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CHANGES IN THE ZOOPLANKTON OF THE NORTH SEA, 1948 TO 1973

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INTRODUCTION

A routine, monthly, synoptic survey of the zooplankton of the North Sea and the Northeast Atlantic has been carried out using Continuous Plankton Recorders (Glover, 1967) for the period from 1948 to the present.

Plankton recorders are towed at a standard depth of 10 m behind merchant ships and Ocean Weather Ships along a number of more or less fixed routes, and as far as possible at monthly intervals. The recorders collect a continuous sample of the plankton which, for purposes of analysis, is divided into sections each representing 10 miles of towing and about 3 m^3 of water filtered. Normally, alternate 10-mile sections are analysed using the methods described by Rae (1952) and Colebrook (1960). The routine processing procedures applied to these data are described by Colebrook (1975b).

As far as possible, the zooplankton are identified as to species but, in some taxonomic groups, identification is confined to genus, family, or even higher categories. The survey provides information about the seasonal, geographical, and annual fluctuations in abundance of the species and other entities in the zooplankton.

Year-to-year changes have been studied extensively in the data from the Continuous Plankton Recorder Survey; Colebrook and Robinson (1964) and Colebrook (1963, 1966, 1972b) all deal primarily with annual fluctuations in abundance. The main emphasis in these studies is the examination of relationships between species and between geographical areas with respect to annual fluctuations in abundance. With the accumulation of data for additional years it has recently become possible to shift the emphasis towards studies of the form and nature of the year-to-year changes themselves; in particular, the results have revealed systematic long-term trends in abundance of many organisms and in the timing of seasonal cycles (see, for example, Colebrook, 1972b; and Glover, Robinson, and Colebrook, 1972). More or less routine data presentations have been developed; these are updated yearly and a report is prepared (see, for example, Colebrook, 1975a).

This paper is confined to a summary presentation of some of the main features of year-to-year changes in the abundance of zooplankton in the North Sea for the period 1948–1973, together with a study of relationships between these changes and those taking place in neighbouring areas outside the North Sea. In addition to presenting some of the long-term trends described previously, an analysis of power spectra reveals cycles of about 3 years' and 7 to 10 years' duration in the abundance of many organisms.

CHANGES IN THE ZOOPLANKTON

In an analysis of variance of data for 13 species and other entities of zooplankton in 4 areas covering the North Sea, for each of the 12 months of the year and for 22 years from 1948 onwards (Colebrook, 1972a), the sums of the variance ratios for the effects, and their interactions for each main effect, were:

Species	278
Months	66
Areas	45
Years	17

These figures indicate that the magnitudes of year-to-year changes are relatively small compared with the variability in the data due to the differences in abundance between species and their seasonal and geographical variations. Two examples are illustrated in Figures 300 and 301, both relating to seasonal variations. Figure 300a is a plot of monthly means of abundance for a copepod, *Pseudocalanus*, in the western central North Sea for the period 1948–1973. The plot shows a clear seasonal cycle in each year while, over the years, there has been a slight decline

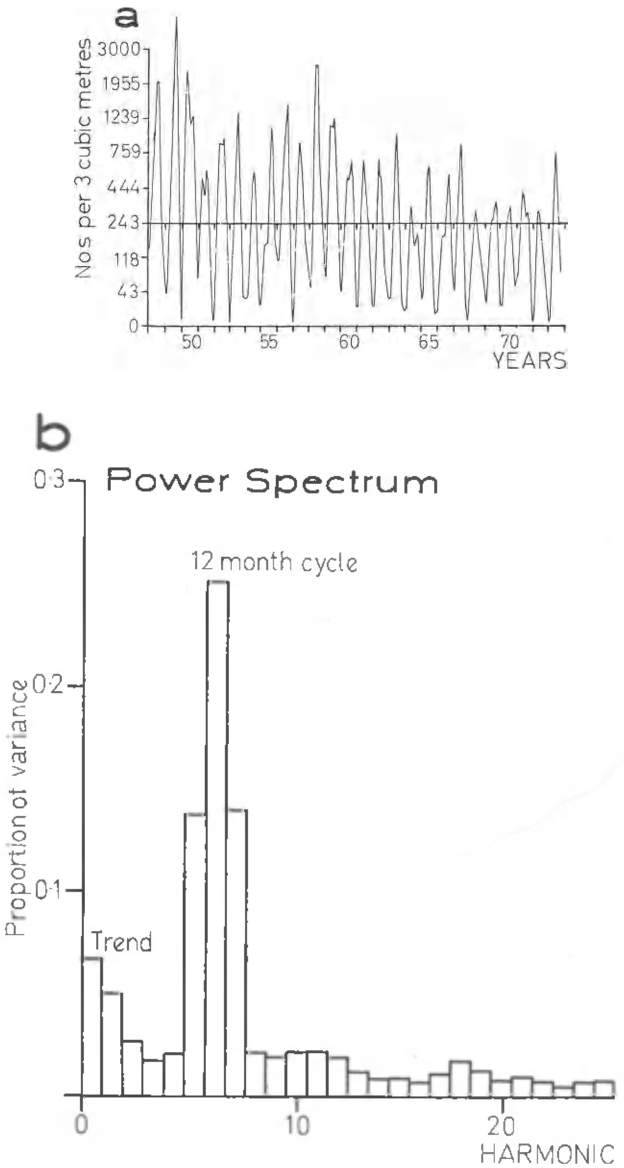

Figure 300. a) A plot of monthly means of abundance of *Pseudocalanus* in the western central North Sea for the years from 1948 to 1973. b) The power spectrum of the variable plotted in Figure 300a.

in its amplitude implying a downward trend in abundance. The power spectrum[1] of the variable indicates that about 60% of the total variability is associated with the 12-month cycle compared with only about 5% associated with the trend.

[1] The power spectrum yields a measure of the distribution of variance in a *time series* over a continuous domain of all possible *wavelengths* from linear trend to twice the interval between successive observations in the series.

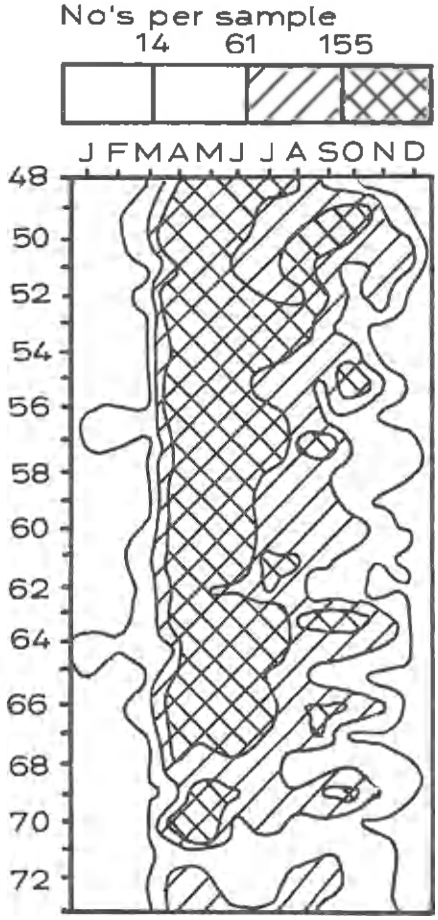

Figure 301. A contoured diagram of the monthly logarithmic means of abundance of *Calanus*, arranged as a monthly/year array, for the western central North Sea for the years from 1948 to 1973. A key to the contours is given.

The second example (Fig. 301) shows, as a contoured month/year diagram, the abundance of the copepod *Calanus* in the western central North Sea. The timing of the spring increase in abundance has remained remarkably constant over the 26-year period in spite of year-to-year changes in abundance: there is no consistent difference in timing between years with high numbers (1950, 1957, 1960, 1963, 1966, and 1969) and years with low numbers (1956, 1962, 1968, and 1971).

It has been shown (Colebrook, 1972a) that year-to-year changes in geographical distribution in the North Sea are also relatively small in magnitude.

In general, therefore, the composition, seasonal cycles, and geographical distributions of the zooplankton have not changed very much over the last 26 years.

Nevertheless, there have been detectable, and in a

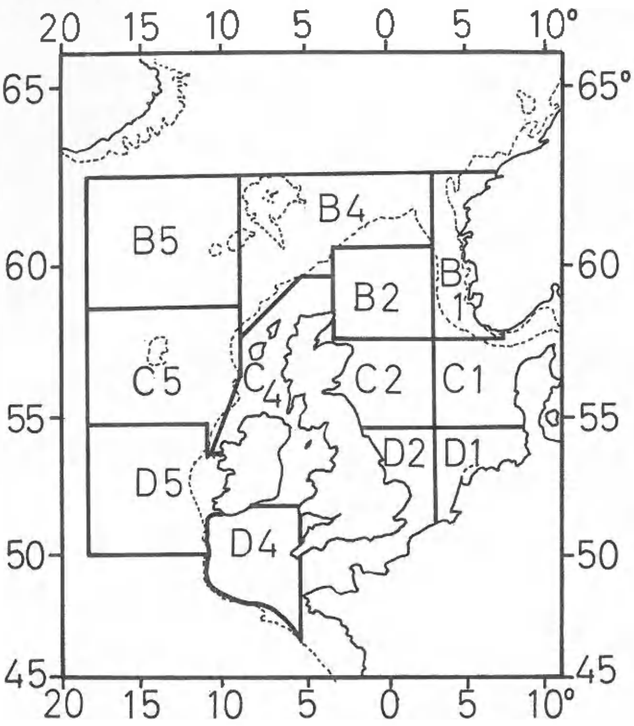

Figure 302. A chart of the Northeast Atlantic and the North Sea showing the subdivision of the survey into standard areas.

few cases fairly considerable, long-term changes in abundance; experience has shown that the best expressions of these changes are obtained by calculating annual means (thus eliminating seasonal changes) for defined standard areas (large enough to give reasonable numbers of samples but small enough not to obscure geographical variations). The set of areas for which virtually complete data are available from 1948 onwards is shown in Figure 302.

The reliability of such expressions of annual fluctuations in abundance can be assessed only on the basis of coherence both within data for the same species in different areas and for different species within the same area.

Analysis indicates that there is, on the whole, fairly considerable coherence within comparable data sets. Two examples are illustrated in Figure 303 by means of half-normal plots of sets of correlation coefficients (Hills, 1969). Figure 303a refers to the correlations between all possible pairs of areas for the year-to-year fluctuations in abundance of *Pseudocalanus* for the years 1948 to 1973. If the data were completely random then the "population" correlation coefficients would be expected to be zero and the z-transformations of the "sample" correlation coefficients should fall on or near a straight line with a slope related to the

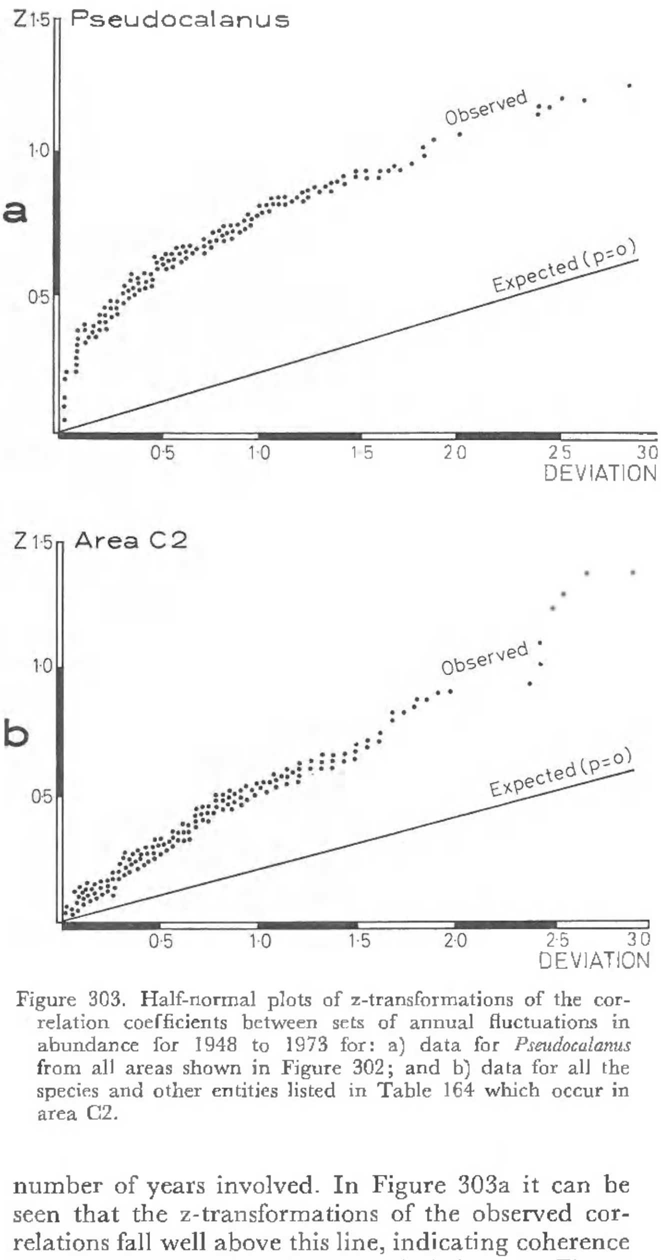

Figure 303. Half-normal plots of z-transformations of the correlation coefficients between sets of annual fluctuations in abundance for 1948 to 1973 for: a) data for *Pseudocalanus* from all areas shown in Figure 302; and b) data for all the species and other entities listed in Table 164 which occur in area C2.

number of years involved. In Figure 303a it can be seen that the z-transformations of the observed correlations fall well above this line, indicating coherence between the data for all the included areas. Figure 303b shows a similar plot for the annual fluctuations in abundance of 18 species and other entities for area C2 (see Fig. 302). Again the observed correlations fall well above the expected straight line, indicating coherence within the data.

Data are available for about 18 species and other entities (see Table 164) for each of the 12 areas shown in Figure 302: a total of 216 data sets. This poses problems of presentation and even greater problems of assimilation. One solution is to use principal components analysis to derive expressions of the main elements of the year-to-year fluctuations in abundance for each area and each species.

Principal components analyses have been done for each of the areas shown in Figure 302 (including data for all species and entities present in each area) and also for each species and entity listed in Table 164 (including the data for each of the areas in which it occurs). In all the analyses, data for the years from 1948 to 1973 were used. In this paper, however, consideration will be restricted to aspects particularly relevant to the North Sea.

Figure 304 contains plots of the first two components for three entities representing major groups of the zooplankton: copepods, chaetognaths, and euphausiids. Polynomials of up to fourth order have been fitted to the components. Also shown are scatter diagrams of the first two eigen-vectors, illustrating relationships between the areas with respect to the components.

The first component for copepods shows a clear downward trend for the whole 26-year period. The terms of the corresponding vector (V1 in the diagram) are all positive and show a relatively small scatter, indicating that this pattern of annual fluctuations in abundance is common to the whole area including Oceanic Atlantic and Continental Shelf areas as well as the North Sea.

The second principal component of copepods also shows a long-term trend, represented by a fourth order polynomial. The corresponding vector shows fairly high positive values for the North Sea areas and negative values for the Oceanic Atlantic areas, indicating that the form of the variation is common to all areas, but it is of opposite sign in the North Sea and the Atlantic.

The components and vectors for chaetognaths tell much the same story. The first component shows a downward trend and the vector terms are all positive but with a larger scatter than for the copepods. The second component shows a fourth order trend similar in form but opposite in sign to that of the copepods, and the vectors indicate a clear inverse relationship between the North Sea and the Oceanic Atlantic.

The first component for euphausiids shows a fourth order trend common in form and sign in most areas, similar in form and sign to the second component for

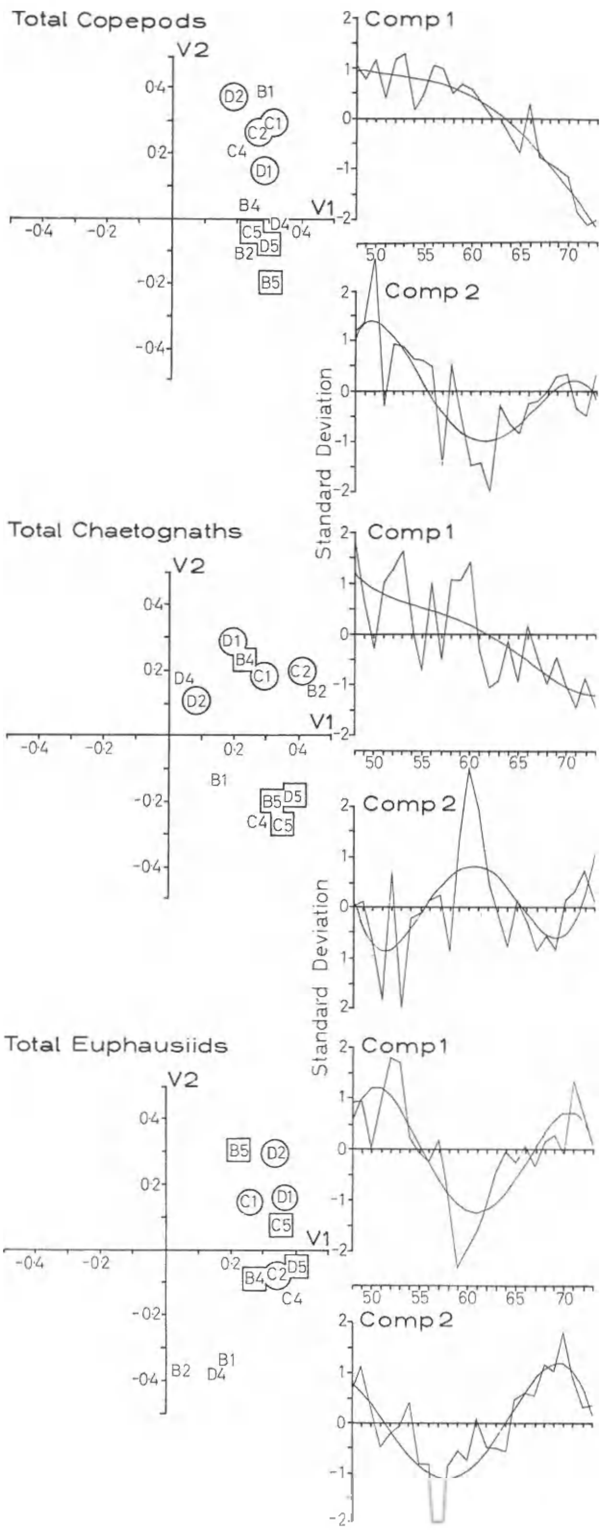

Figure 304. Plots of the first and second principal components, with fitted polynomials, for the annual fluctuations in abundance of total copepods, total chaetognaths and total euphausiids for the years from 1948 to 1973. In each case data from all the areas shown in Figure 302 are included. Scatter diagrams of the corresponding eigen-vectors are also shown. In these plots circles have been drawn around vectors for each North Sea area and squares around those for the Oceanic Atlantic areas.

Table 164. The species and other entities with the areas for which good data for annual fluctuations in abundance are available. The data cover the period 1948 to 1973 unless otherwise indicated by an initial year in the last column. A key to the areas is given in Figure 302

	B5	B4	B2	B1	C5	C4	C2	C1	D5	D4	D2	D1	
Acartia clausi	×	×	×	×	×	×	×	×	×	×	×	×	
Calanus fin. finmarchicus	×	×	×	×	×	×	×	×	×	×	×	×	'58
Calanus helgolandicus	×	×	×	×	×	×	×	×	×	×	×	×	'58
Calanus stages V–VI*	×	×	×	×	×	×	×	×	×	×	×	×	
Total *Calanus* all stages	×	×	×	×	×	×	×	×	×	×	×	–	
Candacia armata	–	–	×	–	×	×	×	×	×	×	–	–	
Centropages typicus	×	×	×	×	×	×	×	×	×	×	×	×	
Euchaeta norvegica	×	×	–	×	×	–	–	–	×	–	–	–	'54
Metridia lucens	×	×	×	×	×	×	×	×	×	×	×	×	
Pleuromamma robusta	×	×	–	–	×	–	–	–	×	–	–	–	
Pseudocalanus elongatus	×	×	×	×	×	×	×	×	×	×	×	×	
Temora longicornis	×	×	×	×	–	×	×	×	–	×	×	×	
Total Copepods	×	×	×	×	×	×	×	×	×	×	×	×	
Podon spp.	×	×	×	×	×	×	×	×	×	×	×	×	'58
Evadne spp.	×	×	×	×	×	×	×	×	×	×	×	×	'58
Total Hyperiidea	×	×	×	×	×	×	×	×	×	×	×	×	
Total Euphausiacea	×	×	×	×	×	×	×	×	×	×	×	×	
Spiratella retroversa	×	×	×	×	×	×	×	×	×	×	×	×	
Total Chaetognatha	×	×	×	×	×	×	×	×	×	×	×	×	

* *Calanus* stages V–VI is an estimate of the total of these stages for *Calanus finmarchicus finmarchicus* and *Calanus helgolandicus*. It is included in addition to these species because observations are available for the whole period since 1948, whereas the species were not identified and counted in routine analysis until 1958.

total copepods but opposite in sign to the second component for the chaetognaths. The second component for euphausiids shows a trend similar in degree but differing in phase from the first component. The lack of any clear geographical pattern suggests that it may be a residual of the first component representing variations in the phase of the trend in different areas.

These three examples are supported by the analyses for most of the other species and also by the analyses of data within the areas. It would appear that there are two basic patterns of events. Firstly, a downward trend in abundance which is common in form and sign in all the areas, occurring not only in the North Sea but also in the Oceanic Atlantic and over the Continental Shelf. Secondly, a fourth order trend, also found throughout the area but varying in sign from species to species; within some species it varies in sign between the Atlantic and the North Sea.

The first principal components for all the entities listed in Table 164 for each of the North Sea areas have been examined for shorter term periodicities. Figure 305 contains plots of the first components for the areas C2, C1, D2, and D1 (see Fig. 302) together with plots of their power spectra following the removal of any linear trend. In each area there are indications of two periodicities: at 2 to 3 years and at 7 to 10 years. Because the data series extends over only 26 years the reality and timing of the latter period must be in doubt.

A few of the more abundant entities occur, in some areas, in sufficient numbers throughout the year to warrant the calculation of anomalies from long-term monthly means in an attempt to remove seasonal variations. In most instances further selective smoothing is required to remove the seasonal variation entirely. Two examples of such time series, free of seasonality, are given in Figures 306 and 307 together with their power spectra (with the linear trend removed for *Pseudocalanus*). These support the evidence from the components for the existence of a periodicity at about 3 years and a longer periodicity, apparent in these examples, at 8 and about 13 years. As with the annual series, problems of resolution throw some doubt on the reality of the longer periodicities, although the evidence for the shorter period, of about 3 years, is strong.

DISCUSSION

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 flucations almost inevitably implies that the year-to-year changes in the abundance of zooplankton in the North Sea are determined to a large extent by physical environ-

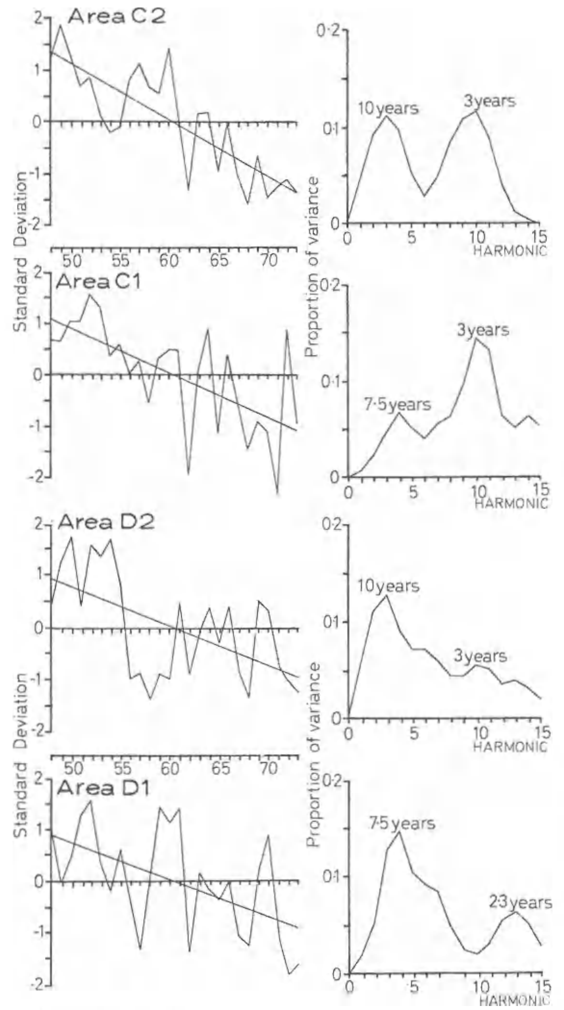

Figure 305. Plots for the first principal components for each of the North Sea areas (see Fig. 302) with fitted linear trends together with the power spectra of the components following the removal of the linear trends.

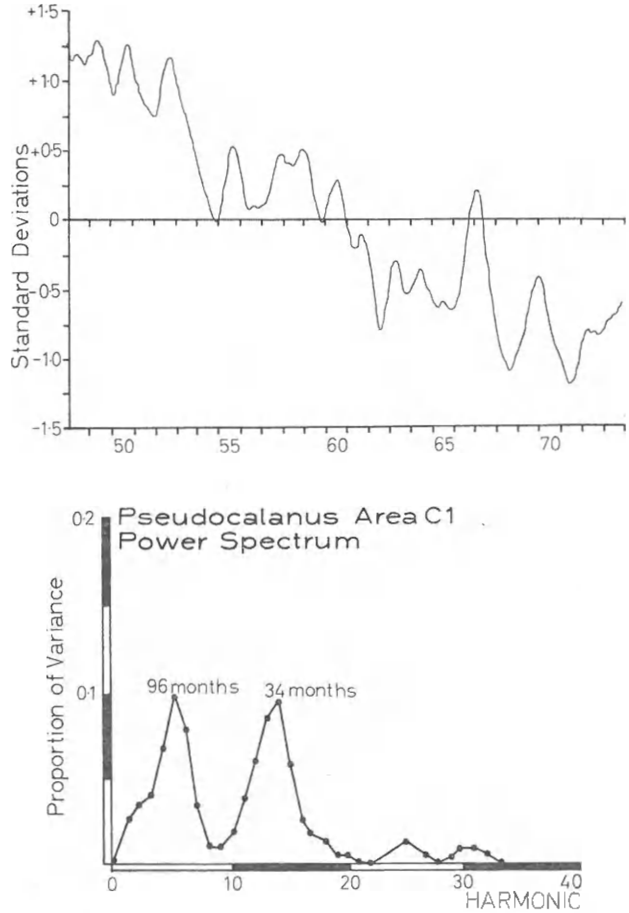

Figure 306. Monthly means of abundance of *Pseudocalanus* for area C1 (see Fig. 302) for the years 1948 to 1973, plotted as anomalies from the long-term means for each calendar month and smoothed, to remove the seasonal cycle. The power spectrum of the variable following the removal of linear trend is also given.

mental changes on a scale comparable with general climatic changes.

Southwood et al. (1974) presented some examples of long-term changes in biological variables in the English Channel apparently related to changes in sea-surface temperatures which in turn were attributed to general climatic changes. Dickson et al. (1975) have suggested a possible relationship between changes in the geographical distribution of some plankton entities in the northern North Atlantic during the years 1966 to 1973 and a change in atmospheric circulation associated with a cell of high-pressure anomalies over Greenland.

Work is in progress in the Continuous Plankton Recorder programme aimed at identifying further relationships of a similar nature. Features similar to most of the year-to-year fluctuations of the plankton have been identified in expressions of fluctuations of sea-surface temperatures. The full extent of the relationships has yet to be determined and it would be premature to present the results here, but it seems likely that they reflect a common response to hydrographic changes related to large-scale (possibly hemispheric) climatic changes.

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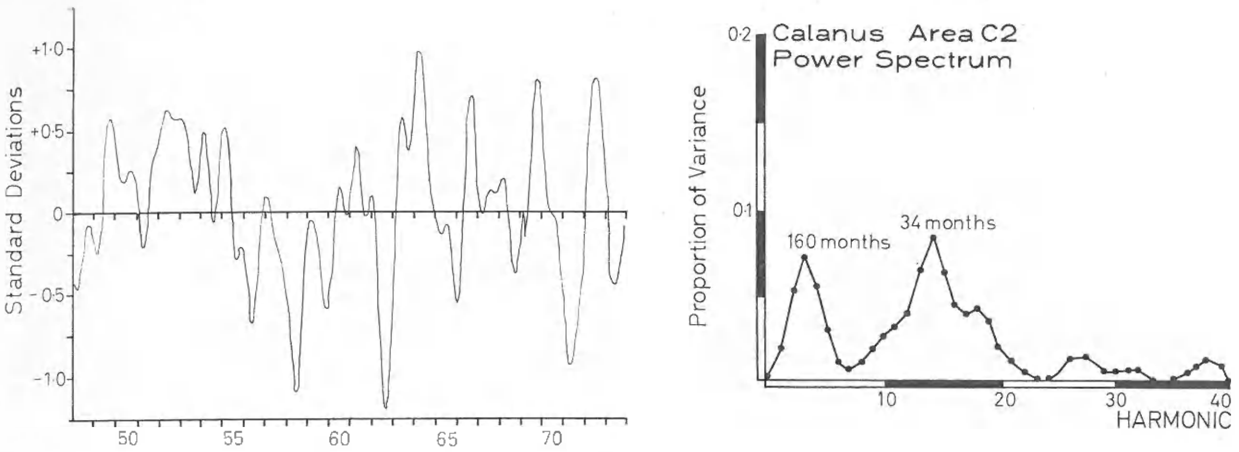

Figure 307. Plots similar to those in Figure 306 for *Calanus* in area C1.

ledge his obvious debt to all those who have been involved in the tremendous task of running the Continuous Plankton Recorder survey during this period and especially to the masters, officers, and crews of the ships without whose willing cooperation the survey would be impossible.

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