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Continuous plankton records: relationships between species of phytoplankton and zooplankton in the seasonal cycle

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Abstract

Seasonal fluctuations in abundance and their geographical variations in the north-east Atlantic Ocean and the North Sea for 49 taxa of both phytoplankton and zooplankton have been studied by multivariate techniques. Most of the observed variability in both seasonal and geographical fluctuations in abundance can be attributed to differences between the taxa with respect to population growth rates modulated by temperature coupled with the distribution of overwintering stocks, with the overall pattern also influenced by the timing of the establishment and breakdown of vertical stability in the water column. The observations indicate that for any species, the similarity between its seasonal cycles in the various areas, which represent a wide range of hydrographic regimes, is appreciably greater than any differences induced by interaction between the species in any particular area.

Introduction

Colebrook (1982 c) presented a study of seasonal variations in the distribution and abundance of the plankton of the North Atlantic Ocean and the North Sea. The data were derived from the Continuous Plankton Recorder survey (Glover, 1967) and the study was based on the presentation of the seasonal variations of a relatively small number of species for a large area, using a fairly high resolution (a grid of 1° latitude by 2° longitude).

In the present study, an alternative approach has been adopted. A total of 49 species and other taxonomic entities of both phytoplankton and zooplankton are included (see Table 1), but for a more restricted area of the north-east Atlantic Ocean and the North Sea and a much coarser set of sub-areas (see Fig. 1).

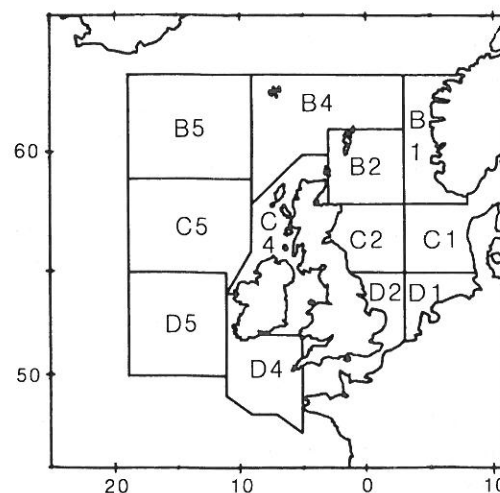The objectives of both studies were, however, much the same: to contribute towards an interpretation of events occurring within the seasonal cycle in order to provide information about the origins of year-to-year variations in the abundance of the plankton of the area (see, for example, Colebrook, 1982 a). The earlier study considered only the more abundant species and provided information about the seasonal variations of the plankton as a whole, while here forms of relationship between species are considered and the way these contribute to the pattern of the seasonal cycle.

Materials and methods

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

Fig. 1. Chart of north-east Atlantic Ocean and North Sea, showing area sub-divisions of the survey used in data processing

Table 1. Alphabetical list of taxa included in the study, with abbreviations used in Figs. 2 and 6

Phytoplankton		Zooplankton	
Asterionella japonica	AJ	*Acartia clausi*	AC
Ceratium furca	FC	*Calanus finmarchicus* V-VI	CF
Ceratium fusus	FS	*Calanus helgolandicus*, V-VI	CH
Ceratium horridum	HR	*Candacia armata*	CD
Ceratium lineatum	LI	*Centropages typicus*	CT
Ceratium longipes	LG	Chaetognatha	CG
Ceratium macroceros	MC	*Clione limacina*	CL
Ceratium tripos	TR	*Corycaeus* spp.	CY
Chaetoceros (Hyalochaete) spp.	HY	*Euchaeta hebes*	EH
Chaetoceros (Phaeoceros) spp.	PH	*Euchaeta norvegica*	EN
Dactyliosolen mediterraneus	DM	Euphausiacea	EP
Nitzschia delicatissima	ND	*Evadne* spp.	EV
Nitzschia seriata	NS	Hyperiidea	HY
Rhizosolenia alata alata	RA	Larvacea	LV
Rhizosolenia alata indica	RI	*Limacina retroversa*	LR
Rhizosolenia alata inermis	RN	*Metridia lucens*	ML
Rhizosolenia hebatata semispina	RP	*Neocalanus gracilis*	NG
Rhizosolenia imbricata shrubsolei	RB	*Oithona* spp.	OI
Rhizosolenia styliformis	RT	*Oncaea* spp.	ON
Skeletonema costatum	SK	*Pleuromamma borealis*	PB
Thalassionema nitzschioides	TN	*Pleuromamma gracilis*	PG
Thalassiosira spp.	TS	*Pleuromamma robusta*	PR
Thalassiothrix longissima	TL	*Podon* spp.	PD
		Pseudocalanus elongatus	PP
		Rhincalanus nasutus	RN
		Temora longicornis	TL
		Total Copepoda	CP

1975). Samples are collected at the standard depth of 10 m and, as far as possible, the organisms are identified to species; however, for some taxonomic groups, identification is to genus, family or even higher categories.

The data used in this study are estimates of abundance, as 25 yr means (phytoplankton) and 35 yr means (zooplankton), for each of the species and other taxonomic entities listed in Table 1. They are based on log-transformed counts of samples averaged for each of the 12 areas shown in the chart in Fig. 1 and for each calendar month.

In most of the processing, data for the phytoplankton and zooplankton are treated separately and, from the point of view of understanding the various analyses, are best regarded as a pair of three-dimensional arrays structured as tables containing rows and columns of estimates of abundance.

To provide the basis for this study, sets of principal components analyses were performed with the data arranged as:

(1) Tables for each area, containing a row for each taxon and a column for each month.

(2) Tables for each month, containing a row for each taxon and a column for each area.

(3) Tables for each taxon, containing a row for each area and a column for each month.

(4) Tables for each taxon, containing a row for each month and a column for each area.

Nearly 150 analyses were performed, and it is clearly impractical and unnecessary to present all the results obtained. What has been done is to try to reduce this mass of information by a variety of means and to present what appear to be the most significant results. It should be stressed that behind the relatively simple presentations included in the figures is a considerable body of data that have been used to confirm that the various short-cuts, groupings, etc. given in the diagrams represent reasonable procedures and representative selections.

In view of the confusion in current literature about the naming of the products of principal components analyses, in this paper I have followed Kendall and Stuart (1966) and use the term "vector" for the eigenvectors of the correlation matrix and restrict the use of the term "component" to the linear transforms of the original data.

Results and discussion

Area analyses: relationships between taxa with respect to seasonal variations in abundance

With the data arranged in tables for each area, containing a row for each species and a column for each calendar month, principal components analyses were performed on each table, with separate analyses for phytoplankton and zooplankton, based on correlation matrices between rows.
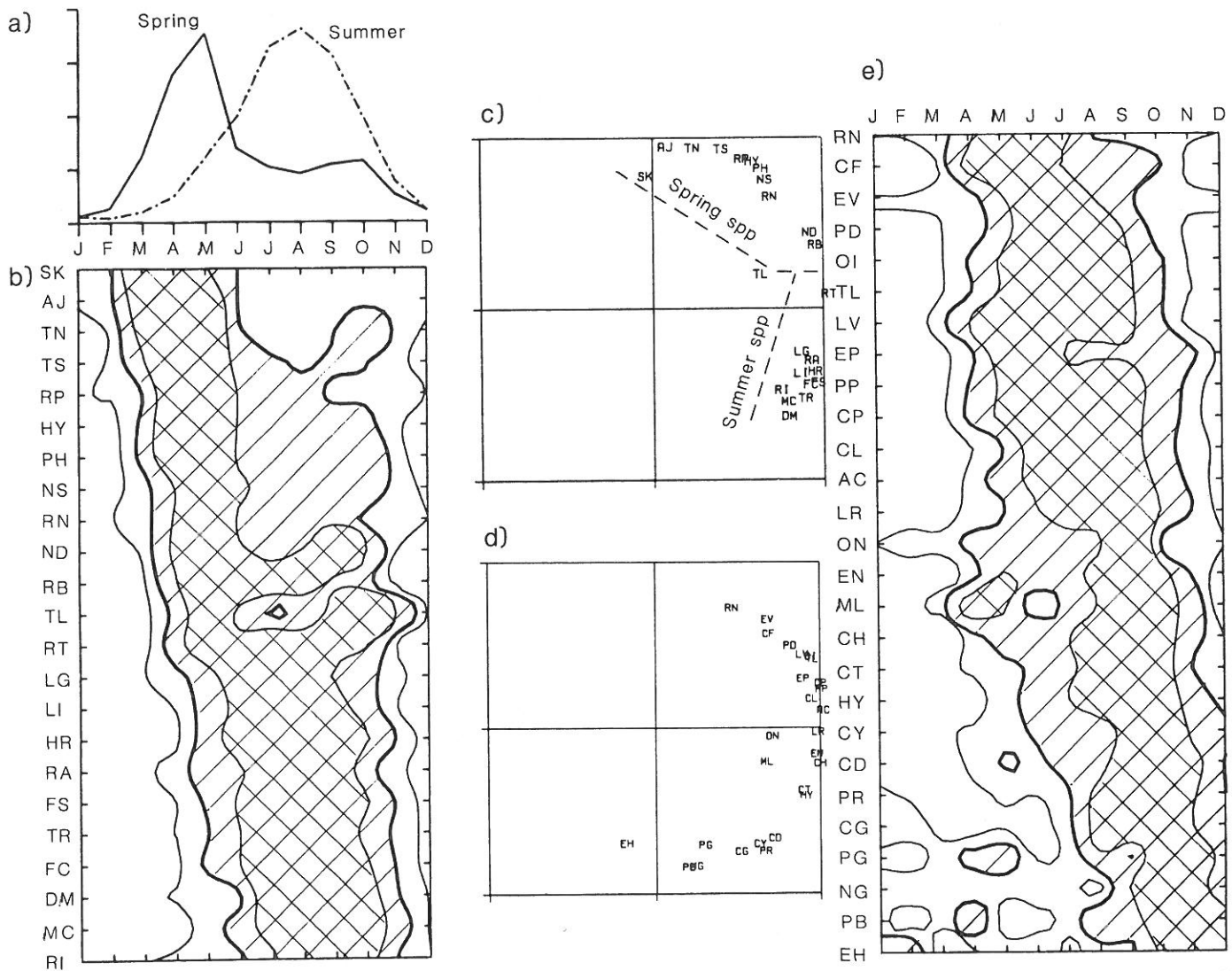
Fig. 2. Seasonal cycles in abundance of phytoplankton and zooplankton, averaged for all areas shown in Fig. 1. (a) Average seasonal cycles for spring and summer groups of phytoplankton. (b) and (c) Phytoplankton, (d) and (e) zooplankton; (b) and (e) are contour diagrams showing the standardised seasonal cycles of each taxon, ranked on the basis of the vector plots in (c) and (d). Abbreviations of taxa names are given in Table 1. Contour levels are $+0.4$ (cross-hatched), -0.8 (hatched) and -0.8 for phytoplankton, and $+0.6$ (cross-hatched), -0.3 (hatched) and -0.8 for zooplankton. The values are deviations from a mean of zero in standard deviation units (see "Results and discussion" for further details)

The resulting components were patterns of monthly variation in abundance and the vectors represent the relationships between the taxa with respect to the components.

As might be expected for temperate waters with a very pronounced seasonal signal, the first components account for a fairly high proportion (about 50% of the total variability) and in the associated vectors, containing a total of 531 values, only 9 were negative; this indicates a high degree of coherence between the species.

The second components represent about a quarter of the total variability (averaging 30% for the phytoplankton and 24% for the zooplankton) and indicate differences between the taxa with respect to timing within the seasonal cycle.

Plots of first against second vectors were produced and these show considerable similarity between the areas and,

in addition, for the phytoplankton, most of the areas show two distinguishable groups of taxa fairly constant in composition, with only three taxa switching between groups in a few areas.

In view of the similarity between the areas and in order to simplify the presentation of the results of these analyses, the data tables were averaged (confounding differences between areas) and principal components analyses were performed for the phytoplankton and zooplankton, respectively.

Fig. 2 contains plots of first against second vectors for these analyses. In the diagram for the phytoplankton (Fig. 2c) the two groups are indicated based on the analyses for each area, omitting *Thalassiothrix longissima* and assigning the three taxa that switched groups to the one in which they occurred most frequently in the area

analyses. Examination of plots of the seasonal cycles of the individual taxa showed that the distinction between the groups is basically between taxa associated with the spring bloom and those that peak appreciably later in the year. The seasonal cycles of the averages of the two groups are shown in Fig. 2 a.

Fig. 2 b is a contour diagram of the seasonal cycles of abundance of the phytoplankton, with differences in abundance between the taxa removed by reducing each row to zero mean and unit variance, with the taxa ranked in the order in which they occur in the vector plot (Fig. 2 c) and with minor changes to the order, by trial and error, to achieve smooth contours.

Fig. 2 d and e are equivalent diagrams for the zooplankton. In this case there are no clear groupings of species, but rather a more or less continuous sequence. The gap between Hyperiidea (HY) and *Candacia armata* (CD) does not occur in most of the vector plots for the individual areas. In Fig. 2 e, the species are ranked, based on the order of the vector plot, with minor changes to achieve smooth contours.

Comparing the two contour diagrams (Fig. 2 b and 2 e), both show a remarkably uniform progression in the peak of the seasonal cycle from early to late in the year, although, throughout, the phytoplankton are a month to two months earlier than the zooplankton.

For the phytoplankton (Fig. 2 b), the first two contours run nearly parallel both with each other and with the seasonal maximum for the whole of the diagram, while the timing of the final seasonal decline is more or less constant for 19 of the 23 taxa, from *Rhizosolenia semispina* (RP) to *Rhizosolenia alata indica* (RI).

The zooplankton (Fig. 2 e), on the other hand, show almost the reverse of this situation, the first two left-hand contours run nearly vertically for the first 16 taxa from *Rhincalanus nasutus* (RN) to *Metridia lucens* (ML). Only for the last 11 taxa do the contours begin to match the seasonal peak. In contrast to this, the contours illustrating the autumn decline in numbers run more or less parallel with the seasonal peak.

The main differences between the phytoplankton and the zooplankton, apart from the obvious difference in the timing of their seasonal cycles, involve the spring and the late autumn, times when there are marked changes in abundance. Thus, it might be expected that changes in geographical distribution should provide useful information about the relationships.

Species analyses: seasonal variations in geographical distribution

With the data arranged in tables for each taxon, containing a row for each month and a column for each area, principal components analyses were performed on each table based on correlation matrices between rows. The resulting components are patterns of geographical distribution and the vectors represent the relationships between months in the seasonal evolution of the geographical distributions.

In addition, analyses were performed on the averaged data for the spring and summer phytoplankton taxa, and these data provide a convenient starting point for the discussion of the seasonal changes in geographical distribution.

Fig. 3 a and b are contour diagrams, for the spring and summer groups, of the seasonal variations in abundance in each of the areas (see Fig. 1). The areas have been ranked, from left to right as oceanic (B5 to D5), shelf (B2 to D4), and North Sea (C2 to D1) and, within each subgroup, the areas are ranked from north to south. Area B1 is omitted as it does not fit into this sequence.

Fig. 3 c and d are contour diagrams of the same data, but with differences between months removed by reducing each month to zero mean and unit variance. These diagrams contain, therefore, only the relative changes in geographical distribution through the year.

It is clear that both the spring and summer groups show similar patterns of geographical change. Both show higher stocks in the North Sea in winter. Increasing abundance causes a relative shift in distribution to the shelf areas in March and April and to the open ocean by May and June. These shifts in distribution reflect the effects of the timing of the development of vertical stability in the water column (Robinson, 1970; Ellett, 1979) and of temperature on growth rate (see, for example Eppley, 1972; Smayda, 1976). The contrast in the surface temperatures between the open ocean and the North Sea is shown in Fig. 7 f. The pattern of decline occurs in a different order, with relatively low abundance in the shelf areas already apparent by June, followed by a steady shift in distribution from the open ocean back to the North Sea from July to January.

Fig. 3 f is a plot of the first against the second vectors for the combined spring and summer groups. This shows that, passing from winter to summer, the spring group is slightly ahead of the summer group, but not by as much as would be expected from the seasonal variations in abundance (Fig. 3 e). This diagram shows that the spring group increases in abundance much faster than the summer group and their peaks are separated by 3 mo. Fig. 3 f indicates that their distributions are at most only 1 mo apart, the spring group in May being similar to the summer group in June, both starting from similar distributions in January. In the second half of the year, the spring group lags behind the summer group, converging to show similar overwintering distributions by December.

Combining the evidence from Fig. 2 b, the ranked seasonal cycles, and Fig. 3 f suggests that, in spite of the considerable differences in the timings of the peaks of the seasonal cycles of the phytoplankton in any particular area, they all start to increase at roughly the same time within appreciably less than a month, and they nearly all show a final decline at about the same time. These time
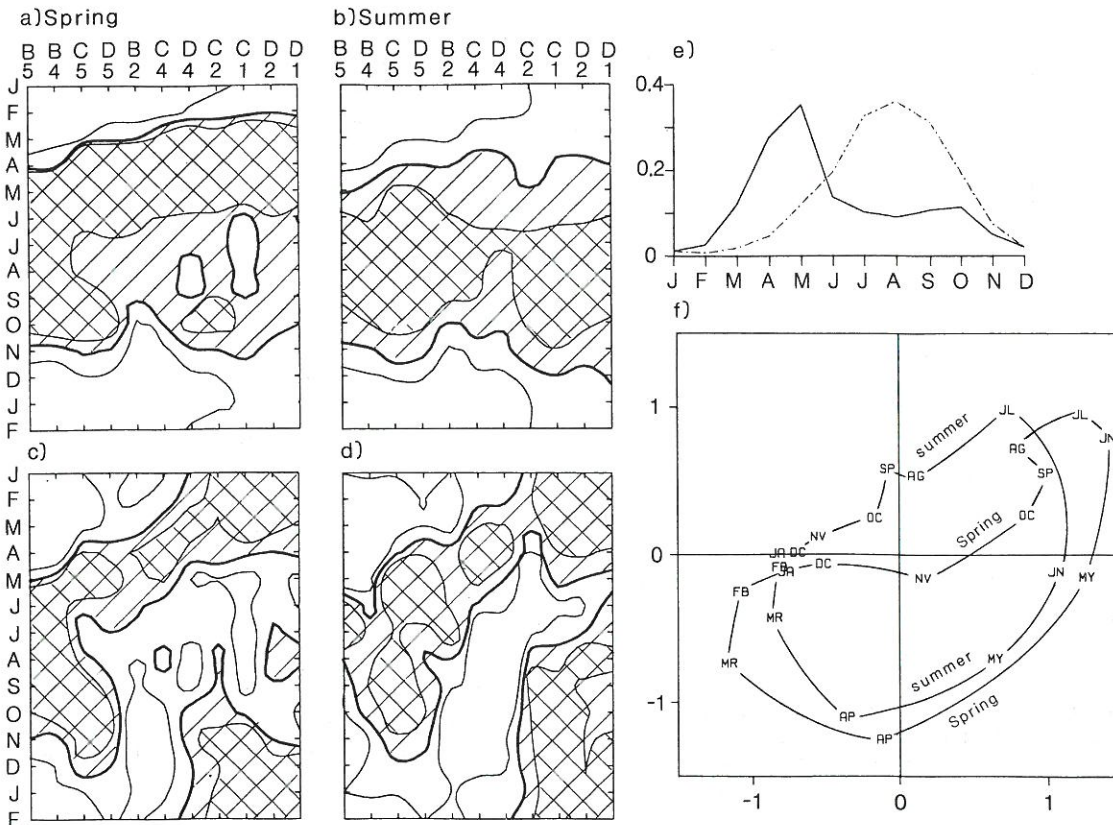
Fig. 3. Seasonal cycles of spring and summer groups of phytoplankton. Contour diagrams (a) and (b) show the seasonal cycles in each of the areas, ranked from oceanic on left to North Sea on right. Contour levels are 0.106 (cross-hatched), 0.029 (hatched) and 0.006 for spring, and 0.058 (cross-hatched), 0.037 (hatched) and 0.015 for summer, all being logarithmic means for subsamples of 1/17500 of samples of 3 m³. Contour diagrams (c) and (d) are equivalent to (a) and (b), but with data for each month reduced to zero mean und unit variance; contour levels are +0.6 (cross-hatched), −0.1 (hatched) and −0.8 for spring, and +0.5 (cross-hatched), −0.2 (hatched) and −0.7 for summer, the values being deviations from a mean of zero in standard deviation units. Scatter plot (f) shows the first two vectors of the combined data from contour diagrams (c) and (d). Graph (e) shows the average seasonal variations in abundance, for all areas in Fig. 1, of spring (continuous line) and summer (dashed line) groups of phytoplankton

limits are presumably set by the onset and breakdown, respectively, of vertical temperature stratification of the water column. This is well known for phytoplankton as a whole, but has not previously been established for all or nearly all the species that make up the phytoplankton in an area.

It follows that the prime distinction between the species that make up the spring bloom and those that peak later in the year is a difference in population growth rate, as opposed to the time at which the population starts growing.

Analyses similar to the set of principal component analyses of taxa have already been described by Colebrook (1982a). In the set described here, two more years of data and a few more taxa have been included but the results are substantially the same. In the previous study the taxa were ranked on the extent of seasonal variation in their geographical distributions, based on the extent of the scatter of points in vector plots. In this rank, the three taxa showing the greatest range of variation were *Hyalochaete* spp., *Rhizosolenia styliformis* and *Thalassiosira* spp. Plots of the first against second vectors for these taxa are given in Fig. 4 showing, in each case, a roughly circular pattern of months. Also shown in Fig. 4 is a vector plot for the

average of the three taxa. This is probably a reasonable estimate of the fullest expression of seasonal variation in geographical distribution shown by any planktonic organism in the study area, and may be used as a standard for comparison with the variations in the distributions of the other taxa.

The comparisons were done by performing a principal components analysis for each taxon, whereby tables contained data for the seasonal variations in geographical distribution of the taxon together with average data for the three taxa, representing the standard. A representative selection of plots of first against second vectors from these analyses are given in Fig. 5. In these diagrams, the points for the average of the three taxa are joined by a continuous line representing the "standard" profile in terms of the vector space. The extent of the scatter of points for the individual taxa represents the range of geographical variation through the year, and their locations relative to the standard profile indicate the relationship between the geographical distribution and the standard.

The rank presented by Colebrook (1982a) indicated that, with few exceptions, the phytoplankton show a greater range of variation than do the zooplankton. This is confirmed by the present study, which also demonstrates
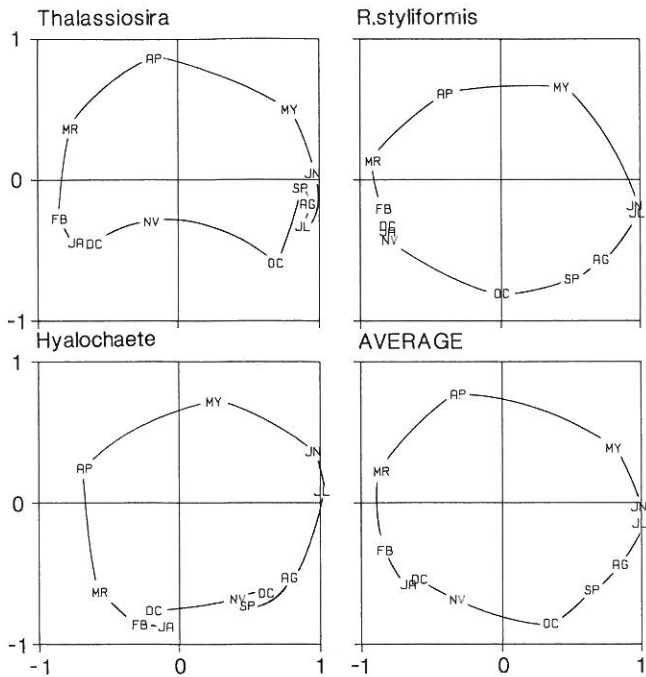
Fig. 4. Vector plots for *Thalassiosira* spp., *Rhizosolenia styliformis*, *Chaetoceros* (Hyalochaete) spp. and the average of these taxa, showing the relationships between months with respect to seasonal variations in geographical distribution. JA: January, ... DC: December

that the vector points for most of the phytoplankton fall on or inside the standard profile. Also, the phytoplankton can be arranged in a loose sequence of increasing variability, with their vector points generally coincident with the standard in winter, and with the other months conforming with a reduced version of the standard profile. For the taxa showing the most variation, the months are also coincident with the standard profile in summer.

The zooplankton, however, show a very different picture. For most of the taxa the vector points fall on or outside the standard profile and are associated with a limited extent of the profile, usually confined to a span of less than 3 mo. Many of the zooplankton are associated with the March to May section of the profile, and four examples of these are included in Fig. 5. Fig. 5 also includes one example (*Pseudocalanus elongatus*) of several taxa showing very limited ranges of variation, all of which are equivalent to the standard winter. Also shown is the vector plot for *Acartia clausi*, one of the few zooplankton taxa to show extensive geographical variation and roughly equivalent to the standard autumn.

It is clearly impractical to present the vector plots of all these analyses, as over 50 taxa are involved. However, an interesting aspect of the relationship between phytoplankton and zooplankton is involved and, therefore, further comparisons with the standard profile were performed using average geographical distributions to simplify the problem of presentation. For the zooplankton, the averages for all twelve months were calculated, while for the phytoplankton data for April to September were averaged.

This excludes the winter period, when nearly all the phytoplankton look like the standard winter.

The resulting vector plots are given in Fig. 6. The geographical distributions of both the phytoplankton and the zooplankton conform more or less to the standard profile, although the zooplankton do show an extended distribution on the second vector axis. Of greater significance is the scatter of the taxa around the standard profile. The zooplankton are more evenly distributed, with some concentration near April and September. For the phytoplankton, however, only 2 taxa (*Rhizosolenia alata alata* and *Skeletonema costatum*) occur on the profile between February and May, as opposed to 12 zooplankton taxa. All the remaining taxa occur between May and February with an obvious concentration near June and July.

Superimposing on these diagrams the ranks of the taxa on the timing of their seasonal peaks in abundance (Fig. 2) indicates that, in spite of the apparent conformity of the distributions to a seasonal pattern, there is no relationship between the geographical distributions and the timing of the seasonal cycles. For example, *Calanus helgolandicus* (CH) occurs close to March in the standard profile, while its peak abundance is in September. Similarly, the group of phytoplankton taxa corresponding to June and July contains taxa varying in rank from 3 to 21 in Fig. 2b.

The apparent mismatch between the geographical distributions of the phytoplankton and zooplankton is highlighted in Fig. 7, which contains contoured diagrams in the same format as those in Fig. 2. Fig. 7a shows seasonal variations in the geographical distribution corresponding to the standard profile (i.e., the average of *Hyalochaete* spp., *Rhizosolenia styliformis,* and *Thalassiosira* spp.); Fig. 7c shows the seasonal variations in the abundance of the average of all the zooplankton taxa; and Fig. 7b shows the seasonal variation in the geographical distribution of the average of all the zooplankton taxa (i.e., the data in Fig. 7c) with each month reduced to zero mean and unit variance. There is clearly a big difference between Fig. 7a and b.

To set this difference in the context of the relative abundance of phytoplankton and zooplankton through the seasonal cycle, the graphs in Fig. 7d and e show the seasonal cycles for the oceanic (B5 to D5), shelf (B2 to D4) and North Sea (C2 to D1) zones, respectively, for the spring and summer groups of phytoplankton (d) and the average of all the zooplankton taxa (e). These graphs show that the apparent mismatch between the phytoplankton and the zooplankton is due to differences that are quite marked but are, at the same time, fairly small compared with the amplitude of the seasonal cycles.

General discussion

The results discussed above and presented in Figs. 4 to 7 pose a number of questions:

(1) Why do most of the zooplankton show much less seasonal variation in geographical distribution than most of the phytoplankton?
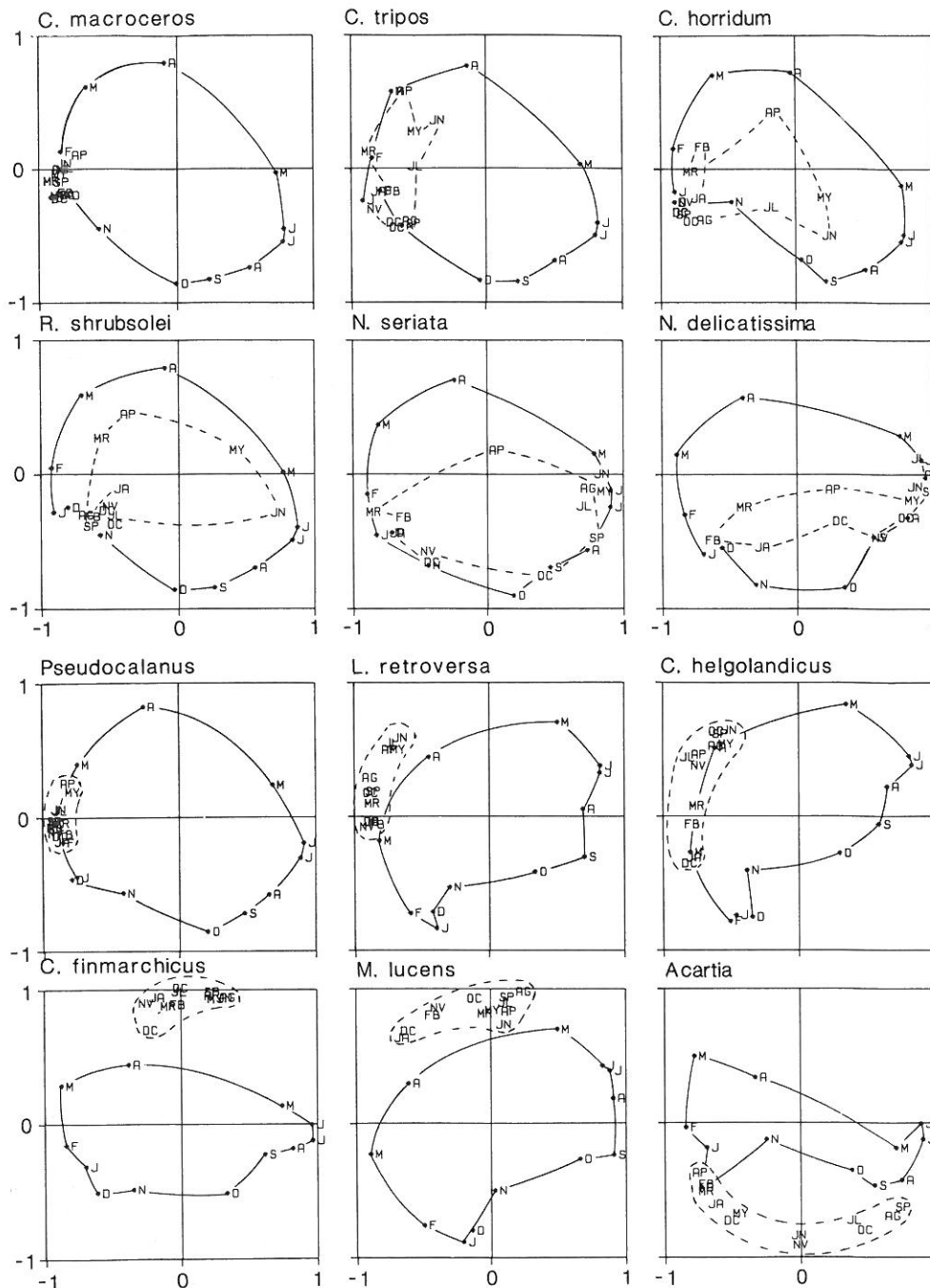
Fig. 5. Vector plots showing relationships between months with respect to seasonal variations in geographical distribution for 6 phytoplankton and 6 zooplankton taxa, compared with a standard sequence (continuous lines), being the average of the 3 taxa shown in Fig. 4. The full names of the taxa are listed in Table 1, and their vectors are either enclosed or joined in sequence by dashed lines

(2) Why is there an apparent mismatch between the geographical distributions of the phytoplankton and the zooplankton?

(3) In spite of the conformity of the geographical distributions of both the phytoplankton and the zooplankton to a pattern clearly relating to seasonal phenomena, why is there no relationship between the geographical distributions and the timing of the seasonal cycles?

The answers to the first two questions may be connected. Colebrook (1982 b), in a study of the seasonal cycles of *Acartia clausi* and *Pseudocalanus elongatus,* suggested that temperature and overwintering stocks played a major role in determining the distribution and dynamics of these species. In both the 1982 b study and in Colebrook (1982 a) it was argued that zooplankton stocks exhibit persistence. The implication is that inherent limitations to the rate of growth of populations reduce the ability of species to respond to the relatively rapid changes in environmental conditions associated with the seasonal cycles, in particular, of temperature and vertical stratification.

It follows that the factors that influence the size of overwintering stocks play a major role in determining both the distribution and the seasonal variations in the distribution of species that are limited in this way.

Fig. 7 e shows that for the average of all the zooplankton the overwintering stocks (for January, February and March) are lowest for the open ocean, higher for the shelf
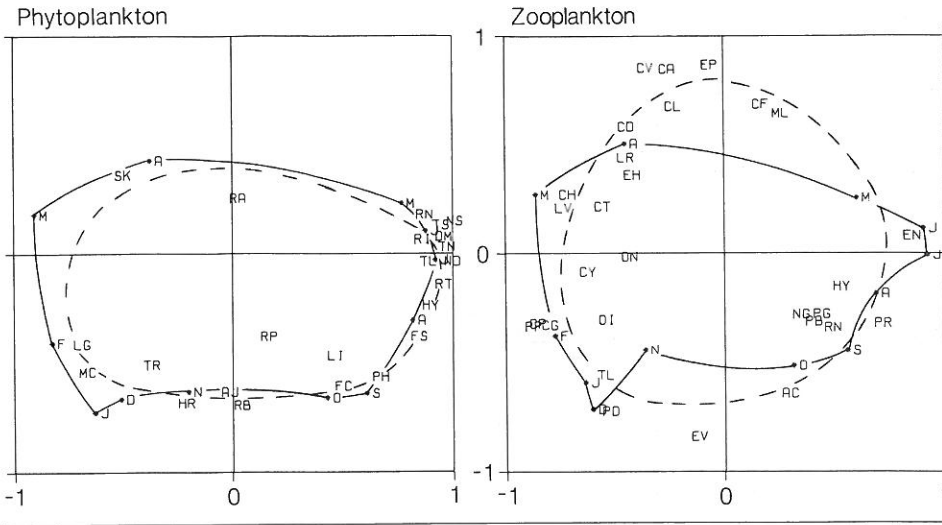
Fig. 6. Vector plots of geographical distributions of phytoplankton and zooplankton, with the sequence of taxa indicated by dashed lines, compared with the standard seasonal cycle (continuous line); see "Average" in Fig. 4. Abbreviations are given in Table 1 and months here are abbreviated as J: January, ... D: December
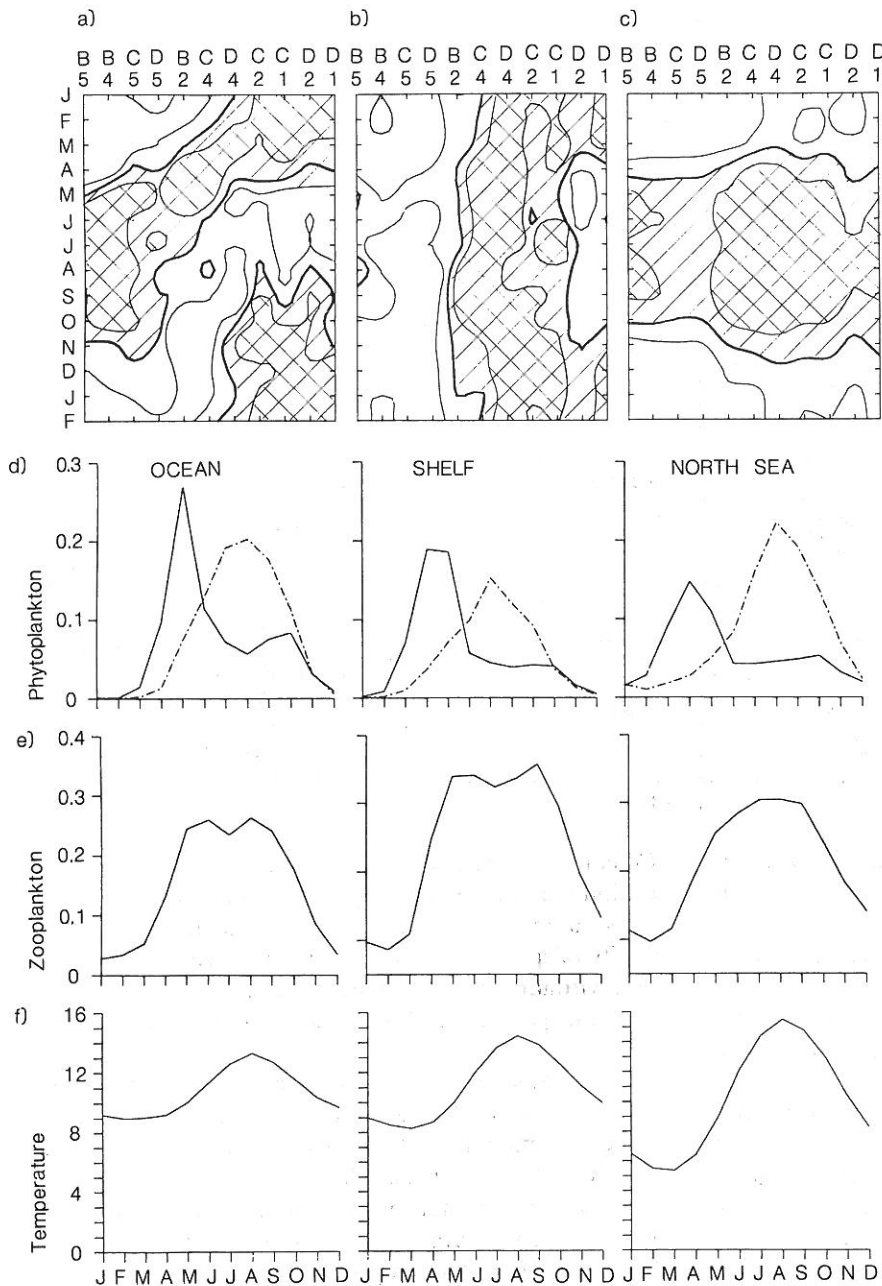

Fig. 7. Contour diagrams (a), (b) and (c) are similar in arrangement to those in Fig. 3; (a) Standard seasonal variation in geographical distribution (see "Average" in Fig. 4); the contour levels are +0.6 (cross-hatched), −0.2 (hatched) and −0.8 standard deviation units. (b) Average for all the zooplankton taxa with data for each month reduced to zero mean and unit variance; contour levels are +0.7 (cross-hatched), +0.1 (hatched) and −0.9 standard deviation units. (c) As (b), but data not standardised; contour levels are 0.26 (cross-hatched), 0.17 (hatched) and 0.10 logarithmic means for subsamples of 1/40 of samples of 3 m³. (d) Seasonal cycles of spring (continuous lines) and summer (broken lines) groups of phytoplankton for oceanic, shelf and North Sea zones, as logarithmic means for subsamples of 1/7 500 of samples of 3 m³. (e) Seasonal cycles of average for all zooplankton taxa for same zones, as logarithmic means for subsamples of 1/40 of samples of 3 m³. (f) Seasonal variations in sea-surface temperature (°C), also for the same zones
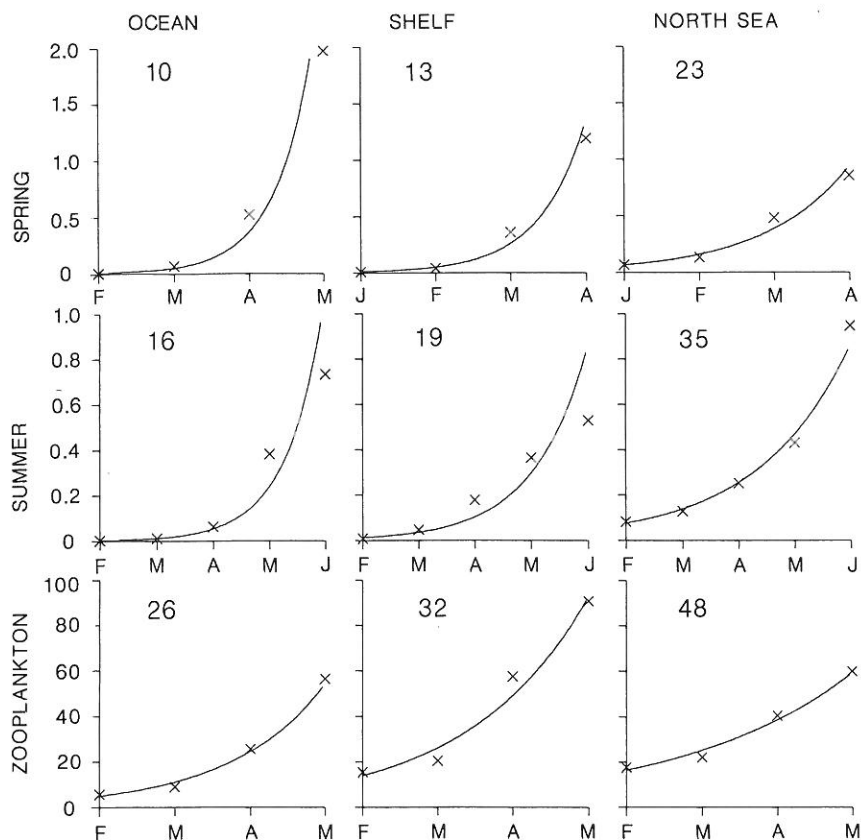
Fig. 8. Exponential curves fitted to sub-sets of data plotted in Fig. 7 (d) and (e), representing the first few months following winter minima. Ordinates are numbers in subsamples of 1/7 500 of samples of 3 m³ for the spring and summer phytoplankton and numbers per sample for zooplankton. Values inside graphs are growth rates, expressed as doubling times in days

and highest in the North Sea. The corresponding temperatures are 9.0°, 8.5° and 5.8 °C; the North Sea in winter is appreciably colder than the shelf and oceanic areas. Fig. 6 shows that most of the more abundant zooplankton taxa have distributions corresponding to the standard winter and early spring. The only abundant taxa that do not are *Acartia clausi* and Hyperiidea, and both of these show extensive seasonal variations in geographical distribution (the vector diagram for *A. clausi* is given in Fig. 5) and both overwinter in the North Sea.

It is suggested, therefore, that the limited seasonal variation in geographical distribution shown by most zooplankton is due to inherent limitations in population growth rate; that the pattern of distribution of zooplankton is strongly influenced by the distribution of overwintering stocks and, within these, some taxa are limited to the shelf areas to avoid the low winter temperatures in the North Sea (see Fig. 7 f).

This also goes some of the way towards explaining the mismatch in distribution between the phytoplankton and the zooplankton.

Fig. 8 shows, for the spring and summer groups of phytoplankton and for the average of all the zooplankton taxa and, for the oceanic, shelf and North Sea zones, exponential curves fitted to the first three or four months following the winter minima. The data are subsets of those plotted in Fig. 7 d and e. Entered on each graph in Fig. 8 is the growth rate converted to doubling time in days.

Given only four or five points in each graph, no great precision can be claimed for the estimates of doubling

times, but relative to each other they are probably satisfactory.

All three entities show the shortest doubling times for the open ocean, almost certainly reflecting the mild winters of the open waters of the north-east Atlantic. The doubling times for the shelf are a few days longer, but those for the North Sea are more or less twice as long. Given that the doubling times refer to periods of 100 plus days it is clear that the fairly high final stocks of all three entities in the North Sea is largely a function of the high initial, overwintering stocks.

There is also a marked difference between the phytoplankton and the zooplankton in the levels of overwintering stocks in the shelf areas. High overwintering stocks of phytoplankton appear to be much more limited to the North Sea than those of the zooplankton.

The low overwintering stocks of phytoplankton coupled with the fact that growth in the open ocean is at least a month behind the shelf (see Fig. 7), giving temperature differences of 1 to 1.5 C° for the equivalent states of growth between the zones, may be sufficient to account for the observed differences in doubling times. The available data, however, are not capable of providing quantitative arguments to demonstrate this.

Although such arguments may explain the relatively low phytoplankton stocks over the shelf they do not explain the paucity of phytoplankton species with distributions equivalent to the shelf zooplankton. But, given the greater mobility throughout the year of the geographical distributions of the phytoplankton, it seems possible that
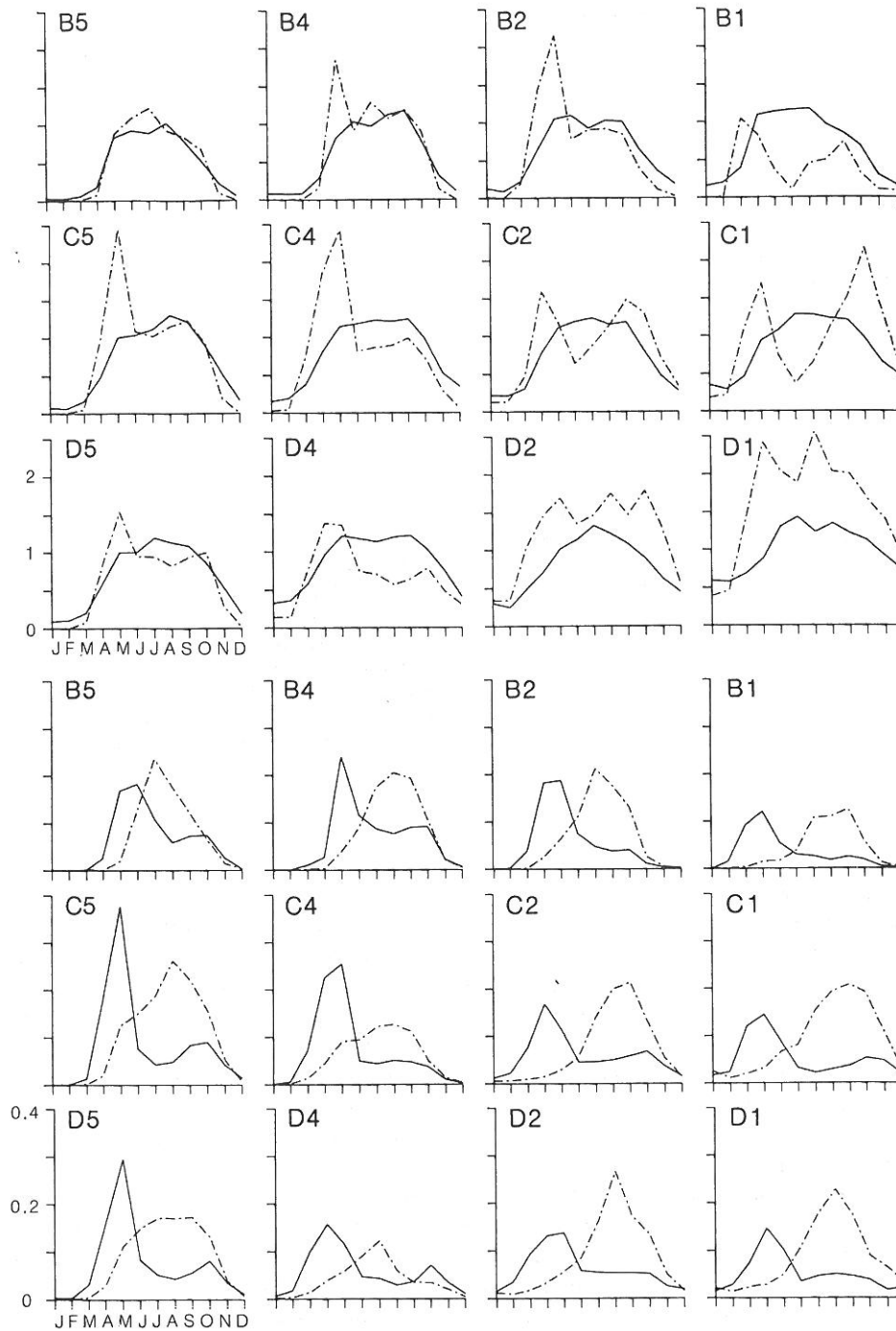
Fig. 9. Upper graphs: seasonal cycles of an index of abundance of phytoplankton (dashed lines), based on estimates of the green colouration of the original samples, compared with the total abundance of copepods (continuous lines); *y*-axis scale for phytoplankton is arbitrary, while for copepods, values are logarithmic means for subsamples of 1/40 of samples of 3 m³. Lower graphs: seasonal cycles of abundance of spring (continuous lines) and summer (dashed lines) groups of phytoplankton; *y*-axes are logarithmic means of subsamples of 1/7 500 of samples of 3 m³

the differences between the phytoplankton and zooplankton may be of no great significance to their relative dynamics in a particular area.

With respect to the third question, about the lack of a relationship between geographical distributions and the timing of the seasonal cycles, it is obvious that, in the study area, several factors showing little or no seasonal variation, such as depth and salinity, are correlated with factors that are important elements in the seasonal cycle, such as temperature and vertical stratification. It is perhaps not so surprising, therefore, to find patterns of differentiation of geographical distribution showing an apparent relationship with some elements of the seasonal cycle.

What is really being sought in trying to answer this question is some indication of the extent to which the geographical distributions and seasonal cycles are influenced by interactions between species, by competition, food supply etc.

It is clear that both geographical distributions (Fig. 6 and Colebrook, 1972) and the seasonal cycles (Fig. 3) are systematically differentiated. It is significant in this context that the analyses suggest that if diagrams like those in Fig. 2 b and e were produced for each area, the timing of the spring increase and the duration of the season would vary but the ranks of the taxa would be much the same in all the areas. Consideration of the differences in the

relative abundance of the taxa in the various areas, as reflected by their geographical distributions (Fig. 6) and the variations in the amplitude of the seasonal cycles (Fig. 7), leads to the conclusion that interaction between species does not play a major role in the timing of the seasonal cycles.

To this can be added the observation that the geographical distributions of many of the zooplankton taxa are determined largely by overwintering stocks rather than by any aspect of their dynamics during the productive season.

The plankton ecosystem gives the impression of consisting of a collection of species responding individually, with respect to their own preferences and tolerances, to a physico-chemical syndrome with, at the level considered here, little or no interaction between them.

What the data indicate, at the very least, is that for any species the similarity between its seasonal cycle in the various areas, which represent a wide range of hydrographic regimes, is appreciably greater than any differences induced by interaction between the species in any particular area.

A similar conclusion was reached by Colebrook (1975) in relation to the annual fluctuations in the abundance of zooplankton (the data relating to the same areas as in this study).

Colebrook (1979) has shown that, relative to the North Sea, the spring bloom of phytoplankton in the open waters of the north-east Atlantic appears to be underexploited by grazing. Davies and Payne (1984) have now shown that in the northern North Sea the spring bloom is similarly underexploited with, on the occasion of their observations, about 35% of the primary production dropping to the bottom. This implies that, with the possible exception of the most northerly oceanic area (see Fig. 9), where *Calanus finmarchicus* overwinters in deep cold water and migrates into the upper layers in considerable numbers in the early spring, inherent restrictions to the growth rate of the zooplankton coupled with low overwintering stocks are the main factors in limiting their ability to exploit the spring bloom. The evidence from growth rates (Fig. 8) and the restricted range of geographical variation through the year of most of the zooplankton (Fig. 5) suggest that temperature has an important influence on population growth but, at the same time, few of the taxa achieve a steady state with respect to the increase in temperature during the spring and early summer (see also Colebrook, 1982 c).

Given the underexploitation by grazing, it would appear that temperature coupled with the development of vertical stability in the water column also plays a major role in the population growth rates of most of the phytoplankton. Due to their higher growth rates, most of the phytoplankton respond to temperature differences and variations much more rapidly than do the zooplankton.

Colebrook (1982 a, c) has suggested that, following the spring bloom, and associated with relatively stable stocks of phytoplankton in the open ocean and shelf areas from about June to October (see Fig. 9), an equilibrium is established, with zooplankton grazing roughly matching the daily primary production and with feed-back to the phytoplankton involving nutrient regeneration. It may be significant, as shown in Fig. 9, that the spring group of phytoplankton show a relatively stable period of abundance from about June to October in nearly all the areas, while for the phytoplankton as a whole this is restricted to the shelf and open ocean.

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