

NEARSHORE ZONATION OF BENTHIC FAUNA, ESPECIALLY NEMATODA, IN LOCH ETIVE

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(Text-figs. 1-5)

The vertical distribution of the benthic fauna, including Nematoda, of soft sediments in shallow water was studied along nearshore transects at two sites in Loch Etive and compared with transects worked there previously. The mathematical techniques of hierarchical classification and reciprocal averaging ordination were applied to the species abundances along the transects in an attempt to summarize the data and describe the faunal zonation in a clear and objective way. The inverse reciprocal averaging ordination of pooled transect data described the zonation for all species at each site as a faunal gradient with a single large step at a depth where hydrographic conditions were most variable. This was the most satisfactory description of zonation since it indicated the pattern of sharp faunal change at these critical depths better than previously and allowed direct comparison between transects.

The vertical distribution of the Nematoda alone could be simplified to a pattern which paralleled that of the other fauna. A single step or break demarcated a shallow brackish assemblage from a typically marine assemblage found in deeper water. Comparison with brackish fauna of the Baltic and from British estuaries illustrate the coherent nature of the brackish component. Zonation of many nematode species paralleled closely previously published descriptions of zonation in the Exe estuary, indicating the dominant effect of salinity governing distribution along the Etive transects.

Classification techniques based on faunal indices of affinity between stations along the transects were less satisfactory. Different indices of faunal similarity yielded different patterns of hierarchy, although an index based on presence/absence data yielded results similar to reciprocal averaging.

A group of species intermediate between the brackish and marine elements was isolated from the non-nematode component, but this was not reflected in the nematodes.

INTRODUCTION

The marked pattern of vertical zonation in the nearshore distributions of benthic fauna in sea-lochs seems to be controlled by the degree of fluctuation and extent of depression in salinity (Gage, 1974). The different vertical patterns in the abundances of species can be related to their known tolerances to reduced and fluctuating salinity. An overall faunal discontinuity seems to occur at a depth which roughly corresponds to the maximum depth to which markedly brackish conditions are experienced.

This paper reports the results of further sampling in Loch Etive, West Scotland, at two of the sites of the previous survey in order to better describe these trends. A slightly different sampling design was used and the analysis included smaller sized species than

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before. Particular attention was paid to the Nematoda which were relatively numerous in the present samples but which had not been identified earlier.

A sharp faunal discontinuity occurring deeper than about 5 m depth was not previously described adequately because the sampling intervals with depth increased from 1 to 5 m at that depth. Two sites were chosen for the present study, Transects 4 and 5 of Gage (1974) in Loch Etive. From the earlier study one seemed to only just contain the faunal discontinuity within the belt of samples taken at 1 m depth intervals. In the other the discontinuity appeared to occur between the 5 and 10 m samples and thus was not defined accurately. It was hoped that a 1 m spacing of samples with depth, from the surface down to 10 m, would yield an improved description of any discontinuity and of faunal zonation in shallow water.

The numerical methods applied to the sample data include the same method of classification as was used earlier. Other methods, including an eigenvector method of ordination (reciprocal averaging), were applied in an effort to find the most efficient way to describe the transect data. Gage (1974) gives a map showing the transect positions and a description of bottom topography and sediment granulometry along the transects, together with a summary of observations of the hydrographic conditions made near the transect sites.

MATERIAL AND METHODS

Samples were taken by diving as described for the previous investigation (Gage, 1974), each sample consisting of 2 cores taken using plastic core tubes, measuring 78 cm² in cross-section, which were pushed at least 15 cm deep into the bottom sediment. Depths were carefully measured and referred to mean tide level (M.T.L.) at Oban. Samples were taken at 1 m depth intervals from 10 m depth to the water's edge. Although it was not possible to follow the exact line of the previous transects, the present transects, which will be referred to as 3A and 4A, were located within the same 100 m stretch of shore. Transect 3A was worked on 11 February 1969 and 4A on 21 October 1971. On both occasions the tide was about 30 cm above M.T.L.

The sediment cores were washed through a 500 μ m aperture sieve and the material retained was fixed with 7% formalin. After staining the entire material with Rose Bengale the animals were picked out, identified as far as possible and counted.

While it is generally accepted (McIntyre, 1969) that a 500 μ m sieve mostly separates macrofaunal taxa from those which comprise the meiofauna, many meiofaunal species may be retained by 500 μ m or even 1000 μ m sieves. This was the case for the present samples, and by far the most numerically conspicuous of these were nematode worms, with more than 300 specimens being found in one sample. Some of them were large enough to have been retained by a 1000 μ m aperture sieve as well. Indeed Gage (1974) found small numbers of Nematoda in samples washed using a 1000 μ m sieve, but these specimens were not identified. The present 500 μ m sieved samples cannot be considered quantitative for nematodes, but are simply a selection of the larger species. The Nematoda have been identified but the small number of other meiofaunal species, mainly harpacticoid copepods, have not.

Data analysis

Ninety-two species, or putative species, were identified from Transect 3A, and 41 from 4A. Of these, 34 from T. 3A and 10 from T. 4A were Nematoda. The smaller meshed sieve used in the present study retained the smaller more juvenile elements and there were consequently higher numerical abundances in the samples than previously. Because of the difficulty of summarizing the information in the listing of the species and their abundances in the samples, multivariate techniques were applied in order to condense the data objectively and describe the main trends without serious loss of information.

Two approaches may be employed in summarizing and hopefully clarifying such ecological data. One involves applying methods of classification and the other of ordination. Their choice of application is said (Pielou, 1969) to depend on a conceptual interpretation of the ecological situation. The result of a classification cannot itself indicate that the samples came from distinct communities, nor can an ordination itself indicate a continuum of imperceptible merging of communities. Because Gage's (1974) study indicated sharp changes in environmental conditions along the Etive transects with associated marked changes in the fauna, a classification seemed to provide a satisfactory summary and was in fact applied in the previous study. However, because the conditions along a transect might also be described as a complex of environmental gradients which alter in intensity with changes in depth, an ordination may seem at least as appropriate. Sophisticated techniques of ordination such as principal components analysis have, however, been more successful as an ecological tool when applied to a narrow range of environment and near-homogeneous communities (Greig-Smith, 1964; Kershaw, 1973). Reciprocal averaging (Hill, 1973), an eigenvector method similar to principal components, is claimed more suitable in displaying stronger faunal gradients. This technique is conceptually similar to direct gradient analysis (Whittaker, 1967) involving ordination on the basis of an evident and apparently important environmental gradient. However, it remains a technique of indirect ordination where the axes extracted, accounting for the principal variability in the data, may as easily correspond to a complex of environmental factors as one readily identifiable factor. Although in reciprocal averaging (unlike principal components) the axes are neither orthogonal nor independent, it is questionable whether this makes them ecologically less meaningful, notwithstanding any difficulty in interpreting them in terms of isolated physical factors (Beals, 1973). Another advantage is that reciprocal averaging, unlike other methods, provides sample and species ordinations ('normal' and 'inverse' analyses) simultaneously and symmetrically.

Because of the lack of independence of the samples taken along the transect, and because of a lack of fit of the parent populations to the multivariate normal distributions, the application of significance tests to the eigenvectors extracted was inappropriate. However, the analysis itself makes no such assumptions. In any case, because of the nature of the physical gradients thought to control the data variability, it was considered highly likely that the first few vectors extracted would account for most of the variation present.

For the classification of the samples, dendrogram representations of relative sample affinity were evolved from a matrix of indices of faunal similarity for all possible pairs of samples in each transect. Two faunal similarity indices were applied, one employing quantitative and the other presence/absence data only. The latter is generally attributed to Sørensen (1948) and takes the form $2j/(a+b) \times 100$ where j is the number of species in common between two samples each containing a and b species respectively. The other was Morisita's (1959) index $C\lambda$. This was employed as the most satisfactory of the many available for quantitative data because its mathematical formulation assumes a log-normal distribution of abundances amongst the species. Benthos sample species abundance data shows reasonable fit to the truncated log-normal as has been demonstrated by Warwick & Buchanan (1970) for Nematoda and by Gage & Tett (1973) for macrobenthos. The dendrogram clustering strategy was the same as applied previously (Gage, 1974).

RESULTS

A listing of species with their abundances in the samples is given in Table 1.

Reciprocal averaging ordination

The primary axis scores obtained by reciprocal averaging of the total data for each transect successfully ordinated the samples (normal analysis) along the depth gradient (Fig. 1). Fig. 1 also shows that the pattern was essentially the same whether quantitative, standardized or presence/absence data was employed, although standardization seemed to provide the least clear grouping. Elimination of the Nematoda or the faunal elements considered motile similarly had little effect, although the nematodes considered alone

NEMATODE ZONATION

TABLE 1 (cont.)

Rank	Species	Score	Axis value	Eigen- value	Depth (m)											
					0	1	2	3	4	5	6	7	8	9	10	
Transect 4A																
N	1 <i>Adoncholaimus fuscus</i> (Bastian)	0		2	
N	2 <i>Gammanema rapax</i>	0		6	
N	3 <i>Bathyporeia pilosa</i> Lindstrom	0		2	
N	4 <i>Enoploides spiculohamatus</i>	1		5	2	
N	5 <i>Adoncholaimus lepidus</i>	2		107	11	3	.	.	.	3	
N	6 <i>Gammaridea</i> sp.	2		7	.	1	
N	7 <i>Enoplus brevis</i>	4		79	60	23	1	.	1	1	
N	8 <i>Jaera albifrons</i>	4		2	2	1	
N	9 <i>Nereis diversicolor</i> O. F. Müller	4		17	50	8	
N	10 <i>Corophium volutator</i>	7		91	48	29	18	2	
N	11 <i>Mya arenaria</i>	8		2	.	2	
N	12 <i>Fabriociola baltica</i>	9		112	120	17	6	10	10	1	.	6	.	.	.	
N	13 <i>Oncholaimus brachycercus</i>	10		1	9	1	.	.	1	
N	14 <i>Phalodrilus monospermathecus</i>	10		372	574	208	66	33	28	18	
N	15 <i>Pygospio elegans</i>	11		131	92	42	26	25	
N	16 <i>Retusa alba</i>	17		3	.	1	.	.	1	
N	17 <i>Hydrobia ulvae</i>	20	1	0.89	22	116	1	.	1	13	.	1	14	4	6	
N	18 <i>Macoma balthica</i>	36		.	16	10	36	15	9	2	3	2	.	.	.	
N	19 <i>Pelosclex benedeni</i>	64		.	.	7	20	20	18	8	8	28	12	2	.	
N	20 <i>Capitellides giardi</i>	74		.	.	1	4	17	119	114	30	36	14	.	.	
N	21 <i>Aricidia catherinae</i>	83		1	3	2	.	.	
N	22 <i>Nereis virens</i> M. Sars	87		1	.	2	.	.	
N	23 <i>Diastylis rugosa</i>	89		1	.	.	.	
N	24 <i>Capitomastus minimus</i>	90		1	7	16	7	
N	25 <i>Amphitrite johnstoni</i> (Malmgren)	91		2	.	.	
N	26 <i>Anticoma</i> sp.	93		2	.	
N	27 <i>Ophiura</i> sp.	96		4	4
N	28 <i>Pholoe minuta</i>	96		8	9
N	29 <i>Scoloplos armiger</i>	97		1	.	4
N	30 <i>Goniada maculata</i>	97		2	1
N	31 <i>Pontonema vulgare</i>	100		4
N	32 <i>Glycera alba</i>	100		2
N	33 <i>Prionospio cirrifera</i>	100		10
N	Dorylaimidae sp.	1		1
N	<i>Paratinkomoetes</i> sp.	1		1

yielded a slightly different pattern (Fig. 5). The eigenvalues obtained (Table 1) indicated that the first axis accounted for the bulk of the variance in the data. Scores obtained in succeeding axes tended to reflect differences in overall sample abundance or numbers of occurrences.

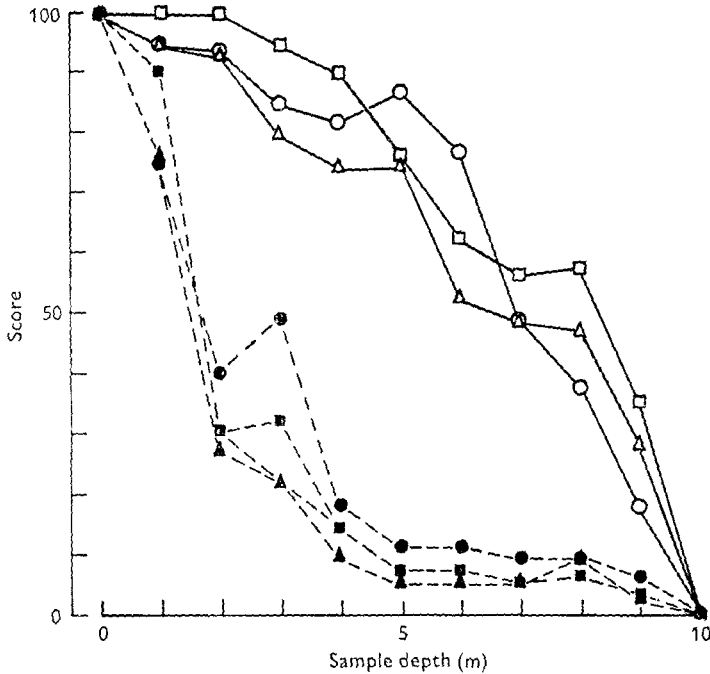


Fig. 1. Normal analysis ordination of samples from Transects 3A (filled symbols) and 4A (open symbols) using quantitative (\square), standardized (Δ) and presence/absence (\circ) data.

The first axis scores of the inverse analysis separated the species into two main groupings for both transects (Table 1). These were easily identifiable as groups of predominantly shallowly or predominantly deeply occurring species. For T. 3A an intermediate group of five species also could be recognized corresponding to an intermediate group of samples (2 and 3 m) in the normal analysis. For T. 4A such a group could not be distinguished, although the score for one species (*Macoma balthica*) alone could be regarded as intermediate, this species occurring also in the intermediate group for T. 3A.

For both transects the use of unstandardized quantitative data yielded better inverse ordinations than those from standardized or presence/absence data. For T. 3A the second and third axis scores were also informative. Fig. 2 shows a plot of species as spatial points in a three-dimensional coordinate frame. The first axis scores may be seen to have separated the points largely into two clusters lying towards either pole of Axis 1. The analysis may therefore be said to have classified the species into two disjoint groups with an intermediate group lying between. The two succeeding axes ordinated each main group in turn. The relevant points are shown projected back onto the plane surfaces composed of Axis 1-2 or Axis 1-3 in Fig. 2 in order to represent these ordinations more clearly. Positions of each intermediate species are shown projected back on both Axis 1-2

and 1-3 planes. It is clear that their relative positions are informative only with regard to the first axis.

The scores of the species for each group have been used to provide a ranking in Table 1. Species with less than two individuals in each transect are omitted because such occurrences carry the least amount of information. Nematode singletons are, however, listed separately in Table 1 as these records are of value in other respects.

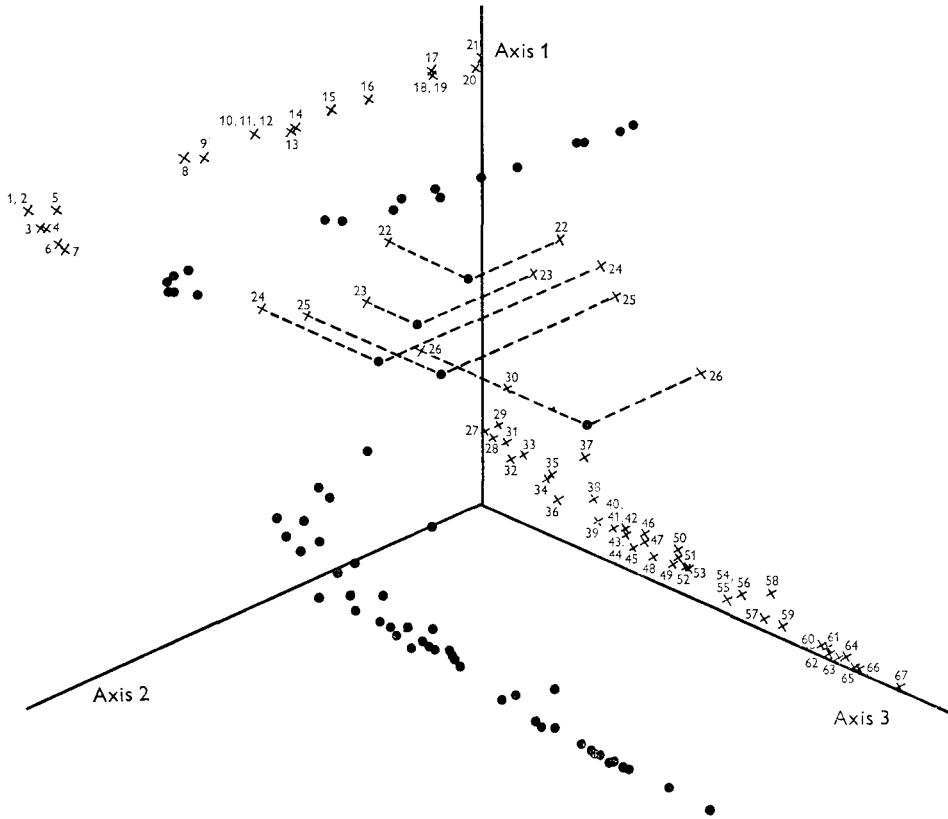


Fig. 2. Plot of Transect 3A species (filled circles) from their first, second and third axis scores in a three-dimensional coordinate frame from an inverse analysis using quantitative data. Back projections of the positions on either the Axis 1-2 or 1-3 planes of those species comprising the two main groupings are shown with numerals by which they may be identified from Table 1.

Singleton species are omitted from the projections onto the Axis 1-2 and 1-3 planes in Fig. 2, although they were utilized in the reciprocal averaging analyses for each transect.

Although the first axis scores for T. 4A were concentrated into two groupings like those for 3A, there was a sufficient range of values to allow an ordination along the depth gradient directly (Table 1) rather than by means of higher axis scores. It was found that reduction of the data by omitting from the analysis species abundances totalling less than either 10 or 50 had little effect on the pattern of normal or inverse scores. Plots of normal scores from such reduced quantitative data along the transect yielded closely similar patterns to those shown in Fig. 1. Plots of inverse scores similarly still showed a

clear separation into two major and an intermediate grouping as shown in Fig. 2 and a ranking showed exact concordance with a ranking of the relevant scores in Table 1. It seems clear that most of the information relating to the structure of the ordination is carried by the most abundant species as was concluded by Austin & Greig-Smith (1968) and Kershaw (1973). Reduction of the data to species abundances totalling > 50 along the transect left only 14% of the original fauna of T. 3A and 29% of T. 4A. It is thus obvious that a considerable saving in effort might have been effected by ignoring the rare species in these analyses.

Overall the ordinations summarized in Fig. 1 and Table 1 suggest that the species occurrences are controlled by a factor or factor complex related to depth with a break occurring along a gradient tending to separate the fauna into two distinct groupings.

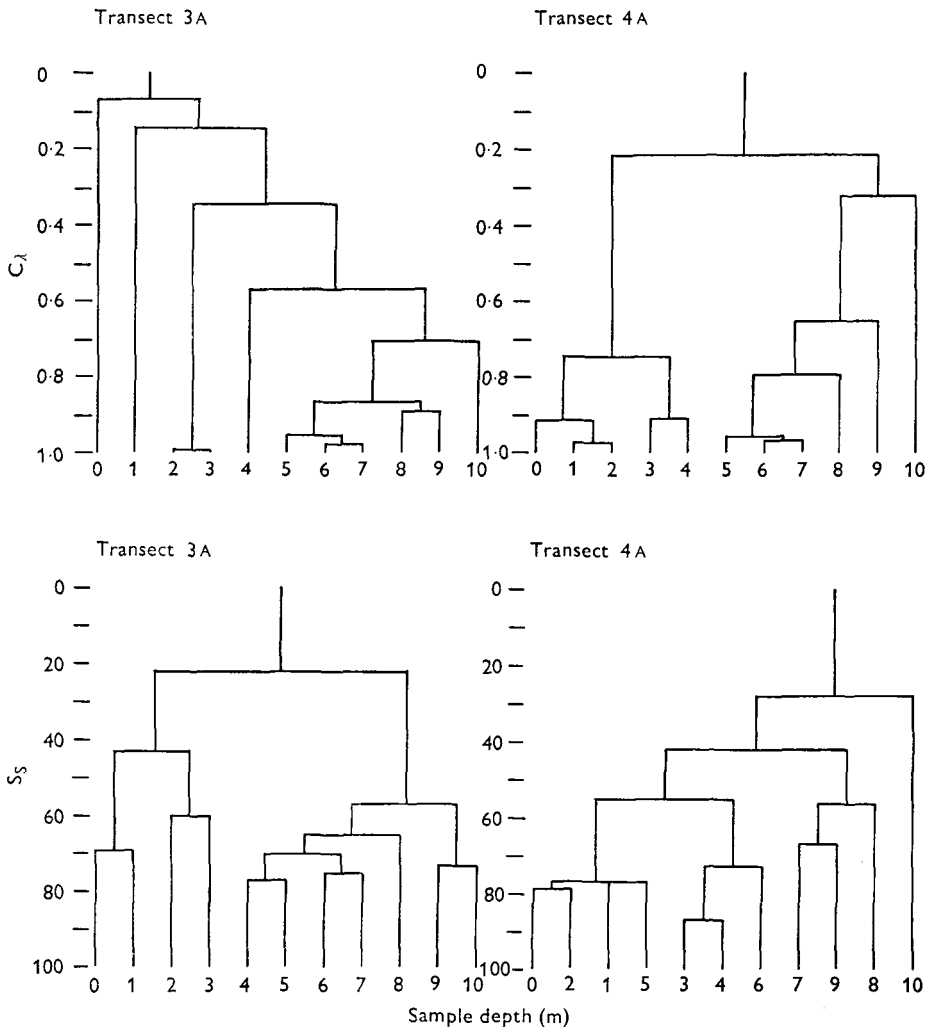


Fig. 3. Dendrogram classifications of transect sample similarity using Morisita's index C (top) and Sørensen's index S_s (bottom).

Hierarchical classification

Dendrogram classifications of the transect samples, with the species abundances taken as sample attributes, are given in Fig. 3. It is clear that concordance between the presence/absence (Sørensen's index) method and that using quantitative data (Morisita's index) is not high. However, the presence/absence dendrograms show a pattern of sample zonation closest to that from reciprocal averaging. An inverse (species as individuals) classification was not attempted because of the rather unsatisfactory results from sample classification, keeping in mind the heavy computational labour necessary with a relatively long species list.

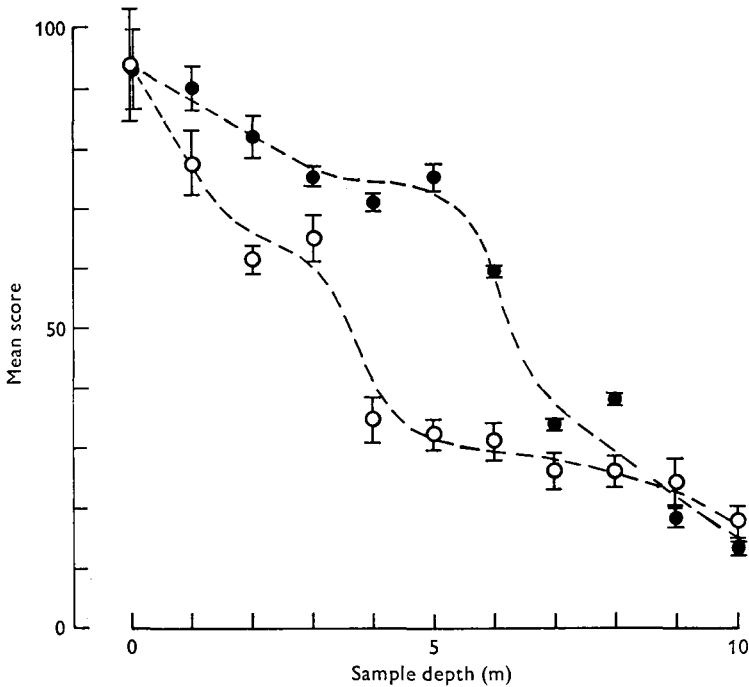


Fig. 4. Ordination of samples extracted from mean scores in an inverse analysis of pooled transect data. Transect 3A, open circles; T. 4A, filled circles. Vertical bars show ± 1 S.E. of the mean. Hand fitted curves represent the faunal gradient.

Reciprocal averaging of pooled transect data

One difficulty in a comparison of the results of reciprocal averaging scores from different analyses, even when from identical sample designs as in the present study, is that the scores from any given axis may not be directly comparable with each other. This is because the axes compared may not reflect the same source of environmental variation. This problem was solved by pooling the data from both transects. A direct comparison of the inverse analysis scores of the species occurring in each transect could then be made.

Fig. 4 shows a plot of the mean of the scores for all species occurring at each depth level, separating those of T. 3A from those of 4A. A distinctive pattern emerged for each

transect, each somewhat resembling the pattern of plots of the normal analysis scores for each transect (Fig. 1). That for T. 3A shows an initial steep gradient from the shallowest depth sampled, then levelling out with a sharp break occurring between 3 and 4 m depth, thereafter with only a moderate slope. Transect 4A shows a basically similar pattern but with the break after a levelling out occurring between 5 and 7 m depth. There was a rather steeper gradient in mean score after the break than for T. 3A. The best result was obtained using quantitative data. Standardized and presence/absence data yielded the same pattern but with narrowed differences between mean score values for each transect.

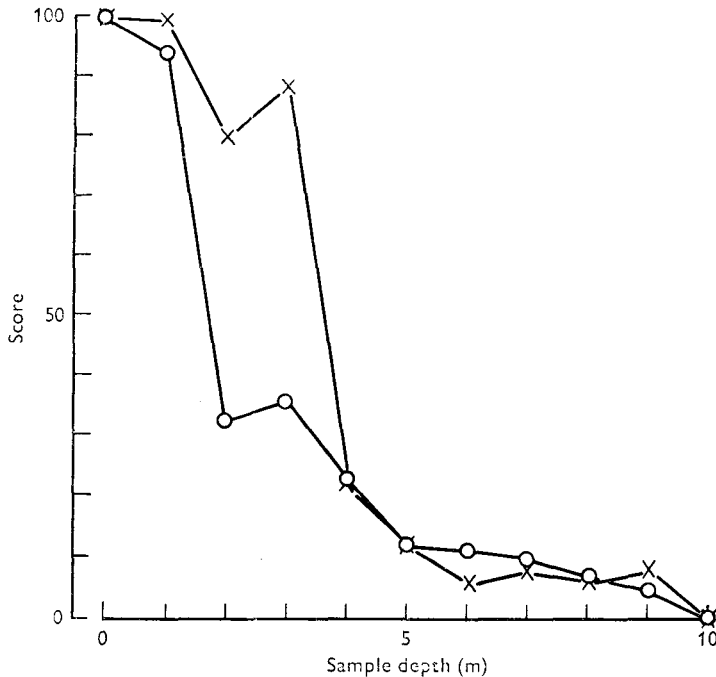


Fig. 5. Ordination of samples from normal analysis using quantitative nematode data only (x) and excluding both nematodes and faunal elements considered mobile from analysis (o).

Reduction of the data to include only the abundant species did not improve the pooled data analyses, with a greater variance occurring between mean scores of adjacent samples tending to obscure the stepped gradient.

The mean score for each depth level provides an intuitively satisfying summary of the zonation. The values relate to position along a faunal gradient while the difference between adjacent scores indicates the local steepness of the gradient.

As salinity was considered previously to be the overriding environmental variable controlling nearshore zonation in Loch Etive, it is of interest to see how the present eigenvector description fits in with what is known of the salinity regime in the Loch. Envelopes of the salinity range from observations at different depths made by the Scottish Marine Biological Association over 5 years are given by Gage (1974). These suggest a strong correlation between the pattern of salinity range and mean score with depth.

Ordination of Nematoda

In order to see whether the zonation pattern of the Nematoda resembled that of the total fauna, a reciprocal averaging analysis was applied to this faunal component alone. The data was insufficient to allow an analysis of T. 4A nematodes. The results from T. 3A showed a marked grouping of both samples and species roughly corresponding to that obtained from the total fauna. The group separation occurred between the 3 and 4 m samples and between the same species that were grouped together in Table 1. The slightly different pattern obtained in a plot (Fig. 5) of the normal analysis scores for the samples compared to those for the total fauna (Fig. 1) may be a consequence of the absence of species with an 'intermediate' distribution, which seem to have the effect of inserting a step in the gradient. The first axis scores in an analysis with quantitative data yielded a ranking of the deeper marine group species almost identical to that given in Table 1. Likewise the third axis scores yielded a ranking of the shallow group very similar to Table 1.

It may be mentioned here that hierarchical classification of the nematode data using both Sørensen's and Morisita's index also yielded dendrograms showing a major dichotomy between the 3 and 4 m samples.

DISCUSSION

Ordination and classification

It may be concluded from the present study that reciprocal averaging ordination effectively described the main pattern of faunal zonation by the primary axis scores. In general, unstandardized quantitative data gave the most satisfactory ordinations. The two groups of species separated by the primary axis scores could be identified as comprising either brackish or marine species and could therefore be interpreted in terms of the salinity conditions prevailing along the transects. Higher axis scores, which ordinated each main group in turn, may or may not be meaningful in terms of environmental gradients. Although with the present data the higher axes scores of an inverse analysis did ordinate one main group against the other, this may possibly depend on a primary axis separation into roughly symmetrical groupings.

It was found that an inverse analysis of the mean of the scores for all the species occurring at a particular depth level seemed to provide at least as reasonable a summary of faunal zonation as that provided by the normal analysis scores. Comparison of data from the two transects, with identical sampling designs, was adequately achieved by pooling the data in this way and then comparing the mean scores of the species originating from each set of data.

The results of classification provided less satisfactory results. The two different indices of faunal similarity yielded differing patterns of hierarchy, although the index utilizing presence/absence data provided a pattern most similar to that from reciprocal averaging, and intuitively the most acceptable summary of zonation.

Faunal zonation

The earlier study (Gage, 1974), on the basis of hierarchical classification of data, postulated a faunal discontinuity between shallow brackish and deeper marine associations of species occurring between 3 and 4 m depth at the site corresponding to T. 3A and between 5 and 10 m depth at the site of T. 4A. The present results of ordination as summarized in Fig. 3 would instead postulate a faunal gradient but with a local break or sharp change in gradient occurring at a depth, for Transect 3A, exactly corresponding to the discontinuity. For T. 4A the observed break occurring between 5 and 6 m depth adds precision to the earlier estimate.

Such an ordination model is more ecologically acceptable than one involving discrete faunal 'communities'. Even if a series of discrete faunal units could exist contiguously on the sea-bed as a response to an intensely vertically structured water mass as in Loch Etive, the effect of diurnal tides and the consequent vertical oscillation of the water mass in contact with the bottom would surely blur any sharp long-term response possible in terms of the spatial distribution of sedentary benthic populations. Because of this, any grouping of the samples or species, as is given in Table 1, must become somewhat arbitrary at its boundaries, and also will tend to conceal any trends or changes within the group. They are retained in the subsequent discussion only because they permit easier discussion of the faunal constituents of the gradient.

The present study tends to confirm conclusions reached by earlier study that the nearshore faunal distribution limits are controlled by the extreme rather than the average value of salinity. The depth of the major constriction in the range of salinity observations for the relevant stations given in Gage (1974) occurs a little deeper than the steepest slope in the reciprocal averaging representation of the faunal gradient. This may simply be because the depth of the observations was not corrected to M.T.L. and includes observations made over a full range of tidal levels. The present results also showed a steeper gradient in the shallowest (0-2 m depth) part of the faunal gradient for T. 3A than for 4A. The explanation may again be because the salinity observations showed a constant and steep decrease in the range from the surface to 3 m depth while for T. 4A the observations showed that, although the maximum salinity range was measured at the surface, the range remains roughly constant until the constriction occurring at about 8 m depth. Consideration of the rankings and groupings of the species themselves in Table 1 would also suggest that the stepped gradient model of faunal zonation may be directly interpreted in terms of their varying euryhalinity. However, because the responses of the species to salinity are for the most part imperfectly known, it is not possible to measure any correlation.

The present results for T. 3A (Table 1) corroborate the existence of the intermediate group of species postulated earlier. This subgroup was comprised of samples with species whose zonation maxima were concentrated at the deeper end of the shallow brackish zone and the upper part of the marine zone. This group was thought to reflect abundance maxima of species less euryhaline than those found in the shallowest samples. The species ordinations of the present study now allow the positive identification of these species (Table 1). For T. 3A these include *Capitellides giardi* and *Macoma balthica* as

expected on the basis of the previous study. The failure of the analysis to include species such as *Peloscolex benedeni* and *Scoloplos armiger* within this grouping may be explained by the sampling design: the previous result seemed to indicate an abundance peak at a slightly deeper level than for *Capitellides* and *Macoma*. Sampling would need to be continued deeper than 10 m in order to separate these species clearly from the deeper grouping. The inclusion of *Eteone longa* and *Marinogammarus* sp. in the intermediate group may reflect an invasion of these mobile species into shallower water than normal, which may have been permitted by the salinity conditions at the time. The inclusion of *Hydrobia* reflected a rather puzzling bimodal distribution with individuals found down to 2 m depth, as would be expected from the previous results, and then reappearing in samples from 5 to 9 m depth. The bottom sloped very steeply into deep water below 2 m depth (see Fig. 6 in Gage, 1974) and these animals may have been rolled or swept down the slope from the narrow shallow water platform by waves and currents.

The species typically comprising the two main groups in the present investigation (Table 1) were the same as delineated before (Gage, 1974), the inverse ordinations now allowing them to be positively associated with a particular grouping.

The species concentrated towards either pole of Axis 1 for T. 4A were also typical members of the brackish and marine assemblages. Ordinated between these two clusters were species which had appeared in the intermediate group for T. 3A, with others whose abundances in the samples were too low to allow conclusions to be drawn.

Nematoda

The shallow assemblage contains a high proportion of species which are recorded either from the Baltic (records in Gerlach & Riemann, 1973, 1974) or from the lower salinity regions of British estuaries (Capstick, 1959 [Blyth estuary]; Warwick, 1971 [Exe estuary]). Species common to the Baltic and British estuaries include *Enoplus brevis*, *Paracanthonus caecus*, *Sphaerolaimus balticus*, *Mesotheristus setosus*, *Anoplostoma viviparum*, *Adoncholaimus thalassophygas*, *Trefusia longicaudata*, *Viscosia viscosa*, *Hypodontolaimus balticus* and *Adoncholaimus fuscus*. Two species, *Adoncholaimus lepidus* and *Gammanema rapax*, are recorded from the Baltic but not from the British estuaries. Estuarine species not found in the Baltic include *Oncholaimus brachycercus*, *Enoploides spiculohamatus*, *Halichoanolaimus robustus*, *Axonolaimus paraspinosus* and *Calyptronema (Catalaimus) maxweberi*. The deep assemblage contains few species which are common in brackish water, except for *Enchelidium marinum* which has been recorded from the Baltic, and *Spirinia (Spirinia) parasitifera* and *Monoposthia costata* which are found in the Blyth estuary. It would thus seem that, as for the macrofauna, salinity is the major factor involved in the zonation of nematode species in Loch Etive.

This view is substantiated by a more detailed comparison of the zonation of nematode species along T. 3A in Loch Etive with the zonation in the Exe estuary described by Warwick (1971). Fortunately, several species are common to both areas. *Ocholaimus brachycercus*, which has an abundance maximum at 0 m in the Etive samples, has similar abundance maxima at MHWST in the middle (Lymptone) and lower (Shelly Bank) reaches of the Exe. This tide level in the Exe is subject to low fluctuating salinities. *Enoploides spiculohamatus*, most numerous at the 0 and 1 m levels in Etive, is confined

to MHWNT in the middle reaches of the Exe and is absent from the lower reaches. *Axonolaimus paraspinosus* has an abundance peak at 1 m in Etive. It is present at all tide levels in the middle reaches of the Exe, with a maximum at M.T.L., but is not found at all in the lower reaches. *Mesotheristus setosus*, confined to the 0 m samples from Etive, is common to all tide levels in the upper reaches (Topsham) of the Exe and is most abundant on the upper and lower shore in the middle reaches. The upper and lower shore are subjected to lower and more fluctuating salinities than the middle shore in this region. This species is again absent from the lower reaches of the estuary where salinities are higher. *Anoplostoma viviparum*, confined to the 0 and 1 m samples from Etive, is the dominant species in the upper reaches of the Exe and is found in smaller numbers in the middle reaches. It is again absent from the higher salinity zones. *Calyptronema (Catalaimus) maxwerbi* has a similar distribution to *Anoplostoma viviparum* in Etive. In the Exe it is found in the middle reaches and the upper shore of the lower reaches. *Adoncholaimus thalassophygas* is restricted to the 0 m level in Etive and the upper reaches of the Exe. *Trefusia longicaudata* is confined 0 m in Etive and the upper shore in the lower reaches of the Exe. *Viscosia viscosa* is again restricted to 0 m in Etive and is only found in the middle reaches of the Exe. Finally *Hypodontolaimus balticus*, found at 1 m in Etive, is confined to the middle reaches of the Exe. These similarities in distribution confirm beyond reasonable doubt the existence of a coherent brackish element in the nematode fauna of Loch Etive.

The marine assemblage is less clearly defined when compared with that of the Exe. The two dominant species from the lower assemblage, *Enchelidium marinum* and *Rhabdodemania minor* are not found in the Exe and are probably more typical of the sublittoral. Furthermore, several of the Etive taxa were not identifiable to specific level because of the absence of males. The only species common to the two areas is *Mono-posthia costata*, which is found only below 6 m in Etive and is confined to the higher salinity shore levels of the lower reaches of the Exe.

Comparison of T. 4A with the Exe zonation is more difficult in that nematodes are less abundant and the discontinuity is only just included at the bottom end of the transect. However, the brackish assemblage is very similar in species composition to that of Transect 3A. One additional species, *Adoncholaimus fuscus* was found. This species is recorded from both the Baltic and the Blyth and Exe estuaries. In the Exe it is confined to the middle reaches and the upper shore in the lower reaches. *Pontonema vulgare* appears at the bottom end of the transect: this large nematode is typical of open coasts around Britain and has not been recorded in either of the estuaries studied.

The nematode nomenclature used in this paper follows that of Gerlach & Riemann (1973, 1974).

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