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Calanus and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*

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ABSTRACT: Spatial and temporal patterns of *Calanus finmarchicus* and *C. helgolandicus* (Copepoda, Calanoida) were investigated in the northeast Atlantic and the North Sea from 1962 to 1992. The seasonal cycle of *C. finmarchicus* is characterised by a single peak of abundance in spring, whereas the seasonal cycle of *C. helgolandicus* shows 2 abundance maxima, one in spring and one in autumn. The former species mainly occurs in northern regions (limited by the 55° N parallel in the North Sea and by the 50° N parallel in the open ocean). The latter species shows 2 types of spatial patterns, occurring in the Celtic Sea during spring and in the Celtic Sea plus the North Sea in autumn. Differences in seasonal spatial patterns of *Calanus* species may result from different responses to the environment, ultimately due to different life cycle strategies, different vertical distributions, opposite temperature affinities and interspecific competition. Futhermore, results reveal that annual means of abundance are closely related to annual maxima and to spatial extensions of the species. It also appears that the long-term trends of the 2 *Calanus* species are opposite: *C. finmarchicus* shows a clear downward trend in abundance, while *C. helgolandicus* presents an upward one.

KEY WORDS: *Calanus* · Long-term changes · Seasonal spatial patterns · Eastern North Atlantic · North Sea · Continuous Plankton Recorder survey

INTRODUCTION

The high variability at low frequencies of plankton communities has been quite recently described by means of long-term monitoring (Russell et al. 1971, Cushing & Dickson 1976, Bernal 1979, 1981). Long-term fluctuations of zooplankton appear to result from environmental changes, rather than purely biological processes (Colebrook 1978, Chelton et al. 1982). Recent studies demonstrated the importance of environmental factors such as sea temperature, oceanic currents, turbulence, wind stress and nutrients on plankton changes (Colebrook & Taylor 1979, 1984, Colebrook 1982, 1985, 1986, Dickson et al. 1988, Radach et al. 1990, Fransz et al. 1991).

In most of these works, zooplankton was considered as a whole and the behaviour of total zooplankton was principally studied. Our purpose was to determine the specific responses of individual zooplankton species that have different physiological and biological properties to environmental changes. We studied 2 calanoid copepod species, *Calanus finmarchicus* and *C. helgolandicus*. These species were chosen because: (1) they constitute the major component of the northeast Atlantic and North Sea zooplankton in terms of biomass, numbers and trophic role (Williams et al. 1994, Gislason & Astthorsson 1995); (2) they are closely related, play a similar role in the ecosystem and their biology and physiology have been largely described (Marshall & Orr 1972, Williams 1985).

To understand the specific responses of these 2 *Calanus* species to their environment, we first have to describe their spatial and temporal patterns. The pur-

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pose of this article is to identify and compare seasonal cycles, spatial patterns, and long-term fluctuations in abundance of the 2 species, as well as their potential link to environmental variables.

METHODS

Sampling. Data were provided by the Continuous Plankton Recorder (CPR) survey. The CPR is a high-speed plankton sampler designed to be towed from commercially operated 'ships of opportunity' over long distances. CPR are towed in the surface layer (7 to 8 m depth) and, due to mixing induced by the ship towing the CPR, the 0 to 20 m layer is sampled (H. G. Hunt pers. comm.). Plankton samples are collected every 20 nautical miles (37 km), corresponding to about 3 m^3 of filtered water. The survey started in 1931 in the North Sea, and was extended over the North Atlantic at the end of the 1950s (Warner & Hays 1994). However, *Calanus finmarchicus* and *C. helgolandicus* species were not routinely distinguished until the late 1950s, thus we have only used the data collected during the period 1962 to 1992. Only stage V copepodites and adults are routinely identified to species level in the CPR survey, and we present here data on these stages only. We focused on the eastern North Atlantic, where the sampling was constant and regular during 1962–92 (see Warner & Hays 1994) and where the 2 species commonly occur (Oceanographic Laboratory Edinburgh 1973, Colebrook 1986). Plankton data consist of about 72 000 samples (~2300 per year).

The CPR survey provides information on the sub-surface distribution of species. Therefore, changes in abundance presented in this study only refer to the sub-surface layer. However, *Calanus* species undergo ontogenetic vertical migrations (Williams & Conway 1980, Hirche 1983, Williams 1985) and consequences of this behaviour on sub-surface changes in *Calanus* abundance will be discussed.

Analyses. Species abundances in each sample were log-transformed using the $\log(x+1)$ function (Colebrook 1975). Monthly data were interpolated in order to obtain a series of regular grids. Interpolation was performed by kriging, the most suitable method for a nonstandard sampling (Cressie 1993). A total of 372 grids were calculated, 1 for each month from 1962 to 1992, and resulted in 372 maps. In the eastern North Atlantic, grid nodes (map pixels) with a minimum of 70% of data during 1962–92 were selected. Remaining missing values were estimated using the ZET method (Zagoruiko & Yolkina 1982), an iterative multiple regression model. The final grid consisted of 224 nodes representing a map of 224 pixels of 8575 km^2 surface each (Fig. 1).

In order to assess variations in the spatial extension of each species, we defined a variable called 'spatial coverage'. For each monthly map, pixels with at least 1 individual were coded 1 and others were coded 0. Spatial coverage of each monthly map was defined by the ratio of pixels coded 1 to the total number of pixels and was given as a percentage (0% indicates that there is no pixel with at least 1 individual, 100% indicates that there is at least 1 individual in every pixel).

Annual abundances correspond to the mean of abundance from January to December. Annual maxima of abundance are defined as the highest monthly abundances of each year. Seasonal cycles are calculated from the means of each month of the 1962–92 series.

Comparison of long-term series was done using the Pearson correlation on original series and detrended ones. Correlations on detrended series were used to reveal relationships that were not due to long-term trends. Cross-correlation was tested by a Monte-Carlo approach (5000 simulations).

RESULTS

Seasonal cycles

The mean seasonal cycle of *Calanus finmarchicus* abundance, calculated from the 1962–92 series, shows

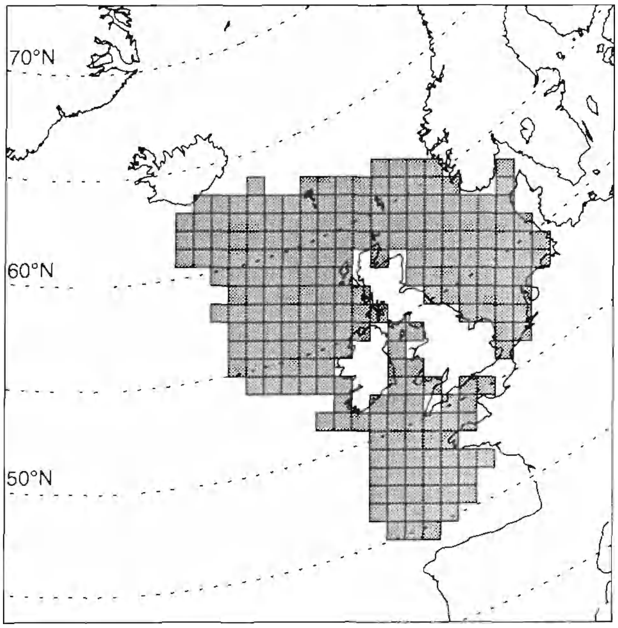

Fig. 1. Study area. Selection of pixels in this area was based on the regularity of the Continuous Plankton Recorder (CPR) survey from 1962 to 1992 and on the numbers of missing values by pixels

a clear peak of abundance during spring, i.e. April to June, and a plateau from July to September (Fig 2a). The seasonal cycle of spatial coverage follows the same pattern, indicating that these 2 variables are closely related and that the number of organisms per surface unit is constant all through the year (Fig. 2a).

The mean seasonal cycle of *Calanus helgolandicus* abundance is quite different (Fig. 2b). There are 2 abundance maxima during the year The first one occurs from May to June, and the second and major one from September to October. Contrary to *C. finmarchicus*, abundance and spatial coverage are not totally similar (Fig. 2b). The shapes of the 2 curves are close, but spatial coverage is at a higher level during autumn. This result indicates either that the mean number of organisms per surface unit is lower during this period or that the species spatial dispersal is higher or that there has been a reorganisation of the species vertical distribution.

The seasonal pattern of *Calanus finmarchicus* is reproducible from year to year; in 90% of the cases the annual maximum of abundance occurs around May. For *C. helgolandicus* the situation is a bit more complicated, with annual maximum abundance generally occurring around September (75% of cases), but in some years around June (25% of cases). For both species, mean abundance is very low during winter, but organisms are still present in the surface layer.

Seasonal spatial patterns

Calanus finmarchicus

During winter, abundances in the surface layer are low and the species distribution is restricted to northern areas, south of Iceland and south of Norway (Fig. 3a). At the beginning of spring, abundances and spatial extension increase, mainly in the northern North Sea and between Scotland and Iceland. The annual abundance maximum appears clearly on the May-June map. The spatial distribution is characterised by 2 areas of very high abundances, south of Iceland and south of Norway. The southern limit is around the 55° N parallel in the North Sea and the 50° N parallel in the open ocean. During summer, there is a general decline in abundance and spatial extension decreases in the open ocean (southern limit of the distribution moves north to around the 55° N parallel). In autumn, rather high abundance always occurs in the northern North Sea and spatial restriction continues, organisms being confined further north than in summer. In November-December, there is a drop in abundance and *Calanus finmarchicus* is limited to the northern North Sea.

Calanus helgolandicus

During winter, the species distribution is confined mainly in the south of the area studied and in the eastern part of the North Sea (Fig. 3b). At the beginning of spring, there is a rise in abundance. Populations extend further south into the Bay of Biscay and disappear from the North Sea surface waters. From May to June, a strong increase in abundance occurs in the Celtic Sea, and populations expand from the south of the area to the North of Ireland. Summer is marked by a decline in abundance and changes in the spatial pattern: organisms move northward, penetrate into the North Sea and vanish from the Bay of Biscay surface waters. Maxima of abundance and spatial coverage, corresponding to the second peak of abundance, are illustrated by the September-October map. As in spring, organisms are numerous in the Celtic Sea. However, this period is characterised by high abundance in the surface water of the North Sea and the Shetland-Orkney Isles that was not observed in spring. In November-December, abundances and spatial coverage decline; remaining organisms are located in the Celtic Sea and the North Sea.

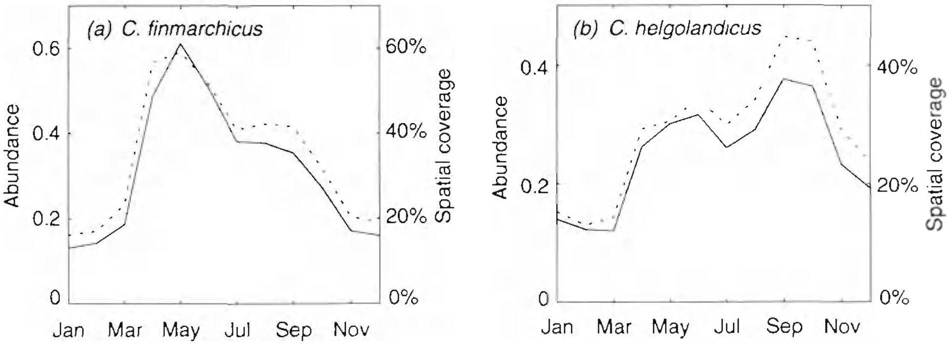

Fig. 2. Mean seasonal cycles of (a) *Calanus finmarchicus* and (b) *C. helgolandicus* calculated over the entire area from 1962 to 1992. Solid lines: $\log(x+1)$ of abundances; dashed lines: spatial coverage (percentage of pixels containing at least 1 individual)

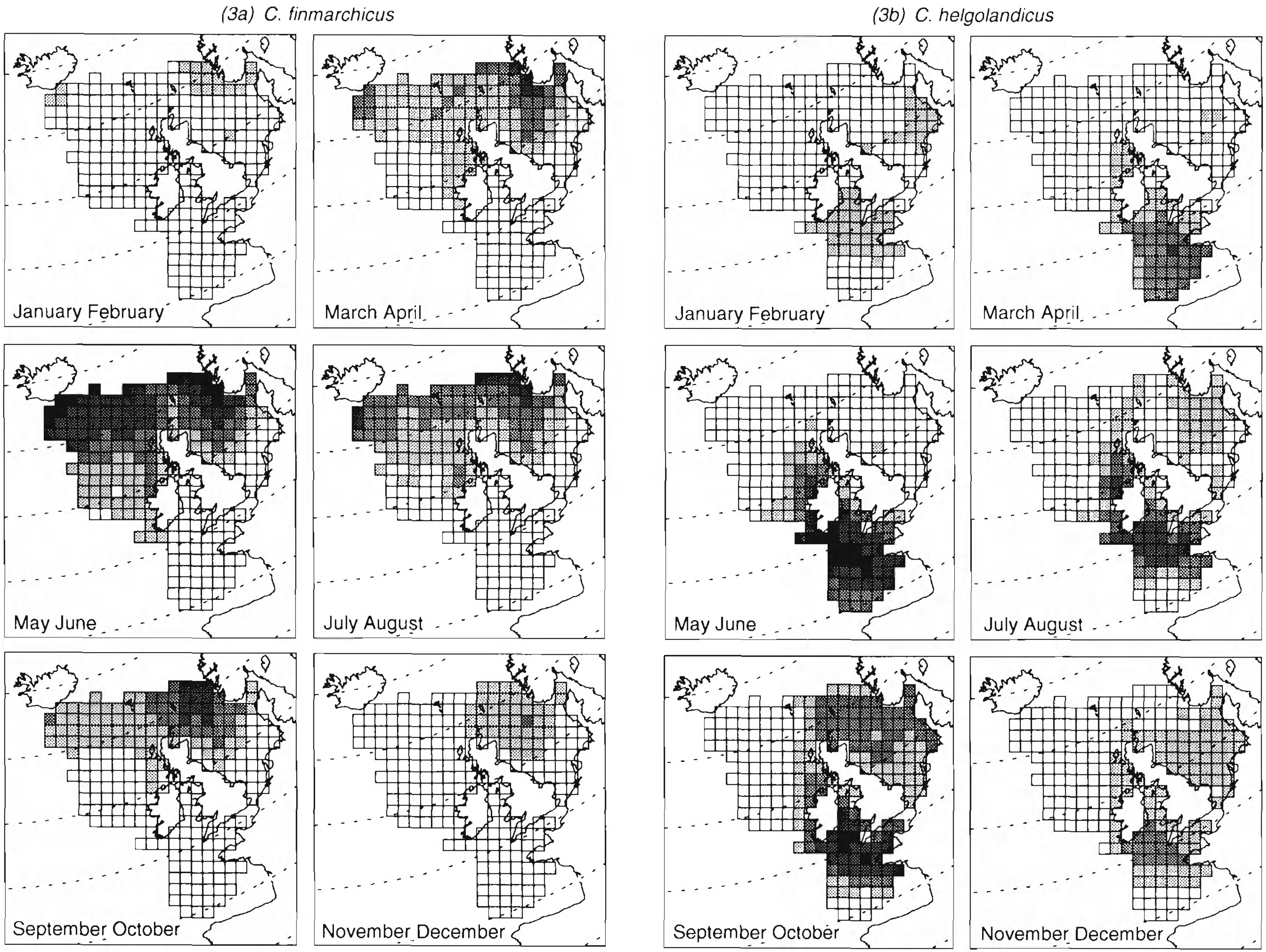

Fig. 3. Mean seasonal spatial patterns of (a) *Calanus finmarchicus* and (b) *C. helgolandicus* calculated over the entire area from 1962 to 1992. Intensity of grey is proportional to the log of the number of organisms

Calanus finmarchicus versus *C. helgolandicus* spatial patterns

Mean spatial coverage of *Calanus finmarchicus* and *C. helgolandicus* was 33.2 and 28.5% of the studied area respectively, but the 2 species can temporarily cover larger areas, mainly in spring for *C. finmarchicus* (up to 77% of the studied area in June 1978) and in autumn for *C. helgolandicus* (up to 82% of the studied area in September 1984). Nevertheless, the 2 species do not reside in the same regions (Rees 1957, Jaschnov 1970, Colebrook 1986). To assess the geographical affinity of each species and their area of co-occurrence, we computed from the 1962–92 series the following index (I) for each pixel:

$$I = \left|\frac{f-h}{f+h}\right|$$

where f is the number of months in which the abundance of *C. finmarchicus* in the pixel is equal to or greater than 1 (organism per sample); h is the number of months in which the abundance of *C. helgolandicus* in the pixel is equal to or greater than 1 (organism per sample). Index values are included between 0 and 1. The value of the index for a pixel is 0 when *C. helgolandicus* occurs as often as *C. finmarchicus* in the pixel. Conversely, when only 1 of the 2 species occurs, the value of the index is 1.

The map of this index (Fig. 4) indicates a latitudinal gradient with a zone of co-occurrence of the 2 species in the middle of the studied area and 2 specific regions, north and south. *Calanus helgolandicus* is preferentially located in southeastern areas and specifically around Brittany, whereas *C. finmarchicus* is dominant in northwestern areas and specifically to the south of Iceland. Specific zones do not exactly match the regions of maximum abundance, situated in the Celtic Sea for *C. helgolandicus* and south of Iceland and south of Norway for *C. finmarchicus*. The region of co-occurrence is very wide and extends over the North Sea and in the eastern North Atlantic from 52 to 57° N. The 2 *Calanus* species co-occur in surface waters of the eastern North Atlantic during spring only and in the surface waters of the North Sea during summer and autumn only (Fig. 3).

Long-term changes

Annual variations in the 2 species' abundance over the entire area from 1962 to 1992 are shown in Fig. 5. *Calanus finmarchicus* displays a clear downward trend over the period (Fig. 5a). The main periods of high abundance are 1962–66 and 1977–80. Years 1967–76 and 1981–86 are characterised by average abundances and 1987–92 by low numbers. On the other hand, *C. helgolandicus* shows a clear upward trend (Fig 5b). The period 1967–76 also displays average abundance, whereas low abundances occur in 1962–66 and 1977–81. In contrast, the end of the series, 1982–86 and 1989–92, is marked by the highest abundances.

Although for both species most of the variability occurs at the scale of a few years, autocorrelation analyses (Legendre & Legendre 1984) do not reveal any dominant cycle. Correlation between the 2 species is significant at the 5% level ($r = -0.4$). This correlation vanishes when it is calculated on detrended series ($r = -0.03$), indicating that the opposite relationship between the 2 series is mainly due to long-term trends. Nonetheless, cross-correlation between *Calanus finmarchicus* abundance and *C. helgolandicus* abundance in the following year is higher ($r = -0.55$) and significant for both original ($p < 0.01$) and detrended series ($r = -0.4$, $p < 0.05$). Cross-correlations with a lag greater than 1 yr are not significant. Thus, the opposition between annual fluctuations in abundance of the 2 species mainly occurs with a delay of 1 yr.

We calculated the correlation between the annual mean abundance and the annual maximum abundance on the 1962–92 series. For both species, correlations are significant at the 1% level ($r = 0.77$ for *Calanus finmarchicus* and $r = 0.62$ for *C. helgolandicus*). Thus, annual abundances of both species are strongly linked to spring abundance for *C. finmarchicus* and spring/autumn abundance for *C. helgolandicus*.

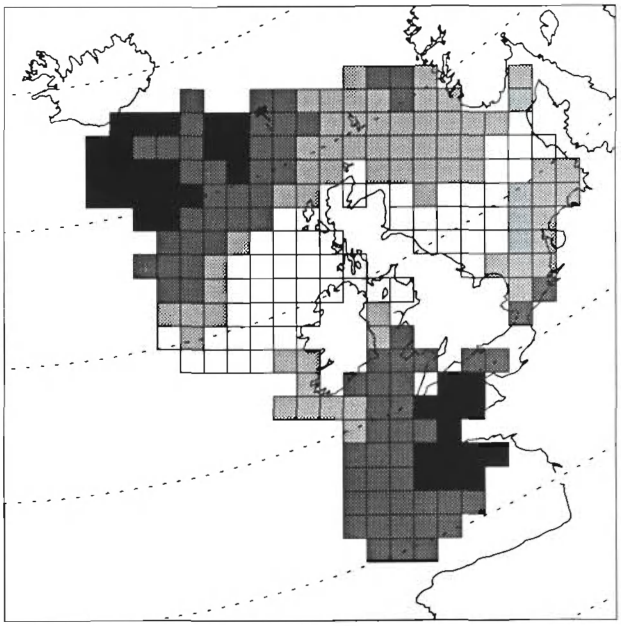

Fig. 4. Co-occurrence of *Calanus finmarchicus* and *C. helgolandicus*. Intensity of grey is proportional to the species ratio (see index I in the text). White squares: *C. helgolandicus* occurs as often as *C. finmarchicus*; black squares: 1 of the 2 species predominates

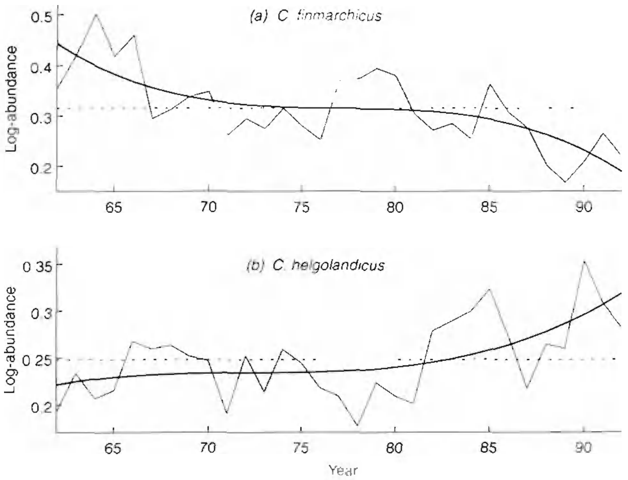

Fig. 5. Annual log of abundances (January to December means) of (a) *Calanus finmarchicus* and (b) *C. helgolandicus*. Solid lines: year-to-year fluctuations and polynomial fits; dashed lines: means over the 1962–1992 period

Correlations between annual abundance and spatial coverage are very high (r = 0.96 for *Calanus finmarchicus* and r = 0.97 for *C. helgolandicus*, $p < 1 \times 10^{-9}$). This very strong link indicates that fluctuations in abundance cannot be dissociated from fluctuations in spatial extension.

DISCUSSION

Relationship between phytoplankton and *Calanus*

The spring phytoplankton bloom occurs in the surface layer of the whole studied area, as noted by Colebroók (1982), and both *Calanus* species take advantage of this spring increase in phytoplankton abundance. Nevertheless, the 2 populations mainly remain spatially apart, with *C. finmarchicus* in the North Sea and the eastern North Atlantic and *C. helgolandicus* mainly to the south of the British Isles. During summer, there is a general decline in phytoplankton biomass (Colebrook 1982) that would explain the decrease in the abundance of the 2 copepods. The autumn period is crucial and is characterised by a higher level of phytoplankton biomass in the North Sea (Colebrook 1982). However, high abundance of *C. finmarchicus* in the near-surface layer only occurs in the northern North Sea, while *C. helgolandicus* is abundant in both southern regions and North Sea. The spatial extent of the latter species is probably supported by the North Sea phytoplankton production during this period. Finally, phytoplankton resources are generally exploited by the 2 species in geographically separated regions, except north of Ireland during spring and in the northern North Sea during autumn, where the 2 copepod species occur simultaneously.

Relationship between temperature and *Calanus*

The 2 *Calanus* species have specific physiological responses to temperature (Hirche 1987, 1990, Carlotti et al. 1993). *C. finmarchicus* is known to be a cold-temperate water species whereas *C. helgolandicus* is a warm-temperate one (Rees 1957, Jaschnov 1961, 1970, Matthews 1967, 1969, Colebrook 1982, Williams 1985). Although the 2 species tolerate a large temperature range, their geographical distribution is related to the geographical temperature gradient (Jaschnov 1961, Williams 1985). Thus, the northern location of *C. finmarchicus* and its limitation south by the 50 to 55° N parallel during its period of maximum spatial coverage probably result from the species' affinity to cold temperatures. Its peak of maximum abundance occurs in spring when temperatures are relatively low and phytoplankton abundant. In autumn, while phytoplankton abundance is maintained at a sufficient level, temperatures are probably too high to allow a second peak of abundance of *C. finmarchicus*. Conversely, the opposite spatial distribution of *C. helgolandicus* can be explained by its warm-temperate temperature affinity. Its preferential zone is located in the south. During spring, while temperatures are relatively low and phytoplankton abundant, this species remains in southern waters. Conversely, summer-autumn warming probably allows the species to extend north and graze the important phytoplankton biomass of the North Sea. Competition for resources between *C. finmarchicus* and *C. helgolandicus* in the North Sea is probably related to the temperature seasonal cycle, *C. finmarchicus* and *C. helgolandicus* being respectively favoured in spring and in autumn. However, Williams & Conway (1980) give evidence that the vertical temperature gradient is responsible for differences in vertical distributions between the 2 *Calanus* species and between stages within species. The development of the seasonal thermocline also affects both species' vertical distribution and results in their separation in the water column (Williams 1985). Furthermore, the life cycle of *Calanus* species is characterised by seasonal ontogenetic vertical migration and overwintering strategies (Hirche 1983). Thus, differences in life cycles and overwintering strategies between *C. finmarchicus* and *C. helgolandicus* (Hirche 1983, 1984) are likely to be responsible for different reponses of the 2 species to seasonal changes in temperature. Nonetheless, fluctuations in abundance of *Calanus* species in the surface layer probably reflect true changes in abundance that can be altered by seasonal vertical migration of the stage V copepodites and adults.

Relationship between currents and *Calanus*

Seasonal and spatial changes of both *Calanus* species are related to temperature and phytoplankton changes but also to advective transport. Hydrodynamism in the area is characterised by the inflow of North Atlantic waters into the North Sea through the northwestern North Sea and the English Channel, and an outflow along the Norwegian coasts (Otto et al. 1990, Backhaus et al. 1994). This feature provides a physical support to the penetration of *C. helgolandicus* into the North Sea during summer. Residual circulation cells south of Norway and in the Celtic Sea (Otto et al. 1990) probably favour the persistence of *Calanus* populations in these regions all through the year.

Seasonal and spatial distributions of the 2 *Calanus* species probably result from specific biological processes (reproduction, feeding, overwintering) and changes in environmental conditions (resource availability, sea temperature, stratification and advective transport). It is reasonable to postulate that abundance and spatial coverage of each species are maximal when optimal environmental conditions are encountered. *C. finmarchicus* reaches its higher abundances in spring when phytoplankton is abundant and temperature relatively low. In autumn, phytoplankton is probably sufficient to support a second peak in abundance but temperature conditions might not be optimal for this species. Furthermore, a high proportion of stage V copepodites have probably already migrated to deeper water to constitute the overwintering stock (Hirche 1983). This can explain the unimodal seasonal cycle of *C. finmarchicus* and its restriction to northern areas since July, despite a current regime propitious to a southern extension. *C. helgolandicus* takes advantage of the spring phytoplankton bloom only in southern regions where temperatures are highest. Although *C. helgolandicus* is advected into the North Sea through the year, it mainly expands into this basin in autumn. The species probably takes advantage of the North Sea phytoplankton production in autumn when temperatures are higher. Furthermore, the species benefits from the relatively low abundance of *C. finmarchicus* in the surface layer during this period. Thus, differences in seasonal spatial patterns of *Calanus* species might result from different responses to the environment, ultimately due to different life cycle strategies, different vertical distributions, opposite temperature affinities and interspecific competition.

Long-term changes

Our results show important year-to-year fluctuations in abundance that are associated with variations in annual abundance maxima and changes in spatial coverage. Annual abundance maximum appears to control total annual abundance. A drop in maximum abundance is not compensated by high abundance during other periods of the year These copepods have several cohorts per year (Marshall & Orr 1972), and these results indicate that a perturbation during the period of maximum abundance may have some important repercussions on the following generations.

An increase in the abundance of both species is always associated with a rise in their spatial coverage. Although long-term changes in abundance and in spatial coverage are closely related, seasonal cycles of these 2 variables are similar in *C. finmarchicus*, but not in *C. helgolandicus*. These results indicate that the number of organisms per surface unit stays constant all through the year for the former species, but varies for the latter. In autumn, the dispersal of *C. helgolandicus* is higher than in spring and the number of individuals per pixel is lower Thus, the autumn peak of abundance probably results from the species' capacity to extend spatially, rather than from local increases in abundance. This suggests that annual abundance in near-surface waters depends on the spatial extension of optimal environmental conditions.

A noticeable result is the opposition in long-term trends of the 2 *Calanus* species' abundance. *C. finmarchicus* is the most abundant copedod and follows a clear downward trend, similar to that described by Colebrook et al. (1984) and Dickson et al. (1988) for total copepods and total zooplankton. On the contrary, *C. helgolandicus* shows a clear upward trend that was unexpected in view of these previous works. This opposition in long-term trends is confirmed by the significant negative correlation between the 2 species. Furthermore, cross-correlation on the detrended series, *C. finmarchicus* and *C. helgolandicus* in the following year, is also significant. This indicates that the opposition between the 2 species also occurs at a shorter time scale. This is clear during the years 1962–66, 1977–80 and 1987–92. Thus, temporal patterns of the 2 species are opposite at short and long time scales but the causes of opposition and of the delay of 1 yr are rather obscure.

CONCLUSION

It emerges from our results that these 2 *Calanus* species, which fulfil a comparable function in the ecosystem, display different and sometimes opposite spatial and temporal patterns. Previous works showed that global events could control marine populations. Dickson et al. (1988) postulated that the long-term increase in the northerly wind component over the eastern North Atlantic, between 1950 and 1980, induced a decline of both phytoplankton and zooplankton. If the long-term decline of *C. finmarchicus* fits with this scheme, this mechanism is not adequate to explain *C. helgolandicus* long-term increase.

A large-scale atmospheric oscillation, which modifies winds regime, occurs in the North Atlantic (Rogers 1984, 1990, Lamb & Randy 1987, Mann & Lazier 1991). This oscillation is comparable to another global atmospheric event, the El Niño Southern Oscillation (Rasmusson & Wallace 1983, Enfield 1989, Mann & Lazier 1991), which changes wind stress, hydrodynamism and sea temperature over the Pacific and is known to impact pelagic communities (Cushing & Dickson 1976, Barber & Chavez 1983, McGowan 1985, Dandonneau 1986, Mysak 1986). This oscillation could be responsible for the changes in abundance of *Calanus* species observed in the present work. However, the studied area is situated in a heterogeneous environment, strongly affected by coastal influences such as regional temperature gradient, local currents, tide effects, pollutant discharges and freshwater inflows. This regional frame could locally control zooplankton abundance fluctuations.

Finally, it has to be determined whether *Calanus finmarchicus* and *C. helgolandicus* populations respond to different local environmental conditions or if they specifically respond to hydrological and climatical changes induced by the North Atlantic Oscillation.

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