

COMMUNITY PATTERNS OF EPIPELAGIC FAUNA ACROSS THE
NORTH PACIFIC SUBARCTIC FRONTAL ZONE: 170°E - 145°W

by

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ABSTRACT

Data from the 1990-1991 monitoring program of Japanese squid driftnet fisheries were used to assess interrelationships among fauna along the North Pacific Subarctic Frontal Zone (SFZ). Correspondence analysis (an ordination method), generally revealed a gradient in similarity patterns among individual driftnet operations and taxa, implying the existence of an underlying environmental gradient affecting community structure in the SFZ. Salmon (*Oncorhynchus* spp.) and pelagic armorhead (*Pentaceros richardsoni*), however, were atypical; they were seldom located near or along the gradient and often characterized fishing operations tangential to the gradient. The two most abundant taxa, neon flying squid (*Ommastrephes bartrami*, the target species of the fishery) and Pacific pomfret (*Brama japonica*), were also the two most pervasive taxa among the individual operations. They were also nearly equal in catch per unit effort (CPUE) between operations for each month and year of the sampling program. Average linkage cluster analysis revealed that driftnet operations could be classified into at least two taxa assemblages, one representing cool sea surface temperatures (SSTs) in the western part of the fishery and the other representing warmer SSTs in the east. The assemblages were most often differentiated by one or two characteristic taxa (in particular, pelagic armorhead or salmon) and abundance patterns of several other key taxa. However, due to gradual and overlapping similarity patterns between assemblages, community variation of the pelagic fauna in the SFZ, where our sampling occurred, is best viewed from the continuum paradigm.

Key Words: Epipelagic Community Variation, North Pacific Squid Driftnet Fishery, Subarctic Frontal Zone, Multivariate Methods.

identify, where possible, distinct groupings of operations (hereafter referred to as clusters or assemblages) based on occurrences of taxa; (3) examine the relationship between community variation, spatial position, and SST; and (4) compare results of (3) across months and years to identify broad patterns of community attributes.

METHODS

The Driftnet Data

The International North Pacific Fisheries Commission (1991 and 1992), and Pella et al. (1992) previously described the Japanese squid driftnet observer program and data collection methods. The pertinent data consists of measurements of the following variables for each observed fishing operation: abundances (counts) of each species caught, latitude and longitude (to the nearest minute), date, and sea surface temperature (SST). An operation usually consisted of 10 consecutively placed net sections (about 1000 standardized 50 m tans) deployed for an overnight soak. Nets had an average stretched mesh diameter of 114 mm (standard error = 0.05). Observers were instructed to monitor 6-7 sections (700-800 standardized 50 m tans) selected at random from those deployed. We retained only decked and/or positively identified specimens in the species data. Soaks beyond one day (i.e., the second day of "tome amis") were not analyzed. Net locations (latitude and longitude) are the mean of two records entered at the beginning and end of net deployment. Date was recorded at the beginning and end of an operation; we used the beginning date. The mean and range of the four SST measurements taken during an operation (SST was measured before and after net deployment and before and after net retrieval) were calculated. General sea conditions (e.g., beaufort state) were also recorded. We used data collected in summer (June to August) in the present analysis; this period accounted for most of the total sampling effort (86% in 1990; 81% in 1991). The number of observed driftnet operations in 1990 was 2474 (755 in June, 1082 in July, and 637 in August) and in 1991 was 2176 (579 in June, 932 in July, and 665 in August).

Fig. 1 shows the monthly sampling pattern of observed operations for 1990 and 1991 data. We performed statistical analyses for each year separately. Also, since legal boundaries of the fishery moved north on a monthly basis we conducted separate analyses by month to avoid confounding location with time. Initially, two approaches to selecting subsets of data were taken. First, we analyzed all data within legally established boundaries. Second, since northern boundaries usually differed between eastern and western sides of the fishery, only data collected south of the southern-most northern boundary were used. This latter approach provided monthly subsets of data with equivalent latitudinal coverage. Because our analyses gave similar results for both methods and because a large number of fishing operations were

INTRODUCTION

Assessment of pelagic community attributes, particularly with regard to oceanographic features, has become a major goal in marine ecology. Various groups of organisms have been studied, including plankton (e.g., McGowan, 1986; Austen et al., 1991), shrimps (Krygier and Wasmer, 1988), midwater fishes (Willis et al., 1988), seabirds (e.g., Pocklington, 1979; Ainley and Boekelheide, 1983), and nekton (e.g., Backus et al., 1970). Some researchers have focused on North Pacific communities. Wahl et al. (1989), for example, found that spatial distributions of seabird assemblages are associated with water-mass types and overlap to an extent relative to similarities in oceanographic conditions. Pearcy (1991) reviewed the general biology and compositional patterns of zooplankton and nekton associated with transitional areas between subarctic and subtropical waters and described a close link between water-mass type and species assemblages. Shimazaki (1986) studied gillnet catch along two meridional transects in the western North Pacific and found that epipelagic fish communities differ between subarctic, transitional, and subtropical domains. Kubodera (1986) found similar results with squid assemblages.

In recent years extensive data on nekton and seabirds of the central North Pacific Ocean have been collected through observer monitoring of high-seas squid driftnet fisheries. Although monitoring of the Japanese fishery first began in 1989, a more comprehensive sampling program was undertaken in 1990 that involved monitoring of 74 fishing vessels in 1990 (Int. North Pac. Fish. Comm., 1991) and 61 vessels in 1991 (Int. North Pac. Fish. Comm., 1992). The driftnet observer program has provided an extensive database of driftnet-caught epipelagic species abundances during summer (primarily) and fall fishing operations; concurrent physical data has included sea surface temperature (SST).

We considered the efficacy of using squid-driftnet data to perform a community-level analysis. The fishery uses gear selected to catch a particular size-class of squid (primarily *Ommastrephes bartrami*; Ignell, 1991a). However, driftnets also entrap a wide variety nekton and some sea birds (Int. North Pac. Fish. Comm. 1991), providing a sample of large epipelagic fauna from pelagic communities in the North Pacific Ocean. Areas covered by the fishery are subject to legal constraints. Northern boundaries of the fishery change (typically move north 2-3°) on a monthly basis, resulting in areas of comparable data that cover up to 90° of longitude and only 2-3° of latitude. The fishery occurs from 170°E to 145°W longitude, with maximum northern boundaries from 40°N to 46°N latitude (Fig. 1; also see Pennoyer, 1990).

In the present study we assess interrelationships among epipelagic taxa (species or genus level) using Japanese squid-driftnet data collected in June, July, and August of 1990 and 1991. We addressed the following objectives: (1) Evaluate multi-taxa similarity patterns among individual driftnet operations; (2)

paradigm of discrete taxa assemblages, and ordination, which follows the continuum paradigm in ecology. Although community variation is generally viewed as being continuous across environmental gradients (e.g., Pielou, 1977; Digby and Kempton, 1987), the two techniques provide a complementary approach to summarizing community structure patterns.

Average linkage cluster analysis (CLA) on a simplified Morisita similarity (SM) matrix (Horn 1966) was used to classify operations into compositionally distinct taxa assemblages. The SM index was chosen since it remains relatively unaffected by differences in diversity and total abundance between SUs (Wolda, 1981; Krebs, 1989) and works well with log transformed data (Wolda, 1981). Three criteria -- R^2 , Pseudo- F , and Pseudo- t^2 -- were uniformly evaluated to determine the number of clusters in each subset of data (Milligan and Cooper, 1985). A consensus among the three statistics was sought -- a local peak in pseudo- F , high t^2 in the next cluster grouping, and a relatively high or sharp increase in R^2 . The analysis was accomplished by inputting a distance matrix (1-SM) into SAS Procedure CLUS (version 6.06). For comparative purposes the approach was also applied using the Jaccard coefficient of resemblance (see Krebs, 1989) on the binary taxa data. Here we present only results using the SM index and note that the Jaccard index provided similar cluster assignments. Both indices are unaffected by zero-zero matches in the data (Krebs, 1989; also see Ludwig and Reynolds, 1988). CPUE data in assigned clusters were then pooled and graphically presented using a modified dominance-diversity curve (Whittaker, 1965). Unclassified operations (singlets and small clusters) were excluded from subsequent graphical and statistical analyses.

Three approaches were used to help interpret results of the cluster analyses. First, SUs identified by cluster assignment were plotted in the explanatory variable space (location and SST). Only SUs occurring within the joint inter-quartile range (midrange) of the explanatory variables were included to reveal the central tendency of the clusters. Second, discriminant function analysis (DFA) was used to determine the degree of separability of assemblages (defined by CLA) using the explanatory variables. Results were evaluated based on the strength of canonical correlation(s) and the success rate of re-classification using a quadratic discriminant function with a jackknife (cross-validation) procedure. Finally, multivariate analysis of variance (MANOVA) followed by pair-wise Bonferroni t -tests were used to separate cluster means. The last two analyses were performed using SAS Procedures DISCRIM and GLM (version 6.06), respectively.

Correspondence analysis (COA) was used to simultaneously ordinate operations and taxa. COA is a dimension reduction method that arranges SUs and taxa along coordinate axes such that the relative position provides information about their ecological similarity. By identifying operations similar (or dissimilar) to one another based on coordinate position, we looked for underlying biological or environmental factors that may influence the

removed when the data were constrained to the southern-most northern boundary (decreasing precision of our analyses), results of only the first approach (legal boundaries) are presented here. All operations occurred within 37° and 46° N. latitude and 170°E and 145°W longitude. This area is bisected by the subarctic frontal zone (Roden, 1991), extends into the Transition Zone (south) and Subarctic Domain (north), and covers approximately 45° of longitude.

The primary sampling unit (SU) in our study was the observed portion of a fishing operation, which ranged in size from 90 to 1248 standard tans ($\bar{X} = 784$) in 1990 and 189 to 1050 standard tans ($\bar{X} = 797$) in 1991. Species counts were therefore standardized to catch per 1000 tans (CPUE) to give equivalent-scaled catch rates. (Hereafter we use the terms "operation" and "SU" interchangeably.) Soak times, timing of net placement, and retrieval techniques also varied to some extent among operations. We note these probable sources of sampling error but assume that they are relatively small compared to natural variation (see Gauch, 1982).

Several observed species occurred in only a few (<1%) of the operations, resulting in zero entries in the original data matrix. Uncommon or rare species can cause several problems in a statistical analysis (e.g., spurious pair-wise correlations; see Legendre and Legendre, 1983; Ludwig and Reynolds, 1988; Clarke and Green, 1988; Krebs, 1989). We used a combination of corrective measures with the intention of retaining as much information in the data as possible. First, statistical methods that remain relatively unaffected by zero entries were used whenever possible (Krebs, 1989); this approach is discussed further in the section on statistical analyses. Second, rare species were either deleted or, where practical, pooled to higher taxonomic levels until occurrence rates improved (Clarke and Green, 1988; Warwick, 1988). For example, sea turtles, which occurred in only 5 operations, were deleted; salmonids (*Oncorhynchus* spp.) were pooled into one taxon. Rare species were never pooled with common species, however, since that would bias the latter. For example, bluefin tuna (*Thunnus thynnus*), which occurred in only 2.5% of the operations, were not pooled with albacore (*Thunnus alalunga*), which occurred in 64% of the operations. Table 1 gives scientific names, common names, and abbreviation codes (used in graphs) of the 36 selected taxa.

CPUE data were routinely transformed to $\ln(\text{CPUE}+1)$ to help control extreme positive skewness of sample distributions and de-weight abundances of very common taxa (Wolda, 1981; Clarke and Green, 1988; Krebs, 1989). Abundances were also converted to binary (presence/absence) data for some of the analyses.

Statistical Analyses

We used multivariate methods described, variously, in Gauch (1982), Manly (1986), Digby and Kempton (1987), Ludwig and Reynolds (1988), Clarke and Green (1988), ter Braak and Prentice (1988), Krebs (1989), and Warwick and Clarke (1991). We examined community variation using techniques of classification, which follows the

canonical correlation was primarily weighted by longitude and the second by SST (Table 3). The total misclassification rate was lowest for cluster 2 (13.1%). Most misclassifications occurred between clusters 1 and 3 (12.1%), and, to a lesser extent, between clusters 1 and 2 (10.2%). These results are also apparent in the midrange plots where clusters 2 and 3 appear fairly distinct in location and SST.

The first three dimensions of COA accounted for 44.6% of the total variation in the June 1990 data. A plot of the first two COA dimensions (Fig. 4) showed transition zones between the assemblages, although the results were generally consistent with CLA. This transition is associated with a similar gradient in taxa similarities and positioning. Note the near-origin position of neon flying squid, pomfret, and sunfish suggesting that these are non-characteristic taxa as indicated by CLA. Cluster 3 operations were arranged tangential to those of clusters 1 and 2, due primarily to the influence of pelagic armorhead.

Canonical Correlation Analysis (CCA) between the first 3 community (COA) indices and the 3 explanatory variables gave the following canonical correlations: $r_1=.791$ ($P<.001$) and $r_2=.423$ ($P<.001$). The first pair of canonical variates primarily represents community index 1 and longitude. The second pair of canonical variates primarily represents community indices 2-3 and SST (Table 4).

July 1990

Operations were grouped into two assemblages (97.5% classified) by CLA. Salmon differentiated cluster 1 whereas pelagic armorhead was generally unique to cluster 2; the remaining taxa were fairly non-characteristic (Fig. 5). The two clusters differed highly ($p<.001$) in longitude and latitude, but not in SST ($p=.79$). Cluster 1 was located principally in the western portion of the fishery and cluster 2 in the eastern portion (Table 2; Fig. 6).

DFA using only latitude and longitude correctly assigned 78.7% of the observations. The first canonical correlation was primarily weighted by longitude (Table 3). The misclassification rate was lowest for cluster 2 (11.4%).

The first three dimensions of COA accounted for 39.2% of the total variation in the July data. Operations associated with the two assemblages were fairly separate when plotted on the first two COA dimensions (Fig. 7A). This separation occurred primarily along the second COA dimension. Except for salmon and pelagic armorhead, taxa were also generally arranged along the area of transition between the two clusters (Fig. 7B). Once again, neon flying squid and pomfret were non-characteristic, although common and highly abundant.

Correlations coefficients from CCA were $r_1=.73$ ($P<.001$) and $r_2=.47$ ($P<.001$). These correlations primarily represent, respectively, the association between COA dimension 1 and longitude, and the association between COA dimension 2 and latitude and SST (Table 4).

community structure. COA was used in conjunction with CLA to assess similarity patterns of taxa and operations relative to cluster assignment. Plots of operations and taxa using the two major COA dimensions (axes) were then produced. The first three dimension scores of each analysis were retained for later use.

The relationship between major COA ordinate scores and position and SST was evaluated using canonical correlation analysis (CCA). This method detects trends and associations among sets of continuous variables and thus provided a way to assess the environmental dispersion of communities (Gittins, 1979 and 1985). The analysis was conducted using SAS Procedure CANCECORR (version 6.06).

Results from CLA and COA were used to identify three general types of taxa: (1) characteristic -- those generally unique to or highly abundant in a particular assemblage and peripheral on the COA plot; (2) key -- those common to or abundant in some but not all assemblages and moderately distant from the origin of the COA plot; and (3) non-characteristic -- those fairly evenly dispersed among operations and near the origin of the COA plot. Note that we may define important taxa (in terms of relatively high CPUE) as non-characteristic.

RESULTS

June 1990

The cluster analysis (CLA) aggregated most SUs (98.8%) into three assemblages. Characteristic taxa were: salmon and eight-armed squid (*Gonatopsis borealis*), cluster 1; blue shark (*Prionace glauca*), yellowtail (*Seriola lalandi*) and albacore, cluster 2; and pelagic armorhead (*Pentaceros richardsoni*) and lancetfish (*Alepisaurus ferox*), cluster 3 (Fig. 2). Non-characteristic taxa included neon flying squid (*Ommastrephes bartrami*), ocean sunfish (*Mola mola*), and to some extent Pacific pomfret (*Brama japonica*). Salmon shark (*Lamna ditropis*) may be viewed as a key taxon since it was abundant in clusters 1 and 3, but not cluster 2.

The assemblages differed in SST and location. For SST and longitude, pair-wise comparisons showed highly significant differences ($p < .001$) between each pair of clusters, whereas only clusters 1 and 2 differed significantly in latitude. These differences are easily seen in the midrange plots (Fig. 3). Cluster 1 occurred principally in the northwestern part of the fishery in moderately cool SSTs, cluster 2 occurred in the eastern portion of the fishery along a range of latitudes and in warmer SSTs, and cluster 3 occurred in the central portion of the fishery in cool SSTs (Table 2; Fig. 3).

Discriminant function analysis (DFA) using the three explanatory variables -- latitude, longitude and SST -- assigned 82.3% of the operations into the correct assemblage. The first

represents the association between COA dimension 1 and explanatory variables SST and longitude (Table 4). The second correlation primarily represents the association between COA dimension 3 and latitude.

July 1991

Operations were aggregated into two assemblages by CLA. Salmon, salmon shark, pelagic armorhead, and eight armed squid generally characterized cluster 1 (Fig. 14). Skipjack tuna characterized cluster 2 and several other subtropical taxa such as albacore, yellowtail and blue shark were considerably more abundant in this cluster than in cluster 1. Non-characteristic taxa included flying squid, pomfret, lancetfish, Pacific saury (*Cololabis saira*), and louvar (*Luvarus imperialis*; Fig. 14). The two assemblages differed highly ($p < .001$) in longitude and SST. Cluster 1 was located principally in the central portion of the fishery and in cool waters. Cluster 2 was generally located in more eastern and warmer waters (Table 2; Fig. 15).

DFA using longitude and SST as explanatory variables assigned 80.9% of the operations to the correct cluster. The first canonical correlation was primarily weighted by SST (Table 3). The misclassification rate was lowest for cluster 2 (10.3%) while 26.1% of cluster 1 operations were misclassified into cluster 2.

Almost half (45.32%) of the total variation between sampling units or taxa abundances was accounted for by the first three dimensions of COA. Most of the separation between sampling units occurred along COA dimension 1 (Fig. 16). Salmon and pelagic armorhead, while both indicative of cluster 1, were highly dissimilar and apparently associated with different operations (Fig. 16).

Canonical correlations were $r_1 = .89$ ($P < .001$) and $r_2 = .44$ ($P < .001$). The first correlation was primarily related to COA dimension 1 and SST and longitude, and the second correlation was primarily related to COA dimension 2 and latitude and longitude (Table 4).

August 1991

Three taxa assemblages were identified by CLA. Skipjack and pelagic armorhead characterized cluster 3 (Fig. 17). Several key taxa, such as albacore and blue shark, were abundant in two clusters. Cluster 1 may best be described by the lack of various subtropical taxa such as skipjack, albacore, blue shark, and pelagic armorhead. Cluster 2 is similar to cluster 3 in taxa composition and abundances, except for a lack of pelagic armorhead and skipjack (Fig. 17). The communities differed highly ($p < 0.001$) in SST, latitude, and longitude. Pair-wise comparisons showed significant differences among all pairs of assemblages in SST, and significant differences among clusters 1-2 and 2-3 in latitude and longitude. The central tendencies of the three assemblages were, respectively: (1) western portion of the fishery and cool SST; (2) western portion and moderately cool SST; and (3) eastern portion and

August 1990

Almost all operations (98.6%) were grouped into three assemblages by CLA. Cluster 1 was characterized by salmon, cluster 2 by pelagic armorhead and buller's shearwater (*Puffinus bulleri*), and cluster 3 by yellowtail and skipjack (*Euthynnus pelamis*; Fig. 8). Key taxa included pomfret, albacore, blue shark, dark shearwater, and salmon shark (see Fig. 8). The clusters differed highly in SST, latitude, and longitude ($p < .001$), and each of these differences persisted in the pair-wise comparisons. Central tendencies of the three clusters were, respectively: (1) western portion of the fishery; (2) eastern portion and cool SST; and (3) central portion and warm SST (Table 2; Fig. 9).

DFA using all three explanatory variables correctly classified 86.7% of the operations. The first canonical correlation was primarily weighted by longitude and the second correlation by SST (Table 3). The total misclassification rate was lowest for cluster 2 (5.7%) and highest for cluster 3 (30.8%).

The first three dimensions of the COA accounted for 37.7% of the total variation in the August 1990 data. Plots of the first two COA dimensions showed a broad transition in SU and taxa attributes (Fig. 10). The plots also showed a somewhat poor separation between clusters 1 and 3, despite the wide spatial separation (Fig. 9).

Correlations coefficients based on CCA were both highly significant: $r_1 = .77$ ($P < .001$) and $r_2 = .73$ ($P < .001$). The first correlation primarily represents the association between COA dimension 2 and longitude, and the second correlation primarily represents the association between COA dimension 1 and latitude and SST (Table 4).

June 1991

CLA grouped fishing operations into two assemblages. Characteristic taxa for the cluster 1 were albacore, swordfish (*Xiphias gladius*), bigeye tuna (*Thunnus obesus*) and dolfinfish (*Coryphaena hippurus*), and for the cluster 2 pelagic armorhead, salmon shark, and salmon (Fig. 11). The two assemblages differed highly in SST and longitude: cluster 1 was associated with eastern, warmer waters and cluster 2 was associated with western, cooler waters (Table 2; Fig. 12).

DFA using only longitude and SST correctly classified 90.4% of the observations. The first canonical correlation was primarily weighted by longitude (Table 3). The misclassification rate for cluster 2 was 8.1% while 14.6% of cluster 1 operations were misclassified.

The first three dimensions of the COA accounted for only 33.03% of the total variation in June 1991 data. Of these three, only the first COA dimension was useful in separating SUs and evaluating taxa (Fig. 13). Separation of the clusters appeared good with some overlap near the origin.

Canonical correlations were both highly significant: $r_1 = .79$ ($P < .001$) and $r_2 = .42$ ($P < .001$). The first correlation primarily

COA scores of flying squid and pomfret along any of the first three dimensions were typically near the origin, revealing that these taxa were non-characteristic or neutral with respect to any environmental gradient in the survey area. Other taxa such as blue shark, saury, and sunfish were occasionally non-characteristic for a particular month.

CLA generally classified the driftnet operations into at least two groups of taxa assemblages, one representing operations in cool SSTs and in the western part of the fishery and the other representing operations in warmer SSTs in the east. When a third cluster was identified, its component operations were generally located in eastern, but cool waters. This occurred in August (both years) and in June 1990.

The clusters were most often differentiated by longitude and/or SST. For each month, Bonferroni t-tests showed highly significant differences in longitude and SST between each pair of clusters. This differentiation is easily visualized in the midrange plots where there is typically a high degree of separation in longitude and SST values between clusters. The canonical correlation and discriminant analyses showed longitude and then SST as the two best predictors of cluster assignment. The importance of longitude in explaining community variation is also reflected in the spatial distribution of individual species. Ignell (in prep) used Generalized Additive Models (GAM) to estimate the relative effect of SST, latitude, and longitude on catch rates of 9 bycatch species in the 1990-91 Japanese driftnet fishery. His results indicate that most of the species have zonal patterns of abundance. Some species (e.g., yellowtail, skipjack, and blue shark) are primarily abundant along the eastern portion of the fishery, some (e.g., salmon) are primarily abundant along the western portion, and some (e.g., pelagic armorhead) exhibit peak abundances within the fishery. These patterns are independent of SST and the latitudinal position of the 5° isotherm at 100 m, and for some species, even persist across months and years.

Comparison of results between months should be viewed with caution since boundaries of the fishery moved northward 2-3° each month. However, variation in community composition across months was largely determined by monthly changes in species abundance patterns. For example, months in which skipjack tuna, bigeye tuna, and dolfinfish were not identified as characteristic were also months in which catch rates or occurrences of these species were too low to be included in the cluster analysis or ordination. Other species such as albacore and salmon shark exhibited monthly changes in abundance pattern -- abundance peaks vary from the eastern to western edge of the fishery (Ignell, in prep) -- thus they may or may not be uniquely associated with a particular assemblage of taxa.

The importance of longitude in explaining community patterns and species characteristics may result from its role in integrating environmental and geographical effects on species distributions. Physical variables such as subsurface salinity and temperature,

moderately cool SST (Table 2; Fig. 18).

Using the three explanatory variables, DFA correctly classified 70.9% of the observations. The first canonical correlation was primarily weighted by longitude and the second by SST (Table 3). The total misclassification rate was lowest for cluster 3 (14.8%) and highest for cluster 1 (42.4%); 31.9% of cluster 1 operations were incorrectly classified into cluster 2.

The first three COA dimensions accounted for 39.17% of the total variation in August 1991 data. A plot of the first two COA dimensions showed a transition in taxa attributes between clusters 1 and 2 (Fig 19A), which is associated with a similar gradient in taxa dispersions (Fig. 19B). Similar to the results of June 1990 (Fig. 4), cluster 3 operations were arranged tangentially to those of clusters 1 and 2 due to the influence of pelagic armorhead (Fig. 19B).

Canonical correlations were $r_1=.70$ ($P<.001$) and $r_2=.51$ ($P<.001$). The first correlation was primarily between COA dimension 1 and latitude and longitude and the second correlation was primarily between COA dimension 2 and SST and longitude (Table 4).

DISCUSSION

The community ordination (COA) generally revealed a one-dimensional gradient or belt in SU and taxa similarities, although a few strongly characteristic taxa caused divergences from this pattern. When plotted along the first two COA dimensions, the presence of the belt implies the existence of an underlying environmental gradient affecting taxa composition, thus community structure, in the SFZ. The gradient also appeared slightly curvilinear in some months suggesting non-linear taxa-abundance patterns over the environmental gradient of the area surveyed. Fishing operations were generally arranged along the gradient of distribution of taxa. Where this occurred, operations at opposite ends of the belt were always assigned to separate groups by the clustering procedure (CLA).

Characteristic taxa included pelagic armorhead, salmon, and, in August samples, skipjack tuna. Their positions in COA space were peripheral and seldom located near or along the gradient formed by the other taxa. When fishing operations were grouped into three rather than two clusters, the additional cluster was always defined by the inclusion of pelagic armorhead and located in COA space tangential to and distinct from the gradient comprised of the remaining operations.

The two most abundant taxa caught in observed driftnet operations, neon flying squid and pomfret, were also the two taxa most pervasive among the assemblages. (We anticipated this finding for neon flying squid since it is the target species of the fishery.) CPUE values for these taxa were also nearly identical between clusters for each month and year of the sampling program.

three COA dimensions. Plots of the first two COA dimensions generally showed a gradient in taxa and SU similarities. Finally canonical correlation analysis revealed a strong relationship between the COA dimensions and explanatory variables SST and longitude. These results imply that, within the SFZ, community variation can be viewed from the continuum paradigm, where groups of organisms change continuously and are thus amenable to ordination-based statistical methods. However, the persistence of longitudinal differences in species distributions, that may not be fully explained by changes in the physical environment, point toward the existence of distinct assemblages in the SFZ (especially the "third" cluster) defined by one or two characteristic taxa. This pattern may be due to changes in forage abundance and related to a zoogeographical province.

Our results differ somewhat from those of Mishima et al. (1981), the only previous study of nekton assemblage patterns across an East-West portion of the SFZ (Shimazaki's (1986) data has no longitudinal component as his data was only collected along the 175°30'E meridian). Although Mishima et al.'s (1981) data is not directly comparable to ours -- it was collected further westward (from 145°E to 170°E longitude) -- they found no apparent spatial pattern to their groupings of sample stations, neither was there any clear spatial separation between groups. Their designation of important (dominant) fish species was based solely on abundance; they did not include characteristic taxa as in our study. However, their dominant fish species for each of four groups were blue shark, flying fish, Pacific saury, and flying squid, respectively. If we were to adopt their method of designation, then all 15 assemblages identified in our study would be characterized by flying squid and pomfret. Environmental data were not included in Mishima et al. (1981), which limits a more rigorous comparison between the studies.

Our results also lead to a number of management implications pertinent to the development of any new fishery in the region studied. The first implication is that any fishery targeting one of the two most abundant species of the SFZ -- neon flying squid or pomfret -- and using non-selective fishing methods will necessarily catch large numbers of other species. There is no possible way to shape a fishery in terms of time and area restrictions to avoid this bycatch.

A second (and more general) implication is that a fishery targeting on any one of the species located in the SFZ will necessarily catch substantial numbers of other species. A few species can be avoided by restricting the permitted fishing area to certain SST and longitudinal ranges. These restrictions are, at best, crude management measures due to the occasional breadth of the underlying ecological gradient affecting species compositions in the SFZ.

The final implication is that salmon and pelagic armorhead can, for the most part, be avoided within the SFZ by restricting fishing to particular areas. To avoid salmon, fishing should be restricted to waters east of 180° longitude. To avoid pelagic

which were not measured in the sampling program and have been shown to be important in the distribution of marine species in the SFZ (Ignell 1991b; Carlson et al., in Prep), not only change meridionally, but also zonally (especially towards the eastern portion of the fishery where the Subarctic Current begins to divide into two branches (Ware and McFarlane, 1989)). This zonal change is slight within the driftnet fishing area, however, and cannot fully explain the marked change in abundances of some species along the eastern portion of the fishery (Ignell, in prep). Another possible ecosystem effect is a change in forage abundance and composition, perhaps due to a nearby change in water mass. Krygier and Wasmer (1988) have identified Eastern Pacific Central waters, located approximately between 20-40°N latitude and 133-157°W longitude, as a distinct zoogeographical area. Although this region lies primarily outside the boundaries of our study area, it may still affect species distributions in the southeast portion of the driftnet fishery and thus explain much of the longitudinal patterns that we observed. Longitude may also reflect the localized distribution of some taxa. From a comparison of table 4 with the COA ordination figures we find that months in which spatial variables (longitude or, in the case of August, 1991, latitude) principally define community structure are also months where one of the taxa assemblages or clusters is defined by the inclusion of pelagic armorhead. Moreover, the location of the additional cluster is relatively constant; for the three months in which fishing operations are grouped into three clusters, the cluster defined by the inclusion of pelagic armorhead was located in the central-eastern portion of the fishing ground, near 160°W longitude. Previous research on salmonids have shown their abundances in the SFZ are also highly related to geography within a given SST range (Ignell, 1991b; Ignell and Murphy, 1993).

The importance of SST in controlling the dispersion taxa in our sampling area during the summer is likely caused by several factors. First, although most species can be found within a wide range of temperatures, the highest catches are generally found within a comparatively narrow range (Brodeur, 1988). Second, although the SFZ's southern boundary in winter is clearly identifiable by either salinity or temperature data, the sharp temperature gradient usually disappears in the summer due to radiative heating and cooling of surface waters. As the temperature of the upper mixed layer (approximately 50 m deep) warms, many fish and invertebrate species seen only in subtropical waters in winter migrate northward into the SFZ and some even into the subarctic domain (Shimazaki, 1986). This temperature-stimulated "crossing over" (Mishima, 1981) is a prominent event in the North Pacific ecosystem, and provides an explanation for the temperature-related arrangement of taxa in our community analyses.

With the exception of salmonids and pelagic armorhead, the dispersion of taxa in the area sampled was strongly associated with a gradient in the physical environment (SST and possibly factors associated with longitude). About 40% of the total catch variation in fishing operations each month were accounted for by the first

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armorhead, fishing should not occur in the central-eastern portion of the fishing grounds (145-175°W).

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Table 3. Results of the canonical discriminant analysis conducted following average linkage cluster analysis based on taxa distributions. Data are from the 1990 and 1991 monitoring program on Japanese squid driftnet vessels.

Year	Month	Canonical Variate 1				Canonical Variate 2			
		r	Lat	Long	SST	r	Lat	Long	SST
1990	June	0.69	-0.49	0.89	0.37	0.41	-0.01	-0.33	0.93
	July	0.53	0.65	0.92	--				
	August	0.68	0.25	0.94	-0.74	0.51	-0.63	0.31	0.67
1991	June	0.72	--	0.92	0.81				
	July	0.66	--	0.56	0.93				
	August	0.67	0.67	0.79	-0.21	0.31	0.61	-0.56	-0.74

Table 2. Number of fishing operations (n) and average position (in decimal degrees) and sea surface temperature (°C) for each assemblage identified by the cluster analyses. Note that only two clusters were identified in some months. Data are from the 1990 and 1991 monitoring program on Japanese squid driftnet vessels.

Year	Month	Cluster 1				Cluster 2				Cluster 3			
		n	Lat	Long	SST	n	Lat	Long	SST	n	Lat	Long	SST
1990	June	396	39.4	173.4	15.3	212	40.0	160.4	16.1	132	39.3	166.3	14.2
	July	598	41.7	171.9	15.5	437	42.0	162.7	15.4				
	August	390	44.3	176.0	15.2	209	44.5	156.9	14.0	27	42.9	166.4	17.4
1991	June	541	39.4	161.0	17.0	165	39.4	177.0	15.3				
	July	594	42.3	168.9	14.8	467	42.3	162.1	16.5				
	August	191	44.5	173.2	14.7	301	44.1	174.6	15.3	189	44.6	163.7	15.0

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Table 1. Scientific names, common names, and abbreviation codes of the 36 taxa used in the study. Some species have been pooled to higher taxonomic levels to increase occurrence frequencies. See text for discussion.

Scientific Name	Common Name	Code
<i>Ommastrephes bartrami</i>	Neon Flying Squid	nsq
<i>Gonatopsis borealis</i>	Eight-armed Squid	esq
<i>Onchoteusthis borealijaponica</i>	Boreal Clubhook Squid	csq
Order Octopoda	Octopuses	oct
<i>Lamna ditropis</i>	Salmon Shark	ssk
<i>Isurus oxyrinchus</i>	Short-finned Mako	mak
<i>Prionace glauca</i>	Blue Shark	bsk
<i>Oncorhynchus</i> spp.	Salmon	slm
<i>Alepisaurus ferox</i>	Longnose Lancetfish	lct
<i>Cololabis saira</i>	Pacific Saury	sry
<i>Lampris guttatus</i>	Opah	oph
<i>Seriola lalandi</i>	Yellowtail	ytl
<i>Naucrates ductor</i>	Pilotfish	plt
<i>Coryphaena hippurus</i>	Dolphinfish	dlf
<i>Brama japonica</i>	Pacific Pomfret	pom
<i>Pentaceros richardsoni</i>	Pelagic Armorhead	plr
<i>Euthynnus pelamis</i>	Skipjack Tuna	skp
<i>Thunnus alalunga</i>	Albacore	alb
<i>Thunnus obesus</i>	Bigeye Tuna	big
<i>Thunnus thynnus</i>	Bluefin Tuna	bfm
<i>Xiphias gladius</i>	Swordfish	swd
Istiophoridae	Billfishes	bll
<i>Luvarus imperialis</i>	Louvar	lvr
<i>Psenes pellucidus</i>	Blackrag	brg
<i>Icosteus enigmaticus</i>	Ragfish	rag
<i>Mola mola</i>	Ocean Sunfish	sun
<i>Diomedea</i> spp.	Albatrosses	abt
<i>Puffinus griseus/tenuirostris</i>	Dark Shearwaters	dsh
<i>Puffinus carneipes</i>	Pale-footed Shearwater	psh
<i>Puffinus bulleri</i>	Buller's Shearwater	bsh
<i>Oceanodroma</i> spp.	Storm-Petrels	stp
<i>Fratercula</i> spp.	Puffins	puf
<i>Callorhinus ursinus</i>	Northern Fur Seal	nfs
<i>Phocoenoides dalli</i>	Dall's Porpoise	dal
<i>Lissodelphis borealis</i>	N. Right-Whale Dolphin	rwd
<i>Lagenorhynchus obliquidens</i>	Pac. White-sided Dolphin	wsd

Table 4. Results of the canonical analysis between the three primary correspondence (COA) dimension scores and three environmental variables. For each month, the two highest canonical correlations (R) are given along with the correlations between the canonical variate and the original variables. Data are from the 1990 and 1991 monitoring program on Japanese squid driftnet vessels.

Year	Month	R	Canonical Variate	Correlation			Canonical Variate	Correlation		
				COA1	COA2	COA3		Lat	Long	SST
1990	June	0.79	V1	0.82	-0.53	0.32	W1	-0.55	0.76	0.58
		0.42	V2	0.57	0.62	-0.48	W2	0.08	-0.53	0.81
	July	0.73	V1	-0.93	0.20	0.32	W1	0.17	0.97	0.52
		0.47	V2	0.20	0.98	-0.05	W2	0.74	0.23	-0.71
	August	0.77	V1	0.10	-0.90	0.43	W1	-0.39	0.85	0.00
		0.73	V2	0.99	0.09	-0.02	W2	0.72	0.52	-0.99
1991	June	0.85	V1	-0.98	0.11	0.16	W1	-0.07	0.83	0.88
		0.54	V2	-0.13	0.20	-0.97	W2	0.82	-0.19	0.38
	July	0.89	V1	-0.95	-0.32	-0.06	W1	0.12	0.64	0.87
		0.46	V2	0.32	-0.93	0.24	W2	0.74	0.76	-0.41
	August	0.70	V1	0.99	0.11	-0.05	W1	0.74	0.64	-0.41
		0.51	V2	-0.11	0.98	0.14	W2	0.21	-0.76	-0.88

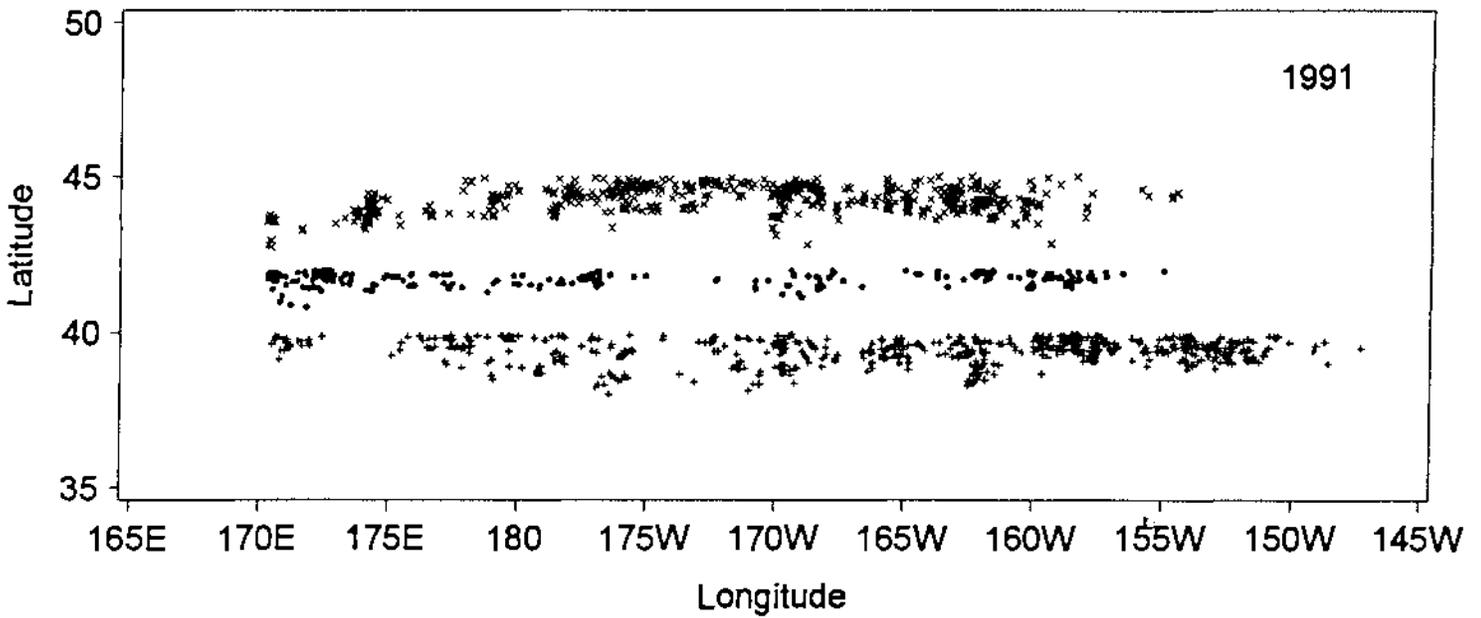
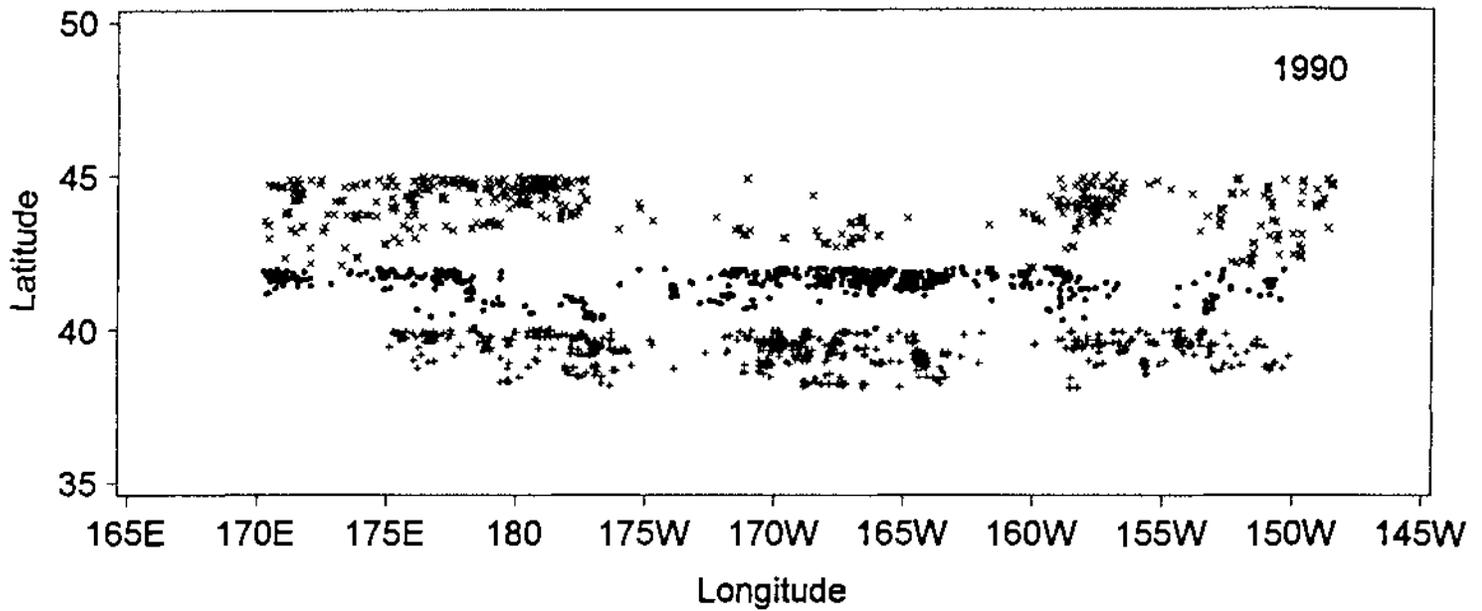


Fig. 1. Locations of fishing operations sampled by observers aboard Japanese squid driftnet vessels, July-August, 1990 and July-August, 1991.

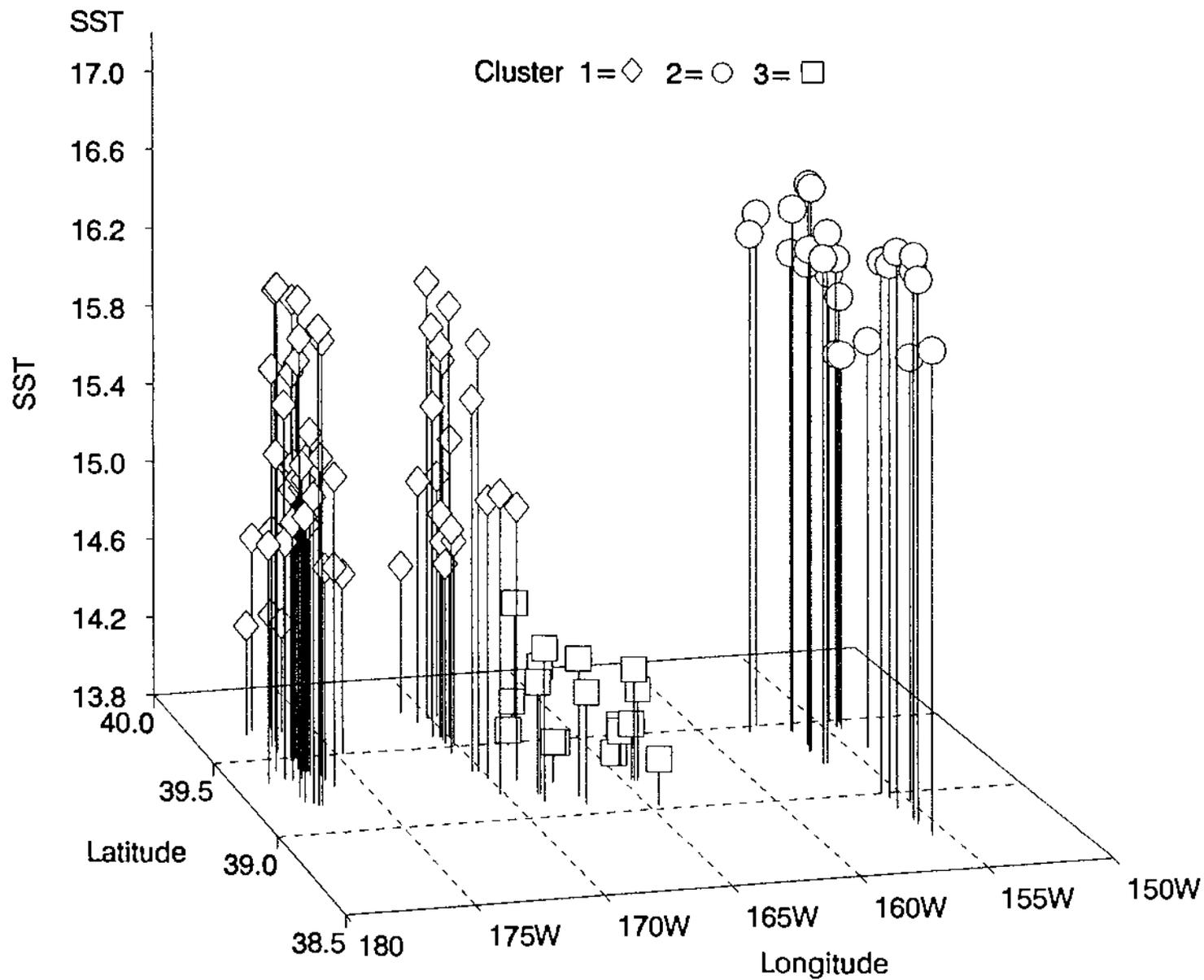


Fig. 3. Midrange plots of June 1990 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

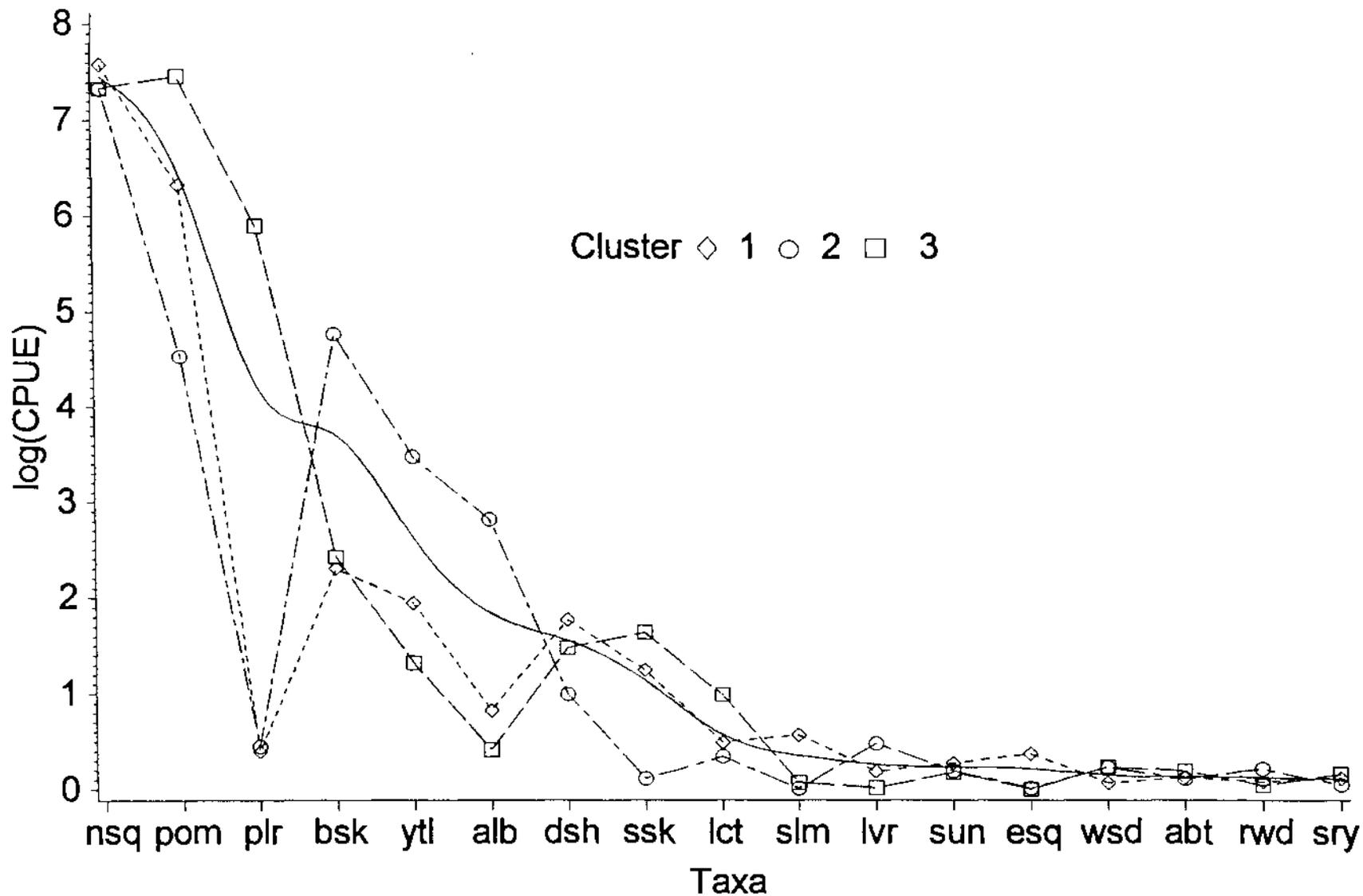


Fig. 2. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in June 1990 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

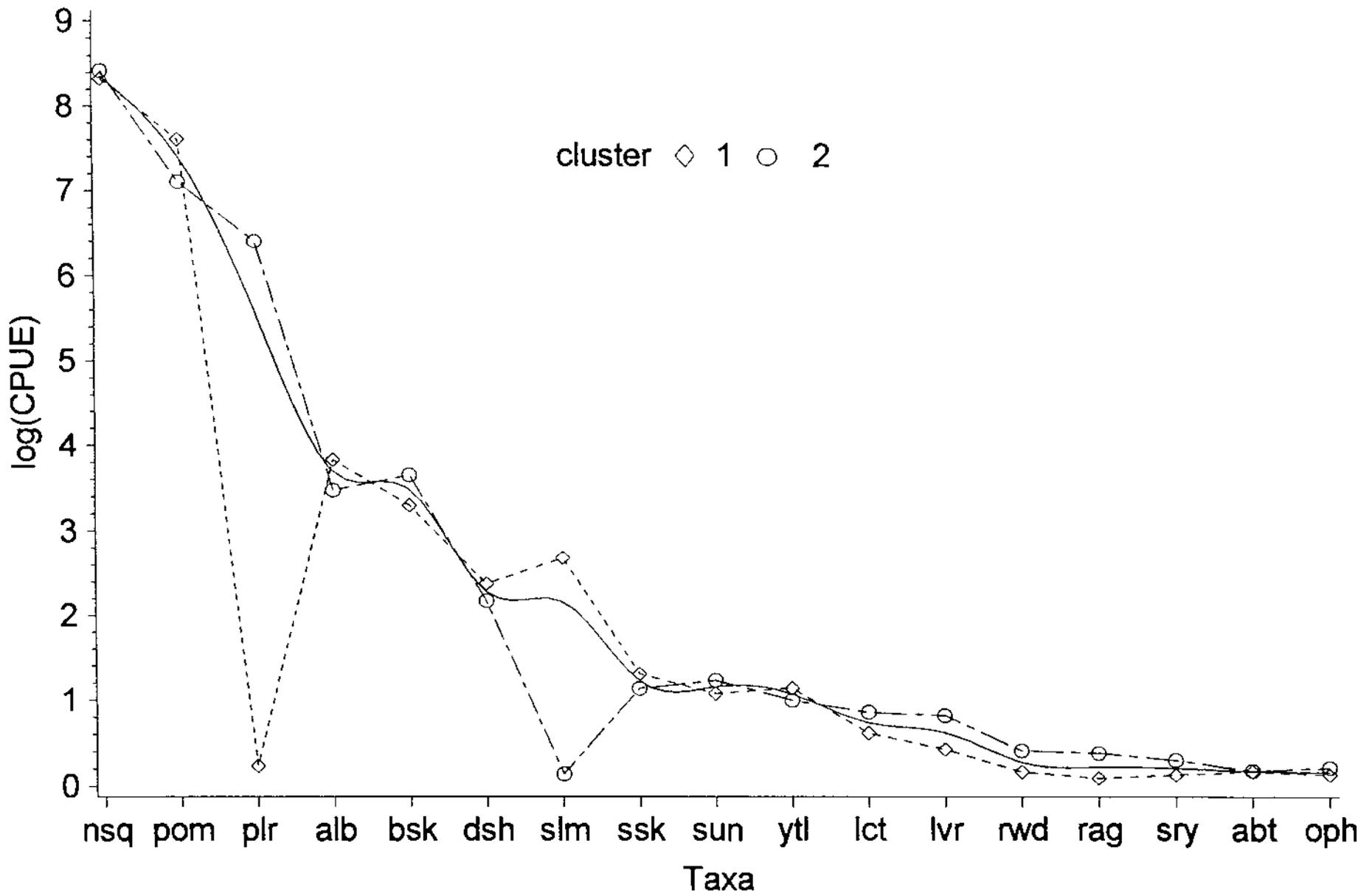


Fig. 5. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in July 1990 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

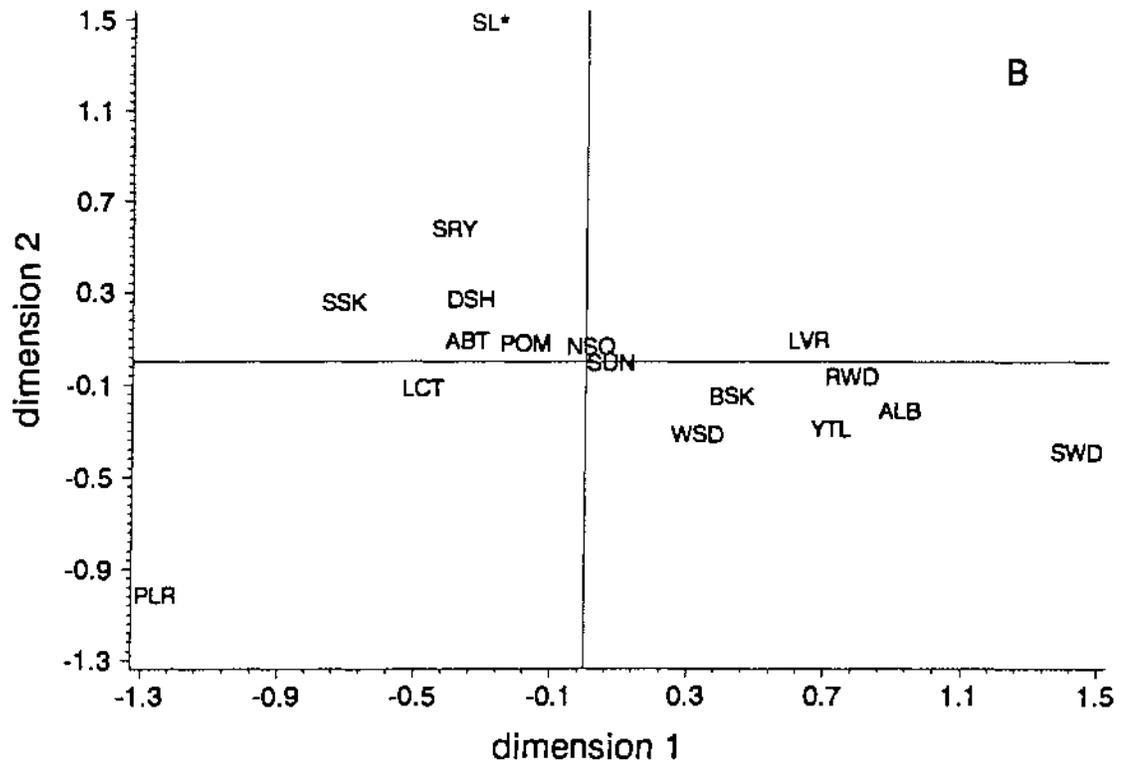
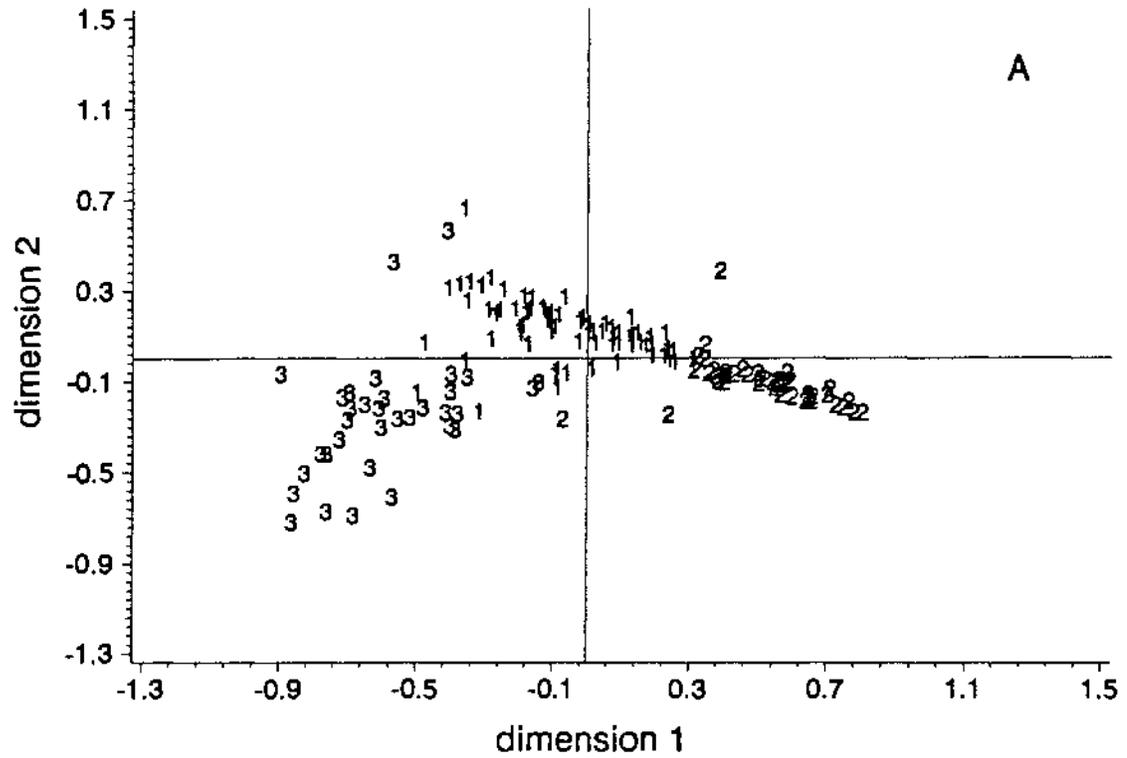


Fig. 4. Correspondence analysis ordination (COA) of June 1990 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B). See Table 1 for taxa abbreviations.

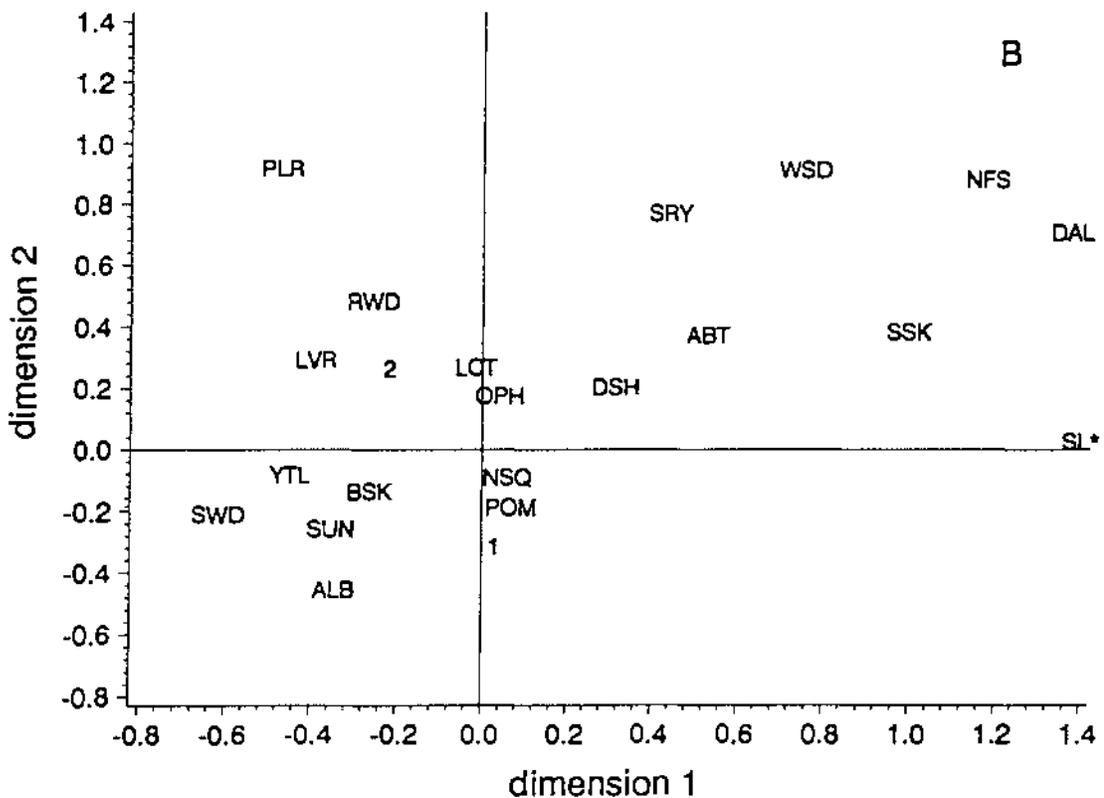
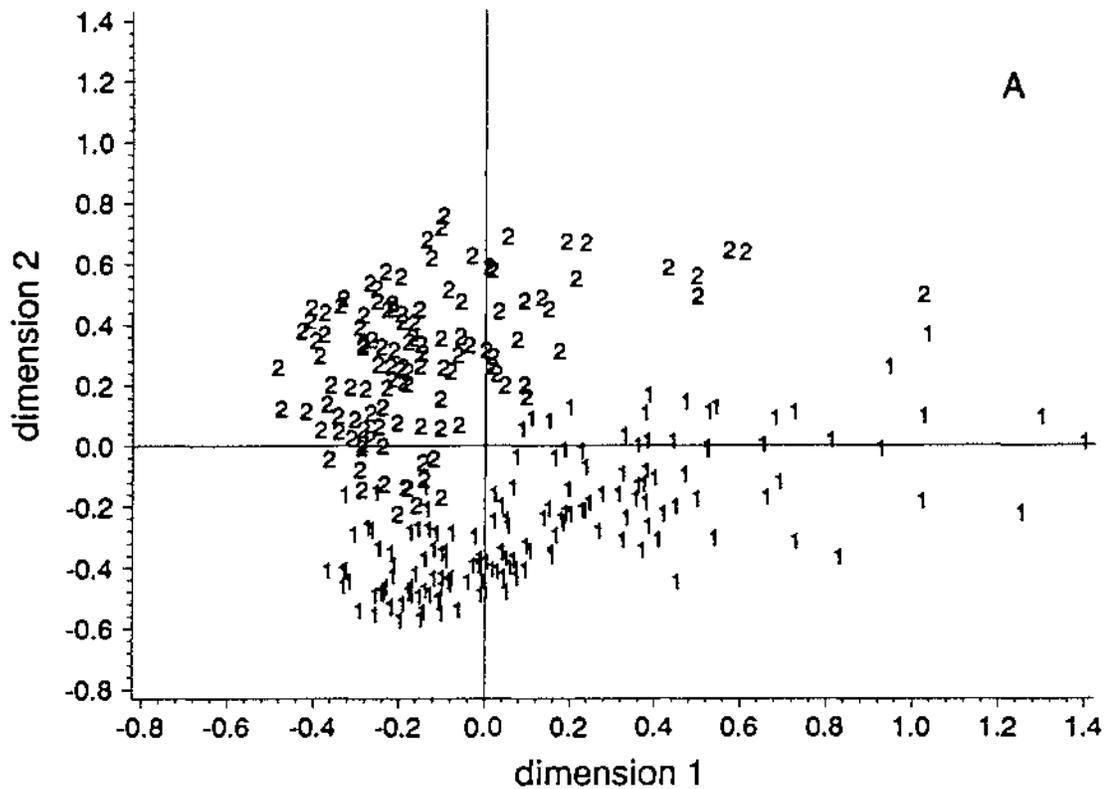


Fig. 7. Correspondence analysis ordination (COA) of July 1990 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B); SL* lies along the vector of the taxa salmon and was beyond the plotting range used for dimension 1. See Table 1 for taxa abbreviations.

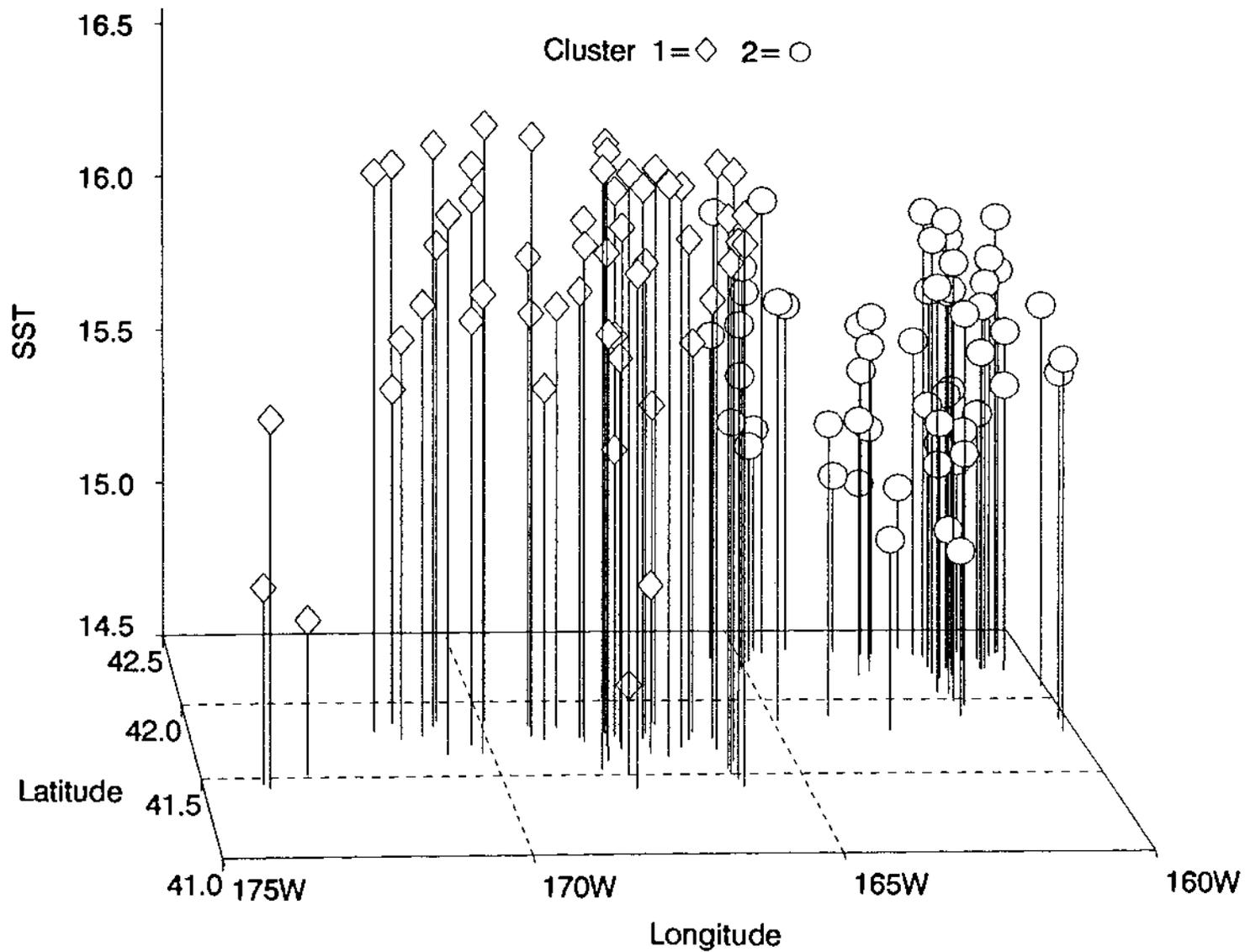


Fig. 6. Midrange plots of July 1990 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

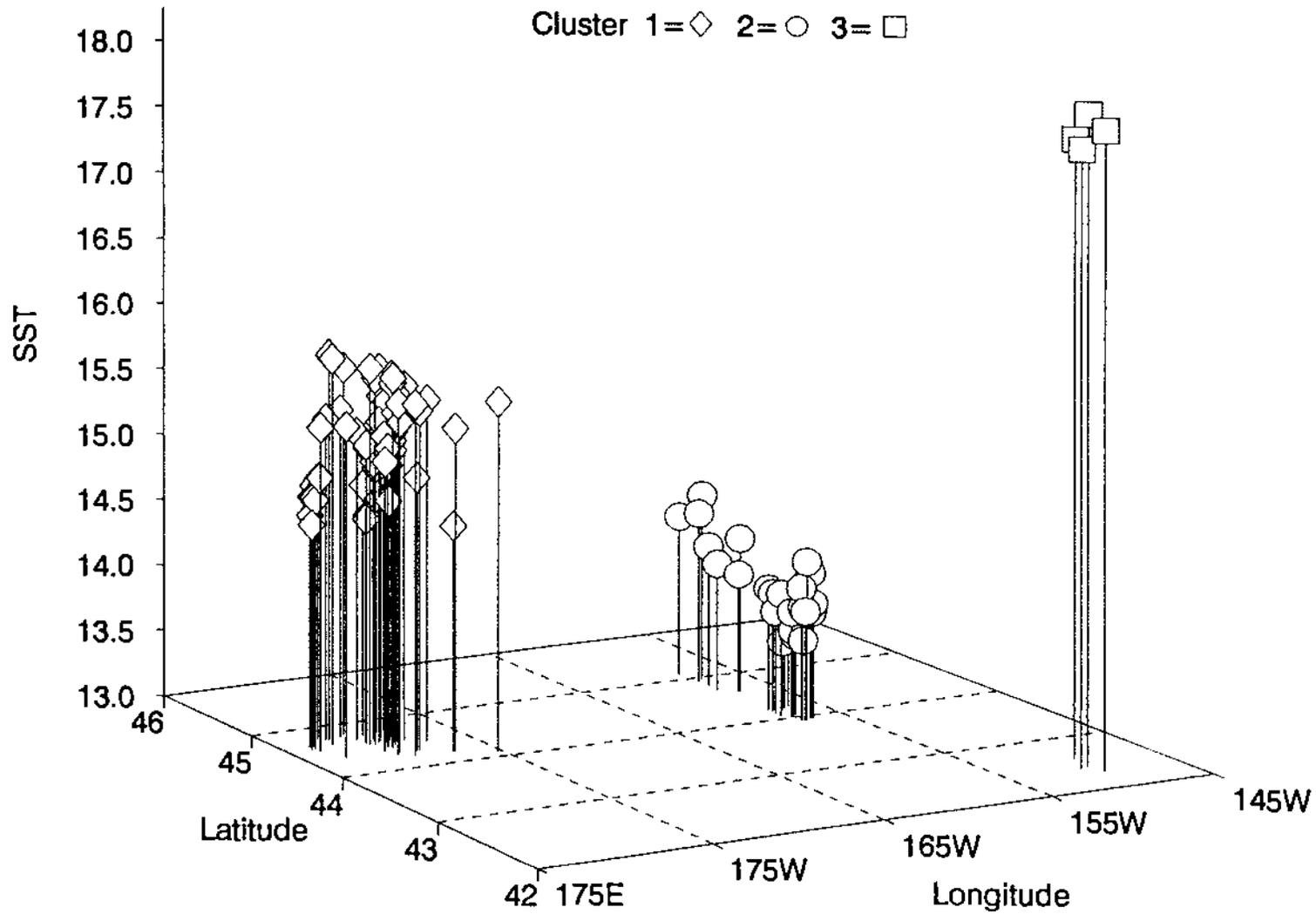


Fig. 9. Midrange plots of August 1990 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

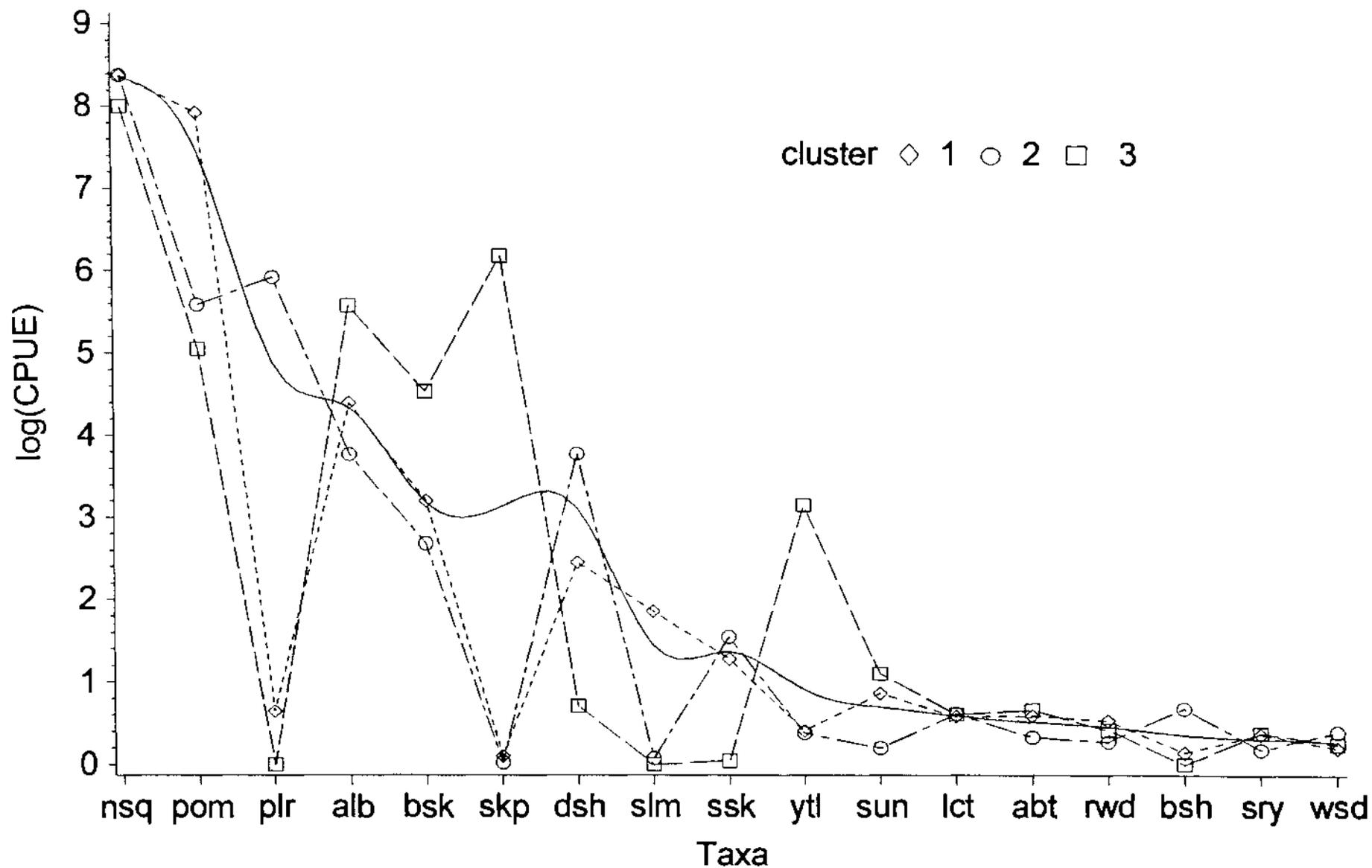


Fig. 8. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in August 1990 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

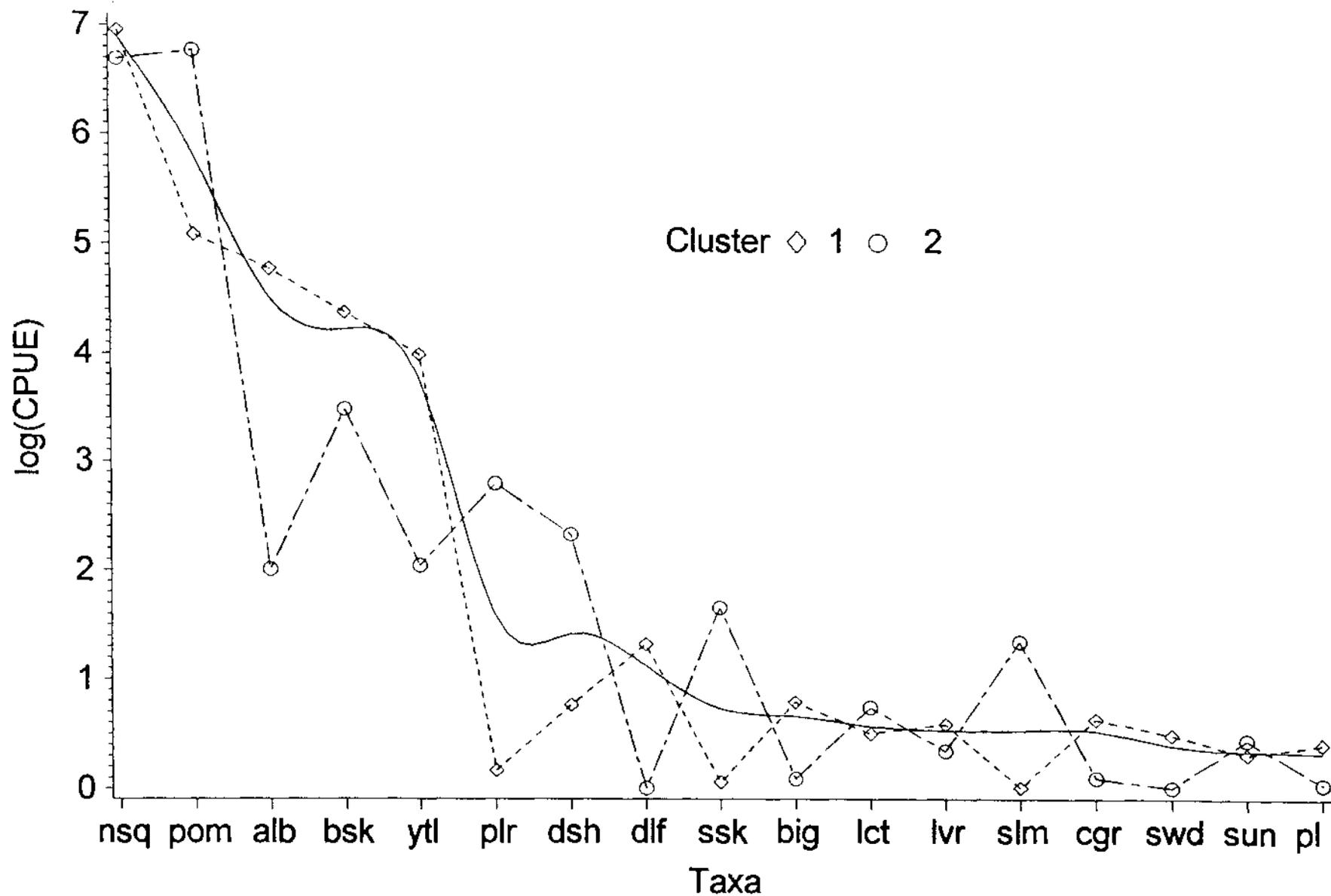


Fig. 11. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in June 1991 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

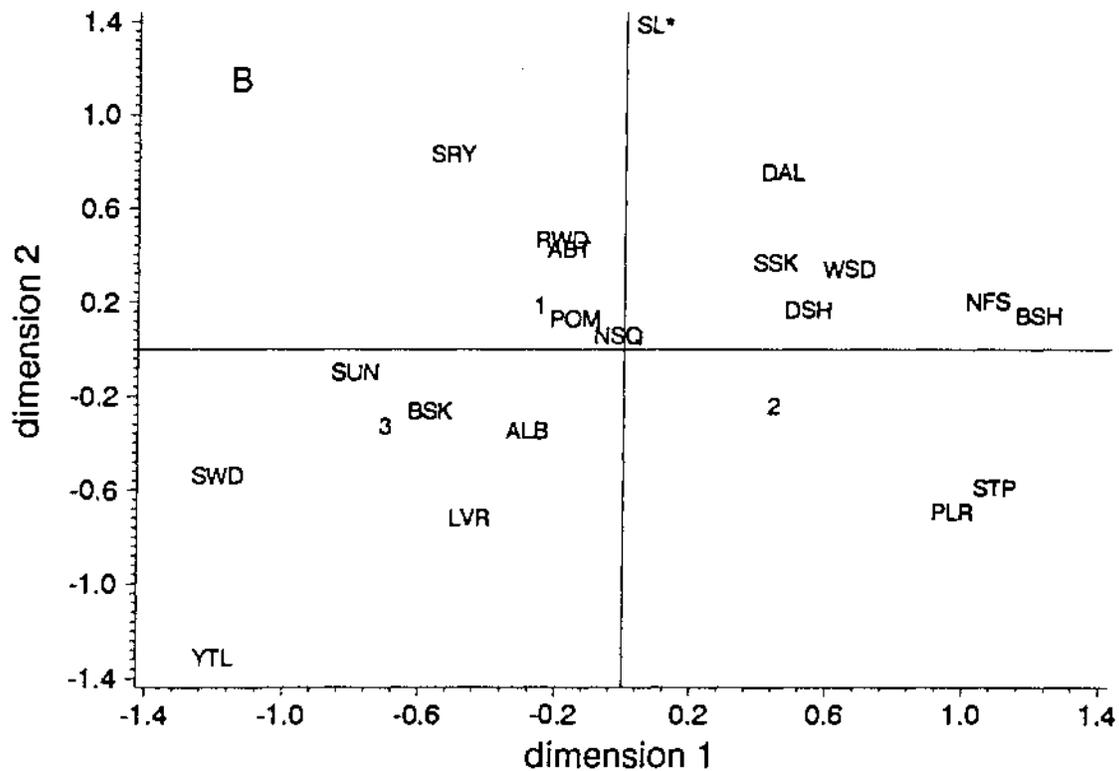
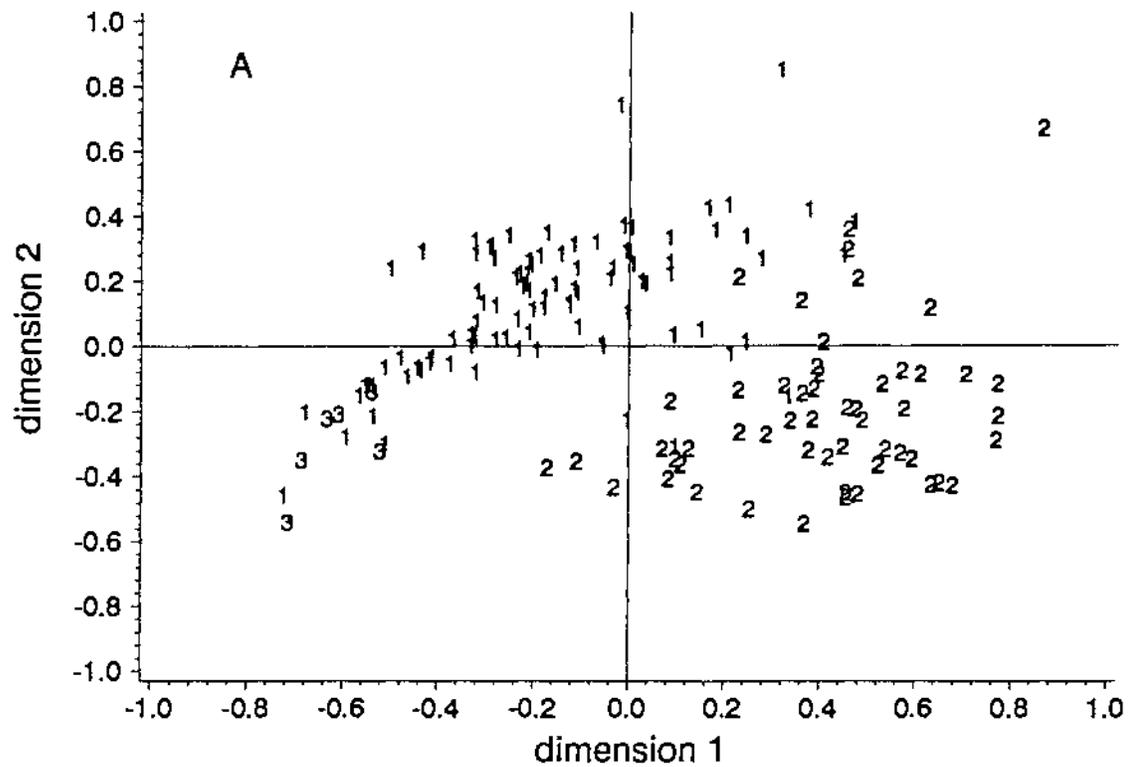


Fig. 10. Correspondence analysis ordination (COA) of August 1990 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B); SL* lies along the vector of the taxa salmon and was beyond the plotting range used for dimension 2. See Table 1 for taxa abbreviations.

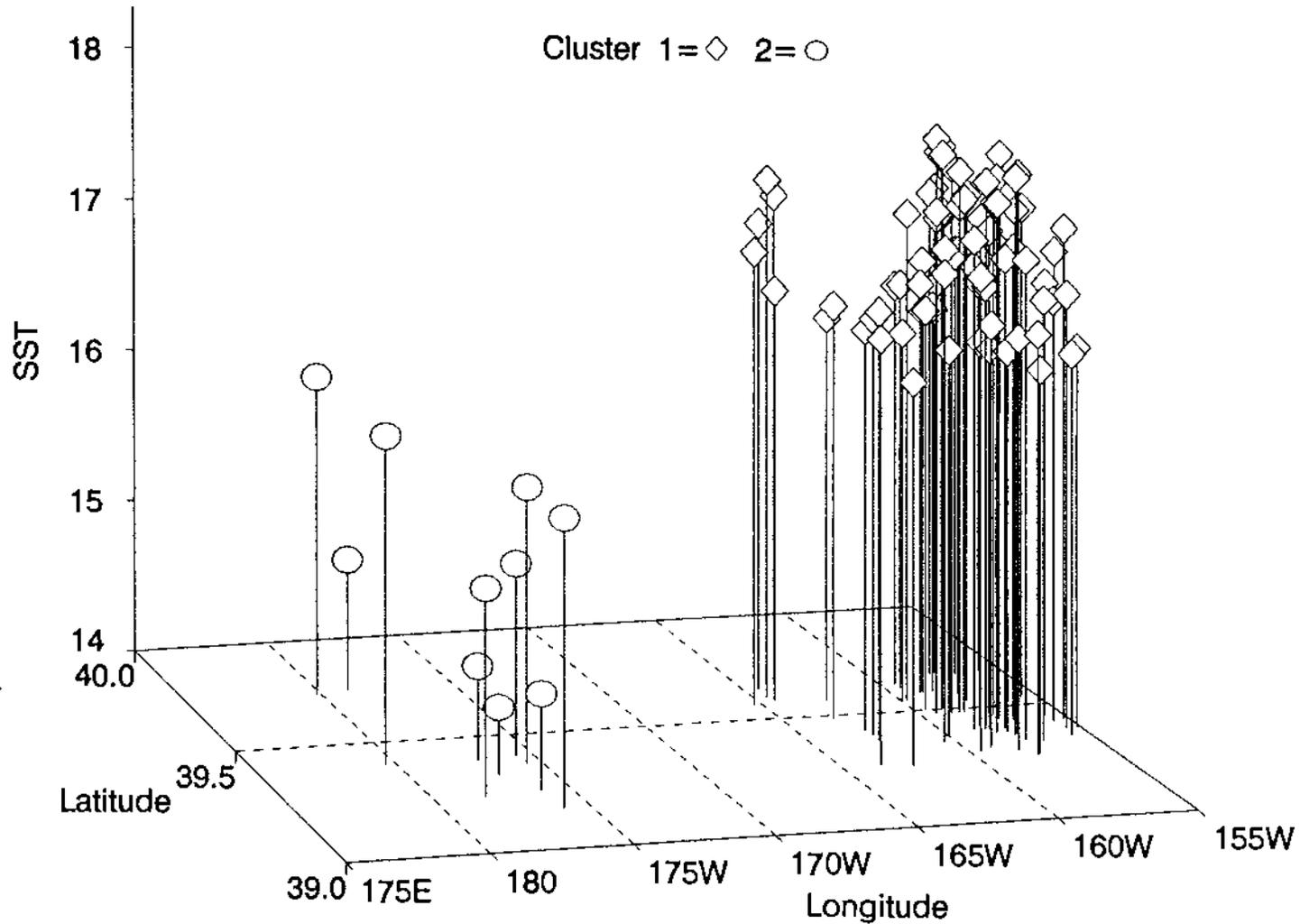


Fig. 12. Midrange plots of June 1991 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

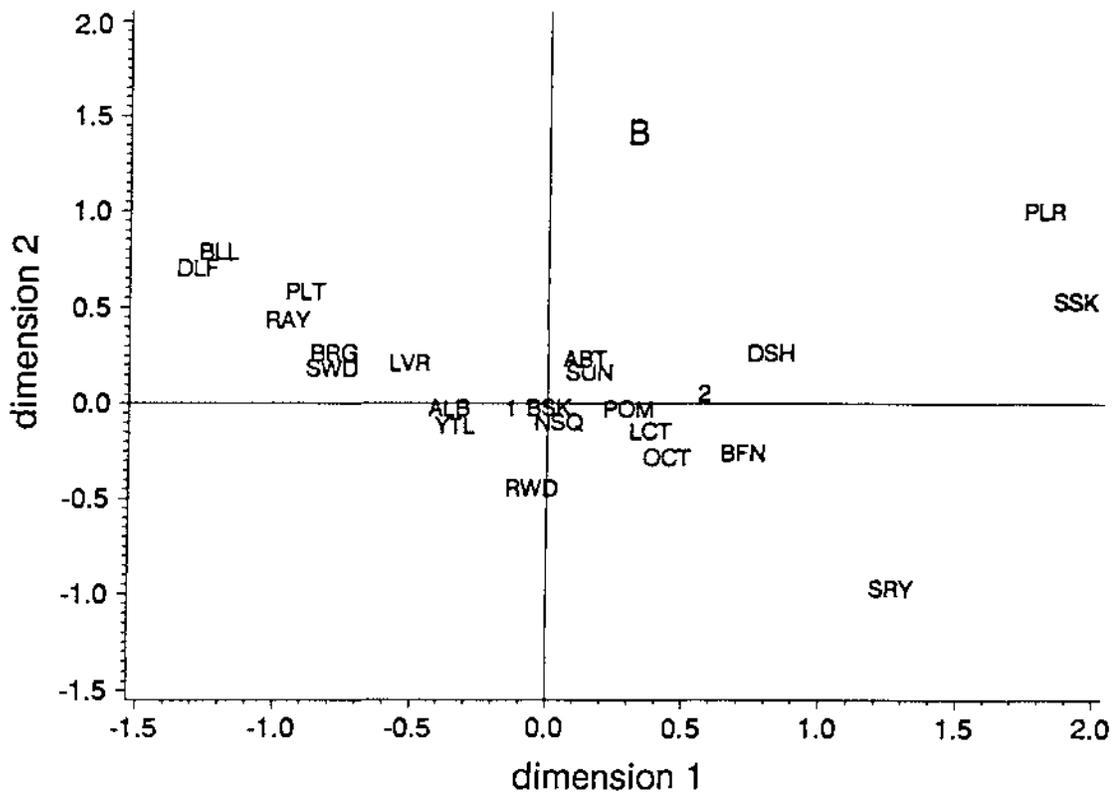
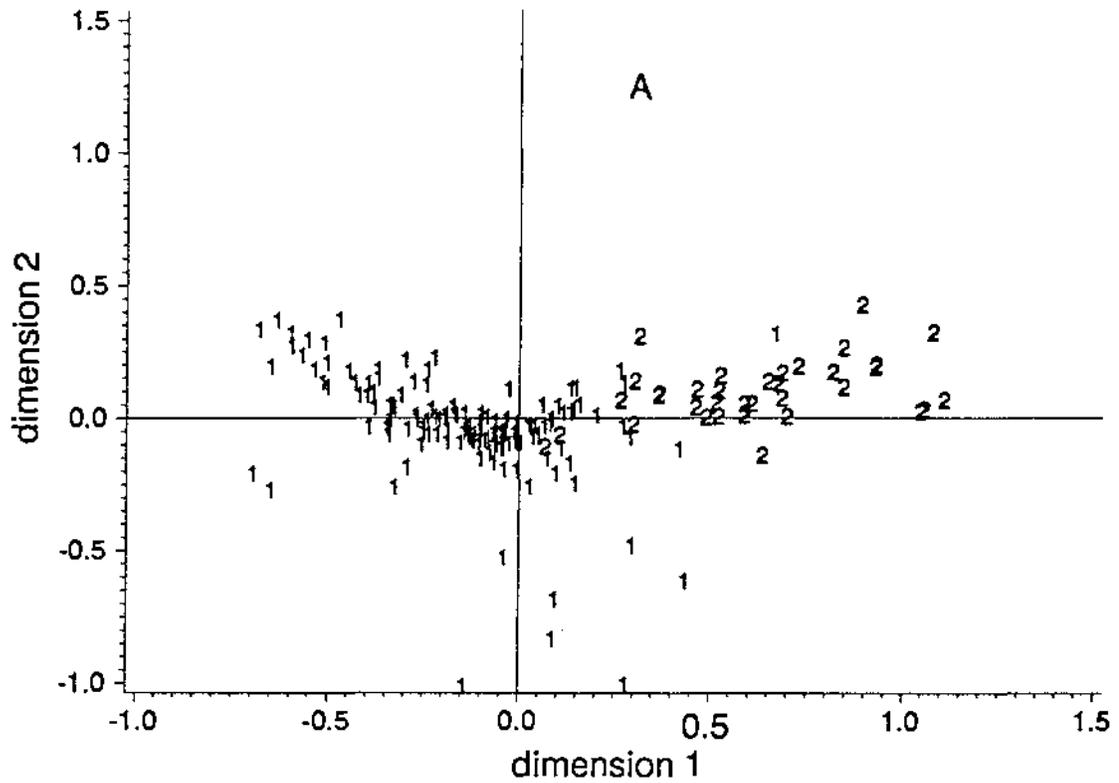


Fig. 13. Correspondence analysis ordination (COA) of June 1991 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B). See table 1 for taxa abbreviations.

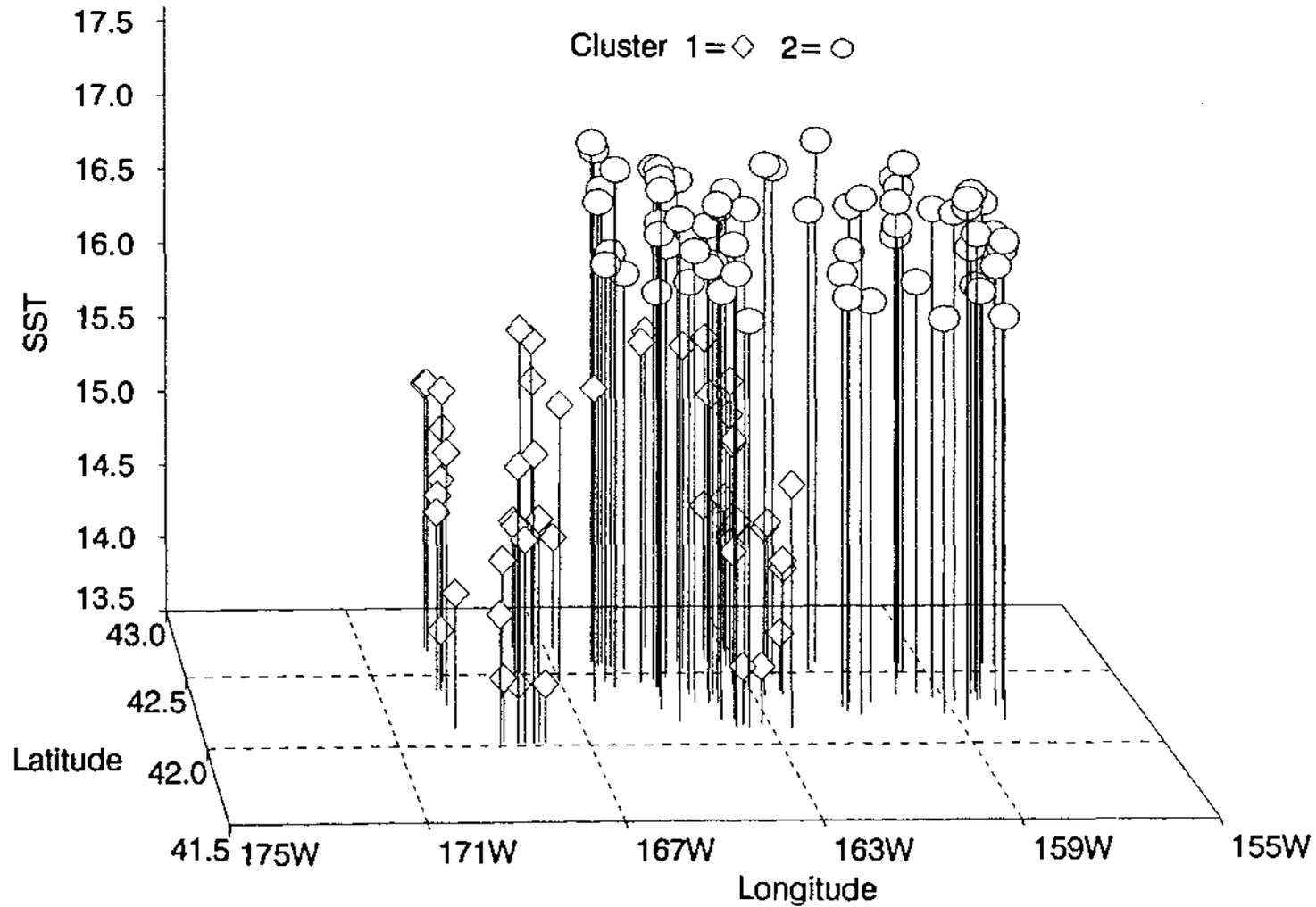


Fig. 15. Midrange plots of July 1991 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

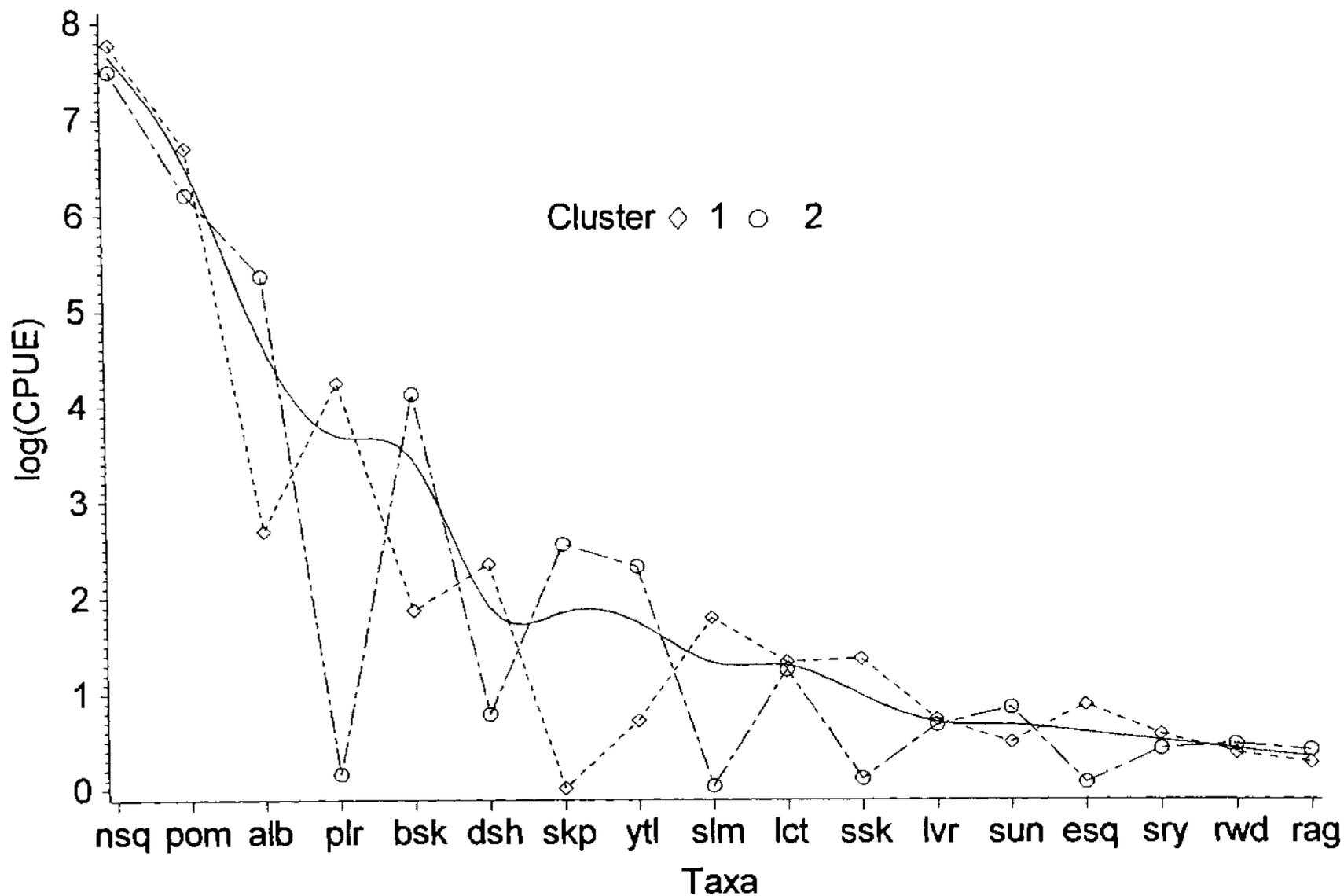


Fig. 14. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in July 1991 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

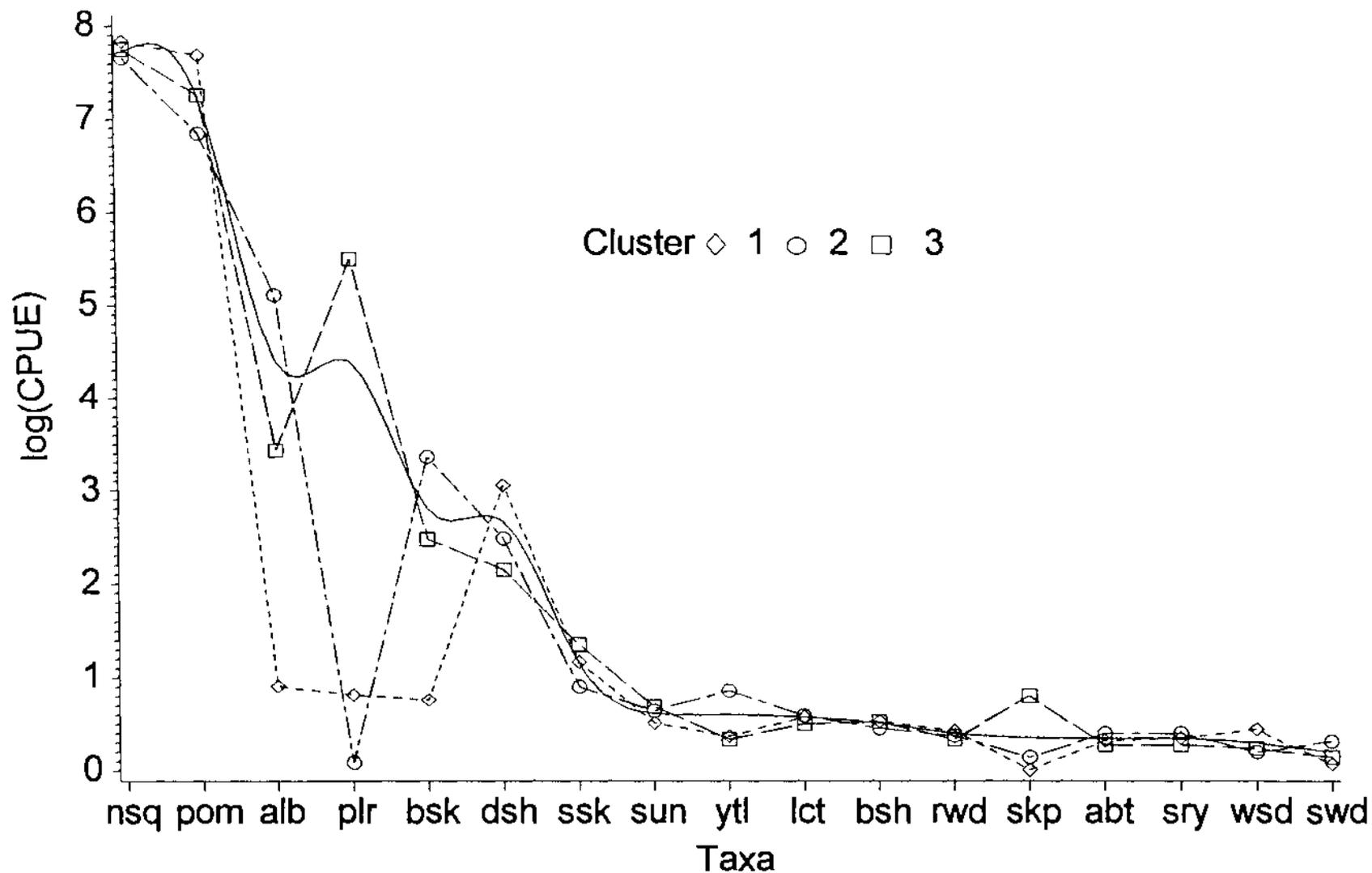


Fig. 17. Catch per unit effort (CPUE = \ln transformed catch per 1000 tans of gillnet) of the major nekton species caught in August 1991 fishing operations. CPUE values are averaged for the three groupings of fishing operations identified by cluster analysis. Table 1 gives taxa abbreviations.

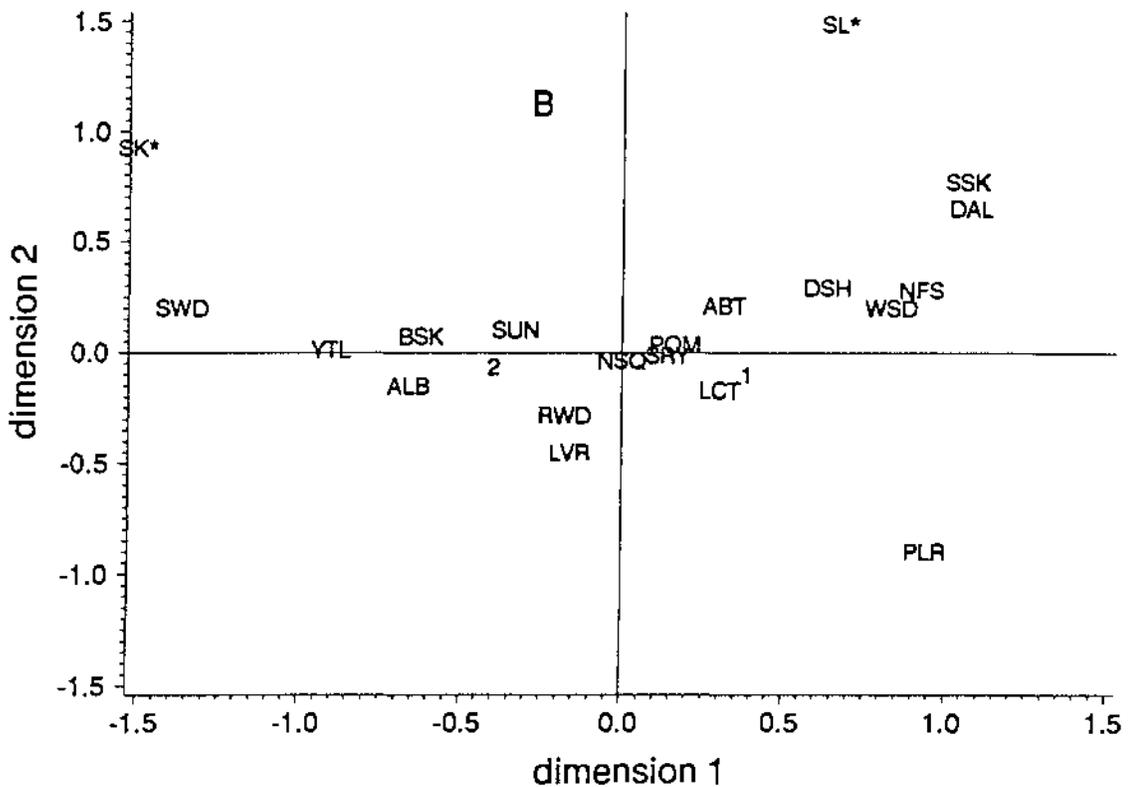
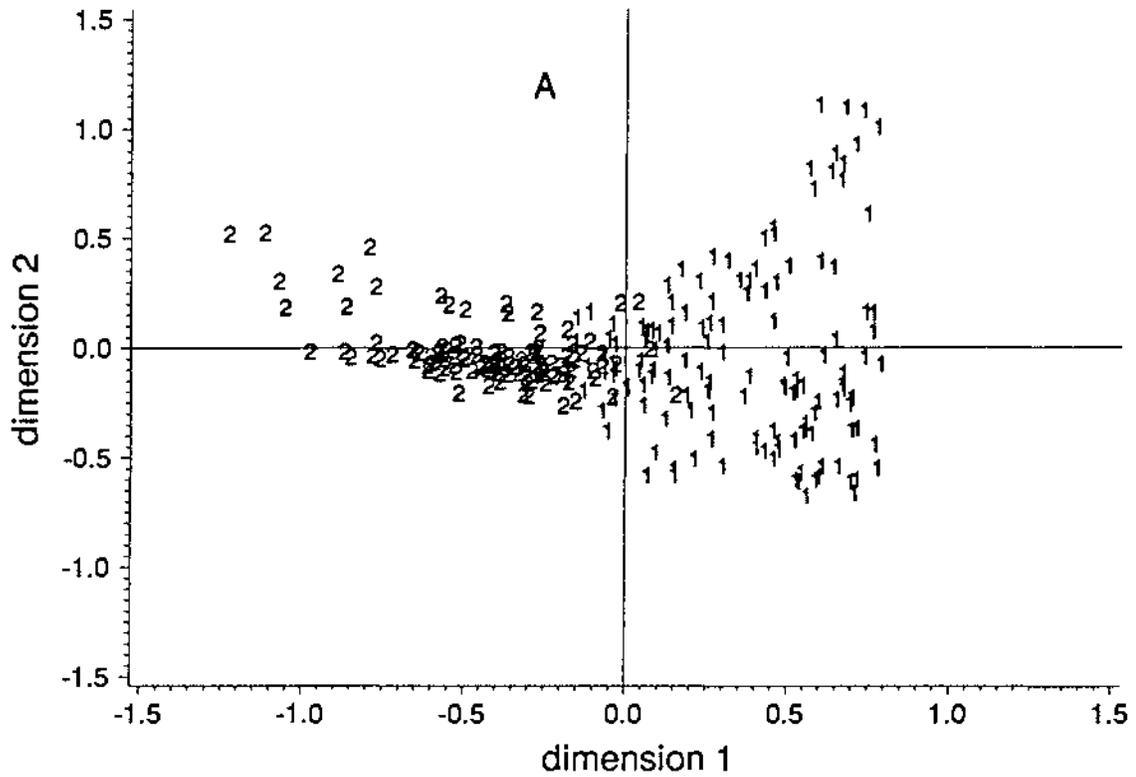


Fig. 16. Correspondence analysis ordination (COA) of July 1991 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B). SL* lies along the vector of the taxa salmon and SK* lies along the vector of the taxa skipjack; both points were beyond the range of values used for plotting. See Table 1 for taxa abbreviations.

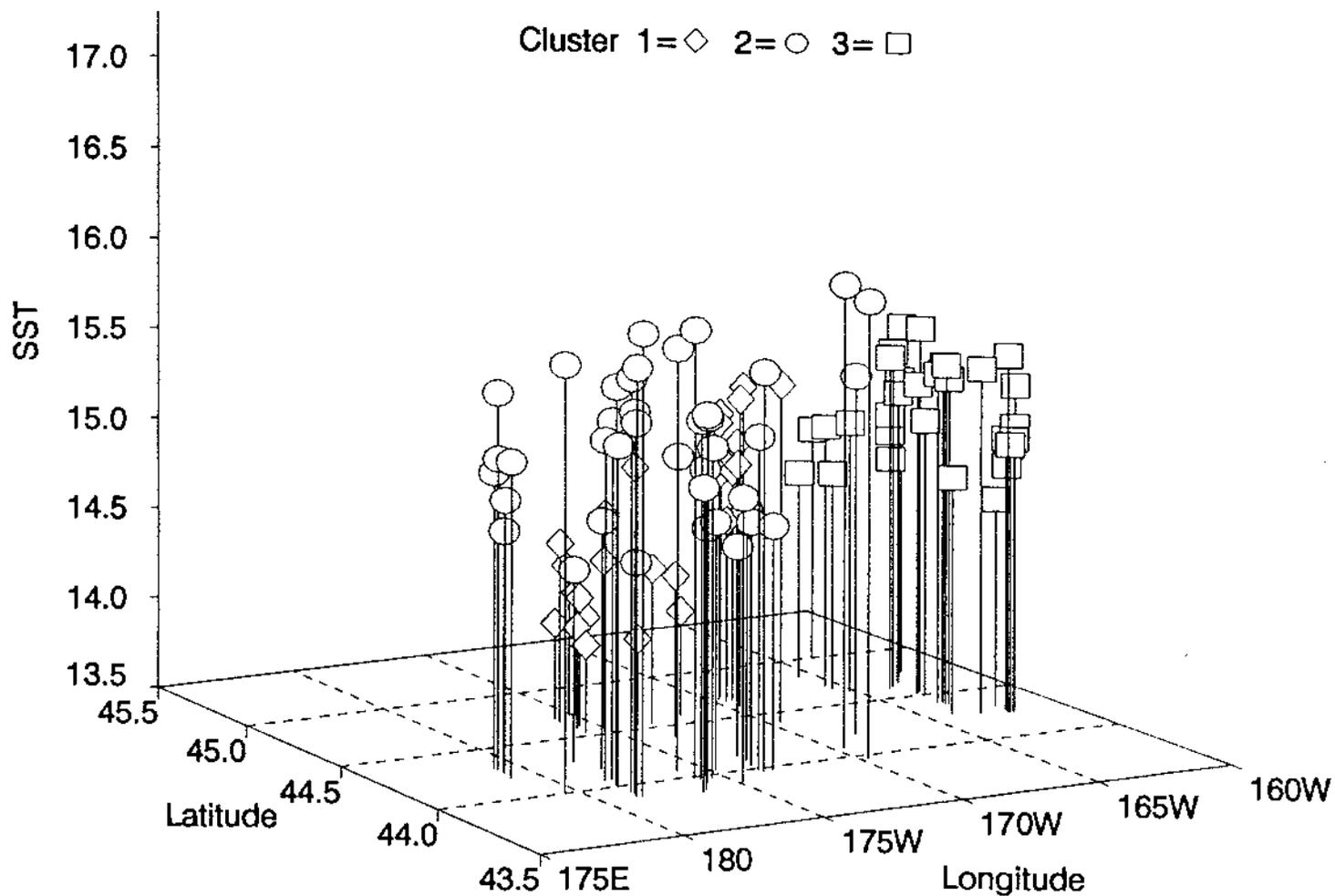


Fig. 18. Midrange plots of August 1991 fishing operations grouped into three assemblages by cluster analysis. Only observations occurring within the joint inter-quartile range of the environmental variables are included for each cluster.

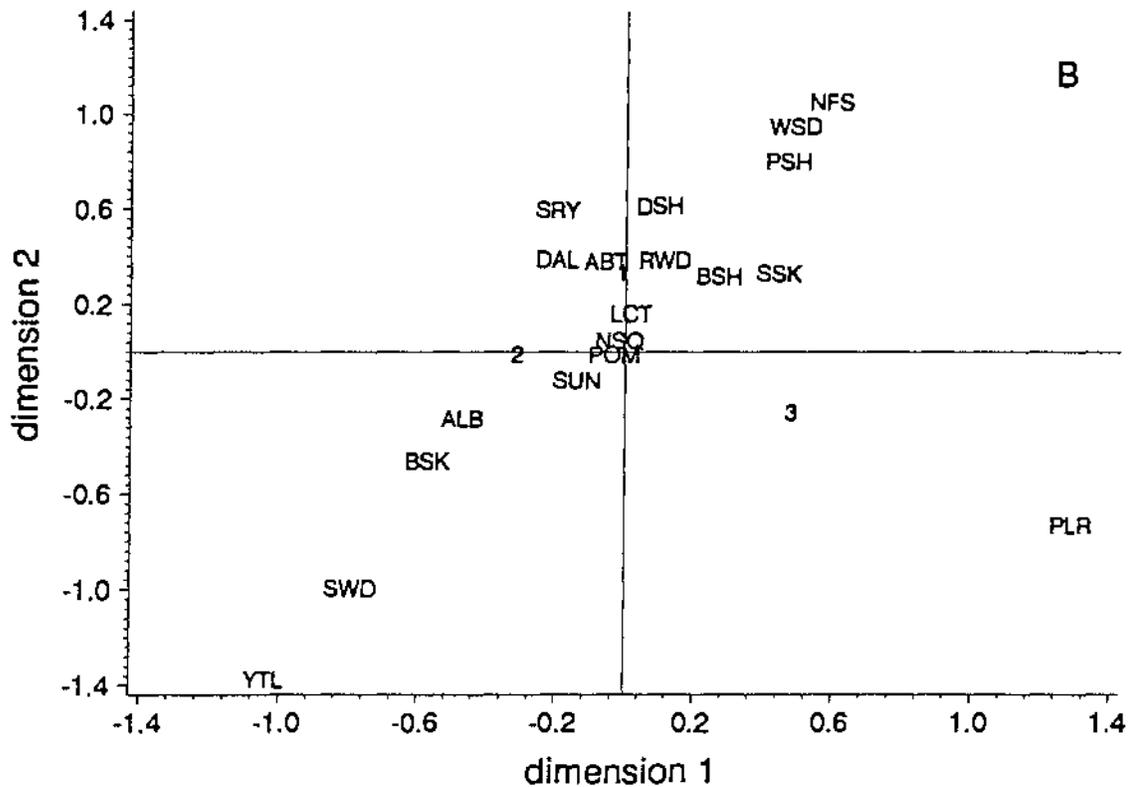
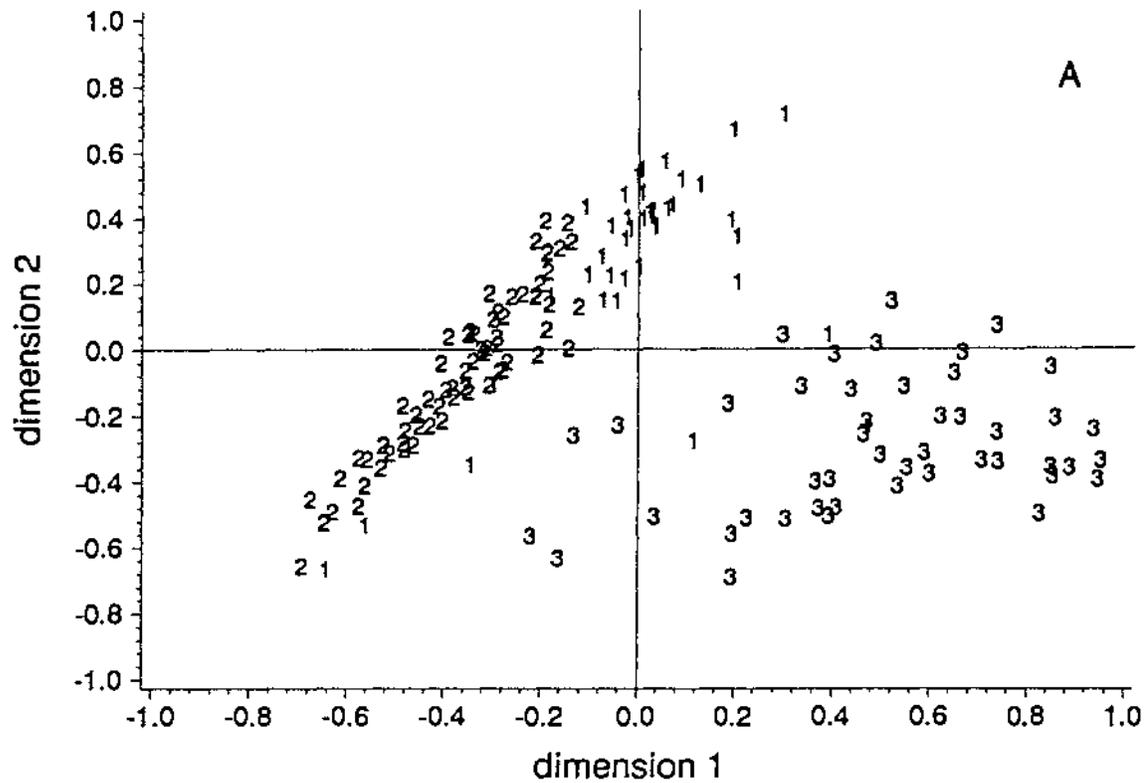


Fig. 19. Correspondence analysis ordination (COA) of August 1991 data. Fishing operations identified by cluster assignment are plotted along the first two COA dimensions (A). Taxa coordinates are plotted along the two primary COA dimensions (B). See table 1 for taxa abbreviations.