Long-term changes in zooplankton and the climate of the North Atlantic

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Long-term variations in zooplankton abundance in the north-east Atlantic, the North Sea, and in freshwater UK lakes are investigated by means of the Continuous Plankton Recorder survey and the Windermere and Esthwaite lakes data. Inter-annual variability of plankton abundance in these data sets shows strong correlation with two modes of climatic variability in the North Atlantic: the latitudinal shifts of the north wall of the Gulf Stream and the North Atlantic Oscillation. Detailed analyses reveal that the connection between environmental forcing and plankton response depends on various mechanisms, i.e., timing and intensity of the spring phytoplankton bloom resulting from changes in stratification levels, changes in temperature, and, in the case of the copepod *Calanus finmarchicus*, advection of the population into the North Sea at the end of the winter season. Future attempts to predict changes in marine ecosystems on the basis of climate scenarios will require focusing major effort on biological–physical modelling and large-scale plankton population ecology. The maintenance of long-term monitoring programmes is also essential to determine whether the climate–plankton connections observed during several decades will persist in the future or will be overruled by other mechanisms and principally human-induced perturbations.

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Introduction

The permanent increase of human activities raises the question of possible long-lasting anthropogenic changes in ecosystems. Forecasting anthropogenic effects on marine ecosystems requires a prior understanding of their natural fluctuations, since human-induced changes can only be perceived as a departure from a natural variability baseline. Measuring these fluctuations at scales ranging from regional to planetary, and from decades to millennia, demands sampling at appropriate scales.

The longest records of changes in marine life have traditionally been associated with commercial fishing activities. However, interpreting changes in fish populations is difficult since variations in abundance reflect the integrated effects of natural causes and of fishing. Furthermore, the life duration of many species is such that the variations in stocks integrate several years of environmental forcing. Plankton species have a shorter life-cycle and are not yet commercially exploited, which means that the study of their responses to climate variations is more accessible.

Long-term climate–plankton connections have been detected in the Pacific in the CalCOFI programme (e.g., Bernal, 1981; Roemmich and McGowan, 1995) and in the North Atlantic in the Continuous Plankton Recorder (CPR) programme (e.g., Colebrook, 1978; Cushing, 1990; Taylor, 1995). The effects of climate on plankton can take place on a world-wide scale (Genin *et al.*, 1995) and may be transferred from plankton to higher trophic levels; for example, by fish or bird populations (Aebischer *et al.*, 1990; Veit *et al.*, 1996).

In the Pacific Ocean, the biological effects of the El Niño Southern Oscillation (ENSO) have been the subject of intensive study. The ENSO is a global atmospheric event that modifies windstress, sea temperature, and hydrodynamics (Cane, 1983; Rasmusson and Wallace, 1983), and consequently impacts pelagic communities (Barber and Chavez, 1983; Mysak, 1986). The
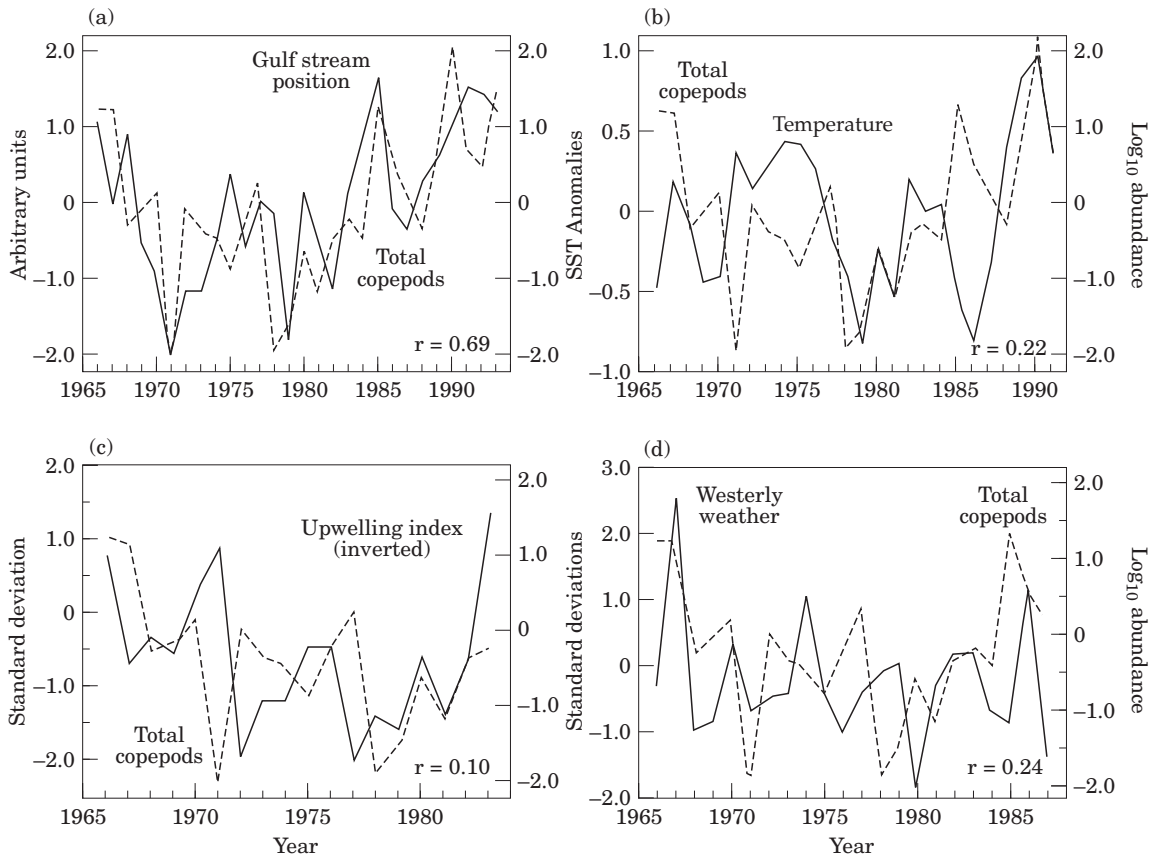
Figure 1. Logarithm of copepod abundance in the central North Sea (broken line; right-hand scale) according to the CPR survey (area C1, cf. Fig. 8) compared with different physical parameters (solid lines; left-hand scale). Correlation coefficients (r) between data pairs are indicated (from Taylor, 1995). (a) Annual value of the Gulf Stream first principal component (1966–1993); (b) annual mean sea-surface temperature anomaly (°C) in area C1 (1966–1991); (c) inverted normalized April–September upwelling index at Porto, Portugal (1966–1983, from Dickson *et al.*, 1988); (d) normalized frequency of westerly weather (1966–1987, from Aebischer *et al.*, 1990).

meteorological and biological effects extend to the northern hemisphere (Jacobs *et al.*, 1994; Karl *et al.*, 1995).

Here, we present two examples of large-scale environmental changes in the North Atlantic: the latitudinal shifts of the Gulf Stream and of the North Atlantic Oscillation (NAO). The Gulf Stream signal and the NAO index are both connected with changes in zooplankton communities in European waters, but the processes involved are different. Spatial and temporal analyses as well as results from modelling studies are used to investigate the nature of the links between these large-scale climate fluctuations and the variations in plankton in the North Atlantic.

North–south shifts of the Gulf Stream north wall

Recently, the latitude of the north wall of the Gulf Stream close to the coast of the USA has been shown a

valuable climatic indicator for understanding inter-annual biological changes on the European Continental Shelf (Taylor and Stephens, 1980; Taylor *et al.*, 1992; Hays *et al.*, 1993; Taylor, 1995). The index of Gulf Stream position was obtained by applying principal components analysis to data extracted from charts of the north wall published in *Gulf Stream Monthly Summary*, *Gulf Stream*, or, most recently, *Oceanographic Monthly Summary* (Taylor, 1995). Year-to-year changes in the CPR estimate of abundance of total copepods in the central North Sea are very similar to changes in the north wall index (Fig. 1a) and the positive correlation accounts for as much as 45% of the variance of the annual plankton abundance. This association is one of the strongest relationships between plankton time series from the CPR survey and the physical environment. For example, the relationship with the Gulf Stream position is much clearer than with local sea surface temperature or with two indices which have been shown to display long-term trends generally similar to those of the
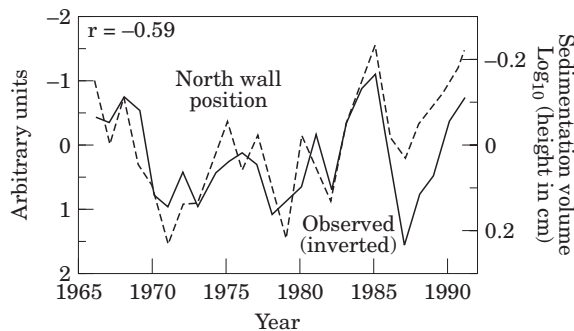
Figure 2. Logarithm (inverted) of the mean summer (May–September) biomass of zooplankton in Lake Windermere (linear trend removed, from Taylor *et al.*, 1996; solid line) compared with the latitude of the north wall of the Gulf Stream (broken line).

zooplankton data (Fig. 1; Dickson *et al.*, 1988; Aebischer *et al.*, 1990). The association is seen in other areas of the North Sea except for the southern part, where there is no thermal stratification (Taylor *et al.*, 1992). Also, it appears to be widespread across different zooplankton species (Taylor, 1995) with the exception of *Calanus finmarchicus* (discussed in the next section).

As any time-lag between shifts in the north wall and the changes in plankton abundance in the central North Sea is less than one month, the connection has to be via the atmospheric circulation. This conclusion is supported by an equally long time series of zooplankton data from Lake Windermere, a freshwater lake in northwest England, showing a significant negative correlation with the latitude of the Gulf Stream (Fig. 2, George and Taylor, 1995). The reversed sign in this case may be due to the life cycle of *Daphnia*, the dominant zooplankton species (George and Harris, 1985). Year-to-year correlation with the north wall of the Gulf Stream has also been reported for a long series of zooplankton data collected off the Northumberland coast (Frid and Huiselan, 1996) and in a terrestrial vegetation data set (Willis *et al.*, 1995).

It seems likely that the onset of spring and the start of seasonal stratification are the processes responsible for the association with the latitude of the north wall. George and Harris (1985) have argued that the timing of spring stratification is the main cause of year-to-year differences in zooplankton abundance in Windermere, and CPR estimates of total copepods in the unstratified southern North Sea show no correlation with the position of the Gulf Stream. George and Taylor (1995) have constructed an index of the onset of seasonal stratification by analysing the thermal characteristics of Lake Windermere at the onset of stratification at the beginning of June. The stratification index (*SI*) was obtained by combining three measurements from early June profiles:

$$SI = G - (R + D)$$

where: G is the depth of the maximum temperature gradient, R the rate of deepening of the 9°C isotherm in the thermocline, and D the difference in depth between the 9 and 10°C isotherms in the thermocline. G, R, and D were standardized to zero mean and unit variance.

This index is clearly correlated with the abundance of zooplankton in Windermere (Fig. 3a) and with Gulf Stream position (Fig. 3b). Indices derived from data from a nearby smaller and shallower lake (Esthwaite Water), from the northern North Sea, and from temperature profiles produced by a one-dimensional model of thermal stratification (Mellor and Yamada, 1974), when driven by hourly meteorological observations (1966–1994) from Dublin airport (Taylor *et al.*, 1996), show the same general relationship with Gulf Stream position as the index from Windermere.

The Dublin data series has also been used to carry out a 29-year run of the Irish Sea model of Prestidge and Taylor (1995). The results (Fig. 4) reveal how this model responds to differences in weather patterns between years (Taylor *et al.*, 1996), perhaps the most noticeable feature being the tendency for higher peaks to be reached in years with an early spring bloom than in years with later blooms. An explanation may be that there is a greater chance of mixing events early in the year providing extra nutrients for phytoplankton growth if nutrients have become depleted by an already developing bloom. In Figure 4, a distinction is made between years with a northerly (Gulf Stream index>0.4) and with a southerly (index< − 0.4) displacement. Intermediate years have been omitted. The model results corresponding to northerly and southerly Gulf Stream years lie on different lines because spring blooms tend to be earlier when the Gulf Stream is further to the south. This is in agreement with the Mellor–Yamada model, which indicated earlier stratification in these years. Confidence in the conclusions reached is, of course, limited by the simplicity of the model, which does not have zooplankton explicitly represented. Nevertheless, the conclusions may still be useful as a more realistic model of the system would be sensitive to the same kinds of inter-annual weather patterns, even though the response might be different.

These results suggest that the timing of spring phytoplankton bloom on the European Shelf is related to the latitude of the Gulf Stream off the US coast. Although the mechanism responsible for the association is not clear, one important factor is likely to be the NAO.

North Atlantic Oscillation (NAO)

The NAO was first identified by Walker (1924) at the time when the ENSO was also detected. It is the
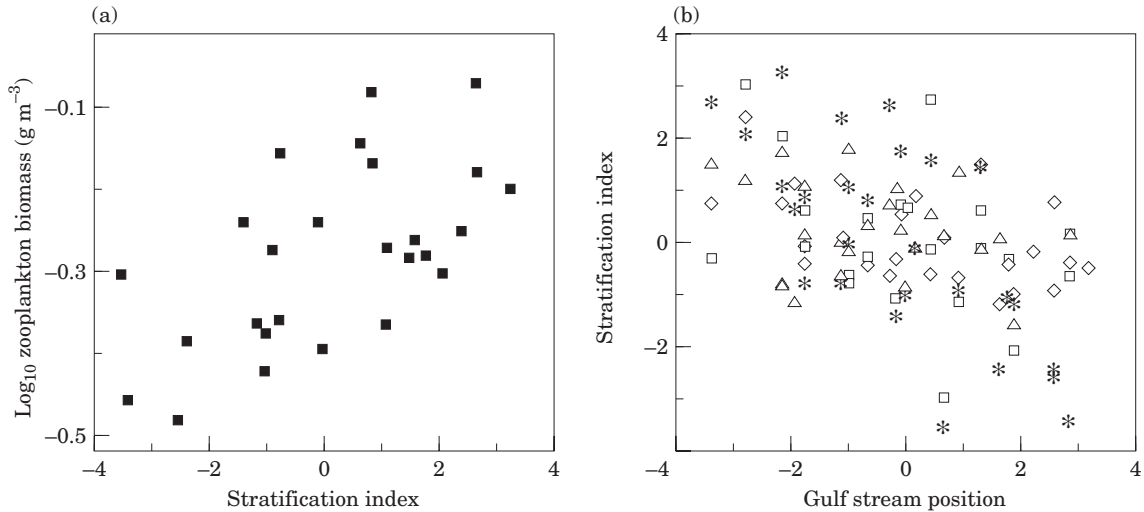
Figure 3. (a) Scatter plot relating the logarithm of the mean summer biomass of zooplankton in the North Basin of Windermere to the index of the onset of stratification in Windermere (r=0.59). A linear trend has been removed from the biomass data to correct for the observed increase in abundance caused by nutrient enrichment of the lake (George and Harris, 1985). (b) Scatter plot relating various indices of stratification (stars: Lake Windermere; triangles: Estwaite water; squares: North Sea; diamonds: Mellor–Yamada mode results) to the position of the north wall of the Gulf Stream (r=0.61) (from Taylor *et al.*, 1996).
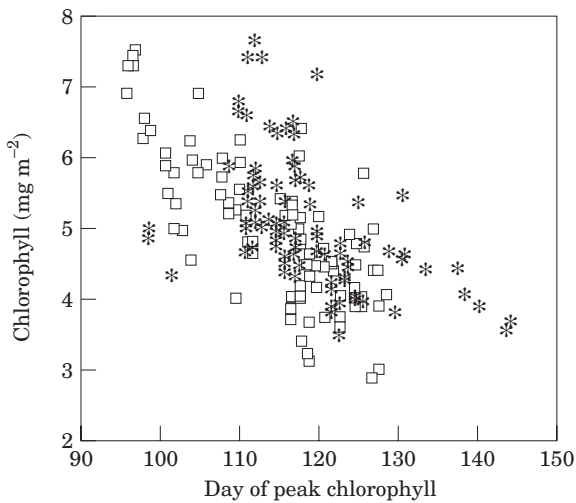

Figure 4. Relationship between the intensity of the spring bloom and its timing predicted for several locations south-west of the Isle of Man by the Prestige–Taylor model of the Irish Sea when forced by meteorological data from Dublin Airport, 1966–1994 (from Taylor *et al.*, 1996). Stars and squares indicate years when the Gulf Stream was shifted northwards and southwards, respectively.

dominant mode of inter-annual changes in sea level pressure pattern over the North Atlantic region (Van Loon and Rogers, 1978; Rogers, 1984; Lamb and Randy, 1987; Rogers, 1990; Hurrell, 1995). Like the ENSO, the NAO is a basin-wide scale atmospheric alternation of atmospheric mass. It takes place between the subtropical high pressures centred on the Azores and

the sub-polar low pressures centred on Iceland. Its state determines the speed and direction of the westerlies across the North Atlantic, as well as the level and direction of moisture transport and winter temperatures on both sides of the basin (Mann and Lazier, 1991; Hurrell, 1995). A high NAO index corresponds to accentuated winter pressure difference between the Azores and Iceland associated with stronger wind circulation than normal in the North Atlantic, high temperatures in western Europe and low temperatures on the east coast of Canada. Conversely, a low NAO index corresponds to a reduced pressure difference during winter and is associated with the opposite effects. The NAO index (Fig. 5; Rogers, 1984; Hurrell, 1995) is the difference in normalized sea level pressures between the Azores (or Portugal) and Iceland during the winter season (December to March).

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). Also, modelling studies suggest that patterns of variations in North Atlantic sea-surface temperature (SST) are connected with the NAO on a millennium scale (Delworth, 1996). Finally, the persistence of an exceptionally strong positive phase of the NAO appears to be the source of recent temperature anomalies and changes in atmospheric moisture transport across the North Atlantic, leading to the dry conditions encountered over southern Europe and the increase in precipitation level in northern Europe and Scandinavia (Hurrell, 1995).

Fromentin and Planque (1996) showed that the NAO index was strongly related to changes in abundance and
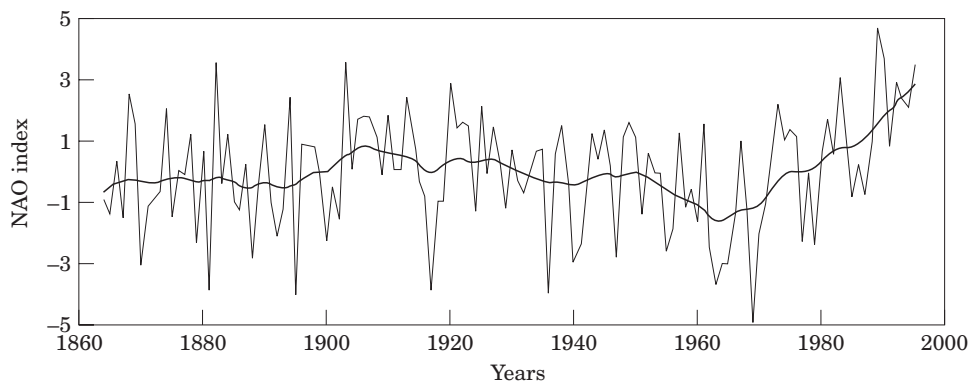
Figure 5. The North Atlantic Oscillation index (difference in normalized sea-level pressure between Portugal and Iceland for the winter period, December–March), 1864–1895. The heavy line indicates the trend estimated by eigen vector filtering with a 10 years window. Data were kindly provided by James W. Hurrell, National Center for Atmospheric Research (Boulder, CO).

distribution pattern of two dominant copepods in the north-east Atlantic, *Calanus finmarchicus* and *C. helgolandicus*. Using 31 years of data (1962–1992) from the CPR survey, 58% of changes in *C. finmarchicus* abundance could be explained by changes in the NAO signal only. The link between the atmospheric variations and species abundance was believed to result from a combination of several factors: (i) changes in west wind stress (WWS) and their effects on primary production, (ii) changes in SST and their effects on interspecific competition between the two species, and (iii) differences in geographical distribution of the two species.

For the period 1962–1992, the average WWS and SST over the north-east Atlantic region are significantly ($p<0.01$) correlated with the NAO signal ($r=0.85$ and 0.51, respectively). Using climatic data from the same Comprehensive Ocean Atmosphere Dataset (COADS, Woodruff et al., 1987), correlations between local time series of WWS/SST during winter/spring for different areas of the north-east Atlantic and the NAO signal were calculated to determine where the link between these was strongest. The resulting correlation coefficients are plotted in Figure 6.

Although the links between NAO and averaged WWS/SST appear to be strong at both short and decadal time scales, the correlation varies within the north-east Atlantic region. Local correlations are significant at the 1% level for WWS over the major part of the region, but drop south of 50N and are not significant below 47°N. Local correlations between NAO and SST are more variable, with significant positive correlation ($p<0.01$) in the entire North Sea, Irish Sea, and the Channel. To the south of the British Isles, correlations are lower and largely not significant, while correlations are negative and generally not significant in the open ocean to the north-west. The NAO effects on WWS and SST are combined in the North Sea region, where

both signals are significantly correlated to the NAO index.

The relationship between the Gulf Stream north wall time series and the NAO has been discussed by Taylor and Stephens (1998) and Planque (1996). While there is little direct similarity between the two series (Fig. 7a), there is significant correlation when the NAO is lagged by 2 years (Fig. 7b). The probability of such a correlation coefficient occurring due to chance at a lead or a lag of up to 2 years, calculated from the binomial distribution, is less than 0.05 (in calculating significance levels of correlation coefficients, degrees of freedom have been corrected for first-order serial correlation using the method of Quenouille, 1952).

A similar delayed response of the Gulf Stream has been observed when attempting to predict changes in the latitude of separation of the current from the US coast. In the two-layer Parsons–Veronis model of this separation, the position at which the Gulf Stream leaves the coast results from a balance between the Ekman drift and geostrophic flow. When Gangopadhyay et al. (1992) compared the inter-annual variations predicted by this model with those observed over the 12-year period (1977–1988), the results concurred only if the Ekman drift was integrated over about 3 years. The latitude of separation, which they estimate at a single longitude close to 75°W, shows a similar trend over this period to the Gulf Stream index (Taylor and Stephens, 1998). Planque (1996) also showed that 54% of the Gulf Stream index variability could be predicted from the NAO index integrated over a 3-year period. Figure 7 suggests that a delayed response has been a feature of the last 30 years. Gangopadhyay *et al.* (1992) have suggested that the time-lag is related to the time for long baroclinic planetary waves to cross the ocean. They have pointed out that the most important of these have length scales of about 1000 km and periods of about 6 months. These

(a)

(b)

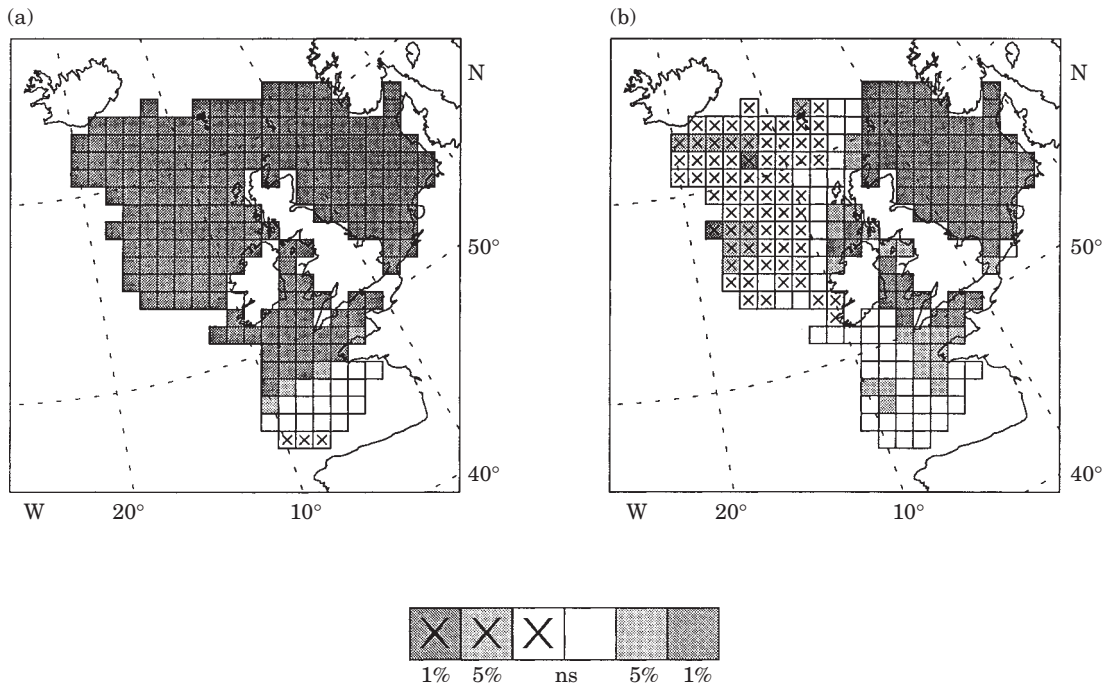| ⊠	⊠	⊠			
1%	5%	ns	5%	1%

Figure 6. Geographic distribution of significance levels (1%, 5%, or not significant; crosses indicate negative coefficients) of correlations between local climatic parameters and the NAO index for the winter–spring months (December–April) during the period 1962–1992. (a) West windstress; (b) sea-surface temperature.

waves travel at several kilometres per day, so that the time scale for them to cross the ocean basin is consistent with the 2-year delay. The Gulf Stream has been shown to respond to ENSO events in the Pacific with a similar time delay (Taylor *et al.*, 1998).

In the north-east Atlantic, changes in strength and direction of winds during winter directly affect the inflow of Atlantic waters into the North Sea. The degree to which this inflow is influenced by the NAO was addressed by using outputs from an integrated depth circulation model forced by wind and sea level pressure data at 6-hour intervals (Proctor and Smith, 1991). The NAO index for 1955–1993 was compared with the average winter flows estimated by the model for three sections in the northern North Sea: sections 1, 8, and 9 in Figure 8. The correlation coefficients between NAO index and winter flows for sections 1, 8, and 9 are -0.78, 0.64, and -0.64, respectively, and are all significant at the 1% level. These high values indicate that the flow between the North Atlantic and the North Sea is strongly connected to the NAO index.

Thus, the NAO is linked to the Gulf Stream latitudinal displacement on the scale of the North Atlantic basin, with an integrated 2 to 3-year lagged response of the Gulf Stream. It is also connected with at least three types of hydro-climatic changes in the North Sea. First, it is linked with variations in the west windstress over the region, with a higher NAO index resulting in higher

windstress. Second, it is associated with changes in SSTs, with a higher NAO index resulting in higher temperatures. Third, it is connected with the inflow of Atlantic Water.

Results from the CPR survey indicate that the two *Calanus* species display contrasting year-to-year changes, where a high NAO index is associated with above average abundance of *C. helgolandicus* and below average abundance of *C. finmarchicus* (Fromentin and Planque, 1996). The connection between NAO index and *C. finmarchicus* is strong when integrated over the north-east Atlantic ($r = -0.76$, $p < 0.01$), but weaker for *C. helgolandicus* ($r = 0.42$, $p < 0.05$). Using CPR data collected during 1962–1992, correlations were calculated between local time series of *Calanus* abundance and the NAO index (Fig. 9) in order to determine whether the association is particularly strong in specific regions. The results indicate that a strong relationship is not uniformly present throughout the north-east Atlantic. *C. finmarchicus* shows a negative correlation in an area including the northern North Sea, the Irish Sea, waters north and west of Scotland and north of Ireland. In contrast, *C. helgolandicus* shows a significant positive correlation in the North Sea, in the waters south of Iceland, and between the Faroes and Shetland Islands.

The links between NAO and WWS/SST suggested that the greatest effects of the NAO on these zooplankton populations might be expected in the northern
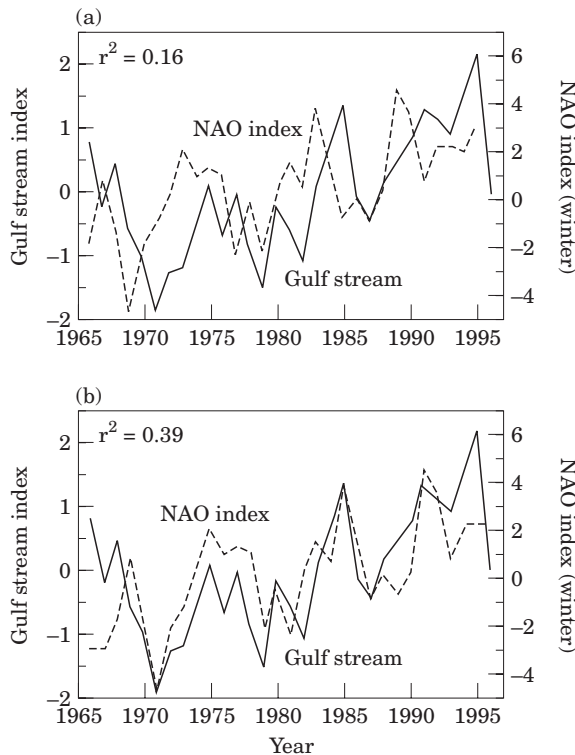
Figure 7. Winter (December–March) NAO index (solid line) compared with the latitude of the north wall of the Gulf Stream (broken line), 1966–1996 (from Taylor and Stephens, 1998). The variance fraction accounted for (r2) by the correlation is indicated. (a) Unlagged NAO index. (b) NAO index lagged by 2 years.

North Sea, where both parameters were significantly correlated to the NAO index. This indeed appears to be the case, although the year-to-year changes in abundance of the two species in this region are opposite.

Since the two species are characterized by distinctly different geographical distributions, Fromentin and Planque (1996) hypothesized that the contrast in their long-term changes in abundance resulted from regional differences in weather changes, particularly in WWS, associated with the NAO, following the scenario proposed by Dickson *et al.* (1988) in which changes in early spring winds alter the timing and intensity of spring primary production. However, the present results indicate that although *C. finmarchicus* is predominant in the northern part of the eastern North Atlantic and *C. helgolandicus* in the southern part, their contrasting time series are observed in the northern North Sea, a region where the two species co-exist. Therefore, regional differences in WWS (and their effects on spring bloom) do not fully explain the observed contrasts.

The morphology of the two species is highly similar, they have identical mouthparts and consequently almost identical food resources. The different responses are therefore likely to result from distinct ecological characteristics rather than from simple variations in the level of food resources during spring. Two ecological features clearly differentiate the two species: their affinity to temperature (Jaschnov, 1961, Williams, 1985) and their overwintering strategy.

With reference to their affinity to temperature, Fromentin and Planque (1996) suggested that changes in SST might modify the competition balance between the two species. This is in accordance with the results presented here, since the maximum contrast is seen in the North Sea where the two species are likely to compete for food and where temperature fluctuations are linked to the NAO, with higher temperature associated with lower abundance of *C. finmarchicus* and higher abundance of *C. helgolandicus*.

The life cycle of *C. finmarchicus* is characterized by a specific overwintering strategy. The population undergoes a seasonal ontogenetic vertical migration and copepodites of stage V of the last summer generation migrate to deep waters where they remain in a low metabolic activity state during the winter period. At the end of winter, individuals migrate to the surface layer, moult into adults and reproduce. The North Sea is a shallow basin and winter populations of *C. finmarchicus* are believed to reside only in deep peripheral areas such as the Faeroes–Shetland Channel (Backhaus *et al.*, 1994). The trough extending along the Norwegian coast into the Skagerrak might also be an overwintering area for the North Sea population, but as yet no evidence has been obtained that a population resides in this region during winter. The location of *C. helgolandicus* populations has been poorly studied, but there is no evidence of overwintering in deep water. Therefore, it seems probable that small numbers of individuals stay in the area inhabited during summer or reside in shallow coastal waters.

The overwintering strategy has important implications for the subsequent spring and summer generations. Modelling studies of *C. finmarchicus* in the Norwegian Sea indicate that the fate of the overwintering stock may depend upon the combination of ontogenetic vertical migration and oceanic circulation patterns (e.g. Slagstad and Tande, 1996). In the North Sea, the success of the summer generations will depend on the advection of overwintering copepodites from off-shelf areas at the end of winter. Results from the circulation model indicate that the winter flow between the Faeroes–Shetland and the North Sea is strongly correlated to the NAO, suggesting that the negative link with the abundance of this species in the North Sea may be partially explained by changes in late winter advection of overwintering populations.

The extent to which populations of *C. finmarchicus* depend upon variations in flow volumes was determined by Stephens *et al.* (1998) for three regions: boxes B1, B2,
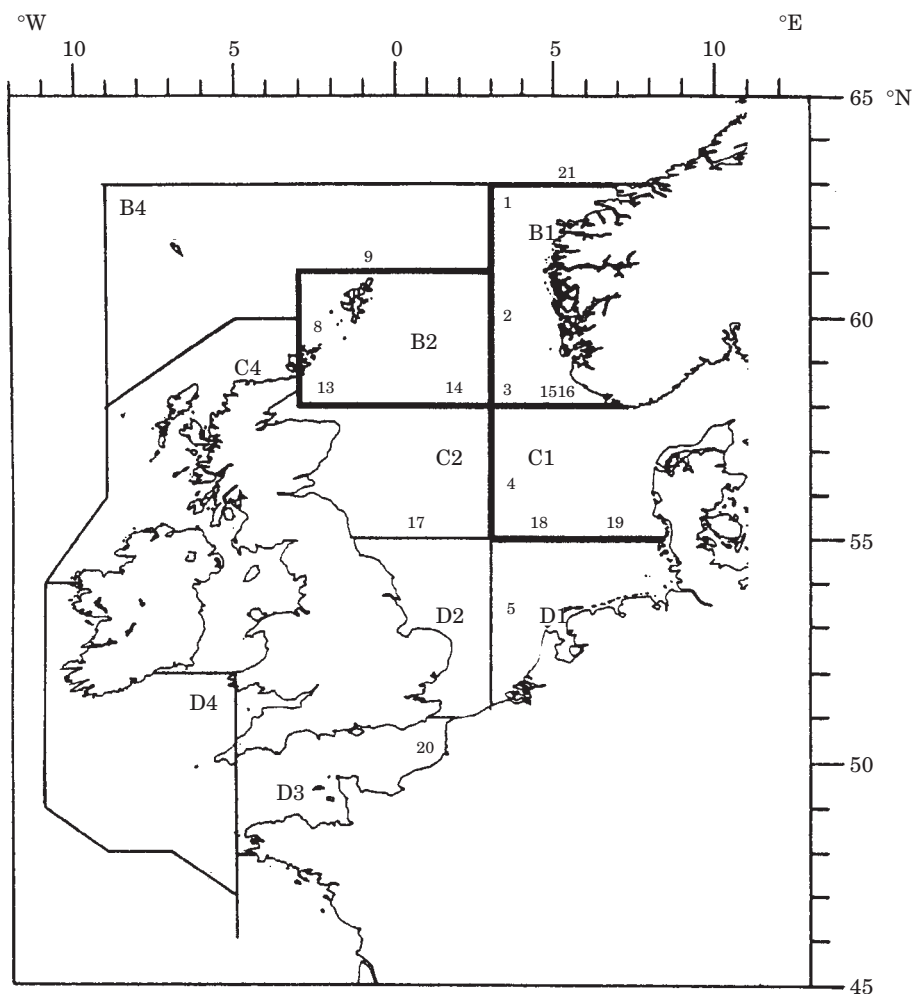
Figure 8. CPR standard boxes and sections used in the oceanic circulation model. Sections 1, 8, and 9 mark the exchange between Atlantic and North Sea waters.

and C1 (Fig. 8). For each region, the year-to-year fluctuations of abundance were modelled by multiregression of flows across the boundaries of the box for the winter, spring, and summer seasons. The squared correlation coefficients between abundance and flows (corresponding to the percentages of variance explained by the model) are given in Table 1. For the three boxes, the highest variance fraction explained by the model is obtained when using the winter flows, and for boxes B1 and B2 the multiple correlation coefficients are significant at the 1% level. The flow model for box C1 does not include the exchange between North Sea and Skagerrak waters. Since populations of *C. finmarchicus* in this region possibly come from deep Skagerrak waters, this limitation in the model could explain why changes in abundance in box C1 are poorly explained by the multiregression model. The model also gives better predictions for *C. finmarchicus* than for *C. helgolandicus*

(not shown). These results support the hypothesis that late winter advection coupled with ontogenetic vertical migration could be an important mechanism in determining annual changes in the abundance of *C. finmarchicus* populations.

In their study, Fromentin and Planque (1996) attributed the year-to-year fluctuations in abundance of *Calanus* to changes in west windstress and SST only. The detailed spatial analysis presented here confirms that temperature changes are locally connected to the fluctuations of the two species in a way that supports the hypothesis of interspecific competition. However, the local correlations reveal that the WWS–primary production scenario is not fully supported since they respond in an opposite way to similar changes in WWS in the North Sea. Additional results on the north-east Atlantic circulation patterns suggest that winter advection of deep overwintering populations of *C. finmar*

(a)

(b)

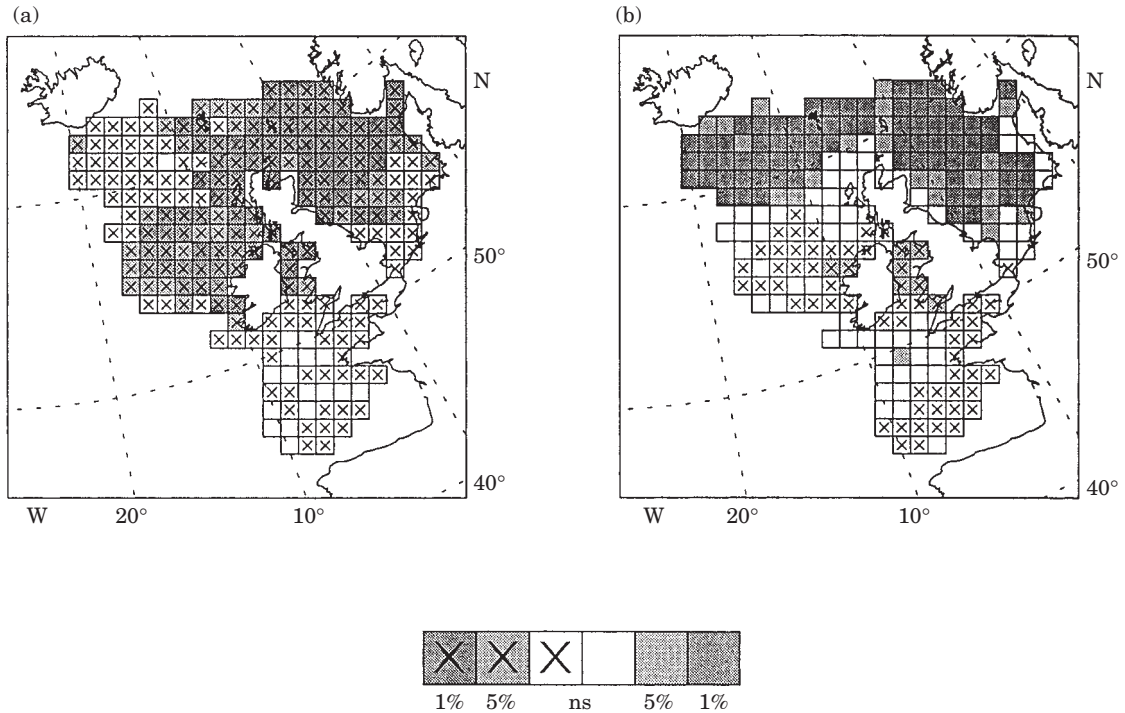| $\times$	$\times$	$\times$			
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Figure 9. Geographic distribution of significance levels (1%, 5%, or not significant; crosses indicate negative coefficients) of correlations between annual (January–December) abundance of *Calanus* and the NAO index for the winter–spring months (December–April) during the period 1962–1992. (a) *C. finmarchicus*. (b) *C. helgolandicus*.

chicus may explain a large part of the variability in annual population abundance. A distinctly different overwintering strategy of *C. helgolandicus* might explain why this species does not respond so strongly to the NAO signal.

Conclusion

Long-term time series of climate indices and plankton are getting more and more accessible to both meteorologists and ecologists and the chance of finding statistical connections between the two types of signals consequently increases. However, the true challenge is now to separate artefacts in statistical connections from true functional relationships.

The examples of the Gulf Stream and the NOA indices presented show that different climatic forcing, although connected on the scale of the North Atlantic Ocean, can be linked in different ways to sympatric plankton populations. The functional connections have been investigated by time-series analysis, coupled physical–biological models, and comparative ecology. It appears that, additionally to changes in primary productivity, life-cycle strategies and large-scale advection processes may be determinant in explaining long-term changes in zooplankton populations.

Table 1. Multiple regression coefficients (squared) between annual abundance of *C. finmarchicus* in CPR boxes B1, B2, and C1 and flows across sections of these boxes for winter (January–March), spring (April–June), and summer (July–September), 1958–1993 (*p<0.05; **p<0.01; ***p<0.001).

Box	Winter	Spring	Summer
B1	0.53***	0.22	0.29
B2	0.57***	0.43**	0.22
C1	0.30*	0.20	0.22

Future attempts at predicting changes in marine ecosystems on the basis of climate scenarios will require important efforts in biological–physical modelling and in large-scale plankton population ecology. The maintenance of long-term monitoring programmes is also essential in determining whether the climate–plankton connections observed over several decades will persist in the future or may be overruled by principally human-induced perturbations.

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