NUMERICAL METHODS IN MARINE ECOLOGY

2. GRADIENT ANALYSIS OF ROCKY SHORE SAMPLES FROM FALSE BAY

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INTRODUCTION

The accessibility of electronic computers has made it possible to analyse vast bodies of data which the human mind cannot consider as a whole and summarise. In recent years many techniques for summarising and ordering ecological information have been developed, mainly by plant ecologists. This series of papers is intended to test some promising techniques to see which methods will be useful in marine studies. The techniques are tested on readily observable situations in the intertidal region; if the results of such tests fit in with what has been firmly established, it is reasoned that the method could be used to study less obvious variations such as those found in the area below the tide marks where direct observation is more difficult. The ultimate aim is to find what environmental factors determine distribution patterns in the sea.

The rocky shore is one of the most convenient situations for analysis of the changes in marine fauna and flora, both in the abundance and distribution of species. In the first paper in this series (Field and McFarlane 1968), "similarity analysis" techniques were tested using rocky shore samples carefully chosen to exclude as far as possible all variables except exposure to wave action. This work demonstrated that similarity analysis methods could be applied to marine studies and it showed quantitatively that the fauna varied with changes in exposure to wave action.

The aim of the present paper is to test whether position vectors analysis, developed by Orloci (1966), might be successfully applied to marine situations. The first paper tested a classificatory technique while this paper deals with a method of ordination. Ordination differs from classification in the presentation of results. A classificatory method such as similarity analysis groups the samples into sets of classes and the relationships between the *classes* are shown on a dendrogram. In an ordination the relationships between the individual samples are presented rather than the relationships between groups of samples. There is much controversy in the literature between the protagonists of the two schools of thought but Anderson (1965) points out that the two approaches may be complementary and that each has its advantages and uses. Most workers would agree that the choice of a technique depends on three criteria: the data being analysed, the requirements of the investigator and the computational facilities at his disposal. These three criteria will be discussed in a later section.

Gradient analysis is a technique evolved to study spatial patterns of vegetation (Whittaker 1967). Its basis is that environmental factors, especially physical factors, are usually continuous and often organisms are distributed along an environmental gradient. Whittaker has shown that if an organism responds to an environmental gradient, a plot of the abundance of the species along the gradient gives a bell-shaped curve with a central peak. The method of sampling along a suspected gradient and plotting the abundance of an organism against a measure of the gradient is called *direct gradient analysis*. This, however, is a lengthy procedure which is not suitable for the analysis of the whole fauna because a separate curve must be plotted for each species.

A better way of analysing trends in the fauna as a whole is *indirect gradient analysis*. The method is also known as comparative ordination. Just as in similarity analysis, the first step in comparative ordination is to compute the similarities between samples (or species in inverse analysis); the similarities may be based both on the species composition and the abundance of species. Analysis of the matrix of similarity coefficients yields "factors" or "vectors". The first vector, corresponding to the largest amount of variation in the matrix, is a measure of the "responsiveness" of the distribution of species to the most important environmental variable (Whittaker 1967). Further vectors may be extracted until the variation in the matrix is exhausted. The vectors are plotted graphically as axes corresponding to the first, second, third . . . etc. vectors – that is, ordinated.

Ordination techniques used in ecological work include principal components analysis, position vectors analysis and simple ordination. Orloci (1966) has compared these three techniques and found position vectors analysis to be about 10% less efficient than principal components analysis which in turn is about twice as efficient as simple ordination. In previous marine studies, Williamson (1961) has used principal components analysis on plankton data and Cassie and Michael (1968) have used principal components analysis and canonical correlation in the analysis of a mud-flat fauna.

The rationale underlying the present work is that if samples are carefully selected along two environmental gradients, the technique should separate from the similarity matrix two vectors which correlate with the two environmental gradients chosen. By analysing the samples along each gradient separately and comparing the results with an analysis of the whole data, the effects of including two major sources of variation could be tested. If the technique succeeds in a simple observable situation, it might be useful in extracting the major environmental gradients affecting distribution in a more complex situation with data taken from random samples.

The two environmental variables chosen were exposure to wave action and vertical height up the shore. In the first paper (Field and McFarlane 1968) analysis of the fauna separated two major groups of samples which were shown to differ significantly with respect to exposure to wave action. The vertical zonation of rocky shore life is a well-established concept which Stephenson (1939, 1944 and 1947) has clearly illustrated by consideration of the dominant species on South African shores. Thus there is good reason to accept that there are changes in the fauna along the two selected environmental gradients.

PROCEDURE

1. *Sites, sampling and data:* The location and method of collecting samples 1–10, which vary in exposure to wave action, is given in Field and McFarlane (1968). Their data were used again in the present work. The area chosen for the vertical transect, which was sampled two years after samples 1–10, is at Oatland Point, near Simonstown. It was selected for the following reasons: firstly the transect could be placed alongside the site from which sample 4 of the previous paper had been collected. This was done in order to relate the exposure to wave action at the transect with the measurements made at samples 1–10. Secondly, the transect crossed a smooth slab of granite without crevices and with a fairly even gradient extending from Mean High Water of Spring tide to Mean Low Water of Springs. Thirdly, a nearby bench mark could be used as a reference point for height related to mean sea level. A diagram of the site is given in Figure 1.

The transect consisted of eleven samples collected in a line 7·45 metres long from 76 cm. below Mean Sea Level to 85 cm. above M.S.L. The line of the transect was at right angles to the shoreline and the top of the transect was limited by a crevice across the rock face; no animals were found above the crevice (i.e. to the left of it in Fig. 1). The lower end of the transect was limited by our inability to sample quantitatively underwater. The samples were collected at low spring tide and the sampling technique was identical to that described for samples 1–10 in the first paper; the transect samples were numbered from 11 at the bottom of the shore to 21 at the top. Sample 14 was located in a slight depression in the rock surface which was heavily colonised by the alga *Bifurcaria brassicaeformis*. Because this might be a complicating factor in the analysis, a further sample (No. 15) was collected from the same level as sample 14 but 15 cm. away from it to the side of the line of the transect, in a position almost free of *Bifurcaria*. It was expected that the analysis would show that sample 15 was typical of this level while sample 14 was not.

A square frame enclosing ·38 sq. m. (side length of two feet) was made of ¼″ rod and painted white to show up in photographs which would help in counting the barnacles. The area of rock surface enclosed by the frame was stripped of organisms using bait knives. Samples were collected along the transect line leaving 6″ (15 cm.) wide strips of uncleared rock surface between successive samples. Material was packed into labelled polythene bags and preserved in 5% neutral formalin. The animals were sorted to species and the number of individuals of each species counted for each sample. The level of the centre of each sample area was surveyed using two transect poles marked at 1″ intervals as described in Day (1969).

The pooled data of samples 1–21 contained 79 species in all, with abundances ranging up to 10,864 individuals of a species (Table 1 on p. 208). In the first paper it was noted that the number of species did not vary with changing exposure to wave action. As the transect data show (samples 11–21) this is not the case for the "emergence factors" (desiccation, temperature stress and illumination in particular) which vary with height up the shore (c.f. Lewis 1964). Samples from higher up the shore had progressively smaller numbers of species and larger numbers of individuals. Thus numbers above 1,000 occur only in samples 18, 19, 20 and 21, and sample 21 contained only four species, two of which were present in numbers exceeding 10,000. This result supports the idea put forward by Sanders (1968)

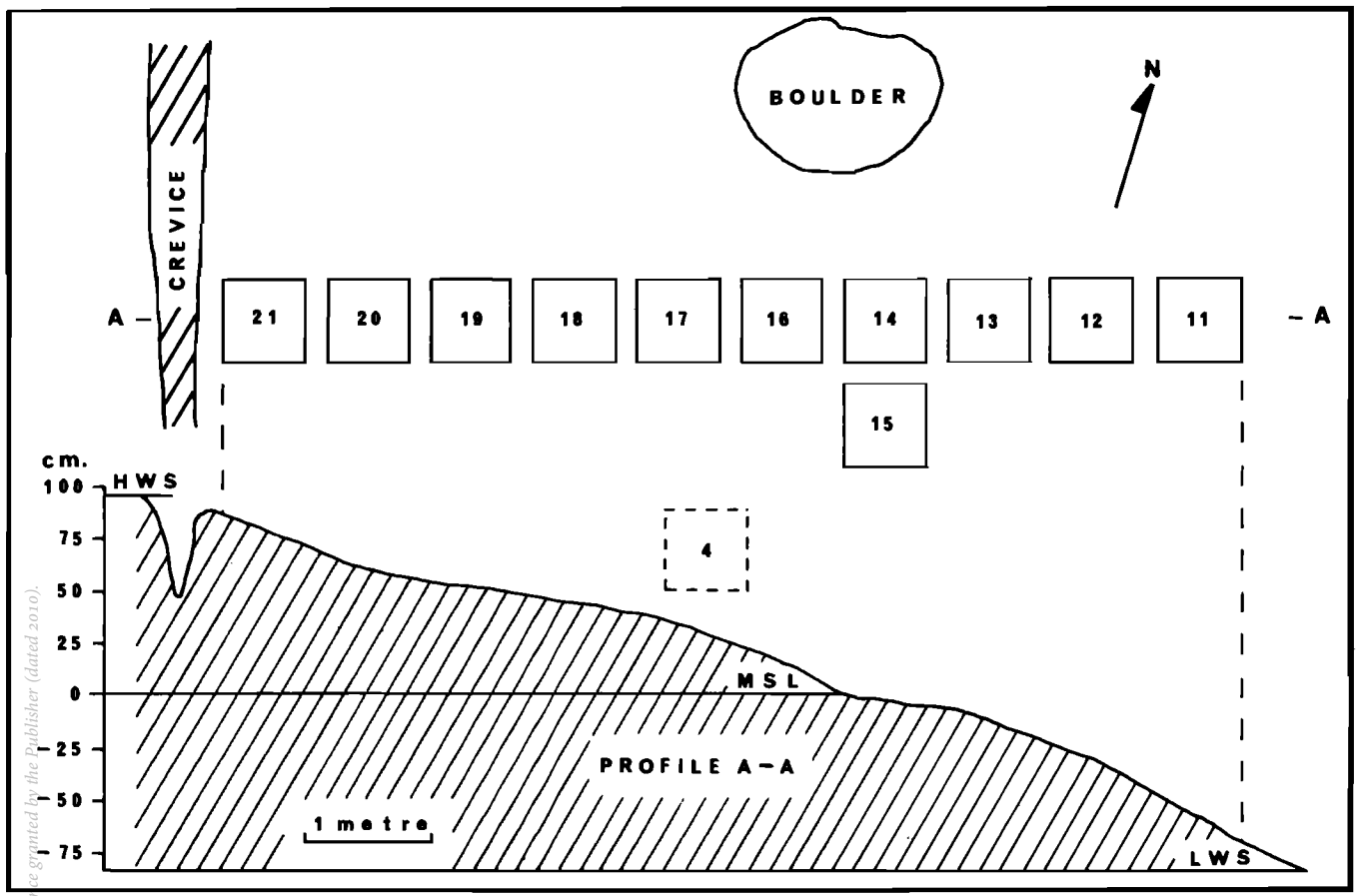


FIGURE 1

Diagrammatic plan and profile of the transect sampling sites which are the squares numbered 11—21. The square numbered 4 shows the position from which sample 4 (of the previous paper) was obtained two years before the transect was sampled. The crevice runs parallel to the shore line. The heights of mean High Water Springs (H.W.S.) and mean Low Water Springs (L.W.S.) are drawn in the profile from figures for the Simonstown area given by Bokenham *et al.* (1939).

that increasing environmental stress (in this case caused by the "emergence factors") results in decreasing diversity because the few species that can withstand the stress do not have much inter-specific competition to contend with and become abundant.

The transect data also show a tendency for the larger animals such as limpets to be confined to the lower reaches of the shore whereas sample 21 at the top of the shore had large numbers of the small winkle *Littorina knysnaensis*, the small barnacle *Chthamalus dentatus* and tiny juvenile bivalves of the genus *Kellya*. Whether samples 20 and 21 belong to the Littorina zone is doubtful, for by the definition of Stephenson (1939), the Littorina zone occurs above the upper limit of barnacles and in samples 20 and 21 it has been noted that both *Littorina* and *Chthamalus* were abundant, occurring in roughly equal numbers. Above sample 21 there were no *Littorina* so it seems that at this locality the Littorina and upper balanoid zones either overlap or the Littorina zone is absent. The crevice which forms the upper limit of the transect might be responsible for this peculiar occurrence.

Histograms of the abundance of three species common at different levels of the transect are shown in Figure 2 (*a*), (*b*) and (*c*). These demonstrate a roughly logarithmic graded change in numbers with varying height up the shore. Reference to the data in Table 1 shows that *Patella cochlear*, after which the cochlear zone is named, does not occur in the samples in sufficient numbers to make graphical presentation worthwhile, so *Oxystele sinensis* has been plotted instead. The data also show that unlike any other species, *Chthamalus* occurred in a well marked band and was either present in numbers exceeding 1,000 or not at all.

2. *Analysis.* The data from samples 1–21 were entered in a matrix and transferred to punch cards for computation. The position vectors method (Orloci 1966) was used to analyse the data. The first step in position vectors analysis is to compute a matrix of similarities between samples from the raw data. The weighted similarity coefficient is used as a measure of similarity between samples:

$$\text{W.S.C.}_{jh} = \sum_{i=1}^{N} (Y_{ij}-\bar{y}_i)(Y_{ih}-\bar{y}_i) \qquad \text{(Orloci 1966)}$$

where W.S.C._{jh} is the similarity coefficient between sample j and sample h, and Y_{ij} is the measure of abundance of the ith species in the jth sample, Y_{ih} is the measure for the hth sample and $\bar{y}_i$ is the mean abundance measure for the ith species over all samples.

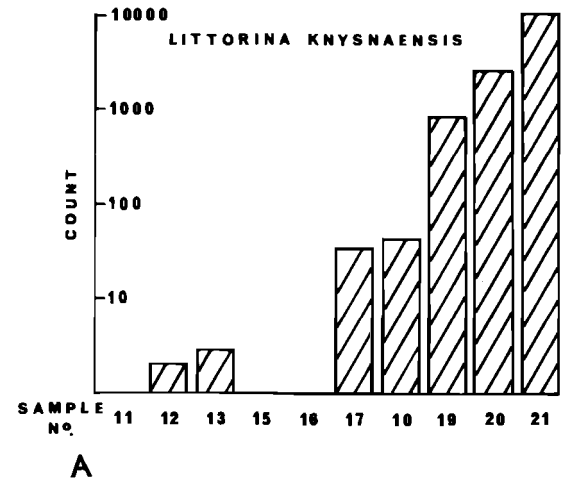
Successive vectors were extracted from the coefficient matrix in the manner described by Orloci (1966). Running time for a full analysis was about 15 minutes using the I.C.T. 1301 computer at the University of Cape Town programmed by one of us (J.G.F.) in Manchester AutoCode (MAC).

Actual and log-transformed numbers were used in separate analyses as measures of the abundance of each species in each sample, the log-transformation being:

$Y_{ij} = \log_e (C_{ij}+1)$ where C_{ij} is the count of the ith species in the jth sample.

so that when C = O, Y = O and negative logarithms are avoided. Separate analyses were performed on the "wave-exposure data" (samples 1–10), the transect data (samples 11–19) and on samples 1–19 and 1–21.

After extracting the vectors by computer one is able to plot the samples as points along



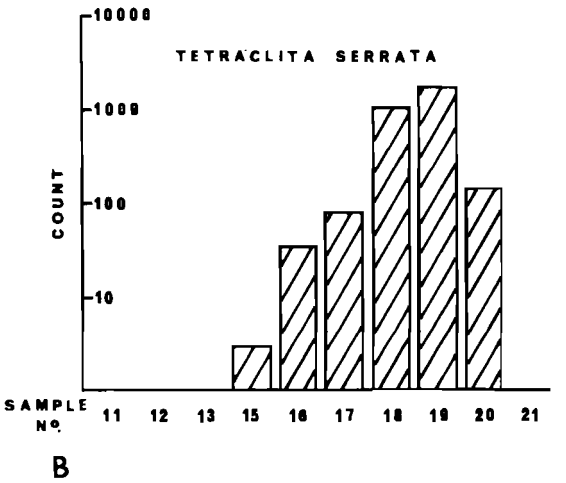
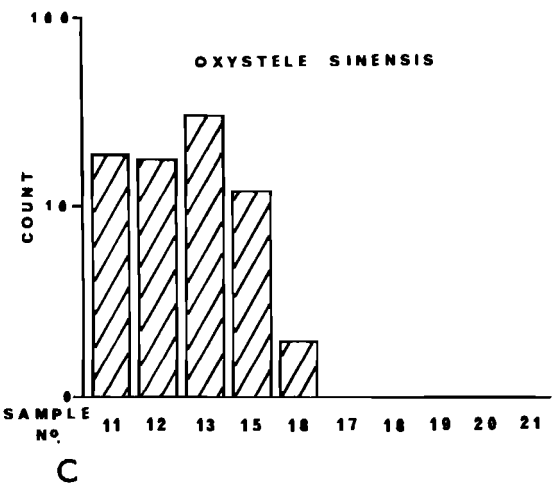


FIGURE 2
Direct gradient analysis: histograms showing the changing abundance with height of three species common at different levels on the shore. The abundance scale is logarithmic.



the axes of a graph. Each axis corresponds to a vector so that the "multi-dimensional" relationships between samples can be represented on a two-dimensional graph and a simplified, visual picture obtained. There is inevitably some distortion in this simplification, which has led to criticism of ordination methods.

Rank Correlation: Correlations were performed to determine whether particular vectors correspond with environmental variables, using Spearmans Rank Correlation Coefficient:

$$r_s = \frac{\Sigma x^2 + \Sigma y^2 - \Sigma d^2}{2\sqrt{\Sigma x^2 . \Sigma y^2}} \qquad \text{(Siegel 1956)}$$

where $\Sigma x^2 = \frac{N^3 - N}{12} - \Sigma T_x$

$$\Sigma y^2 = \frac{N^3 - N}{12} - \Sigma T_y$$

d = difference between ranks of corresponding samples

N = No. of pairs of observations (i.e. No. of samples ranked).

$$T_x = \frac{t^3_x - t_x}{12}$$

t_x = No. of observations of variable x tied at a given rank.

The significance of the correlations was determined from Student's t calculated according to the formula:

$$\text{Student's } t = r_s \sqrt{\frac{N-2}{1-r_s^2}} \qquad \text{(Siegel 1956)}$$

Spearmans Rank Correlation is a non-parametric test about 90% as powerful as Pearsons product-moment test (Siegel 1956). It was chosen in preference to product-moment correlation because of the difficulty of obtaining quantitative measures of wave-action at the transect sites and quantitative measures of height at the "wave action sites", 1-10.

The samples were ranked according to their sequence along each vector. For example, if sample 10 had the highest value along vector 1, it would be assigned to rank one. Sample 15 might have the next highest value and its rank for that vector would then be two, and so on. The vector rankings were then correlated with the rankings assigned to each environmental variable. The two sets of environmental variables were made up as follows (Table 2 on p. 210):

(1) *Vertical height:* The samples were ranked from lowest to highest on the shore; samples at the same level were given a tied value. Vertical height obviously has no effect on the fauna itself, but associated factors such as desiccation, temperature stress and others vary with height up the shore and these affect the fauna directly.

(2) *Exposure to wave action:* The samples were ranked according to the mean turbulometer readings given in the first paper. All transect samples were given the same tied rank as the adjacent sample 4 for which a reading was available. This is a crude approximation, but it

is impossible to get comparable measurements of wave action experienced at different levels on the shore.

RESULTS

Although analyses were performed on both actual and log-transformed data, only the results of analysing the log-transformed data are shown in most cases, for reasons which will be given later. Figure 3 shows the graph produced by plotting the samples as points along the first two vectors extracted by analysis of samples 1-10, which were chosen to vary in exposure to wave action. It can be seen that samples 4, 5, 6, 7 and 8 form a closely related cluster and a loose group of samples 3, 9 and 10 is somewhat intermediate between these and samples 1 and 2 with respect to vector 1. The most sheltered stations are on the left and the most exposed on the right of the graph. This agrees well with the results of similarity analysis given in the first paper. Figure 4 shows the very significant correlation of vector 1 with exposure to wave action. The efficiency shows that this vector accounts for 50% of the variation in the data. Vector 2 shows no significant correlations and presumably accounts for some of the random variation between samples. Vector 3 is only just significantly correlated with wave action. The method appears to work well on these data.

Figure 5 shows the graph of the first two vectors extracted from analysing transect samples 11-19, samples 20 and 21 were omitted for reasons which will become apparent. Generally there is a trend from the stations lowest on the shore on the left of the graph to the highest stations on the right. There are two stations out of sequence at either end of the graph, but this may be due to random variations for samples 11, 12 and 13 are all close together and correspond to a fairly homogeneous cochlear zone at the bottom of the intertidal region. Samples 15, 16, 17, 18 and 19 are spread out across the graph indicating a progressive change from the lower to upper balanoid zone. From this analysis it appears that the balanoid zone is much more heterogeneous than the cochlear zone. Sample 14, which was taken from a depression in the rock face, is well off the main trend from left to right and appears to have been separated by vector 2. The rank correlations (Fig. 6) show that only vector 1 has any significant correlation with vertical height.

The graph obtained by plotting the vectors extracted by analysis of the pooled data from samples 1-19 is given in Figure 7. The transect samples are almost in sequence from the top of the shore on the left of the figure to the cochlear zone samples on the right. The "wave action samples" (samples 1-10 of Field and McFarlane 1968) also agree with the previous analysis of those data alone; the most exposed samples are at the top and the group of sheltered samples near the bottom. This is confirmed by the rank correlations shown in Figure 8. Vector 1 is very significantly correlated with vertical height and vector 2 correlates with wave action. Vectors 3 and 4 are not significant and probably account for random variation. Samples 17 and 4, which were collected from adjacent sites at about the same level on the shore (see Fig. 1), are not as close as one might have expected; this can be explained by the fact that they were collected at different times, two years apart so that this difference is probably caused by variation in the fauna with time. The result is, therefore,

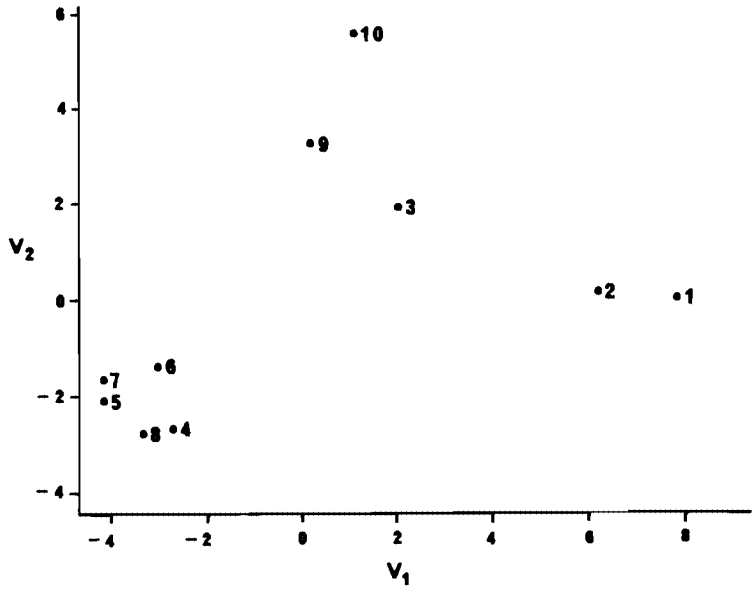


FIGURE 3
Position vectors analysis of log-transformed data of samples 1—10. The samples (numbered) are plotted as points with co-ordinates given by the first two vectors (V_1 and V_2). The vector scales are ratios related to values of the weighted similarity coefficient.

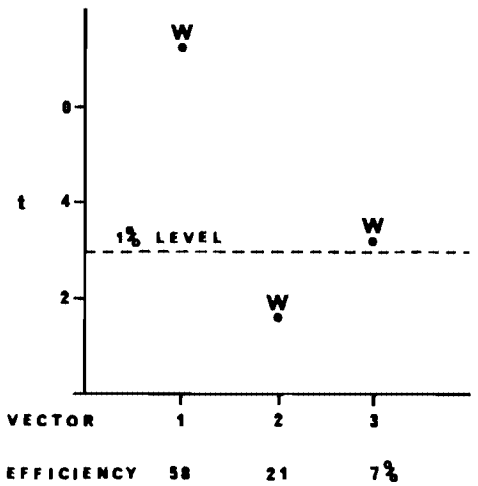


FIGURE 4
The significance of rank correlations between vectors 1, 2, and 3 formed by analysis of samples 1—10, and wave action (W). The "efficiency" of each vector is the percentage of total variation accounted for by each vector; it is calculated according to the formula of Orloci (1966).

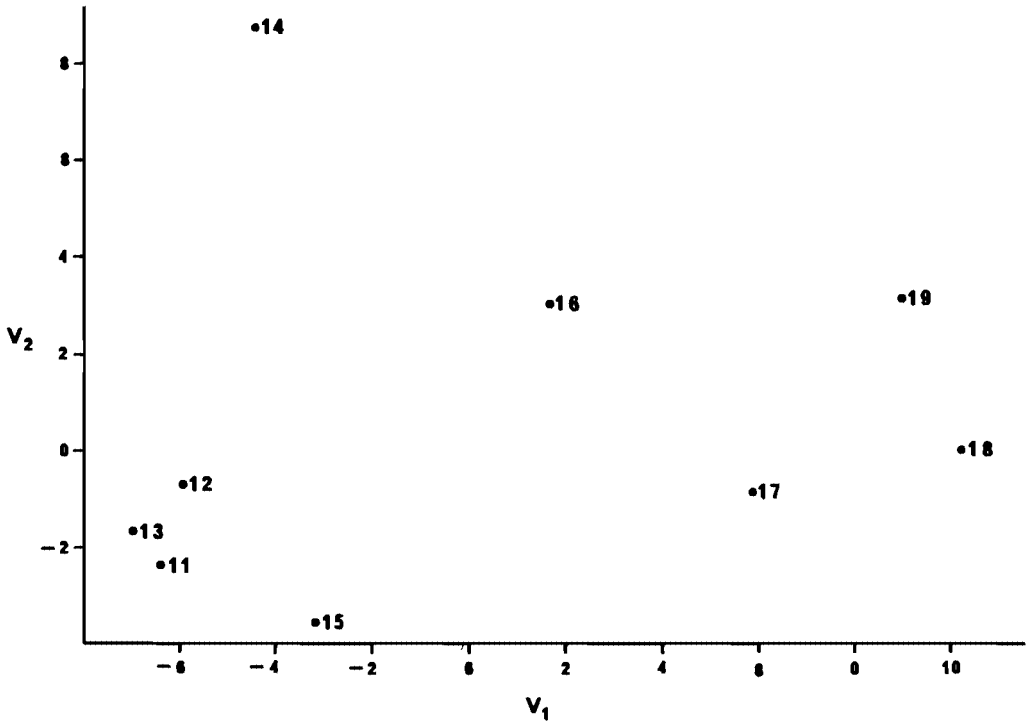


FIGURE 5
Ordination of the first two vectors formed by analysis of log-transformed data of samples 11—19. The numbered points represent samples.

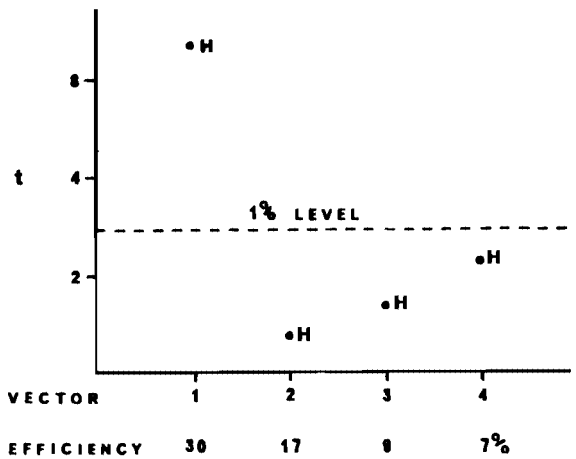


FIGURE 6
The significance of rank correlations between vectors 1, 2, 3 and 4 formed by analysis of samples 11—19, and vertical height (H).

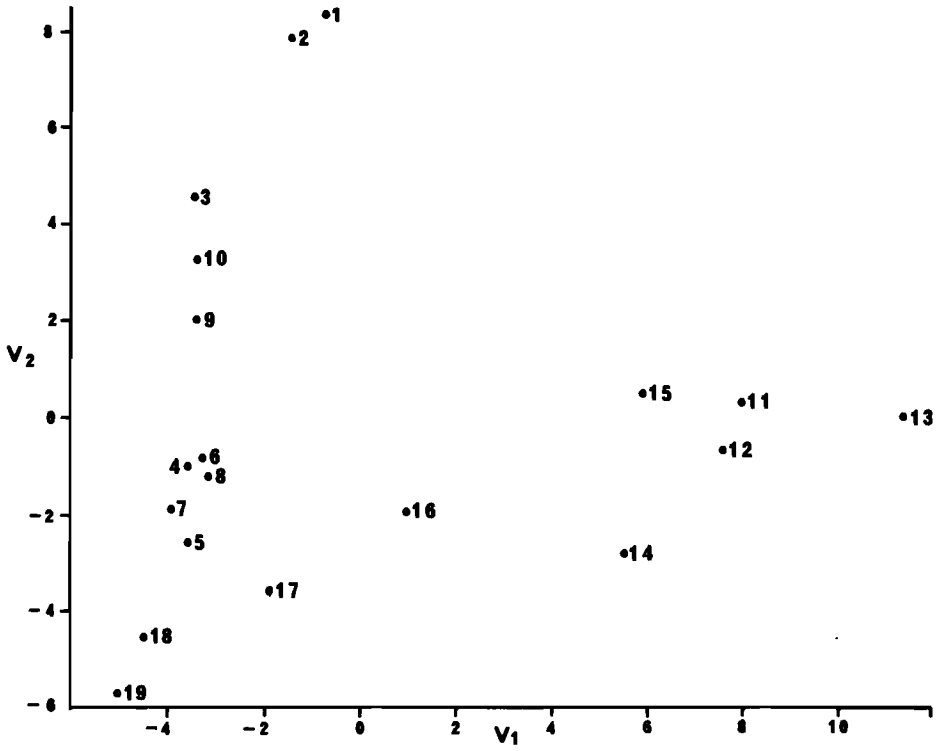


FIGURE 7
Ordination of the first two vectors formed by analysis of the log-transformed data of samples 1—19. The numbered points represent samples.

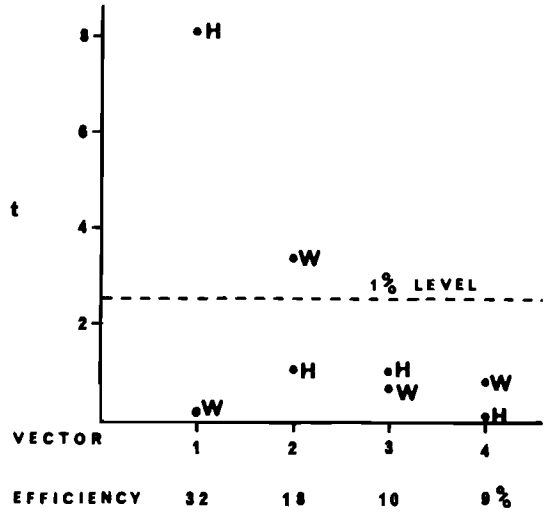


FIGURE 8
The significance of rank correlations between vectors formed by analysis of samples 1—19, and the environmental variables vertical height (H) and wave action (W).

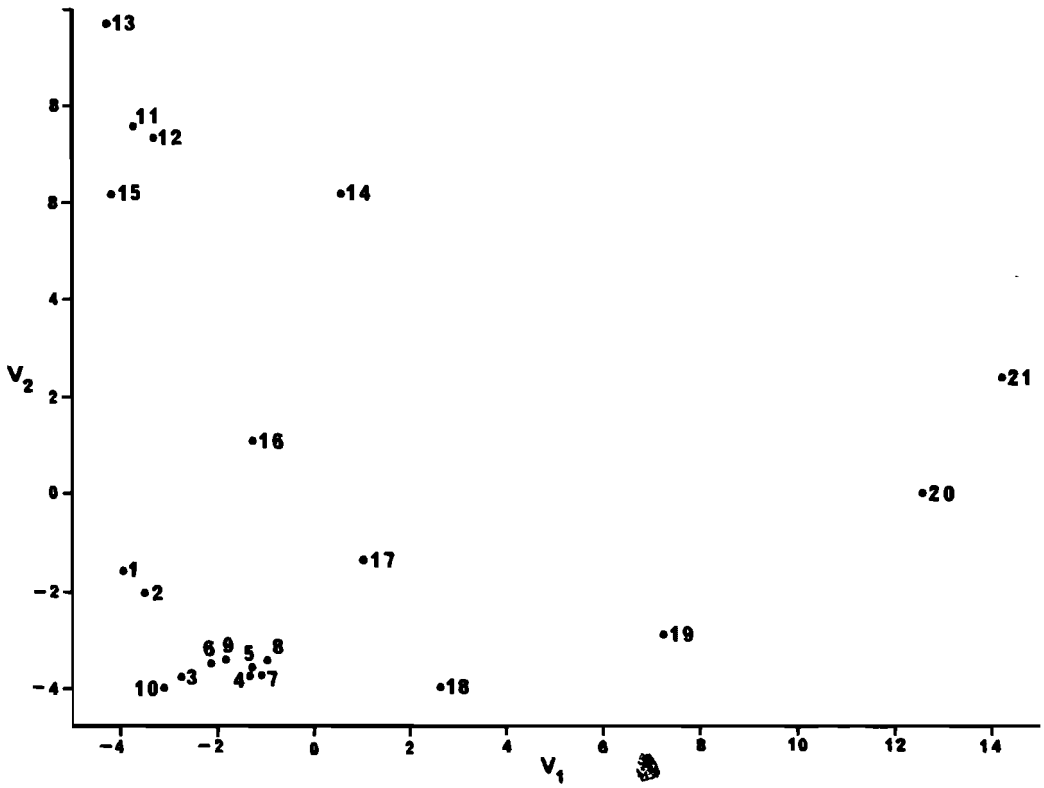


FIGURE 9
Ordination of the first two vectors formed by analysis of the log-transformed data of samples 1—21. The numbered points represent samples.

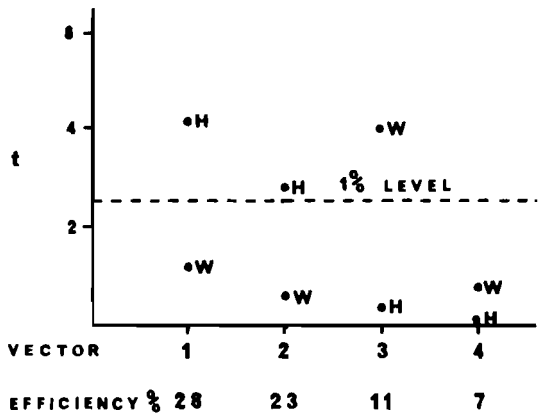


FIGURE 10
The significance of correlations between vectors formed by analysis of the log-transformed data of samples 1—21, and the environmental variables vertical height (H) and wave action (W).

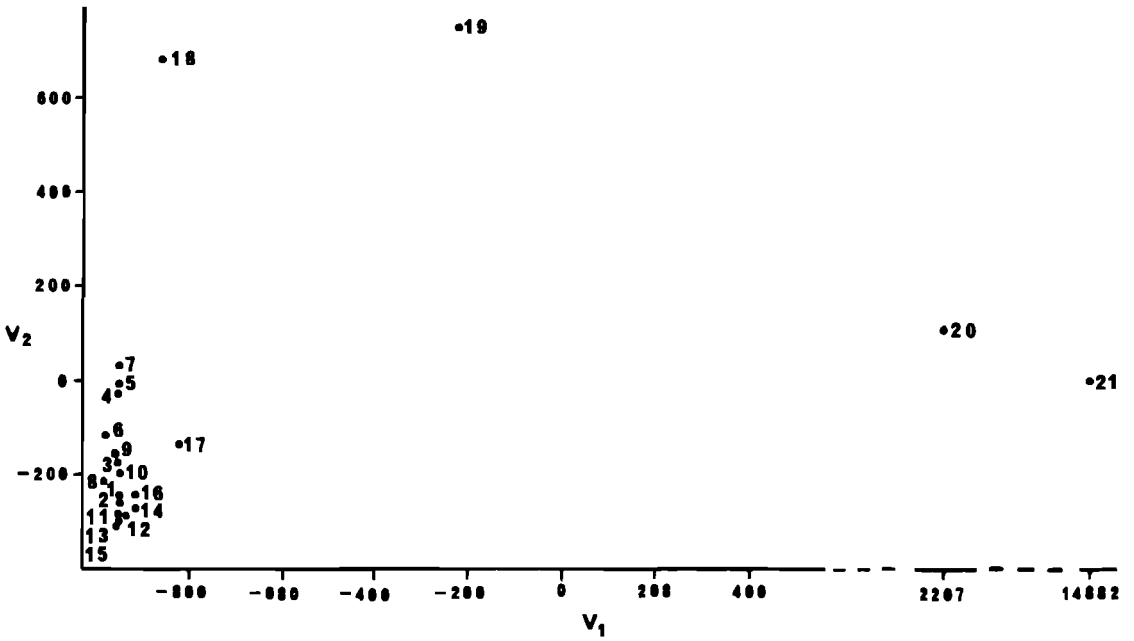


FIGURE 11
Ordination of the first two vectors formed by analysis of the actual counts of each species in samples 1—21. The numbered points represent samples. Note that the scale of vector 1 is not continuous.

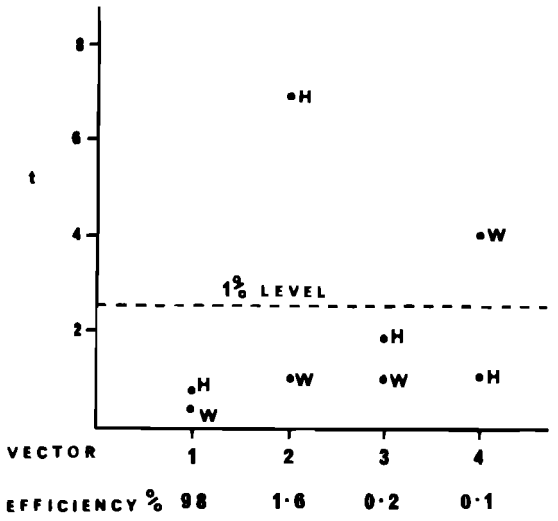


FIGURE 12
The significance of correlations between vectors formed by analysis of the untransformed counts of samples 1—21 ,and the environmental variables vertical height (H) and wave action (W).

what one might have expected of a successful analysis, except that sample 13 is out of sequence.

When all twenty-one samples are analysed together the picture is not as clear. Plotting the first two vectors (Fig. 9) shows the transect samples in an arc from the cochlear zone samples (11, 12 and 13) at the top left to samples 20 and 21 at the right while the exposed and sheltered samples overlap. Figure 10 shows that the first two vectors both correlate with vertical height and only the third vector is significantly correlated with wave action. It appears that samples 20 and 21 introduce so much variation into the data that two vectors are needed to remove this variation before other trends can be exposed. Probably the large numbers of a few species in samples 20 and 21 and the absence of most of the other species in these two samples complicate the analysis.

The results presented so far have been of the analysis of log-transformed data. Figure 11 shows the first two vectors extracted by analysis of the actual counts of individuals in all 21 samples. There is a tight bunch of samples at the left hand side of the graph and samples 18, 19, 20 and 21 are widely scattered. The correlations in Figure 12 shows that vector 1 does not correlate with either variable, vector 2 correlates with height (although this is not clear from the ordination in Fig. 11) and only vector 4 correlates with wave action. Similarly other ordinations and correlations of analyses performed on actual counts did not conform as closely to the results we expected as did the same analyses of the log-transformed data.

DISCUSSION

The work was designed to test a method of analysis. If the technique operated successfully the first two vectors formed by analysis of the whole data should correlate with the two gradients along which the samples were taken.

Clearly the analyses of log-transformed data yielded results which were closer to what was expected than the analyses of the untransformed counts. Log-transformation of the data was also found to give more useful results in similarity analysis (Field and McFarlane 1968). Cassie (1962) and Cassie and Michael (1968) have reasoned that this transformation may be appropriate for most populations of organisms. For these reasons, only analyses of the log-transformed data will be considered further.

The results of position vectors analysis of samples 1-10 confirm the obvious fact that the fauna does vary from sample to sample and show that this variation corresponds with changes in wave action. In the similarity analysis performed on these data in the first paper, groups of samples were formed which differed significantly with respect to wave action, but it is not evident from the dendrogram that samples 3, 9 and 10 (semi-exposed) had a fauna intermediate between that of samples 1 and 2 (exposed) and samples 4, 5, 6, 7 and 8 (sheltered), this could only be inferred. Position vectors analysis shows clearly that this fauna is intermediate between the other two.

Analysis of transect samples 11-19 shows a significant correlation with vertical height up the shore. This does not mean that vertical height itself affects shore animals but that factors which vary with height up the shore, the "emergence factors", do. As has been

mentioned, the samples below Mean Sea Level (cochlear zone samples) are more closely clustered than those above M.S.L. (balanoid zone samples). This may be interpreted as meaning that the cochlear zone is indeed a true relatively homogeneous zone but that the balanoid zone is a region of progressive change in fauna with height. This has of course been subjectively recognised by the subdivision into upper-, mid-, and lower balanoid zones (Stephenson 1939). This sort of finding would be useful in analyses of the benthos where direct observation is not easy.

When both sets of data were analyses together without samples 20 and 21, the extraction of neither trend was affected, in fact the first vector had a slightly higher correlation with vertical height than in the analysis of the transect data alone. Thus position vectors analysis was very successful not only in separating two vectors which correlated well with the original environmental gradients, but also in separating a distinct sample (No. 14) which did not form part of either trend. However, when samples 20 and 21 were included in the analysis it took two vectors to extract the large amount of variation correlated with height, and only after that was the variation due to wave action separated. If such a situation arose in a large analysis with several sources of variation affecting the data, it would be difficult to get good correlations when only a few individuals are isolated from the main cluster, so that interpretation would be difficult. Moreover it would be necessary to look at several graphs showing vectors 1, 2, 3, 4 . . . to get a proper perspective of the situation. Therefore, one might well have reservations about using this technique on data containing very aberrant samples. Classificatory methods probably present the results of analysis of such heterogeneous data more clearly than ordination (see Greig-Smith 1964, pp. 177-178). On theoretical grounds, too, one has doubts about coefficients of similarity based on deviations from a mean when the data bear no resemblance to a normal frequency distribution. So it seems that if little is known about the data prior to analysis, a classification based on a simple, distribution-free coefficient of similarity may be the safest way of doing a first analysis. If this reveals similar or homogeneous groups, these may then be analysed by more sophisticated methods.

The nature of the data is one criterion in the choice of a method of analysis. Another is the aim of the investigator. When environmental variables can be measured on a graded scale or ranked, then ordination methods may be useful because correlations can be performed, but if the environmental data can only be expressed in the form of a contingency table (i.e. they fall into discrete categories) then there seems to be little point in extracting graded vectors. The investigator may be more interested in the groups of samples or species than in graded relationships between individuals, in which case classification is called for.

The computational facilities available, the third criterion, are also important and in the case of this paper prevented the use of a more powerful method of ordination such as principal components analysis.

One may conclude that position vectors analysis has worked successfully in analysing faunal gradients on a rocky shore. However, there are doubts about its usefulness when the samples under analysis differ widely in their faunal content. It will probably be most useful in the analysis of trends or clines within a fairly homogeneous set of samples.

SUMMARY

The series of papers is aimed at testing different numerical methods to see which might be useful tools in the study of marine distribution patterns. The first paper (Field and McFarlane 1968) tested similarity analysis methods, this one tests position vectors ordination.

The method was tested by choosing samples along two environmental gradients which were known to influence the composition of the fauna. The gradients chosen were vertical height up a rocky shore, sampled by means of a transect, and exposure to wave action, for which the data of the first paper were used again. Different analyses of these data showed that there was a statistically significant correlation between the main trends of variation in the fauna and the gradients along which the samples were collected. This correlation was good whether the transect and wave-action sets of data were analysed separately or pooled, but the analysis was not entirely satisfactory when the two "aberrant" samples at the top of the shore were included in the data.

Three criteria in the choice of a method of analysis are discussed. It is concluded that position vectors ordination is most likely to be useful for analysing trends in fairly homogeneous sets of data but that similarity analysis probably gives a simpler and clearer result when heterogeneous data are analysed.

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See tables on following pages

TABLE 1: NUMBERS OF ANIMALS PER SAMPLE

Species	Samples 11	12	13	14	15	16	17	18	19	20	21
1. *Bunodosoma capensis* (Lesson)	11	4	6	7	2	1	—	—	—	—	—
2. *Bunodactis reynaudi* (M. Edw.)	—	—	1	—	—	—	—	—	—	—	—
3. *Pseudactinia flagellifera* (Hertwig)	2	36	96	29	17	8	—	—	—	—	—
4. *Planocera gilchristi* Jacubowa	—	—	—	1	—	2	—	2	12	—	—
5. *Pseudonereis variegata* Grube	10	10	31	27	99	42	56	18	5	—	—
6. *Lysidice natalensis* Kbg.	3	5	4	—	—	1	—	—	—	—	—
7. *Nereis willeyi* Day	20	3	13	—	2	—	—	—	—	—	—
8. *Syllis variegata* Grube	—	15	—	—	1	2	—	—	—	—	—
9. *S. armillaris* O.F.M.	42	4	107	—	45	—	—	—	—	—	—
10. *S. armata* Quatref	—	—	—	1	—	—	—	—	—	—	—
11. *Nicolea macrobranchia* (Schm.)	—	3	4	—	—	—	—	—	—	—	—
12. *Pomatoleios kraussi* (Baird)	1	—	2	2	2	2	—	—	—	—	—
13. *Lepidonotus clava* Willey	20	40	34	10	14	5	1	—	—	—	—
14. *Bhwania goodei* Webster	—	—	—	—	1	—	—	—	—	—	—
15. *Cirriformia capensis* (Schm.)	12	7	61	8	100	97	1	—	—	—	—
16. *Boccardia polybranchia* (Haswell)	—	—	—	—	—	—	—	1	—	—	—
17. *Tetraclita serrata* Darwin	—	—	—	—	3	36	81	1,002	1,750	142	—
18. *Chthmalatus dentatus* Krauss	—	—	—	—	—	—	—	—	—	1,799	10,864
19. *Hyale grandicornis* (Kroyer)	11	69	12	—	17	22	110	93	—	—	—
20. *H. saldanha* Chilton	45	39	9	5	—	—	—	—	—	—	—
21. *Lysianassa ceratina* (Walker)	8	26	2	7	—	—	1	—	—	—	—
22. *Amaryllis macrophthalma* Haswell	5	14	1	13	—	—	—	—	—	—	—
23. *Paramoera capensis* (Dana)	—	3	3	18	—	—	—	—	—	—	—
24. *Macropisthopous stebbingi* Barnard	5	—	—	12	—	—	—	—	—	—	—
25. *Iais pubescens* (Dana)	—	—	—	—	—	—	4	—	—	—	—
26. *Parisocladus perforatus* (M. Edw.)	4	2	4	—	11	40	68	72	5	—	—
27. *P. stimpsoni* (Heller)	—	—	3	9	—	—	11	50	200	6	—
28. *Dynamenella dioxus* Barnard	—	—	—	—	—	—	—	8	7	10	16
29. *D. huttoni* (Thomson)	10	14	28	—	25	23	—	—	—	—	—
30. *D. scrabicula* (Heller)	—	—	—	—	—	—	—	3	3	2	—
31. *D. australis* Richardson	—	—	—	—	1	—	—	—	—	—	—
32. *Cymodocella pustulata* Barnard	9	4	—	1	—	—	—	—	—	—	—
33. *Paridotea fucicola* Barnard	—	1	2	50	—	—	1	—	—	—	—
34. *Plagusia chabrus* (Linn.)	—	—	—	2	—	—	—	—	—	—	—
35. *Acanthochiton garnoti* (Blainville)	1	—	—	—	—	1	—	—	—	—	—

(continued)

(Table 1 continued)

Species	Samples 11	12	13	14	15	16	17	18	19	20	21
36. *Ischnochiton oniscus* (Krauss)	2	3	—	—	2	1	1	—	—	—	—
37. *Perna perna* (Linn.)	4	8	10	—	22	51	63	3	—	—	—
38. *Choromytilus meridionalis* (Krauss)	3	5	—	—	—	2	—	—	—	—	—
39. *Modiolus philippinarum* Hanley	—	2	—	—	1	1	—	—	1	—	—
40. *Saxicava rugosa* (Linn.)	—	—	1	—	5	1	1	—	—	—	—
41. *Thecalia concamerata* (Brug.)	—	—	—	1	—	—	—	—	—	—	—
42. *Burnupena delalandii* (Kiener)	1	4	1	—	2	5	—	9	3	—	—
43. *B. limbosa* (Lam.)	—	—	—	—	—	2	—	—	—	—	—
44. *Thais squamosa* (Lam.)	1	7	3	16	—	—	—	—	—	—	—
45. *T. dubia* (Krauss)	—	—	—	10	—	—	3	3	20	9	—
46. *Kellya* sp.	—	2	—	5	1	34	336	205	626	982	5,548
47. *Pyrene kraussi* (Sowerby)	—	2	3	25	—	—	1	—	—	—	—
48. *Turbonilla trachealis* Gould	—	—	—	1	—	—	1	—	—	—	—
49. *Afrocominella elongata* (Dunker)	—	—	—	—	—	1	—	—	—	—	—
50. *Marginella biannulata* (Fabricius)	—	—	—	1	—	—	—	—	—	—	—
51. *Oxystele variegata* (Anton)	—	—	—	1	8	34	66	139	177	6	—
52. *O. sinensis* (Gmelin)	19	18	30	90	11	1	—	—	—	—	—
53. *O. tigrina* (Chemnitz)	5	6	11	—	—	—	—	—	—	—	—
54. *Littorina kynsnaensis* Philippi	—	2	3	39	—	8	37	44	860	2,605	10,068
55. *Gibbula multicolor* Krauss	1	—	1	—	—	2	—	2	2	—	—
56. *Tricolea capensis* (Dunker)	—	—	—	7	—	—	1	—	—	—	—
57. *Turbo sarmaticus* Linn.	—	—	1	3	—	—	—	—	—	—	—
58. *Fissurella mutabilis* Sowerby	27	13	27	8	21	3	2	—	—	—	—
59. *Helcion pectunculus* (Gmelin)	—	5	1	—	—	—	—	—	—	—	—
60. *Crepidula porcellana* Lam.	—	—	—	6	1	—	—	—	—	—	—
61. *Patella barbara* Linn.	3	0	5	0	2	—	—	—	—	—	—
62. *P. tabularis* Krauss	5	1	—	—	—	—	—	—	—	—	—
63. *P. cochlear* Born.	17	3	19	—	6	—	—	—	—	—	—
64. *P. granularis* Linn.	—	—	—	—	—	—	—	3	—	—	—
65. *P. oculus* Born.	—	—	1	1	4	1	3	—	—	—	—
66. *Siphonaria aspera* Krauss	—	—	2	—	—	—	2	1	3	2	—
67. *Parechinus angulosus* (Leske)	3	12	3	34	2	1	2	—	—	—	—
68. *Asterina exigua* (Lam.)	1	2	8	8	1	1	2	—	1	—	—
69. *Ophiarachnella capensis* (Bell)	—	—	2	2	1	—	—	—	—	—	—
70. *Potamageton sp.*	—	—	1	—	7	15	185	55	—	—	—

TABLE 2

RANKS ASSIGNED TO SAMPLES FOR RANK CORRELATIONS. THE RANKS WERE MODIFIED APPROPRIATELY WHEN ONLY SOME OF THE SAMPLES WERE USED IN CORRELATION.

	Rank	
Sample Number	*Vertical height*	*Wave action*
1	12	1
2	12	2
3	12	3
4	12	12
5	12	12
6	12	19·5
7	12	21
8	12	19·5
9	12	4·5
10	12	4·5
11	1	12
12	2	12
13	3	12
14	4	12
15	5	12
16	6	12
17	12	12
18	18	12
19	19	12
20	20	12
21	21	12