

A COMPARISON OF SOME METHODS FOR ANALYSING CHANGES IN BENTHIC COMMUNITY STRUCTURE

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Statistical methods for analysing changes in community structure fall under the three general headings of univariate, graphical/distributional and multivariate. These methods are applied to a variety of benthic community data (macrobenthos, meiobenthos, corals, demersal fish), from a variety of localities (intertidal/subtidal, temperate/tropical) and over both spatial and temporal scales. Four general conclusions emerge from this comparative study:

(1) The similarity between sites or times based on their univariate or graphical/distributional properties is usually different from their clustering in multivariate analyses.

(2) Species dependent (multivariate) methods are much more sensitive than species independent (univariate and graphical/distributional) methods in discriminating between sites or times.

(3) In examples where more than one component of the fauna has been studied, univariate and graphical/distributional methods may give different results for different components, whereas multivariate methods tend to give the same results.

(4) By matching multivariate ordinations from subsets of environmental data to an ordination of faunistic data, the key environmental variables responsible for community change may be identified.

INTRODUCTION

Natural communities of animals and plants generally comprise a large number of species, and changes in community structure are determined by a suite of different environmental variables to which each of the species in the community may respond differently. The community ecologist is thus faced with a rather complex problem of characterising community attributes, analysing changes in them over spatial or temporal scales, and relating these changes to potentially causal environmental variables. A wide variety of different solutions to these problems has been developed, but broadly the available methods fall into three categories:

(1) Univariate methods. Relative abundances of the different species at each site or time are reduced to a single index.

(2) Graphical/distributional methods. Relative abundances or biomasses of different species are plotted as a curve, which retains more information about the distribution than a single index.

(These two methods are not species specific, and two communities with a completely different taxonomic composition could have the same univariate or graphical/distributional structure.)

(3) Multivariate methods of classification and ordination which compare communities on the basis of the identity of the component species as well as their relative importance in terms of abundance or biomass.

For each of these classes of methods there are appropriate statistical tests to determine the significance of differences between replicated community samples in either time or space. For univariate indices, classical ANOVA is appropriate, and for graphical and multivariate methods there are multivariate equivalents, including the simulation/permutation test ANOSIM (Clarke & Green, 1988; Clarke, 1990) which does not make the assumption of multivariate normality in the data.

This paper compares these classes of methods by applying them to a broad range of studies on various components of the marine benthos from a variety of localities in order to address the questions of whether species dependent and species independent attributes of community structure behave the same or differently in response to environmental changes, and which are the most sensitive. Within each class of methods there is a very wide variety of different techniques employed, and to make this comparative exercise more tractable we have chosen to examine only one method for each class; the Shannon Wiener diversity index $H' = -\sum p_i (\log_e p_i)$ (Shannon & Weaver, 1949), k -dominance curves (Lambshhead *et al.*, 1983) and non-metric Multi-dimensional Scaling Ordination (MDS) (Kruskal & Wish, 1978) on a Bray-Curtis similarity matrix of appropriately transformed species abundance or biomass data. All of these methods are now very commonly employed in community studies. The example studies referred to will only be described briefly, as more detail can be found in the relevant publications, which are referenced.

SENSITIVITY

The first four examples compare the relative sensitivities of these methods in detecting community change.

Ekofisk oil-field macrobenthos

Changes in community structure of the soft-bottom benthic macrofauna in relation to oil drilling activity at the Ekofisk platform in the North Sea have been described by Gray *et al.* (1990). The positions of the sampling stations around the rig are coded by shading conventions in Figure 1 according to their distance from the currently active platform. It can be seen from Figure 2 that species diversity is significantly reduced only in the black zone, closer than 250 m from the rig, and that the three outer zones do not differ from each other in terms of species diversity. Similarly, the k -dominance curves (Figure 3) indicate a significant effect only within the black zone, the curves for the three outer zones being closely coincident. These methods of data analysis, which are commonly employed in pollution studies, suggest that the effects of the oil rig on the benthic fauna are extremely localised. However, in the MDS analysis (Figure 4) community composition in all of the zones is distinct, and there is a clear gradation of change from the (black) inner to the (open circle) outer zones. Formal significance testing (using ANOSIM) confirms statistically the differences between all zones. The MDS is clearly more sensitive, and can detect differences in community structure up to 3 km away from the rig.

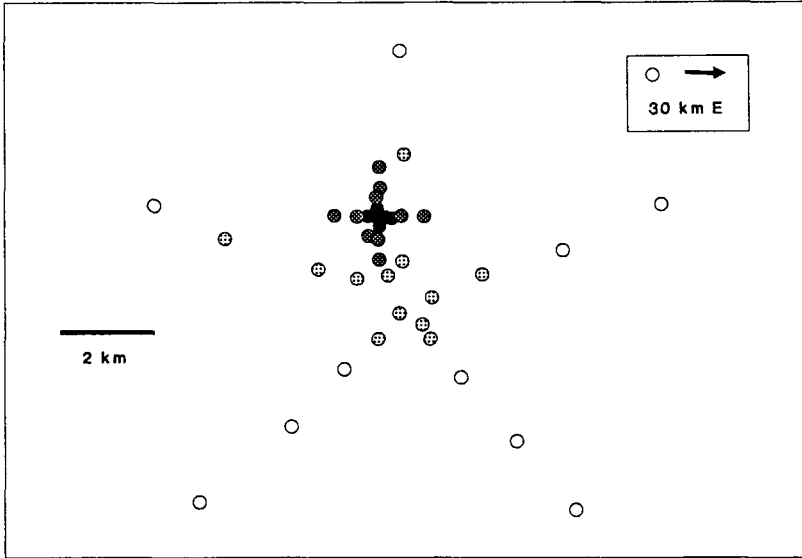


Figure 1. Map of sampling stations around the Ekofisk oil rig. Stations are represented by circles shaded according to their distance from the rig, which is situated at the centre of the black circles.

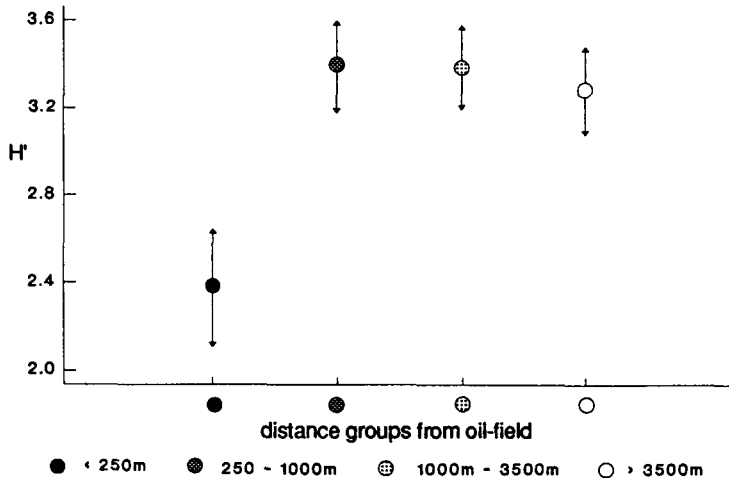


Figure 2. Shannon diversity of the macrobenthos (mean and 95% confidence limits) in each distance-zone around the Ekofisk rig.

Frierfjord macrobenthos

As part of the GEEP/IOC Oslo Workshop on the biological effects of pollutants (Gray *et al.*, 1988), macrobenthos samples were collected at a series of six stations in Frierfjord/Langesundfjord, station A being the outermost and station G the innermost (station F was not sampled for macrobenthos). For a map of the sampling locations see figure 2 in

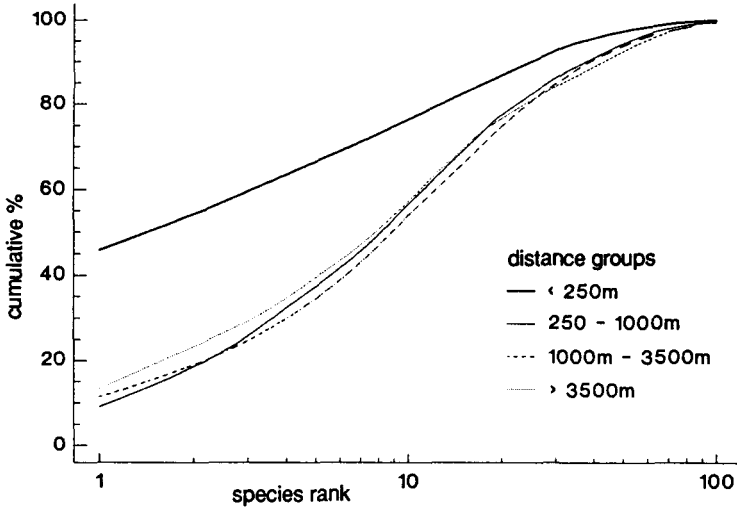


Figure 3. Mean k -dominance curves for the macrobenthos in each distance-zone around the Ekofisk rig.

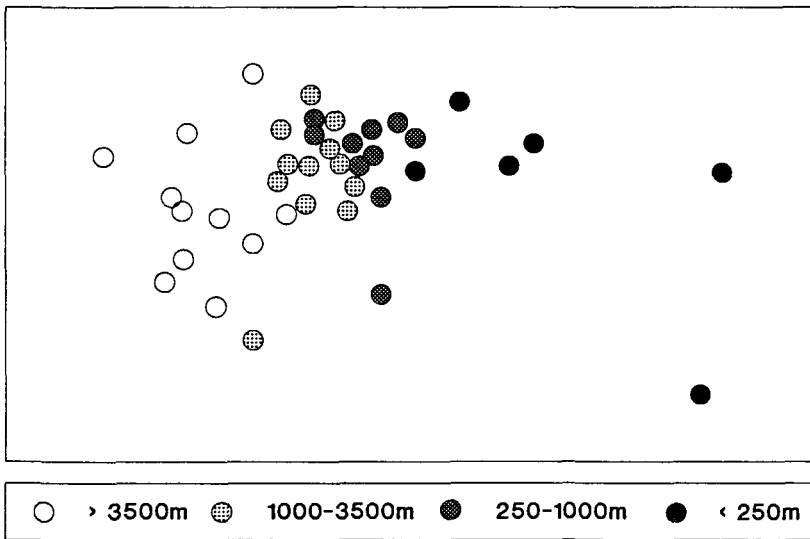


Figure 4. MDS ordination by stations of the root-transformed macrobenthos species abundance data for the Ekofisk oil-field.

Follum & Moe (1988). Site A had a higher species diversity and site C the lowest but the others were not significantly different (Figure 5). A comparison of the juxtaposition of k -dominance curves for species abundances and species biomasses (the ABC method of Warwick, 1986 and Warwick *et al.*, 1987) indicated that stations C, D and E were most stressed, B was moderately stressed, and A and G were unstressed (Figure 6). An MDS of all 24 samples (four replicates at each station), supported by the ANOSIM test, showed

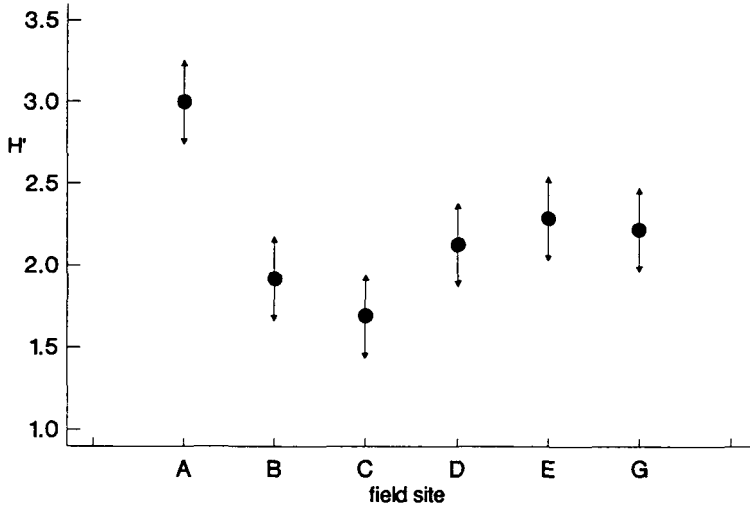


Figure 5. Shannon diversity of the macrobenthos (mean and 95% confidence limits) for stations in Frierfjord/Langesundfjord.

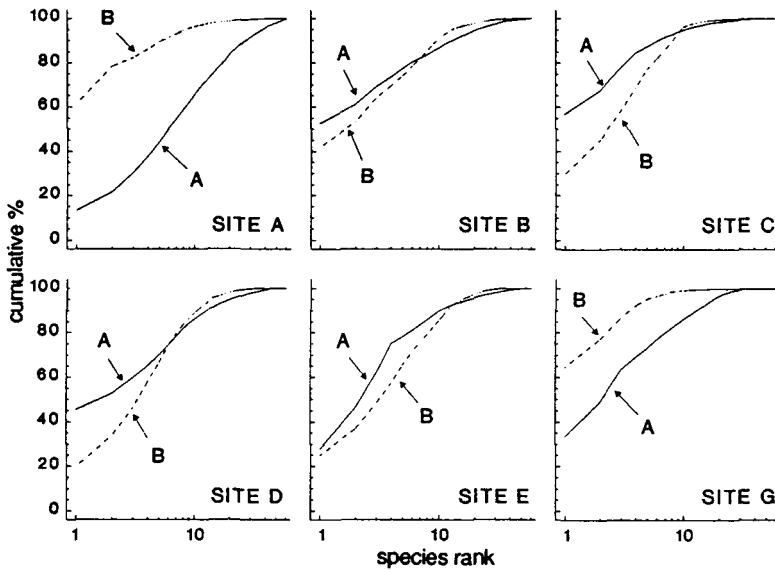


Figure 6. ABC curves for the macrobenthos species data at each station in Frierfjord / Langesundfjord. Solid lines, abundance; broken lines, biomass.

that only stations B and C were not significantly different from each other (Figure 7). Thus, the MDS was much better at discriminating between stations than the diversity measure, but perhaps more importantly, sites with similar univariate or graphical/distributional community structure did not cluster together on the MDS. For example E and G had different ABC plots but clustered together, and diversity at E was not significantly different from D although they are furthest apart on the MDS.

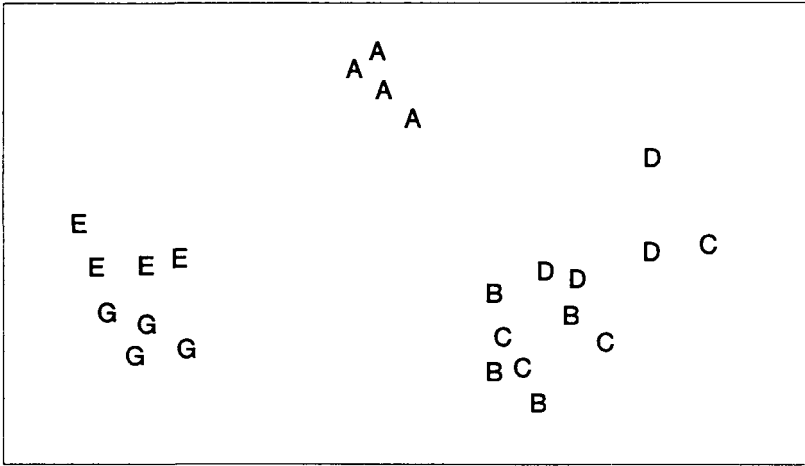


Figure 7. MDS ordination by stations (four replicates at each) of the double-square-root transformed macrobenthos species abundance data in Frierfjord/Langesundfjord.

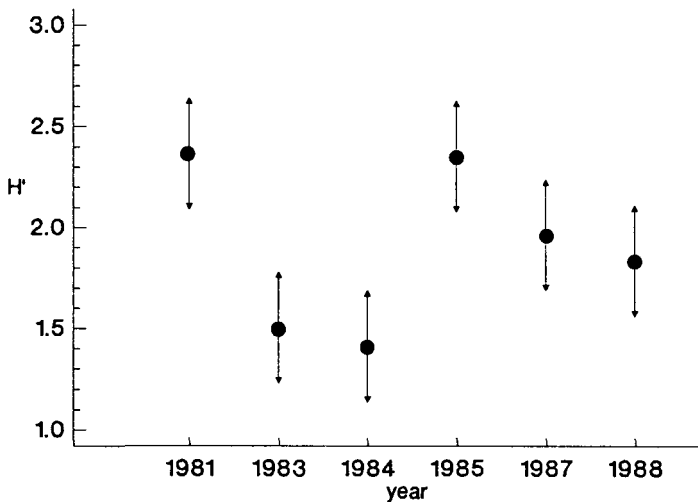


Figure 8. Shannon diversity (mean and 95% confidence limits) of coral species, based on area of cover, from 1981-1988 at Pari Island, Indonesia.

Pari Island corals

Warwick *et al.* (1990b) analysed coral community responses to the El Niño of 1982-83 at two reef sites in the Thousand Islands, Indonesia. At Pari Island there was an immediate reduction in diversity in 1983, apparent full recovery by 1985, with a subsequent but not significant reduction (Figure 8). The mean k -dominance curves were similar in 1981 and 1985, with the curves for 1983, 1984, 1987 and 1988 more elevated (Figure 9). The ANOSIM test confirmed the significance of differences between 1981 and 1985 curves from other years, but the other years were not distinguishable from each

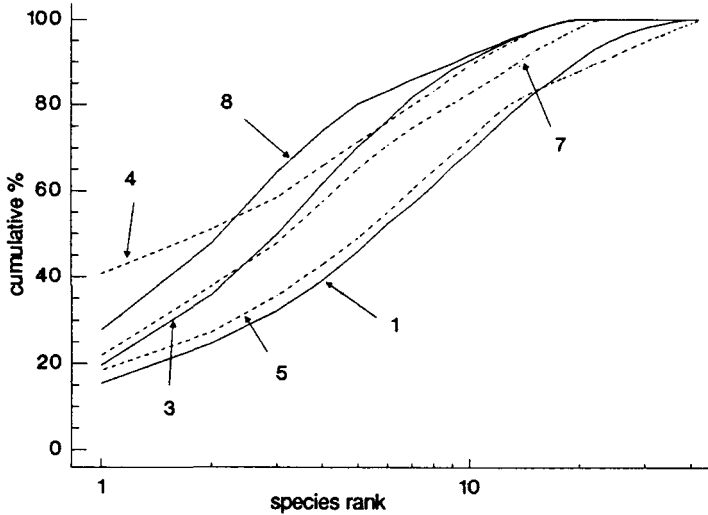


Figure 9. Average *k*-dominance curves for coral species, based on area of cover, from 1981 (=1) to 1988 (=8) at Pari Island, Indonesia.

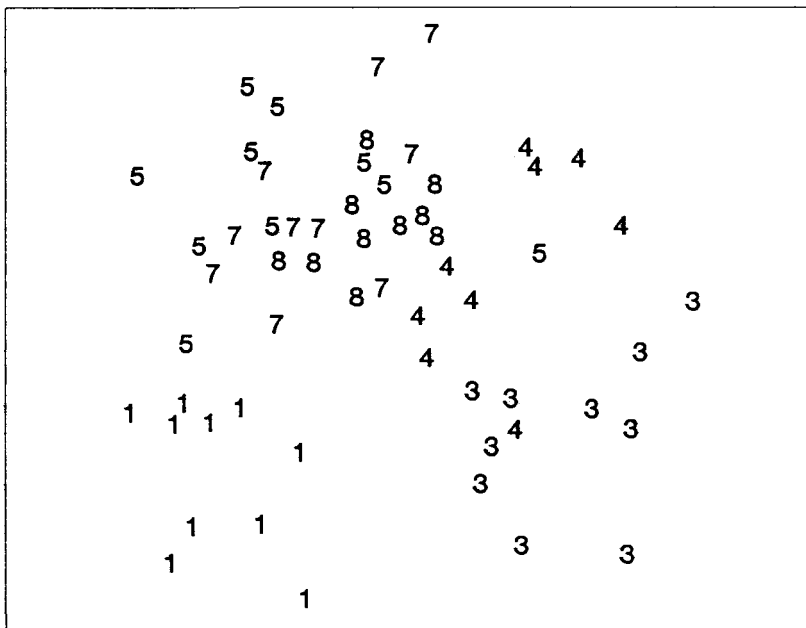


Figure 10. MDS by years (10 replicates each) of root transformed coral species cover data at Pari Island, Indonesia. 1=1981, 3=1983 etc.

other. The MDS showed an immediate location shift in community composition at the ten replicate sites between 1981 and 1983, and ANOSIM indicated significant differences between all pairs of years. Recovery proceeded in the pre-El Niño direction but was not complete by 1988 (Figure 10). Thus, although all the methods showed the immediate and dramatic post El Niño bleaching effect, the multivariate method was more sensitive in monitoring the recovery phase.

Maldives reef fish

In the Maldivian islands, Dawson Shepherd *et al.* (in press) compared reef-fish assemblages at 23 coral reef-flat sites, 11 of which had been subjected to coral mining for the construction industry and 12 were non-mined. The reef-slopes adjacent to these flats were also surveyed. No differences in diversity (Figure 11) or k -dominance curves (Figure 12) between mined and non-mined sites could be detected. The MDS (Figure 13), however, clearly distinguished mined from non-mined sites on the reef-flats, and also to a lesser degree even on the slopes adjacent to these flats; ANOSIM confirmed the significance of this difference.

Conclusions

These examples share two common features. Firstly, the similarity in community structure between sites or times based on their univariate or graphical/distributional

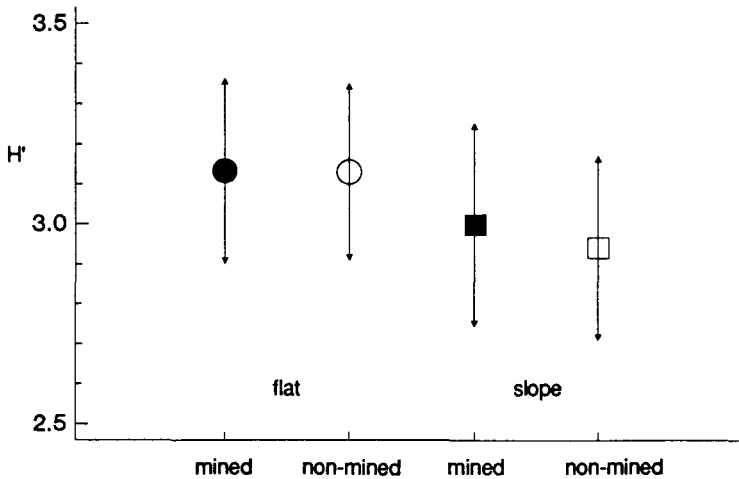


Figure 11. Shannon diversity (mean and 95% confidence limits) of coral fish assemblages at mined and non-mined reef-flat and slope sites in the Maldives.

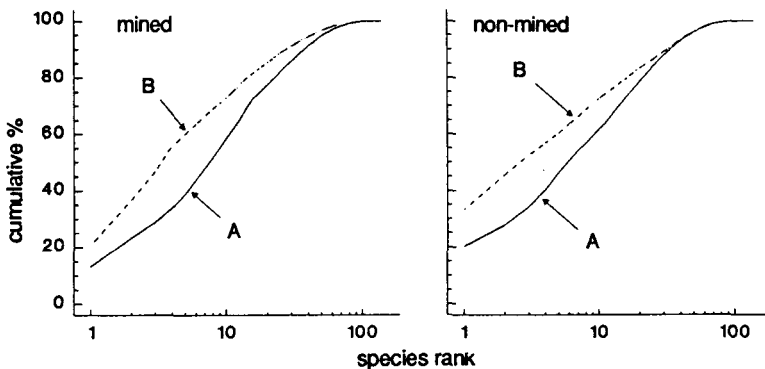


Figure 12. Average k -dominance curves for abundance and biomass of coral fish assemblages at mined and non-mined reef-flat sites in the Maldives.

attributes is different from their clustering in the multivariate analysis. Secondly, the species dependent multivariate method is much more sensitive than the species independent methods in discriminating between sites or times.

COMPARISON OF DIFFERENT FAUNAL COMPONENTS

Often in environmental impact studies, the general 'health' of the system is inferred from an analysis of just one component of the fauna, for example the macrobenthos or meiobenthos, or even a single taxonomic component of the latter, because of the taxonomic problems involved in sample analysis. The next three examples, while serving to reinforce the conclusions drawn above on the comparative performance and sensitivity of the methods of data analysis, are included mainly to examine the question of whether different components of the fauna give similar or different results in terms of their response to community change when subjected to these three types of analysis.

Isles of Scilly seaweeds

Dr J.M. Gee and colleagues at the Plymouth Marine Laboratory analysed the entire metazoan fauna (macrofauna + meiofauna) from five species of intertidal macro-algae (*Chondrus*, *Laurencia*, *Lomentaria*, *Cladophora*, *Polysiphonia*) each collected at eight sites near low water from rocky shores on the Isles of Scilly (unpublished data). The meiofauna and macrofauna showed clearly different diversity patterns with respect to weed type; for the meiofauna there was a trend of increasing diversity from the coarsest (*Chondrus*) to the finest (*Polysiphonia*) weed, but for the macrofauna there was no clear trend and *Polysiphonia* had the lowest diversity (Figure 14). These differences were also reflected in the *k*-dominance curves which had different sequencing for these two faunal components, for example the *Polysiphonia* curve (numbered 5 in Figure 15) was the lowest for meiofauna and highest for macrofauna. However, the MDS plots for meiobenthos and macrobenthos were very similar, with the algal species showing very similar

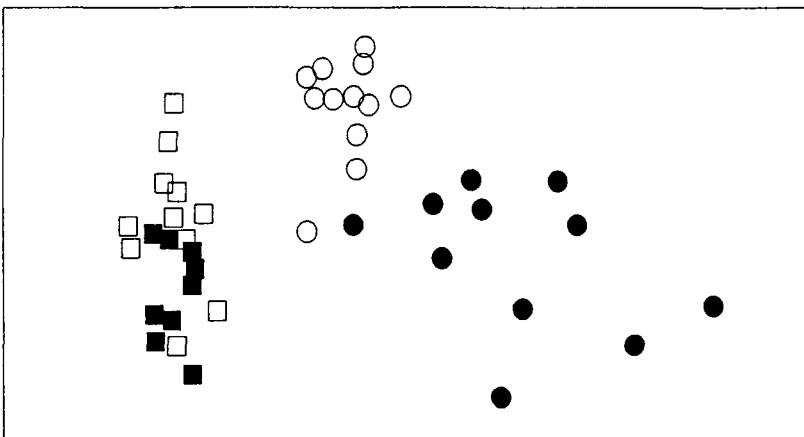


Figure 13. MDS by sites of the double-square-root transformed coral fish species abundance data in the Maldives. Symbols as in Figure 11, i.e. circles, reef-flat; squares, slope; solid, mined; open, non-mined.

relationships to each other in terms of their meiofaunal and macrofaunal community structure (Figure 16).

Tamar estuary meiofauna

Austen & Warwick (1989) compared the structure of the two major taxonomic components of the meiobenthos, nematodes and harpacticoid copepods, in the Tamar estuary for six replicate samples at a series of ten intertidal soft-sediment sites (site 1 at the mouth of the estuary and site 10 at the head). The average k -dominance curves show no clear sequencing of sites for the nematodes, for example the curve for site 1 is closely coincident with that of site 10 (Figure 17). For the copepods, however, the curves become increasingly elevated from the mouth to the head of the estuary. In the MDS, both

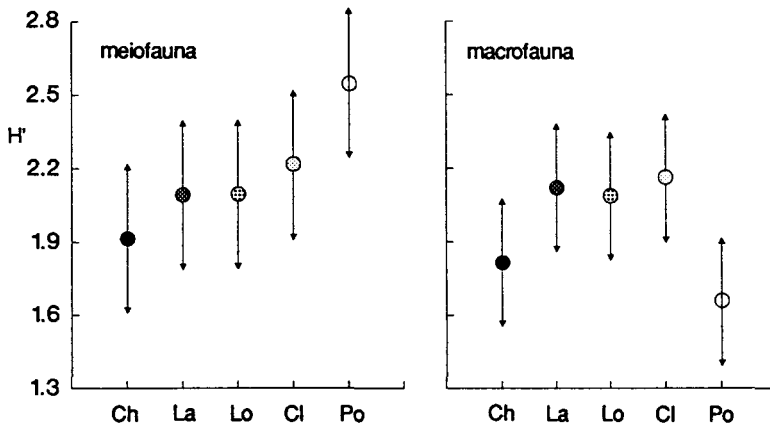


Figure 14. Shannon diversity (mean and 95% confidence limits) for the meiofauna and macrofauna of intertidal seaweeds on the Isles of Scilly. Ch, *Chondrus*; La, *Laurencia*; Lo, *Lomentaria*; Cl, *Cladophora*; Po, *Polysiphonia*.

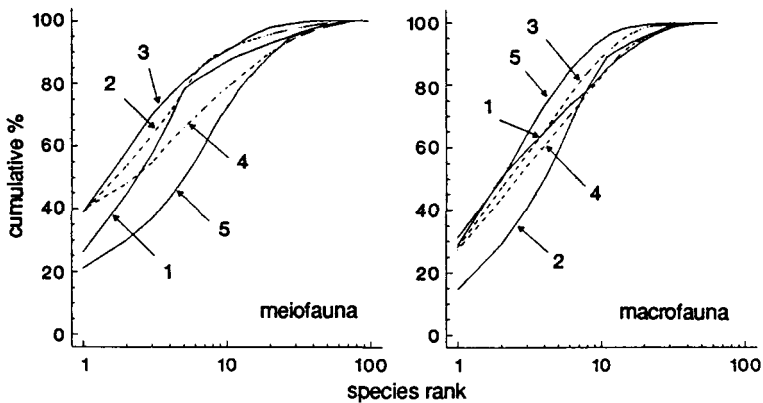


Figure 15. Average k -dominance curves for meiofauna and macrofauna species abundances in five species of intertidal seaweeds on the Isles of Scilly.

nematodes and copepods show a similar horse-shoe shaped sequencing of sites from the mouth to the head of the estuary (Figure 18).

Eaglehawk neck meiofauna

Warwick *et al.* (1990a) studied the effect of disturbance by soldier-crabs on the structure of the nematode and copepod components of the meiobenthos at an intertidal sandflat at Eaglehawk Neck, on the Tasman Peninsula, Australia. The crabs disturbed the sediment in discrete patches, and samples were collected in a blocked design, the four blocks having two samples inside and two outside a disturbed patch, as shown schematically in Figure 19. Two-way ANOVA showed a significant reduction in species

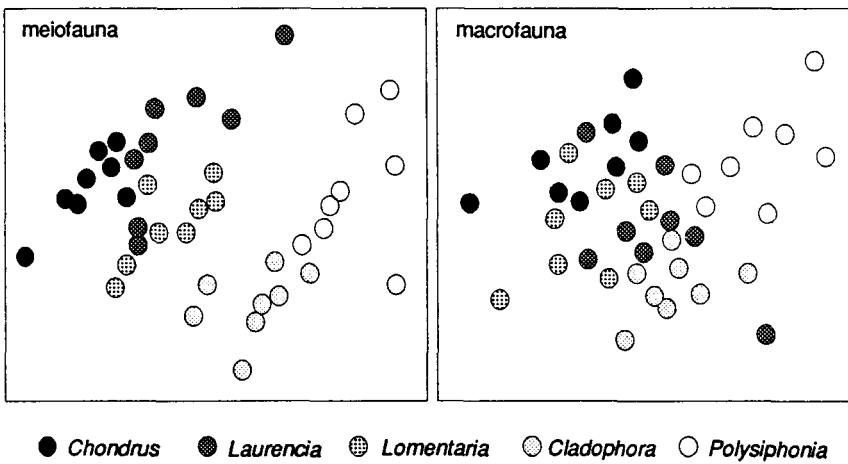


Figure 16. MDS by sites of the standardised double-square-root transformed meiofauna and macrofauna species abundance data from the Isles of Scilly. The five seaweed species are indicated by different shading conventions.

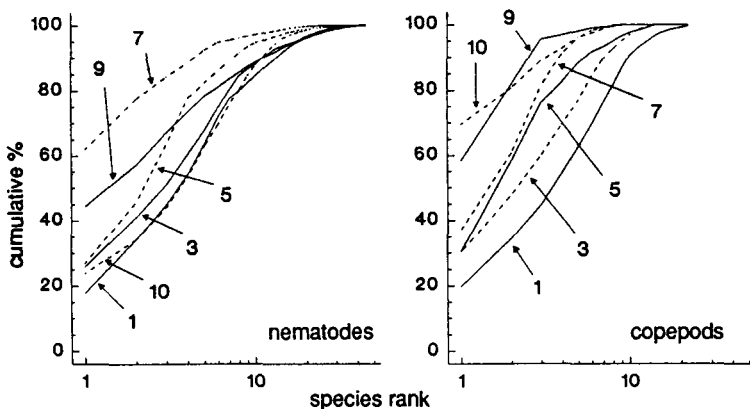


Figure 17. Average k -dominance curves for nematode and copepod species abundance data at ten stations in the Tamar estuary. For clarity of presentation, some sites have been omitted (see Austen & Warwick, 1989, for details).

diversity in the disturbed areas for the nematodes, but not for the copepods. The k -dominance curves were also significantly elevated in disturbed blocks for the nematodes (Figure 20), as tested by two-way ANOSIM, but not for the copepods (Figure 21). However, the MDS configurations for nematodes and copepods both showed a similar pattern to that of the 'total meiofauna' (nematodes+copepods), with the disturbed sites in each block positioned above the undisturbed sites (except for one copepod sample in the block designated by diamond-shaped symbols) and the same left-right sequencing of blocks (Figure 22).

Conclusions

In these examples where more than one component of the fauna has been studied, a general feature is that the univariate and graphical methods gave different results for different components, whereas the multivariate method gave the same results.

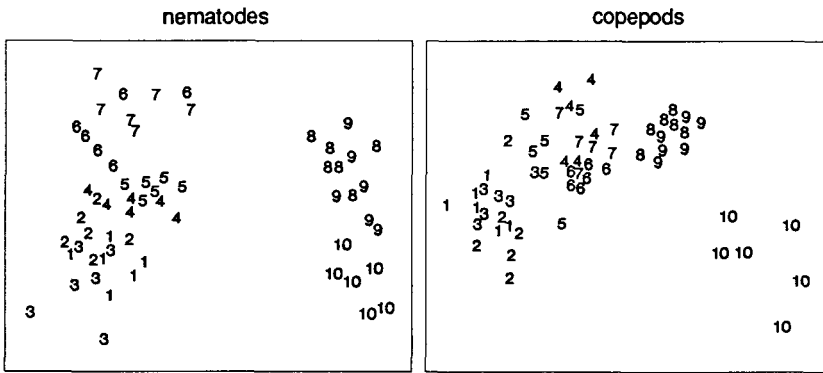


Figure 18. MDS by sites (each with six replicates) of double-square-root transformed nematode and copepod species abundance data from the Tamar estuary.

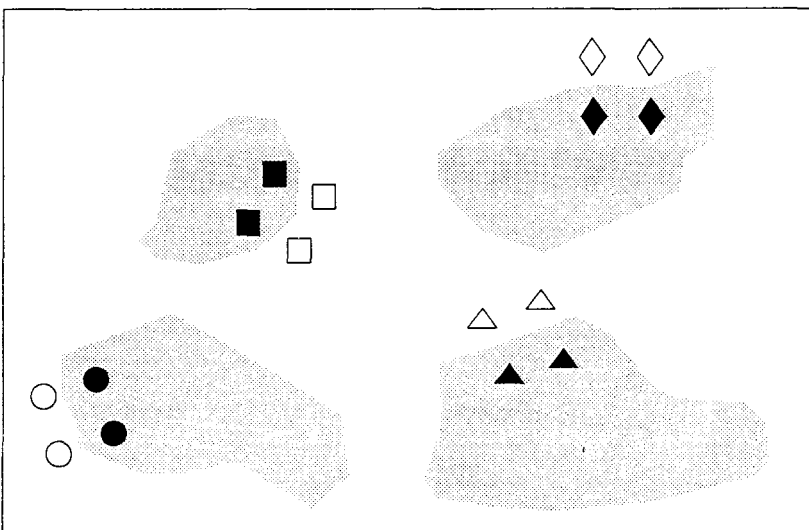


Figure 19. Schematic representation of blocked sampling design for meiofauna cores collected on the sandflat at Eaglehawk Neck, in relation to patches of sediment disturbed by soldier crabs (stippled).

RELATING FAUNISTIC ORDINATIONS TO ENVIRONMENTAL VARIABLES

The above examples indicate that multivariate methods are not only more sensitive in detecting the responses of benthic communities to environmental change, but also give similar results regardless of the component of the fauna being analysed. The sensitivity and generality of multivariate methods make them particularly valuable tools in the

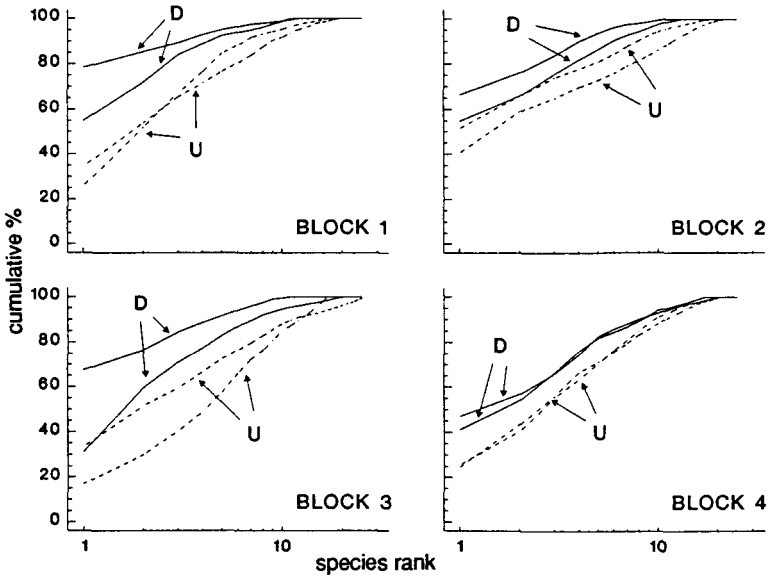


Figure 20. *k*-dominance curves for nematode species abundances in the four samples of each block at Eaglehawk Neck. D, disturbed; U, undisturbed.

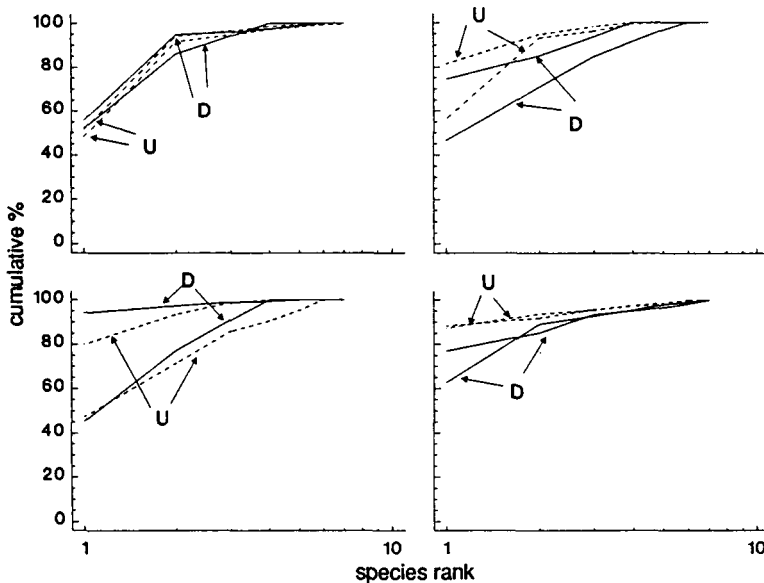


Figure 21. *k*-dominance curves for harpacticoid copepod species abundances in the four samples of each block at Eaglehawk Neck. D, disturbed; U, undisturbed.

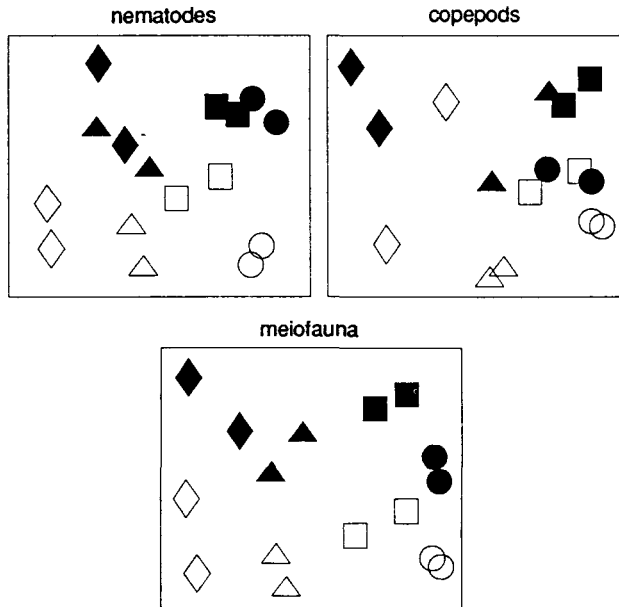


Figure 22. MDS by core samples of root transformed meiofaunal species abundance data at Eaglehawk Neck. Symbols as in Figure 19, *i.e.* solid, disturbed; open, undisturbed; shapes, four different blocks.

assessment of community change; however, there is a need to relate this community change to measured environmental change. The reason why MDS configurations for different components of the fauna are similar must imply that the balance of species within these communities is being affected in the same way by the same combination of key environmental variables. This too is a multivariate problem, and has been tackled formally in a number of ways, under the general heading of 'canonical' analyses (*e.g.* Redundancy Analysis and Canonical Correspondence Analysis, Jongman *et al.*, 1987). These techniques are associated with particular forms of multivariate ordination (*e.g.* Principal Components Analysis and Correspondence Analysis, respectively), and are naturally suited to problems and data structures for which these ordination methods are appropriate. For example, they operate on linear combinations of environmental variables directly related to the species abundances in the original data matrix, and the chosen ordination technique dictates the (implicit) definition of dissimilarity of two samples (*e.g.* 'Euclidean' or 'chi-squared' distance).

Here, we have preferred the converse formulation: biological considerations suggest an appropriate transformation and choice of dissimilarity coefficient for the faunal analysis (Field *et al.*, 1982), and subsequent ordination is based only on the (rank) dissimilarity matrix. A relationship is therefore sought between the faunal MDS and pattern in the environmental variables. Informally, one might expect that, if the relevant environmental variables which determine community composition are correctly identified, then an ordination of these variables should closely resemble the faunistic ordination. Experimenting with these variables in different combinations might also

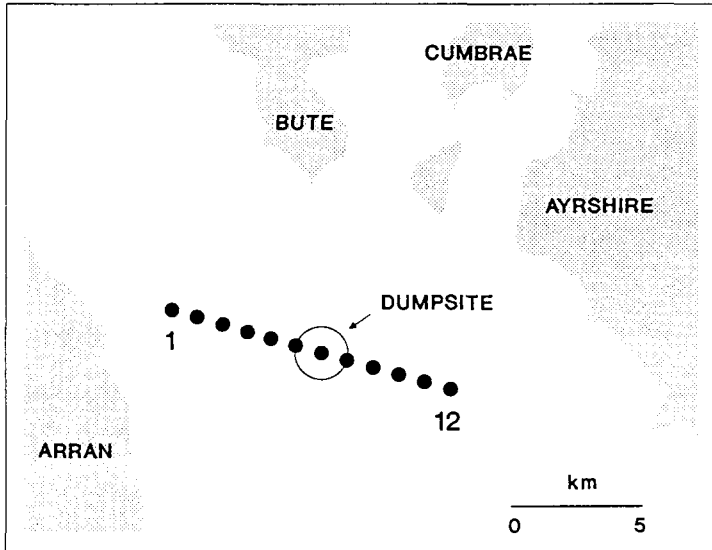


Figure 23. Map of macrobenthos sampling sites in relation to the Garroch Head sewage sludge dumping ground.

enable us to choose which of these combinations matches the faunistic ordination most closely, and hence to identify which are the most responsible for community differences. The omission of a key variable will lead to an inferior match, as will the inclusion of variables with a significantly different pattern across sites but which have no effect on species composition. The following four examples explore these ideas.

Macrobenthos of the Garroch Head sewage-sludge dumping ground

Figure 23 shows the positions of 12 stations across the Garroch Head sewage-sludge dumping ground in the Firth of Clyde which were sampled for macrobenthos in 1983 (Pearson & Blackstock, unpublished SMBA Report, 1984). The MDS for macrobenthos species biomasses (Figure 24) shows a gradation of change in community structure from station 1 to station 7 (the dump-centre) and then back again to station 12, which is compositionally close to station 1. A correlation-based Principal Components Analysis (PCA) on the measured environmental variables (carbon, nitrogen and eight metals) in the sediment (Figure 24) closely resembles the structure of the faunistic MDS, suggesting that these are the variables that 'explain' the changes in community structure across the dump-site. As might be expected, the PCA for C and N alone (Figure 24) is very one dimensional, whereas the PCA for metals (Cu, Mn, Co, Ni, Zn, Cd, Pb, Cr) more closely reproduces the three dimensional structure of the faunistic MDS. This suggests that, although organic enrichment has been considered the main determinant of benthic community structure at such sites, the toxic effects of heavy metals may also be of importance.

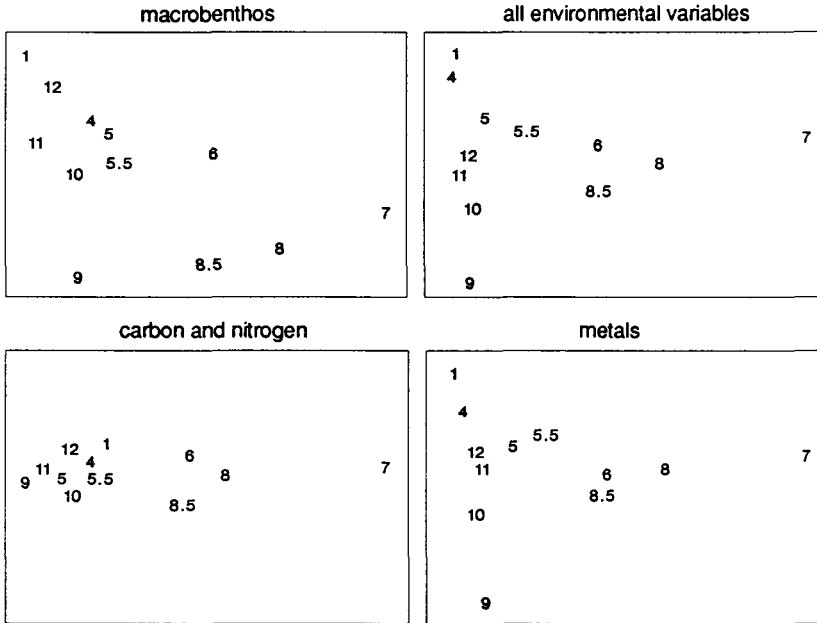


Figure 24. MDS ordination by stations of double-square-root transformed macrobenthos species biomass data for the Garroch Head transect, together with PCA ordinations for various combinations of environmental variables measured in the sediments.

Exe estuary nematodes

Field *et al.* (1982) re-analysed the data of Warwick (1971) which described the distribution of nematodes at 19 intertidal sediment sites in the Exe estuary. The PCA for just four environmental variables (sediment grain size, interstitial salinity, organic content, blackened H_2S depth) produced the most similar grouping of stations to the faunistic MDS (Figure 25), indicating that these are the most important in determining nematode distributions. The only notable difference is in the positions of stations 5 and 10 relative to the others.

Macrobenthos of estuaries in south-west Britain

Warwick *et al.* (in press) showed that a PCA for seven environmental variables reproduced the main features of the faunistic MDS for intertidal macro-invertebrate communities at 38 intertidal sediment sites from six estuaries in south-west Britain (Figure 26), although there were some differences in detail. A feature of both ordinations was the clear separation of the Severn estuary sites (29-38) from the other five estuaries. The PCA for purely 'static' environmental variables such as grain size and organic content did not reproduce this separation, suggesting that dynamic features of the Severn estuary (current speed as indexed by tidal range and wave climate as indexed by wind-fetch distance) are responsible for its uniqueness.

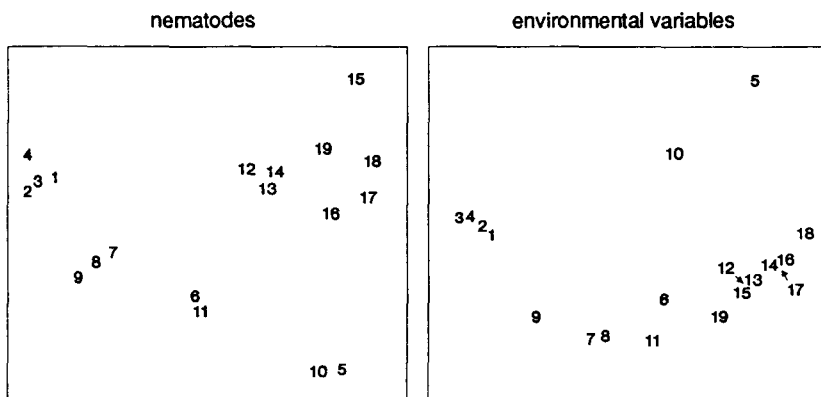


Figure 25. MDS ordination by sites of standardised root transformed nematode species abundance data from the Exe estuary, together with PCA ordination of four environmental variables (see text).

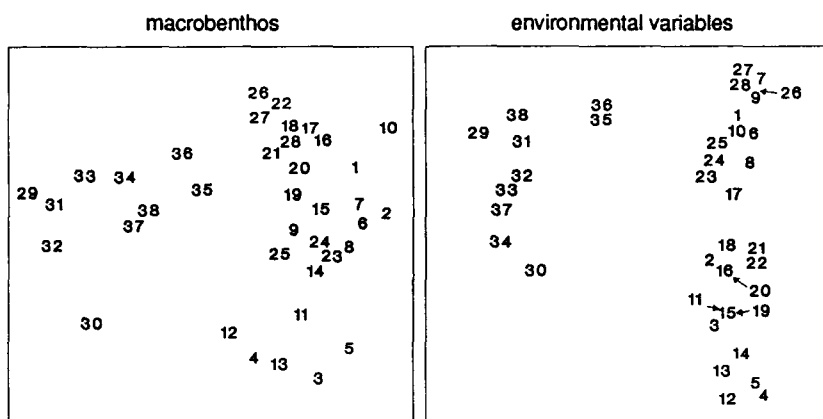


Figure 26. MDS ordination by sites of double-square-root transformed macrobenthic species abundance data from 38 sites in six estuaries in south-west Britain, together with PCA ordination of seven environmental variables.

Ekofisk oil-field macrobenthos

Returning to the first example used in this paper, the fact that stations arranged concentrically around the rig cluster together in the MDS configuration suggests, in itself, that the community differences are a direct result of the drilling activity. Such situations are rare in pollution-effects studies, and it is usually more difficult to distinguish community changes induced by natural and by anthropogenic variables. The PCA for just three variables in the Ekofisk sediments which can be directly attributed to the drilling activity (total hydrocarbons, barium and 'mud' content) shows a very good match (Figure 27) to the faunistic MDS (Figure 4), providing strong correlative evidence for cause and effect.

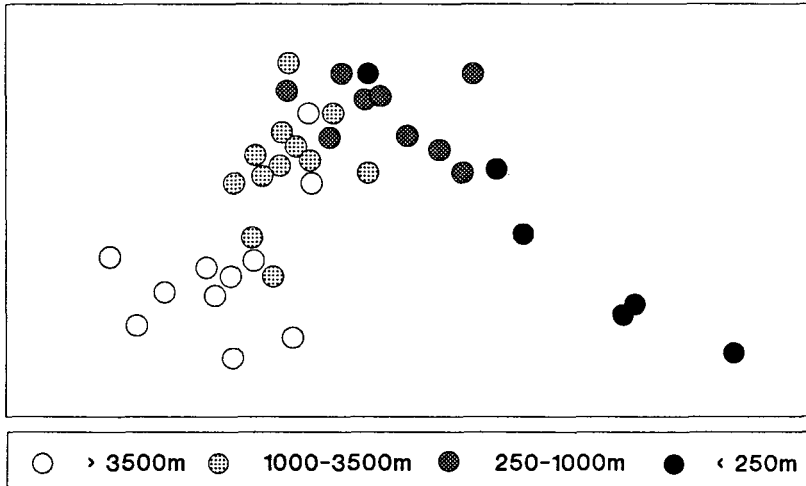


Figure 27. PCA ordination by sites of total hydrocarbons, barium and mud content of the sediments of the Ekofisk oil field. Compare with faunistic MDS in Figure 4.

Conclusions

These examples show the close correspondence between ordinations of sites with respect to their faunistic attributes and to environmental data, and suggest one means by which the most important environmental variables responsible for community change might be identified.

DISCUSSION

The species independent methods of community analysis, although less sensitive in detecting change than multivariate methods, do have the clear advantage that some value judgement can be attached to the changes observed. Thus, the reduction in species diversity or the elevation of k -dominance curves are usually regarded as detrimental responses. The fact that changes in community response of different components of the fauna may differ, indicating differential responses to stress, may in some instances be turned to advantage in that it may enable the cause of stress to be identified. For example, stress responses in the macrobenthos but not the meiobenthos have been used as evidence for physical disturbance as the cause, since the macrobenthos may depend more on habitat stability to maintain high species diversity (Austen *et al.*, 1989; Warwick *et al.*, 1990c).

Multivariate methods have the advantages of great sensitivity and generality of response, but in themselves are indicative only of community change which can be difficult to interpret in terms either of value judgements (detrimental or otherwise) or of the possible cause. There is a clear future research requirement for the development of community level stress indices which retain the multivariate information which is lost in univariate or graphical measures, and which will be more sensitive than the latter. Also, there is a need to formalise the optimal linking of environmental and faunistic

ordinations, in the framework of the non-metric multivariate methods adopted here; such work will be reported elsewhere.

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