Continuous plankton records: zooplankton and environment, North-East Atlantic and North Sea, 1948-1975

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ABSTRACT

Principal components analyses are used to describe the major year-to-year changes in the abundance of the zooplankton of the North-East Atlantic and the North Sea for the period 1948 to 1975. There is a marked degree of coherence both between species and between different parts of the area. The changes show persistence from year-to-year in the form of long term trends. The main pattern of differentiation between the species is related to their geographical distributions.

Interpretations of the year-to-year changes are presented, based on empirical associations with climatic factors, which suggest that changes in the North Atlantic current, and more localised wind-driven advection play a major role in determining the year-to-year changes. It would appear the variations in abundance are influenced primarily by density-independent factors.

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Prélèvements en continu de plancton :
zooplancton et environnement,
Atlantique Nord-Est et Mer du Nord
1948-1975

RÉSUMÉ

La méthode en composantes principales est utilisée pour décrire des variations annuelles du zooplancton dans l'Atlantique Nord-Est et la Mer du Nord pendant la période 1948-1975.

Il existe un fort degré de cohérence à la fois entre les espèces et les différentes parties de la zone. Les variations montrent une certaine persistance d'année en année sous la forme de tendances à long terme. La caractéristique principale de discrimination entre les espèces est liée à leurs répartitions géographiques.

Des interprétations des variations annuelles sont présentées. Elles sont fondées sur des associations empiriques avec des facteurs climatiques, ce qui suggère que des changements dans le courant Nord Atlantique et des phénomènes d'advection à échelle locale sous l'effet du vent jouent un rôle important en provoquant des variations annuelles. Il semblerait que les variations d'abondance soient influencées principalement par des facteurs indépendants de la densité.

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INTRODUCTION

Colebrook (in press), in a discussion of long term fluctuations in the abundance of zooplankton for the North Atlantic region, stated that "the commonality in the form of annual fluctuations in abundance over such a wide area including oceanic, Atlantic shelf and North Sea areas and the existence of trends and periodicities in the fluctuations almost inevitably implies that the year-to-year changes in the abundance of the zooplankton are determined to a large extent by physical environmental changes on a scale comparable with general climatic changes".

This has been confirmed by subsequent work. Garrod and Colebrook (in press) presented, in summary form, the current status of interpretative studies with respect to the determination of inter-annual changes in the fish stocks and the plankton of the North Atlantic ocean over the last three decades. The main conclusions, albeit based on empirical relationships were that an appreciable proportion of the fluctuations could be attributed to changes in the strength and/or direction of the North Atlantic Current and to wind-driven advection associated with large scale, medium term, variations in the distribution of atmospheric pressure.

This raises the question of the extent to which between-year variations in the abundance of zooplankton are determined by density-independent processes, as opposed to presumably density-dependent interactions between species. The object of this paper is to present, in greater detail than was possible within the scope of either of the above papers:

1) the evidence for coherence in annual changes in abundance both geographically and between the more abundant species of the zooplankton;

2) the form and extent of relationships with marine and atmospheric climatic variables;

3) a search for indications of the relative roles of density-independent and density-dependent processes in determining year-to-year changes in abundance.

DATA

A routine, monthly, synoptic survey of the plankton of the North Sea and the North-East Atlantic has been carried out from 1948 to 1975 using Continuous Plankton Recorders towed by merchant ships and Ocean Weather Ships on regular routes (Glover, 1967). Methods of counting and data processing are described by Rae (1952), Colebrook (1960) and Colebrook (1975 a).

As far as possible, the zooplankton are identified to species but, in some taxonomic groups, identification is confined to genus, family or even higher categories.

Figure 1 is a chart of the subdivisions of the survey area for which virtually complete date are available from 1948 and in Table 1 are listed the taxa together with an indication of the areas in which each occurred in sufficient abundance for the estimation of annual means. This list includes all the zooplankton taxa which occur in sufficient abundance to provide satisfactory estimates of year-to-year changes in at least four of the areas, see Colebrook (1975 b). The species Calanus f. finmarchicus and Calanus helgolandicus were not separated in the analysis of the samples prior to 1958 and, therefore, an estimate of total Calanus stages V-VI, which is available for the whole period, is also included.

For each X in Table 1 there is a data set consisting of the logarithmic means of abundance for each year from 1948 (or as indicated in the Table) to 1975. There are 194 such sets and clearly it is not possible to present all these data

Figure 1

A chart showing the standard sub-areas of the North-East Atlantic and the North Sea for which virtually complete data are available from the Continuous Plankton Recorder Survey for the years 1948 to 1975.
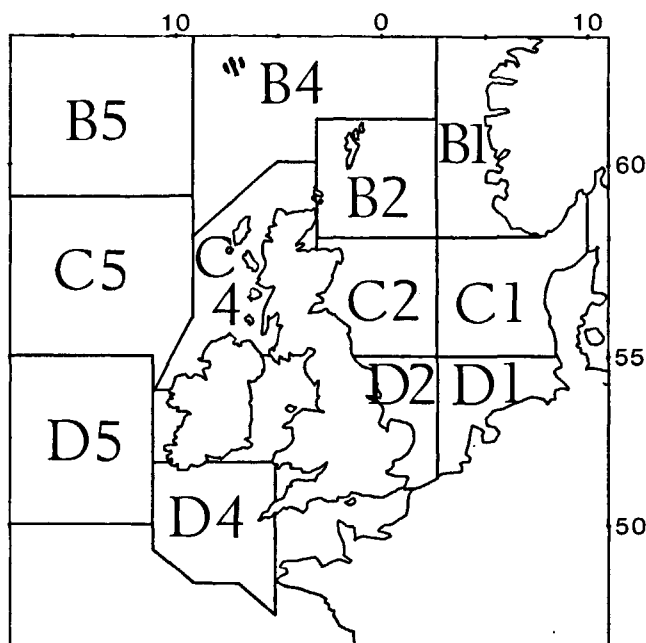
here. Details of the current position with regard to the availability of these and other routine data formats are published in an annual inventory, a limited number of copies of which are available, on request, from the Director, Institute for Marine Environmental Research, Prospect Place, The Hoe, Plymouth.

Principal components analyses were used to extract from these data the main patterns of year-to-year changes in abundance. The data input to each analysis consisted of a set of variables representing annual fluctuations in abundance as continuous time-series from 1948 to 1975 (with the exceptions noted in Table 1). Analyses were carried out on arrays consisting of the data sets for: 1) all the areas for each species and 2) all the species for each area. The compositions of the data sets can be obtained by extracting each row and each column from Table 1. The analyses were all based on correlation, as opposed to covariance, matrices involving the standardisation of each variable to zero mean and unit variance. The purpose of this is to eliminate differences in abundance between species and between areas, leaving only the relative year-to-year changes in abundance.

The output of the principal component analyses consists, in each case, of a sequence of eigenvectors and an associated set of components. The first principal component can be regarded as the best possible single representation of the annual fluctuations in abundance for all the entities included in the analysis. The subsequent components are orthogonal (uncorrelated) representations with progressively decreasing variances. The eigenvectors produced by each analysis are sequences of variables in order of decreasing importance. For the area analyses each vector consists of values corresponding to each species and for the species analyses each vector consists of values corresponding to each area. The vector values are weights by which the standardised annual fluctuations are multiplied and the resulting weighed variables are summed to give the components. In any vector, similar values indicate similarities between the corresponding species or areas with respect to the

associated component. The first few vectors for each analysis can be used, therefore, to study the relationships between species or areas with respect to their annual fluctuations in abundance.

The results of principal components analyses indicate the degree and nature of relationships between the input variables and, to the extent that they involve logical patterns relating to all or nearly all the variables, they may be said to be *coherent*. In many cases it is apparent that there is a measure of similarity between the input variables indicating *commonality*. In neither case is it at all easy to provide precise measurements but the terms are convenient to use, in a relative sense, in comparing the results from a number of analyses.

THE ZOOPLANKTON

Pseudocalanus and Hyperiidea

Figures 2 and 3 contain illustrations of the data and the products of principal components analyses for two taxa, *Pseudocalanus* and Hyperiidea. The data (*a* in both figures) are plotted in standardised form with zero means and unit variances for each area. These two taxa were selected as being representative with respect to both the relationships between data and components and the degree of coherence within the data. They are described in some detail to illustrate how components, eigenvectors and data are related *within* each analysis to provide a background to the subsequent examinations, which are concerned primarily with relationships *between* the results of the analyses.

For *Pseudocalanus*, the first principal component (Fig. 2 *d*) represents a form of variation common to all the areas (all the first vector values are positive) which can be seen clearly in the data, whereas the second component represents a pattern of variation with some geographical differentiation. The high positive values for the second vector include most of the oceanic and

Table 1

A listing of the taxa including: a) a standard abbreviation of the names used in several of the figures; b) the first year for which data are available, and c) lists of the areas for which the data are adequate to permit the calculation of annual means of abundance. A key to the areas is given in Figure 1.

|			*c*											
	a	*b*	B5	B4	B2	B1	C5	C4	C2	C1	D5	D4	D2	D1
Acartia clausi	AC	'48	X	X	X	X	X	X	X	X	X	X	X	X
Calanus f. finmarchicus	CF	'58	X	X	X	X	X	X	X	X	X	X	X	X
Calanus helgolandicus	CH	'58		X	X	X	X	X	X	X	X	X	X	X
Calanus spp. Stages V-VI	CL	'48	X	X	X	X	X	X	X	X	X	X	X	X
Candacia armata	CA	'48			X		X	X	X	X	X	X		
Centropages typicus	CT	'48	X	X	X	X	X	X	X	X	X	X	X	X
Euchaeta norvegica	EN	'54	X	X		X	X			X			.	
Metridia lucens	ML	'48	X	X	X	X		X	X	X	X	X	X	X
Pleuromamma robusta	PR	'48	X	X			X			X				
Pseudocalanus elongatus	PS	'48	X	X	X	X	X	X	X	X	X	X	X	X
Temora longicornis	TL	'48	X	X	X	X		X	X	X		X	X	X
Total copepods	TC	'48	X	X	X	X	X	X	X	X	X	X	X	X
Podon spp.	PD	'58	X	X	X	X	X	X	X	X	X	X	X	X
Evadne spp.	EV	'58	X	X	X	X	X	X	X	X	X	X	X	X
Hyperiidea	HY	'48	X	X	X	X	X	X	X	X	X	X	X	X
Euphausiacea	EP	'48	X	X	X	X	X	X	X	X	X	X	X	X
Spiratella retroversa	SP	'48	X	X	X	X	X	X	X	X	X	X	X	X
Chaetognatha	CG	'48	X	X	X	X	X	X	X	X	X	X	X	X
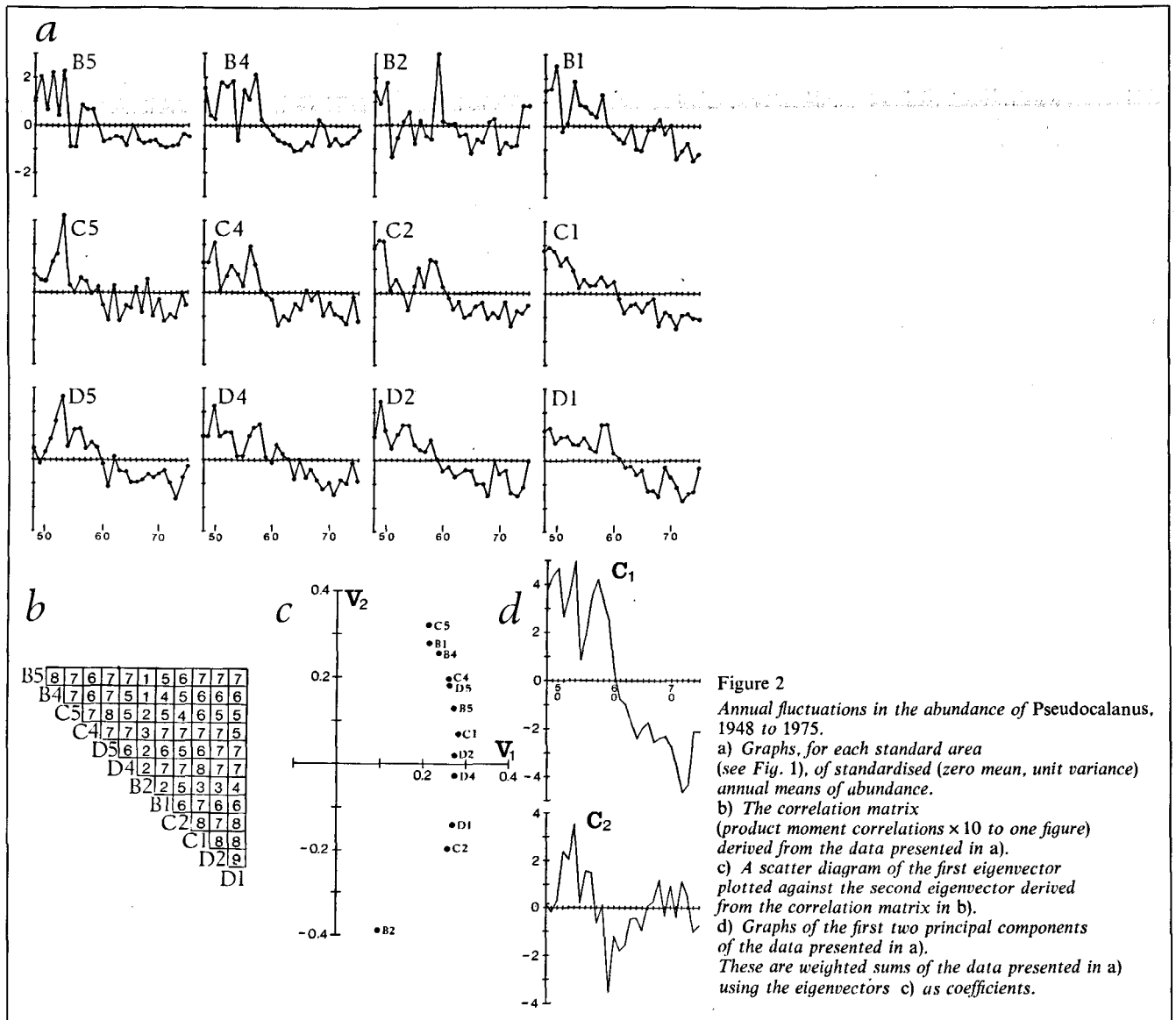
Figure 2

Annual fluctuations in the abundance of Pseudocalanus,
1948 to 1975.
a) *Graphs, for each standard area*
(see Fig. 1), of standardised (zero mean, unit variance)
annual means of abundance.
b) *The correlation matrix*
(product moment correlations × 10 to one figure)
derived from the data presented in a).
c) *A scatter diagram of the first eigenvector*
plotted against the second eigenvector derived
from the correlation matrix in b).
d) *Graphs of the first two principal components*
of the data presented in a).
These are weighted sums of the data presented in a)
using the eigenvectors c) as coefficients.

Atlantic shelf areas while the North Sea areas and the Celtic Sea show low positive or low negative values, only B2 shows a high negative value. The second component can be recognised, as a residual from the first, in the data for areas B5, B4, C5, C4 and D5. The extent to which this pattern is genuinely represented in its negative form is uncertain. The distribution of areas in the vector plot (Fig. 2 c) does not provide very convincing evidence and the only features clearly visible in the data are high values for 1969 in areas B2 and C2 corresponding with the lowest value in the second component. The correlation array primarily reflects the general similarity between the areas.

While the coherence is not so marked as for *Pseudocalanus*, the first component for Hyperiidea (Fig. 3 d) also represents a pattern of variation common to a considerable area, only the vector term for area D4 being negative. The pattern is clearly visible in the data for several areas and it is obviously different from the first component for *Pseudocalanus*. The second component (Fig. 3 d) represents a clearer differentiation between oceanic and North Sea areas than that for *Pseudocalanus* and in its positive form it is visible in the data for areas C2, C1 and B2. The magnitude of the negative terms of

the second vector (Fig. 3 c) and the fact that they refer to geographically contiguous areas suggests that there is a real inverse relationship between oceanic and North Sea areas with respect to this component.

There is a significant correlation (at the 0.1% level) between the first component for Hyperiidea and the second component for *Pseudocalanus*. This provides further confirmation for the reality of the *Pseudocalanus* component. The implications will be considered later in an examination of the associations between all the species. Compared with that for *Pseudocalanus*, the correlation array (Fig. 3 b) for Hyperiidea reflects the generally lower level of coherence and the more marked geographical differentiation in the data.

The sets of principal component analyses

In comparing the results obtained from a set of comparable principal components analyses an element of selection is involved. Firstly, the signs of components are indeterminate: each has a mean of zero and it may be plotted as it appears in the output from the analysis or it may be inverted. In the analyses considered here the assignation of signs to the first components seldom poses much of a problem. Reference to the relevant vectors or
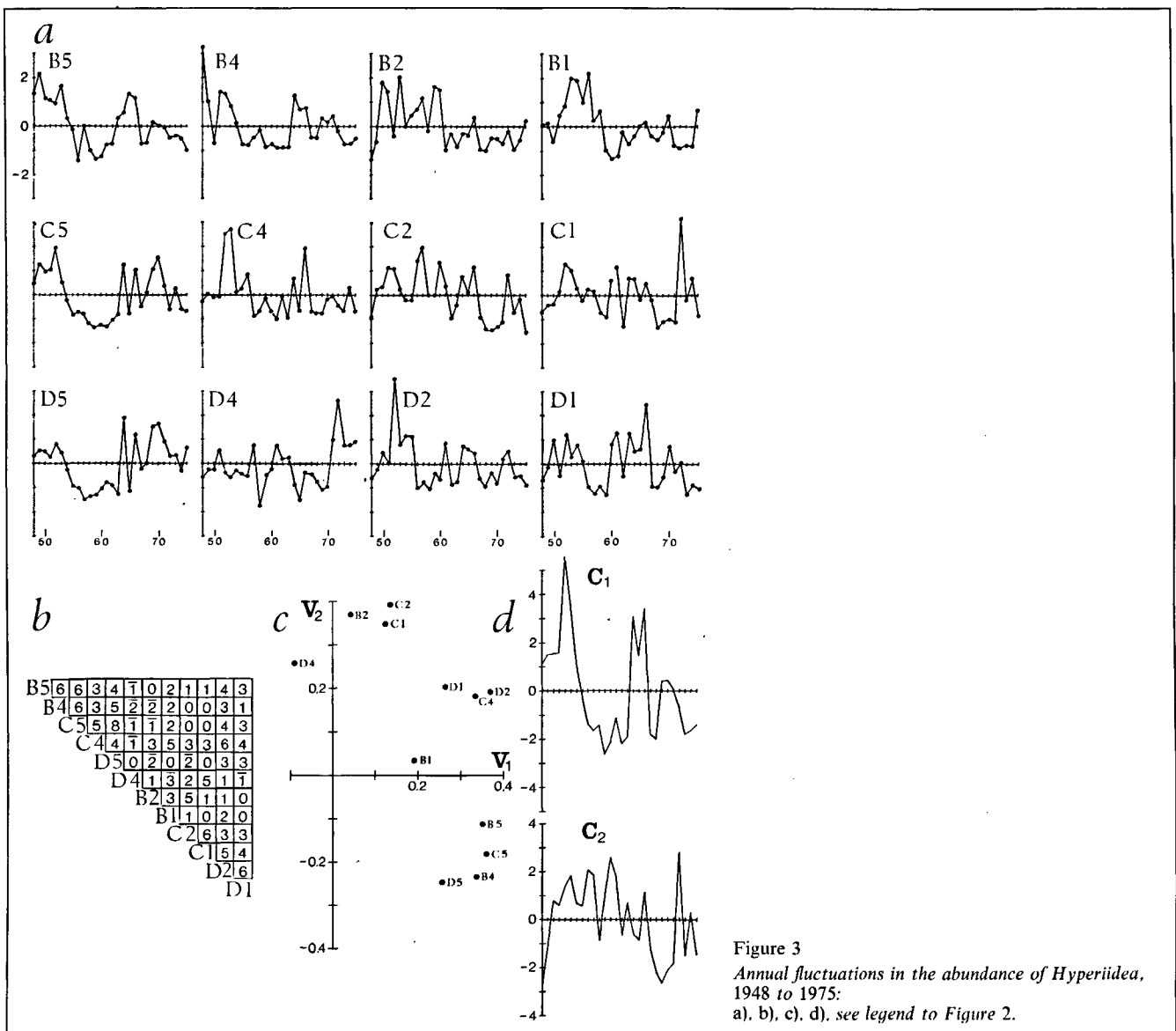
Figure 3

Annual fluctuations in the abundance of Hyperiidea, 1948 to 1975:
a), b), c), d), *see legend to Figure 2.*

to the original data generally makes it obvious which way up the component should be plotted to give the better representation of the variability in the data. The results illustrated in Figures 2 and 3 are typical. The second components can present more of a problem, again the results illustrated in Figures 2 and 3 provide typical examples. In the case of *Pseudocalanus*, the sign was chosen to give the majority of vector terms positive. The form of the component given in Figure 2 can be recognised in some of the data and it has a positive correlation with the first component of Hyperiidea, the sign of which is not in doubt. For the second component of Hyperiidea there is a clear suggestion from the vector of a real negative relationship between areas in which case the sign of the component is arbitrary. However, as will be shown below the component as given in Figure 3 has a positive correlation with the first components of both *Acartia* and *Metridia* and, therefore, this is probably the form to be preferred.

Secondly, it must be stressed that the rank of a component, whether it is the first or second, etc. is determined only by its variance. It is quite possible, therefore, for common elements of variability in two data sets to be represented by components of different rank. If the first components of two different data sets are similar, the implication is not only that there is an element of variability common to both sets but also that it is the largest element of variability within each set that can be represented by a single component, which adds to the quality of the relationship.

In practice, the main patterns of relationship are found between components of equal rank, with very few exceptions. This adds considerably to the evidence for the reality of such patterns but leads to possible confusion in nomenclature and, for the sake of simplicity, such patterns will be referred to the rank of the majority of the components involved. Exceptions will be indicated in the text.

Area components

These are the components derived from analyses of data sets for all the taxa in each area (the columns of Table 1). Figure 4 contains plots of components for the areas, arranged in two sets. The search for coherent sets was restricted to the first two components in each case and B4 is the only area for which a switch of components is involved. Superimposed on each plot is a smoothed form of the component derived, in each case, from the first eigenvector filter for a maximum lag of 4 years (see
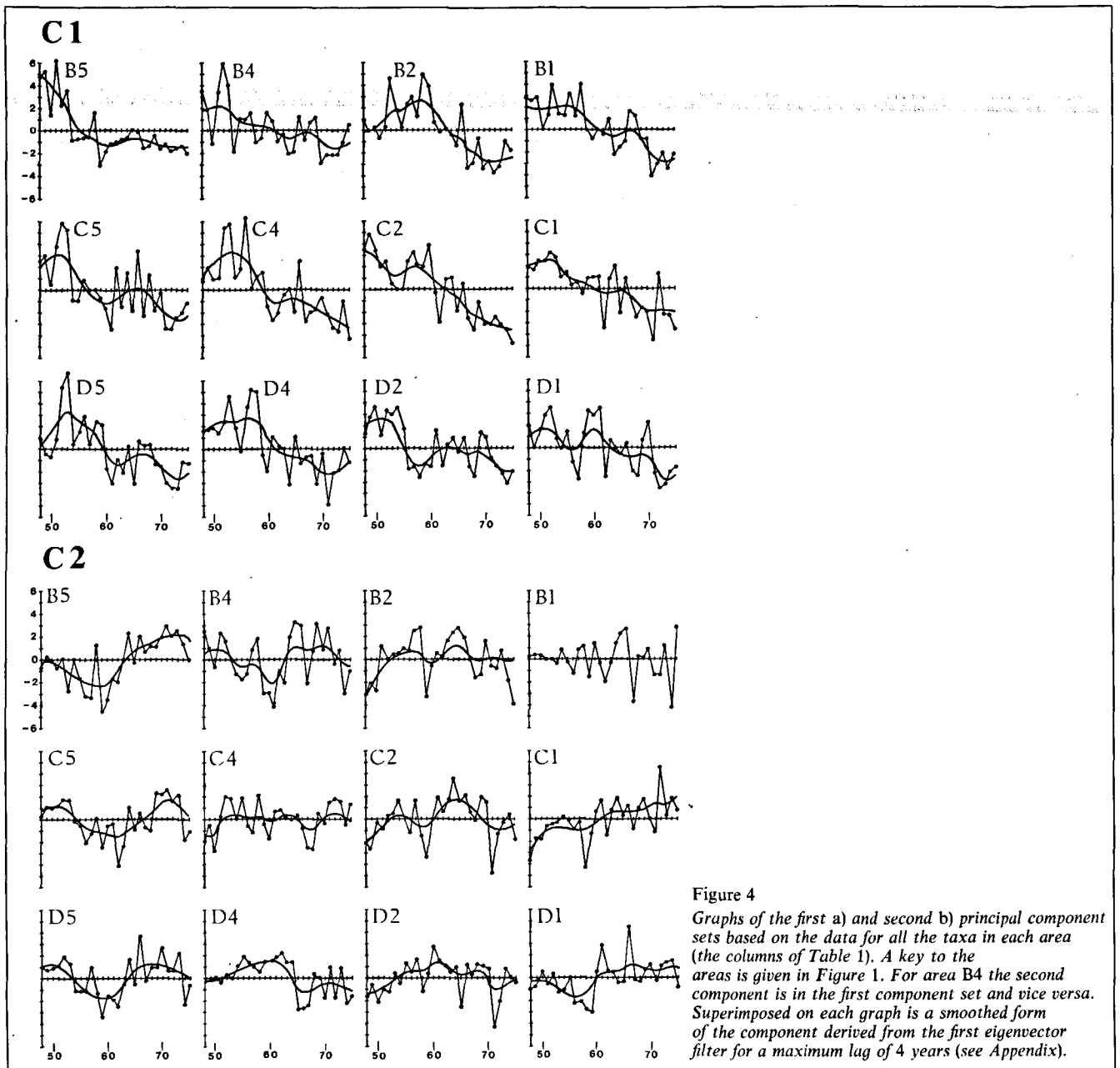
Figure 4

Graphs of the first a) and second b) principal component sets based on the data for all the taxa in each area (the columns of Table 1). A key to the areas is given in Figure 1. For area B4 the second component is in the first component set and vice versa. Superimposed on each graph is a smoothed form of the component derived from the first eigenvector filter for a maximum lag of 4 years (see Appendix).

Appendix). For area B1, in the second component set a linear filter appeared as the fourth eigenvector, accounting for only 11% of variability; it has therefore been omitted in Figure 4. In addition to the filter analysis, power spectra and the coefficients of up to fifth order orthogonal polynomials were calculated for each component. These confirmed that, with the sole exception of the second component for area B1, low frequencies accounted for a considerable proportion of the variance of the components. For the first component set an average of 50% of variability was associated with the first three polynomial orders and 51% with the zero and first two harmonics. For the second component set an average of 50% of variability was associated with the first five polynomial orders and 46% with the zero and first three harmonics. For both sets, the form of the eigenvector filters and the proportion of variability accounted for by the smoothed variables suggest that they provide satisfactory representions of the low frequency elements in the components.

The first component set is clearly highly coherent with a large element of variability common to all areas. Figure 5 a is a scatter plot of the first two vectors (weighted by their respective roots to indicate relative variance) of the correlation matrix for the set. This confirms the coherence: there is a tendency for North Sea areas to be positive and oceanic and shelf areas to be negative in the second vector but there are exceptions both ways and the differentiation is small compared with the commonality. This is quite remarkable when it is considered that the taxa whose annual fluctuations in abundance are represented in the components vary from moderately neritic (Temora longicornis) to exclusively oceanic (Pleuromamma robusta) and the areas cover a wide geographical range from open ocean (with summer maximum temperatures of about 16°C in the South to about 12°C in the North) to shelf waters, to the shallow neritic waters of the southern North Sea. The high proportion of variability associated with the smoothed variables argues at least for considerable persistence from year-to-year and the similarities between them suggest real long term trends in the fluctuations in abundance.
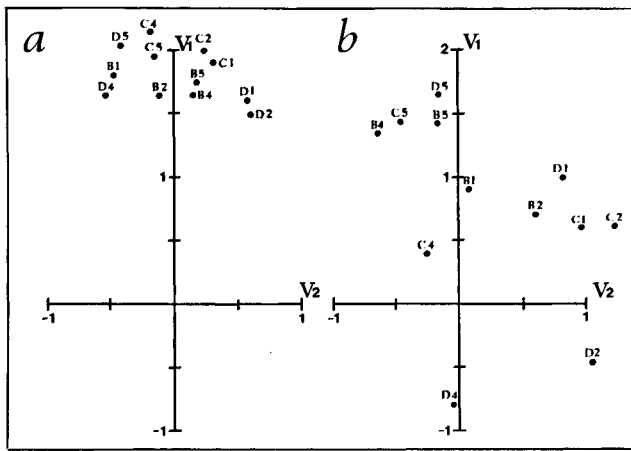
Figure 5

Scatter diagrams of the first and second eigenvectors weighted by their respective roots for: a) *the first area component set (Fig. 4 a) and* b) *the second area component set (Fig. 4 b).*

The plot of vectors for the second component set (Fig. 5 b) shows a much wider scatter of the points than for the first components. Geographically contiguous areas appear as near neighbours and a differentiation between oceanic and North Sea areas is indicated, which is visibly reflected in the plots in Figure 4. Again there are indications of long term trends, less pronounced and more variable than for the first components but, nevertheless. clearly visible in the data and supported by the power-spectra and the eigenvector filter analyses.

Area vectors

Figure 6 shows a scatter plot for the first vector against the second vector for each area. In these plots, data for total copepods have been omitted and *Calanus* is represented by the species *Calanus f. finmarchicus* and *Calanus helgolandicus.* For the first vectors (Y-axes), out of the total of 170 entries only 23 (13.5 %) are negative and only 7 (4 %) are less than −0.1. Of the 23 negative values 17 are accounted for by just four taxa, *Temora longicornis* (4), *Acartia clausi* (5), *Evadne* (3) and *Podon* (5). This indicates that the first components (Fig. 4 a)

represent a pattern of annual fluctuation in abundance common to a considerable majority of the taxa/area data sets. In addition, the scatter plots show a fair measure of similarity in the juxtaposition of the taxa in each area, although the orientation with respect to the coordinates varies somewhat. In most of the areas the taxa can be regarded as falling on a sequence from negative values on v_2 to positive on v_1 to positive on v_2. An approximate mean rank of the taxa can be derived by listing them in this sequence for each area and averaging their ranks. The resulting list is presented in Table 2, and it implies that while all the taxa share in the common element of annual fluctuations in abundance, those close together in the list show a greater similarity than those further apart.

Table 2

The rank of the taxa derived from the vector plots given in Figure 6, see text.

1. *Podon* spp.
2. *Evadne* spp.
3. *Acartia clausi*
4. *Temora longicornis*
5. *Pseudocalanus elongatus*
6. *Centropages typicus*
7. *Calanus helgolandicus*
8. Chaetognatha
9. *Spiratella retroversa*
10. *Candacia armata*
11. *Metridia lucens*
12. *Pleuromamma robusta*
13. Euphausiacea
14. Hyperiidea
15. *Calanus f. finmarchicus*
16. *Euchaeta norvegica*

This rank could be quite fortuitous; it seems more likely, however, to reflect some aspect of the standing of the taxa in the ecosystem and there are a number of obvious features of variability with which this rank can be compared. These are, the relative abundance of the taxa, the timing of their seasonal cycles, and their geographical distributions. Abundant and less common taxa occur throughout the list with no obvious associations.
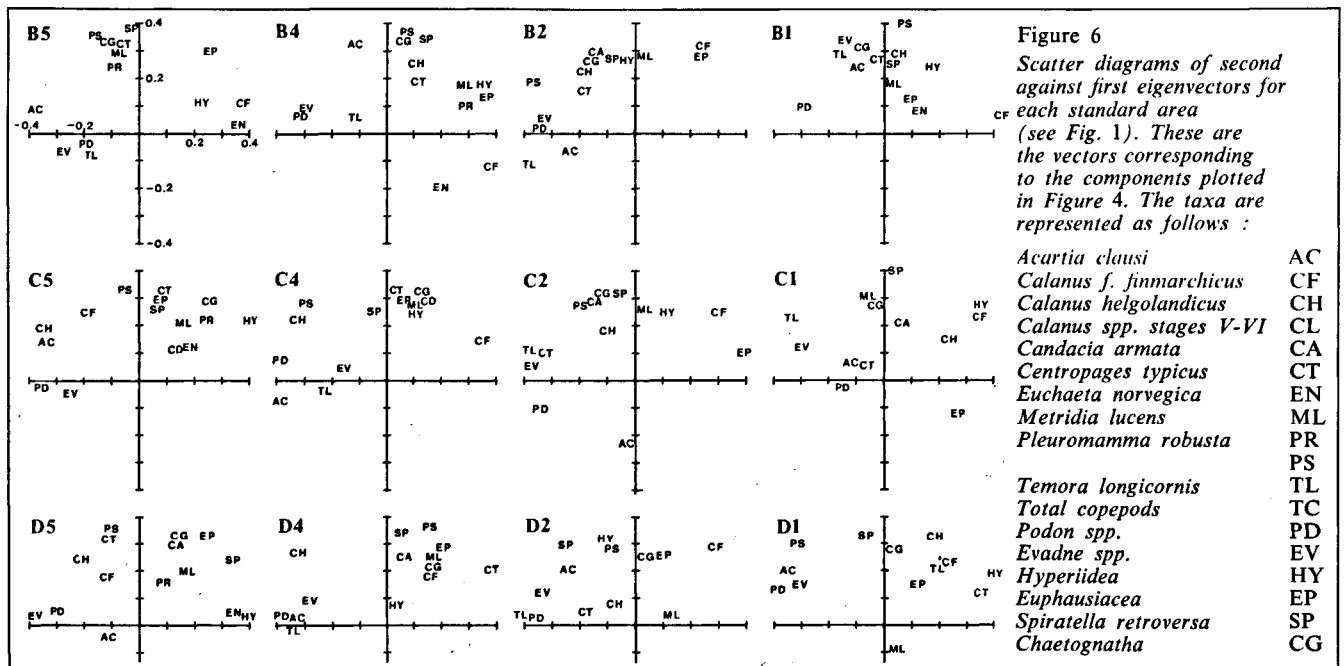

Figure 6

Scatter diagrams of second against first eigenvectors for each standard area (see Fig. 1). These are the vectors corresponding to the components plotted in Figure 4. The taxa are represented as follows :

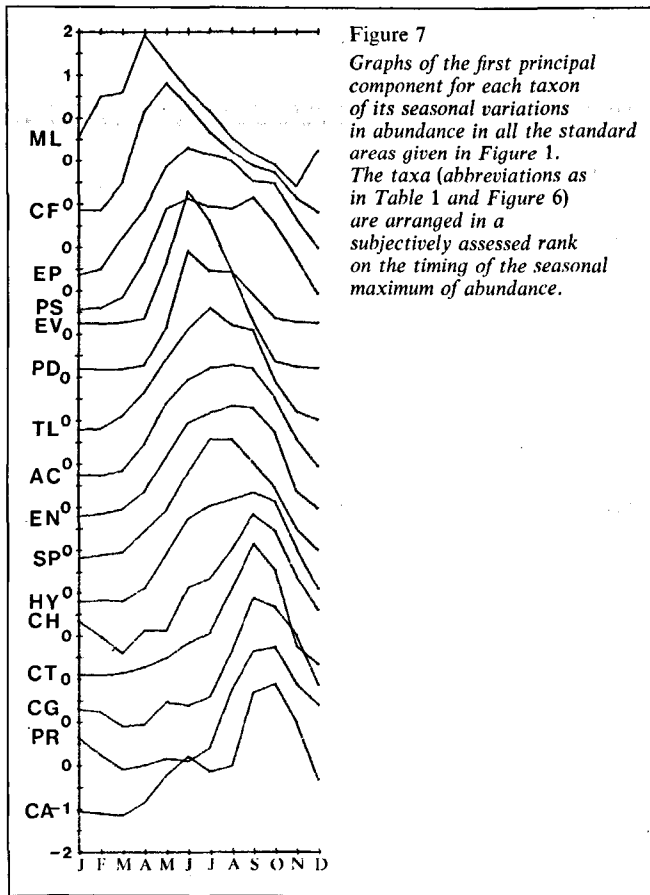|	
Acartia clausi	AC
Calanus f. finmarchicus	CF
Calanus helgolandicus	CH
Calanus spp. stages V-VI	CL
Candacia armata	CA
Centropages typicus	CT
Euchaeta norvegica	EN
Metridia lucens	ML
Pleuromamma robusta	PR
	PS
Temora longicornis	TL
Total copepods	TC
Podon spp.	PD
Evadne spp.	EV
Hyperiidea	HY
Euphausiacea	EP
Spiratella retroversa	SP
Chaetognatha	CG

Figure 7

Graphs of the first principal
component for each taxon
of its seasonal variations
in abundance in all the standard
areas given in Figure 1.
The taxa (abbreviations as
in Table 1 and Figure 6)
are arranged in a
subjectively assessed rank
on the timing of the seasonal
maximum of abundance.

Figure 7 contains plots, for each species, of the first principal component of the seasonal variations in abundance in a subjectively assessed rank of the timing of the seasonal maximum. Again there is no relationship with the rank in Table 2.

Colebrook (1972 a) presented the results of an analysis of the geographical distributions of 51 planktonic taxa which did not, however, include all those listed in Table 2. This analysis has, therefore, been repeated incorporating only data for zooplankton but including all the required taxa and based on a combination of the data for the years 1969 to 1975. Compared with the earlier analysis, a considerably larger area of the open ocean South of 49°N is included due to improved sampling. Principal components analysis was used to extract from the data the main patterns of geographical distribution and the associated relationships between the taxa. A scatter plot of the values of the first and second vectors for the taxa listed in Table 2 is given in Figure 8 a and for each taxon is given its rank derived from this table. There is a clear association between the ranks and the position of the taxa in the diagram. This means that when comparing the annual fluctuations in abundance of taxa within a limited area there is a greater similarity between the fluctuations of those taxa which show similar geographical distributions.

Figure 8 b and c are charts of the first two principal components of geographical distribution (based on data for 43 taxa of zooplankton, an extract of the vectors of
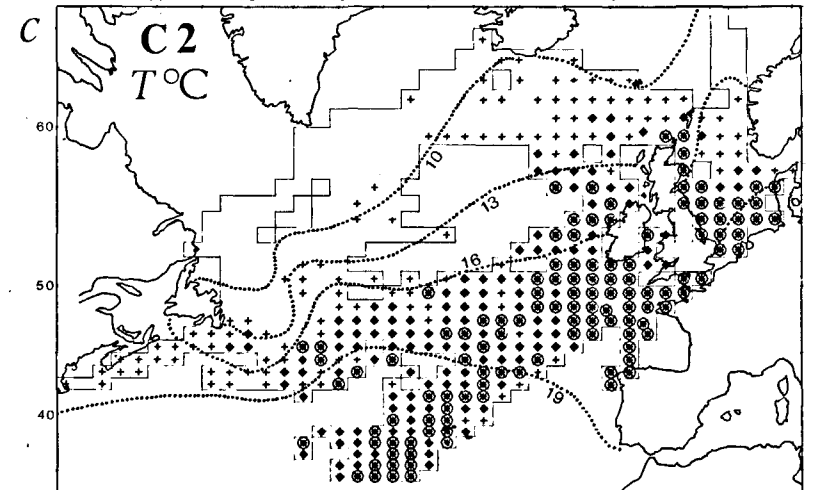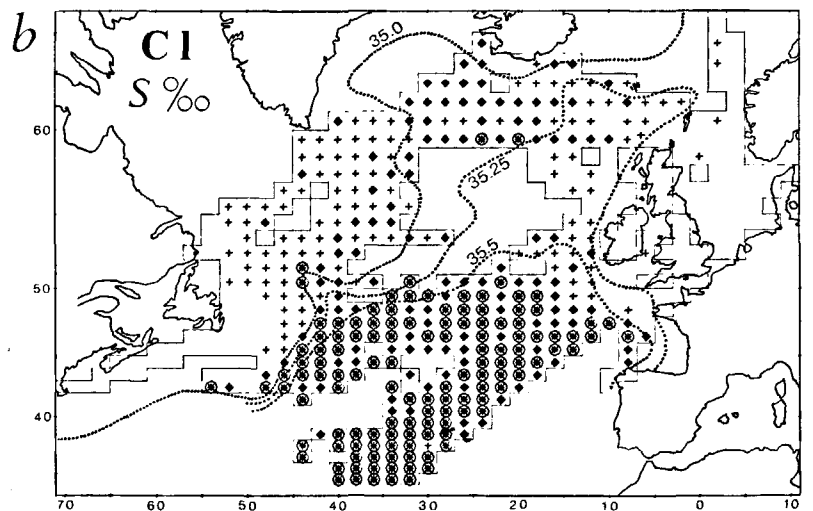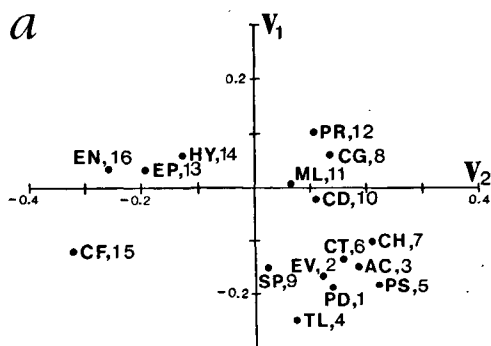
Figure 8

a) A scatter diagram of the first two
eigenvectors derived from the correlation matrix
for the mean geographical distributions of each
of the taxa listed in Table 1 (using the
abbreviated species names given in the Table).
Beside each taxon name in the
plot is its rank taken from Table 2.
b), c) are charts of the principal components
corresponding to the eigenvectors plotted in a).
The values are represented by graded symbols:

highest quarter   circle
second quarter   cross
third quarter   dot
lowest quarter   blank

Chart b) also shows contours of mean
surface salinity in the range 35 to 36°/oo.

Chart c) also shows surface isotherms for
the month of August in the range 10 to 22°C.

which are shown in Figure 8 *a*). Superimposed on the distributions are, respectively, surface isohalines and isotherms for the month of August (as a typical summer month). The distribution of temperature and salinity is clearly correlated in the open ocean sector and, therefore, cannot be expected to correspond precisely with the distributions of orthogonal components but it is clear, nevertheless, that considered as a coupled pair the first two components reflect the distributions of these factors quite closely. This confirms the results presented by Colebrook (1964) of yet another analysis of geographical distribution which, while based on a different set of species of zooplankton, covered an area corresponding closely with the area considered in the present analysis of annual fluctuations in abundance.

Thus, the differentiation between taxa with respect to their annual fluctuations in abundance represented in Table 2, can be related to environmental factors; the taxa at the head of the rank being associated primarily with warm low salinity water (negative v_1, positive v_2 in Figure 8 *a*), those in the centre with warm higher salinity water (positive v_1, positive v_2) while those at the bottom of the list are associated with colder waters (negative v_2). An obvious inference from this is that the major pattern of differentiation between species with respect to their annual fluctuations in abundance does not contain any clear density-dependent element, as it would if, say, the associations between taxa were related to the timings of their seasonal cycles.
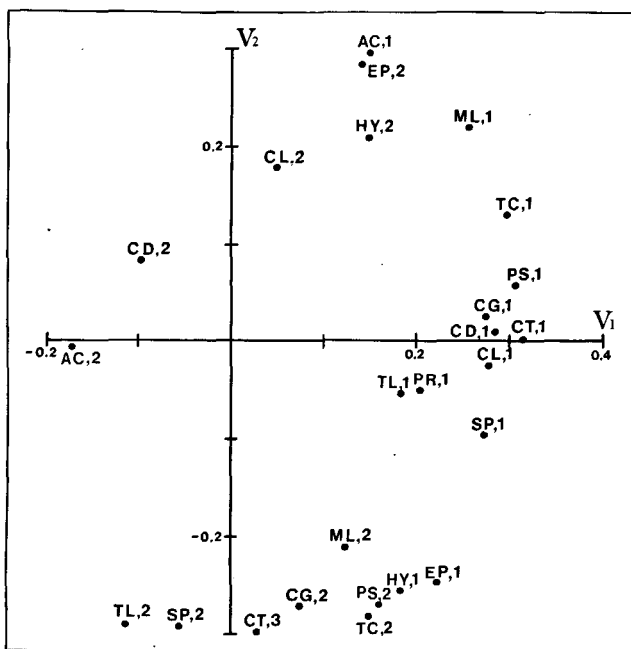
Taxon Components

These are the components derived from analyses of data sets for all the areas for each taxon (the rows of Table 1). To facilitate the selection of component sets, only those taxa were considered for which complete runs of data were available. With one exception, the component sets were based on a study of the first two components and for only one species (*Temora longicornis*) was it necessary to switch components. For *Centropages typicus* it was found that its third component showed appreciably greater coherence within the second component set than did its second component. The second component of *Pleuromamma robusta* was omitted since this species is present in only four of the twelve areas.

Figure 9 is a scatter diagram of the first two eigenvectors of the correlation matrix of the two combined component sets. It must be remembered that the component pairs for each species are orthogonal. Figure 10 gives plots of the components arranged to correspond as closely as possible with the relative positions of their vector values in Figure 9. As in Figure 4, superimposed on each plot is
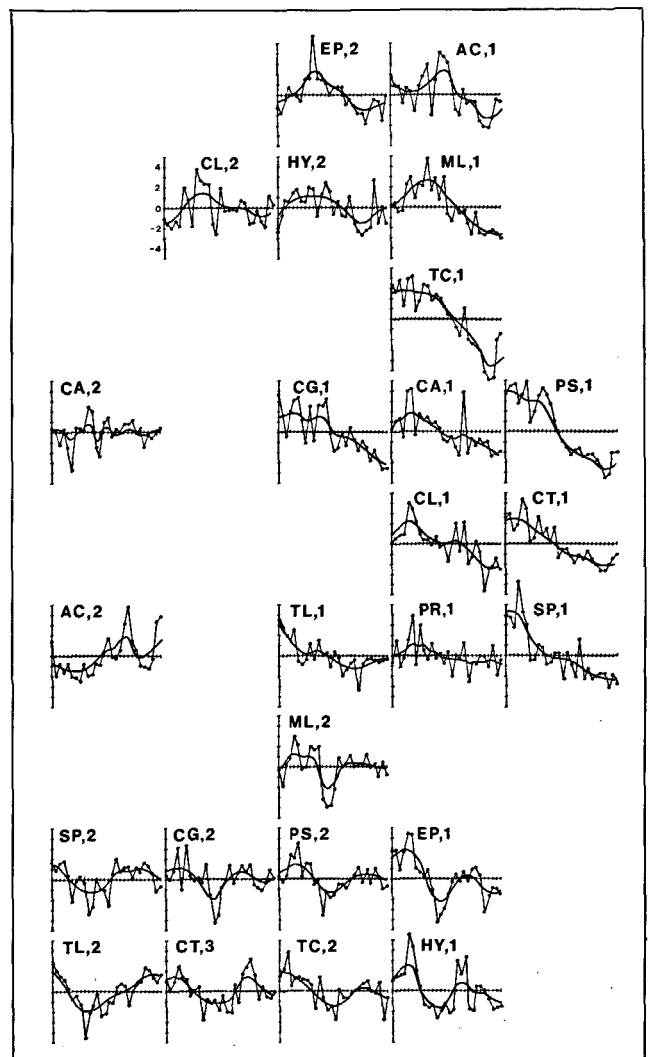
Figure 9

A scatter diagram of the first two eigenvectors of the components included in the first and second component sets derived from the data for all the areas for each taxon (the rows of Table 1). Only taxa for which complete time series of data are available are included:

Acartia clausi	AC	Temora longicornis	TL
Calanus spp. stages V-VI	CL	Total copepods	TC
Candacia armata	CA	Hyperiidea	HY
Centropages typicus	CT	Euphausiacea	EP
Metridia lucens	ML	Spiratella retroversa	SP
Pleuromamma robusta	PR	Chaetognatha	CG
Pseudocalanus elongatus	PS		

With suffix 1 or 2 indicating first or second component set.

Figure 10

Graphs of the first and second component sets. The graphs are located to correspond as closely as possible to the vector plot in Figure 9. Superimposed on each graph is a smoothed version of the component derived from the first eigenvector filter with a maximum lag of 4 years (see Appendix). The abbreviations of the species names are given in Figure 9 and Table 1.

a smoothed form of the component derived in each case from the first eigenvector filter for a maximum lag of 4 years (see Appendix).

Comparison with Figure 4 indicates that the pattern of fluctuation of the first component set is clearly visible in the group of taxon first components in the centre of Figure 10. The values of the corresponding vectors indicate that the pattern is common to virtually all the data sets involved as was the case with the equivalent area vectors. Similarly, the dominant pattern for the oceanic areas (B5, B4, C5, D5) of the second area set is clearly visible in the group of first and second components at the bottom on Figure 10. In this case the vectors do not present any consistent geographical pattern but among the taxa concerned there are high positive vector terms in all the areas except D4 which supports the isolation of this area in the vector plot in Figure 5 b. The group of components at the top of the figure represents, on the other hand, a pattern of variability not visible in the area components. Again, the corresponding vectors do not show any consistent geographical pattern but among the taxa there are fairly high positive values for all the areas.

There is clear evidence from the results presented here. deriving from both commonality and rational patterns of differentiation, for the existence of consistent patterns of year-to-year fluctuations in the abundance of the zooplankton of the North-East Atlantic and the North Sea. The graphs of the principal components given in Figures 4 and 10 provide a description of the main patterns of change.

THE ENVIRONMENT

Sea-surface temperatures

Colebrook and Taylor (in preparation) have shown that there is a marked contrast between the mechanisms involved in determining sea-surface temperatures in the open North Atlantic as compared with the shelf and shallow seas around the British Isles. In the latter area the surface temperatures appear to be determined to a large extent by direct heat exchange with the atmosphere and mediated primarily by the meridional component of the surface winds. The area involved includes most of the areas covered by the plankton data discussed in the previous section. There is, however, little or no relationship between year-to-year changes in temperature and the abundance of the zooplankton as represented by the principal components given in Figures 4 and 10.

For the open ocean, Colebrook and Taylor presented the first three components of monthly anomalies of sea-surface temperature at the nine North Atlantic Ocean Weather Stations for the period 1951 to 1974 as providing valid representations of the major long term patterns of temperature change. Garrod and Colebrook (in press) have shown that there were high correlations between the first principal components for the zooplankton and the sum of the first two temperature components representing a pattern of temperature change characteristic of the whole mid-latitude zone of the open ocean.

The first three temperature components and the mean of the first two were recast as annual means, and graphs of these variables are given in Figure 11. Correlations were calculated with all the zooplankton components illustrated in Figures 4 and 10 and the results are given in Tables 3 and 4.

In Table 3, the correlations between the temperature components and the zooplankton area second components are scarcely different from what would be expected from zero relationships. The correlations with the first zooplankton components, however, contain a high proportion of significant values and associations must be assumed. By far the clearest is with the combined first and second temperature component, with most of the higher values occurring in the oceanic and shelf areas (the first two columns). The individual first and second components reflect this to some extent, while the third component shows higher correlations for the North Sea than for most of the other areas.

In Table 4 the species are tabulated in the same position as in Figure 10, reflecting their interrelationships. There is a clear differentiation within the taxon components with respect to their associations with the first two temperature components. The third temperature compo-
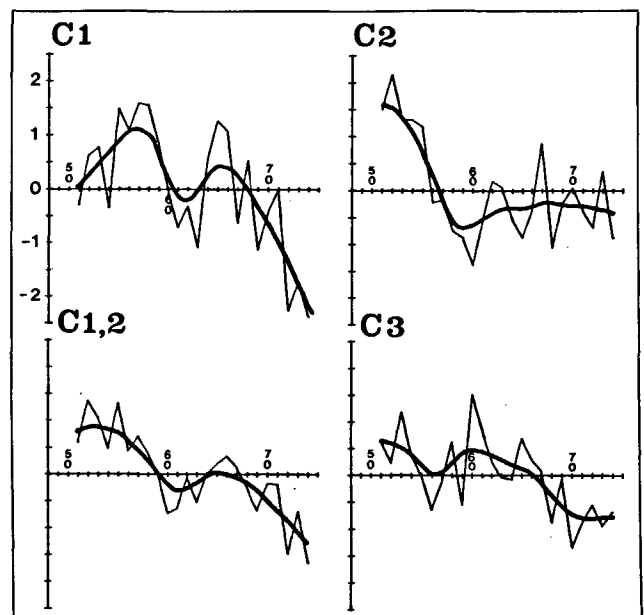

Figure 11
Graphs of annual means of principal components of sea-surface temperature at the nine North Atlantic Ocean Weather Stations. Superimposed on each is a smoothed version derived from the first eigenvector filter for a maximum lag of 4 years (see Appendix). The graphs represent the first (C1), second (C2) and third (C3) components and the mean of the first and second (C1, C2).

nent shows weaker but nevertheless coherent relationships within a set of neighbouring taxon components.

The interpretation of the associations indicated in Tables 3 and 4 presents a number of problems. Firstly, the patterns of temperature change represented in the components refer primarily to the open ocean. None of the nine Ocean Weather Stations occurs in the area from which the plankton data were collected and only two of them occur at all close to it. Therefore, none of the associations with the plankton can be attributed to the influence of temperature as such: the components have to be regarded as indices of other aspects of hydrographic change and complete identifications are not yet available. The first temperature component shows significant relationships with fluctuations in wind stress associated with both the North-East Trades and the mid-latitude

westerlies and can, therefore, be regarded as an index of variations in the strength and/or direction of the North Atlantic Drift. The vector pattern associated with the component is consistent with this hypotheses (Colebrook, Taylor, in preparation) and a study of vertical temperature profiles at the Ocean Weather Stations (*op. cit.*) indicates that the pattern of temperature change associated with the first component persists to depths of at least 250 m. Changes of this nature and scale coupled with persistence in time as indicated by the element of trend are clearly capable of influencing the characteristics of the water masses of the whole of the area and may provide at least a partial explanation of the high degree of commonality represented in the zooplankton first components (Figs. 4 *a*, 5 *a*) which, as stated on p. 14 involve areas covering a wide geographical range, and

Table 3
Correlations between the first and second area components and the first three temperature components. A key to the areas is given in Figure 1.

Zooplankton area first components

	1st component (T)					2nd component (T)					3rd component (T)			
	5	4	2*	1**		5	4	2	1		5*	4	2**	1
B	.23*	.28**	.47**	.50		.55*	.36*	.01	.35		.43	.36	.51**	.34**
C	.44**	.53*	.48	.29		.47**	.41	.13***	.35		.24	.19	.53	.54*
D	.53	.40	.16	.26		.48	.26	.64	.20		.24	.36	.34	.40

	1st + 2nd component (T)			
	5**	4*	2	1***
B	.53***	.44***	.35*	.60*
C	.62***	.66*	.44**	.43
D	.70	.46	.51	.32

Zooplankton area second components

	1st component (T)				2nd component (T)				3rd component (T)			
	5	4	2	1*	5	4	2	1	5*	4	2	1
B	.35	.25	−.36	.43**	.02	.11	−.16	−.04	.39	−007	−.24	.27
C	−.13	−.05	.02	.52*	.24	−.32	−.11	.19	−.08	−.09	−.22	.13
D	.00	−.17	−.06	.40	.26	−.01	.09	.07	−.16	−.12	−.15	−.02

	1st + 2nd component (T)			
	5	4	2	1
B	.28	.26	−.37	.29**
C	.05	−.23	−.05	.51
D	.16	−.14	.01	.35

taxa whose geographical distributions range from neritic to exclusively oceanic.

The high correlations between the combined first and second temperature components and the zooplankton area first components (Table 3) together with the form of the differentiation in the associations with the species components (Table 4) suggest coupling within the component pairs either for the temperature or for the plankton, or indeed both, similar to that shown by the geographical components in relation to temperature and salinity illustrated in Figure 8. Until an identification of the second temperature component is available, which should assist in resolving the coupling, the associations with the plankton will remain uninterpretable, with the exception of the evidence for a link with the flow of the North Atlantic Drift.

Atmospheric pressure

Garrod and Colebrook (in press) described a complex relationship between the zooplankton area first components and an index of atmospheric pressure distribution provided by changes in the frequency of days per year of westerly weather type over the United Kingdom (Lamb, 1969, and pers. comm.). It was shown that the association contained two elements, a positive relationship between the long term trends and an inverse relationship with a quasi-cyclical variation with a period of about 3 years. If the fluctuations in days of westerly weather type are lagged by 2 years with respect to the plankton components then the cyclical elements are brought more or less into phase and correlations provide estimates of positive association with respect to both elements.

Table 4

Correlations between the first and second zooplankton components and the three temperature components. The taxa are tabulated in the same positions as in Figure 10, abbreviations as in Table 1.
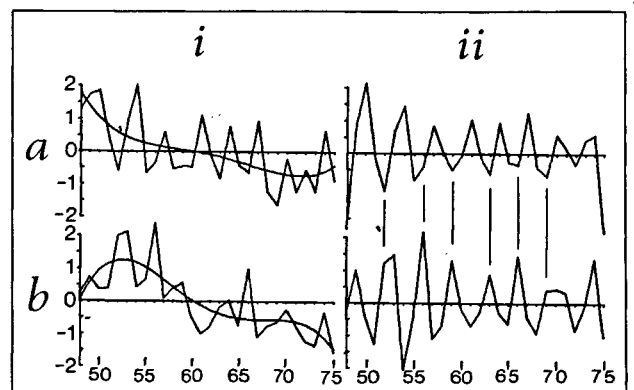
1st component (T)

					EP2	.50**	AC1	.23***		
		CL2	.04	HY2	.09	ML1	.59***
						TC1	.60**	***
CA2	.10			CG1	.46*	CA1	.54*	PS1	.60*
						CL1	.41**	CT1	.47
AC2	−.30			TL1	−.09	PR1	.50	SP1	.29
				ML2	.23
SP2	−.21	CG2	.06	PS2	.09	EP1	.22
TL2	−.40	CT2	−.11	TC2	.20	HY1	.24

2nd component (T)

				EP2	.04	AC1	−.07		
		CL2	−.12	HY2	.07	ML1	.20
						TC1	.27
CA2	−.16			CG1	.22	CA1	.34*	PS 1	.36*
						CL1	.43	CT1	.43**
AC2	−.20			TL1	.37*	PR1	.36	SP1	.48
				ML2	.40***			***
SP2	.09	CG2	.38	PS2	.59**	EP1	.67**
TL2	−.03	CT2	.31	TC2	.50	HY1	.49

3rd component (T)

				EP2	.28*	AC1	.41*		
		CL2	.04	HY2	.41	ML1	.45**
						TC1	.54
CA2	−.20			CG1	.56**	CA1	.29*	PS1	.42*
						CL1	.43	CT1	.45*
AC2	−.08			TL1	.17	PR1	.26	SP1	.41
				ML2	−.17
SP2	−.28	CG2	−.02	PS2	.03	EP1	.16
TL2	−.34	CT2	−.07	TC2	−.08	HY1	.25

Figure 12

Graphs a) refer to the frequency of days of westerly weather type over the United Kingdom. Graphs b) refer to the mean of the first principal component set for areas (see Fig. 4 a). For details see text p. 21.

Table 5 lists the correlations between the lagged frequencies of days of westerly weather type and all the zooplankton components. Significant correlations are found for all but two of the area first components and all but three of the species first components. The element in these correlations relating to the long-term trend can probably be linked with the climatic change in the North Atlantic associated with the temperature variations and, as far as the plankton are concerned, these probably provide the better index. The main interest in the relationship with the westerly weather index lies, therefore, in the quasi-periodic element.

Garrod and Colebrook showed that this variability is represented in the mean of the zooplankton area first components. The graphs marked *i* in Figure 12 show the original variables (*a* is the westerly weather index and *b* is the mean first component) with fitted polynomial trends illustrating the positive relationship between them. Graphs *ii* show the periodic element of each extracted using eigenvector filters with a maximum lag of 4 years. There is an obvious inverse relationship.

Although it would be possible to employ band-pass filters in the analysis of the individual components, it was considered preferable to use eigenvector filters (see Appendix, which includes a documented example of the analysis of one of the components in question). By this method, a filtered variable showing a particular frequency will appear only if an appreciable proportion of the variability of the component is associated with that periodicity. Figure 13 contains plots of all the zooplankton components, for areas or taxa, for which an approximately 3-year periodicity appears in the filtered variables, given a maximum lag of 4 years. The figure also shows the periodic element of the westerly weather index, which has been inverted to give positive similarity with the plankton variables. The phase relationships are quite close in each case, confirming the inverse
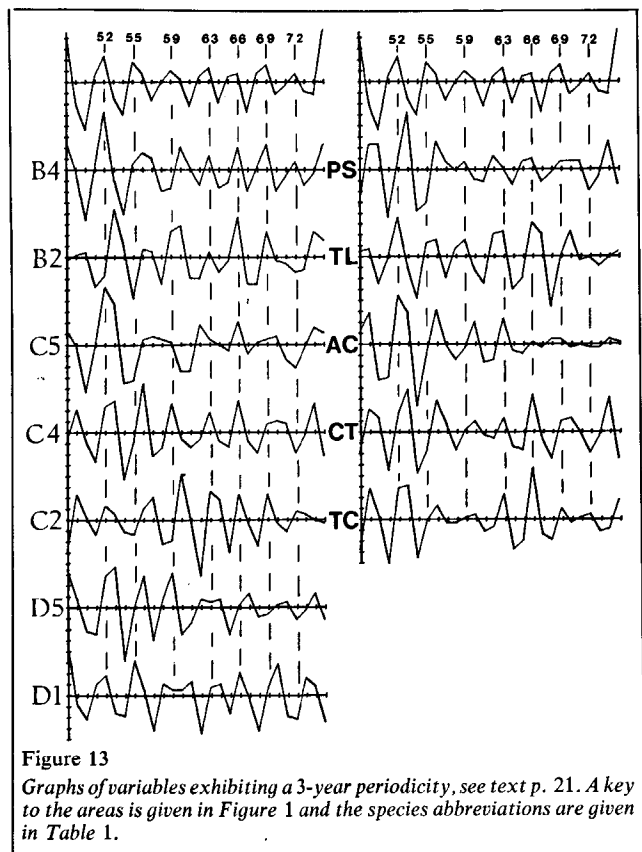

Figure 13

Graphs of variables exhibiting a 3-year periodicity, see text p. 21. A key to the areas is given in Figure 1 and the species abbreviations are given in Table 1.

relationship between the periodic element in the index and this element in the year-to-year fluctuations in the abundance of the zooplankton.

Colebrook and Taylor (in preparation) described an analysis of fluctuations in quarterly means of atmospheric pressure (Namias, 1975) for 1947 to 1974 for 17 positions covering the area 50°N to 60°N and 10°E to 10°W. It was shown that the second and third principal
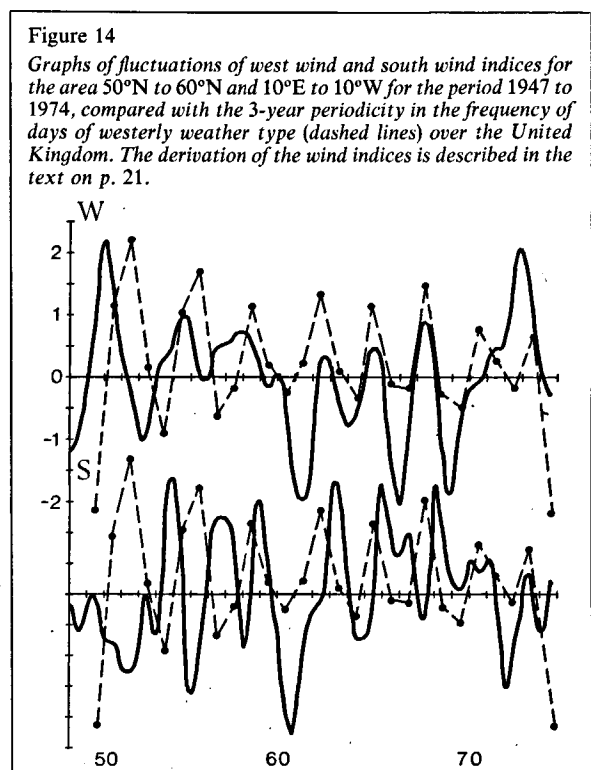
Table 5

Correlations between the zooplankton components and the annual frequency of days of westerly weather type over the British Isles, lagged by 2 years, see text.

Area first components

	5	4	2	1
	**	**		*
B	.52	.57	.36	.47
	*	***	***	***
C	.51	.69	.60	.61
	**		*	*
D	.54	.25	.43	.47

Taxa components

CA2	−.20
AC2	−.22
SP1	.19	CG2	.26
TL2	−.30	CT2	.27

| | CL2 |
| CA2 | −.20 |

EP2	.24
	*
HY2	.42		.00
	CL2
CG1	.54
	**
TL1	.50
ML1	.35
PS2	.35
	*
TC2	.38

Area second components

	5	4	2	1
B	.30	.10	.00	.09
C	.04	.02	−.07	.11
D	.08	−.10	−.05	.08

ACI	.31
	*
ML1	.40
	**
TCI	.59
	**			**
CA1	.55	PS1	.56
	***		***
CL1	.63	CT1	.63
			***
PR1	.19	SP1	.70
		**
EP1	.48
HY1	.37

Figure 14

Graphs of fluctuations of west wind and south wind indices for the area 50°N to 60°N and 10°E to 10°W for the period 1947 to 1974, compared with the 3-year periodicity in the frequency of days of westerly weather type (dashed lines) over the United Kingdom. The derivation of the wind indices is described in the text on p. 21.

components of the data represented fluctuations in westerly and southerly anomaly winds respectively. Smoothed plots of these components are given in Figure 14 and compared with the periodic element of the westerly weather index. Neither of the pressure components shows a significant long-term trend. Over most of the period the second (West wind) component shows a positive relationship with the westerly weather index. From 1948 to about 1956, however, there is a closer inverse relationship with the third (South wind) component. With respect to the plankton this would suggest wind-driven advection, either of populations of organisms or of factors affecting populations, as a possible mechanism underlying the relationships between abundance and the westerly weather index.

It may be worth noting that the period of close relationship with the southerly anomaly winds, from 1948 to about 1956 corresponds, in the plots for *Pseudocalanus* and *Centropages typicus* in Figure 12, with a consistent sequence of about three relatively large amplitude cycles and that, as Colebrook and Taylor have shown, the South wind anomaly has a marked influence on sea-surface temperatures of the North Sea and the Atlantic shelf.

The eigenvector analysis revealed possible biennial oscillations in a few of the components and a periodicity of between 5 and 6 years in quite a number of components, possibly reflecting interaction between biennial and three year periods. In the absence of any obvious interpretations, however, the quality of the data precludes any more intensive efforts at resolution.

DISCUSSION

The previous sections of this paper provide descriptions of the main patterns of year-to-year fluctuations in the abundance of species of zooplankton for the period 1948 to 1975 for the North-East Atlantic and the North Sea (Figs. 4 and 10). First level interpretations of these fluctuations are proposed, based on empirical associations with physical environmental factors relating to medium and long-term changes in climatic factors operating on a large geographical scale (Tables 3 to 5, Figs. 12 and 14).

If these associations can be confirmed by the establishment and evaluation of mechanisms by which the abundance of the zooplankton is determined, this will imply that about half of the observed variability in the annual means can be attributed to density-independent, physical environmental processes. Of the remaining variability, an unknown but certainly not trivial proportion can be attributed to uninterpretable "noise" relative to the time and space scales of the pattern of sampling. The role of density-independent processes in determining year-to-year changes in abundance is also indicated by the fact that species which show similar annual fluctuations tend to have similar geographical distributions (see p. 16).

There is, at first sight, a conflict between these conclusions and the emphasis commonly placed on the role of trophic interactions and density-dependent processes in the plankton ecosystem (see, for example,

Steele, 1974). In this study of year-to-year fluctuations, the variability related to seasonal changes and to differences in abundance between species have been deliberately eliminated, by averaging and standardisation. Compared with these sources, in which density-dependent processes can be presumed to play a major role, the magnitude of year-to-year changes in abundance is small (Colebrook, 1972 b).

The most plausible implication of the apparent importance of density-independence in long-term changes is that the density-dependent processes are extremely stable, either through low efficiency or, more likely, through extensive buffering and that year-to-year changes have to be regarded as due to relatively minor, but nevertheless significant, perturbations of a primarily density-dependent system.

Acknowledgements

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Figure

a) *Is a graph of the original variable with the filtered variable derived from the first eigenvector superimposed.*

b) *Is a graph of the original variable with the filtered variable derived from the second eigenvector superimposed.*

c) *Is the power spectrum of the original variable (maximum lag 14, N = 28).*

d) *Is the power spectrum of the filtered variable derived from the first eigenvector (maximum lag 14, N = 28).*

e) *Is the power spectrum of the filtered variable derived from the second eigenvector (maximum lag 14, N = 28).*

APPENDIX

Eigenvector filters

In this paper the method of eigenvector filters has been used extensively, both for smoothing data sets to emphasise trends, and for the extraction of characteristic frequencies. The method is a development of principal components analysis and the operations involved are as follows:

1) given a variable x_i with $i = 1(1)n$, form the lag matric with successive rows:

$$x_m x_{m+1} \cdots x_n, x_{m-1} x_m \cdots x_{n-1}, \ldots, x_1 x_2 x_{n-m}$$
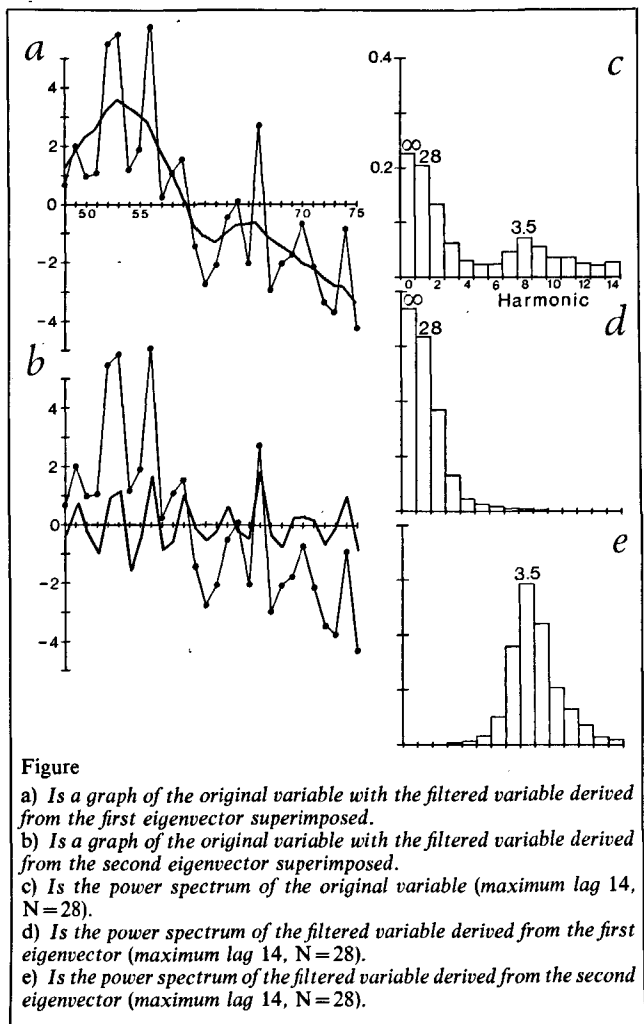
where m is a specified maximum lag;

2) perform a principal components analysis on the lag matrix using the variance/covariance matrix. Each vector contains m terms and each component $n - m$ terms;

3) for a specified vector and component form the matrix VC. This contains the same number of rows and columns as the lag matrix;

4) the filtered variable is formed by averaging diagonals of elements in VC corresponding to the successive terms of the original variable. Thus the first and last $m - 1$ terms of the filtered variable are based on averages of fewer than m terms and are less well estimated than the remainder.

The eigenvectors function in a manner similar to that of band-pass filters. In this form of analysis, however, the first eigenvector of the variance/covariance matrix produces a filtered variable with the largest possible variance and successive eigenvectors produce filtered variables with progressively smaller variances. In trials on a number of variables, employing varying lags it was found that there was no tendency for particular frequencies to be associated with particular lags. At the same time. in the analysis of short time-series, such as all those considered in this paper, the use of large lag values led to over-resolution producing instability in the frequencies in the filtered variables. Provided relatively low lag values are used, however, the frequency bands associated with successive filtered variables are determined entirely by the magnitudes of frequencies in the original time-series.

An example of an analysis is illustrated in appendix Figure. The variable is the first principal component of zooplankton in area C4 (see paper, Fig. 4) consisting of a sequence of 28 annual values (Figs. *a* and *b*). The major periodic elements in the variable are associated with the zero and first harmonics with a lesser peak at the eighth harmonic. equivalent to a period of 3.5 years (Fig. *c*). The filtered variable derived from the first eigenvector (maximum lag of 4) contains only the low frequency element (Figs. *a* and *d*), while the filtered variable derived from the second eigenvector contains only the higher frequency element (Figs. *b* and *e*).

The periodic structure of the original variable has been successfully resolved into realistic frequency bands and the variances of the filtered variables reflect the proportion of variance in the original associated with the resolved frequencies. It must be stressed that the only parameter selected for the analysis was the maximum lag, the value of which effects the band widths of the resolution but has little influence on the frequencies in or the variances of the filtered variables.

The use of power spectra and the application of any frequency resolution method on variables with fewer than 30 points clearly has to be regarded with considerable caution. Throughout the paper the resolutions have been deliberately kept as low as possible, comparisons between power spectra of the filtered variables and the originals was a standard procedure, and evidence for patterns of variability is invariably based on multiple occurences in independent data sets.