CANONICAL CORRELATION ANALYSIS OF MARINE
MACROBENTHOS SURVEY DATA

GARY C. B. POORE[1] and M. C. MOBLEY

Marine Studies Group, Ministry for Conservation, 605 Flinders Street, Melbourne, Victoria 3000, Australia

Abstract: Canonical correlation analysis is applied to measurements of environmental variables and species distributions made during a survey of macrobenthos around a sewage-treatment farm drain. The implications of data reduction, necessary to enable the method to proceed, are discussed. The amount of data was reduced by discarding the rarest species, discarding species occurring at fewest stations, and including only those species and environmental variables which correlated highly with the greatest number of other variables. Only the third data-reduction scheme gave ecologically sensible results. Use of station scores on the first two canonical variates (CV1 and CV2) enabled the sampling grid to be divided into a group of nearshore stations, a group of intermediate depth, and a group of deep offshore stations. Loadings of environmental variables on the canonical variates were found to be unstable but correlations between these variables and canonical variates enabled the variates to be interpreted: CV1 as a gradient of depth and associated changes in sediment characteristics, CV2 with depth- and nutrient-related components, and CV3 as patchiness in sediment characteristics different from that normally expected with depth. Use of correlations between species and canonical variates enables definition of two major species groups, one confined to nearshore environments and a second offshore. These groups (and their sub-groups) related well to groups defined previously by hierarchical classification. It is concluded that, with careful attention to the method of data reduction, canonical correlation analysis can be an effective tool in the analysis of marine benthic survey data.

INTRODUCTION

Descriptive ecological surveys are often undertaken with the stated objective of describing the distribution of plants and animals in terms of physico-chemical features of the environment. To this end, surveys are designed to collect information divided a priori into two sets, biotic data and abiotic data. But in spite of the stated objective and possession of data divided conveniently into two parts, ecologists have not been particularly successful in relating biotic and abiotic data. In marine benthic ecology where complex statistical methods are widely used there has been little progress in this field. Although benthic surveys have frequently been carried out as part of marine environmental research, relationships between animal distributions and environmental disturbance or pollutants have been rarely shown other than by subjective methods.

[1] Present address: Department of Crustacea, National Museum of Victoria, 71 Victoria Crescent, Abottsford, Victoria 3067, Australia.

Mathematical methods for looking for pattern in sets of data of a single type are well developed. Classification and ordination have been widely applied with success to the biological half of the data, usually counts of species in samples. Data on abiotic variables have been treated separately and differently or not at all. The basic problem of reducing the two data sets to a comprehensible size and then relating them in a meaningful way has rarely been considered in marine benthic ecology.

Canonical correlation analysis is a statistical method conceptually appealing in its ability to ascertain the extent to which one set of measurements is related to another and to determine the particular attributes which have been responsible for these relationships. The method, developed by Hotelling (1935), is an extension of principal components analysis.

Linear functions of the two sets of variables are selected so that the (canonical) correlation between the two functions is maximized. Furthermore, pairs of linear functions that are uncorrelated with previous pairs and have the maximum correlation possible may also be found. Geometrically, the method looks at the relative positioning of the subjects in the two measurement spaces (Cooley & Lohnes, 1971, p. 169). Usually the variables with the highest coefficients in each of these linear functions are assumed to define that function and hence the key features relating the two data sets may be assessed from a pair of coefficient vectors (Pielou, 1969; Cooley & Lohnes, 1971; Clifford & Stephenson, 1975; Williams, 1976).

Canonical correlation analysis has not been especially useful in agriculture or in biology in general (Austin, 1968; Williams, 1976) although Barkham & Norris (1970) and McIntire (1978) found its use encouraging. The method suffers, like many other similar parametric techniques, from the assumption of linear relationships between the variables. Its successful use in this paper may be due to the fact that sampling was from a fixed point on shore (i.e. the drain) seawards.

Cassie & Michael (1968) used canonical correlation analysis on data from a marine intertidal mudflat. Their results took the form of counts of 8 species and 9 sediment parameters for 21 stations. It is more usual in benthic surveys to find many more species than there are stations, in which case the corresponding correlation matrix will be singular and hence no solution will be available. The canonical correlations will be unity for the first one or more pairs of canonical variates calculated. This means that the canonical correlations can be made to appear high simply by making the number of variables included approach the number of stations.

It is therefore necessary to reduce the number of species (and possibly also the number of environmental variables); this may be done in several ways. The simplest approach is to discard the rarest species or species which occur at fewest stations. Species whose distributions correlate weakly with those of other species are unlikely to contribute to an overall pattern and may, therefore, be ignored (Williams, 1976). Species which do not correlate highly with any environmental variable, or vice versa, may be omitted.

This paper describes the use of canonical correlation analysis of data from a marine benthic survey which has previously been analysed using classification and partial correlation (Poore & Kudenov, 1978). The objective then was to describe the distribution of the fauna in terms of abiotic variables and in particular to assess the effect of a sewage-treatment farm drain on the fauna. In this paper this is still an objective, but the main one is to illustrate the stages involved in applying canonical correlation analysis.

METHODS

SAMPLING

A 2-km^2 area was sampled at 36 stations on seven radiating lines during 18–28 November 1975 (Fig. 1). The origin of the grid was near the 145W drain of the Wer-
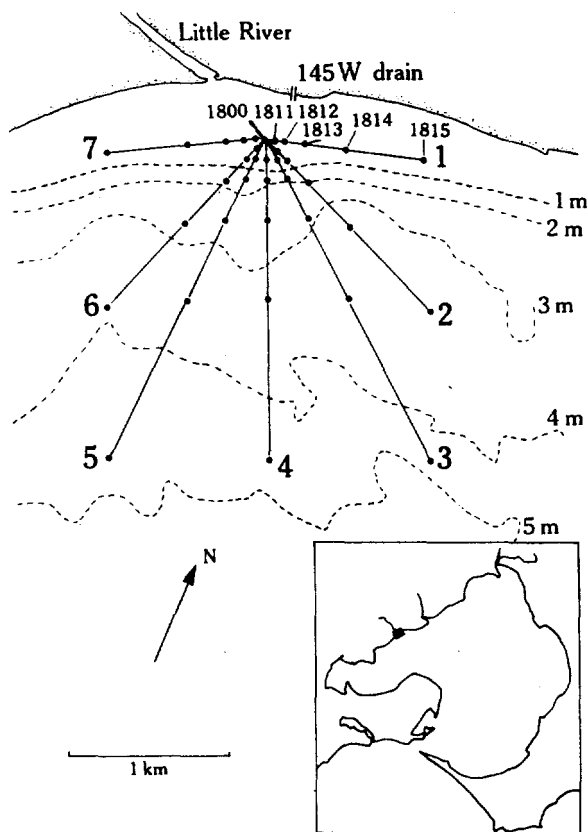

Fig. 1. The area studied and its location in Port Phillip Bay (inset): transects are numbered 1 to 7; the origin (Station 1800) and stations on transect 1 (1811–1815) are labelled (Poore & Kudenov, 1978); the station prefix 18 is not used in subsequent figures.

ribee sewage-treatment farm. About 40 environmental variables were determined and macrofaunal species in 0.05-m² samples were counted (Poore & Kudenov, 1978).

DATA REDUCTION

Thirteen abiotic variables were selected: depth, concentrations of nitrite plus nitrate; ammonia and phosphate in the interstitial water; percentage of carbonate in the sediment; mean particle size; sorting coefficient; percentages of medium sand, fine sand, very fine sand, silt and clay; and percentage of organic matter (Poore & Kudenov, 1978). The list of species was reduced from 246 to 49 first by omitting all species averaging less than one individual per sample.

Three alternative schemes were tried to further reduce the number of variables and canonical correlation analysis was performed on each resulting data set. (1) Species with total counts of fewer than 118 individuals were discarded; this left 22 species and all 13 environmental variables. (2) Only species present in half or more of the stations were included; this resulted in 18 species and 13 environmental variables. (3) Only species which correlated with three or more environmental variables with $|r| > 0.4$ were included. In addition, only environmental variables correlating with seven or more species with $|r| > 0.4$ were included. This process left 22 species and 9 environmental variables in the analysis. It was observed that the species which were omitted were those which also correlated highly with fewest (< 14) other species and the environmental variables omitted correlated highly with at most two other environmental variables.

DATA TRANSFORMATION

As with most multivariate methods, more success can be expected when applying canonical correlation analysis if the data are approximately multivariate normal in distribution. As counts are usually skewed in benthic surveys, a log transformation was decided upon. In fact, log (count + 1) was used. In the case of abiotic variables, those that were percentages (P) had the transformation arctan square root applied to $P/(100 - P)$ (Snedecor & Cochran, 1976, p. 32).

DATA ANALYSIS

For each reduced set of p species variables and reduced set of q environmental variables a canonical correlation analysis was carried out using the SPSS subprogram CANCORR. The output consisted of (1) correlation coefficients between all pairs of $p + q$ variables; (2) correlations between q pairs of linear functions (canonical variates); (3) coefficients (loadings) of the $p + q$ original variables on the q pairs of canonical variates (CVs), and (4) the canonical variate scores for the stations on the first two pairs of CVs.

Considering the first pair of canonical variates for example, if $s_{1i}, s_{2i} \ldots s_{pi}$ are the standardized species counts at Station i and $e_{1i}, e_{2i} \ldots e_{qi}$ are the standardized values of environmental variables at that station, then the output gives the vector of loadings a and b such that

$$z_{1i} = a_1 s_{1i} + a_2 s_{2i} + \ldots + a_p s_{pi}$$

$$z_{2i} = b_1 e_{1i} + b_2 e_{2i} + \ldots + b_q e_{qi},$$

where z_1 and z_2 are the pair of canonical variates. Hence the canonical variate scores for Station i can be evaluated, plus the correlation between z_1 and z_2 (called the canonical correlation coefficient).

Given a pair of canonical variates that are highly correlated it is only necessary to consider the canonical variate scores for one set of data variables. Selecting one set of station scores from each of the first two pairs of canonical variates (environmental CVs in our case), the stations were plotted in the two dimensional space, in order to see if they grouped together. These groups were then marked off on the original map of the sampling area in which the stations occurred (see Fig. 1), to see what interpretation, if any, could be placed on the canonical variates.

Given the correlation matrix for the environmental variables (or species), multiplication by the corresponding vector of loadings, produces a vector of correlations between the environmental variables (or species) and the canonical variate. If one or two of these correlations are high, then the canonical variate may be interpreted.

RESULTS

The initial intuitive interpretation of the results, both environmental and biotic, suggested that the major gradient in the sample grid was with increasing distance from shore and increasing depth. Sediments nearshore (within the 1-m contour) were more sandy, better sorted (lower sorting coefficient) and contained less carbonate than those offshore (Poore & Kudenov, 1978). Interstitial nutrient concentrations were generally greater nearshore than offshore. The stations were also separable into a nearshore group and an offshore group based on their fauna but many species were quite widespread (Poore & Kudenov, 1978).

In the first data reduction scheme both CV1 (the first pair of canonical variates) and CV2 represented several environmental variables but only CV2 was associated with any species. The correlations between these species and environmental variables were not high and were often contradictory in sign. The sample scores plotted for a canonical variate of each pair did not fall into discrete groups or show any spatial trend. The only exception was that the shallowest stations tended to fall together.

Similar results were obtained with the second data reduction scheme although different environmental variables and species were involved. In neither scheme

Loadings on nine environmental variables and 22 species on the first two canonical variates (CV1 and CV2) in the third canonical correlation analysis: species are given with a single-letter code indicating taxon (thus Amphipoda, Bivalvia, Cumacea, Isopoda, Mysidacea, Ostracoda, Polychaeta) and the total number of individuals captured in 36 samples.

Environmental and biotic variables			CV1 $r = 0.993$	CV2 $r = 0.979$
Depth			0.588	0.509
Orthophosphate			0.090	0.530
Ammonia			0.119	−0.316
Percentage carbonate			· 0.037	−0.509
Sorting coefficient			−0.251	−0.257
Percentage medium sand			−0.354	−0.585
Percentage fine sand			−0.851	−0.412
Percentage silt			−0.330	−0.199
Percentage clay			0.530	0.138
Gammaropsis sp. 1	A	1414	−0.072	0.021
Mediomastus sp. 1	P	1026	0.693	−0.327
Caulleriella sp. 1	P	536	−0.428	0.835
Eunice antennata Savigny, 1820	P	269	−0.712	−0.971
Asychis sp. 1	P	217	0.948	−1.011
Dimorphostylis cottoni Hale, 1936	C	199	−0.561	0.129
Euphilomedes sp. 1	O	182	0.239	0.623
Exoediceros sp. 1	A	177	0.102	−0.398
Afromysis australiensis Tattersall, 1940	M	146	0.058	−0.560
Limnoporeia sp. 2	A	138	0.056	−0.390
Notospisula trigonella (Lamarck, 1818)	B	131	0.298	0.531
Magelona sp. 1	P	114	0.584	−0.048
Cirolana woodjonesi Hale, 1924	I	97	0.162	0.445
Gastrosaccus dakini Tattersall, 1940	M	92	0.025	0.334
Oedicerotid sp. 4	A	72	0.788	0.428
Glyphocuma bakeri Hale, 1936	C	71	0.01⁻	−0.151
Paraphoxus sp. 9	A	64	0.40⁻	0.241
Oediceroides sp. 1	A	50	−1.049	−0.317
Ophiodromus sp. 1	P	48	−0.276	−0.481
Dorvillea australiensis (McIntosh, 1885)	P	40	0.988	0.050
Paraphoxus sp. 6	A	39	0.200	0.349
Rutiderma sp. 1	O	39	−0.349	−0.228

could the pattern of stations in the two-dimensional space (defined by the first two canonical variates) be transposed to a map of the stations in real space such that a trend or zones were apparent.

In the third data reduction scheme (Table I) CV1 was dominated by a single environmental feature, the percentage of fine sand, which decreased with increasing distance from shore. Within the 1-m depth contour the percentage of fine sand ranged from 62 to 81% but beyond this line values from 2 to 62% were found. *Dorvillea, Asychis,* and oedicerotid sp. 4 were all negatively correlated with fine sand and were found only beyond the 1-m contour. *Oediceroides* and *Eunice* were also

negatively correlated with fine sand and distributed similarly to the other three so their loadings on variate 1 seem anomalous.

No environmental variables had particularly high loadings on CV2. The three species with high loadings on CV2 were most common at middle to greater depths.

Nevertheless, the station scores plotted for a canonical variate from each pair (Fig. 2) fell into discrete groups which were meaningful in real space (Fig. 3). Group
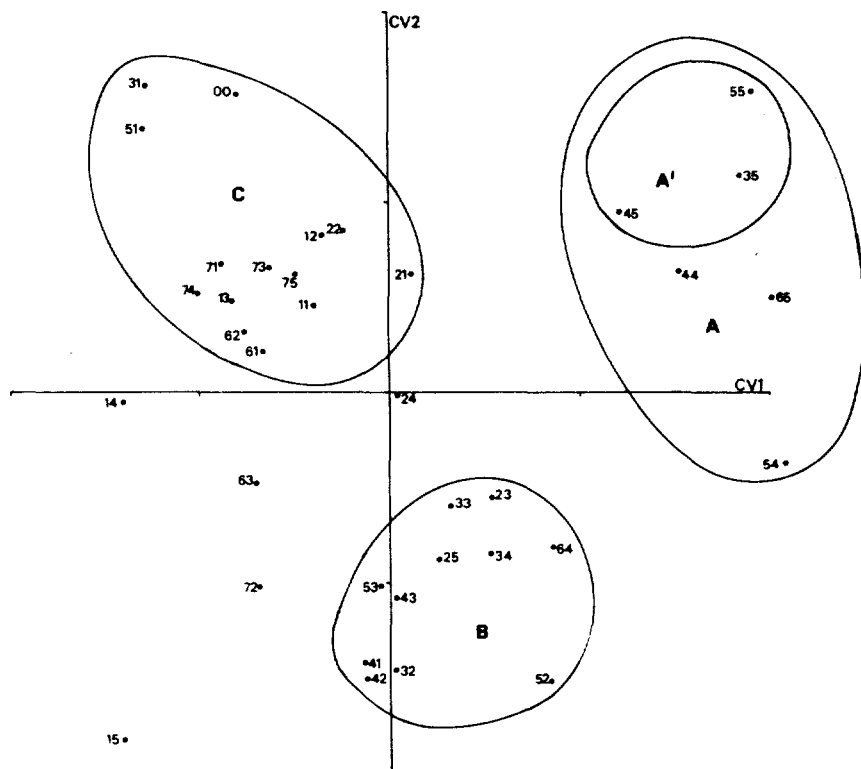

Fig. 2. Sampling stations plotted using scores on canonical variates 1 and 2: data reduction scheme 3; groups of stations obvious by inspection are circled and labelled A, A′, B, and C.

A, with highest positive scores on CV1, included deepest stations. Within this Group A′ comprised the three deepest stations with highest scores on CV2. Stations in Group B had intermediate scores on CV1 and low scores on CV2 and occurred at intermediate depths (Fig. 3). The remaining Group C included most of the stations within the 1-m contour (Fig. 3). Stations 14 and 15 had much lower scores on CV2 than expected. By examination of the original data it could be seen that the percentage of medium sand was greater here than at other stations in Group C. Percentage medium sand was one of the factors associated with CV2. The position of Station 72 cannot be interpreted in this way.

As the plot of scores gave meaningful results, the analysis was extended by computing the correlations between the variables (environmental and species) and the canonical variates. In the first instance this was done for the first two canonical variates and, when these were found to be encouraging, for the third variate as well.
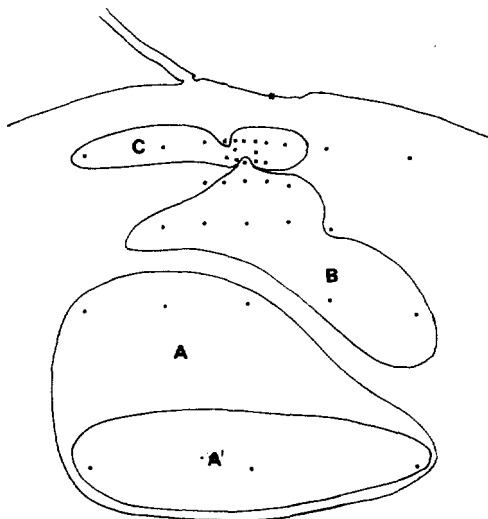

Fig. 3. Station groups (A, A′, B, and C derived from Fig. 2) plotted on the original sampling grid shown in Fig. 1.

The first canonical variate had strong correlations with most environmental variables. High positive correlations were found with silt, depth, and clay and high negative correlation with fine sand (Table II). The variate can therefore be said to represent a gradient of increasing depth and associated changes in sediment characteristics.

Correlations with CV2 were weaker but a positive correlation with phosphate and negative correlations with medium sand and carbonate were apparent (Table II).

TABLE II

Correlations between variables and the first three canonical variates obtained using data reduction scheme 3.

Variable	CV1	CV2	CV3
Depth	0.867	−0.012	−0.427
Orthophosphate	−0.512	0.537	0.423
Ammonia	−0.358	−0.105	0.201
Percentage carbonate	0.459	−0.667	−0.169
Sorting coefficient	0.689	−0.301	0.482
Percentage medium sand	0.262	−0.723	−0.035
Percentage fine sand	−0.827	0.409	−0.153
Percentage silt	0.890	−0.122	0.298
Percentage clay	0.738	−0.051	0.541

species in any sample is small and is more likely due to chance than to similar habitat requirements. Elimination of rare species in fact has an effect similar to that of reduction in sampling effort. We reduced our original species list of 246 to 49 by excluding the rarest species. A further reduction by the same exclusion principle produced answers for the canonical correlation analysis which were difficult to interpret.

The second data reduction scheme eliminates species occurring at fewest stations. This has the disadvantage of removing from the analysis species confined to a single station or to a small group of stations. We suspected in this study that the sewage-farm drain would influence only a few stations. Removal of species confined to these stations defeats the purpose of the investigation and, as expected, gave unsatisfactory results in the canonical correlation analysis.

The third data reduction scheme gave the most easily interpretable results. Variables which do not correlate with each other (or with other variable-sets which are themselves interrelated) behave independently, unconnected with patterns elsewhere in the system. In the search for pattern they may as well be omitted. In addition, this scheme is less arbitrary, depending on examination of data relationships rather than restriction of the community studied. That is, the scheme does not violate the concept of a community as much as the other two schemes and provided us with ecologically sensible results.

Alternative data reduction schemes have been used in canonical correlation analysis. For example, Barkham & Norris (1970) replaced their original data matrix by a smaller matrix of eigenvectors from which those vectors associated with a small eigenvalue were omitted. The loadings of the original variables on the canonical variates can then be derived indirectly but Barkham & Norris were not satisfied with their analytical results.

DATA ANALYSIS

There are at least three ways of giving the canonical variates meaning. One is to look at relative sizes of loadings, another is to plot station scores on the canonical variate. The third is to look at the correlations between original variables and canonical variates. The first approach appears to be unsatisfactory. The loadings are not independent of one another, so removing a particular variable from an analysis causes the loadings of the other variables to change magnitude. It was found that removing a species at random from those used in the third data reduction scheme (thus removing thirty correlation coefficients) changed the loadings reported in Table I out of all recognition.

The use of station canonical scores was a valuable aid to describing our results and relating them to sampling space (see Figs. 2 and 3). Surprisingly, this approach appears not to have been used before in the ecological literature. This is probably because scores are of little value in the sociological problems for which canonical

correlation analysis was developed. An anonymous individual's score on a canonical variate is of no value to the sociologist but in ecology it is possible to relate scores to an extrinsic variable, the stations' spatial relationship to each other.

Computing the correlations between the original variables and their corresponding canonical variates enables us to do two things: first, group together those species with high correlations with some canonical variate, and secondly take the environmental variables correlating highly with the other canonical variate of its pair to explain the factors causing this grouping.

The choice of how many canonical variate pairs to include in the results can be made on the basis of significance tests on the canonical correlation coefficients. The size of the canonical correlation coefficient is dependent upon the relative number of stations and data variables. Hence a value very close to unity may look impressive but, as in the above reduction schemes, is only high because the number of stations is only one or two above the number of data variables. Tests of hypotheses concerning the significance of canonical correlation coefficients are obviously irrelevant if the coefficient is unity. For following pairs of canonical variates they are valid only if the stations are a random sample of the area of interest, which is not the case for transect sampling. Using the significance level produced, however, by the SPSS package as a guide only, the first two or three pairs of canonical variates in each of our data reduction schemes were retained for further analysis.

Geometrically, a canonical correlation of unity implies that the position of the stations on a line in the species-space is identical to the positioning in the environmental-space, apart from a multiplying factor. This does not mean that these canonical variates are important factors in the original spaces. A better measure of the way in which species distributions are determined by the environmental variables measured may be the redundancy (Cooley & Lohnes, 1971, p. 171). In this study, for the first three canonical variate pairs, 48% of the variation in the species was associated with variation in the environmental variables. Total redundancy is analogous to the squared multiple correlation coefficient in multiple regression analysis and in fact canonical correlation analysis reduces to regression analysis when either p or q equals one.

RESULTS OF THIS STUDY

It certainly aids in interpretation if the environmental canonical variates can be explained in terms of few variables as was the case with the third scheme. It was a fault of the first two schemes that several environmental variables had high or similar loadings on the variates. On the other hand, the ecologist wanting to explain the biotic attributes in terms of the abiotic attributes is delighted if several species have high loadings or correlations on a variate explained by a single abiotic variable.

In this study, CV1 represented a gradient of depth and associated sediment properties, CV2 represented depth and nutrients, and CV3 represented changes in sediment

characteristics not associated with depth, i.e. patchiness in the abiotic habitat.

The clear division of the species into two groups along the first three canonical variates enabled characteristic ("indicator") species to be recognized. In Fig. 5 these groups were compared with the six species-groups obtained by classification analysis by Poore & Kudenov (1978, their Table 3). (Note that the species used in the canonical correlation analysis were only a subset of those used in the classification.)
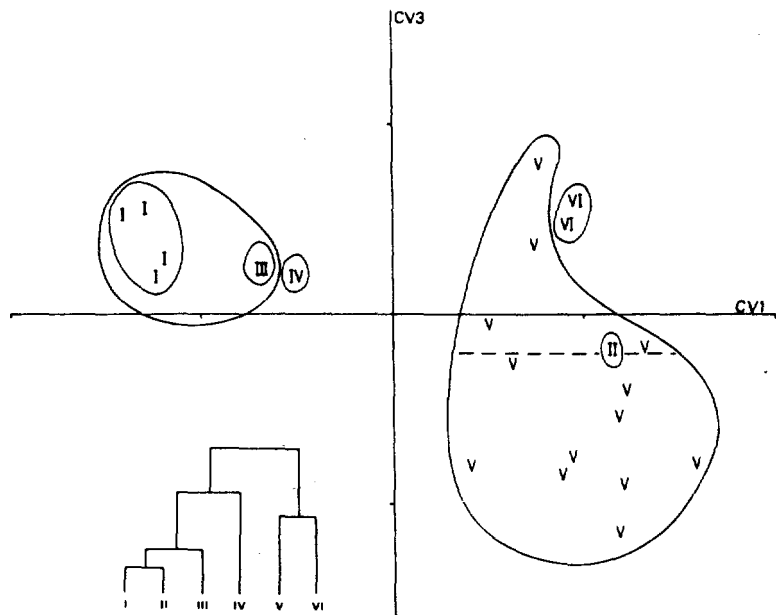

Fig. 5. Species plotted using correlations on canonical variates 1 and 3 (Fig. 4): species are here labelled with the group (I to VI) to which they were assigned in Poore & Kudenov's classification: (1978, their Table 3); the hierarchy of groups (inset) is given and translated to the plot by encircling progressively higher levels in the hierarchy; the position of Group II is anomalous (see text); the dashed line divides sub-groups of Group V; *Dorvillea* was incorrectly given as cf. *Synasterope* sp. 2 by Poore & Kudenov (1978, their Table 3).

The species from Groups I, III, and IV (together combined at higher levels in the hierarchy) were confined to or most dense at shallowest stations. Species in Groups V and VI (the second half of the hierarchy; Fig. 5) were most abundant in deep water. *Mediomastus* (from Group II) was mis-classified in Poore & Kudenov's treatment and is better placed with deep-water species as happens in the canonical correlation analysis.

Species Group V contained the largest number of species and was relatively confined on CV1 and CV2 but had both positive and negative correlations with CV3 (Fig. 5). Subsequent examination of the hierarchical classification indicated that this group can be further divided into two sub-groups, the first of species whose correlations with CV3 were > -0.1 and the second of species whose correlations

with CV3 were < -0.1 as indicated by the dashed line in Fig. 5. The species with highest positive correlations (*Dimorphostylis*, *Paraphoxus* sp. 9) were confined to stations at depths >2 m. The species with highest negative correlation (e.g. *Cirolana*) were more scattered and more widespread.

CONCLUSION

The success of this study suggests that canonical correlation analysis has not received the attention in benthic ecology that it deserves. We have shown how it is possible to erect station groupings, define characteristic species for different habitats and to relate the distribution of species and samples to environmental variables. More popular classification techniques fail to meet the last, and often most important, of these objectives.

It is almost axiomatic that the structure and function of the benthos is determined in the first instance by the nature of sediment. Thorson's (1957) concept of parallel level-bottom communities relies on this proposition but there has been very little research on the particular features of the sediment to which animals respond. Sanders (1958) found that the density of macrobenthos correlated with the percentage of clay, but suggested that high levels of organic matter associated with clay were responsible for the nature of clay-loving fauna. On a gross scale the sediment-fauna relation is probably true, but what rôle do grain size and other sedimentary properties play in determination of patchiness or trends in species distributions over intermediate or small scales? Are their effects masked by interspecific competition? Lie (1974) used principal components analysis of a benthic fauna followed by multiple regression to explore the relations among the extracted components and environmental variables. A correlation was found between one of the components and mean particle size which was independent of depth. Smith & Greene (1976) used similar methods with some success for benthos influenced by a submarine outfall. Few authors have, however, attempted to demonstrate such a statistical relation between biotic and abiotic variables on small scales and use of canonical correlation analysis for this purpose seems well worthwhile.

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