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## Quantifying structural redundancy in ecological communities

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Received: 23 January 1996 / Accepted: 14 July 1997

**Abstract** In multivariate analyses of the effects of both natural and anthropogenic environmental variability on community composition, many species are interchangeable in the way that they characterise the samples, giving rise to the concept of structural redundancy in community composition. Here, we develop a method of quantifying the extent of this redundancy by extracting a series of subsets of species, the multivariate response pattern of each of which closely matches that for the whole community. Structural redundancy is then reflected in the number of such subsets, which we term "response units", that can be extracted without replacement. We have applied this technique to the effects of the Amoco-Cadiz oil-spill on marine macrobenthos in the Bay of Morlaix, France, and to the natural inter-annual variability of macrobenthos at two stations off the coast of Northumberland, England. Structural redundancy is shown to be remarkably high, with the number and sizes of subsets being comparable in all three examples. Taxonomic/functional groupings of species within the differing response units change in abundance in the same way over time. The response units are shown to possess a wide taxonomic spread and, using two different types of randomisation test, demonstrated to have a taxonomically and functionally coherent structure. The level of structural redundancy may therefore be an indirect measure of the resilience or compensation potential within an assemblage.

**Key words** Multivariate analysis · Marine macrobenthos · Oil pollution · Compensation potential · Randomisation test

### Introduction

The detection and monitoring of community responses to environmental change often employ multivariate ordinations in which the sample relationships can be well summarised in two dimensions, reduced from a very much higher-dimensional species space (Clarke 1993). This implies that many species must be interchangeable in the way they characterise the samples, and that an analysis of a small subset of the total number of species may give a similar result to that of the full species analysis. Indeed, Gray et al. (1988) compared the configurations produced from a non-metric multidimensional scaling ordination (MDS) of 110 species of marine macrobenthos at six stations in Frierfjord, Norway, with a similar analysis using less than 20% of these species, selected at random, and showed that the ordinations were remarkably similar in the way in which they discriminated between sites. Thus, for marine macrobenthos at least, there appears to be considerable redundancy in the species which characterise the community composition. This has been widely exploited in environmental assessment programmes in which analysis at taxonomic levels higher than that of species has been shown to reveal similar patterns to the full species analysis (Warwick 1993 and references therein), the inference being that the species within a taxon react in similar ways to environmental variability. If the interchangeable species are also functional equivalents, the level of redundancy may also be a useful measure of assemblage resilience (Chapin et al. 1995), and the redundancy could be regarded as the potential for functional compensation (Menge et al. 1994; Frost et al. 1995). Our objective here is to develop a method of quantifying the level of structural redundancy in specific studies of, particularly, temporal community response to environmental change, and then to explore its relationship to more functional concepts, such as the potential for compensation.

Our principal example, in exploring the concept of structural redundancy, is of a marine assemblage of soft-bottom macrobenthos, sampled at a station in the Bay

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of Morlaix (Pierre Noire), France, at approximately 3-monthly intervals on 21 occasions between April 1977 and February 1982 (Dauvin 1984; Warwick and Clarke 1993). This spanned the period of the wreck of the *Amoco-Cadiz* oil tanker some 50 km west of the station, in March 1978. Non-metric multidimensional scaling ordination (MDS) has been performed on the species abundance data. Following standard practice (Clarke and Warwick 1994), abundances of the 257 species observed are initially subject to severe transformation (fourth root), to ensure that the multivariate analysis also reflects patterns of variation in the less-abundant taxa rather than being dominated only by the most common species, and Bray-Curtis similarities (Bray and Curtis 1957) are computed between every pair of samples. The MDS ordination (Kruskal and Wish 1978) then attempts to place the 21 samples in an arbitrary 2-dimensional space such that their relative distances apart match, in rank order, the corresponding pairwise similarities: nearby samples have similar communities, and vice-versa. The results of this ordination (Fig. 1) show an immediate post-spill change in total community composition, followed by a gradual, though only partial, reversion of the community to the pre-spill condition. Prior to the spill, and particularly towards the end of the sampling period, regular seasonal changes in community composition are evident from the cyclic patterns superimposed on the recovery trend. Thus the assemblage has responded to two distinct time-scales of environmental variation, a major medium-term change resulting from the pollution incident, and shorter-term seasonal changes.

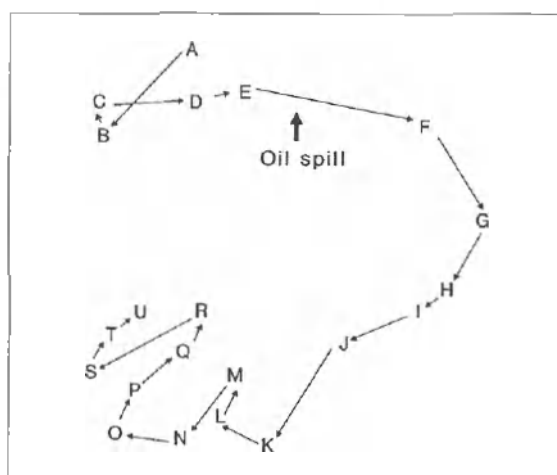


Fig. 1 Non-metric multi-dimensional scaling (MDS) ordination of macrobenthic community samples from the Bay of Morlaix, taken on 21 occasions (A–T), each point representing an average of 5 Hamon grab samples (Dauvin 1984). The ordination is based on Bray-Curtis similarities calculated from 4th-root transformed species abundances (257 species). “Stress” (Kruskal’s formula 1), which reflects inaccurate representation of the among-sample similarities in the 2-d ordination, is low (0.09). From Warwick and Clarke (1993)

A concept of structural redundancy arises naturally in questioning the extent to which the overall pattern of community change through time is expressed by a smaller number of species: is there only one subset of species accounting for the principal features of the MDS plot of Fig. 1, or are there many such mutually exclusive subsets? The technical problems here are, firstly, to define a suitable measure of the match between the community pattern derived from the full data set and that for any reduced set of species, and secondly, to search the space of species subsets for “good” matches, i.e. those for which the measure exceeds some threshold value.

## Methods I

### Selecting species subsets

The subset selection procedure is shown schematically in Fig. 2. In the non-parametric context of matching MDS configurations for species data to the multivariate patterns of associated environmental variables, it has been argued (Clarke and Ainsworth 1993) that an appropriate measure of agreement is the simple Spearman rank correlation coefficient ( $\rho$ ), computed between the corresponding entries in the two underlying triangular matrices of between-sample similarities. This correlation is calculated with the standard adjustment for tied ranks (Kendall 1970) but note that  $\rho$  does not have standard distributional properties because the elements of a similarity matrix are not independent of each other.

Employing the measure  $\rho$  here, it is natural to define a “response unit” as the smallest species subset for which the rank correlation with sample similarities for the full species set exceeds, say, 0.95. It would rarely be computationally feasible to search the full space of  $2^s - 1$  possible subsets, where  $s$  is the total number of species, so a stepwise procedure is adopted. This is analogous to stepwise multiple regression, in which subset selection proceeds incrementally. At each iterative stage, the single species which maximally increases  $\rho$  is added to the existing subset, and there is also an elimination step in which the effect of dropping one species at a time is considered.

This “forward selection/backward elimination” algorithm is exemplified in Table 1 for a data set of six species: the hypothetical

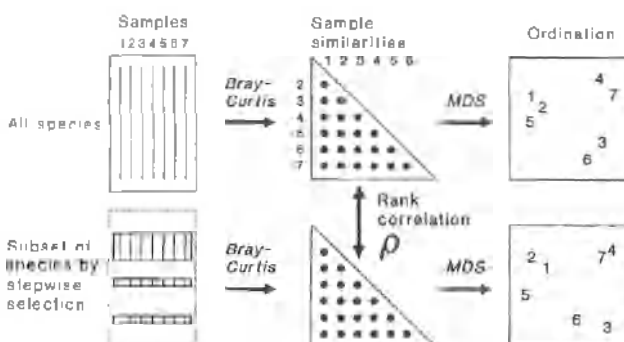


Fig. 2 Schema for multivariate analysis and the matching procedure. For the full set of species (top), the abundance data matrix (left) is converted to a triangular matrix of similarities between all pairs of samples (centre), the ranks of which are used to derive the non-metric MDS plot (right). The same steps can be carried out for any subset of species (bottom) and the match to the full set determined by rank correlation ( $\rho$ ) of the elements of the two similarity matrices

**Table 1** Hypothetical illustration of stages in the stepwise algorithm (forward selection *F*/backward elimination *B*) to select a subset of species with a good match of the sample pattern to that for the full set (6 species). At each stage, **bold type** indicates the subset with the best

$\rho$  and the *italics* denote a backward elimination step that fails (decreases  $\rho$ ) and is therefore ignored. The selection ends when  $\rho$  attains the value 0.95. (A forward selection step which did not increase  $\rho$  would also have terminated the algorithm.)

Step	Direction	Species sets						Best $\rho$
1	F	1	2	3	4	5	6	0.6
2	F	2+1	2+3	<b>2+4</b>	2+5	2+6		0.65
3	<i>B</i>	2	4					0.6
4	F	2+4+1	2+4+3	<b>2+4+5</b>	2+4+6			0.7
5	<b>B</b>	2+4	2+5	4+5				0.8
6	<i>B</i>	4	5					0.55
7	<b>F</b>	4+5+1	4+5+2	4+5+3	4+5+6			0.85
8	<i>B</i>	4+5	4+1	5+1				0.8
9	F	4+5+1+2	4+5+1+3	<b>4+5+1+6</b>				0.9
10	B	4+5+1	4+5+6	4+1+6	<b>5+1+6</b>			0.92
11	B	5+1	5+6	1+6				0.93
12	<i>B</i>	5	6					0.55
13	F	5+6+1	<b>5+6+2</b>	5+6+3	5+6+4			0.94
14	<i>B</i>	5+6	5+2	6+2				0.93
15	F	5+6+2+1	5+6+2+3	<b>5+6+2+4</b>				0.95
16	<i>B</i>	5+6+2	5+6+4	5+2+4	6+2+4			0.94
17	STOP	$\rho = 0.95$ threshold reached, for species subset <b>2+4+5+6</b>						

$\rho$  values are implausible (though not inconsistent) but are chosen to illustrate the full workings of the algorithm. It first selects the single species 2, adds species 4 then 5, drops 2, adds 1 then 6, drops 4 then 1, adds 2 then 4, at which stage the subset consists of species 2, 4, 5, 6 and the algorithm terminates, having attained the threshold "match" of  $\rho = 0.95$ . Of the 63 ( $= 2^6 - 1$ ) possible species subsets, the algorithm has considered about half of them and this proportion drops dramatically as the number of species increases to realistic levels (100+) and a full evaluation becomes impossible ( $2^{100}$  combinations). Clearly, even if a unique minimal-sized subset exists that satisfies the  $\rho > 0.95$  criterion, there is no guarantee that a stepwise procedure will find it. A degree of "redundancy" is expected, in the sense of species responding in parallel ways to the time-scales of environmental change, and there are likely to be many near-optimal subsets which are never considered. Note that the algorithm may also terminate prematurely, before  $\rho = 0.95$  is attained, if the  $\rho$  value does not increase at any of the forward selection steps (i.e. no single species addition improves the match, though two or more may do so).

In response to some of these difficulties it is desirable to repeat the stepwise procedure several times, starting with different initial species subsets chosen at random, so that the algorithm explores different regions of the massive parameter space. The examples given later use 40 such random starts and an initial subset of approximately 10% of the full species list (formally, each species has independent probability 0.1 of being selected for the initial list). A typical run of the algorithm (termed BVSTEP) is more orderly than the illustration of Table 1. There is usually an initial elimination phase, removing several of the starting set, followed by a steady forward selection phase (with only occasional backward steps), adding species until the  $\rho = 0.95$  threshold is attained. Failure to reach the threshold can occur but usually does so in a minority of runs; this is genuinely premature termination since there must exist a species set with  $\rho > 0.95$ , namely the full set (for which  $\rho = 1$  of course). Of those repeat runs for which the  $\rho > 0.95$  criterion is reached, the one with the smallest number of species is selected as giving the minimal species subset "best" capturing the full community pattern.

### Exploring structural redundancy

Having identified a minimal-sized subset of species (the first response unit) encapsulating the sample relationships in the community as a whole, a natural next step is to exclude these species

and ask whether there exists a further subset (the second response unit) which replicates the full community pattern and, if so, at what level of matching. The BVSTEP algorithm is therefore re-run for the reduced species matrix against the full set and, since this time a match for which  $\rho > 0.95$  is not guaranteed to exist, the algorithm may terminate according to the second stopping rule, at a genuine optimum for  $\rho$ . The selection from the several (40) random starts is then made purely on the basis of the largest  $\rho$  obtained, irrespective of the size of the species subsets. The resulting second response unit is now excluded (along with the first set) and the "peeling" procedure repeated, the whole process eventually yielding a set of successive response units whose number reflects the degree of structural redundancy in the community matrix.

## Results I

### Morlaix oil-spill data

For the Morlaix data, the best subset found by the BVSTEP procedure comprises only nine species and the sample MDS based on this subset is shown in Fig. 3b; the very close match seen to the wider community pattern (Fig. 3a) substantiates the use of a  $\rho > 0.95$  matching criterion. Excluding these 9 species (the first response unit) and re-applying the entire stepwise procedure gives a second set of 11 species, and the component plots of Fig. 3 show the results of continuing this peeling, by cumulative removal of the response units generated at each stage. Four units can be found which attain the  $\rho > 0.95$  criterion (Fig. 3b-e); after this point one additional subset can be found which has a clear visual affinity with the overall multivariate pattern (optimum  $\rho = 0.91$ , Fig. 3f). The remaining two optimisations give rapidly degrading matches to Fig. 3a, with the final plot (Fig. 3i) being based on the residual, unselected species after seven peels. Note that the heavy computational constraints in the stepwise procedure required an initial reduction of the species complement to the 125 "most important", in the sense of non-neg-

ligible percentage abundance in any one sample, and this reduced set is the basis of the plot in Fig. 3a and all subsequent selections. (The omitted 127 species were all rare, accounting for only 0.2% of the total abundance and, on average, being absent from all five grab samples

for 90% of sampling times. Their exclusion had negligible effect on the overall community pattern:  $\rho = 0.99$  for the comparison of Fig. 3a with Fig. 1. Also, a run of the stepwise selection procedure on the omitted species failed to find any convincing match with Fig. 3a; at best  $\rho = 0.65$  with around one-third of the species selected.)

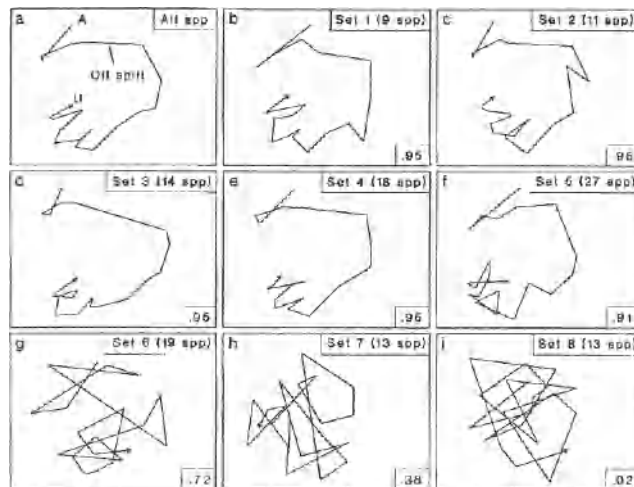


Fig. 3 Non-metric MDS plots from the Bay of Morlaix macrobenthic samples, showing the remarkable extent to which a the overall community pattern, a complex mixture of seasonal and pollution signals across the 5-year time period, is reproducible by b-f a succession of five small, mutually exclusive subsets of species, generated by the peeling procedure (see text), after which g-i the pattern breaks down. The matching coefficient ( $\rho$ ) to a is shown in the bottom right corner of each plot and the size of the species subsets given in the top right corner. The MDS stress values are a 0.09, b-d 0.08, e, f 0.12, g 0.21 and h, i 0.24

### Structure of response units

The response units which attain a good match are seen to be of steadily increasing size (9, 11, 14, 18 and 27 species). One might hypothesise that the overall picture is dictated by certain key species, with a relatively strong "signal-to-noise" ratio through time, which can be substituted by species from similar taxonomic or functional groups, but which have abundance patterns with weaker signal-to-noise ratios. The later subsets may therefore require two or three representatives to mirror the effect of single species from earlier sets. The demonstration of group coherence of this type across the subsets is central to the interpretation of redundancy and is a testable hypothesis.

Figure 4 divides the species subsets from the first five peels into a simple taxonomic/functional grouping. The categories are essentially phyletic but the polychaete worms, crustaceans and molluscs are each divided into two functional/taxonomic groups: A = Cnidaria (sea-anemones); B = Sipuncula; C = sedentary Polychaeta (Sedentaria), which are deposit feeders; D = motile Polychaeta (Errantia), which are mainly carnivores;

Fig. 4. Species lists (response units), from the Bay of Morlaix macrobenthic analysis, for each of the first five subsets extracted by the peeling procedure, divided into nine major taxonomic/functional faunistic groupings (A Cnidaria, B Sipuncula, C sedentary Polychaeta, D motile Polychaeta, E small, burrowing Crustacea, F large, epibenthic Crustacea, G gastropod Mollusca, H bivalve Mollusca, I Echinodermata)

	Subset 1	Subset 2	Subset 3	Subset 4	Subset 5
A					<i>Renarda c. californica</i>
B					
C	<i>Chironomus tentans</i> <i>Scirpulus girardi</i> <i>Amphipoda acutifrons</i> <i>Levinseni clausi</i>	<i>Ocenebra fusiformis</i> <i>Mulinia pinnata</i> <i>Heterocirculus alatus</i>	<i>Stylaroides plumosa</i> <i>Myrionecta sp.</i> <i>Thalassia cinctonatus</i> <i>Artedea minuta</i>	<i>Notomastus lateralis</i> <i>Polycirrus sp.</i> <i>Sipunculus lamellatus</i> <i>Scoloplos armiger</i> <i>Artedea cernuilli</i>	<i>Marginalia belti</i> <i>Cyanea lumbricoides</i> <i>Parvulus kefersteinii</i> <i>Spiniflorus</i> <i>Lancea conchiliga</i> <i>Mediomastus fragilis</i> <i>Terebellides stroemii</i>
D	<i>Harmothoe lunulata</i> <i>Eteone longa</i>	<i>Odontostylis gibba</i>	<i>Hydrotus bilineata</i> <i>Nephtys hombergi</i> <i>Phyllodoce lineata</i> <i>Koronae hebes</i>	<i>Leptonereis glauca</i> <i>Syllis cornuta</i> <i>Sthenolite limicola</i>	<i>Gomada maculata</i> <i>Eulalia sanguinea</i> <i>Eumelasma impudens</i> <i>Glyceria convoluta</i> <i>Lumbriculus latreilli</i>
E	<i>Ampelisca tenebris</i> <i>Phoronis longicauda</i>	<i>Ampelisca brevicornis</i> <i>Bathyporeia tenuipes</i> <i>Isocobina tincta</i> <i>Periclimenacis typicus</i>	<i>Bathyporeia rana</i> <i>Megaloporeia ugilis</i> <i>Ampelisca typica</i>	<i>Urechis pulchellus</i> <i>Ampelisca tenuicornis</i> <i>Ampelisca rana</i> <i>Ampelisca spinipes</i> <i>Orchamene rana</i>	<i>Anguilla hamulus</i> <i>Bathyporeia elegans</i> <i>Dicathys larvis</i> <i>Aora tygaca</i> <i>Phoronis maris</i> <i>Periclimenacis longimanus</i> <i>Aphrodite ovalipes</i>
F	<i>Phoronis aspinosa</i>	<i>Phoronis bispinosa</i>	<i>Gastropoda inchoata</i> <i>Myrtilus aspinosa</i>	<i>Anapagurus hyndmanni</i>	<i>Pagurus bernhardus</i> <i>Microgaster purpureus</i>
G		<i>Nassarius reticulatus</i>			
H		<i>Thracia flexuosa</i>	<i>Venus mytila</i>	<i>Thracia flexuosa</i> <i>Abra alba</i> <i>Cultellus pallidus</i> <i>Nucula luteola</i>	<i>Cardium edentatum</i> <i>Cardium gibba</i> <i>Cardium edentatum</i> <i>Spisula ovalis</i>
I					<i>Astrocardia brachyloca</i>

**Table 2** For the five response units from the Morlaix macrobenthic analysis, the number of species falling within each of eight taxonomic/functional groupings (the observed frequencies from Fig. 4, omitting group B for which all frequencies are zero). The figures in brackets are the expected frequencies under the usual null hypothesis of "no interaction" in a 2-way contingency table

Taxonomic/ functional group	Response unit					Total
	1	2	3	4	5	
A	0 (0.1)	0 (0.1)	0 (0.2)	0 (0.2)	1 (0.3)	1
C	4 (2.6)	3 (3.2)	4 (4.1)	5 (5.2)	7 (7.9)	23
D	2 (1.7)	1 (2.1)	4 (2.7)	3 (3.4)	5 (5.1)	15
E	2 (2.4)	4 (2.9)	3 (3.7)	5 (4.8)	7 (7.2)	21
F	1 (0.8)	1 (1.0)	2 (1.2)	1 (1.6)	2 (2.4)	7
G	0 (0.1)	1 (0.1)	0 (0.2)	0 (0.2)	0 (0.3)	1
H	0 (1.1)	1 (1.4)	1 (1.8)	4 (2.3)	4 (3.4)	10
I	0 (0.1)	0 (0.1)	0 (0.2)	0 (0.2)	1 (0.3)	1
Total	9	11	14	18	27	79

E = small, relatively sedentary, burrowing Crustacea (amphipods, cumaceans, tanaids and leptostracans), which are mainly deposit feeders; F = large, wide-ranging, epibenthic Crustacea (decapods and mysids), which are scavengers; G = gastropod Mollusca; H = bivalve Mollusca; I = Echinodermata (all brittle-stars in this case). The species ordering within the cells is according to their match ( $p$ ), as single variables, to the pattern of community change derived from all species in the relevant subset.

The numbers of species within each cell of Fig. 4 are listed in Table 2, omitting category B, which is absent from all 5 subsets. The question of interest is whether the total counts within each subset (the column totals) are more consistently apportioned to the taxonomic/functional groups than would be expected by chance, i.e. do the response units have a coherent structure?

## Methods II

### Testing for coherence: $\chi^2$ statistic

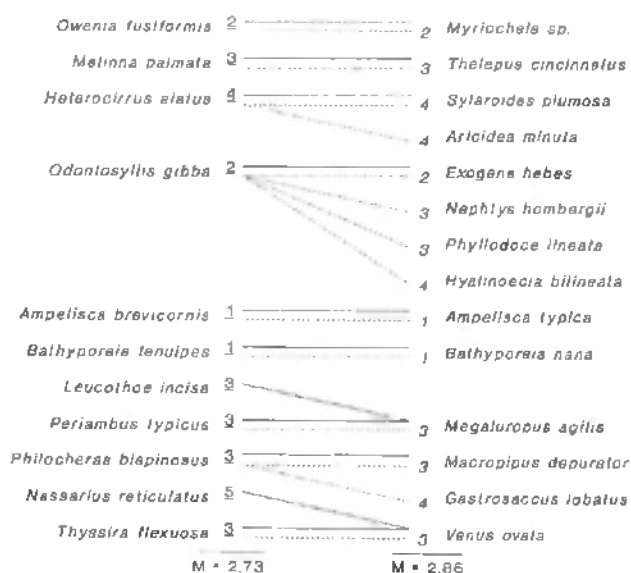
The observed frequencies within the cells of Table 2 form a standard two-way contingency table, with fixed marginal totals. The null hypothesis under test is that of no coherence, i.e. the species falling within successive subsets are, in effect, randomly selected (without replacement) from the full set of species in the table. The random selection retains the differing response unit sizes (e.g. as in the column totals of Table 2) and, of course, the differing faunistic group sizes (as in the row totals). This is the hypergeometric model for a contingency table, and a test can be based on the usual chi-squared statistic,  $\chi^2 = \sum (O-E)^2/E$ , where  $O$  represents the observed number of species in a cell of the two-way table and  $E$  its expectation (the corresponding row total multiplied by the column total and divided by the grand total). There are, however, two non-standard features in this case. Firstly, the alternative hypothesis postulates that the allocation of species to the faunistic groups is more coherent (i.e. regular) across subsets than would be expected by chance. Thus, the alternative hypothesis is favoured if the value of  $\chi^2$  is significantly small, in contrast to the standard "interaction" test which rejects the null hypothesis for significantly large values (the latter would correspond here to a test for a significantly different faunistic composition in each subset). Secondly, the observed

frequencies, and those expected under the null hypothesis, are likely to be too low to justify the usual approximation of a  $\chi^2$ -distribution for the test statistic. Instead, the exact distribution is simulated by a randomisation/permutation test in which a large number (2000) of random re-allocations of the full species set are made (without replacement) to the response units, and the  $\chi^2$  value recomputed for each. The null hypothesis of no coherence is then rejected, at the 0.05 level, if the observed  $\chi^2$  is smaller than all but 5% of the simulated values.

### Testing for coherence: taxonomic mapping

The contingency table test could be criticised for an element of subjectivity in the choice of the mixed functional and taxonomic attributes in the faunistic groupings, so an alternative, based purely on standard taxonomy, has also been developed. (An analysis based purely on functional attributes is not possible without a better understanding of the functional roles of many of the macrobenthic species involved.) This alternative test has the additional advantage of using the full hierarchy of taxonomic relations between the subsets rather than a single-level categorisation. The question posed is whether, within successive response units, each species has an analogue, or analogues, to which it is more closely related (taxonomically) than would be expected by chance.

The question is answered by defining an "optimal taxonomic mapping" statistic,  $M$ . This is illustrated in Fig. 5, which uses as an example just two subsets of species, of sizes 11 and 14 respectively (in fact, these are two of the five response units from the Morlaix macrobenthic analysis). For each species in the first subset, its closest taxonomic relative in the second subset is identified (continuous line in Fig. 5), scoring 1–5 for a species of the same genus, family, order, class and phylum, respectively, and 6 if it has no phyletic counterpart (as in Warwick and Clarke 1995). These scores are averaged over all the species from the first subset (underlined numbers in Fig. 5,  $M = 2.73$ ). This is not a reversible "one-to-one



**Fig. 5** Illustration of "taxonomic mapping", using just the second (left) and third (right) subsets of species obtained by the peeling procedure, from the Morlaix macrobenthic analysis (Fig. 4). Continuous lines represent the best "many-to-one" map of the left-hand subset onto the right, with the underlined number showing the taxonomic distance between connected species (distances are from a simple Linnean classification, counting 1 for species in the same genus, 2 for species in the same family, and so on). Dashed lines and italic numbers represent the mapping of the right-hand set onto the left

map", e.g. two species could have the same closest relative (*Leucothoe incisa* and *Perianthus typicus* both map onto *Megaluropus agilis* in Fig. 5), so the complementary average is also taken of the optimal mapping of the second subset onto the first (dashed lines and italic numbers in Fig. 5,  $M = 2.86$ ). These two values are averaged ( $M = 2.80$ ) and a grand mean  $M$  is then computed over all successive pairs of response units. The use of simple averaging on the  $M$  values for consecutive pairs largely eliminates artefacts which could arise from mapping very disparately sized subsets onto each other.

Under the null hypothesis of no coherence, the distribution of possible values of  $M$  was determined by the same randomisation procedure as previously. The full set of species in all response units was allocated at random to those units, preserving the different subset sizes, and the overall value of  $M$  calculated for each simulation. Again, 2000 randomisations were performed and the true value of  $M$  referred to the simulated distribution, a sufficiently small value indicating rejection of the null in favour of the alternative hypothesis, of coherent subset structure.

## Results II

### Coherence of Morlaix response units

The five response units from the Morlaix peeling procedure (Fig. 4) give rise to the observed and expected frequencies shown in Table 2, with a resulting  $\chi^2$  value of 16.6. The randomisation procedure generates the null distribution of  $\chi^2$  shown in Fig. 6a. The observed  $\chi^2$  is clearly in the lower tail of this distribution, with only 28 of the 2000 simulations generating smaller values; the null hypothesis is rejected ( $P < 0.014$ ) in favour of the alternative of coherence of the response units.

Similarly, the taxonomic mapping procedure generates an observed value of  $M = 2.92$ , on averaging over all consecutive pairs of units, which can be compared to the simulated distribution in Fig. 6b; the null hypothesis is again rejected ( $P < 0.002$ ) in favour of the coherence alternative.

### Abundance trends for Morlaix data

The question arises as to whether the abundances of the same taxonomic/functional groups of organisms in different response units are negatively correlated, which would be indicative of compensation between the units, or whether there is positive correlation across the response units (synchrony). In Fig. 7 we have summed the fourth-root transformed abundances of species within each cell of Fig. 4 and plotted these abundances against time. This shows that, in each response unit, given taxonomic/functional groups of species change in abundance in a similar way, although the pattern of change differs among these faunistic groups within each unit.

### Macrobenthic time series from Northumberland

To explore the generality of the observations noted about redundancy structure in the Morlaix series, we

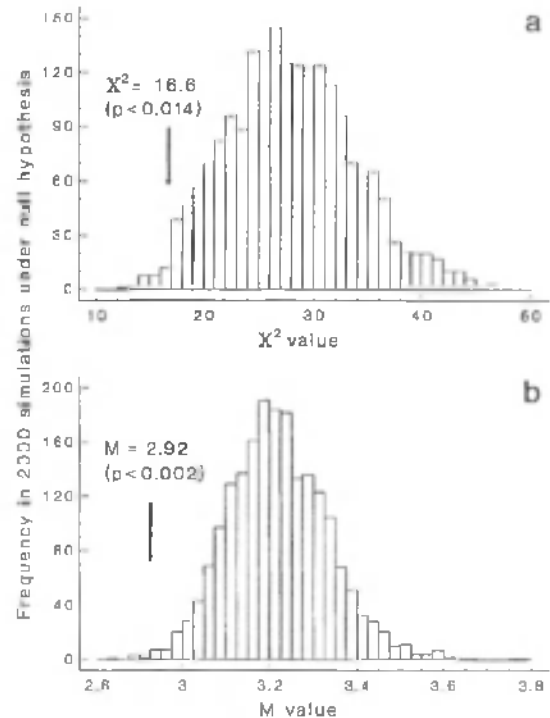


Fig. 6 For the Morlaix macrobenthic data, histograms of 2000 simulated values for the test statistics: a  $\chi^2$ , from a two-way layout of response units by taxonomic/functional category; b  $M$ , from an optimal taxonomic mapping of the species in successive response units onto each other. The simulations are under the null hypothesis of "no coherence in faunistic structure", and are the result of a (constrained) random allocation of species to the units. The true values of the two statistics fall in the lower tails of their respective distributions, leading to rejection of the null hypothesis in both cases

have conducted a similar analysis of macrobenthic time series data from two stations off the coast of Northumberland, north-east England (Buchanan 1993; Buchanan and Moore 1986a, b; Buchanan and Warwick 1974; Buchanan et al. 1974, 1986). Station P is at a depth of 80 m, and the sediment has a median particle diameter of 0.056 mm, corresponding to the Wentworth grade "silt". Station M1 is at a depth of 54 m, median particle diameter 0.145 mm ("fine sand"). For consistency, data have only been analysed for years in which both stations have been sampled: 1973–1985 omitting 1977. Station P was sampled annually in January–February and station M1 in March–May. There have been no obvious local anthropogenic impacts at either of these stations during the sampling period, and community changes reflect general inter-annual variability.

The MDS for 4th-root-transformed abundances of all species ( $s = 138$  at P,  $s = 194$  at M1) shows a sequential change in community structure at both stations (Fig. 8). The samples from the 1980s are separated from those for the 1970s on both plots and represent the rather abrupt switch in community structure at the turn of the decade which is known to have occurred in several components of the North Sea biota (Austen et al. 1991). An MDS plot of the two stations combined (Fig. 9)

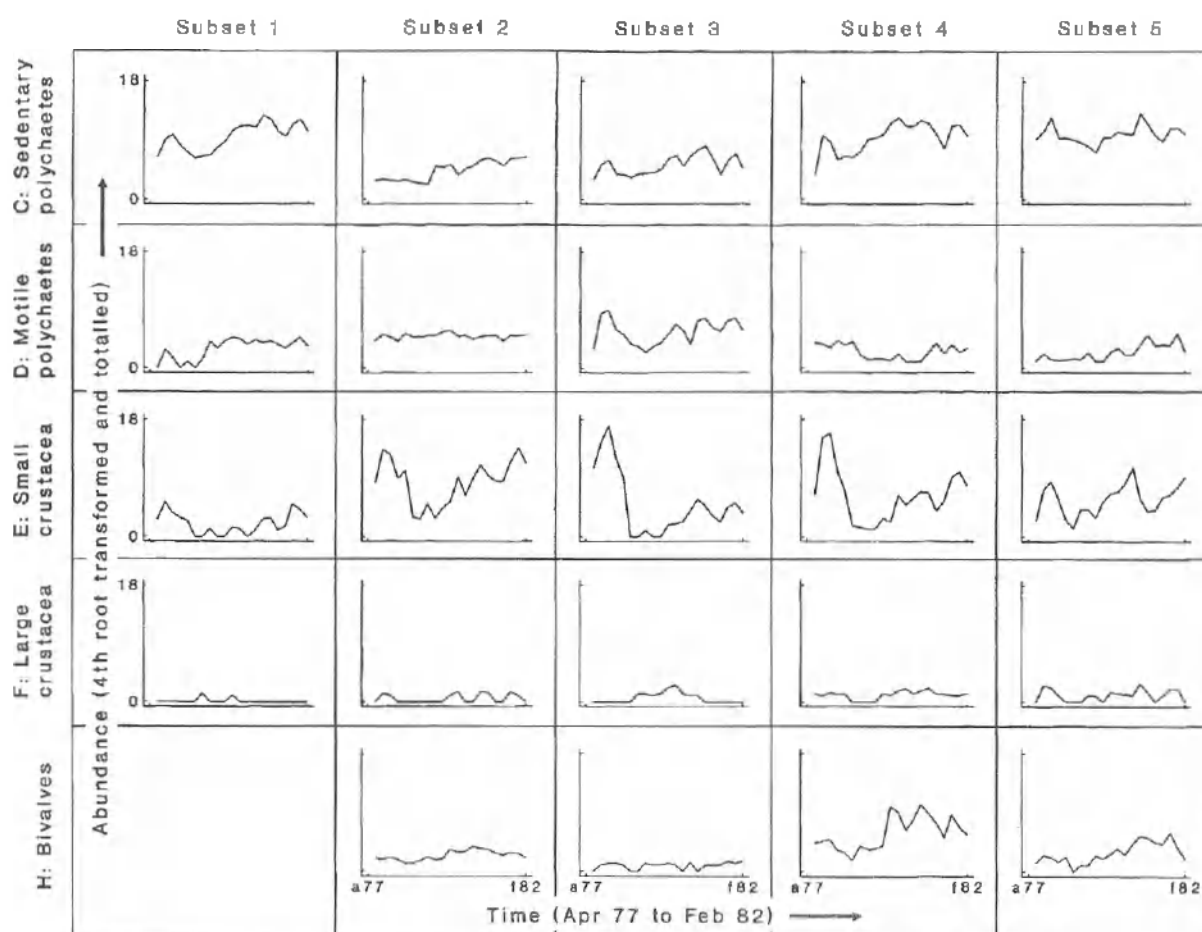


Fig. 7 For the Morlaix macrobenthos, sums of the 4th-root transformed abundances of species within specific taxonomic/functional groups and "response unit" subsets (as in Fig. 4), plotted against time

shows that, although the clusters for each station are far apart, indicating quite different species compositions, the direction of community change through time is the same at both.

For station P, the first subset extracted by the peeling procedure comprises 10 species (listed in Table 3), and the MDS plot for these 10 (Fig. 10b) shows a very close match to the wider community pattern exhibited by the 125 most abundant species (Fig. 10a). Two more subsets of 15 and 21 species respectively meet the  $\rho > 0.95$  matching criterion (Figs. 10c, d), and a fourth set of 24 species achieves a maximum correlation of 0.91 (Fig. 10e), after which the match rapidly declines (Figs. 10f, g, h). For station M1, the first subset comprises 9 species (listed in Table 4), and the MDS plot for these 9 (Fig. 11b) again shows a very close match to the wider community pattern (Fig. 11a). Three more subsets of 12, 15 and 23 species respectively meet the  $\rho > 0.95$  criterion (Figs. 11c, d, e), and a fifth set of 14 species achieves a maximum correlation of 0.91 (Fig. 11f), after

which the match declines (Figs. 11g, h). For stations P and M1 combined, the first subset comprises 7 species, listed in Table 5, with  $\rho$  of 0.95 (the MDS plots for these subsets are not presented since the two clusters of points are very collapsed, as in Fig. 9, making the fine structure of the time courses hard to distinguish). Three more subsets of 9, 10 and 12 species, respectively, meet the  $\rho > 0.95$  matching criterion, and a fifth set of 25 species achieves a maximum correlation of  $\rho > 0.94$ , after which the match declines with a set of 23 species ( $\rho = 0.85$ ), the remaining 36 species giving only  $\rho = 0.24$ .

As with the Morlaix data, the subsets extracted from the Northumberland stations are coherent in that they comprise taxonomically and functionally matching species with a wide taxonomic spread. At station P, the subsets typically comprise a large coelenterate (*Virgularia*, *Cerianthus*, subsets 1 and 2 only), polychaete species which are surface deposit-feeders, subsurface deposit-feeders and carnivores, small crustaceans (cumaceans and amphipods), bivalve molluscs and echinoderms (Table 3). The subsets at station M1 have a similar taxonomic/functional composition except that the large coelenterates may either be replaced with other taxa (nemertines, polyclads, subsets 2 and 4) or be absent.

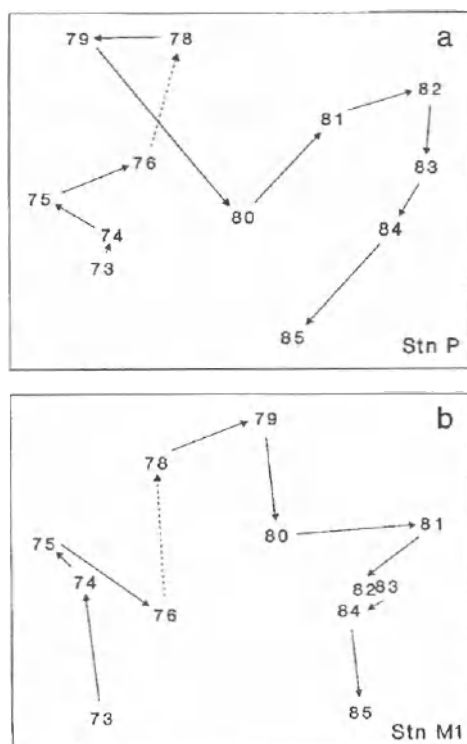


Fig. 8 Non-metric MDS ordinations for the sub-tidal macrobenthic community samples taken at two Northumberland sites (Buchanan 1993), over the 12 years 1973–1976, 1978–1985: a station P, sampled in January–February, b station M1, sampled in March–May. The ordinations are based on Bray-Curtis similarities from 4th-root transformed abundances of a 138, b 194 species, with resulting stress values of a 0.12, b 0.10

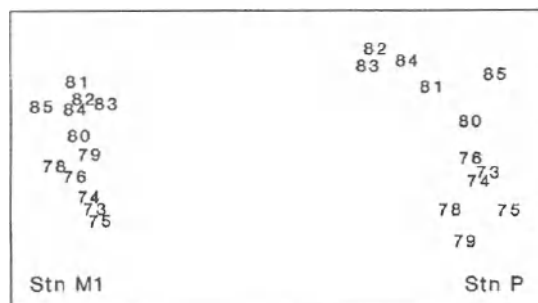


Fig. 9 Combined non-metric MDS ordination for the samples from both Northumberland stations P (right) and M1 (left), over the 12 years 1973–1976, 1978–1985 (207 species). Note that, in spite of the substantially different community composition at the two sites (left to right), a consistent time trend is apparent (bottom to top). Stress value: 0.06

## Discussion

The above analyses of structural redundancy have revealed a number of consistent features among the different time-series data sets.

1. The number of subsets of species extracted by the peeling procedure, which correlate to the wider com-

munity pattern (of 125 species) with a matching coefficient  $> 0.95$ , is similar in all cases, namely Morlaix: 4 (5); Northumberland station P: 3 (4); Northumberland station M1: 4 (5); Northumberland stations P and M1 combined: 4 (5). The numbers in brackets include "near misses", where  $\rho > 0.90$ .

2. The numbers of species in each of the subsets is also similar, namely Morlaix: 9, 11, 14, 18; Northumberland P: 10, 15, 21; Northumberland M1: 9, 12, 15, 23; Northumberland P and M1 combined: 7, 9, 10, 12. The fact that the numbers of species in the subsets tend to be smaller for the combined Northumberland data reflects the relatively large differences in community composition between the two stations, in comparison with the changes at each over time: a relatively few abundant species are likely to characterise this difference.

3. Regularity of taxonomic composition across successful "peels" is a subtle and difficult alternative hypothesis against which to test, given the relatively small number of species involved (e.g. in the  $\chi^2$  test). Nonetheless, coherence has been demonstrated beyond reasonable statistical doubt, by two objective tests designed to utilise somewhat different attributes of the data and, indeed, clear links do seem apparent from inspection of Fig. 4 and Tables 3, 4 and 5.

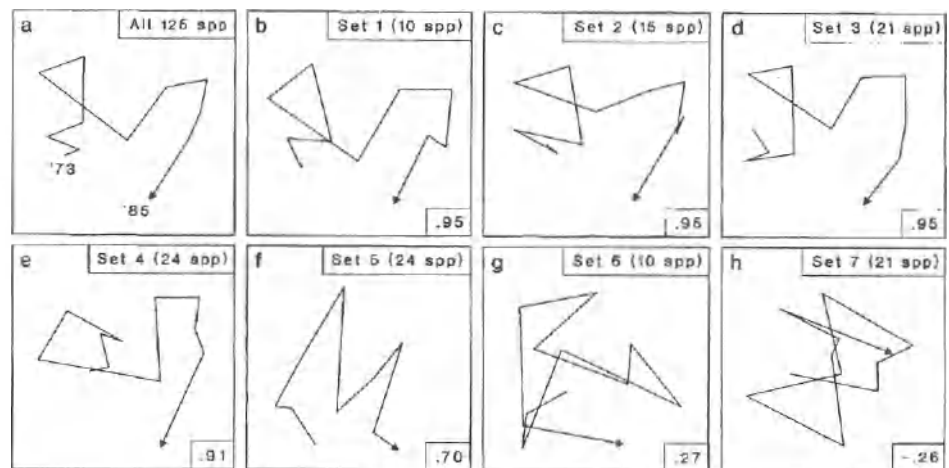
4. Each of the response units encompasses a wide taxonomic and functional spread, and it is evident that the total community pattern does not simply result from trends in one group of organisms which is particularly sensitive to environmental change.

The link between structural redundancy and functional redundancy/potential for functional compensation is difficult to make from observational studies of this kind. The exact functional (e.g. trophic) role of each species within an assemblage of benthic macrofauna is not known, and we can only construct broad categorisations based on what is known about a few species and inferences that physiognomically similar species behave in the same way. Successive response units have been shown to contain representatives of all the functional groups which might be expected to occur in such habitats (surface and subsurface deposit-feeders, carnivores, scavengers) and also span the range of differential sensitivities to pollution/disturbance known to occur among major taxa, from the most sensitive crustaceans to the most tolerant deposit-feeding polychaete worms (Warwick and Clarke 1993). However, it is a large leap from concepts of functional redundancy (Walker 1992; Lawton and Brown 1993) to the potential for functional compensation (Menge et al. 1994; Frost et al. 1995), since it is only by experimental removal of species of a specific functional type from a particular response unit that it can be shown that species of the same functional type from another response unit will compensate for this function. All we can say at the present time is that each response unit does contain species or groups of species which, from what is known of their biology, do appear to be the functional equivalents of species in other response units, and that these

**Table 3** Taxonomic composition of species subsets from the peeling procedure (see text), at Northumberland Station P. The first three subsets attain the  $\rho > 0.95$  criterion, for the match of similarities to those for the full set of 125 species, but the fourth subset has  $\rho = 0.91$

Subset 1	Subset 2	Subset 3	Subset 4
Coelenterates <i>Virgularia mirabilis</i>	Coelenterates <i>Cerianthus lloydii</i>	Sedentary polychaetes <i>Paecilochaetus serpens</i>	Sipunculans <i>Golfingia vulgaris</i>
Sedentary polychaetes <i>Spiofanus hutchinsoni</i>	Sedentary polychaetes <i>Apistobranchius tullbergi</i>	<i>Polydora</i> spp.	Sipunculid spp.
<i>Spionidae</i> sp.	<i>Prionospio multibranchiata</i>	<i>Spiofanus kroyeri</i>	Priapulids <i>Priapulid caudatus</i>
<i>Ophelina modesta</i>	<i>Chaetozone setosa</i>	<i>Prionospio malmgreni</i>	Sedentary polychaetes <i>Laonice cirrata</i>
<i>Ampharete baltica</i>	Cirratulid sp.	<i>Spio filicornis</i>	<i>Magelona minuta</i>
Errant polychaetes <i>Eteone longa</i>	<i>Ophelina acuminata</i>	<i>Euclymene affinis</i>	<i>Caulerella caputecoris</i>
<i>Goniada maculata</i>	Errant polychaetes <i>Pholoe minuta</i>	<i>Polycirrus medusa</i>	<i>Tharyx</i> sp.
Crustaceans <i>Eudorella truncatula</i>	<i>Nereis longissima</i>	Errant polychaetes <i>Sthenelais lineicola</i>	<i>Scalibregma inflatum</i>
<i>Harpinia antennaria</i>	Crustaceans <i>Leucon nasica</i>	Phyllodocidae sp.	<i>Heteromastus filiformis</i>
Gastropod molluscs <i>Odostomia</i> sp.	<i>Physica marina</i>	<i>Gyptis brevipalpa</i>	Amparetidae spp.
	<i>Nephrops norvegicus</i>	<i>Glycera rousii</i>	Errant polychaetes <i>Linopherus hemuli</i>
	Bivalve molluscs <i>Montacuta ferruginosa</i>	<i>Lumbrineris gracilis</i>	Hesionidae sp.
	Gastropod molluscs <i>Cylichna cylindracea</i>	Crustaceans <i>Eudorella emarginata</i>	<i>Synelmis klatti</i>
	Echinoderms <i>Amphiura filiformis</i>	<i>Distylis lucifera</i>	<i>Glycinde nordmannii</i>
	<i>Amphiura chiajei</i>	Isepid sp.	<i>Lumbrineris hibernica</i>
		<i>Lembo longipes</i>	<i>Schistomeringos caecus</i>
		Photidae sp.	Oligochaetes <i>Oligochaete</i> spp.
		Bivalve molluscs <i>Nucula tenuis</i>	Crustaceans <i>Diastylis rugosa</i>
		<i>Kellia suborbicularis</i>	Aplacophoran molluscs <i>Chaetoderma nitidulum</i>
		Echinoderms <i>Leptosynapta bergensis</i>	Bivalve molluscs <i>Venus striatula</i>
			Bivalve sp.
			Gastropod molluscs <i>Prosobranch</i> sp.
			Echinoderms <i>Ophiura affinis</i>
			<i>Brissopsis lyrifera</i>

**Fig. 10** Non-metric MDS plots from Northumberland station P samples, over the 12 years, showing the precise way in which a the overall community pattern is reproducible in b–e consecutive species subset peels, before f–h the pattern breaks down. The matching coefficient  $\rho$  to a is given in the bottom right corner of each plot and the number of species in each subset is shown top right. Stress values for the ordinations are a 0.11, b 0.09, c 0.08, d 0.12, e 0.14, f 0.19, g, h 0.13



species appear to respond in similar ways to environmental change. The number of successful peels may thus in some sense be regarded as a measure of the potential for functional compensation, if not the capacity for it.

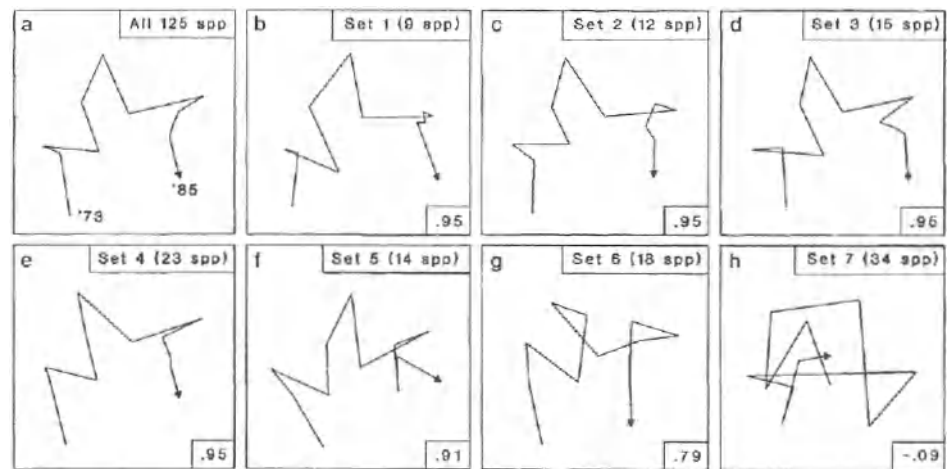
Even if we refrain from defining a formal redundancy index based on the number of successful peels,

and turn our back on any functional implications, the methodology still seems a useful way of demonstrating the scale of redundancy inherent in any analysis of community structure. On that basis, the benthic macrofauna data examined here would appear to provide striking examples of the degree of redundancy observable in practice.

**Table 4** Taxonomic composition of species subsets from the peeling procedure, at Northumberland Station M1. The first four subsets attain  $\rho > 0.95$  but the fifth (smaller) group only has  $\rho = 0.91$

Subset 1	Subset 2	Subset 3	Subset 4	Subset 5
Sedentary polychaetes <i>Apistobanchus tullbergi</i> <i>Spiophanes bombyx</i> <i>Chaetopterus variopedatus</i> <i>Diplocirrus glaucus</i> <i>Ampharete haltica</i>	Nemertines Nemertea spp. Sedentary polychaetes <i>Orbinia setulata</i> <i>Paradoneis lyra</i> <i>Terebellides stroemi</i>	Sedentary polychaetes <i>Polydora</i> spp. <i>Tharyx</i> sp. <i>Ophelina modesta</i> <i>Heteromastus filiformis</i> <i>Rhodine gracilior</i>	Platyhelminthes Polyclad spp. Sedentary polychaetes <i>Scoloplos armiger</i> <i>Spiophanes kroyeri</i> <i>Prionospio</i> <i>multibranchiata</i> <i>Magelona minuta</i> <i>Magelona mirabilis</i> <i>Chaetozona setosa</i> <i>Capitomastus minimus</i> <i>Capitellidae</i> sp. <i>Pectinaria auricata</i> <i>Polycirrus medusa</i>	Sedentary polychaetes <i>Levinsonia gracilis</i> <i>Prionospio malmgreni</i> <i>Cirratulidae</i> spp. <i>Euclymene affinis</i>
<i>Sabellides octocirrata</i> <i>Lanice conchilega</i> Bivalve molluscs <i>Myssella bidentata</i> Gastropod molluscs <i>Odostomia</i> sp.	Errant polychaetes <i>Pholoe minuta</i> <i>Glyptis brevipalpa</i> <i>Nephtys</i> spp. Crustaceans <i>Diastylis rathkei</i> Aplacophoran molluscs <i>Chaetoderma nitidulum</i> Bivalve molluscs <i>Lucinoma borealis</i> Gastropod molluscs <i>Turritella communis</i> <i>Cylchma cylindracea</i>	Errant polychaetes <i>Linopherus hemuli</i> Polynoidae sp. <i>Synelmis klatti</i> Crustaceans <i>Diastylis lucifera</i> <i>Amphiscia tenuicornis</i> Photidae spp. Bivalve molluscs <i>Myssia undata</i> <i>Spisula subtruncata</i> <i>Abra nitida</i> Echinoderms <i>Echinocyamus pusillus</i>	Errant polychaetes <i>Sphaerodorum flavum</i> <i>Glyceria rouxii</i> <i>Glycinde nordmanni</i> <i>Lumbrineris hibernica</i> <i>Lumbrineris gracilis</i> Oligochaetes Oligochaete spp. Bivalve molluscs <i>Chlamys opercularis</i> <i>Kellia subarhicularis</i> <i>Cultellus pellucidus</i> <i>Mya truncata</i> <i>Thracia villasiuscula</i> Echinoderms <i>Amphiura filiformis</i>	Errant polychaetes <i>Aphrodita aculeata</i> <i>Eteone longa</i> <i>Nereis longissima</i> Crustaceans <i>Ampelisca brevicornis</i> <i>Maera loveni</i> Bivalve molluscs <i>Nucula tenuis</i> <i>Thyasira flexuosa</i> Phoronids <i>Phoronis mulleri</i> Echinoderms <i>Echinocardium flavescens</i> Hemichordates <i>Glossobalanus marginatus</i>

**Fig. 11** MDS plots from Northumberland M1 samples over the 12 years, again showing the clear way in which b-f successive species peels can be found to match a the overall community structure, before g-h the pattern begins to break down. Stress values are a, b 0.08, c 0.07, d, e 0.09, f 0.10, g, h 0.15



**Acknowledgements** This work forms part of the Marine Biodiversity project of the Plymouth Marine Laboratory, Natural Environment Research Council, United Kingdom, and is part-funded by the UK Ministry of Agriculture, Fisheries and Food (contract number AE1113). We would like to thank two anonymous referees and Professor Peterson for many searching and invaluable comments, which led to a much extended and improved manuscript. The BVSTEP algorithm for species subset selection was initially

coded in APL 11-386 by one of us (K.R.C.) and a much more efficient FORTRAN version coded by Charles Green and Martin Carr, to whom we are indebted; it is intended to make this available in the next version of the PRIMER community analysis software package, from the Plymouth Marine Laboratory. We would also like to thank Dr. J.B. Buchanan for allowing us free access to the Northumberland time series data from the 1970s and early 1980s.

**Table 5** Taxonomic composition of species subsets from the peeling procedure, at Northumberland Stations P and M1 combined. The first four subsets attain  $\rho$  values of 0.95, the fifth has  $\rho = 0.94$  and the sixth,  $\rho = 0.85$

Subset 1	Subset 2	Subset 3	Subset 4	Subset 5	Subset 6
Coelenterates	Sedentary polychaetes	Sedentary polychaetes	Coelenterates	Nemertines	Sedentary polychaetes
<i>Virgularia mirabilis</i>	<i>Tharyx</i> sp.	<i>Apistobranchus tullbergi</i>	<i>Halacampa crysanthemum</i>	Nemertea spp.	<i>Orbinia seriulata</i>
Sedentary polychaetes	<i>Ophelina acuminata</i>	<i>Prionospio malmgreni</i>	Sedentary polychaetes	Sipunculans	<i>Levinsonia gracilis</i>
<i>Prionospio multibranchiata</i>	<i>Euclymene affinis</i>	<i>Scalibregma inflatum</i>	<i>Spiophanes bombyx</i>	<i>Galfingia elongata</i>	<i>Poecilochaetus serpens</i>
<i>Rhodine gracilior</i>	<i>Myriochele oculata</i>	<i>Ampharete holtica</i>	<i>Magelona minuta</i>	<i>Galfingia vulgaris</i>	<i>Spiophanes kroyeri</i>
Errant polychaetes	<i>Trichobranchus glacialis</i>	Errant polychaetes	<i>Chaetozone setosa</i>	Sipunculid spp.	<i>Spio filicornis</i>
<i>Eteone longa</i>	Errant polychaetes	<i>Nereis longissima</i>	Errant polychaetes	Sedentary polychaetes	<i>Caulerella caputesocis</i>
Crustaceans	<i>Limnophorus hemuli</i>	<i>Nephtys</i> spp.	Phyllodoctidae sp.	<i>Polydora</i> spp.	<i>Diplocirrus glaucus</i>
<i>Diastylis rugosa</i>	<i>Pholoe minuta</i>	Crustaceans	<i>Lumbrineris hibernica</i>	<i>Pectinaria koreni</i>	<i>Heteromastus filiformis</i>
Bivalve molluscs	Crustaceans	<i>Leptognathia</i> sp.	Crustaceans	Hesionidae sp.	Errant polychaetes
<i>Nucula tenuis</i>	<i>Ampelisca tenuicornis</i>	<i>Calocaris macandreae</i>	<i>Leucon nasica</i>	Errant polychaetes	<i>Sthenelais limicola</i>
<i>Lucinoma borealis</i>	Bivalve molluscs	Aplacophoran molluscs	Bivalve molluscs	<i>Synelmis klatti</i>	<i>Glyptis rosea</i>
	<i>Cultellus pellucidus</i>	<i>Chaetoderma nitidulum</i>	<i>Thyasira flexuosa</i>	<i>Glycera rouxii</i>	<i>Glycinde nordmanni</i>
		Bivalve molluscs	<i>Kellia suborbicularis</i>	<i>Goniada maculata</i>	<i>Drilonereis filum</i>
		<i>Venus striatula</i>	<i>Myrella hidentata</i>	<i>Lumbrineris gracilis</i>	Crustaceans
			Phoronids	Crustaceans	<i>Eudorella emarginata</i>
			<i>Phoronis mulleri</i>	<i>Eudorella truncatula</i>	<i>Pericolodes longimanus</i>
			Echinoderms	<i>Diastylis lucifera</i>	<i>Lembos longipes</i>
			<i>Amphiura filiformis</i>	<i>Ampelisca macrocephala</i>	<i>Protomedea fasciata</i>
				<i>Horpinia antennaria</i>	Bivalve molluscs
				<i>Corophium affinis</i>	<i>Montacuta ferruginosa</i>
				Photidae spp.	<i>Cardium scabrum</i>
				<i>Nephtys norvegicus</i>	<i>Hiatella arctica</i>
				Bivalve molluscs	Gastropod molluscs
				<i>Ahra nitida</i>	<i>Odosornia</i> sp.
				Gastropod molluscs	Prosobranch sp.
				<i>Turritella communis</i>	Echinoderms
				<i>Natica alderi</i>	<i>Ophiura affinis</i>
				<i>Cylichna cylindracea</i>	Hemichordates
				Echinoderms	<i>Glossobalanus marginatus</i>
				<i>Amphiura chiajei</i>	
				<i>Echinocardium cordatum</i>	
				<i>Brissopsis lyrifera</i>	

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