heterogeneity not found in the other station groups. For example, in the silt fraction values range from 4.17% (station 935) to 45.06% (station 72).
- OSG -- Sediment samples from OSG, with sand/gravel percentages ranging from 36% to 77%, did not show the degree of consistency found in the nearshore groups. This group is probably not safely separable from MSG on the basis of the parameters chosen. It shows lower concentrations (\bar{x} = 59.96%) of sand and correspondingly higher (\bar{x} = 31.26%) percentages of silt than were found in MSG. This increase in the fraction of fine-grained sediments in OSG is in accord with the postulated transport of fine particles to offshore areas.

CONCLUDING DISCUSSION

THE DETERMINATION OF FINAL STATION GROUP BOUNDARIES

Inspection of the plots resulting from principal coordinate and principal component analyses (Figures 10, 13, 16, 19) reveals a problem often encountered when using ordination techniques to produce station groupings. If one envisions these plots without the different symbols marking the affinities already suggested by the cluster analysis, it becomes apparent that gradations between major groups makes group differentiation (if groups may be distinguished) difficult if not impossible. This result is probably due as much to the large number of stations involved as it is to any inherent lack of structure in the data.

Chardy et al. (1976) used ordination methods, unaided by other types of analysis, to classify benthic infaunal distributions off the Brittany coast. They were successful in their efforts to discern community relations, but were dealing with only 30 stations. Given the larger number of stations involved in the present study, the use of ordination methods largely in the capacity of a confirmation of the cluster analysis results is unavoidable. Other uses of ordination methods are: (1) in defining the relations

between groups previously delineated by cluster analysis and (2) in determining the relationships between outliers and main groups or occasional group members to construct group members. In this case the graphic output of the ordination methods is especially useful.

Minor modifications of the cluster interpretations are suggested by the results of ordination output. In particular, stations 61 and 62 invariably exhibit a strong affinity for IG1, while stations 82 and 83 are generally found near MSG. Stations 3, 8, and 10 are strongly transitional between groups IG1 and IG3.

A map of the communities incorporating the combined information derived from cluster analysis and ordination techniques is presented in Figure 23. The link between station 4 and IG3 is not strong, so station 4 has been left outside of IG3. The transitional nature of stations 3, 8, and 10 is indicated by the dashed line linking them to MSG. Stations 61 and 62 and stations 82 and 83 have been incorporated in IG1 and MSG respectively. Although not indicated on the map, the entire OSG assemblage is less distinct than any of the other major groups. The similarities of stations 14 and 35 to OSG are not acknowledged as these links are admittedly tenuous.

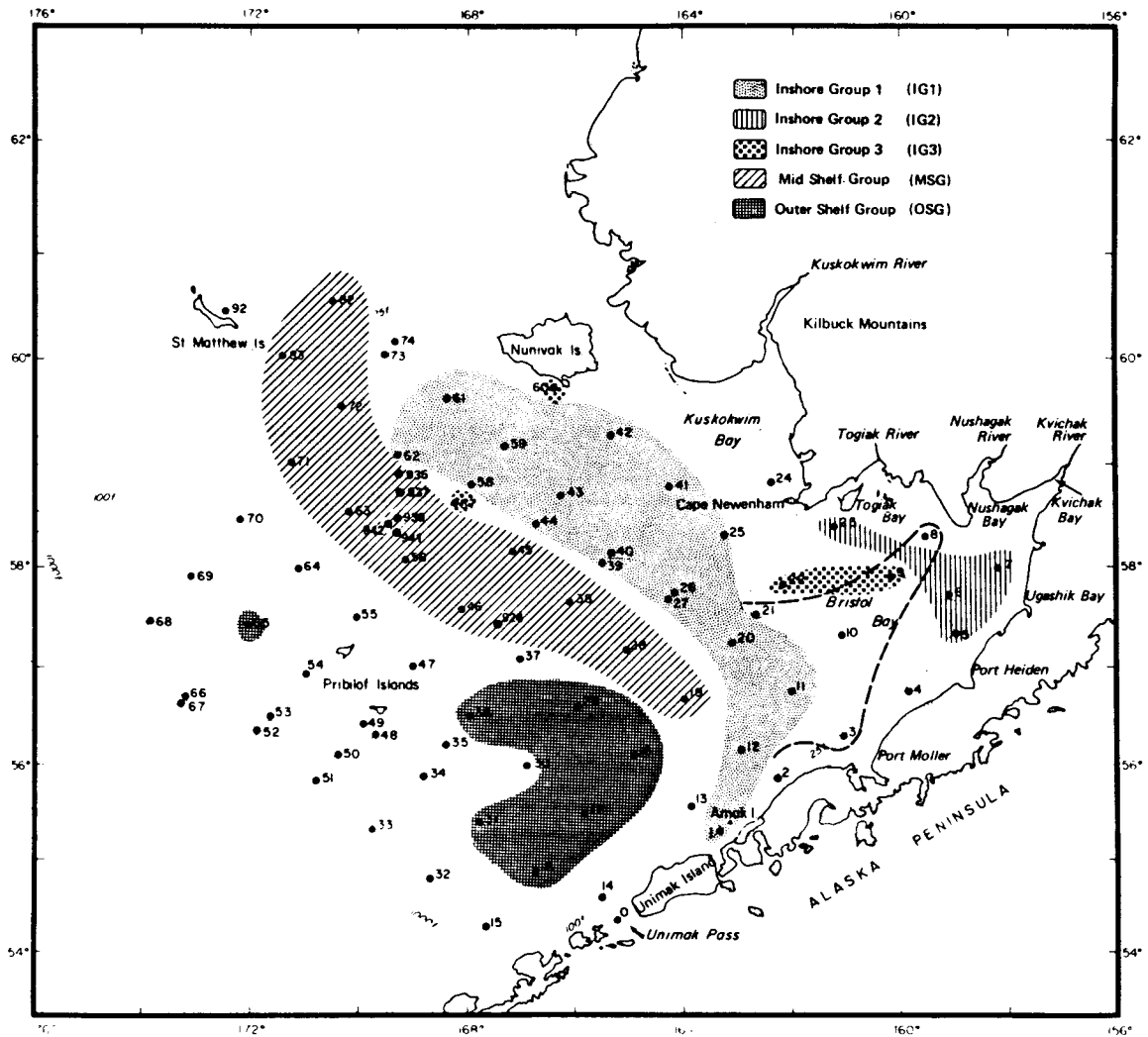


Figure 23. Station groups delineated by the combined use of cluster, principal components, and principal coordinates analyses. The dashed line linking stations 3, 8, and 10 to Inshore Group 1 indicate that these stations are only weakly associated with Inshore Group 1.

Most techniques used suggested the same relationship between outliers and the core groups. A summary of the affinities of unclassified singleton stations and station pairs to the major station groups is presented in Table 13.

Stations 2 and 4 are weakly linked to each other and all the inshore station groups. Stations 14 and 15 are also linked to each other and more generally to OSG. This tie to the outer shelf group is consistent with their position near the shelf edge, although considering the extreme water depth associated with station 15 (1,500 m), it is surprising that station 15 shows a similarity to any of the other stations or groups. Station 24 is characterized by a fauna that is dissimilar to most other stations and the relationship between 24 and the other stations and groups remains ambiguous. During collection, the grabs from this station were noticeably atypical for the varied substrate type brought up. Given the proximity of station 24 to the mouth of the Kuskokwim River and the Alaskan coast, it is possible that ice rafting tends to maintain a significant heterogeneity in the substrate. Station 35 is clearly most similar to stations 30, 49, and 15 and to OSG.

With the exception of the pair of stations 30 and 49 (which are decidedly shelf break in orientation), the station pairs that were suggested (see Table 3) are not

Table 13. Bering Sea benthic stations not classified by cluster analysis at .30 similarity level. Station affinities are indicated by cluster, principal components, and principal coordinates analyses.

Unclassified Stations	Type of Analysis and Indicated Affinity					
	Cluster Analysis		Principal Coordinates Analysis		Principal Components Analysis	
	Czekanowski Distance	Canberra Metric Distance	Czekanowski Distance	Canberra Metric Distance	Covariance Matrix	Correlation Matrix
2	none	IG2*	IG1,IG3,4	none	IG2,14,15	13,15,30,49
4	none	IG2*	IG1,IG3,2	IG1	14,15,IG2*	IG2
13	IG3	14,15	none	14,35	none	2,15,30,49
14	15,35	15,35	13,15	35,OSG	15	35,OSG
15	none	13,14	13,14	14,35	OSG	2,13,30,49
24	none	none	IG1	55*	61,IG1*	MSG
35	OSG*	14,15	30,OSG*	14	none	14,OSG
30,49	64,70,OSG	none	35,OSG	OSG	OSG	2,13,15
47,55	IG1	IG1,IG3*	24,47	MSG*	IG1*	MSG*,IG1*
64,70	OSG	MSG	29,47	29,18,OSG*	MSG*	MSG*

*Indicates a weak link to the stations or groups noted.

amenable to easy classification. Stations 47 and 55 are weakly associated with MSG and IGl. Stations 64 and 70 are more closely related to the midshelf group and to several stations from OSG (i.e., stations 18 and 29). Stations 18 and 29 are further from the shelf break than are any other members of OSG. This positioning suggests a link to 64 and 70, which are also removed from the shelf edge.

THE INTERPRETATION OF THE RESULTS OF ORDINATION

Some insight into the interactions between ordination procedures may be obtained from an examination of the above-mentioned station affinities. The associations of stations 82 and 83 are illustrative. Station 83 is clearly the more diverse of the two, with an enriched fauna in terms of both the number of species and number of individuals (see Table 6) present at the station. Under analysis of the principal components of the covariance matrix, MSG is split into two contingents, the smaller composed of stations 37, 38, 73, and 924 (see Figure 17). Station 82 projects onto the first axis in the general vicinity of these four stations, while station 83 is found among the rest of MSG. Stations 37, 38, 73, and 924 show the lowest number of individuals/m² for stations in IGl, while station 82 has only half the number of individuals that 83 has.

The positions of 82 and 83 relative to the rest of MSG reverse under the complementary ordering (i.e., principal components of the correlation matrix). Station 83 is now found on the fringe of MSG while station 82 is nearer the group center (see Figure 19). The explanation for this effect lies in the effect of the correlation coefficient on the larger numbers of individuals found at station 83. An important point in this interpretation is that the stations are largely populated by the same species; hence, their greatest similarity is to each other.

A result less easily explained is the response of OSG to ordination. Stations 29 and 18 are found displaced from the rest of OSG by principal coordinates of the Czekanowski distance matrix (see Figures 12 and 18) and the principal components of the covariance matrix. Again, the complementary techniques involving reduction in the effects of dominance and abundance leads to the migration of stations 29 and 18 towards the rest of OSG. This is not difficult to explain since stations 18 and 29 register the greatest number of individuals per square meter in the group (see Table 14) and are among the stations showing the lowest Brillouin diversity for OSG.

Use of techniques that reduce the effect of high abundances and dominance would be expected to result in a

Table 14. Dominance, diversity, and species richness for Bering Sea stations classified into major station groups. Calculations based on 180 species used in cluster and ordination analyses.

Station Group	Station	Brillouin Diversity Index	Simpson Dominance Index	Total Number of Species	Total Number of Individuals/m ²	Species Richness
IG1	1	2.91	.078	53	2354	6.70
	3	2.81	.083	39	752	5.74
	8	2.61	.105	40	2382	5.02
	10	2.84	.070	34	446	5.41
	11	2.83	.099	45	578	6.92
	12	2.54	.145	45	1460	6.04
	20	2.79	.095	44	932	6.29
	25	2.62	.118	44	1674	5.79
	27	2.16	.178	33	1098	4.57
	39	2.53	.114	37	1154	5.11
	40	2.52	.122	45	1410	6.07
	41	1.87	.303	49	3570	5.87
	42	3.05	.070	54	960	7.72
	43	2.71	.111	46	2240	5.83
	59	2.99	.065	43	1320	5.85

Table 14. continued

Station Group	Station	Brillouin Diversity Index	Simpson Dominance Index	Total Number of Species	Total Number of Individuals/m ²	Species Richness
IG2	5	2.25	.125	16	460	2.45
	6	1.76	.227	17	296	2.81
	7	1.35	.378	13	190	2.29
	23	2.00	.170	16	250	2.72
IG3	9	2.41	.178	50	984	7.11
	22	2.76	.065	50	525	7.82
	57	1.93	.246	44	1370	5.95
	60	2.19	.184	33	318	7.46
MSG	19	2.72	.101	58	3706	6.94
	28	1.40	.545	50	4120	5.89
	37	2.87	.061	32	358	5.27
	38	2.17	.241	38	548	5.87
	45	2.51	.125	50	2306	6.33
	63	2.57	.114	40	2178	5.07
	71	2.72	.100	43	2578	5.35
	72	2.73	.094	39	1320	5.29
	73	2.59	.086	35	492	5.48

Table 14. continued

Station Group	Station	Brillouin Diversity Index	Simpson Dominance Index	Total Number of Species	Total Number of Individuals/m ²	Species Richness
MSG	924	2.60	.113	37	538	5.73
	935	2.66	.152	42	2126	5.35
	937	2.57	.112	36	1452	4.81
	939	2.51	.105	29	1154	3.97
	941	2.56	.094	27	754	3.92
	942	2.64	.078	25	758	3.62
OSG	16	2.72	.106	40	562	6.16
	17	2.84	.071	40	732	5.91
	18	2.81	.104	56	1438	7.56
	29	2.50	.168	54	4198	6.35
	31	3.27	.050	72	816	10.74
	36	3.14	.068	59	900	8.53
	65	2.63	.370	43	814	6.27

more compact OSG. It is difficult to say whether or not OSG is more compact in Figure 19 (based on the principal components of the correlation matrix) than in Figure 18 (based on the principal components of the covariance matrix) as fully half of this axis is involved in removing variance associated with OSG. A complete examination of this situation would require an analysis of the actual components extracted from the correlation matrix, but this cursory view leads to the knowledge that OSG is intrinsically more heterogeneous than the other station groups in terms of abundances. Since OSG is also fairly well separated by the principal coordinates analysis based on the Canberra metric coefficient (see Figure 13), it seems likely that the abundance differences are in species held in common by most stations in the group. If these species were not constantly occurring within the group, then such a change in distance measure would not be expected to greatly change the station projections relative to other members in the group.

The view of stations 3, 8, and 10 is also complicated. If it may be assumed that differences within a station group are primarily based on abundances rather than species composition, we would expect the most disparate stations (compared to other stations in the group) in terms of the numbers of individuals present (i.e., stations 3 and 10; see

Table 14) to be affected most strongly by the correlation standardization. Also, stations exhibiting the highest degree of dominance will respond to differences in distance measures. IGI is poorly defined by the covariance-based analysis (see Figure 16) with stations 3, 8, and 10 seemingly far removed from the group centroid. Definition is improved by the correlation standardization (see Figure 19) and the distances between 3 and 10 and the group centroid have reversed. Station 8 seems unaffected. A similar trend occurs in the principal coordinate solutions as stations 3 and 10 shift to nearer the group centroid when using a dominance-reducing distance measure (the Canberra metric) and station 8 remains in the group periphery. The Simpson dominances for these stations (3, 8, and 10), are low (see Table 14); thus, the contributions of several key dominant species at other stations in the group must have been reduced.

The different ordination alternatives lead to rearrangements of the stations within a particular group, while the relations of the groups to each other are generally constant. Differences between (as opposed to within) groups are largely determined by species composition rather than by abundances of species held in common. It is probable that the distance between station 8 and the rest

of the group was largely determined by species differences, a hypothesis that is in part borne out by inspection of the raw data and also by the fact that station 8 remains separate from the group under all the ordination alternatives. Again, access to information detailing which species are most influential in producing the output is only available through the inspection of factors associated with the principal components analysis.

As mentioned earlier, an additional use of ordination techniques is in clarifying relations between station groups. The most obvious relationship is the constant close association between the nearshore and Bristol Bay groups (IG1, IG2, and IG3). This is most evident in Figures 12 and 21. MSG is generally closest to IG1, although under the principal components of the covariance matrix (see Figure 16) ordering the relation between MSG and the other groups is difficult to discern.

OSG has already been described as somewhat diffuse. Under none of the ordination alternatives is OSG clearly affiliated with either MSG or the nearshore groups (IG1, IG2, IG3). Thus, an inshore/offshore polarity is indicated, with IG1, IG2, and IG3 being closely related and MSG less clearly allied to IG1.

BIOTIC AND ABIOTIC FACTORS AFFECTING COMMUNITY STRUCTURE

Differences in the trophic structure of the infaunal communities were seen between several of the station groups outlined by the numerical analysis. An increase in the ratio of abundances of suspension feeding organisms to those of other trophic levels from 0.18 to 0.45 (Table 10) was found in the offshore progression from IGI to MSG. A subsequent decrease in this ratio, from 0.45 to 0.23 was found in moving from MSG to the outer shelf group, OSG.

The results of several benthic community studies have addressed the relationship between sediment characteristics and sedimentation rate to community structure. Rhoads and Young (1970) and Levinton (1975) reported the exclusion of suspension feeding organisms from certain areas of Buzzards Bay, Massachusetts. Their studies suggest that instability in silt/clay sediments facilitates tidal-current resuspension of sediments which in turn adversely affect suspension feeders by clogging filtering apparatus and burial of larval forms. Rhoads and Young (1970) indicate that a resuspension of sediments may also be effected by detrital feeders in the process of foraging.

Feder et al. (1978) have implicated sediments in the exclusion of suspension feeders in certain areas of

continental shelf of the Gulf of Alaska and Prince William Sound, Alaska. These areas are subject to direct input of glacier-borne sediments from streams draining coastal glaciers and from the discharge of the Cooper River. The resulting high sedimentation rates are thought to effectively limit suspension feeders, again by suffocation and burial. Thus, exceedingly high rates of sedimentation related to specific characteristics of the abiotic environment may result in adverse effects on suspension-feeding organisms. Such effects resemble closely those caused by the action of detrital-feeding communities on a coincident suspension-feeding community. It should be emphasized that in both Buzzards Bay and the Gulf of Alaska, silt/clay fractions are commonly higher than 50% and the water content of the sediments is also high [over 50% in the first 2 cm (G. E. M. Matheke, pers. comm.)]. Although no data on water content of sediments is available for the Bering Sea study area, silt/clay fraction in the area of fine-particle deposition (OSG), averages only 40% (see Table 11).

Sokolova (1959) has hypothesized that community structure on the slope and floor of the Kurile-Kamchatka Trench and the Bering Sea is largely determined by food supply, which is in turn linked to sedimentation rates. High sedimentation rates are thought necessary to insure

adequate food input to the detrital-feeding communities. High suspended loads are required to insure the food source for suspension feeding communities. Sokolova was primarily interested in community structure from deep benthic environments. These are areas in which the very high sedimentation rates experienced in Prince William Sound and the high tidal current velocities found in Buzzards Bay are generally not found. High sediment rates and high bottom currents do not, in the work of Sokolova, refer to levels sufficiently high to adversely affect the suspension-feeding community.

Thus, community structure may be intimately related to overlying current structure, as it is the bottom currents that maintain the suspended load. It has been assumed that suspension feeders actively feed at varying heights in the water above the sea floor. Many may also actively feed on the detrital layer at the sediment surface if a food source superior to that of the water column may be reached. This occasional detrital feeding by suspension feeders will be limited by exhaustion of local food resources, especially for those suspension feeders that are sessile. Relocation on the part of motile or discreetly motile suspension feeders may be energetically unfavorable, especially if significant effort is required for the construction of tubes.

Jumars and Fauchald (1977) also suggest that food supply is related to community structure in the polychaete communities off the coast of southern California, but their observations deal more with the requirements of mobility to increase the extent of foraging areas as the organic carbon content of the sedimentary environment decreases. Their hypotheses did not deal directly with the problem of trophic structure since suspension feeders were never numerically important in their study areas.

In contrast to the theories outlined above, the observed changes in distributions of suspension feeders from IGl to MSG seem, for several reasons, to be unrelated to sedimentation rates or sediment types. The compact sand bottom of IGl should be conducive to the establishment of a suspension feeding community. Such sandy, compact sediments provide a firm substrate for the construction and placement of tubes, and should not resuspend easily. Also, the combined absence of coastal glaciers in this area and the advection of the Kuskokwim River outflow to the northern shelf area means that sedimentation rates in IGl are probably not high enough to exclude suspension feeders.

One explanation for the observed paucity of suspension feeders in IGl may be based on storm-wave induced turbulence. Sharma (1975) has calculated that bottom current velocities of

approximately 30 cm/sec may commonly occur in water depths of 94 m in the Bering Sea. However, most stations of IGL are at depths less than 50 m. Significant wave heights and periods of 6-7.5 m and 8-9 sec. constitute 1% of all observed waves for this area in the month of November (Brower et al. 1977). Further, waves of 8-9.5 m with significant periods of 13 sec. have also been observed. Calculations of maximum bottom currents induced by such waves may be made as follows:

$$\mu_{\max} = a\delta \frac{\cosh k(zth)}{\sinh kh}$$

where a equals amplitude, δ equals $2\pi/T$, T equals period, k equals $2\pi/L$, z equals depth for which μ is being calculated (z is positive upward), and h equals bottom depth (McLellan 1965). Maximum horizontal bottom current velocities corresponding to such waves would be approximately 24 cm/sec. for the smaller wave and over 150 cm/sec. for the larger (calculated for one meter above bottom, with a bottom depth of 50 m). Such high velocities could cause significant mortality among the suspension feeding community, especially on organisms attached to the sediment surface. Wave scour has been shown to inflict significant damage to benthic infaunal communities of the North Wales coast (Rees et al. 1977), although the study concentrated

on bottoms shallower than 15 m. Mortality, in this case, would be due to direct washing of organisms from the sediment surface, exposure of sediment-dwellers to predators, or possible burial of mature or larval forms. A detailed knowledge of the habits of these organisms and especially of their tolerance to disturbance is unavailable at this time.

The preceding discussion is highly speculative. The actual effects of wave-induced turbulence on benthic organisms is not well known. In addition, the magnitude of wave-induced turbulence in the area of IGl is uncertain. Ice cover over much of the winter may effectively shield the bottom from the effects of winter storms. Such a shielding would result in a relatively undisturbed benthic environment. Rhoads et al. (1978) noted that slow-growing detrital feeding organisms are often characteristic of undisturbed bottoms, while fast-growing opportunists, many of which are suspension feeders, characterize environments subject to disturbance. If ice cover does shield the bottom in the area of IGl, then a depauperate suspension-feeding community might be expected. It seems unlikely, however, that the area covered by IGl is well-shielded from winter storms, as the ice front ice is usually not far advanced by mid-November, the time for which the wave-induced bottom currents were calculated above.

The increase in the ratio of suspension feeders to other trophic types from 0.18 in IGl to 0.45 in MSG may well be attributable to a damping of storm-wave-induced turbulence with depth. Another potential factor in this situation is seasonal productivity. As mentioned earlier, retreat of ice in the spring is followed by an intensive bloom. The algal populations are apparently not completely utilized by the zooplankton in the area and have been found to sink to within several meters of the bottom (Alexander 1978, Taniguchi et al. 1976). Although it is not likely that these populations continue to actively photosynthesize, they represent, while suspended just above the bottom, a potentially significant food resource for benthic suspension feeders. After sinking to the sediment surface, any remnants of the bloom will be accessible to both detrital feeders and some suspension feeders. The implication is that an adequate food source probably exists for the suspension feeding community; in addition, adverse effects of the presence of a detrital feeding community are not yet felt. Although the sediments from MSG are finer in size than those of IGl, they are still classified as fine sand and are compact enough to prevent easy resuspension. Thus, the type of amensalism noted by Rhoads and Young (1970) is not likely to occur in MSG. As noted above, Levinton (1975) reported disturbance of suspension feeding

communities on bottom with greater than 50% silt/clay fractions, while the silt/clay fraction from the area of MSG is only 37%.

Uncertainties concerning the effect of turbulence in the area of MSG also exist. Many of the stations of this group are found at depths less than 70 m, for which substantial storm-induced turbulence may exist. Threshold levels for disturbance of this type need be known to assess the role of turbulence in such marginal situations.

The causes for reduction in abundance of suspension feeding individuals in OSG is probably related to the considerations outlined by Sokolova (1959). This area is not ice-covered in an average year, although at times the pack ice will extend into it. Thus, a direct introduction of primary productivity to the greater depths of the OSG stations is probably not a regular occurrence. Also, with increasing depth, the effect of storm-induced turbulence is negligible. Thus, the bottom community in this area is not subjected to the extreme events characteristic of station groups nearer to shore. Bering Sea source water enters outer Bristol Bay through this area, implying that current velocities strong enough to keep some material suspended do exist. Sediments from this region clearly show a higher percentage of fine particles than do sediments from other

areas included in the major station groups. However, OSG sediments are still coarser than those from study areas in Quisset Harbor, Massachusetts, in which elimination of suspension feeders has been linked to the action of detrital feeders (Levinton 1977). It seems, then, that neither the detrital feeding nor suspension feeding mode should be clearly favored, a prediction substantiated by the ratio of 0.24.

Several hypotheses concerning the near absence of suspension feeders from IG2 are forthcoming on the basis of sediment information. Sediments from this group are primarily gravel and coarse sand. This condition may result from the presence of substantial currents in the overlying water. Myers (1976) has proposed an Eckman-related upwelling scheme which may explain the existence of locally high currents in the Bristol Bay area. Also, the proximity of these stations to the Alaska Peninsula may result in a high gravel content since this region is tectonically active. The exceedingly high sand/gravel fraction coupled with periodic high bottom currents could result in unstable bottom conditions that are not favorable to the maintenance of a suspension feeding community.

An analysis of the underlying causes of the distribution of species groups is beyond the scope of this study.

Research on the part of Russian workers has covered both trophic classification and zoogeographic affinities of the organisms in this area. Semenov (1968) concluded that, along a transect extending out of Bristol Bay, changes in the infaunal communities were related to both temperature and food availability. Predominance of certain trophic groups was found to coincide with changes in zoogeographic complexes, and both effects were attributed to characteristics of the overlying water masses. Neiman (1963) outlined a similar relationship. Her work covered a larger area (the entire eastern Bering Sea shelf and continental slope), and did not detail community structure in much of the area under consideration in the present study. The dominance zones of zoogeographic complexes delineated by Semenov (1968) are in agreement with the distributions of the three water masses previously described for this area. The water mass distributions also coincide with the inshore/offshore trends in species composition and trophic structure suggested by this study. While much work remains to be done on the effect of turbulence, food availability and temperature, it seems likely that these parameters will ultimately be found the most important in determining the structure of benthic communities in this area.

SUMMARY

The combined use of the techniques of cluster analysis, principal components, and principal coordinates analysis led to several conclusions concerning the existence of biological provinces and species assemblages in the study area.

1) Five major station groups were found to encompass 47 of the 62 stations under study. Three main groups account for 39 of these stations. These three groups occupy adjacent bands whose long axis roughly parallels the bathymetry, defining contiguous areas of increasing depth. Two smaller groups (4 stations each) are found in the vicinity of the head of Bristol Bay and around Nunivak Island.

2) Fifty-six species assemblages have also been delineated. The distribution of thirteen of these show strong correlations with the major station groups. Two broad classes of the species groups are obvious: (a) those with distributions generally confined to a single station group, and (b) those considered ubiquitous but showing marked changes in numbers at the different station groups.

Several ecological differences between the main station groups are evident.

(a) An inshore/offshore polarity exists, with high numbers of individuals being found in the coarse sand

bottoms of the inshore areas and progressively lower abundances in the finer sediments of the offshore areas (MSG and OSG).

(b) An increase in the ratio of suspension-feeding organisms to other trophic types was seen in the midshelf area. This ratio was 0.45 in MSG, 0.18 in IG1, and 0.24 in OSG. The differences between groups is thought to be based on a difference in food supply and differences in the effect of storm-wave-induced turbulence on the shallow-dwelling suspension feeding community.

(c) A near absence of suspension feeding individuals in the coarse sand and gravel areas at the head of Bristol Bay (IG2).

(d) A low diversity in the midshelf area (MSG) when compared to both the inner and outer shelf groups (IG1 and OSG). In the former case, high diversity stems from the large number of individuals present, while in the latter case it results from high species richness (i.e., high numbers of species found at each station).

APPENDIX I. Station location, sampling date, and
depth of stations used in Bering Sea
infaunal studies.

Station	Latitude	Longitude	Date Sampled	Depth (m)
1	55°18'	163°18'	7 June 75	47
2	55°51'	162°17'	7 June 75	43
3	56°17'	161°02'	8 June 75	52
4	56°46'	159°52'	8 June 75	52
5	57°21'	158°58'	8 June 75	45
6	47°43'	159°05'	8 June 75	47
7	57°58'	158°15'	8 June 75	35
8	58°17'	159°32'	8 June 75	24
9	57°55'	160°08'	9 June 75	53
10	57°19'	161°06'	9 June 75	65
11	56°45'	161°59'	9 June 75	71
12	56°09'	162°56'	9 June 75	83
13	55°33'	163°49'	7 June 75	67
14	54°39'	165°25'	7 June 75	165
15	54°18'	167°36'	29 May 75	1,006
16	54°53'	166°44'	28 May 75	205
17	65°29'	165°50'	28 May 75	121
18	56°06'	164°54'	28 May 75	95
19	56°40'	163°57'	10 June 75	77
20	57°15'	163°05'	10 June 75	54
22	57°50'	162°11'	10 June 75	45
23	58°20'	161°21'	10 June 75	31
24	58°46'	162°29'	10 June 75	73
25	58°19'	163°13'	11 June 75	35

APPENDIX I. continued

Station	Latitude	Longitude	Date Sampled	Depth (m)
27	57°40'	164°16'	11 June 75	53
28	57°10'	165°04'	11 June 75	70
29	56°36'	165°57'	28 May 75	84
30	56°00'	166°51'	27 May 75	133
31	55°22'	167°47'	6 June 75	165
35	56°13'	168°20'	5 June 75	163
36	56°31'	167°55'	27 May 75	117
37	58°40'	169°00'	16 June 75	75
38	57°40'	166°06'	11 June 75	66
39	58°03'	165°29'	11 June 75	51
40	58°08'	165°16'	12 June 75	47
41	58°47'	164°15'	12 June 75	34
42	59°16'	165°20'	12 June 75	22
43	58°42'	166°17'	12 June 75	38
45	58°10'	167°10'	12 June 75	67
47	56°58'	169°01'	18 August 75	84
49	56°25'	169°56'	4 June 75	110
55	57°29'	170°08'	20 August 75	73
57	58°36'	168°13'	13 June 75	53
59	59°12'	167°18'	13 June 75	38
60	59°43'	166°24'	13 June 75	24
61	59°39'	168°22'	13 June 75	39
62	59°06'	169°15'	13 June 75	53
63	58°33'	170°10'	14 June 75	73
64	58°01'	171°08'	14 June 75	90
65	57°25'	172°05'	14 June 75	105
70	58°29'	172°11'	21 August 75	106
71	59°04'	171°10'	21 August 75	82

APPENDIX I. continued

Station	Latitude	Longitude	Date Sampled	Depth (m)
72	59°34'	170°19'	24 August 75	68
73	60°02'	169°29'	23 August 75	48
82	60°33'	170°29'	22 August 75	60
83	60°02'	171°26'	23 August 75	73
924	57°28'	167°28'	22 May 75	73
935	58°50'	169°19'	24 May 75	68
937	58°41'	169°18'	25 May 75	65
939	58°29'	169°19'	25 May 75	71
941	58°20'	169°19'	25 May 75	70
942	58°28'	169°23'	25 May 75	70

APPENDIX II. Sample data sheet from Bering Sea

BERING SEA BENTHOS -- DISCOVEREE CRUISE 808 -- JUNE 1975

CRUISE 808	STATION 007	PERCENTS REFER TO
TAXON CODE	TAXON NAME	SAMPLE DATE SAMP NO.
40000000000	RHYNCHOCOFLA	06/08/75 0003
44000000000	NEMATODA	06/08/75 0004
43010000000	POLYCHAETA	06/08/75 0004
43011201040	AMAITIDES MACOSA	06/08/75 0006
43011202050	ETEPONE LONGA	06/08/75 0004
43012401030	HEPHTYS CAFFA	06/08/75 0003
43013901010	HAPLOSCOLOPIOS PANAMENSIS	06/08/75 0002
43013901010	HAPLOSCOLOPIOS PANAMENSIS	06/08/75 0004
43013901010	HAPLOSCOLOPIOS PANAMENSIS	06/08/75 0003
43013901010	HAPLOSCOLOPIOS PANAMENSIS	06/08/75 0006
	SUBTOTAL	
43014210030	SPIOPHANES CIRNATA	06/08/75 0002
43015603010	OPHELIA LIMACINA	06/08/75 0002
43015603010	OPHELIA LIMACINA	06/08/75 0007
43015603010	OPHELIA LIMACINA	06/08/75 0005
43015603010	OPHELIA LIMACINA	06/08/75 0003
43015603010	OPHELIA LIMACINA	06/08/75 0004
43015603010	OPHELIA LIMACINA	06/08/75 0006
	SUBTOTAL	
43015604020	TRAVISIA FORBESII	06/08/75 0004
43015604020	TRAVISIA FORBESII	06/08/75 0006
43015604020	TRAVISIA FORBESII	06/08/75 0002
	SUBTOTAL	
43016608020	POLYCIRRHIS MEDUSA	06/08/75 0003
43016808000	SARFILA SP.	06/08/75 0005
43000000000	MOLLUSCA	06/08/75 0004
43042401170	MACOMA BALTICA	06/08/75 0005
43042401170	MACOMA BALTICA	06/08/75 0004
	SUBTOTAL	
43042402010	TELLINA LUTEA ALTERNIDENTATA	06/08/75 0006
43042402010	TELLINA LUTEA ALTERNIDENTATA	06/08/75 0003
43042402010	TELLINA LUTEA ALTERNIDENTATA	06/08/75 0002
	SUBTOTAL	
43050604020	SOLAFIELLA ORESCURA	06/08/75 0003
43050604020	SOLAFIELLA ORESCURA	06/08/75 0006
	SUBTOTAL	

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TOTAL COLLECTIONS AT THIS STATION

COUNT		WET WEIGHT		PER SQ METER	
NO.	PCT	GRAMS	PCT	NO.	WWGT
1	0.63	0.001	0.00	1	0.001
1	0.63	0.001	0.00	1	0.001
1	0.63	0.002	0.01	1	0.003
1	0.63	0.009	0.05	1	0.013
1	0.63	0.000	0.00	1	0.001
1	0.63	0.146	0.79	1	0.208
4	2.52	0.007	0.04	6	0.010
2	1.26	0.004	0.02	3	0.006
3	1.89	0.009	0.05	4	0.013
4	2.52	0.008	0.04	6	0.011
13	8.19	0.028	0.15	19	0.040
1	0.63	0.000	0.00	1	0.000
14	8.81	0.170	0.92	20	0.244
1	0.63	0.	0.	1	0.
2	1.26	0.010	0.06	3	0.015
1	0.63	0.002	0.01	1	0.002
1	0.63	0.011	0.06	1	0.016
1	0.63	0.002	0.01	1	0.002
20	12.58	0.195	1.05	29	0.279
1	0.63	0.008	0.04	1	0.011
5	3.14	0.037	0.20	7	0.053
2	1.26	0.035	0.19	3	0.050
8	5.03	0.080	0.43	11	0.115
1	0.63	0.004	0.02	1	0.006
1	0.63	0.000	0.00	1	0.000
1	0.63	0.001	0.01	1	0.002
1	0.63	0.004	0.02	1	0.005
1	0.63	0.001	0.01	1	0.002
2	1.26	0.005	0.03	3	0.007
1	0.63	1.119	6.04	1	1.599
2	1.26	2.959	15.96	3	4.228
1	0.63	0.252	1.36	1	0.359
4	2.52	4.330	23.35	6	6.186
1	0.63	0.010	0.05	1	0.014
1	0.63	0.006	0.03	1	0.008
2	1.26	0.015	0.08	3	0.022

ME 1975

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PERCENTS REFER TO TOTAL COLLECTIONS AT THIS STATION

SAMPLE DATE	SAMP NO.	COUNT NO.	PCT	WET GRAMS	WEIGHT PCT	PER NO.	SO METER WWGT
06/08/75	0003	1	0.63	0.	0.	1	0.
06/09/75	0003	1	0.63	0.065	0.35	1	0.093
06/08/75	0002	1	0.63	0.001	0.00	1	0.001
06/08/75	0006	1	0.63	0.005	0.02	1	0.007
SUBTOTAL		2	1.26	0.005	0.03	3	0.008
06/08/75	0002	1	0.63	0.001	0.00	1	0.001
06/09/75	0002	2	1.26	0.007	0.04	3	0.010
06/09/75	0006	1	0.63	0.020	0.11	1	0.028
06/09/75	0005	1	0.63	0.004	0.02	1	0.006
06/09/75	0003	4	2.52	0.	0.	6	0.
06/08/75	0004	3	1.89	0.006	0.03	4	0.009
SUBTOTAL		11	6.92	0.037	0.20	16	0.053
06/08/75	0002	1	0.63	0.000	0.00	1	0.000
06/08/75	0004	1	0.63	0.033	0.18	1	0.047
06/09/75	0005	1	0.63	0.049	0.26	1	0.070
06/09/75	0006	1	0.63	0.292	1.57	1	0.417
SUBTOTAL		3	1.89	0.373	2.01	4	0.533
06/09/75	0004	1	0.63	0.000	0.00	1	0.000
06/09/75	0005	1	0.63	0.013	0.07	1	0.018
SUBTOTAL		2	1.26	0.013	0.07	3	0.018
06/08/75	0005	12	7.55	4.403	23.75	17	6.291
06/08/75	0004	27	16.98	7.617	41.08	39	10.882
06/08/75	0006	5	3.14	0.022	0.12	7	0.031
06/08/75	0002	12	7.55	1.091	5.88	17	1.559
06/09/75	0007	15	9.43	0.	0.	21	0.
06/08/75	0003	6	3.77	0.079	0.42	9	0.117
06/09/75	0001	1	0.63	0.018	0.10	1	0.026
SUBTOTAL		78	49.06	13.230	71.35	111	18.900
STATION TOTAL		159		18.544		227	26.491

APPENDIX III. Species used in classification of Bering
Sea benthic stations infaunal studies.

Polychaeta

Gattyana treadwelli
Harmothoe imbricata
Polynof canadensis
Peisidice aspera
Phloe minuta
Anaitides groenlandica
Anaitides mucosa
Anaitides maculata
Eteone spetsbergensis
Eteone longa
Nephtys ciliata
Nephtys caeca
Nephtys punctata
Nephtys Rickettsi
Nephtys longasetosa
Aglaophamus rubilla anops
Glycera capitata
Glycinde picta
Glycinde armigera
Onuphis geophiliformis
Eunice valens
Lumbrinereis similabris
Lumbrinereis zonata
Ninve gemma
Drilonereis falcata minor
Haploscoloplos panamensis
Haploscoloplos elongatus
Scoloplos armiger
Aricidea suecica
Aricidea uschakowi
Paraonis gracilis
Laonice cirrata
Polydora socialis
Polydora concharum
Prionospio malmgreni
Spio filicornis
Spiophanes bombyx
Spiophanes kroyeri
Spiophanes cirrata
Magelona japonica
Magelona pacifica

Polychaeta (cont.)

Tharyx sp.
Chaetozone setosa
Brada villosa
Scalibregma inflatum
Ammotrypane aulogaster
Ophelia limacina
Travisia brevis
Travisia forbesii
Sternaspis scutata
Capitella capitata
Heteromastus filiformis
Maldane sarsi
Maldane glebifex
Nicomache personata
Notoproctus pacifica
Praxillella gracilis
Praxillella praetermissa
Rhodine loveni
Owenia fusiformis
Myriochele heeri
Cistenides brevicoma
Cistenides granulata
Cistenides hyperborea
Ampharete arctica
Ampharete acutifrons
Lysippe labiata
Pista cristata
Pista maculata
Artacama proboscidea
Laphanis boeckii
Proclea emmi
Terebellides stroemi
Chone gracilis
Chone infundibuliformis
Chone cincta
Chone dumeri
Euchone analis
Pseudopotamilla reniformis
Cossura longocirrata

APPENDIX III. continued

Mollusca

Acila castrensis
Nucula tenuis
Nuculana permula
Yoldia amygdalea
Yoldia hyperborea
Yoldia scissurata
Yoldia secunda
Dacrydium pacificum
Modiolus modiolus
Astarte polaris
Astarte esquimaulti
Cyclocardia ventricosa
Cyclocardia crebricostata
Cyclocardia crassidens
Axinopsida serricata
Thyasira flexuosa
Mysella tumida
Mysella aleutica
Odontogena borealis
Clinocardium ciliatum
Serripes groenlandicus
Psephidia lordi
Spisula polynyma
Macoma calcarea
Macoma brota
Macoma moesta alaskana
Macoma lama
Tellina lutea alternidentata
Lyonsia norvegica
Margarites olivaceus
Solariella obscura
Solariella varicosa
Tachyrynchus erosus
Polinices narus
Polinices pallida
Neptunea ventricosa
Neptunea heros
Admete couthouyi
Retusa obtusa
Cylichna occulta
Cylichna alba

Arthropoda

Balanus crenatus
Balanus hesperius
Balanus rostratus
Leucon nasica
Eudorella emarginata
Eudorella pacifica
Eudorellopsis integra
Eudorellopsis deformis
Diastylis alaskensis
Diastylis bidentata
Diastylis cf. D. tetradon
Ampelisca macrocephala
Ampeliscidae birulai
Ampeliscida eschrichti
Ampeliscida furcigera
Byblis gaimandi
Argissa hamatipes
Corophium crassicorne
Erichthonius hunteri
Melita dentata
Melita formosa
Euhaustorius eous
Pontoporeia femorata
Urothoe denticulata
Haustorius eous
Photis spasskii
Photis ninogradovi
Protomedea fascata
Protomedea grandimana
Protomedea fasciatoides
Protomedea chaelata
Anonyx nugax
Hippomedon kurilious
Orchomene nugax
Orchomene lepidula
Bathymedon nanseni
Monoculodes zernovi
Westwoodilla caecula
Harpinia kobjakovae
Harpinia gurjanovae
Harpina tarasovi

APPENDIX III. continued

Arthropoda (cont.)

Paraphoxus simplex
Paraphoxus milleri
Paraphoxus obtusidens
Thysanoessa raschi

Sipunculida

Golfingia margaritacea
Phascolion strombi

Priapulida

Priapulus caudatus

Brachiopoda

Terebratalia crossei

Echinodermata

Asterias amurensis
Dendraster excentricus
Echinarachnius parma
Amphipholis pugetana
Diamphiodia craterodmeta
Ophiura sarsi
Cucumaria calcigera
Psolus phantapus

Urochordata

Boltenia ovifera
Boltenia villosa

APPENDIX IV. Mathematical operations used in cluster analysis, principal components analysis, and principal coordinates analysis.

For the purposes of this appendix, it will be assumed that data has been gathered for n species from m stations. The data will be contained in the matrix X where x_{ij} represents the number of the i th species found at the j th station. The n rows of this matrix then represent species while the m columns represent stations.

Part 1. Cluster Analysis.

Given the matrix X , a distance matrix S is constructed such that s_{ij} represents the distance between stations i and j (normal analysis) or species i and j (inverse analysis). The Czekanowski and Canberra metric dissimilarity coefficients were used as distance measures in the normal analysis while only the Czekanowski measure was used in the inverse analysis.

Normal analysis:

$$\text{Czekanowski coefficient } s_{ij} = \frac{\sum_{e=1}^m |(x_{ei} - x_{ej})|}{\sum_{e=1}^m (x_{ei} + x_{ej})} \quad (1)$$

$$\text{Canberra metric coefficient } s_{ij} = \frac{\sum_{e=1}^m \frac{|x_{ei} - x_{ej}|}{(x_{ei} + x_{ej})}}{\quad} \quad (2)$$

In the normal analysis, S is $m \times m$ and symmetric.

Inverse analysis:

$$s_{ij} = \frac{\sum_{e=1}^n \frac{|x_{ie} - x_{je}|}{\quad}}{\sum_{e=1}^n (x_{ie} + x_{je})} \quad (3)$$

In the inverse analysis, S is $n \times n$ and symmetric.

The cluster analysis proceeds by joining entities of the matrix S (since S is symmetric, rows and columns represent the same entity). This is accomplished by finding the smallest element in S (corresponding to the smallest distance between entities) and joining these elements. Distance between the newly formed entity and all remaining individuals or entities must be recalculated according to the general formula:

$$d_{hk} = \alpha_i d_{hi} + \alpha_j d_{hj} + \beta d_{ij} + \gamma |d_{hi} - d_{hj}| \quad (4)$$

Entities i and j have been fused and renamed " k "; d_{hk} is the new distance between cluster k and some previously existing cluster, h . The recalculated distances are substituted for the row (considering only the lower triangle of S , since it is symmetric) entries in S corresponding to

one of the fused elements. The row corresponding to the other fused element is removed and the dimension of S are effectively reduced by 1×1 after each fusion procedure.

The specific values of parameters of the update equation (equation 4) used in this study are:

Nearest neighbor strategy

$$(\alpha_i = \alpha_j = +0.5, \beta = 0, \gamma = -0.5) \quad (5)$$

Group average strategy

$$(\alpha_i = n_i/n_k, \alpha_j = n_j/n_k, \beta = \gamma = 0.0) \quad (6)$$

Flexible sorting strategy

$$(\alpha_i + \alpha_j + \beta = 1.0, \alpha_i = \alpha_j, \beta < 1.0, \gamma = 0.0) \quad (7)$$

[see Lance and Williams (1977) and Anderberg (1973)].

Part 2. Principal Components Analysis.

Slightly different procedures are followed to calculate the variants of principal components analysis used in this study. These variants are the principal components analysis based on the covariance matrix and the principal components analysis based on the correlation matrix.

Given the matrix X , row centering to produce the matrix A is accomplished as follows:

$$\text{Covariance matrix} \quad a_{ij} = \frac{x_{ij} - \bar{x}_i}{\sqrt{m-1}} \quad (8)$$

$$\text{Correlation matrix} \quad a_{ij} = \frac{x_{ij} - \bar{x}_i}{\sqrt{\frac{m}{\sum_{e=1}^m (x_{ie} - \bar{x}_i)^2}}} \quad (9)$$

where a_{ij} is an element of the matrix A and \bar{x}_i equals the row mean:

$$\bar{x}_i = \left(\frac{m}{\sum_{e=1}^m x_{ie}} \right) / m \quad (10)$$

A is thus $m \times m$.

The matrix Q is then formed by:

$$Q = A'A \quad (11)$$

where A' represents the transpose of A.

The eigenvalues and eigenvectors of Q are then found. The vector of station projections on the i th axis (component scores on the i th principal component) are found as y_i , where

$$y_i = \alpha_i \quad (12)$$

is the i th eigenvector of Q adjusted such that

$$\alpha_i' \alpha_i = \gamma_i \quad (13)$$

where γ_i is the i th eigenvalue of Q (see Orloci 1967).

Part 3. Principal Coordinates Analysis.

Given the matrix X , the distance matrix S is calculated as in cluster analysis (Part 1, this appendix). S is then transformed to the matrix Q according to the following equation:

$$q_{ij} = s_{ij} - \bar{s}_i - \bar{s}_j + \bar{s} \quad (14)$$

where \bar{s}_j is the mean of the i th row or column of S (S is $m \times m$ and symmetric):

$$\bar{s}_i = \frac{\sum_{j=1}^m s_{ij}}{m} \quad (15)$$

and \bar{s} is the overall mean:

$$\bar{s} = \frac{\sum_{j=1}^m \sum_{i=1}^m s_{ij}}{m} \quad (16)$$

The vector of projections of the m stations (represented by rows or columns of the matrix S) onto the principal axes is found as y_i where

$$y_i = \delta_i \quad (17)$$

and δ_i is the i th eigenvector of Q scaled such that

$$\delta_i' \delta_i = \gamma_i \quad (18)$$

where γ_i is the i th eigenvalue of the matrix Q (see Gower 1966).

APPENDIX V. Matrix of average cell densities. Cells are composed of station groups or unclassified stations and species groups as indicated by cluster

analysis. Density = $\frac{\sum_{i=1}^s \sum_{j=1}^n x_{ij}}{ns}$ where n = number of stations in

cell, s = number of species in cell, x_{ij} = number of individuals of the ith cell species found at the jth cell station.*

Species Group	MSG	30,49	64,70	OSG	IG3	47,55	IG1	4	24	14	35	15	IG2	2	81,82
1	-	-	-	-	0.1	-	-	-	-	5.0	-	-	-	-	-
2	0.4	-	0.8	0.7	0.2	-	0.2	-	-	5.0	-	-	-	-	-
3	0.1	-	-	-	2.8	1.3	-	-	-	0.7	-	-	-	-	-
4	0.6	3.3	-	0.1	33.7	-	1.2	-	-	15.0	-	-	1.5	-	1.8
5	0.1	-	-	0.1	1.2	1.0	0.6	-	-	12.0	1.0	-	0.4	-	-
6	52.9	-	-	0.3	1.3	1.0	0.1	-	-	-	10.0	-	-	-	-
7	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-
8	0.1	-	-	6.2	0.1	-	0.1	-	0.3	3.2	4.8	0.2	-	1.0	-
9	-	-	-	-	-	-	-	-	-	-	2.0	-	-	-	-
10	-	-	-	0.3	0.2	-	-	-	-	2.4	70.0	0.4	-	-	0.2

*(-) indicates zero entry.

APPENDIX V. continued

Species Group	MSG	30,49	64,70	OSG	IG3	47,55	IG1
11	0.6	-	-	1.8	0.4	-	0.2
12	-	-	-	0.3	-	-	-
13	0.2	-	-	0.9	1.4	-	-
14	8.0	-	-	0.1	-	1.0	-
15	0.1	-	1.0	4.3	-	-	-
16	0.1	-	-	0.4	0.3	0.5	1.2
17	0.7	-	-	-	0.2	-	0.9
18	2.3	-	-	-	0.5	-	0.9
19	-	-	-	0.4	0.2	-	22.8
20	0.6	-	-	0.1	-	-	0.8
21	1.4	-	-	0.9	0.3	2.0	1.2
22	0.5	-	-	0.3	-	-	-
23	0.9	-	-	1.6	-	1.0	1.4
24	10.2	-	1.1	10.1	0.2	1.7	0.8
25	40.1	9.2	6.6	14.6	4.3	16.9	26.0
26	11.6	1.5	33.5	5.2	0.6	5.4	2.2
27	3.9	0.1	0.7	0.6	0.2	0.3	0.3
28	45.5	15.2	35.5	26.0	2.7	18.1	10.9

4	24	14	35	15	IG2	2	81,82
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-
-	5.0	1.0	-	-	-	-	-
-	-	-	-	-	-	-	-
-	-	1.0	-	-	-	-	-
-	2.5	-	-	-	13.8	-	-
-	-	-	-	-	-	-	-
-	-	-	-	-	0.2	-	-
3.3	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	1.0
-	2.5	-	-	-	-	-	2.5
-	-	-	-	-	-	-	13.7
3.6	65.7	2.4	1.9	2.1	0.3	2.2	3.3
-	2.0	-	0.4	1.2	-	-	8.2
-	2.9	0.3	0.3	2.6	0.3	3.8	11.3
-	0.3	1.8	6.9	0.9	0.1	-	92.7

APPENDIX V. continued

Species Group	MSG	30,47	64,70	OSG	IG3	47,55	IG1	4	24	14	35	15	IG2	2	81,82
29	-	10.5	-	7.6	-	0.5	0.4	5.0	-	-	4.0	-	-	-	-
30	6.3	6.4	34.2	42.7	0.3	31.0	0.3	-	5.2	0.9	2.4	9.1	-	-	1.2
31	1.4	-	-	0.2	0.2	179.3	0.4	-	-	-	-	-	-	-	-
32	1.7	-	-	0.2	2.0	7.7	5.3	-	-	-	0.7	0.7	-	-	0.3
33	-	-	-	0.4	0.3	3.0	0.1	-	-	-	-	-	0.5	26.7	-
34	-	-	-	0.1	0.2	0.5	0.5	61.0	116.3	2.0	1.0	1.0	-	3.3	-
35	2.8	-	-	1.4	0.3	-	1.5	13.3	16.3	-	8.0	-	-	-	0.5
36	0.7	-	-	0.7	4.4	3.0	7.3	-	22.5	0.7	20.7	-	-	-	-
37	0.2	-	0.5	0.6	1.2	1.8	1.9	2.5	1.3	-	-	2.0	-	-	-
38	1.3	-	-	-	-	4.0	14.6	-	-	-	-	-	0.2	-	-
39	20.2	-	0.2	0.3	3.3	9.1	29.1	1.5	2.2	0.2	0.7	0.7	8.0	1.9	-
40	2.8	4.5	1.1	7.4	13.3	17.1	30.4	4.8	12.7	1.1	2.3	1.0	12.3	0.4	0.3
41	0.1	0	128.0	-	36.7	39.0	3.6	-	-	-	-	-	-	-	-
42	0.6	-	-	-	38.2	-	38.2	-	-	-	-	-	-	-	-
43	0.1	-	-	1.6	0.8	-	0.1	-	-	-	-	18.0	0.2	-	-
44	-	21.3	-	0.1	0.5	-	0.7	-	-	-	-	1.0	-	-	-
45	1.7	-	7.0	-	-	-	0.1	-	-	-	-	-	-	-	-
46	-	1.5	34.3	2.7	-	0.5	1.1	-	-	-	-	-	-	-	-

APPENDIX V. continued

Species Group	MSG	30,47	64,70	OSG	IG3	47,55	IG1	4	24	14	35	15	IG2	2	81,82
47	-	-	1.7	0.3	-	-	-	-	-	-	-	-	-	-	-
48	0.1	-	2.7	-	-	3.0	0.6	-	-	-	-	-	-	-	-
49	-	-	-	0.1	-	-	-	32.5	-	-	-	-	-	-	-
50	-	-	-	-	-	-	1.6	3.3	-	10.0	-	-	-	-	-
51	-	-	-	0.3	0.4	-	0.8	3.3	-	-	-	1.2	-	-	-
52	-	-	-	-	0.3	-	0.1	-	-	-	-	-	-	-	-
53	-	-	-	-	114.6	-	-	-	-	-	-	-	-	-	-
54	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-	-
55	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-
56	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-

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