

North Atlantic
Calanus finmarchicus
 Long-term changes
 Space-time interactions
 Continuous Plankton Recorder

Océan Atlantique nord
Calanus finmarchicus
 Changements à long terme
 Interactions spatio-temporelles
 Continuous Plankton Recorder

Long-term time series in *Calanus finmarchicus* abundance – a question of space?

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ABSTRACT

Year-to-year changes in abundance of the copepod *Calanus finmarchicus* in the North Atlantic are studied by means of the Continuous Plankton Recorder (CPR). Using data collected during the years 1962 to 1974, the spatial heterogeneity of long-term trends is studied by numerical analysis: Mantel test, Mantel correlogram, and spatio-temporal clustering.

Results reveal that (1) interannual changes of *C. finmarchicus* abundance are spatially autocorrelated; (2) the spatial structures have a radius varying between 400 and 1100 km; and (3) there is a high variability in the annual changes observed between the different zones detected by clustering.

These results show that observations made in the Northeast Atlantic cannot be extrapolated to the whole North Atlantic basin, and suggest that identification of the size and location of an "homogeneous zone for long-term changes" should be taken into account when determining factors responsible for year-to-year fluctuations in abundance of *C. finmarchicus*.

RÉSUMÉ

Variations à long terme de *Calanus finmarchicus* – une question d'espace ?

Les changements interannuels d'abondance du copépode *Calanus finmarchicus* sont étudiés à l'aide du « Continuous Plankton Recorder » (CPR). À partir des échantillons collectés de 1962 à 1974, les variations spatiales de ces changements sont étudiées par plusieurs analyses numériques: test de Mantel, autocorrélogramme de Mantel et classification spatio-temporelle.

Les résultats montrent (1) qu'il y a autocorrélation spatiale entre les séries à long terme, (2) que les structures spatiales relatives aux variations interannuelles ont une dimension de 400 à 1100 km de rayon et (3) qu'il existe une variabilité élevée entre les différentes zones détectées par la classification.

Les observations réalisées dans l'Atlantique nord-est ne sont donc pas extrapolables à l'ensemble de l'Atlantique nord. L'identification et la caractérisation (taille et position géographique) des zones homogènes vis-à-vis des changements à long terme devraient permettre de mieux définir les facteurs responsables des fluctuations interannuelles d'abondance de *C. finmarchicus*.

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INTRODUCTION

Since 1931, the abundance and distribution of plankton in the North Atlantic and the North Sea have been sampled by the Continuous Plankton Recorder (CPR) survey. Samples collected within the survey have been used to identify seasonal and long-term fluctuations of plankton abundance (Colebrook, 1978; 1979; 1982; Colebrook *et al.*, 1984; 1986), as well as large-scale geographical patterns of plankton spatial distribution (Oceanographic Laboratory of Edinburgh, 1973). In the North Atlantic, zooplankton is largely dominated by copepods. The present work focuses on the copepod species, *Calanus finmarchicus*. *C. finmarchicus* is widely distributed over the North Atlantic and the North Sea and its biomass can reach up to 92% of the total zooplankton (Gislason and Asthorsson, 1995). Seasonal and annual fluctuations as well as the spatial distribution of *C. finmarchicus* abundance have been reported in numerous previous works (Jaschnov, 1970; Colebrook, 1986; Hassel, 1986; Tande and Slagstad, 1992). However, these studies were generally oriented distinctively on spatial or temporal fluctuations but did not show any clear relationships between spatial and temporal processes. As an increasing number of studies focus on the global understanding of oceanic processes, it seemed necessary to develop a suitable methodology dedicated to the production of synoptic results on spatio-temporal processes.

Previous studies (Matthews, 1969; Planque *et al.*, in press), pointed out the relationship between seasonal changes in abundance of *C. finmarchicus* and the geographical distribution of the species. These works showed that geographical heterogeneity of environmental conditions, such as sea-surface temperature, phytoplankton outbreak timing, or oceanic currents, were associated with temporal shifts of the species' seasonal cycle. These results raise the question whether long-term changes also depend on the geographical distribution of the species. The aim of the present paper is to identify the characteristics of *C. finmarchicus* long-term changes in the North Atlantic. It is focused on the following questions:

- Are there relationships between long-term changes in abundance and spatial distribution patterns?
- If so, can we describe these relationships?
- Can we identify oceanic regions that show distinct long-term fluctuations?

Sampling

Each month, several ships tow Continuous Plankton Recorders along routes in the North Atlantic and the North Sea. The CPRs are towed at high speed (11-33 km.h⁻¹) in near-surface water. Plankton is retained inside these recorders on a continually moving band of silk mesh of nominal aperture 270 μ m. After each tow this silk roll is unwound and cut into sections corresponding to 18.5 km of tow; the abundance of *Calanus finmarchicus* copepodites stage V and adults is then quantified in a routine manner for alternate 18.5 km sections (Rae, 1952; Colebrook, 1960). The location of CPR deployment and retrieval is

recorded for each tow, from which the location for the mid-point of each sample is calculated. The abundance of *C. finmarchicus* in every sample is log-transformed using the $\text{Log}(x + 1)$ function (Colebrook, 1975). In the present study, we have used samples collected over the North Atlantic and the North Sea from January 1962 to December 1974. During this period, oceanic coverage of the CPR survey was at its maximum (Warner and Hays, 1994).

METHODS

Preliminary data processing

In order to perform further analysis, a series of transformations and matrix constructions is first carried out (Fig. 1).

Step 1: Because of the CPR sampling procedure, locations of samples collected each month may vary and comparisons between distinct monthly data sets is difficult. To solve this problem, each monthly spatial distribution of *C. finmarchicus* has been re-estimated on a regular grid identical for every month. The spatial regulation of each map is performed by interpolation on a regular grid composed of 50 \times 50 nautical mile squares (8575 km²).

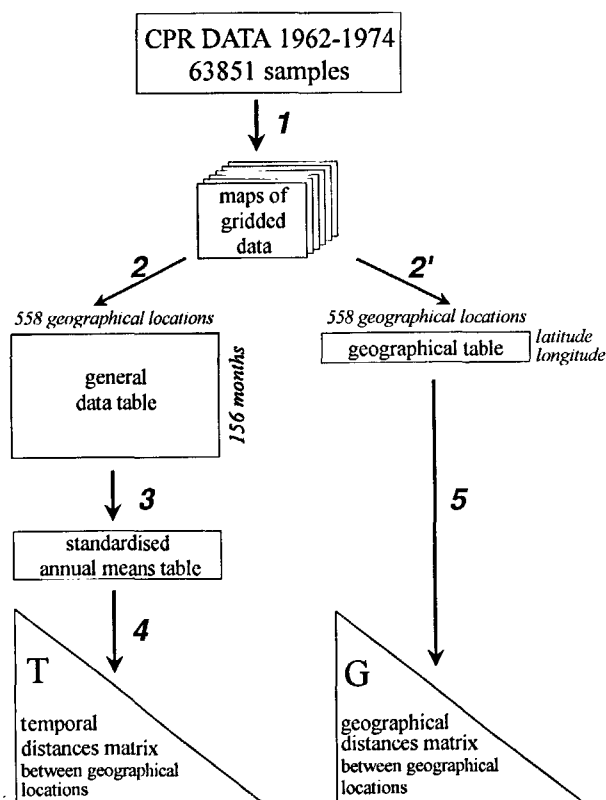


Figure 1

Successive steps (arrows) of the CPR data preliminary processing. 1: monthly data-set cartography and interpolation procedure; 2: selection of geographical 'pixels' and construction of a general data table; 2': construction of the geographical table. 3: annual means calculation and standardization (zero mean and unit variance); 4: computation of the temporal matrix of Euclidean distances T. 5: computation of the matrix of geographical distances G. See text for details.

The grid is represented on a map using the Lambert conical 'equivalent' projection, so that the cartographic and terrestrial surfaces are proportional and distances are only slightly affected (Richardus and Adler, 1972).

Interpolation is done by kriging, an ideal tool for mapping CPR data for two reasons: (i) sampling is not carried out following a classic sampling plan (random, regular, stratified, and so on); and (ii) data are spatially autocorrelated (*i.e.* not independent because they are structured in space). Kriging also provides the Best Linear Unbiased Estimator (Cressie, 1993). For each grid square (pixel), the estimated abundance is calculated using a maximum of ten neighbouring samples and a maximum distance between estimator and samples (search radius) of 370 km. Accuracy of kriging estimation depends on the number and distance of surrounding samples, and if no sample can be found in the neighbourhood of a grid node, no estimation of abundance is returned for this node.

Step 2: From the 156 maps of gridded data obtained, only grid nodes (pixels) with sufficient data are retained. Selected pixels (558) have a maximum of 30% missing values and a maximum of six successive missing values. Remaining missing values are replaced by estimations calculated with an iterative multiple regression method, the ZET algorithm (Zagoruiko and Yolkina, 1982). The ZET algorithm results in a 156×558 matrix in which each row represents a month of a particular year and each column a geographical location on the map.

Step 2': A table containing the geographical locations (longitude and latitude) of selected pixels is also constructed.

Step 3: From the 156×558 table, annual means of abundance are calculated, leading to a 13 (years) \times 558 (geographical locations) matrix. Each column is standardized to zero mean and unit variance to eliminate differences in absolute abundance between oceanic locations.

Step 4: The matrix of Euclidean distances between pixels is computed using standardised annual values. This matrix is now termed the temporal distances matrix T .

Step 5: The matrix of geographical distances G is also computed from the geographical coordinates of the selected pixels. The two matrices T and G are used to assess relationships between long-term trends and spatial distribution of the species.

Mantel test

The Mantel test (Mantel, 1967) is based on the comparison of two distance matrices – one relevant to spatial distances and the other to ecological distances – and can be used to test the hypothesis of independence between temporal processes and their spatial distribution. The normalized Mantel statistic r is given by

$$r = \frac{1}{n-1} \sum_i \sum_{j \neq i} \frac{(g_{i,j} - \bar{g})}{S_g} \cdot \frac{(t_{i,j} - \bar{t})}{S_t}$$

where i and j are the row and column indices, n the number of elements in the matrices (diagonal excluded),

$g_{i,j}$ and $t_{i,j}$ the elements of matrices G and T at row i and column j . S_g and S_t are the standard deviations of values in matrices G and T (diagonal excluded).

The null hypothesis (absence of correlation between temporal distances and spatial distances) is tested by comparing the r value to an empirical distribution of 1000 values obtained after random permutation of one of the two matrices.

Mantel correlogram

By extension of the Mantel statistic, Sokal (1986) proposed the Mantel correlogram function that can be used to depict the relationship between temporal processes and spatial scales. The Mantel correlogram results from the computation of several Mantel tests, each test being relevant to a spatial scale (distance class). From the geographical matrix G and for each class of spatial distance, a model matrix X is calculated such that if the geographical distance between samples i and j ($g_{i,j}$) is included in the distance class, the element of the model matrix $x_{i,j}$ is coded 0; if not, the element $x_{i,j}$ is coded 1. Mantel tests are computed between the temporal matrix T and the model matrices X .

Spatio-temporal clustering

The Mantel test and the Mantel correlogram were used to test and depict the relationship between spatial scales and temporal processes. The purpose of the spatio-temporal clustering is to identify the oceanic zones in which interannual changes follow similar patterns. The clustering is based on the temporal distance matrix T cited above. From these distances, pixels are gathered by hierarchical agglomerative flexible clustering (Lance and Williams,

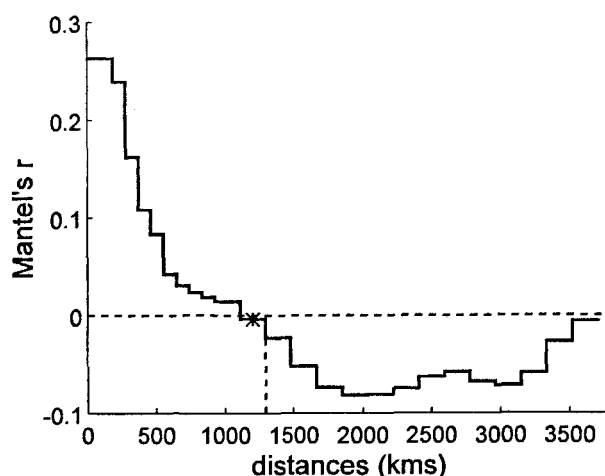


Figure 2

Mantel's correlogram between distance matrices T and G . The correlogram depicts interactions between long-term changes and their spatial distribution. If Mantel's r is positive for a geographical distance, it indicates that the similarities (of long-term time series) between the couples of sites separated by this distance is higher than the average similarity between every possible couples of sites. '*' indicates that r is not significant at the 1% level. The vertical dotted line indicates the distance from which Mantel's r starts to be significantly negative (1% level).

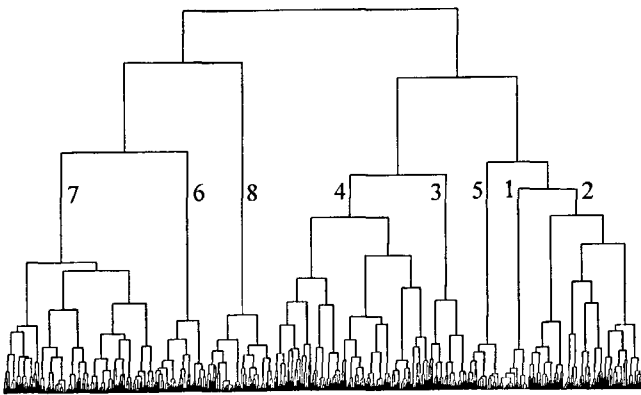


Figure 3

Dendrogram resulting from the classification of the pixels by reference to their long-term time series. Eight groups are retained with sizes varying from 0.4 to $3.9 \times 10^6 \text{ km}^2$.

1966). The major groups are identified on the resulting dendrogram and a map of their spatial distribution is drawn.

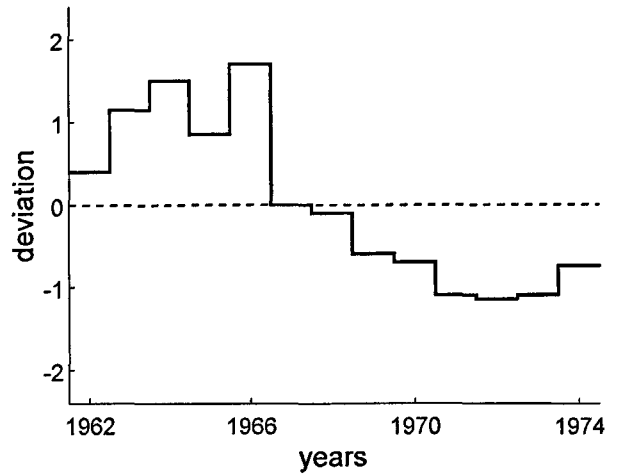


Figure 4

Standardized (zero mean, unit variance) annual changes in abundance of *C. finmarchicus* from 1962 to 1974 over the North Atlantic and the North Sea calculated from raw CPR data. The geographical distribution of samples is not taken into account.

RESULTS

The Mantel r statistic between the two matrices T and G has a value of 0.342 and is significant at the 1% level. This result indicates that interannual changes of

Calanus finmarchicus population abundance in the North Atlantic and the North Sea are not independent of space. In neighbouring regions, interannual changes are more similar than in regions that are geographically far apart.

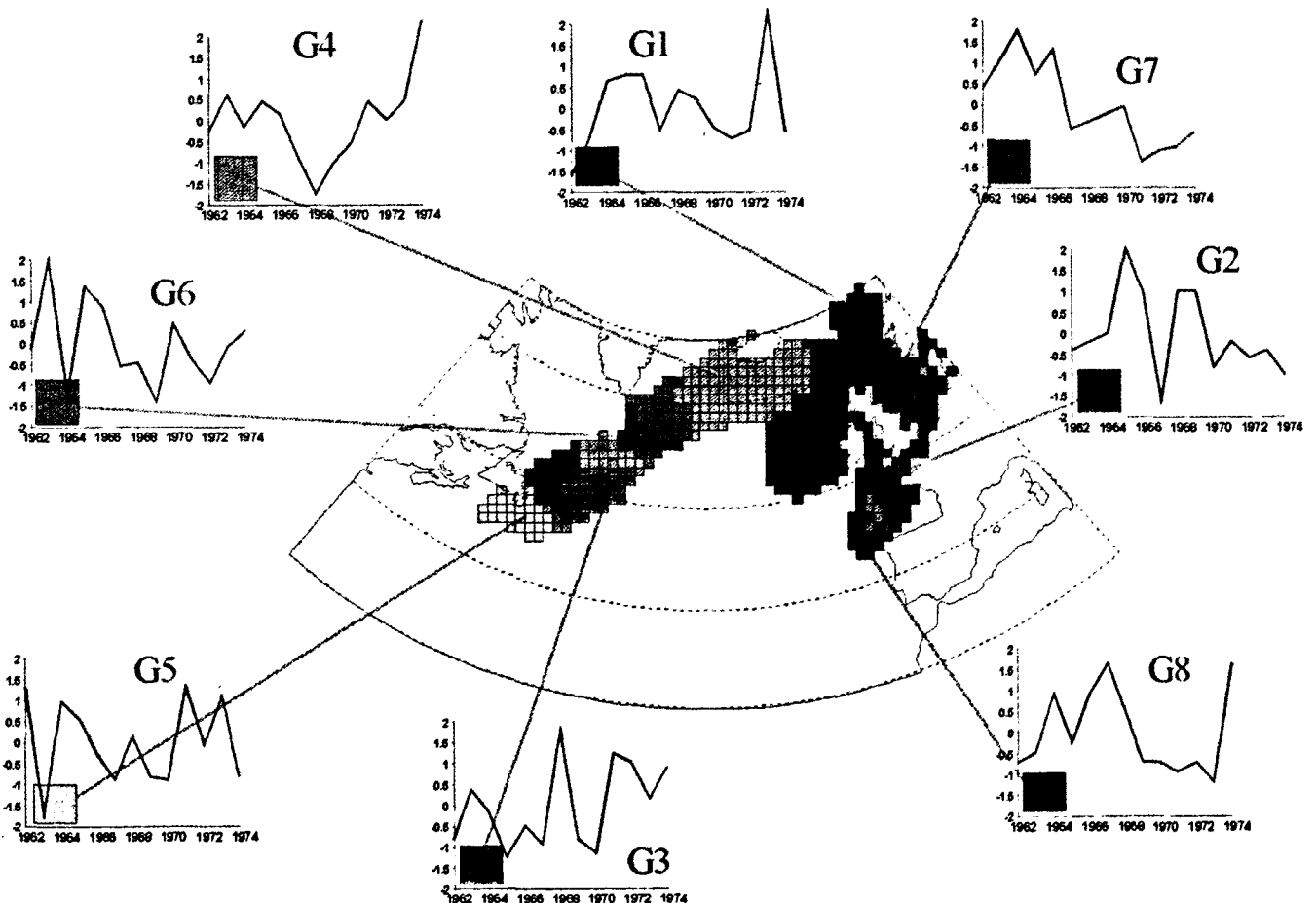


Figure 5

Spatial localization of the eight groups defined by clustering. For each group, interannual changes of *C. finmarchicus* abundance (standardized to zero mean and unit variance) are indicated.

The Mantel correlogram (Mantel r vs. geographical distance between pixels) furnishes information on the levels of similarity occurring for each distance class (Fig. 2). When stations are located less than 1100 km apart the Mantel r is positive, indicating a similarity of the interannual fluctuations between these stations. This coefficient rapidly decreases from the first class of distance (0 to 185 km, $r = 0.26$) to the fourth class of distance (370 to 460 km $r = 0.11$). This suggests that interannual changes in the abundance of *C. finmarchicus* will be homogeneous in areas of 370 km radius or less. In larger areas (between 370 and 1100 km radius), interannual changes are more heterogeneous but still remain in agreement in terms of general trends. For the distance class 1100-1300 km, r is not different from zero at the 1% level. Thus, there is statistical independence between long-term time series. Finally, in locations from 1300 to 3700 km apart Mantel r is negative similarity between sites is lower than expected when all distance classes are considered. The Mantel autocorrelogram function suggests that regions where long-term changes are similar should have a size between 370 and 1100 km radius, respectively 0.4 and 3.9×10^6 km². Identification of these regions was done by clustering.

The clustering method results in the construction of a dendrogram (Fig. 3) in which eight groups of pixels are defined. Sizes of groups vary from 0.6 to 3.6×10^6 km², in accordance with the sizes previously defined by the Mantel correlogram. Average time-series of *C. finmarchicus* abundance (standardized to zero mean and unit variance) are calculated for the entire data set and for each of the eight groups.

The general trend calculated without reference to the spatial distribution of the species (Fig. 4) is characterized by a high level of abundance from 1962 to 1966, followed by a decrease from 1967 to 1972 and a stabilization until 1974.

The groups generally comprise sets of contiguous pixels (Fig. 5), confirming that annual changes are organized in space. Group 7 (in red), which is the largest group constituted of contiguous pixels, covers the entire North Sea, the Irish Sea and a large part of the Atlantic waters west of Ireland and Scotland. In these areas, the CPR sampling intensity is maximum. In this group, long-term changes are characterized by a decrease in the abundance of *C. finmarchicus* from 1964 to 1972. This trend is very similar to that obtained when averaging all the CPR data without regard to their spatial distribution (Fig. 4). The Pearson correlation coefficient between these two series is $r_p = 0.95$ (significant at the 5% level). Group 4 is the second major group defined by the clustering, and comprises a large region south of Iceland and a smaller one southeast of Greenland. Annual changes in this group (Fig. 5) are different from the average trend (Fig. 4), as the mean abundance of *C. finmarchicus* increases from 1968 to 1974. Groups 1, 3, 5, 6 and 8 are located in restricted areas and show distinct long-term trends. Group 2 is constituted by three distant regions and its ecological meaning is difficult to assess. There is a high variability between the eight pluriannual series, as indicated by the low Pearson correlation coefficients between them: the maximum positive correlation is between groups 4 and 6: $r_p = 0.43$ (not significant at the 5% level).

DISCUSSION

Year-to-year changes in the abundance of *C. finmarchicus* have been shown (1) to be spatially autocorrelated; (2) to be similar in regions of 1100 km radius or less; and (3) to be highly variable between oceanic regions located far apart. In a previous study on the annual variability of *C. finmarchicus* around the British Isles, Colebrook (1963) reported that annual changes in areas of the North Sea were different from Atlantic ones. He hypothesized that regional changes could result from the existence of separate populations, the occurrence of different water masses, and the co-occurrence of *C. finmarchicus* and *C. helgolandicus* that were not distinguished in the CPR survey at this time. Later, Colebrook (1985) pointed out the relationship between sea-surface temperature and zooplankton, the role of overwintering populations on annual fluctuations of abundance (Colebrook, 1985), and the effect of westerly weather frequency and phytoplankton abundance (Colebrook, 1986). Dickson *et al.* (1988) also highlighted the long-term effects of northerly wind increase on the decline of zooplankton biomass around the British Isles. Similar effects of changes in temperature and stratification on zooplankton in the California current have been reported by Roemmich and McGowan (1995). Other external events, such as the latitudinal displacement of the Gulf Stream (Taylor and Stephens, 1980) and storm track displacements (Taylor *et al.*, 1992) have been related to long-term fluctuations of plankton abundance in the Northeast Atlantic. Considering these previous studies, there appear to be several possible interpretations of the location and size of the "homogeneous regions for long-term changes" that are identified in the present work. A first hypothesis is that the spatial distribution of these regions can be directly linked to the spatial distribution of environmental variables, so that each region is typical of a peculiar environmental situation. A second hypothesis is that the spatial location of groups is controlled by the existence of distinct *C. finmarchicus* populations that are geographically separated. The combined effects of spatial distribution of environmental factors with distinct populations of *C. finmarchicus* are likely to be responsible for the spatial heterogeneity of long-term changes.

The purpose of this study was more to assess the spatial properties of *C. finmarchicus* long-term trends than to identify factors responsible for these fluctuations. However, these two points of view are closely linked, and we must define their spatial scales prior to understanding long-term ecological processes.

Most of the studies on long-term fluctuations of plankton cited above were conducted in the North Sea and the North East Atlantic areas (corresponding to groups 7 and 2). It is the case for the downward trend of plankton revealed by the CPR survey as a general decline of plankton abundance from the early 1950s to the early 1980s in the Northeast Atlantic and the North Sea (Colebrook, 1982; 1984; Aebischer *et al.*, 1990). However, as shown by the interannual series of *C. finmarchicus*, results obtained in the Northeast Atlantic cannot be easily extended to other areas of the North Atlantic. Thus, the spatial extension

of this long-term trend is probably limited to the areas surrounding the British Isles, and different or opposite trends may occur in other regions of the North Atlantic.

As large-scale, long-term studies are increasingly important for the assessment of changes in the global ecosystem, it seems essential to establish a clear distinction between ecological changes that occur at regional scales (hundreds of kilometres) and others that occur at global scales (size of the Atlantic ocean). Further research should also be conducted to determine whether regional plankton changes result from regional or global climatic causes.

It appears from the present work that plankton changes at the scale of an oceanic basin cannot be easily extrapolated from regional observations. The maintenance of long-term plankton surveys at an oceanic-basin scale is crucial

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