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Calanus and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*

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ABSTRACT: The influence of the North Atlantic Oscillation (NAO) on 2 major zooplankton species of the eastern North Atlantic and the North Sea, *Calanus finmarchicus* and *C. helgolandicus* (Copepoda, Calanoida), was investigated. Our results confirm that from December to April, west wind stress (WWS) intensity and temperature are strongly related to the NAO. If these results were expected, more striking were the close relationships between NAO and *Calanus* species abundance. Fluctuations in abundance of *C. finmarchicus* mainly result from the combination of 2 factors, both driven by the NAO: WWS effects on spring primary production and temperature. The case of *C. helgolandicus* is more complicated, as the links between this species and the NAO result from the combination of several factors. Two of these factors, spatial heterogeneity of WWS strength over the area and temperature, are directly driven by the NAO. The third one, competition between the 2 *Calanus* species, is indirectly influenced by the NAO. Biogeographical boundaries of the 2 copepods are also modified by the NAO. Thus, in a comparable way to the El Niño Southern Oscillation in the Pacific, the NAO impacts the pelagic ecosystem of the eastern Atlantic and the North Sea.

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

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INTRODUCTION

In a previous study Planque & Fromentin (1996, this issue) showed that *Calanus finmarchicus* and *C. helgolandicus* spatial and temporal patterns in the eastern North Atlantic and in the North Sea are different. *C. finmarchicus* reaches highest abundance in the surface layer during spring in the north of the area, while *C. helgolandicus* takes advantage of the spring phytoplankton bloom only in southern regions and extends into the North Sea surface waters in autumn. Differences in seasonal spatial patterns of *Calanus* species might result from different responses to the environment, ultimately due to different life cycle strategies, distinct vertical distributions, opposite temperature affinities and interspecific competition. Furthermore, long-term trends in the abundances of the 2 copepods are opposite. *C. finmarchicus* shows a downward trend, and *C. helgolandicus* an upward one, but the mechanisms causing such differences remain unexplained.

The aim of the present work is to examine whether *Calanus finmarchicus* and *C. helgolandicus* respond to different local environmental conditions or respond differently to the same global phenomenon. Indeed, recent studies showed that some global atmospheric changes, such as El Niño Southern Oscillation (ENSO), influence pelagic communities (Barber & Chavez 1983, McGowan 1985, Mysak 1986, Mann & Lazier 1991, Karl et al. 1995). In the North Atlantic, a comparable atmospheric phenomenon, the North Atlantic Oscillation (NAO), occurs (Van Loon & Rogers 1978, Rogers 1984, 1990, Lamb & Randy 1987). The NAO is a large-scale alternation of atmospheric mass between the North Atlantic region of subtropical high surface pressures, centered on the Azores, and subpolar low surface pres-

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sures, centered on Iceland. The state of the NAO determines the speed and direction of the westerlies across the North Atlantic, as well as winter temperatures on both sides of the North Atlantic (Mann & Lazier 1991). An accentuated pressure difference between the Azores and Iceland (corresponding to a high positive NAO index) is associated with strong wind circulation in the North Atlantic, high temperatures in western Europe and low temperatures on the east coast of Canada. Recently, Greenland ice core data have revealed large decadal climate variations over the North Atlantic that can be related to the NAO (Barlow et al. 1993). It also appears that the persistence of an exceptionally strong positive phase of the NAO is the source of recent temperature anomalies and changes in atmospheric moisture transport (Hurrell 1995).

The clear effects of ENSO on pelagic ecosystems, together with clear evidence that changes in wind conditions affect Atlantic plankton communities (Dickson et al. 1988), suggest that the NAO might control plankton abundance. This work tests the hypothesis that the NAO affects the spatial and temporal patterns of the 2 dominant copepods of the eastern North Atlantic and the North Sea: *Calanus finmarchicus* and *C. helgolandicus*.

METHODS

Plankton data were collected by the Continuous Plankton Recorder (CPR) survey from 1962 to 1992. Species abundances in each sample were log transformed using the $\log(x+1)$ function (Colebrook 1975). CPRs are towed in the surface layer (7 to 8 m depth) and we present here data on stage V copepodites and adults. More details on methods and content of this data set were described by Planque & Fromentin (1996).

The NAO index is the difference in normalised sea level pressures (SLP) between Ponta Delgadas (Azores) and Akureyri (Iceland) and is usually calculated on the winter season (Rogers 1984). SLP from 1895 to 1992 were provided by the World Weather Archive. Because this study focused on the NAO effect on plankton, we extended the calculation of the index to December-April.

Meteorological data were provided by the Comprehensive Ocean Atmosphere Data Sets (COADS). We considered 3 variables: air temperature, sea surface temperature (SST) and the west component of the wind stress (WWS). To depict the relationship between the NAO index and these variables, we only took into account the mean of the months December to April. Meteorological data were interpolated identically to plankton ones within the area defined by Planque & Fromentin (1996, Fig. 1).

Eigenvector Filtering (EVF) was performed to detect general trends in the NAO secular series (Colebrook 1978, Ibanez & Etienne 1992). This method uses Principal Component Analysis on the autocovariance matrix of the series. The series estimated from the first principal component was taken as the general trend. For the 31 yr series, trend was detected by a third-order polynomial fit.

Meteorological time series were considered from 1962 to 1992 to match plankton series. Relationships between the NAO index and WWS, temperatures and the 2 *Calanus* species were investigated using Pearson correlations on original series and detrended ones. Correlations on detrended series were used to reveal relationships that were not due to long-term trends.

RESULTS

NAO index

The general trend of the index was calculated using EVF with a lag of 10 yr. The first component, which corresponds to the general trend, accounts for 18.3% of the total variance. Three major periods can be distinguished from this trend (Fig. 2): (1) 1895-1919 is characterised by a plateau above the mean of the series, (2) 1920-1962 presents a 40 yr downward trend, interrupted by a slight increase from 1940 to 1950, (3) 1963-1992 shows a clear upward trend, particularly in the last few years. How-

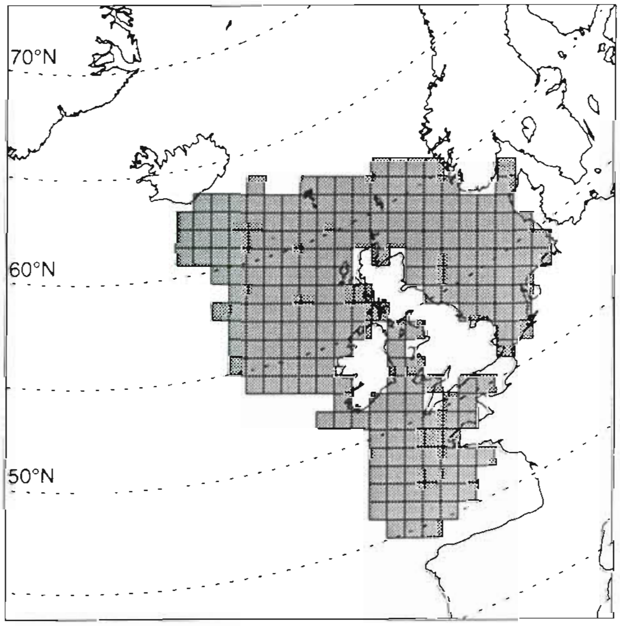

Fig. 1. Study area. Selection of this area was based on the regularity of the Continuous Plankton Recorder (CPR) sampling from 1962 to 1992

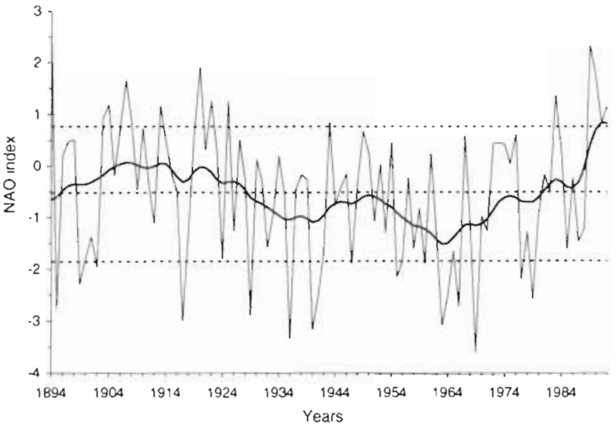

Fig. 2. North Atlantic Oscillation (NAO) December–April index based on the average pressure difference between the Azores and Iceland from 1895 to 1992. Dashed lines indicate the mean of the series (middle line) plus and minus standard deviation (upper and lower lines)

ever, this trend accounts for a small amont of the total variability and most of the variance occurs at shorter scales (less than 10 yr). The index sometimes varies largely from one year to another, e.g. 1902–1903, 1924–1925, 1967–1969, 1988–1989. Very high values of the index (above the mean plus the standard deviation) are encountered at the beginning (1903–1925) and the end (1989–1992) of the series. Very low values (below the mean minus the standard deviation) are found all along the series, especially during the periods 1895–1903, 1929–1941 and 1962–1969. These results are similar to those described by Rogers (1984) for the winter index from 1895 to 1983.

The period 1962–1992, on which the study is focused, corresponds to the third part of the increasing NAO index. Nevertheless, all types of NAO pattern occur during these 31 yr: very low values of the index in 1963, 1964, 1966, 1969, 1977 and 1979, and very high values in 1983 and 1989–1992.

NAO index and meteorological factors

We compared long-term fluctuations of the NAO with WWS and temperature to determine the intensity of the relationships among these variables in the studied area from 1962 to 1992. NAO index and WWS show a similar upward trend, more pronounced at the beginning and at the end of the period (Fig. 3a). There is a very strong correlation between the 2 series, r = 0.85 ($p = 1 \times 10^{-9}$; Table 1a). Furthermore, year-to-year variations are perfectly synchronous; strong WWS are observed in years with high NAO index and vice versa. This result is corroborated by the significant correlation on the detrended series ($r = 0.84$, $p = 1.10^{-9}$; Table 1b).

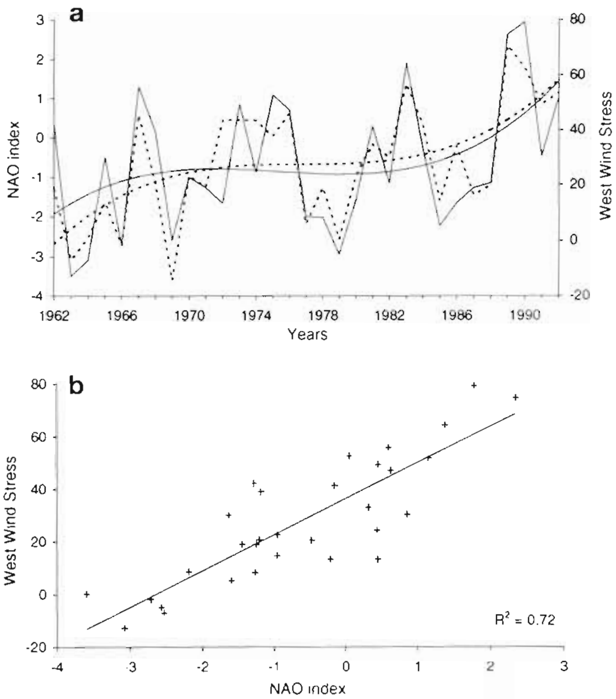

Fig. 3. (a) Average west wind stress (WWS) in $m^2 s^{-2}$ over the study area (solid line) and NAO index (dashed line) from 1962 to 1992. Third-order polynomial fits are superimposed. (b) Linear regression plot between the NAO index and the WWS

Table 1. Pearson correlation coefficients between long-term series (1962–1992) of the NAO, west wind stress (WWS), air temperature, sea surface temperature (SST), *Calanus finmarchicus* (*C. fin.*) and *C. helgolandicus* (*C. helgo.*) without and with a delay of 1 yr. Correlations significant at the: **1% level; *5% level; ns: not significant. Correlations on (a) original series, (b) detrended series (original series minus polynomial trends). Cross-correlations on *C. helgolandicus* tested by a Monte-Carlo approach (5000 simulations)

	NAO	WWS	Air temp.	SST	*C. fin.*
a					
NAO	–	–	–	–	–
WWS	0.85^{**}	–	–	–	–
Air temp.	0.55^{**}	0.5^{**}	–	–	–
SST	0.51^{**}	0.54^{**}	0.89^{**}	–	–
C. fin.	-0.76^{**}	-0.71^{**}	-0.44^{*}	-0.46^{**}	–
C. helgo.	0.42^{*}	0.31^{ns}	0.09^{ns}	0.3^{ns}	-0.4^{*}
C. helgo. (with 1 yr lag)	0.53^{**}	0.57^{**}	0.34^{ns}	0.52^{**}	-0.55^{**}
b					
NAO	–	–	–	–	–
WWS	0.84^{**}	–	–	–	–
Air temp.	0.54^{**}	0.44^{*}	–	–	–
SST	0.41^{*}	0.46^{**}	0.87^{**}	–	–
C. fin.	-0.6^{**}	-0.68^{**}	-0.39^{*}	-0.31^{ns}	–
C. helgo.	0.15^{ns}	0.1^{ns}	-0.12^{ns}	0.05^{ns}	-0.03^{ns}
C. helgo. (with 1 yr lag)	0.41^{*}	0.5^{**}	0.38^{*}	0.47^{**}	-0.4^{*}

The regression emphasizes a strong linear relationship, and the NAO explains 72% of the interannual variability in WWS ($r^2 = 0.72$; Fig 3b). Correlations between the NAO index and both air temperature and SST are also significant ($p < 0.01$; Table 1a) and remain significant (at the 1% or 5% level) for the detrended series (Table 1b).

These results confirm that WWS, air temperature and SST are closely associated with the NAO in the studied area from 1962 to 1992.

NAO index and long-term fluctuations of *Calanus* species

Calanus finmarchicus

NAO index displays an upward trend (see above) whereas *Calanus finmarchicus* displays a downward one (Planque & Fromentin 1996; Fig. 4a). Therefore Fig. 4a shows the 2 series with the NAO index on a reverse scale. The match between the 2 series indicates that: (1) the trends are exactly opposite and (2) variations at shorter time scales are synchronous. This is confirmed by strong negative correlations, significant at the 1% level for both raw data and detrended series (Table 1). Periods of accentuated pressure difference between the Azores and Iceland, i.e. positive NAO index, are associated with low abundances of *C. finmarchicus*, e.g. 1972–1976, 1983 and 1989–1992. Conversely, periods of low pressure difference, i.e. negative NAO index, are associated with high abundances of *C. finmarchicus*, e.g. 1962–1966 and 1977–1980. The regression reveals that 58% of the interannual variability of *C. finmarchicus* abundance is explained by the NAO ($r^2 = 0.58$; Fig. 4b).

Calanus helgolandicus

The relationship between *Calanus helgolandicus* and NAO is less obvious than that for *C. finmarchicus* (Fig. 5). The 2 series are positively correlated at the 5% level, but this correlation is primarily due to the long-term increases of both parameters; correlation on the detrended series is close to zero (Table 1). Indeed, year-to-year variations are not synchronous (Fig. 5a). High abundances of *C. helgolandicus* do not always match high values of the NAO index, e.g. 1976, 1981 and 1989. The regression indicates that the relation-

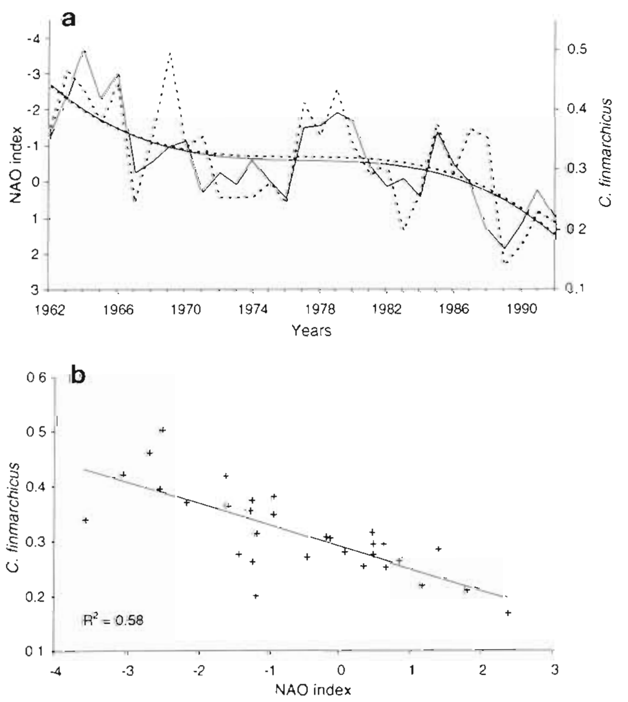

Fig. 4. (a) Average log abundance [$\log(x+1)$] of *Calanus finmarchicus* over the study area (solid line) and NAO index on a reverse scale (dashed line) from 1962 to 1992. Third-order polynomial fits are superimposed. (b) Linear regression plot between the NAO index and *C. finmarchicus* log abundance. Each annual value is based on ~2300 samples

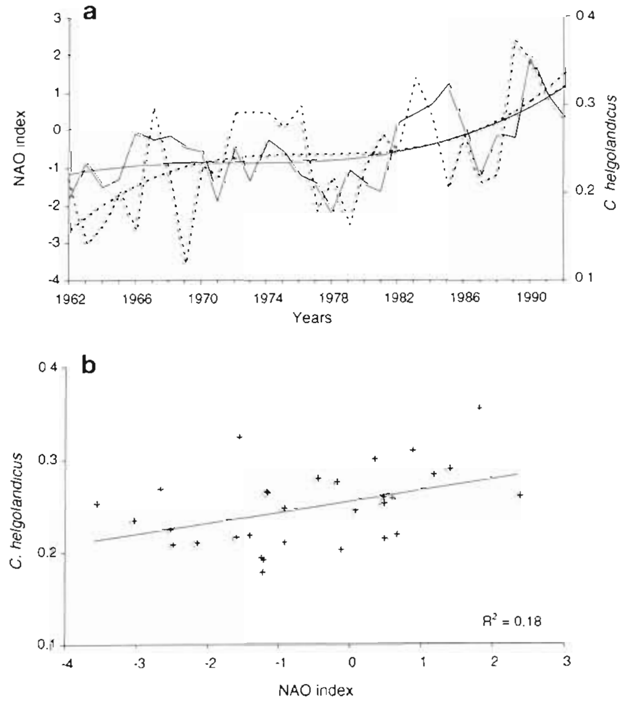

Fig. 5. (a) Average log abundance [$\log(x+1)$] of *Calanus helgolandicus* over the study area (solid line) and NAO index (dashed line) from 1962 to 1992. Third-order polynomial fits are superimposed. (b) Linear regression plot between the NAO index and *C. helgolandicus* log abundance. Each annual value is based on ~2300 samples

ship is weak; only 18% of the variability of *C. helgolandicus* is explained by the NAO ($r^2 = 0.18$; Fig. 5b). Nonetheless, cross-correlation between the 2 series (NAO and *C. helgolandicus* in the following year) is higher and significant for both original and detrended series (Table 1). This reveals that the connection between the NAO and *C. helgolandicus* abundance mainly occurs with a delay of 1 yr.

Calanus species abundances versus NAO patterns

Annual and seasonal *Calanus* species abundances during periods of extreme NAO patterns were investigated in order to examine the link between *Calanus* species and NAO. High NAO years, 1983 and 1989–1992, are characterised by extreme positive NAO indices, above the mean plus standard deviation of the secular series (Fig. 2). Low NAO years, 1963, 1964, 1966, 1969, 1977 and 1979, are on the other hand characterised by extreme negative NAO indices, below the mean minus standard deviation of the secular series.

Annual abundances

Mean of the total *Calanus* species abundance is significatively greater during a low NAO than during a high one (Fig. 6a). There is a significant deficit of 18.5% of the total abundance during a high NAO (Student test: p = 0.006). This deficit results from an important drop (44%) in *C. finmarchicus* abundance that is not fully compensated for by the increase (30%) in *C. helgolandicus* abundance.

Seasonal abundances

Spring and autumn total abundances also decrease during high NAO (Fig. 6b, c). However, these declines are not statistically significant because variability within years of a particular NAO pattern is higher (seasonal confidence intervals are higher than annual ones). In spring and autumn, declines of *Calanus finmarchicus* abundance during high NAO are significant (Student tests: p = 0.003 for spring, p = 0.0003 for autumn). These deficits in abundance are important, reaching 33% in spring and 57% in autumn. In contrast, *C. helgolandicus* abundance is greater during high NAO by about 33% in spring and 37.5% in autumn. Although autumn increase is statistically significant (p = 0.004), the spring rise is not significant due to an important variability within years of high and low NAO.

Thus, NAO extreme patterns are associated with drastic changes in *Calanus* species abundances. *C. finmarchicus* abundance is significatively higher during low NAO, whereas *C. helgolandicus* abundance increases during high NAO. Finally, total *Calanus* species abundance variations, which result from the 2 species' opposite responses, are driven by changes in *C. finmarchicus*, the most abundant of the 2 copepods.

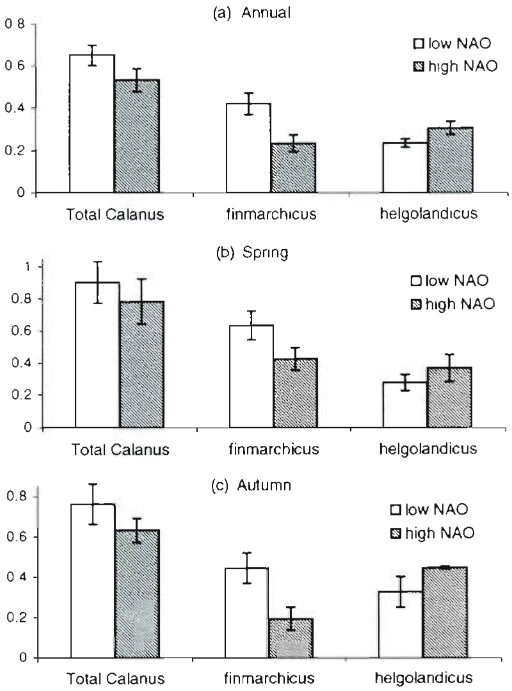

Fig. 6. (a) Mean annual log abundance of total *Calanus* species, *C. finmarchicus* and *C. helgolandicus*, during low (1963, 1964, 1966, 1969, 1977, 1979) and high (1983, 1989, 1990, 1991, 1992) NAO years, with confidence intervals at the 5% level. (b) Mean spring log abundance with confidence intervals. (c) Mean autumn log abundance with confidence intervals

DISCUSSION

Variations in both meteorological and biological factors are related to the NAO. WWS are closely connected to the NAO; high NAO induces high WWS and vice versa. SST and air temperature are significantly correlated with NAO, and from low to high NAO years temperature rise is about 0.4 to 1.1°C. These results confirm that the effects of the NAO on the direction and the strength of the westerlies are clearly pronounced over the studied area. While these results are expected in view of previous studies, this work establishes the presence of a tight relationship between NAO and zooplankton. Nevertheless, ecological processes that link *Calanus* abundance to the NAO still have to be determined.

Calanus finmarchicus is the species which is most connected to the NAO. This relationship can be partially explained by extending the analysis of Dickson et al. (1988) on the linkage between winds and plankton production. During a high NAO pattern, the wind stress is reinforced, generating a strong mixing of the surface layer in winter and spring (Fig 7a). The enhanced mixing delays the spring phytoplankton bloom and reduces primary production (Sverdrup 1953, Dickson et al. 1988). A decline and delay of the spring phytoplankton bloom might be one of the causes of drop in the abundance of *C. finmarchicus* in the surface layer. Furthermore, westerlies being pushed farther south, air and sea surface temperatures are higher than normal. This situation is probably unfavorable to *C. finmarchicus*, which is a cold-temperate water species (Hirche 1987, 1990, Carlotti et al. 1993, Planque & Fromentin 1996). Thus, the significant decline of this species, about 44% from low to high NAO years, is likely to result from a combination of these 2 negative circumstances. The situation is reversed during a weak NAO (Fig 7b). Indeed, a low WWS allows an earlier stratification of the surface layer and hence an earlier initiation of the spring phytoplankton bloom. Westerlies being pushed far north of their average position, air and sea surface temperatures are lower than normal. This ecological context is probably favorable to higher abundance of *C. finmarchicus* in the surface layer. Finally, the link between NAO and *C. finmarchicus* seems relatively direct and appears to result from a combination of 2 factors both driven by the NAO: WWS effects on spring primary production and temperature fluctuations.

However, this scenario cannot explain the connection between NAO and *Calanus helgolandicus* abundance in the sub-surface waters. Firstly, because the abundance of this species is higher during high NAO than during low ones. Secondly, because there is a 1 yr delay between NAO situations and *C. helgolandicus* response. These results can be interpreted if we consider the spatial heterogeneity of the NAO effects within the studied area. Amplitude of the WWS response to NAO is largely greater in the north of the area than in the south. In northern regions, where *C. finmarchicus* is predominant, WWS increase by 180% of their average values during high NAO years, but only increase by 50% of their average values in southern regions, where *C. helgolandicus* is predominant.

The effects of high NAO on the water column stratification are thus less pronounced in southern regions and spring phytoplankton production is probably less perturbed than in northern ones. Furthermore, *Calanus helgolandicus*, a warm-temperate species (Rees 1957, Matthews 1969, Jaschnov 1970, Planque & Fromentin 1996), might take advantage of the high NAO warming effect. These 2 circumstances constitute a favorable context for this species.

Moreover, during autumns of high NAO years, there is a competitive advantage of *Calanus helgolandicus* over *C. finmarchicus*. Indeed, during high NAO autumns *C. finmarchicus* abundance drops by 57%, probably due to a poor spring recruitment. This competitive advantage mainly happens in the North Sea, where the 2 species co-occur in autumn (Planque & Fromentin 1996), and might contribute to the 37.5% increase in *C. helgolandicus* sub-surface abundance during autumns of high NAO years.

We can also hypothesize that: (1) hydrodynamism is reinforced during high NAO, inducing a better dispersion of *Calanus helgolandicus*, especially into the North Sea; (2) that high NAO are propitious to maintain a higher level of *C. helgolandicus* overwintering stocks and, hence, a persistently high population level the following year (Colebrook 1985). This last point is supported by the 1989-1990 case. These 2 years are characterised by 2 successive high NAO. In autumn 1989, *C. helgolandicus* abundance was very high in the North Sea. The warm winter 1989-1990 probably allowed the persistence of the stocks in the North Sea and hence some exceptional abundances in that region during spring 1990 in comparison to a normal year. Moreover, *C. helgolandicus* were probably able to take advantage of the remarkable low abundance of *C. finmarchicus* in the North Sea during spring 1990. This might explain the radical opposition between the 2 species' annual abundances during that particular year. Finally, the link between *C. helgolandicus* and NAO might result from a combination of 3 factors. Two of these factors, spatial heterogeneity of WWS intensity over the area and temperature, are directly driven by the NAO. The third one, competition between the 2 *Calanus* species, is indirectly influenced by the NAO. Furthermore, *C. helgolandicus* re-

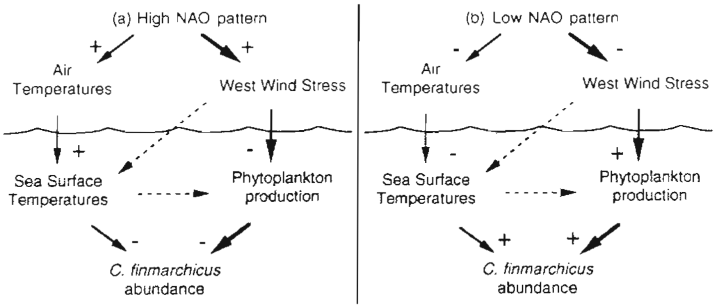

Fig. 7. General scheme of the connections between NAO and *Calanus finmarchicus* during (a) high and (b) low NAO patterns

sponse to the NAO seems to occur mainly in autumn and during the following winter, which explains the 1 yr delay observed between this species and NAO, as between the 2 copepod species.

Besides the effects of the NAO on *Calanus* species abundance, NAO also modifies the biogeographical boundaries of the 2 copepod species. During high NAO, temperatures are higher and *C. helgolandicus* extends farther north (see spring 1990 situation described above), whereas this species is confined in southern regions during low NAO. In contrast, *C. finmarchicus* is confined in northern regions during high NAO, and extends farther south during low NAO. This is revealed by the strong negative correlation between *C. finmarchicus* spatial extension (as defined in Planque & Fromentin 1996) and the NAO index (r^2 = 0.57, indicating that 57% of the spatial extension variability is due to NAO). This result fits some previous works on the effects of climate changes on the competitive advantage of the species (Cushing & Dickson 1976, Southward 1980, Southward et al. 1988).

Nevertheless, variations in abundance in the surface layer might also be altered by changes in the vertical distribution of both species. The 2 *Calanus* species can take up different positions in the water column, depending on the vertical temperature gradient, overwintering strategy and inter-specific competition (Williams & Conway 1980, Hirche 1983, 1984, Williams 1985). Furthermore, increases in turbulence can modify the contact rate between copepods and phytoplankton cells (Denman & Gargett 1995). These processes are likely to affect the NAO-plankton relationship presented above, but could not be tested within the framework of this study, as CPR samples are collected only in the subsurface layer.

CONCLUSION

In a way comparable to the Niño Southern Oscillation, there are some connections between NAO and plankton fluctuations in the eastern North Atlantic and North Sea. The 1982–1983 ENSO event has been associated with a reduced phytoplankton biomass in both the western and eastern Pacific (Barber & Chavez 1983, Dandonneau 1986). It has also been linked with a rise in temperature and a reduced flow of the Californian current that induces radical changes in zooplankton biomass (Bernal 1981, Chelton et al. 1982, McGowan 1985, 1990, Mullin 1994). The ENSO and the Aleutian low also affect fish production in the Pacific (Sinclair et al. 1985, Mysak 1986, Beamish & Bouillon 1993). Our results demonstrate that *Calanus* species fluctuations are closely linked to the state of the NAO. There is a significant and important decline (18.5%) in total *Calanus* species abundances from low to high NAO years. However, relationships between NAO and zooplankton are complex and would result from interactions of physical mechanisms with biological and physiological processes. Differences in the responses of the 2 *Calanus* species to the NAO are due to their specific seasonal cycles, opposite temperature affinities and different geographical locations (Planque & Fromentin 1996).

Further investigations should be conducted to determine relationships between NAO and other zooplankton populations as well as fish stocks. Indeed, *Calanus* species constitute the main resources for fish juveniles and regulate fish recruitment in the studied area (Cushing 1973, Brander & Hurley 1992). Furthermore, fluctuations in wind-induced turbulence and temperature are known to modify prey capture efficiency and growth and development of fish larvae (Sundby & Fossum 1990, Dickson & Brander 1993, Conover et al. 1995, Sundby 1995).

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