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Continuous Plankton Records: Seasonal Cycles of Phytoplankton and Copepods in the North Atlantic Ocean and the North Sea

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Abstract

Data from the Continuous Plankton Recorder survey of the North Atlantic Ocean and the North Sea are used to study geographical variations in the amplitude, duration and timing of the seasonal cycles of total phytoplankton and total copepods. It is shown that the distribution of overwintering stocks influences the distributions throughout the year. There is a relationship between the timing of the spring increase of phytoplankton and the amplitude of the seasonal variation in sea surface temperature. In the open ocean, the timing of the spring increase of phytoplankton corresponds with the spring warming of the surface waters. In the North Sea the spring increase occurs earlier, associated, perhaps, with transient periods of vertical stability, resulting in a relatively slower rate of increase. It is suggested that in the open ocean the higher rate of increase is under-exploited by copepods due to low overwintering stocks and longer generation times. Exceptionally early spring increases of phytoplankton off the west coast of Greenland and over the Norwegian shelf are probably associated with permanent haloclines. A high and late autumn peak of phytoplankton off the coast of Portugal may be associated with coastal upwelling.

Introduction

Colebrook and Robinson (1965) described the seasonal cycles of gross estimates of the standing stocks of phytoplankton and copepods in the north-eastern Atlantic Ocean and the North Sea using data from the Continuous Plankton Recorder survey (Glover, 1967) for the period 1948 to 1960. Since then, the area of the survey has extended to cover most of the Atlantic Ocean north of 45°N, and Robinson (1970) described the geographical variation in the seasonal cycle of the phytoplankton for this larger area. He showed that the timing of the spring increase was, in part, related to the development of stability of the surface waters as measured by the rate of increase of surface temperature in spring and early summer (Craig, 1960). In the period since the publication of Robinson's paper, data have been acquired for 11 more years (up to 1976) providing better estimates of the seasonal cycles; moreover, better temperature data have become available from the ICES Hydrographic Service and the UK Meteorological Office (Colebrook and Taylor, in preparation).

In view of this, the earlier study of Colebrook and Robinson (1965) has been repeated, covering the extended period of 16 years and giving particular emphasis to the investigation of relationships with temperature.

Data and Analysis

The methods used in the analysis of the samples collected by Continuous Plankton Recorders have been described by Rae (1952) and Colebrook (1960) and routine data processing methods have been described by Colebrook (1975). Briefly, the estimates of the abundance of copepods used in this study are means of transformed counts [$y = \log_{10}(x + 1)$] of the numbers of copepods in samples of 3 m^3, based on all the samples taken in each month, averaged over all the years of sampling (1948 to 1976), in each of a set of standard areas (see Fig. 1). The measure of phytoplankton was obtained from a visual assessment of the green

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coloration of the filtering silks; these are expressed in numerical equivalents (Robinson, 1970) and processed in the same way as the counts of copepods (but without transformation). These data cannot with any degree of reliability be translated into any form providing comparability between phytoplankton and copepods; they can only be used as estimates of relative changes in abundance in different areas and months.

All the samples are taken from a standard depth of 10 m. The results are, therefore, subject to variability due to changes in vertical distribution. Some species of copepods carry out clear diurnal vertical migrations and only occur in samples taken at night. These species are, however, not very abundant and their contribution to the estimate of total copepods is generally unimportant. Of the species known to carry out seasonal vertical migrations, only *Calanus finmarchicus* is sufficiently abundant to influence significantly the estimates of total copepods. In general however, experience in analysing the samples indicates that the increase in numbers of copepods in spring is due primarily to the appearance of young stages. This suggests that reproduction and advection are the dominant processes involved in variations in distribution and abundance during the spring increase.

The seasonal variations in abundance of phytoplankton and copepods for each of the areas in Fig. 1 are shown in Fig. 2.

As would be expected for temperate latitudes, there is a clear seasonal cycle with some latitudinal variation in amplitude. There are also fairly clear variations in timing, season length and abundance and it is these variations which are studied in detail in the subsequent sections of this paper.

The data presented in Fig. 2 were arranged in the form of a table with a column for each of the areas and two rows for each month containing the data for phytoplankton and copepods, respectively.

These data were subjected to principal component analyses, as follows:

(1) Each row of the table was standardised to zero mean and unit variance, removing differences in abundance both between months and between phytoplankton and copepods, leaving in the data only variability associated, within each month, with differences between areas. A principal components analysis was performed, based on product moment correlation coefficients between rows.

The eigenvectors contain values for months and the principal components are representations of geographical distributions.

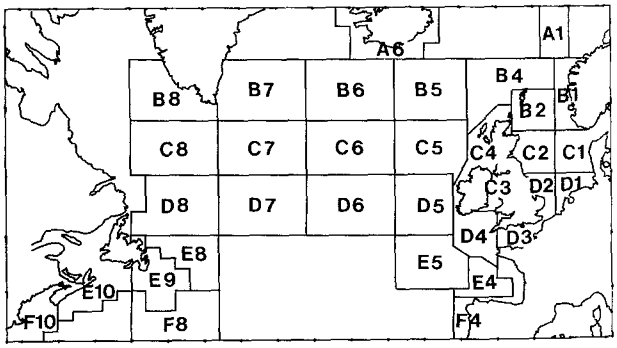

Fig. 1. Chart of North Atlantic Ocean, showing sub-division into areas used throughout this study

(2) For C, the copepod data and P, the phytoplankton data, each column of the table was standardised to zero mean and unit variance leaving in the data only variability associated with differences between months. Principal components analyses were performed, based on product moment correlation coefficients between columns, on the two data sets. In both analyses the eigenvectors contain values for areas and the principal components are representations of seasonal cycles.

In addition to these analyses, a set of parameters was established to characterise the major features of the differences between the seasonal cycles. These are essentially the same as those used by Colebrook and Robinson (1965) and are:

(1) Mean abundance of phytoplankton (A_p) and copepods (A_c) in each area as $\Sigma x_m/12$, where m is the month number (January = 1 to December = 12).

(2) Timing of the spring increase, estimated as the month coordinate of the centre of gravity of the area below graphs of monthly means for January to June and calculated by $T = \Sigma(m.x_m)/\Sigma x_m$, where $m = 1\ (1)\ 6$.

(3) Season duration, estimated as the standard deviation of the timing for the whole year and calculated by $L = \sqrt{\{\Sigma x_m (m-T)^2/\Sigma x_m\}}$, where T is calculated as above with $m = 1\ (1)\ 12$.

Timing and season duration were calculated for both phytoplankton (T_p, L_p) and copepods (T_c, L_c).

Sea surface temperature data, in the form of long-term monthly means for each of the areas shown in Fig. 1, averaged over the years 1948 to 1976, were treated in much the same way as the plankton data. Similar principal components analyses were performed and param-

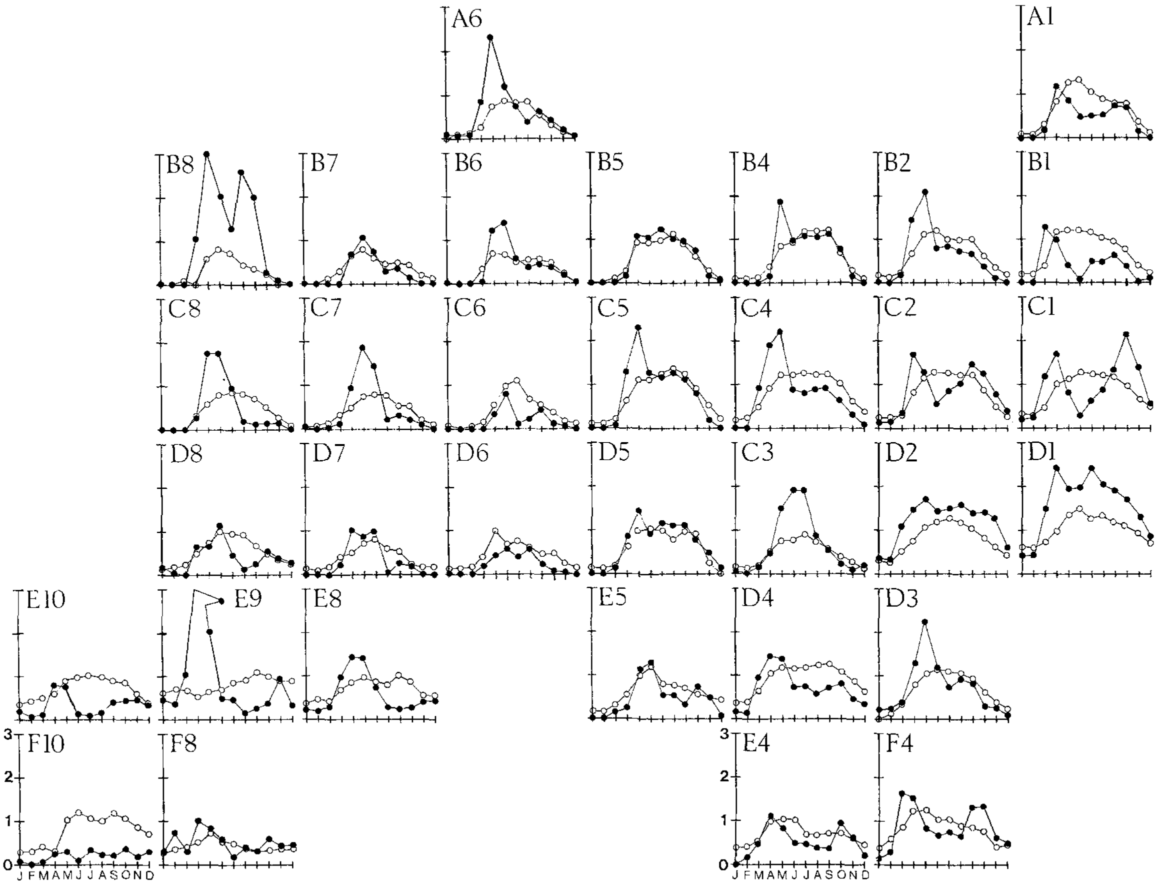

Fig. 2. Seasonal variations in abundance of phytoplankton (filled circles), and copepods (open circles) in each of areas shown in Fig. 1. Phytoplankton data are arbitrary units of greenness and copepod data are logarithmic means of numbers

eters of timing of the spring warming, season duration and annual means were calculated in the same way as for phytoplankton and copepods.

Robinson (1970) established a relationship between the timing of the spring increase of phytoplankton and a parameter called "temperature difference" (Craig, 1960). This is calculated as the mean surface temperature for May, June and July minus the surface temperature for March and was intended by Craig to provide an estimate of relative variations in the intensity of vertical stratification covering the period of the spring warming. The standard deviation of the seasonal cycle of temperature can similarly be used to estimate the intensity of stratification covering the whole season. Trials indicated that, for the areas shown in Fig. 1, "temperature difference" and the standard deviation of temperature were linearly related with a highly significant correlation suggesting that, in the context of empirical interpretation, there was little to choose between the two parameters. Standard deviations are preferred, however, because they are based on all of the data (instead of 4 months in the calculation of the "temperature difference") and they are also independent of variations in the timing of the seasonal cycle. They have, therefore, been used in this study.

Tomczak and Goedecke (1964) and Schroeder (1965) have presented diagrams for each month giving the vertical distribution of temperature along selected transects covering the North Sea and the North Atlantic Ocean, respectively. These have been used to prepare diagrams for selected locations, with temperature contoured in a frame of depth against time, illustrating seasonal variations in the extent of vertical stratification. Diagrams have been prepared for as many as possible of the areas shown in Fig. 1, selecting locations as close as possible to the centre points of the areas. Some examples of the profiles are given in the lower graphs in Fig. 3.

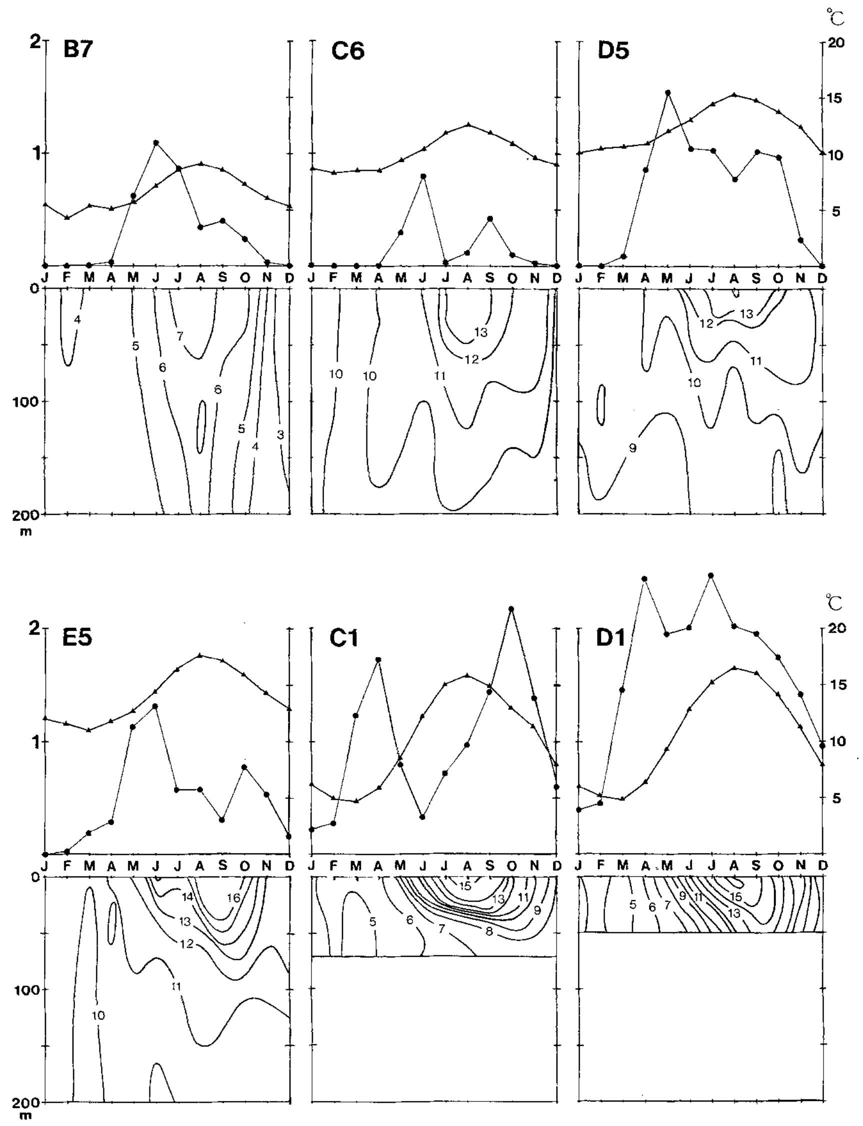

Fig. 3. Seasonal variations in phytoplankton (circles) and sea surface temperature (triangles) compared with seasonal temperature profiles (contours at 1 C^{o} intervals) in the top 200 m for 6 of the areas shown in Fig. 1. Phytoplankton data are arbitrary units of greenness

Results

It was clear from an examination of the results of the various analyses described above that there is a general geographical pattern representing major aspects of differentiation of the seasonal cycles; a number of more localised features are also reflected in the data. Both aspects contain useful information about interrelationships between phytoplankton and copepods and their association with temperature changes, and the following account is presented from this point of view. Full accounts of the types of analyses performed on the data have already been presented by Colebrook and Robinson (1965) and Robinson (1970).

Fig. 3. shows the seasonal cycles of phytoplankton compared with depth-time temperature profiles for 6 of the areas in Fig. 1. These show a consistent difference in the relative timing of the spring increase of phytoplankton compared with the timing of the onset of vertical temperature stratification as between the open ocean areas (B7, C6, D5, E5) and the shallow water areas (C1, D1). In both sets of areas the spring increase in the phytoplankton occurs well before the establishment of a clear thermocline. In the open ocean areas, however, the spring warming is under-way before the peak in the phytoplankton has occurred, whereas in the shallower waters the timing of the spring increase

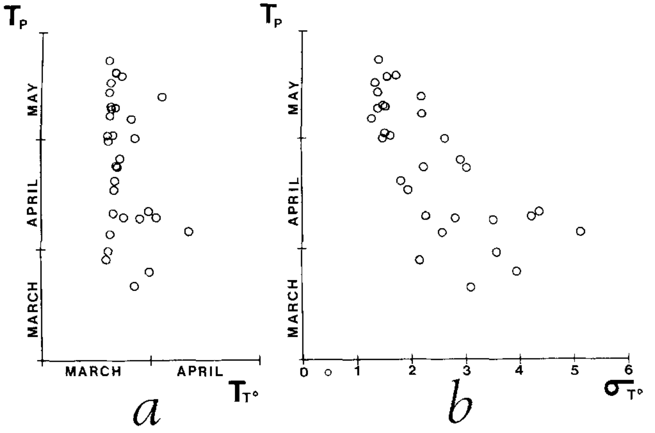

Fig. 4. Scatter diagrams of (a) timing of spring warming of the sea surface (T_T) plotted against timing of the spring increase of phytoplankton (T_p), and (b) standard deviations of seasonal variation in sea surface temperature (σ_T) plotted against timing of the spring increase of phytoplankton (T_p), for each of areas shown in Fig. 1. (The method of estimating timing is described in the text)

is appreciably earlier relative to the spring warming.

Fig. 4a shows a scatter plot of the timing of the spring warming against the timing of the spring peak of phytoplankton. The correlation between the two variables is -0.37, which is just significant at the 5% level. However, the range of timing of the phytoplankton is much greater than that for the spring warming, indicating the generality of the feature represented by a few examples in Fig. 3. This makes it difficult to attribute more than a minor contributory role to the timing of the spring warming in relation to the geographical variation in the timing of the spring increase in phytoplankton. Fig. 4b shows the relationship between the standard deviation of the seasonal cycle of temperature and the timing of the spring peak in phytoplankton. The correlation is -0.75, which is significant at the 0.1% level and is comparable with the relationship described by Robinson (1970) which he attributed to the well-established connection between the spring phytoplankton outbreak and vertical stability of the water column (see, for example, Gran and Braarud, 1935; Riley, 1957).

There are two obvious problems. Firstly, the variation in the timing of the spring increase of phytoplankton is not matched by an equivalent range of variation in the timing of the spring warming. Secondly, the timing of the spring increase of phytoplankton is much more strongly correlated with variation in the intensity of stratification, as estimated by the standard deviation of temperature, which is not manifest in the long-term mean data until well after the increase in the phytoplankton. The data presented by Williams (1973-1977) on chlorophyll a and temperature at Ocean Weather Station (O.W.S.) India (50°N; 19°W) in individual years (1971 to 1975) also show that the phytoplankton increase precedes the establishment of a clear thermocline. This renders it unlikely that averaging over years, as is the case for all the data presented here, is obscuring the timing of the onset of clear stratification to any significant extent. If the relationship presented in Fig. 4b is accepted as real, one is obliged in this context to regard the standard deviation of temperature as an estimate of the potential for vertical stability in the upper layers, realised in the form of weak or transient thermal structure, that is poorly represented in diagrams based on whole degree isotherms, but which is, nevertheless, sufficient to sustain increases in the phytoplankton stocks. The difference in the timing of the spring increase of phytoplankton in relation to the spring warming in the deep waters of the open ocean as compared with the shallower waters of the continental shelves and the North Sea is consistent with this interpretation.

The variation in the timing of the spring increase of phytoplankton is reflected in a seasonal change in geographical distribution which can in turn be compared with changes in the distribution of copepods. A representation of the relationships between the geographical distributions of phytoplankton and copepods in each month is given in Fig. 5, which is a scatter diagram of the first two eigenvectors from Analysis 1 (see "Data and Analysis"). The components corresponding to these two vectors account for 48 and 16% of total variability, respectively, a total of 64%. With the exception of the distribution of phytoplankton in June, there is a common element in the distributions, as indicated by positive values for the first eigenvector. There is also a changing pattern of distribution with a seasonal succession. In winter, spring and autumn the pattern of change is common to both copepods and phytoplankton; only in summer is there any marked divergence. The variations may be illustrated in summary form by presenting a series of distributions; these are calculated as the sum of the weighted first two principal components, using mean eigenvector values

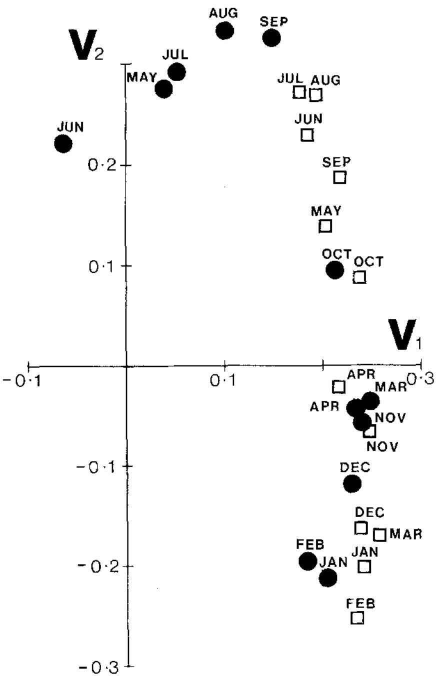

Fig. 5. Scatter diagram of first two eigenvectors of a principal components analysis of geographical distribution in each month of phytoplankton (circles) and copepods (squares)

as weights for groups of months representing (a) November to April for phytoplankton and copepods (all months with negative values in the second vector), (b) May to August for phytoplankton, and (c) May to August for copepods. The distributions for these groups of months are given in Fig. 6.

In winter, spring and late autumn, the distributions of both phytoplankton and copepods show above-average abundance in the North Sea and over most of the European and American shelf areas and below-average abundance in most of the open ocean areas. The summer distributions both show higher values in the open ocean relative to the shelf areas, the difference for the phytoplankton (Fig. 6b) being more pronounced than for the copepods (Fig. 6c).

The extent of the differences in abundance relative to the amplitude of the seasonal cycle is shown in Fig. 7. Each plot is the weighted sum of the first two principal components of Analyses 2P and C (months, phytoplankton and months, copepods see "Data and Analysis"), using as weights typical eigenvector values for the open ocean and for the North Sea. For copepods it is clear that, compared with the amplitude of the seasonal cycle, the differences in abundance between the North Sea and the open ocean are small.

For the phytoplankton the differences are appreciably larger and can be attributed primarily to a higher rate of increase in standing stock between April and May in the open ocean compared with the North Sea. This could be related to the later timing of the spring increase relative to the timing of the spring warming in the open ocean compared with shallower waters. It seems possible that the establishment of vertical stability sufficient to maintain phytoplankton increase may be more persistent in the open ocean as it occurs during periods of rising temperature, whereas in the shallower water areas a sequence of transient periods of vertical stability may be involved resulting in a slower increase in phytoplankton. It is also possible, however, that differences in grazing may be involved. R. Williams (personal communication) estimates that the spring herbivore population in the northern North Sea (data from the Fladen Ground experiment, 1977) is considerably larger than that at O.W.S. India (59°N; 19°W).

The general grazing relationship is indicated by the fact that the seasonal variations in the geographical distribution of copepods do follow those of the phytoplankton but, as would be expected by the considerable difference in generation times, both the extent (Fig. 5) and the amplitude (Fig. 7) of the changes are less marked.

Fig. 5 shows that, with one exception, all the first vector terms are positive, indicating an element of geographical distribution common to all months. The summer distributions result from differential increases in standing stock, due to reproduction and advection, from the winter minima. The common element of distribution can, therefore, be regarded in terms of the influence of the distribution of overwintering stocks on the pattern for the whole year. Again, the effect appears to be greater for the copepods than for the phytoplankton.

It would seem to follow that the relatively higher rate of increase in phytoplankton in the open ocean is probably under-exploited by copepods (and probably, by analogy, other zooplankton), and, due to low overwintering stocks and longer generation times, the copepods are unable to increase quickly enough to graze down the phytoplankton within the limited duration of the growing season. Thus, based on purely circumstantial evidence, there would appear to be a surplus of phytoplankton in the open ocean for most of the summer.

The implied poor relationship between overall abundance of phytoplankton and

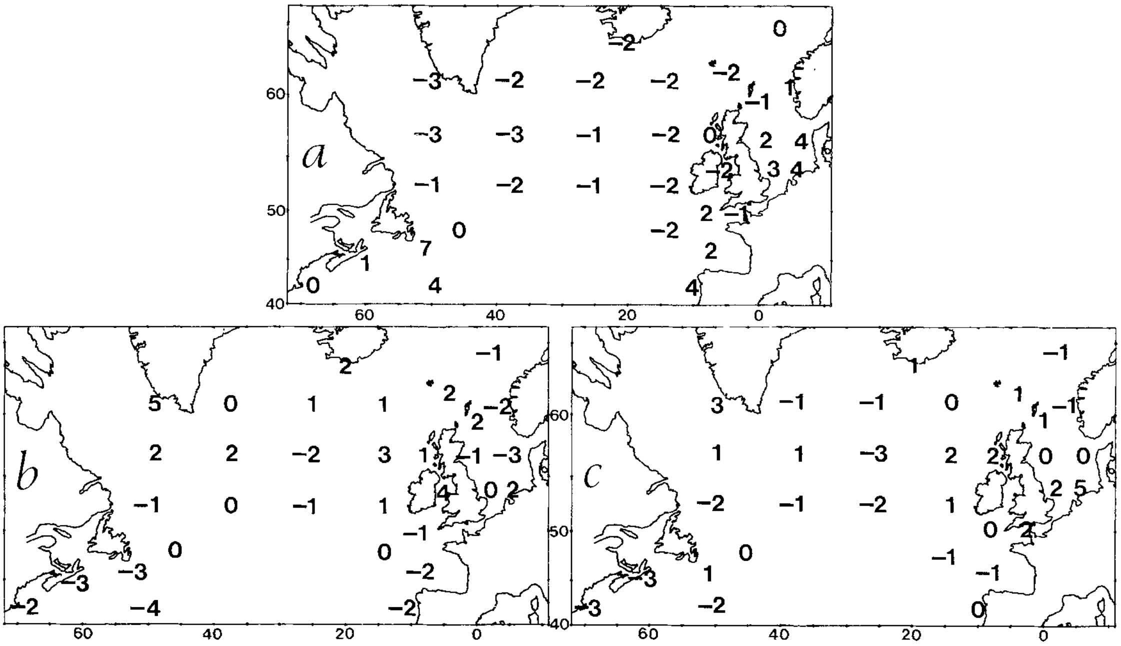

Fig. 6. Average geographical distribution of phytoplankton and copepods in groups of months, calculated as the sum of the weighted first two principal components of Analysis 1, using mean eigenvector values as weights, then standardised to zero mean and unit variance, x 10. The month groups are: (a) Phytoplankton and copepods, winter (November to April); (b) phytoplankton, summer (May to August); (c) copepods, summer (May to August)

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copepods is confirmed by Fig. 8, which is a scatter plot of the first two eigenvectors of a principal components analysis of the geographical distributions of the season duration, timing of spring increase and mean abundance for phytoplankton and copepods together with the month-group mean distributions shown in Fig. 6. The corresponding components account for 90% of the variability of the 9 input variables. The season duration and timing parameters for both phytoplankton and copepods together with the winter distribution (Fig. 6a) form a coherent group close to the axis of the first eigenvector. The distribution of whole-year means for copepods also has a high value in the first eigenvector. This suggests that the first principal component provides a good representation of the dominant geographical pattern in the differentiation of the seasonal cycles associated with these variables; this is illustrated in Fig. 9. As would be expected, the component shows very clearly the difference between open ocean and shallow water areas. It also, however, shows some latitudinal variation indicating later timings and shorter seasons in northern waters.

The clear association between the timing and season duration parameters shown

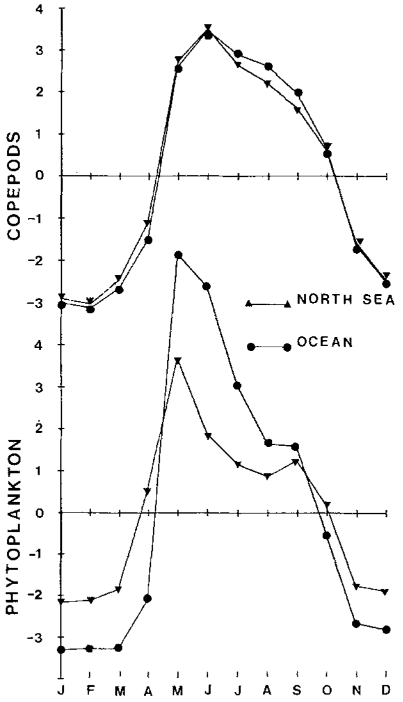

Fig. 7. Differences between seasonal cycles of phytoplankton and copepods in the open ocean and the North Sea. Method of derivation is described in text. The *x*-axes are in standard deviation units

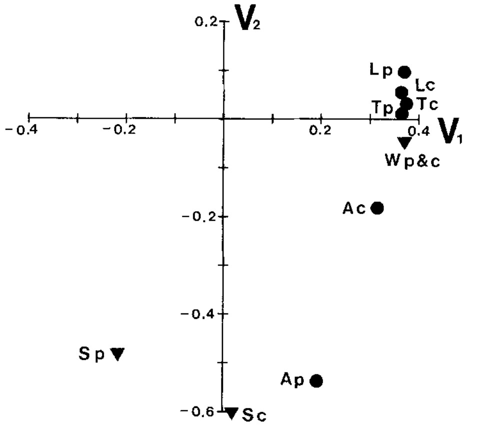

Fig. 8. Scatter diagram of first two eigenvectors of a principal components analysis of geographical distributions (based on areas shown in Fig. 1) of parameters of the seasonal cycles of phytoplankton and copepods (circles) and month-group means (triangles) in Fig. 6. L_p season duration of phytoplankton; L_c season duration of copepods; T_p timing of spring increase of phytoplankton; T_c timing of spring increase of copepods; A_p mean abundance of phytoplankton; A_c mean abundance of copepods; $W_{p\ \&\ c}$ phytoplankton and copepods, winter; S_p phytoplankton, summer; S_c copepods, summer

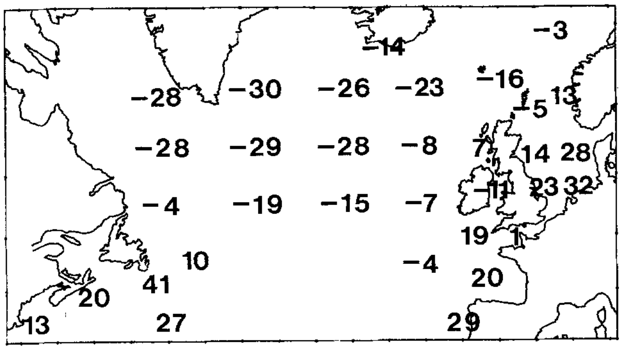

Fig. 9. Chart showing first principal component of the geographical distribution of the variables listed in legend to Fig. 8. Component is presented as standard deviation x 10

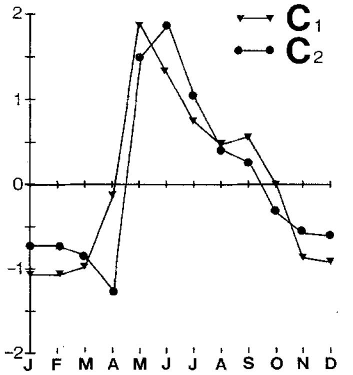

Fig. 10. Graphs of first two principal components (C_1, C_2, both reduced to zero mean and unit variance, x-axis, in standard deviations) of the seasonal variation of phytoplankton in areas shown in Fig. 1

in Fig. 8 raises the question of the timing of the autumn decline in relation to the timing of the spring increase. Colebrook and Robinson (1965) suggested that the season duration was determined primarily by the timing of the spring increase, implying a more or less constant autumn decline. The wider geographical coverage now available seems to indicate that, at least for the phytoplankton, there is a tendency for an early spring increase to be associated with a later than average autumn decline. The first principal component of Analysis 2P (months, phytoplankton) represents a seasonal cycle common to all the areas (all the eigenvector values are positive and range from 0.095 to 0.223). The second eigenvector is highly correlated (r = 0.87, significant at 0.1%) with the first component of the parameters (Fig. 9). This implies that the second component of Analysis 2P represents differences between areas with respect to timing and season duration. Fig. 10 shows plots of the two components, and it is clear that seasonal variations of phytoplankton calculated as weighted sums of these two components, with the weights applied to the second component varying in sign as well as amplitude, would show differences in the timing of the spring increase and inversely related changes, although of smaller amplitude, in the timing of the autumn decline. A similar examination of the corresponding components for the copepods shows little potential variability in the timing of the autumn decline, indicating that the season duration is determined almost entirely by the timing of the spring increase.

The graphs in Fig. 2 indicate that several of the coastal areas show particular features unrelated to the principal geographical pattern presented in Fig. 9. The most obvious are given below.

West Greenland (Fig. 2, Area B8)

The tracks of the Continuous Plankton Recorder tows in this area lie over the continental shelf or only just off it, and Fig. 2 indicates that in this region there is an exceptionally high standing stock of phytoplankton relative to copepods for the whole of the productive season. The area also shows a pronounced halocline at a depth of about 25 m (U.S. Naval Oceanographic Office, 1967), presumably providing enough vertical stability to trigger an early spring increase in phytoplankton, about a month earlier than over deep water to the east of Greenland (Fig. 2, Area B7). This, coupled with low temperatures restricting the development of copepods, produces what appears to be a complete break-away from grazing control for the whole season.

Norwegian Shelf (Fig. 2, Area B1)

An exceptionally early spring increase of phytoplankton can again be associated with the presence of a halocline connected, in this instance, with Baltic outflow water. It seems probable that the large stock of *Calanus finmarchicus* overwintering in deep water in this area (Sømme, 1934) provides sufficient grazing pressure to prevent the development of large phytoplankton stocks as off the west coast of Greenland.

Southern North Sea (Fig. 2, Areas D1 and D2)

Colebrook and Robinson (1965) suggested that the long season duration and absence of a clear autumn peak of phytoplankton may be attributed to continuous exchange between surface and bottom in this very shallow area. Tomczak and Goedecke (1964) show that there is only slight vertical temperature stratification over most of the area.

Portuguese Coastal Zone (Fig. 2, Area F4)

Compared with the other European continental shelf areas there is a high and late autumn peak of phytoplankton. Wooster *et al.* (1976) have presented evidence for coastal upwelling along the eastern boundary of the North Atlantic Ocean. This indicates that off Lisbon (38°N) there does appear to be upwelling from July to September. Sea surface temperature data made available by the U.K. Meteorological Office indicate that going northwards from Lisbon the period of upwelling changes, being about 1 month later off Cape Finisterre (43°N). This period of upwelling corresponds with the timing of the autumn peak of phytoplankton.

The Grand Banks (Fig. 2, Area E8)

This area is characterised by a very sharp and high spring peak of phytoplankton which may be attributable to the shallowness of the region coupled with the low temperature, restricting the growth of copepods. The reasons for the marked decline between April and June are not clear, but it may be produced by nutrient limitation due to the pronounced and shallow thermocline which develops in this area (Schroeder, 1965).

Nova Scotian Shelf and Gulf of Maine (Fig. 2, Areas E10 and F10)

This is a region of considerable local variability in the seasonal cycle. Presentation in the form of averages in just two areas is probably adequate in relation to the general geographical relationships described in this paper but, for any greater detail, reference should be made to the fairly extensive literature available. Sherman (1965) and Smayda (1973) are good source papers.

Discussion

In general, the results derived from the examination of the parameters are similar to those of the earlier study by Colebrook and Robinson (1965), even though data for nearly twice the number of areas are included, and the same conclusions can be drawn: that the key factor is the timing of the spring increase of phytoplankton and that the abundance of copepods is determined more by the length of time during which food is available than by the amount available. This is explained here in terms of an apparent surplus of phytoplankton in the open ocean in summer.

In the earlier study, however, the relationship with the overwintering stocks was not recognised. Fig. 5 clearly illustrates the influence of overwintering on distributions throughout the year, but there is also the question of a possible causal basis for the high correlations with the parameters of timing and season duration. The timing of the phytoplankton increase has been shown to be correlated with the seasonal range of temperature (Fig. 4b), interpreted as an indicator of vertical stability. The inverse of vertical stability is mixing, and it seems reasonable to expect winter survival to be influenced by vertical mixing processes through losses to deep water. If this is so, then the correlation between winter distribution and the timing and season duration parameters is the result of a common causal process and not of a direct link.

Two main points have emerged from this study compared with those of Colebrook and Robinson (1965) and Robinson (1970). Firstly, there would appear to be a rapid spring increase in the standing stock of phytoplankton over most of the open ocean which, compared with shallow water areas, is under-exploited by grazing. Secondly, there is clear evidence to suggest that the distribution of overwintering stocks has a marked influence on the distribution, particularly of copepods, throughout the year.

Colebrook (1978), in a study of year-to-year changes in the abundance of zooplankton, has shown that species which show similar annual fluctuations in abundance tend to have similar geographical distributions and do not necessarily show similar seasonal cycles. He has also shown that an appreciable proportion of the annual changes in abundance may be related to changes in advection associated with either variations in the North Atlantic drift or smaller scale wind-driven effects. In this context, the role of overwintering stocks provides a possible mechanism whereby relatively small advected changes in populations in winter may be magnified into marked differences in the following summer.

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