Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*

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ABSTRACT

The population of *Calanus finmarchicus* in the North Sea is replenished each spring by invasion from an overwintering stock located beyond the shelf edge. A combination of field observations, statistical analysis of Continuous Plankton Recorder (CPR) data, and particle tracking model simulations, was used to investigate the processes involved in the cross-shelf invasion. The results showed that the main source of overwintering animals entering the North Sea in the spring is at depths of greater than 600 m in the Faroe Shetland Channel, where concentrations of up to 620 m^{-3} are found in association with the overflow of Norwegian Sea Deep Water (NSDW) across the Iceland Scotland Ridge. The input of this water mass to the Faroe Shetland Channel, and hence the supply of overwintering *C. finmarchicus*, has declined since the late 1960s due to changes in convective processes in the Greenland Sea. Beginning in February, animals start to emerge from the overwintering state and migrate to the surface waters, where their transport into the North Sea is mainly determined by the incidence of north-westerly winds that have declined since the 1960s. Together, these two factors explain a high proportion of the 30-year trends in spring abundance in the North Sea as measured by the CPR survey. Both the regional winds and the NSDW overflow are connected to the North Atlantic Oscillation Index (NAO), which is an atmospheric climate index, but with different time scales of response. Thus, interannual fluctuations in the NAO can cause immediate changes in the incidence of north-westerly winds without leading to corresponding changes in *C. finmarchicus* abundance in the North Sea, because the NSDW overflow responds over longer (decadal) time scales.

INTRODUCTION

The copepod *Calanus finmarchicus* constitutes up to 70% of the mesozooplankton biomass over a wide area of the north-east Atlantic during summer, and forms a large part of the diet of many species of planktivorous fish (Fransz *et al.*, 1991). Its annual abundance in the North Sea has declined steadily since the late 1950s and attempts at correlating the trends in *C. finmarchicus* abundance with indices of North Atlantic climate have indicated a relationship with westerly winds, the North Atlantic Oscillation Index (NAO), and shelf circulation patterns (Colebrook, 1985, 1986; Dickson *et al.*, 1988; Arbischer *et al.*, 1990; Fromentin and Planque, 1996; Stephens *et al.*, 1998). However, the decline in abundance in the North Sea is not a universal phenomenon across the range of distribution in the North Atlantic. In other areas, the abundance has remained relatively stable or increased over the same period (Planque and Ibanez, 1997). None of the correlative studies undertaken so far has been able to inform on mechanisms involved in the patterns of changes in abundance, and hence they are not necessarily robust in a situation where a combination of processes may be involved in the long term spatio-temporal dynamics of the species.

The life cycle of *C. finmarchicus* involves a period in diapause state during the winter (Gran, 1902; Sömme,

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1934; Marshall and Orr, 1955; Hirche, 1983). In some areas, e.g. Gulf of Maine and Nova Scotia (Durbin *et al.*, 1995; Herman *et al.*, 1991), concentrations of diapause animals are found in deeper parts (>200 m) of the shelf waters during winter but no corresponding accumulations are found in the North Sea (Williams and Lindley, 1980; Krause and Martens, 1990; Fransz *et al.*, 1991). Instead, high concentrations (~ 50000 m^{-2}) are found at depths of 500 1000 m in ocean waters beyond the shelf edge (Paulsen, 1906; Østvedt, 1955; Krause, 1978; Hirche, 1983, 1996; Heath and Jónasdóttir, 1999) where they inhabit the cold (<0°C) southerly flowing Norwegian Sea Deep Water mass (NSDW), which overflows the submarine Iceland-Scotland Ridge through the Faroe Shetland Channel (Fig. 1). Lower concentrations (~ 5000 m^{-2}) of overwintering animals are also widespread throughout the north-east Atlantic at depths of 400 1500 m (Williams and Conway, 1988; Longhurst and Williams, 1992).

Overwintered animals begin to emerge from diapause in early February in the north-east Atlantic and their ascent to the surface waters takes about 1 month (Heath, 1999). On arrival at the surface the females produce a small number of eggs, utilizing residual lipid reserves, but the main reproductive output from the overwintered stock is triggered by the spring phytoplankton bloom (Richardson *et al.*, 1999). In the surface waters, the animals encounter a different circulation regime from that at the overwintering depth. Those which ascend along the eastern boundary of the North Atlantic and south-eastern Norwegian Sea become entrained in the Continental Slope Jet Current (CSJ), which together with the North Atlantic Current carries warm (>9°C) water poleward into the Norwegian Sea. Branches of the CSJ flow across the shelf edge and into the North Sea, providing a potential transport mechanism for C. *finmarchicus* (Wood, 1932; Williams and Lindley, 1980; Krause and Martens, 1990; Fransz *et al.*, 1991). Backhaus *et al.* (1994) elaborated on this general scheme to incorporate the distribution and sources of overwintering animals in relation to the deep circulation in the north-east Atlantic. Their conceptual model included the scope for conservation of the genetic integrity of C. *finmarchicus* populations through

Figure 1. Bathymetry of the area covered by the hydrodynamic model, and the locations of key geographical features. The NSDW flows south-west through the Faroe Shetland Channel at depths > 600 m and then into the Atlantic passing between the Faroe Islands and Faroe Bank. The NACW flows north-east between the Faroe and Shetland Islands and continues northwards into the northern Norwegian Sea, with a branch extending into the northern North Sea.
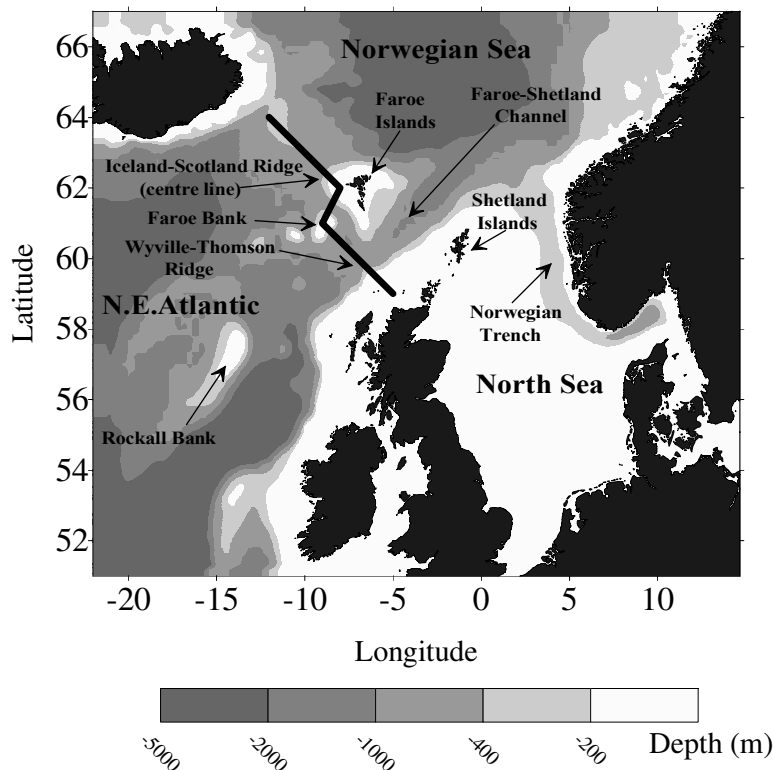
spatial closure of generation lineages over the annual cycle, and the potential for interactions between shelf ecosystems around the North Atlantic.

In this paper we investigate part of the Backhaus *et al.* (1994) hypothesis concerning the spatio-temporal dynamics of *C. finmarchicus*, and its potential to account for the decline in abundance in the North Sea. In particular, we have studied a 120-day period commencing with the onset of the ascent migration from overwintering depth, and determined the aspects of winter distribution and dispersal in the surface waters, which together determine the magnitude of the invasion of the North Sea in spring.

BACKGROUND HYDROGRAPHY OF THE NORTH-EAST ATLANTIC AND NORWEGIAN SEA

The Iceland Scotland Ridge separates the Norwegian Sea basin from the open north-east Atlantic. Each of these areas has a complex circulation and water mass structure, and exchange between the two regions occurs mainly through the Denmark Strait and the Faroe Shetland Channel, which traverses the Iceland Scotland Ridge. Atlantic water flows northwards into the Norwegian Sea in the surface layers, whilst cold, dense subsurface flows carry polar water southwards into the Atlantic through both of these passages.

Five main water masses contribute to the upper and lower layers of the water column in the Faroe Shetland Channel (Fig. 1; Müller *et al.*, 1979; Turrell *et al.*, 1999). The upper layer is composed of North Atlantic Central Water (NACW) and Modified North Atlantic Water (MNAW), which form the surface inflow to the Norwegian Sea from lower latitudes. The NACW is carried by branches of the Gulf Stream and is the warmest and most saline water mass encountered in the area. The MNAW is formed during winter cooling in the subpolar gyre of the North Atlantic. The circulation in the upper layer is to the north-east, into the Norwegian Sea. Between Scotland and Norway, the poleward flow of NACW is focused into a jet current along the continental slope, referred to as the Continental Slope Jet (CSJ). The bottom layer is composed of a mixture of Arctic water masses, with a mean flow to the south-west. NSDW is the coldest ($<0°C$) and most dense water mass contributing to the bottom layer. Mixtures containing varying amounts of Arctic Intermediate/North Icelandic Water (AI/NIW), and East Icelandic Current Water (EICW) are found at mid-depths (Meincke, 1978; Hansen and Jakupsstovu, 1995). The AI/NIW is formed at intermediate depths north of the Iceland Scotland Ridge, whilst the EICW

is a low salinity surface water mass that covers a large part of the southern Norwegian Sea. Temperature-salinity diagrams from the Faroe Shetland Channel display a characteristic inflection at around 3°C, 34.95 35.0 salinity, and a salinity minimum of < 34.9 at 0.5°C. The former represents a mixture of AI/NIW and MNAW at depths of 400 500 m, whilst the latter corresponds to a layer of water at 500 700 m depth formed by subduction of EICW at the subpolar front. The EICW is carried south into the Faroe Shetland Channel as a low salinity layer beneath the AI/NIW, where it gradually mixes with the underlying NSDW. This low salinity layer has been referred to as Norwegian Sea Intermediate Water (NSIW; Martin, 1993).

Turrell *et al.* (1999) have documented changes in the composition of the bottom water in the Faroe Shetland Channel. Salinity at the 800 dbar horizon in the Faroe Shetland Channel fluctuated around a stable long-term mean of approximately 34.925 up to 1967. However, after this date, the values at this horizon declined approximately linearly to around 34.905 in 1995. The origin of this decline in salinity of the bottom water has been attributed to cessation in the late 1960s of the formation of deep water by convection in the Greenland Sea (Schlosser *et al.*, 1991). As a consequence of this, the pool of NSDW in the Norwegian Sea basin, which had previously been maintained by a balance between inflow from the Greenland Sea and outflow through the Faroe Shetland Channel and Denmark Strait, gradually drained away. A deepening, by around 400 m, of the base of the pycnocline delineating the top of the NSDW in the Norwegian Sea has been cited as evidence of this (Turrell *et al.*, 1999), and the consequence has been a progressive decline in the supply of NSDW to the Faroe Shetland Channel. Using time-series of salinity and silicate concentration data, Turrell *et al.* (1999) estimated that up to 1970 the contribution of NSDW to the bottom waters in the Channel had been around 60%, but this had reduced to 40% by 1995 with a corresponding increase in the contribution from NSIW.

MATERIALS AND METHODS

Continuous Plankton Recorder data

Continuous Plankton Recorder (CPR) data (Glover, 1967; Warner and Hays, 1994) on the abundances of *C. finmarchicus* (copepodite stages V and VI, both male and female) in the northern North Sea between 1958 and 1993 were obtained from the Sir Alister Hardy Foundation for Ocean Science (SAHFOS, Plymouth, UK). The CPR analysts record the number of speci-

mens of each species in the samples according to an approximately exponential abundance index. These data are referred to as recorded values. The mean actual numbers of specimens corresponding to each recorded value category, referred to as the accepted value, obtained from tabulated values of geometric mean abundances provided by SAHFOS.

Two different approaches were used to statistically model the data (Beare and McKenzie, 1999a, b). In both cases the aim was to simulate the probability of occurrence of the recorded values. In the first method (Model 1), data were divided into areas of equal sea surface area and the time-dependence (resolved into 73 5-day periods per year) of the resulting spatial aggregation was modelled using a Multinomial Logit Model (MLM; McCullagh and Nelder, 1989; Hastie and Tibshirani, 1990). Where data were available for 36 years of sampling, the model output was therefore in the form of a 73×36 matrix. The recorded values for a sample at time t were denoted by R_t and we then modelled the inverse cumulative distribution function of R_t, i.e. $P(R_t > v) = P_{tv}$. Two versions of the model were investigated (Models 1.0 and 1.1):

$$\ln \frac{P_{tv}}{1 - P_{tv}} = \pi_v + \text{smooth}(t) + \text{smooth}(s) \qquad (1.0)$$

$$\ln \frac{P_{tv}}{1 - P_{tv}} = \pi_v + \text{smooth}(t, s) \qquad (1.1)$$

where π was a factor corresponding to the recorded value of v. The smooth factors were the dependence of the logit of P_{tv} on trend (t) and seasonality (s) estimated either independently (Model 1.0) or simultaneously (Model 1.1). These dependencies were estimated using a locally weighted regression estimator (LOWESS; Cleveland and Devlin, 1988) on both trend and seasonality.

In the second method, Generalized Additive Models (GAMs) were used to statistically model the recorded values directly as a function of latitude (y), longitude (x), long-term trend (t) and seasonality (s) (McCullagh and Nelder, 1989; Hastie and Tibshirani, 1990). Time was again modelled on the basis of 73 5-day periods per year. Following experimentation (Beare and McKenzie, 1999a) it was deduced that the best model was that in which spatial and temporal components depended upon each other. The recorded values were modelled directly using a LOWESS smoother on all four predictor variables of location and time simultaneously, i.e. latitude, longitude, trend and seasonality (Model 2):

$$R_{xyt} = \text{smooth}(t, s, x, y) \qquad (2)$$

Once Model 2 was fitted to the data, a grid of latitudes and longitudes was constructed and the model was used to predict values of copepod abundance at each of the points in the grid. Accepted numbers (i.e. accepted numbers per sample as opposed to the recorded indices of abundance) were estimated from the smoothed recorded values by simple linear interpolation. Synoptic maps for any 5-day period within the 36-year span of the data could then be constructed.

The GAM procedure had two main disadvantages compared with the MLM. The GAM procedure assumed the data were normally distributed, which was clearly not true, while the higher dimensionality could be particularly susceptible to the variations in the distribution of CPR sampling. The advantage of the GAM was that it appears to provide similar results to the MLM at minimal cost in terms of computing power and utilized all the available data.

Field sampling

Field sampling to determine the vertical distribution of *C. finmarchicus* was carried out during five cruises by RV DANA (October 1993, February 1994, December 1994, January 1995 and March 1995) and one by RRS CHALLENGER (May 1995). The survey in January 1995 incorporated a widespread survey of the spatial distribution of overwintering copepodites in the Faroe Shetland Channel and southern Norwegian Sea. On each cruise, plankton samples were collected with net systems (Dunn *et al.*, 1993) capable of filtering material from discrete depth layers (up to 50 discrete layer samples taken in a water column of 1000 m). The mesh size of the collecting net was 200 μm on all cruises. Hydrographic data were collected by a CTD system attached to the towed plankton sampler. Each sample was analysed to determine the abundance of copepodite development stages of *C. finmarchicus*. Further details are presented by Heath (1999) and Heath and Jónasdóttir (1999).

Modelling the distribution of C. finmarchicus *by particle tracking*

A particle tracking model was used to simulate the time-dependent horizontal trajectories of particles programmed to imitate the vertical movements of *C. finmarchicus* copepodites emerging from overwintering. The model was forced with three-dimensional flowfields produced by an implementation of the three-dimensional baroclinic Hamburg Shelf Ocean Model (HAMSOM) (Backhaus and Hainbucher, 1987; Stronach *et al.*, 1993) to represent the north-east Atlantic (Fig. 1; Hainbucher and Backhaus, 1999) with a 14-km horizontal grid resolution and eight depth levels (0 20 m, 20 50 m, 50 100 m, 100 200 m, 200 400 m, 400 600 m, 600 1000 m, >1000 m). The HAMSOM was

configured to simulate quasi-stationary flowfields for various seasonal average temperature and salinity conditions (Levitus, 1982) and wind speed and direction scenarios. A wind speed of 8 m s^{-1} was applied from each of four directions (south-west, north-west, north-east and south-east). In addition, for the south-west direction only, flowfields were simulated for a range of wind speeds between 4 and 16 m s^{-1}. These flowfields were used to calculate the deterministic horizontal advective components of particle velocities using a finite difference scheme. Stochastic horizontal diffusion velocities were derived from the amplitude of current velocities at each node, resulting from a time-dependent model run with M_2 tidal forcing at the model boundary (Gallego et al., 1999).

The vertical trajectory of particles was represented by prescribing their depth as a function of age since release. The aim was to imitate the ascent migration of C. finmarchicus from overwintering depths to the surface waters and the subsequent behaviour in the upper layers. The standard scheme was defined by three parameters: initial (overwintering) depth (D_1), final (spring) depth (D_2) and ascent rate (dD/dt; Gallego et al., 1999). Tracking was initiated at time zero with particles distributed on a regular 15 km grid at the D_1 depth horizon. At each time step the depth of each particle was reduced according to the rate dD/dt until reaching depth D_2 and, thereafter, remained constant. Variants on this scheme included a switch to a sinusoidal migration with a 24-h period between depth limits D_{2a} and D_{2b} on reaching the surface layers, designed to represent a diel vertical migration in the upper layers (Gallego et al., 1999). Each particle was weighted to reflect the abundance of overwintering C. finmarchicus at the release location as estimated from field sampling. The weighting term was lineally related to abundance, and the weighting value of each particle remained constant throughout the tracking run.

The number of particles with simulated trajectories that entered the North Sea was used to derive an index of the spring invasion by C. finmarchicus. A rectangular target area was delineated in the northern North Sea in a region where the CPR data indicated a high abundance of stage V and VI copepodites in the spring, and the invasion index defined as the weighted number of start locations accounting for particles that entered the target area (Gallego et al., 1999). The invasion indices were subject to variability in a six-dimensional parameter space (flowfield scenario, target area, D_1, D_2, dD/dT, and initial weighting). Results of a sensitivity analysis of the invasion index with respect to these parameters have been described elsewhere (Gallego et al., 1999). Briefly, the analysis showed that the index

was robust with respect to the vertical migration and weighting parameters within the range $\pm$ 15% of the mean values estimated from field observations (see below). Imposition of a diel sinusoidal migration once particles reached the surface layer showed that the invasion indices were approximately linearly related to the mean depth of the vertical migration sinusoid and insensitive to the amplitude. Thus, simulating diel behaviour in the upper layers provided no new insight compared with the fixed D_2. The results were highly sensitive to wind direction, but relatively insensitive to wind speed in the range 4 12 m s^{-1}. With stochastic diffusion included in the tracking model, the results were insensitive to the number of particles released at each location for > 25 particles per location, and the results were not significantly different from those obtained by using deterministic advection velocities alone.

Parameterization of the model from field data

Values for the initial weighting of each particle, and the vertical migration parameters D_1, D_2 and dD/dt were derived from field survey data. With respect to the horizontal distribution of overwintering animals, Heath and Jónasdóttir (1999) have shown that in December 1994 and January 1995 the mean abundance of copepodites was 25 times higher in the waters north of the Wyville Thomson Ridge than in the Atlantic waters to the south (north of the Ridge, mean abundance = 22 960 m^{-2}, SD = 13 564 m^{-2}, n = 32 stations; south of the Ridge, mean abundance = 930 m^{-2}, SD = 290 m^{-2}, n = 6 stations; ratio of mean abundance north:south = 25:1). Thus, on the basis of direct observations, all particles originating from south of the Iceland Scotland Ridge were assigned a weighting of 1, and all those from north of the Ridge a weighting of 25. The available data were not adequate to resolve the spatial distribution of initial weighting more finely than this over the range of the model area.

With respect to the overwintering depth parameter (D_1), Heath and Jónasdóttir (1999) showed that north of the Wyville Thomson Ridge, animals were concentrated in the bottom water of the Faroe Shetland Channel and in the upper layers of the NSDW in the southern Norwegian Sea. The σ_t = 28.0 isopycnal delineated the shallow extent of the vertical distribution, and the average depth of this surface in the survey area was around 600 m. In the Atlantic waters south of the Ridge, where polar origin bottom waters were absent, the vertical distribution was more diffuse but the 600 m horizon still represented the upper extent of the distribution. Accordingly, the parameter D_1 was assigned a value of 600 m. In the spring (early May) copepodites that had ascended to the upper layers were

concentrated in the surface 100 m (Heath, 1999). Hence, the parameter D_2 was assigned a value of 36 m, corresponding to the mid-depth of the second level in the hydrodynamic model (20 50 m).

The mean ascent migration rate of copepods (dD/dt) was assigned a value of 15 m day^{-1} based on modelling of vertical distribution data collected during a series of six surveys in the Faroe Shetland Channel covering the period October May (Heath, 1999). This value agreed closely with an independent analysis of potential ascent velocities resulting from an increase in the buoyancy of *C. finmarchicus* copepodites as a consequence of internal biochemical changes on emergence from diapause (Visser and Jónasdóttir, 1999).

Interannual variation in wind forcing and initial weighting

Year-specific indices of *C. finmarchicus* invasion for the north-east North Sea target area were derived by combining the particle tracking model results with data on the incidence of winds from different compass quadrants. First, the number of release locations from north and south of the Iceland Scotland Ridge contributing to the target area were determined for four climate scenarios represented by NW, NE, SE and SW 8 ms^{-1} wind forcing of the winter (December February) configuration of the hydrodynamic model. An annual index of invasion was then calculated by multiplying the weighted number of contributing release locations for each wind direction scenario by the log-transformed seasonal frequency of occurrence of winds from that direction during December February in each year:

$$I_Y = \sum_{a=1}^{a=2} \sum_{w=1}^{w=4} f_{Y,w} \times H_{a,Y,w} \times i_{a,Y}$$

where I_Y is the overall invasion index in year Y (1955 94); w is the wind direction (1 4; north-west, north-east, south-east and south-west, respectively); $f_{Y,w}$ is the geographically averaged seasonal frequency of wind events from direction w in year Y (log-transformed to normalize the data); $H_{a,Y,w}$ is the number of particle release locations in region a ($a = 1$, 2; north of the Ridge, south of the Ridge) contributing to the target area in year Y for wind scenario w; and $i_{a,Y}$ is the weighting value for particles originating from release region a in year Y. The time-series (1955 94) of annual invasion indices (I_Y) was smoothed using a LOWESS routine (Cleveland and Devlin, 1988), corresponding to the smoothing applied to the CPR data with which the model results were compared.

Wind data for the period 1955 94 were obtained from the Meteorological Institute of the University of Hamburg (1982 94, Luthardt, 1987) and from Norwe-

gian sources (1955 81, Backhaus *et al.*, 1985). Wind stress at 6-h intervals during December February for each year was integrated over 2°latitude × 4°longitude cells covering the area 58°N 64°N, 10°W 2°E. The number of 6-h events from each compass quadrant (NW, NE, SE, SW) was positively related to the average stress, indicating that the frequency of events was a reasonable summary of the wind conditions in a given year.

Estimation of year-specific weighting values for the particles was particularly problematic. There are no data comparable with those collected in winter 1994/95 (Heath and Jónasdóttir, 1999) from which to directly estimate values for earlier years. However, the work of Turrell *et al.* (1999), which demonstrates a progressive decline in the composition of the bottom water of the Faroe Shetland Channel, combined with the observations of Heath and Jónasdóttir (1999), which show partitioning of overwintering copepodites between water masses, provides the basis for a hindcast of the year-specific spatial weighting to be applied to model particles.

The two principal assumptions of the hindcast approach were that (i) the spatial distribution of overwintering copepodites is a consequence of both the distribution of prediapause animals in the autumn and the deep circulation patterns, and (ii) there have been no underlying long-term trends in the abundance of *C. finmarchicus* in the source areas in the autumn. Hence, changes in the spatial distribution of overwintering abundance are assumed to be solely a consequence of changes in deep circulation. Evidence in support of these assumptions is as follows. Initial work with the tracking model showed that the origins of particles reaching the North Sea were around Rockall Bank and in the Faroe Shetland Channel (Gallego *et al.*, 1999). Heath (1999) showed that the abundance of overwintering copepodites in the bottom water of the Channel cannot be explained solely through vertical fluxes in the autumn, but must be largely due to horizontal advection at depth. The upstream source of the bottom water in the Faroe Shetland Channel is in the Norwegian Sea (Turrell *et al.*, 1999). Rates of transport in the deep circulation imply that animals carried into the Channel by the deep circulation must have descended from the surface layers in the central and southern parts of the Norwegian Sea basin. Beare and McKenzie (1999b) and Planque and Ibanez (1997) showed from analysis of CPR data that underlying trends in *C. finmarchicus* abundance are spatially heterogeneous, with the central North Atlantic and Norwegian Sea showing little evidence of an underlying long-term decline, in marked contrast to the North Sea. Thus, the hindcast proceeded on the basis that relative to the North

Sea, the concentrations of overwintering copepodites in the open North Atlantic and in the source waters of the Faroe Shetland Channel have been constant over the period 1955 94.

The water column in the Faroe Shetland Channel was assumed to comprise two layers (upper and bottom). The bottom layer ($\sigma_t > = 27.9$) was assumed to be made up of NSDW and NSIW, and the upper layer of NACW, MNAW and AI/NIW. The equilibrium concentration of animals in the Channel (C_{FSC}, m^{-3}) is then given by:

$$C_{FSC}=(f_U((p_{NACW}C_{NACW})+(p_{NACW}C_{MANW})+(p_{AIW}C_{AIW})))+(f_B((p_{NSDW}C_{NSDW})+(p_{NSIW}C_{NSIW})))$$

where, f_B is the proportion of bottom layer water in the Channel, f_U is the proportion of upper layer water in Channel ($f_U + f_B = 1$), p_{NACW} is the proportion of NACW in the upper layer, p_{MNAW} is the proportion of MNAW in the upper layer, p_{AIW} is the proportion of AI/NIW in the upper layer

$$(p_{NACW}+p_{MNAW}+p_{AIW}=1);$$

p_{NSDW} is the proportion of NSDW in the bottom water, p_{NSIW} is the proportion of NSIW in the bottom water ($p_{NSIW}=1$ p_{NSDW}), and C_{NACW}, C_{MNAW}, C_{AIW}, C_{NSIW} and C_{NSDW} are the constant concentrations of overwintering copepodites (m^{-3}) in the NACW, MNAW, AI/NIW, NSIW and NSDW, respectively.

For the purpose described here, the NSDW was defined as the upper part of the NSDW pool in the Norwegian Sea, which contributes to the bottom water of the Faroe Shetland Channel. This water is identifiable on the basis of dissolved silicate concentrations > 11.5 mM m^{-3} and salinity > 34.923 (Turrell *et al.*, 1999). Mean concentrations of CIV-CVI copepodites in the five water masses during winter 1994/95 were as follows: $C_{NACW}=0.66$ m^{-3}, $C_{MNAW}=2.70$ m^{-3}, $C_{AIW}=2.83$ m^{-3}, $C_{NSIW}=13.68$ m^{-3}, $C_{NSDW}=86.23$ m^{-3} (Heath and Jónasdóttir, 1999). The distribution of water in the Faroe Shetland Channel between the upper and bottom layer (f_U and f_B) was estimated from the volume above and below the $\sigma_t > 27.9$ isopycnal in the survey data collected during winter 1994/95 ($f_U = f_B = 0.5$). This distribution is largely determined by the topography and therefore can be regarded as constant in the long term. Similarly, the water mass composition of the upper layer was estimated from the 1994/95 survey data ($p_{NACW}=0.3$, $p_{MNAW}=0.6$, $p_{AIW}=0.1$). These proportions have fluctuated since 1955 (Turrell *et al.*, 1999), but since the concentration of copepodites in all of these water masses is low compared with the bottom layer, the impact of fluctuations in composition of the upper layer is likely to be negligible.

Turrell *et al.* (1999) estimated the proportions of NSDW and NSIW in the bottom water of the Channel (p_{NSDW} and p_{NSIW}) to be 0.4 and 0.6, respectively, during 1990 95. Incorporation of these values in the equation above indicates a depth mean equilibrium concentration of copepodites in the Faroe Shetland Channel of 22.4 m^{-3}. Assuming a mean water column depth of 1000 m, this compares with a measured value of 22.9 m^{-3} in winter 1994/95. Substituting a value of 0.6 for the NSDW contribution to bottom water, such as is implied by the pre-1967 salinity measurements at the 800 db level, yields a mean concentration in the Channel of 29.7 m^{-3}, or a ratio of abundance north:south of the ridge of 32:1, compared with the 1994/95 value of 25:1. On this basis, the weighting of particles originating from north of the Iceland Scotland Ridge was 32 for the years 1955 67, and decreased lineally at a rate of 0.25 per annum from 1968 to 1994. The weighting for particles originating south of the Ridge remained at 1 throughout.
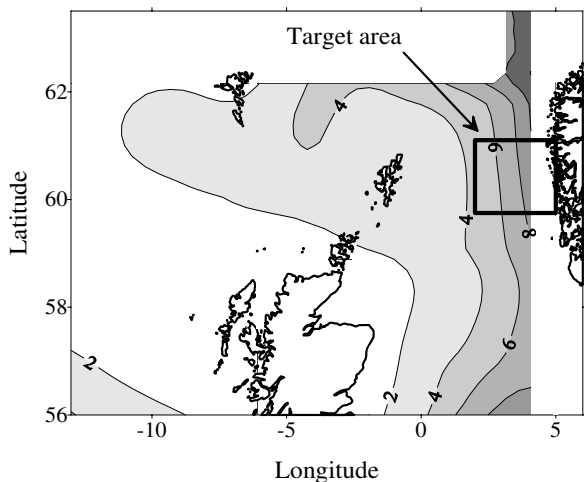
RESULTS

Seasonality and distribution of C. finmarchicus *in the North Sea*

Output from the GAM applied to CPR data (Model 2) was analysed to determine the seasonal distribution patterns of *C. finmarchicus* in the North Sea. The approach demonstrated that the invasion of *C. finmarchicus* has followed a recurring sequence each year with CV and CVI copepodites appearing during March at the shelf edge and spreading into the North Sea from the north, mainly via the Norwegian Trench. The results from this analysis suggested that neither the Fair Isle Channel, nor the East Shetland Atlantic inflow (Turrell *et al.*, 1996) have been important invasion routes. Concentrations of copepodites in the North Sea during the winter have been extremely low.

The distribution pattern seen in March and April in the CPR data (Fig. 2) was confirmed by a field survey carried out in April 1992 (Madden *et al.*, 1999). Both the CPR and the field survey data showed that stage CVI male and female specimens were most abundant in the northern North Sea along the western side of the Norwegian Trench, concident with a zone of inflowing Atlantic water. Juvenile stages were abundant along the leading (southern) edge of the wave of invading *C. finmarchicus*.

On the basis of these results, the target area for the particle tracking model was located at the north-eastern boundary of the North Sea (59°45′N 61°00′N, 2°00′E 5°00′E; Fig. 2). Unfortunately, collection of CPR data

Figure 2. The average distribution of C. *finmarchicus* copepodite stages V and VI during March and April from the Generalized Additive Model of CPR data. Contours represent the estimated number of animals per m^3 at a depth of approximately 7 m. The rectangular compartment in the north-eastern North Sea is the target area used for the particle tracking analysis.

in this area for comparison with model results was discontinued in 1986, so data were only available for a 28-year period, compared with 36 years in some other areas of the North Sea. Nevertheless, there were two compelling reasons for selecting this area. First, the objective of the tracking model was to identify invading particles at the point of entry to the continental shelf waters. Secondly, field survey data (Madden *et al.*, 1999) indicated that in March and April most if not all of the stage CV and CVI copepodites in this area should be survivors from the overwintering stock rather than first generation offspring. This was an important consideration since comparisons between weighted particle concentrations and CPR data on copepodite abundance become less justifiable as the surviving animals from the previous year die off, and spatial and temporal effects on reproductive output influence the distribution and abundance of first and second generation copepodites. MLM analysis (statistical model 1) of data from the target area showed that the underlying long-term trend in spring (March April) abundance was a steady decline from the early 1960s onwards.

Particle tracking model results

The numbers of release locations from north and south of the Iceland Scotland Ridge contributing to the north-eastern North Sea target area were determined for the four climate scenarios represented by NW, NE, SE and SW 8 m s^{-1} wind forcing of the winter

(December February) configuration of the hydrodynamic model. Only the north-west wind scenario resulted in invasion of the target area from release locations north of the Iceland Scotland Ridge. All wind scenarios resulted in invasion from sources south of the Ridge (Fig. 3).

The main feature of the data on interannual variations in wind direction was an increase in the incidence of southerly winds from the mid-1960s onwards, and a corresponding decrease in the incidence of northerly winds (NW + NE). In contrast, the balance between westerly and easterly winds was stable over the same period. Most of the change in balance between northerly and southerly airflows was due to a decrease in north-westerly winds and an increase in south-westerly winds (Fig. 4).

Unweighted particle results

The effect of changes in wind forcing alone on the predicted invasion indices was investigated by applying the same weighting to particle release locations north and south of the Iceland-Scotland Ridge (north:south, 1:1). The results showed a declining trend over the period 1955 94, but the correlation (r^2) with CPR data from 1958 to 1983 was not significant ($P > 0.01$). The homogeneity of the correlation between CPR data and model results was assessed by successively removing years from the beginning of the CPR time-series and repeating the analysis. Discontinuities in the relationship between the time-series should be indicated by rapid changes in the correlation coefficient. The results were not significant over the entire range of years (Fig. 5a, b) suggesting that the unweighted model provided a uniformly poor explanation of the long-term trend in abundance.

Model results with constant weighting

The 25:1 north:south weighting ratio was applied as a constant over all years and the resulting invasion indices compared with the long-term trends in CPR abundance.

The predicted invasion with weighted particles showed an underlying decline over the 40-year period with superimposed periods of high and low magnitude which, in general, coincided with those in the CPR time-series. However, statistical comparison of the entire time-series of observed trend data and corresponding model results was not significant. When years were successively dropped from the beginning of the time-series the correlation between the observed and model data rapidly increased, attaining a plateau at $r^2 \approx 0.7$ ($P < 0.01$) for the years 1967 onwards (Fig. 5c, d). The results therefore indicated a discontinuity in the relationship at around the mid-1960s.
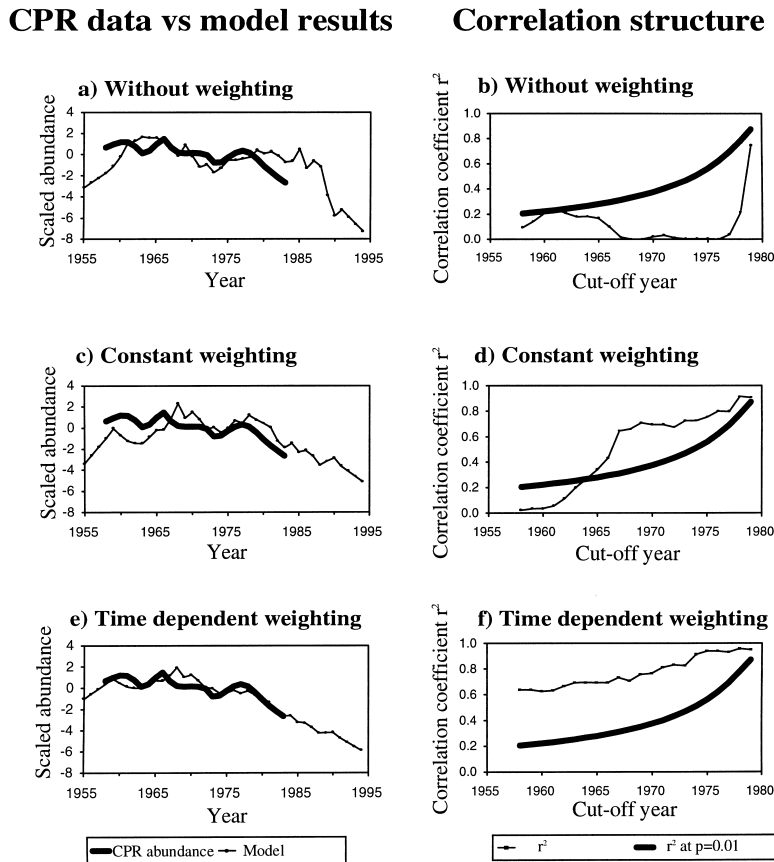
Figure 3. Particle tracking model predictions of the source areas of *C. finmarchicus* entering the north-eastern North Sea target area under different wind directions. Each panel represents a different wind direction (north-west, north-east, south-east, south-west). Particle start locations at the 600 m depth horizon are indicated by the grid of dots, and those from which particles successfully reached the target are highlighted by the dark area of larger symbols. The contour lines show the 600 m isobath.
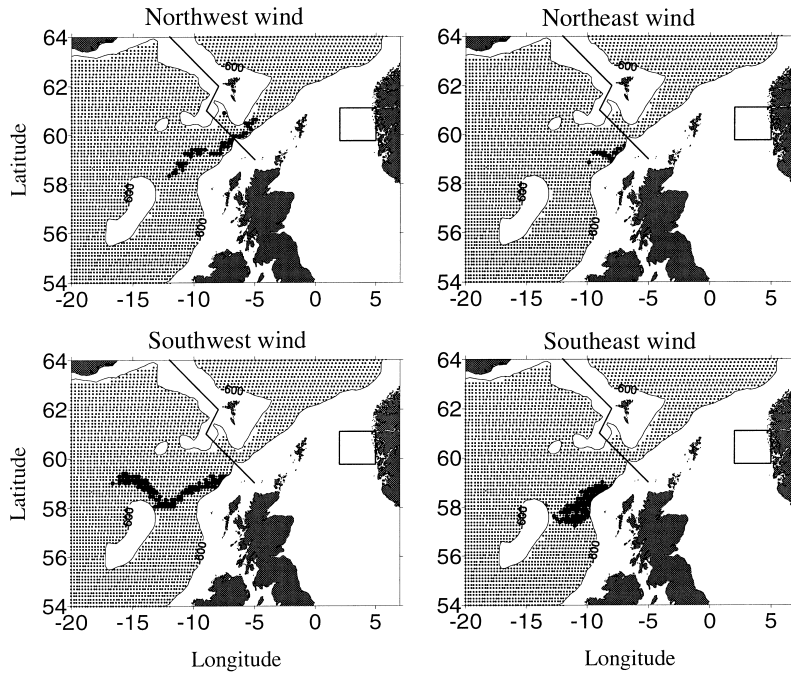
Figure 4. Mean frequency of winds from four compass quadrants during the months December February in successive decades between 1955 and 1994.
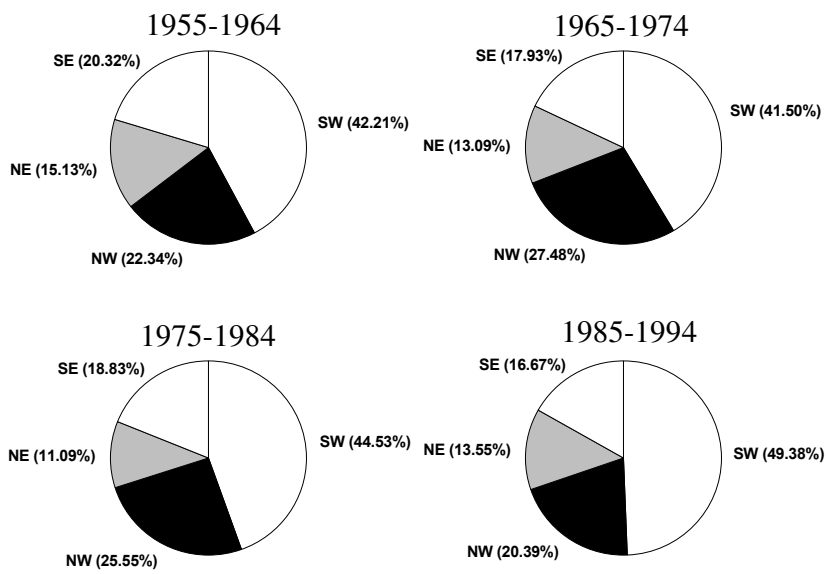
Figure 5. Time-series (left-hand panels) and correlation structure (right-hand panels) of model results and *C. finmarchicus* abundance data from the CPR surveys in the north-eastern North Sea. In the correlation structure panels, the cut-off year refers to the earliest year used to calculate the correlation between model results and CPR data, i.e. cut-off year 1960 refers to years 1960–83 and 1970 refers to years 1970–83.

CPR data vs model results   Correlation structure

a) Without weighting

b) Without weighting

c) Constant weighting

d) Constant weighting

e) Time dependent weighting

f) Time dependent weighting

CPR abundance — Model

r² — r² at p=0.01

Model results with time-dependent weighting

The results obtained using the year specific weighting values for particles originating north of the Iceland Scotland Ridge were highly correlated with the CPR data ($P \ll 0.01$), with no evidence of discontinuity and, hence, provided a significantly better account of the long-term changes in the observed *C. finmarchicus* abundance than the model with constant weighting (Fig. 5e, f).

DISCUSSION

The outcome of the investigation was a strong correlation between the particle tracking model results and CPR data for the period 1958–83 ($r^2 > 0.6$), provided that both time-and space-dependent variations in the concentration of overwintering copepodites were included in the model. Both the tracking model and the CPR data showed a declining abundance of *C. finmarchicus* in the target area from the mid-1960s to 1983. The decline continued to 1994 in the model results, but this could not be compared with observations since CPR sampling in the target area ceased in 1983. However, CPR sampling continued elsewhere in the region, and the abundance of *C. finmarchicus* during March and April has shown a coherent decline throughout the North Sea from the mid-1960s to 1994 (Beare and McKenzie, 1999a). Hence, the abundance of copepodites in the target area probably also declined, as predicted by the model results.

It could be argued that use of a different target area would allow more of the CPR data to be utilized for comparison with the tracking model results. However, this would be inappropriate because the tracking model did not include any representation of reproduction. Hence, for consistency with the model, the target area should be situated in a region where field observations have shown that during the spring, the majority of copepodites are survivors from the overwintering

population rather than first generation offspring. This condition was met only in the inflow region of the north-eastern North Sea, along the western side of the Norwegian Trench (Madden *et al.*, 1999). In addition, Beare and McKenzie (1999a) showed that the seasonal cycle of copepodite stages IV–VI abundance in the north-eastern North Sea has been stable over the period of observation. Hence, changes in the timing of arrival of overwintered animals in the surface waters cannot be involved in the decline in abundance in March and April. In contrast, the seasonal cycle of abundance in the north-western North Sea, which does not receive inflow directly across the northern boundary, was found to be unstable (Beare *et al.*, 1998), suggesting that in the interior of the North Sea other processes may modify the trends in the invasion magnitude. Trophodynamic modelling studies (e.g. Bryant *et al.*, 1997) have indicated that although the number of adults present in the spring is a significant factor determining the abundance of *C. finmarchicus* later in the year, the patterns of phytoplankton production become increasingly important during the season and with distance into the interior of the North Sea. Nevertheless, the annual mean abundance of *C. finmarchicus* in the northern North Sea as a whole (56°N–60°N, 1°W–5°E), which has also shown a coherent decline since the mid-1960s (cf. Fromentin and Planque, 1996; Stephens *et al.*, 1998), is significantly correlated with the trend in spring abundance in the target area ($r^2 = 0.37$, $n = 26$, $P < 0.01$).

The synthesis of a number of studies that is encapsulated in the model described here allows us to address those aspects of the hypothesis of Backhaus *et al.* (1994) that concern the invasion of the North Sea in the spring. The elements of the hypothesis that can be addressed are:

- overwintering copepodites must form a line source at depths of approximately 600 m extending along the continental slope between Scotland and Norway;
- the invasion into the North Sea takes place mainly via two routes (Fair Isle Current and Norwegian Trench);
- the topographic steering of the CSJ at the northern end of the Norwegian Trench results in invasion occurring first in that area;
- the vertical up and down migration of *C. finmarchicus*, together with the up and downwelling at the slope within the CSJ, is the vertical link for the closure of the life cycle;
- the horizontal link in the cycle is provided by the prevailing circulation at the slope and on the shelf;
- overwintering must take place beneath the core of the CSJ in order to make use of the NSDW counterflow.

Our investigations confirm that the interaction between vertical migration and the circulation regime does enable *C. finmarchicus* copepodites overwintering off the continental shelf edge north-west of Scotland to invade the North Sea in a predicatable manner each spring. However, we have no evidence that upwelling within the CSJ is a necessary feature of this process since the HAMSOM hydrodynamic model did not have a sufficiently fine spatial resolution to inform on this detail. The findings of our studies also confirm that the Norwegian Trench is the main invasion route in the spring, and that this is a consequence of the branching of the slope jet current onto the shelf in this area.

Our studies disagree with the aspects of the hypothesis relating to the importance of the Fair Isle Current as an invasion route, and on details of the distribution of overwintering animals. The analysis of CPR data has shown that the Fair Isle Current area has always been of lesser significance in terms of *C. finmarchicus* abundance than the north-eastern North Sea throughout the past 40 years. Abundance in the Fair Isle area declined in concert with the rest of the North Sea in the late 1960s, but was also accompanied by a change in the seasonal pattern of abundance and a shift in the balance between *C. finmarchicus* and the related species *C. helgolandicus*. By the early 1990s, *C. helgolandicus* had assumed predominance over *C. finmarchicus* in the autumn (Beare and McKenzie, 1999a). In the particle tracking model, none of the particles released at the 600 m depth horizon entered the North Sea through the Fair Isle Channel under any wind scenarios. Significantly shallower overwintering depths were required to simulate invasion through the Fair Isle route, and the origins of these particles were in the shelf and slope area west of Scotland and Ireland (unpublished results). Thus, our results suggest that *C. finmarchicus* entering the North Sea via the Fair Isle Current originate from a population with different overwintering behaviour from that in the Norwegian Sea and Faroe Shetland Channel, and distributed further south, perhaps in the Celtic Sea and south-western approaches to the UK (Williams and Conway, 1982, 1988; Williams, 1985).

In the simulations of overwintering at 600 m depth, particles invading the North Sea via the Norwegian Trench clearly originated from sites along the continental slope in the Faroe Shetland Channel and northern Rockall Trough, much as predicted by the Backhaus hypothesis. However, our field observations indicate that in reality these particles represent two distinct groups of animals. The first group are the copepodites in the Faroe Shetland Channel in December and January whose vertical distribution was

delineated by the NSDW element of the bottom water, whilst the second group are animals in the Atlantic water south of the Wyville Thomson Ridge whose vertical distribution showed no clear relationship to water mass structure (Heath and Jónasdóttir, 1999). The Faroe Shetland Channel animals were in a deep diapause state at temperatures of +3.0 to 0.5°C in December and January (Ingvarsdóttir et al., 1999), and had high wax-ester content and body weight. In contrast, the Atlantic animals were at +7 to +9°C, may not have been in deep diapause, and had low wax ester content and body weight (Heath and Jónasdóttir, 1999; Jónasdóttir, 1999). The abundance of copepodites in the Faroe Shetland Channel was 25 times higher than in the Atlantic. The prevailing flow regimes in the region indicate that the parental origins of the animals that ascend to the surface from the Faroe Shetland Channel in February, were in the Norwegian Sea and possibly the fringing continental shelf areas during the previous summer. In contrast, the parental origins of the animals that emerge to the surface south of the Wyville Thomson Ridge were probably in the open North Atlantic.

Clearly, the concept of a continuous line source beneath the CSJ needs to be modified. The prevailing view should be of two main pools of overwintering animals, one in the Norwegian Sea and another in the Atlantic. These pools are redistributed by the deep circulation during the winter, and in particular, the Norwegian Sea pool feeds into the Faroe Shetland Channel. *Calanus finmarchicus* invading the North Sea via the Norwegian Trench are potentially drawn from both pools, the proportions being dependent on wind driven circulation in the upper layers, and the extent of redistribution into the Faroe Shetland Channel from the Norwegian Sea.

Armed with the above conceptual model, we can begin to explain the decline in abundance of *C. finmarchicus* in the North Sea since the late 1960s. The supply of overwintering animals to the Faroe Shetland Channel by the deep circulation is of key importance. Since the concentration of animals in the Norwegian Sea pool is greater (25 times) than in the Atlantic, processes in the Norwegian Sea must to a large extent dictate the scale of the invasion into the North Sea. As the supply of NSDW to the Faroe Shetland Channel bottom water declined from the late 1960s onwards, the contribution to the North Sea from the Norwegian Sea pool of overwintering animals also decreased. Relative to this decline, fluctuation in the supply from the Atlantic would have been of far lesser significance. Trends in the directional pattern of the regional wind field, which dictates the invasion success

of those animals that reach the surface waters, have further modulated the main underlying process.

Our conceptual model of why the magnitude of the North Sea invasion has declined over a 30-year period appears to rely on two quite separate processes changes in the deep circulation and changes in the regional wind field. However, it is quite likely that both are related in a complex way to Atlantic basin scale atmospheric factors. Periodic changes in the atmospheric pressure difference between the subtropical Atlantic high over the Azores and the subpolar low over Iceland (Lamb and Randy, 1987), referred to as the North Atlantic Oscillation (NAO), have been linked to the regional wind field in the north-east Atlantic. Intensification of the latitudinal pressure gradient results in strengthening of the atmospheric circulation in the North Atlantic and increasing dominance of south-westerly winds. The winter NAO index has undergone several phases of fluctuation since the late 19th century, but most recently has shown a persistent underlying increase since the late 1950s, attaining 100 year high values during the mid-1990s. This appears to be the explanation for the change in airflow pattern indicated by our analysis of the incidence of winds from different compass quadrants. However, the decline in supply of NSDW to the bottom water of the Faroe Shetland Channel is also connected to basin scale atmospheric processes, and possibly to the NAO. Relaxation of the wind stress curl over the Greenland Sea in the late 1960s and early 1970s resulted in cessation of the deep convection and the formation of deep water in the Greenland Sea, and ultimately a reduction in the supply of NSDW (Schlosser et al., 1991; Turrell et al., 1999). The relationship between the NAO and wind stress curl over the Greenland Sea is less certain than the link to regional winds in the north-east Atlantic (Dickson, 1997), but is a common factor in the origin of the decadal fluctuation in both factors.

Finally, the conceptual model described here exposes the dangers of relying on correlations between forcing and response variables without an adequate explanation of the underlying mechanisms. Fromentin and Planque (1996) drew attention to a strong inverse correlation between the NAO time-series and the annual abundance of *C. finmarchicus* in the North Sea and northeast Atlantic from CPR data collected during 1962 92 (although the CPR signal was primarily driven by data from the North Sea). Various hypotheses were erected to explain this relationship, including trophic responses mediated by wind stress effects on phytoplankton production. Similarly, Stephens et al. (1998) identified correlations between annual abundance in the northern

North Sea from CPR records (1958 93) and transport rates on the continental shelf simulated by a two-dimensional barotropic storm surge model. The modelled transport rates were entirely driven by the annual wind regime, which in turn could be related to trends in the NAO. However, both of these correlative models failed in the period 1996 97, which saw a major reversal of the NAO to low values and an increase in the incidence of north-west winds, but no corresponding increase in *C. finmarchicus* abundance in the northern North Sea (Planque and Reid, 1998). The reason is quite clear from the model presented here. The reversal of the NAO has not resulted in any immediate increase in the supply of NSDW to the Faroe Shetland Channel bottom water, so the supply of animals to invade the North Sea remains at a low level, despite the ostensibly more favourable regional wind conditions. It would take several years of persistent deep convection in the Greenland Sea to restore the NSDW overflow through the Faroe Shetland Channel, and produce a recovery of *C. finmarchicus* abundance in the North Sea.

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