Continuous plankton records : phytoplankton, zooplankton and environment, North-East Atlantic and North Sea, 1958-1980.

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ABSTRACT

Year-to-year fluctuations in the abundance of phytoplankton in the North-East Atlantic and the North Sea for the period 1958 to 1980 are described. Based on similarities between their annual fluctuations in abundance, the taxa may be divided into two groups, one of 12 species of diatoms and 1 species of *Ceratium*, the other of 5 species of *Ceratium*. The annual fluctuations in abundance of the *Ceratium* group is negatively correlated with a component of sea surface temperature (representing changes in the open ocean) and with the frequency of cyclonic weather over the United Kingdom. The Diatom group shows very similar annual fluctuations to those of most of the zooplankton species. Both groups show a high proportion of long wavelength variability in the form of a more less linear downward trend in abundance over the whole period.

There is evidence to suggest that the high proportion of long wavelength variability shown by the zooplankton is influenced by inherent persistence in stocks from year-to-year. The phytoplankton show little or no persistence. The close relationship between zooplankton and phytoplankton may, therefore, involve feed-back through nutrient recycling so influencing the annual levels of abundance of phytoplankton.

Oceanol. Acta, 1982, **5**, 4, 473-480.

RÉSUMÉ

Prélèvements en continu du plancton : le phytoplancton, le zooplancton et l'environnement, l'Atlantique du Nord-Est et la Mer du Nord, 1958-1980.

Les variations annuelles en abondance du phytoplancton de l'Atlantique du Nord-Est et de la Mer du Nord pour la période de 1958 à 1980 sont décrites. En se fondant sur des similitudes entre leurs variations annuelles en abondance, il est possible de diviser les catégories en deux groupes : un premier de 12 espèces de Diatomées et une espèce de *Ceratium*, et un second formé de 5 espèces de *Ceratium*. La variation annuelle en abondance du groupe de *Ceratium* est négativement corrélée avec une composante de la température de surface (représentant les changements en pleine mer) et avec la fréquence des conditions atmosphériques cycloniques sur le Royaume-Uni. Le groupe des Diatomées présente des variations annuelles comparables à celles de la plupart des espèces zooplanctoniques. Les deux groupes présentent une proportion élevée de variabilité dans les basses fréquences, sous la forme d'une tendance en abondance décroissante de manière plus ou moins linéaire sur toute la période étudiée.

Les données disponibles suggèrent que la proportion élevée de variabilité dans les basses fréquences présentée par le zooplancton est influencée par une continuité propre du stock d'une année sur l'autre. Le phytoplancton présente peu ou pas de continuité naturelle.

La relation étroite entre le zooplancton et le phytoplancton suggère un effet rétroactif par régénération des sels nutritifs pouvant influencer les niveaux annuels de l'abondance du phytoplancton.

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INTRODUCTION

Colebrook (1978) presented the results of a study of the annual fluctuations in the abundance of zooplankton in the North-East Atlantic and the North Sea for the period 1948-1975, based on data from the Continuous Plankton Recorder survey. Empirical associations with climatic variables suggested that changes in the North Atlantic current and more localized wind-driven advection play a major rôle in determining the form of the annual variability of the zooplankton.

Data on phytoplankton from the Continuous Plankton Recorder survey have been used to describe patterns of geographical distribution (Oceanographic Laboratory, Edinburgh, 1973; Colebrook, 1972) and seasonal variations in abundance and distribution (Robinson, 1965). Reid (1977; 1978) has described the year-to-year changes in indices of abundance of total phytoplankton [based on an estimate of greenness of the sample silks (Robinson, 1970)], total diatoms and total *Ceratium* spp. for the period 1958 to 1974.

Due to a change in the method of counting the samples from the survey (Colebrook, 1960) consistent data on the annual fluctuations in abundance of phytoplankton taxa are available only from 1958. Data are now available up to 1980, giving time-series of 23 years. This is just adequate to provide the basis for a study analogous to that of the zooplankton.

This paper, therefore, describes the annual fluctuations in the abundance of phytoplankton taxa in the North-East Atlantic and the North Sea for the period 1958 to 1980. Relationships with both the zooplankton and the environment are considered.

DATA

A synoptic survey of the plankton of the North-East Atlantic and the North Sea has been carried out using Continuous Plankton Recorders towed by merchant ships and Ocean Weather Ships on regular routes at monthly intervals at a standard depth of 10 m (Glover, 1967). Methods of counting and data processing are described by Colebrook (1975); as far as possible, phytoplankton organisms are identified to species, but

for some taxonomic groups, identification is made to sub-species while in others it is confined to genus. The mesh size of the silk used (0.27 mm) is such that most of the phytoplankton passes through the sampler but a representative proportion of the larger diatoms and dinoflagellates is retained (Robinson, 1970).

Figure 1 contains a chart of the sub-divisions of the survey area for which virtually complete data are available from 1958 to 1980, and in Table 1 the phytoplankton taxa are listed together with an indication of the areas in which each occurred in sufficient abundance for the estimation of annual means.

For each X in Table 1 there is a data set consisting of the logarithmic means of abundance for each year from 1958 to 1980. The treatment and methods of analysis of these data are essentially the same as those used for the zooplankton by Colebrook (1978). Principal components analyses were used to extract representations of the main patterns of year-to-year changes in abundance. Analyses were performed on arrays consisting of the data sets for :

a) all the areas for each species (the rows of Table 1); and

b) all the species for each area (the columns of Table 1). The analyses were all based on correlation matrices involving the standardization of each variable to zero mean and unit variance in order to eliminate differences in abundance between species and between areas, leaving only the relative year-to-year changes.

In view of the fact that the length of the time-series for the phytoplankton is restricted to 23 years, compared with 33 years now available for the zooplankton, information relating only to the first principal component is presented here. Studies of relationships between areas and species are based primarily on the first two eigenvectors of principal components analyses of the sets of first components relating to areas and species respectively.

The allocation of signs to the principal components presented no problems. Nearly all the values of nearly all the first eigenvectors corresponding to the components had common signs and, in the relevant figures the components are presented to have positive values for the majority of the terms of the eigenvectors.

Figure 1

Graphs of the first principal components (solid lines) of phytoplankton, standardized to zero mean and unit variance; superimposed (dashed lines) are fitted fourth-order polynomials. The structure of the data sets from which the components are derived is described in the text. A key of the abbreviations of the species names is given in Table 1 and a key to the areas is given in the figure.
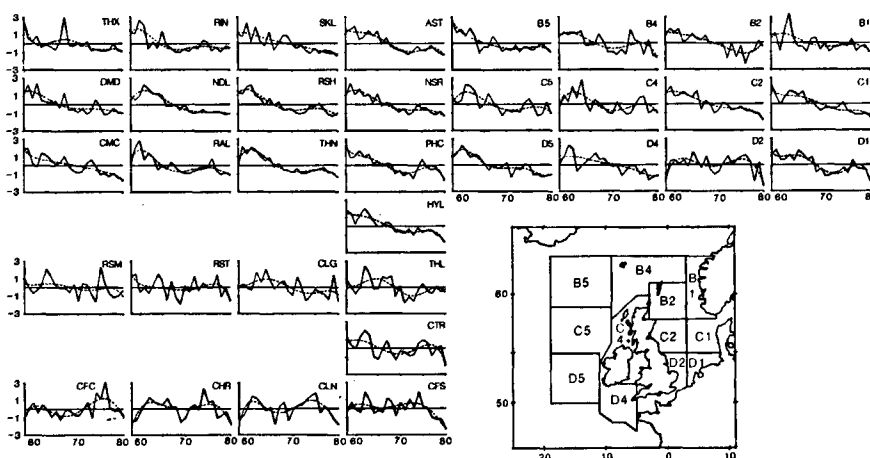
Table 1

A listing of the phytoplankton species included in the study with : a) a standard three letter abbreviation of the names used in several of the figures; b) 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) the first eigenvalues of principal components analyses of the sets of data for each species; d) the first eigenvalues for the data sets for each area. c and d are expressed as percentages of the total variability of the data sets represented in the first principal components.

	a	b												c
		B5	B4	B2	B1	C5	C4	C2	C1	D5	D4	D2	D1	
Skeletonema costatum	SKL	–	X	X	X	X	X	X	X	X	X	X	X	30
Thalassiosira spp.	THL	X	X	X	X	X	X	X	X	X	X	X	X	29
Dactyliosolen mediterraneus	DMD	X	X	X	X	X	X	X	X	X	X	–	–	45
Rhizosolenia imbricata shrubsolei	RSH	X	X	X	X	X	X	X	X	X	X	X	X	45
Rhizosolenia styliformis	RST	X	X	X	–	X	X	X	X	X	X	X	X	24
Rhizosolenia hebetata semispina	RSM	X	X	X	X	X	X	X	X	X	X	X	X	25
Rhizosolenia alata indica	RIN	X	X	–	–	X	X	X	–	X	X	–	–	50
Rhizosolenia alata alata	RAL	X	X	X	X	X	X	X	X	X	X	X	X	50
Hyalochaete spp.	HYL	X	X	X	X	X	X	X	X	X	X	X	X	47
Phaeoceros spp.	PHC	X	X	X	X	X	X	X	X	X	X	X	X	34
Asterionella japonica	AST	X	X	X	–	–	X	X	X	–	X	X	X	30
Thalassiothrix longissima	THX	X	X	X	X	X	X	X	X	X	X	X	X	43
Thalassionema nitzschioides	THN	X	X	X	X	X	X	X	X	X	X	X	X	54
Nitzschia seriata	NSR	X	X	X	X	X	X	X	X	X	X	X	X	41
Nitzschia delicatissima	NDL	X	X	X	X	X	X	X	X	X	X	X	X	59
Ceratium fusus	CFS	X	X	X	X	X	X	X	X	X	X	X	X	34
Ceratium furca	CFR	X	X	X	X	X	X	X	X	X	X	X	X	26
Ceratium lineatum	CLN	X	X	X	–	X	X	X	X	X	X	X	X	24
Ceratium tripos	CTR	X	X	X	X	X	X	X	X	X	X	X	X	25
Ceratium macroceros	CMC	X	X	X	X	X	X	X	X	X	X	X	X	33
Ceratium horridum	CHR	X	X	X	X	X	X	X	X	X	X	X	X	33
Ceratium longipes	CLG	X	X	X	X	–	X	X	X	–	–	X	X	28
	d	53	37	26	35	32	22	45	48	30	31	27	18	

RESULTS

Graphs of the principal components of the phytoplankton are presented in Figure 1. They comprise 34 variables, one for each of the species listed in Table 1 and one for each of the areas shown in the key chart in Figure 1. They represent the best possible single presentations of the year-to-year fluctuations in abundance relating to the species or area. They seldom represent less than a quarter and sometimes more than a half of the total variability in the sets of variables from which they are derived (see Table 1). In Figure 1 the components have been standardized to zero mean and unit variance and fitted fourth order polynomial curves are superimposed to emphasize long-term trends. The species components are arranged to correspond as closely as possible with the placing of the species in a plot of the first two eigenvectors derived from the set of components (Fig. 2 *a*). The area components are arranged in a quasi-geographical layout.

The general impression given by Figure 1 is of clear coherence associated primarily with obvious fits to systematic trends. It should be emphasized that trends similar in form and sign are present in the data from which the principal components are derived. The dominant pattern has the form of a more or less linear downward trend spanning virtually the whole of the 23 year period.

This pattern is shown by all the species in the top four rows of Figure 1 and by all the areas except D2. A
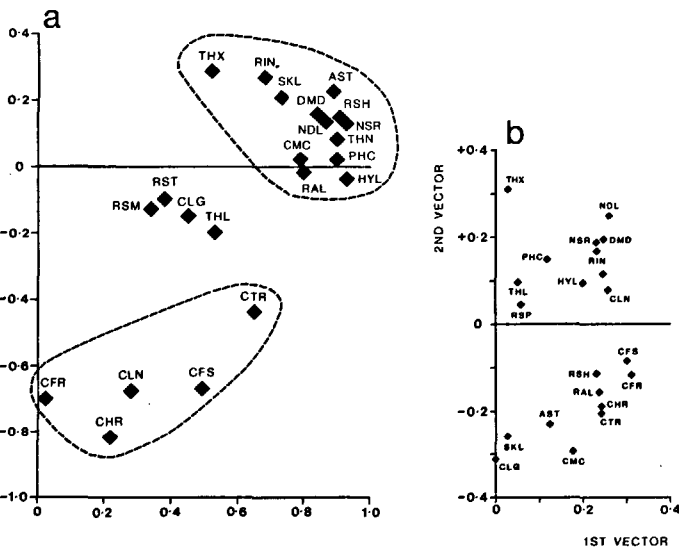

C

Figure 2

a : *A scatter plot of the first two eigenvectors derived from the set of species components (see text).*

b : *A scatter plot of the first two eigenvectors derived from an analysis of the geographical distributions of phytoplankton species (except* Rhizosolenia styliformis) *in the North Atlantic and the North Sea (Colebrook, 1972).*

c : *A rank of species on the basis of the timing of their seasonal cycles of abundance with early species at the top and late species at the bottom.*

A key to the abbreviations used for the species names used in all three diagrams is given in Table 1.

second pattern is shown by area D2 and by the *Cera-tium* spp. in the bottom two rows of Figure 1. The differentiation between the two patterns is indicated by two distinct clusters of species in the eigenvector plot in Figure 2 *a*. There is also a third cluster of four taxa between the two main groups (Fig. 2 *a*); examination of the correlation matrix shows, however, that all four taxa have higher correlations with members of one or both the main groups than they do with each other. They have to be regarded therefore, as showing annual fluctuations in abundance intermediate between the two main groups rather than comprising a third distinct group. For convenience the main groups will be referred to as the Diatom group and the Ceratium group respectively.

INTERPRETATION

In view of the coherence and pattern shown by the components, it would appear that the interpretation problem can be reduced to the identification of the factors involved in determining the two distinct patterns of annual fluctuation in abundance.

As aids to interpretation, plots of the first two eigenvectors of each set of components (species and areas) were prepared, and power spectra of each of the components were calculated.

The vector plot of the area components showed only the obvious difference between area D2 and the remaining areas; no other systematic geographical pattern was detected. The vector plot of the species component is given in Figure 2 *a*. In addition to assisting in the definition of species groups (see above) this diagram can be used in comparisons with information about relationships between species with respect to their geographical distributions and the timing of their seasonal cycles of abundance. Figure 2 *b* is a scatter plot of the first two eigenvectors from a principal components analysis of the geographical distributions of the species, taken from a series of analyses described by Colebrook (1972). There does not appear to be any similarity between this and the pattern of species in Figure 2 *a*, implying that species with similar geographical distributions (species occurring close together in Fig. 2 *b*) do not necessarily show similar annual fluctuations in abundance. In this, the phytoplankton differs from the zooplankton : Colebrook (1978) showed that there was a clear tendency for zooplankton with similar geographical distributions to show similar annual fluctuations.

Figure 2 *c* is a rank of the species with respect to the timing of their seasonal peaks in abundance, with early species (peaking in March to April) at the top and late species (peaking in September to October) at the bottom. Again, there does no appear to be any relationship between this rank and the arrangement of species in Figure 2 *a*, implying that species occurring at the same time of year do not necessarily show similar annual fluctuations in abundance.

The power spectra of the principal components are presented in Figure 3. They are based on annual means, providing time-series containing 23 values; this is rather
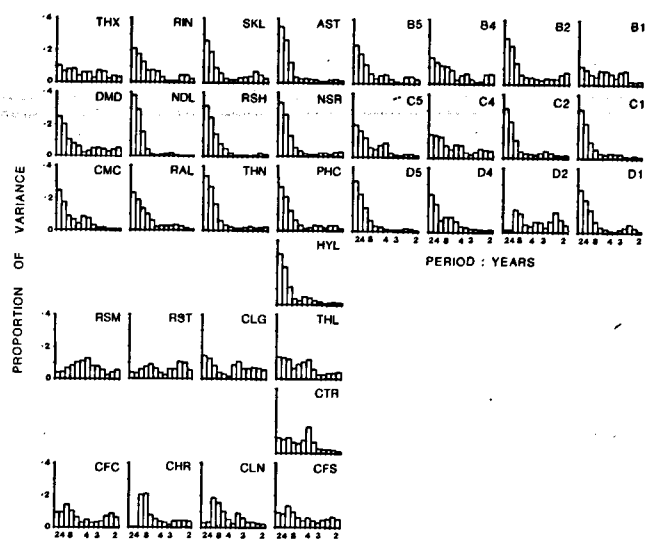

Figure 3

Histograms of the power spectra of the principal components of the annual fluctuations in the abundance of phytoplankton shown in Figure 1. The layout is the same as in Figure 1. The spectra are based on time-series of 23 annual values (1958-1980) and calculated with a maximum lag of 12 years.

short for the application of power spectral analysis and the resolution used is greater than the maximum generally recommended for the calculation of such spectra. However the clear patterns in the spectra, reflecting the species groups, gives some confidence in their reality.

The spectra of the species components reveal a clear contrast between the Diatom group which show predominantly long wave-length variability and the Ceratium group for which the only consistent feature are peaks corresponding to a wave-length of about 12 years.

Variability at about this wave-length has been observed in two environmental variables, the second principal component of sea surface temperature (based on data for the 12 areas shown in Figure 1, for the period 1948 to 1980) and the number of days per year of cyclonic weather type over the British Isles for the same period (Lamb, 1969, and subsequent data published by the Climate Research Unit, University of East Anglia). The second principal component of sea surface temperature is primarily an open ocean pattern, the relevant eigenvector shows large positive values for areas C5 and D5, smaller positive values for B4, C4 and D4, while the North Sea areas all show small negative values (see chart of areas in Figure 1).

Figure 4 shows graphs of the principal components of the Ceratium group of species together with graphs (for the period 1958 to 1980) of the second principal component of sea surface temperature and the frequency of cyclonic weather. All the variables are standardized to zero mean and unit variance and fitted fourth order polynomial curves are superimposed. It is clear that both the environmental variables are negatively correlated with the species of the Ceratium Group.

Maximum Entropy cross-spectral analyses (Strand, 1977) of a subset of species environment pairs indicate that coherence is largely confined to the longer wavelengths of 10-11 years. Variability at this wavelength has been identified in a number of environmental and
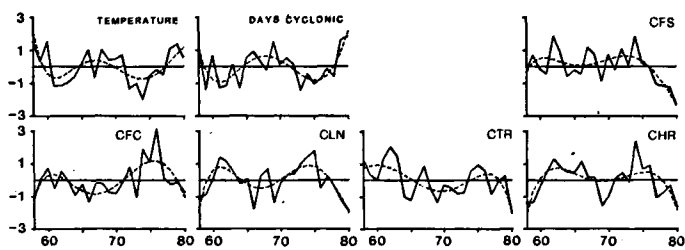
Figure 4

Graphs of the second principal component of sea surface temperature (temperature) derived from annual means for each of the 12 areas shown in the chart in Figure 1, variations in the frequency of cyclonic weather over the British Isles (days cyclonic), and the first principal component of the annual fluctuations in abundance for the Ceratium group of species (Fig. 2 a, key to the species names in Table 1). All graphs are standardized to zero mean and unit variance and superimposed are fitted fourth order polynomials (dashed lines).

biological variables (Southward *et al.,* 1975). The nature of the relationship in this case, with negative correlations confined to a particular wave band presents problems of interpretation and the mechanisms involved in the observed relationships have yet to be identified.

The pattern of annual fluctuation in abundance shown by the diatom group (the first four rows of species in Figure 1) and all the areas except D2 is similar to the main pattern of fluctuation shown by the zooplankton. As examples, Figure 5 shows graphs of the first principal components of the annual fluctuations in abundance, based on data sets equivalent to those of the phytoplankton, for Total Copepods (12 areas), Chaetognatha (12 areas), area B4 (18 species of zooplankton) and area C2 (17 species of zooplankton) for the period 1948 to 1980, compared with the components for *Phaeoceros* spp., *Asterionella japonica* and for all the phytoplankton species in the same areas, B4 and C2. These are typical of a much larger number of relationships between the zooplankton and phytoplankton.

At first sight the interpretation of this relationship seems obvious. As zooplankton depend on phytoplankton for their food it is not surprising that there should appear to be a positive relationship between their
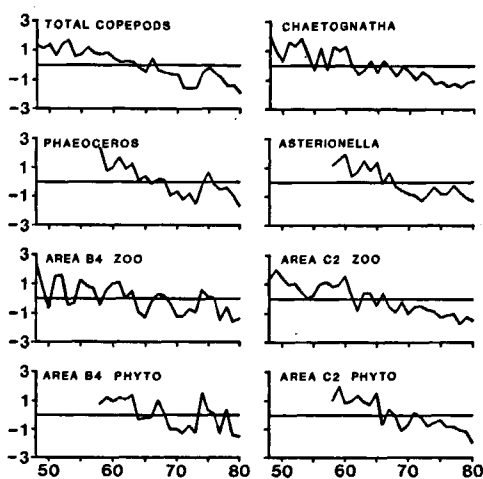

Figure 5

Comparisons of the annual fluctuations in abundance of zooplankton (1948-1980) and phytoplankton (1958-1980). The graphs are first principal components standardized to zero mean and unit variance.

annual fluctuations in abundance. There is, however, some evidence that the relationship is more complicated than this.

Colebrook (1981) has suggested that the form of the annual fluctuations, and in particular the extent of long wavelength variability, in the abundance of many species of zooplankton is influenced by persistence from year to year. It is assumed that, for these species, the rate of population increase from the winter minimum to the summer maximum is such that, irrespective of changes in the environment, the summer maximum is not independent of the size of the overwintering stock. Colebrook (1982) presents a study of two species, *Pseudocalanus elongatus* and *Acartia clausii,* in which it is suggested that the extent of variation in geographical distribution through the seasonal cycle may indicate the relative extent of persistence. For species which show totally different geographical distributions in summer and winter, the summer stocks must be independent of the winter stocks, whereas, for species which show similar distributions in summer and winter, the summer stocks may be dependent on the winter stocks.
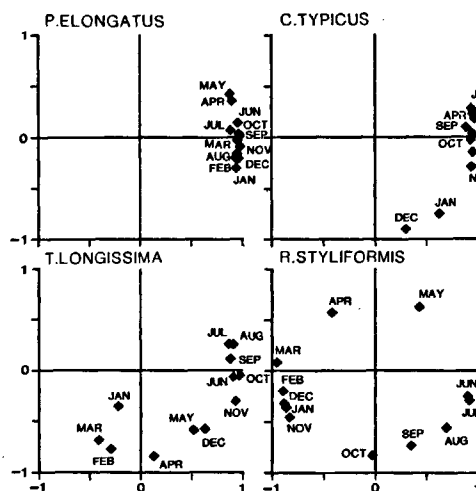

Figure 6

Four examples of 32 plots of the first two eigenvectors representing variations in the extent of seasonal differentiation of geographical distribution of zooplankton and phytoplankton (see Table 2).

For all the phytoplankton species listed in Table 1 which occur in at least 10 of the 12 areas and, similarly for the more abundant zooplankton taxa, long-term monthly means were calculated for each of the 12 areas shown in the chart in Figure 1. These data were arrayed into a table for each species each having a row for each calendar month and a column for each area. For each species, a principal components analysis was performed, based on the correlations between rows (months). For each species a scatter plot of the first two eigenvectors was produced, four of which are shown in Figure 6. The plots were ranked on the basis of the extent of the scatter of the points. The plot for *Skeletonema costatum* showed no systematic seasonal pattern and was excluded from the rank which is listed in Table 2. The plots in Figure 6 relate to the taxa ranking 1, 10, 22 and 32 in the table.

At the top of the rank are species which show considerable similarity between winter and summer. The top

Table 2

Rank of phytoplankton and zooplankton taxa on the extent of seasonal variation in geographical distribution.

1.	*Pseudocalanus elongatus*
2.	*Ceratium macroceros*
3.	*Calanus helgolandicus*
4.	*Chaetognatha*
5.	*Calanus finmarchicus*
6.	*Temora longicornis*
7.	*Metridia lucens*
8.	*Limacina retroversa*
9.	Total copepods
10.	*Centropagos typicus*
11.	*Ceratium tripos*
12.	*Calanus* spp. Stages V-VI
13.	*Calanus* All stages
14.	*Euphausiacea*
15.	*Ceratium horridum*
16.	*Rhizosolenia hebetata semispina*
17.	*Dactyliosolen mediterraneus*
18.	*Phaeoceros* spp.
19.	*Acartia clausi*
20.	*Rhizosolenia alata alata*
21.	*Hyperiidea*
22.	*Thalassiothrix longissima*
23.	*Rhizosolenia imbricata shrubsolei*
24.	*Nitzschia seriata*
25.	*Nitzschia delicatissima*
26.	*Ceratium furca*
27.	*Ceratium lineatum*
28.	*Ceratium fusus*
29.	*Thalassionema nitzschioides*
30.	*Hyalochaete* spp.
31.	*Thalassiosira* spp.
32.	*Rhizosolenia styliformis*

Figure 7

Histograms of the average power spectra of principal components of the annual fluctuations in abundance (1958 to 1980) of the six most persistent zooplankton taxa and for the diatom group of phytoplankton.

six species show average correlations between winter and summer months of over 0.7 (for 12 areas). In the middle of the rank, *Ceratium horridum* to *Dactylosolen mediterraneus,* the correlations between winter and summer are about zero, while at the bottom of the rank they are less than − 0.5. The increase in the scatter of the points in the plots passing down the rank is clearly shown by the examples given in Figure 6.

The main effect of persistence on year-to-year fluctuations is to increase the proportion of variability associated with long wavelengths (Colebrook, 1981). For the zooplankton taxa listed in Table 2 (omitting *Calanus finmarchicus* and *C. helgolandicus* for which data are available only since 1958), power spectra of the annual fluctuations in abundance were calculated for each of the 12 areas shown in the chart in Figure 1. These taxa were ranked with respect to the extent of long wavelength variability, based on the plots of the power spectra. This rank was compared with that of the same taxa in Table 2. The correlation (Spearmans' ϱ) was 0.67 which is significant at the 2 % level. If *Temora longicornis,* which because of its limited geographical distribution may be too high in Table 2, is omitted, then the correlation increases to 0.85 for 11 species which is significant at the 0.1 % level. This relationship clearly supports the assumption that the extent of seasonal differentiation of geographical distribution provides an index of the extent of persistence.

In the rank in Table 2, only two species of phytoplankton, *Ceratium macroceros* and *Ceratium tripos* occur in the section of the rank associated with positive correlations between winter and summer; all the others show zero or negative correlations suggesting little or no persistence from year to year. Given the much shorter
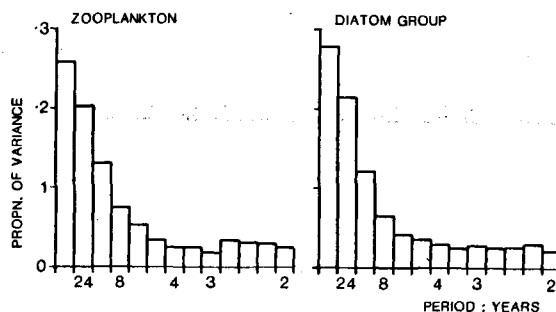
generation times of phytoplankton as compared with most zooplankton species this is not surprising.

However, the Diatom group of species all show patterns of annual fluctuation in abundance containing, as can be seen from Figure 3, a high proportion of long wavelength variability. Figure 7 shows histograms of the average power spectra of the first principal components of the top six zooplankton taxa in the rank based on the extent of long wavelength variability, compared with the average spectrum for the Diatom group of species. Both spectra show 72 % of the total variability associated with wavelengths greater than 6 years.

For the zooplankton a significant proportion of this is attributable to inherent persistence. The phytoplankton, on the other hand, do not show any inherent persistence from year to year and the origin of the long wavelength variability in the phytoplankton presents a problem. If the abundance of zooplankton is determined by that of the phytoplankton through grazing or if both phytoplankton and zooplankton are independently determined by common environmental forcing, or in any combination of these alternatives, the persistence shown by the zooplankton should result in their showing a higher proportion of long wavelength variability thant the phytoplankton. The results presented in Figure 7 show that they do not. The almost inescapable conclusion is that the abundance of phytoplankton is influenced by that of the zooplankton. Instead of visualizing zooplankton and phytoplankton as being respectively dependent and independent variables through the obvious feeding relationship there appears to be a more complex connection involving feed-back from the zooplankton to the phytoplankton thus influencing the annual levels of abundance.

Colebrook (in press) shows that, within the seasonal cycle over a large area of the North-East Atlantic (between about 45 and 58°N) following the spring bloom, the stock of phytoplankton remains fairly constant for a period of about four months. Presumably the zooplankton are grazing at a rate more or less equal to the production of the phytoplankton. It is difficult to conceive how such a system could remain stable for a period as long as four months without some feed-back from the zooplankton.

The mechanism of the feed-back is most probably nutrient recycling from faecal material and other excretory products of the zooplankton.

Very little information is available about the extent of nutrient recycling in temperate open ocean waters. For the Atlantic most estimates refer to upwelling regions (see, for example Smith, Whitledge, 1977). For a station in the North Pacific Jawed (1973) estimated that about 36 % of the total nitrogen requirement of the phytoplankton in summer was supplied by recycling and Eppley (1981) quotes values for the ratio of regenerated production to total production ranging from less thant 0.4 for upwelling regions to over 0.95 for the central North Pacific. All these estimates, however, refer to tropical or sub-tropical waters.

Less direct evidence for nutrient recycling in the northern North Sea is provided by Krause (1981) who found high concentrations of copepod faecal pellets in the top 30 m which appeared to conflict with estimates of their sinking rates (Smayda, 1969). Krause concluded that much of the faecal material must be recycled.

The production of faecal pellets by Calanus finmarchicus and Pseudocalanus elongatus has been estimated to be about 15 % of body weight per day (Petipa et al., 1970). In addition to faecal pellets as a source for recycled nutrients, Copping and Lorenzen (1980) have shown, in an experimental system, that as much as 18 % of the daily phytoplankton loss appears as dissolved organic material primarily from cells damaged while being eaten.

Thus, while it remains to be proved that the rate of nutrient recycling is sufficient to produce the apparent dependence of phytoplankton on the stock of zooplankton in temperate seas, this does appear to be a possibility.

DISCUSSION

This study provides a convenient opportunity to summarise the progress towards the identification of the processes involved in determining the year-to-year changes in the abundance of the plankton of the North-East Atlantic and the North Sea. Many of the aspects considered in recent studies are brought together here : the rôle of climatic changes relating to the environment, the origin of annual changes within the dynamics of the seasonal cycle, the effects of persistence and, introduced in this study, the possible rôle of nutrient recycling in providing feed-back from zooplankton to phytoplankton.

With respect to the effects of changes in climate, the annual fluctuations of the Ceratium group of species are correlated with changes in sea-surface temperature and with variations in the frequency of cyclonic weather. Colebrook (1978) showed that major elements in the annual fluctuations of the zooplankton were correlated with changes in sea-surface temperature, east of about 20°W, and also with variations in the frequency of westerly weather. Due to changes in the deployment of the Ocean Weather Ships in recent years, it is not possible to update the particular estimate of sea surface temperature used in the earlier investigation; data on the frequency of westerly weather are however available

ble, permitting the addition of five more years (1976-1980) to the time-series. In the previous study it was found that there was a positive correlation between long-term trends in the zooplankton and the weather index, together with a simultaneous negative correlation in the wave band between 3 and 4 years. No change in this interpretation is necessary following the updating of the series. As an example, Figure 8 a shows the first principal component of the abundance of 17 zooplankton taxa in area Cl (see Fig. 1) with superimposed, the changes in the frequency of westerly weather for the period 1948 to 1980. The long-term trends in both variables (extracted by eigenvector filters, Colebrook, 1978) are shown in Figure 8 b while the residuals are shown in Figure 8 c. A Maximum Entropy cross spectral analysis (Strand, 1977) of the data confirms that clear coherence between the two variables is found at the long wavelengths and again at about 3.5 years. The phase relationships confirm the obvious positive relationship at the long wave lengths; for the wave band around 3.5 years the phases are consistent with a negative relationship, with the westerlies leading the zooplankton by between 6 months and a year.

The power spectra of the two variables are also presented in Figure 8. While the mechanism of the relationship between the plankton and the frequency of westerly weather has yet to be established, it may be significant that the difference between the spectra is precisely what would be expected in the response of a persistent variable (the zooplankton) to forcing with a frequency structure similar to that of the westerlies. The peaks in the spectra correspond with respect to wavelength but not amplitude, the zooplankton showing an appreciably higher proportion of long wavelength variability.

With respect to the origin of annual fluctuations within the dynamics of the seasonal cycle, the emphasis has been on attempts to identify a particular season of the year which has a dominant influence on the annual levels of abundance. For the oceanic waters of the North-East Atlantic, the spring bloom of phytoplankton appears to be underexploited by grazing (Cole-
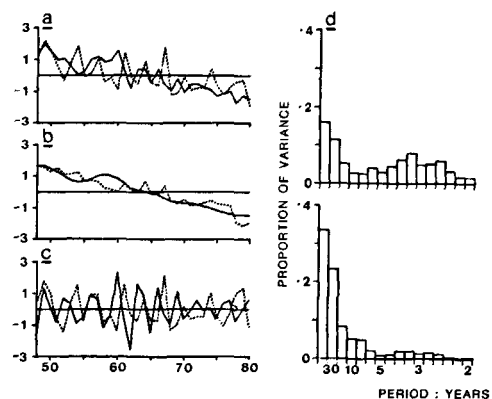

Figure 8

a : Graphs of (solid line) the first principal component of the annual fluctuations in abundance (1948-1980) of zooplankton in area C2 (see Fig. 1) and (dashed line) the variations in the frequency of westerly weather over the British Isles.
b : Long-term trends in the graphs in a extracted by eigenvector filters.
c : The residual variability following the removal of the trends.
All variables standardized to zero mean and unit variance.
d : Histograms of the power spectra of the variables plotted in a.

brook, 1979) and its amplitude is presumably nutrient limited. During the spring increase of the zooplankton, the populations of at least two major species increase exponentially at a rate that appears to be determined primarily by temperature (Colebrook, 1982). It seems unlikely, therefore, that the processes involved in the spring increase could produce the observed close relationship between the year-to-year changes in the abundance of zooplankton and phytoplankton.

The recognition of the extent of persistence in the stocks of many species of zooplankton suggests that events in winter may be important, in that relatively small changes in the stocks may be magnified into marked differences in the following summers. This would seem to imply, however, that the close coupling between zooplankton and phytoplankton in summer is primarily a one-way process with negligible feed-back from phytoplankton to zooplankton through grazing. On the whole, it seems most likely that it is the summer period, following the spring bloom, that has the most pronounced effect on the annual levels of the stocks. During this period, the changes in the zooplankton can be interpreted as being modulated by a feed-back loop involving nutrient regeneration, phytoplankton growth and grazing. On a longer time-scale the annual levels are influenced by persistence from year-to-year through the overwintering stocks.

There remain a number of gaps. The zooplankton-phytoplankton system requires description in terms of nutrient dynamics and pathways, particularly with respect to nutrient regeneration. Secondly, the key to persistence lies in the overwintering stocks and it is not at all clear how these are maintained. Thirdly there is a major gap between correlations with indices of climatic change and descriptions of the physical processes that have a direct effect on the annual levels of the plankton.

Aknowledgements

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