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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.

Key words: Calanus finmarchicus, circulation, modelling, North Atlantic, North Atlantic Oscillation Index, Norwegian Sea Deep Water, plankton, winds

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 (Franz 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,
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; Frantz et al., 1991). Instead, high concentrations (~5000 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. finnarchicus (Wood, 1932; Williams and Lindley, 1980; Krause and Martens, 1990; Frantz 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. finnarchicus 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.
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 Green-
land 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 36years of sampling, the model output was therefore in the form of a 73 x 36 matrix. The recorded values for a sample at time t were denoted by $R_i$ and we then modelled the inverse cumulative distribution function of $R_i$ i.e. $P(R_i > v) = P_{tv}$. Two versions of the model were investigated (Models 1.0 and 1.1):

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

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

where $\pi$ 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):

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

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 copepodes in the Faro 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 copepodes 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; Strohach 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 \(\frac{dD}{dt}\) (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 \(\frac{dD}{dt}\) 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 linearly 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 copepods 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, \(D_1\), \(D_2\), \(\frac{dD}{dT}\), 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 \(\frac{dD}{dt}\) 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 copepods 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 \(\sigma_r = 28.0\) 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) copepods 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 \( C. \ marmaricus \) copepodes 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 \( C. \ marmaricus \) 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 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 Norwegian sources (1955-81, Backhaus et al., 1985). Wind stress at 6-h intervals during December-February for each year was integrated over 2° latitude \times 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 copepodes between water masses, provides the basis for the 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 copepodes is a consequence of both the distribution of pre-diapause animals in the autumn and the deep circulation patterns, and (ii) there have been no underlying long-term trends in the abundance of \( C. \ marmaricus \) 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 copepodes 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 northern 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 \( C. \ marmaricus \) 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
the concentrations of overwintering copepods 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 (σt > 27.9, Turrell et al., 1999) was assumed to be made up of NSDW and NSIWI, 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:

\[ C_{FSC} = (f_U((p_{NSDW}C_{NSDW})+(p_{MNAW}C_{MNAW})+(p_{AI/NW}C_{AI/NW}))) + (f_B((p_{NSDW}C_{NSDW})+(p_{MNAW}C_{MNAW}))) \]

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

\[ (p_{NSDW}+p_{MNAW}+p_{AI/NW} = 1); \]

\( p_{NSDW} \) is the proportion of NSDW in the bottom water, \( p_{AI/NW} \) is the proportion of AI/NIW in the bottom water (\( p_{AI/NW} = 1 - p_{NSDW} \)), and \( C_{NSDW}, C_{MNAW}, C_{AI/NW}, C_{NSDW} \) are the constant concentrations of overwintering copepodes (m^{-3}) in the NACW, MNAW, AI/NIW, NSIWI 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 copepodes in the five water masses during winter 1994/95 were as follows: \( C_{NSDW} = 0.66 \) m^{-3}, \( C_{MNAW} = 2.70 \) m^{-3}, \( C_{AI/NW} = 2.83 \) m^{-3}, \( C_{NSIWI} = 13.68 \) m^{-3}, \( C_{NSIWI} = 86.23 \) 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 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 (\( p_{NSDW} = 0.3, p_{MNAW} = 0.6, p_{AI/NW} = 0.1 \)). These proportions have fluctuated since 1955 (Turrell et al., 1999), but since the concentration of copepods 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 NSIWI in the bottom water of the Channel \( (p_{NSDW} \) and \( p_{NSIWI} \)) 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 copepods 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 CVI and CVII copepodes 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 copepodes 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, coincident 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 copepoides 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 copepoides. 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**

- **a) Without weighting**
  - Abundance: 0-5
  - Model: black line
  - CPR: red line

- **b) Without weighting**
  - Correlation coefficient: 0-1
  - Cut-off year: 1960-1980

- **c) Constant weighting**
  - Abundance: 0-5
  - Model: black line
  - CPR: red line

- **d) Constant weighting**
  - Correlation coefficient: 0-1
  - Cut-off year: 1960-1980

- **e) Time dependent weighting**
  - Abundance: 0-5
  - Model: black line
  - CPR: red line

- **f) Time dependent weighting**
  - Correlation coefficient: 0-1
  - Cut-off year: 1960-1980

**DISCUSSION**

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 ($P \leq 0.01$), 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).

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 copepods 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 copepods 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 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 copepodes 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 copepodes overwintering off the continental shelf edge north-west of Scotland to invade the North Sea in a predictable 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 southwestern 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 copepodes 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 (Ingvardsdóttir 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 copepods 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 Remy, 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 north-east 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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