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The seasonal dynamics of *Calanus finmarchicus*: development of a three-dimensional structured population model and application to the northern North Sea

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Abstract

A weight-structured population model is described for *Calanus finmarchicus*. Results are presented for an area of the northern North Sea for which detailed stage succession data exist, and are discussed in the context of other models of zooplankton population dynamics for that area. The essential simplicity of the model enables embedding in a three-dimensional hydrodynamic scheme representing the northern North Sea ($1^\circ \times 1^\circ$ boxes, split into upper 30 m and below). Results of this spatially-resolved model are discussed in the context of a new statistical analysis of *C. finmarchicus* late-copepodites from the continuous plankton recorder. Crown Copyright © 1997 Published by Elsevier Science B.V.

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1. Introduction

Despite several decades of research the representation of carbon or energy flux through the food web in marine ecosystem models is still not adequate to simulate the relationship between the dynamics of higher trophic levels (e.g. fish) and fluctuations in the autotrophic components of the system implied by empirical studies (Parsons et al., 1984; Nixon,

1988). Modelling has concentrated either on the physics–nutrients–phytoplankton system (Fransz et al., 1991b) or on the fish assemblage (Sissenwine and Daan, 1991), but the two levels have not been satisfactorily connected. Partly, this is due to the complexity of the interconnecting metazoan zooplankton, and partly due to the scarcity of adequate data for establishing the parameters, structure and required performance of such models.

The difficulty of modelling the dynamics of the metazoan zooplankton assemblage stems from the diversity of form, behaviour and function. Reduction of the diversity to tractable proportions by aggregating species has proved very difficult. Zooplankton data are often defined more by the mesh size of nets used to collect them than by the functional status

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of the organisms. Even so, attempts at categorising species on the basis of trophic relationships immediately encounter difficulties since most organisms will feed on a wide variety of prey, and the diets of most species change dramatically during the life cycle. The traditional concept of zooplankton being essentially herbivorous grazers is now recognised to be misleading (Lonsdale et al., 1979; Sherr et al., 1986; Conley and Turner, 1987; Kleppel et al., 1988). Most species can operate as omnivores, which is not helpful for model formulation. Another major problem for zooplankton modelling is that the body size of most species varies by at least two orders of magnitude over the life cycle, with associated allometric scaling of physiological rates. This contrasts sharply with the life cycle of protozoan and autotrophic species where the unit size varies by only a factor of two. The consequence is that whilst the uptake, excretion, growth and mortality dynamics of autotrophic species assemblages can be represented by parameterized models of the bulk biomass, this approach is almost certain to fail for the zooplankton where the parameterization must be heavily dependent on the life-cycle stage composition of the population even at the single species level.

The challenges outlined above have been broadly recognised for many years (e.g. Steele and Mullin, 1977). More recently there has been significant progress towards structured representations of zooplankton (e.g. Fransz, 1981; Carlotti and Sciandra, 1989; Carlotti and Nival, 1992; Carlotti et al., 1993; Henderson and Steele, 1995, 1996; Carlotti and Radach, 1996; Heath et al., 1997). Internal structure has been characterised in terms of age, development stage or body weight. Such models have been operated in isolation driven by time dependent forcing data, or coupled to one-dimensional (vertically) resolved models of a nutrient–phytoplankton ecosystem. All these models have been sensitive to initial and boundary conditions, implying that in reality horizontal dispersal is likely to be critically important. However, there have been few if any three-dimensional spatial implementations of structured zooplankton models. The problems associated with such a development are daunting. Firstly, the prey categories of the structured model must also be provided, either as time resolved three-dimensional

data, or by coupling to an operational three-dimensional model capable of accurately mimicking nutrient and phytoplankton dynamics. Secondly, there is the requirement for spatially resolved initial conditions, and the time resolved boundary conditions of the three-dimensional scheme. There is an essentially similar requirement for independent data to compare against model results, resolved in three-dimensional space, time and developmental stage. Few situations can provide this level of data support to modelling. Finally, the technical modelling problems and computational demands of running a highly resolved structured population model in three-dimensional mode are potentially very considerable.

The North Sea is extremely rich in plankton data and may represent the best opportunity to assemble and test species specific models of zooplankton. For a large part of the year the zooplankton biomass in the northern North Sea is dominated by *Calanus finmarchicus* (Fransz et al., 1991a), which is therefore a obvious target for modelling. This has the added advantage that it is a relatively large, mainly herbivorous copepod, and the copepodite stages of its life cycle are retained by standard sampling nets. High quality time- and stage-resolved data on *C. finmarchicus* are available from the FLEX experiment in 1976 and have already been extensively exploited for modelling (Henderson and Steele, 1995, 1996; Carlotti and Radach, 1996). The influence of advection on FLEX '76 has been re-examined in a subsequent study of plankton dynamics along a drogue drift-track in that area (Fransz and Tijssen, 1983; Fransz and Diel, 1985). In addition, coarse two-dimensional and monthly time resolved data with coarse stage resolution are available from the continuous plankton recorder (CPR) surveys, whilst three-dimensional data with high stage resolution have been collected on a number of synoptic research cruises. Quasi-synoptic zooplankton surveys (May to June and January to March 1987) have covered the entire North sea, with some information on individual species and depth layers (Krause and Martens, 1990; Krause et al., 1995). A large amount of phytoplankton biomass data are available for the North Sea for the assembly of either a forcing data series, or for assessing the performance of a suitable underlying ecosystem model.

Problems specific to modelling the population dynamics of *C. finmarchicus* in the North Sea relate to the discrimination between this species and the related *Calanus helgolandicus* in the data, and representing the seasonal immigration of animals into the North Sea region from across the shelf break. *C. finmarchicus* and *C. helgolandicus* are morphologically similar and are practically distinguishable only in the adult and late copepodite stages, and even then the quality of discrimination is uncertain. The main physiological differences between the two species relate to their temperature responses. Optimum temperatures for a range of physiological processes in *C. helgolandicus* are higher than for *C. finmarchicus*, and the distributions of the two species can be broadly separated by the 14°C summer isotherm (Williams and Conway, 1980; Williams, 1985). Unfortunately, the distributions overlap in the northern North Sea (Williams and Lindley, 1980; Planque and Fromentin, 1996). The life-cycle strategy of *C. finmarchicus* in the North Sea includes a diapause stage which survives through the winter at depths >600 m off the continental shelf edge. In the spring, individuals emerge from diapause, migrate towards the surface and are carried into the North Sea by the surface water circulation (Wood, 1932; Backhaus et al., 1994). Thus, the northern North Sea is reseeded with *C. finmarchicus* each spring from outside the area. It is hypothesised that this phenomenon is extremely important for the success of the shelf population. Evaluation of the role of climatic processes in the success of the invasion is being carried out elsewhere, but so far there has been no quantitative assessment of the population dynamics within the North Sea and the sensitivity to northern inflow.

The model described here represents an initial attempt to evaluate the sensitivity of the in-situ population dynamics of *C. finmarchicus* in the northern North Sea. First, we have formulated a new weight structured population model which retains the important dynamical properties of many more complex models but is less computationally demanding thereby giving us the scope to implement it in a three-dimensional matrix. We have configured the model to be forced by spatially and temporally resolved data on phytoplankton concentration compiled from a variety of sources. This eliminates the

requirement to verify the performance of an underlying nutrient–phytoplankton model, but carries other attendant problems. The whole system was set in the framework provided by the European Regional Seas Model (ERSEM) transport module (Lenhart et al., 1995; Pätsch and Radach, 1997). This represents the North Sea by 85 $1^\circ \times 1^\circ$ areas, 45 of which are split into upper (30 m) and lower compartments, with daily resolved exchange rates derived from the output of a three-dimensional hydrodynamic model (Pohlmann, 1996). Initial and boundary conditions, and data for comparison with model results were compiled from CPR results and from research vessel survey data. It is shown that accurate dynamics can be generated with relative ease for an isolated zero-dimensional scenario with this structured model. An unstructured model (Broekhuizen et al., 1995) is subjected to the same forcing scenario for comparison, to illustrate the features of the dynamics which can be reproduced only by the structured model. The three-dimensional implementation of the structured model exposes crucial areas of weakness in the knowledge of *C. finmarchicus* physiology and biology, and in the quality of the data used to drive and evaluate the model.

2. Data compilation and analysis

2.1. CPR data

Continuous plankton recorder data has been collected by the Sir Alister Hardy Foundation for over sixty years and has provided marine scientists with often the only source of information on the spatial and temporal distributions of many marine plankton taxa. For a detailed overview of the survey see Colebrook (1975) and Warner and Hays (1994). Many different approaches have been used to analyse CPR data (e.g. Colebrook, 1979; Broekhuizen and McKenzie, 1995; Planque and Fromentin, 1996) although none have involved fitting probabilistic models to raw CPR data.

There are numerous problems associated with the analysis of CPR data due to both the method of sampling and the protocols involved in recording the data. The data are collected by voluntary ‘ships of opportunity’ which tow the CPR samplers during their routine business. Spatial coverage around

Britain has been very wide-ranging especially when compared to other datasets available although the generally fixed positions of the tow routes mean that some areas are rarely sampled. Also certain ships on certain tow routes have sailed rather erratically causing considerable data voids in the time-dimension. This non-random sampling distribution is a potential minefield for the unwary analyst, especially when the main intention is to fit statistical models to the data. Furthermore, a good proportion of raw CPR data are zero, even for the common taxa, and actual counts of abundances are binned into 13 categories or 'recorded values', the widths of which increase exponentially (for details see Warner and Hays, 1994).

In this study CPR data for *C. finmarchicus* copepodite V/VI were analysed from the northern North Sea and North East Atlantic (56°N to 64°N and 13°E to 11°W) from January 1958 to December 1993. The 'recorded values' were assumed to be normally distributed and then modelled as a four dimensional smooth function of latitude, longitude, long-term trend (based on 2628 five-day periods) and seasonality (based on 73 five-day periods per year). Fitting was done with a generalized additive model (GAM) (see Hastie and Tibshirani, 1983) coupled with a LOWESS smoothing function (Cleveland, 1979). The fitted statistical model was then used to interpolate values at $1^\circ \times 1^\circ$ resolution for 1992, from 56°N to 62°N and 5°W to 10°E (Fig. 1). 'Accepted numbers', which approximate to the original (actual) counts, were estimated from the smoothed 'recorded values' by simple linear interpolation.

The year (long-term trend), time of year (season) and place of sampling (longitude and latitude) are all important in predicting plankton abundance. A good representation of the main spatial and temporal gradients in CPR data was our requirement here and, notwithstanding the inherent sampling problems of CPR data, we believe the approach reflects the main features of the distribution of *C. finmarchicus*.

2.2. Phytoplankton forcing data

Previous attempts to model *Calanus* population structure and dynamics (e.g. Henderson and Steele, 1995; Carlotti and Radach, 1996) have included a simple nutrient–phytoplankton dynamic substrate.

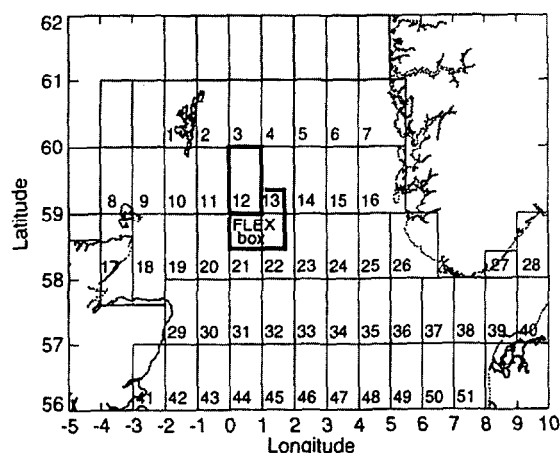


Fig. 1. The northern North Sea model area indicating northern/northwestern boxes for which explicit boundary conditions were available. The whole of the southern North Sea (not shown) is included in the hydrodynamic transport scheme. The area investigated during FLEX '76 is indicated.

These models have no horizontal resolution and, in those particular examples, the zooplankton are constrained to fixed level(s) in the vertical dimension. Obtaining useful results from a spatially-resolved zooplankton model coupled to its substrate requires that that substrate has appropriate spatial and seasonal dynamics. That in turn depends on the identification of statistically-robust patterns in the phytoplankton (and possibly detritus) data. No model has the proven capability to simulate phytoplankton dynamics at our (fine) scale for the northern North Sea. In the absence of this we chose to force the phytoplankton level of the model with time-series data available for each spatial area of the model.

The phytoplankton forcing data consisted of chlorophyll determinations aggregated over 36 years (1960–1995) supplied as monthly arithmetic means by J. Pätsch of Institut für Meereskunde, Hamburg. For most of the $1^\circ \times 1^\circ$ rectangles of the model area there were adequate sample sizes within the upper 30 m compartment. For some areas several months were missing or there was a low sample size, and in both cases we used data from an adjacent rectangle to fill the gap. Where there were several adjacent rectangles with missing or sparse data (29, 30, 42 and 43) we used chlorophyll data which had been analysed in the same way but for the 15-box ERSEM

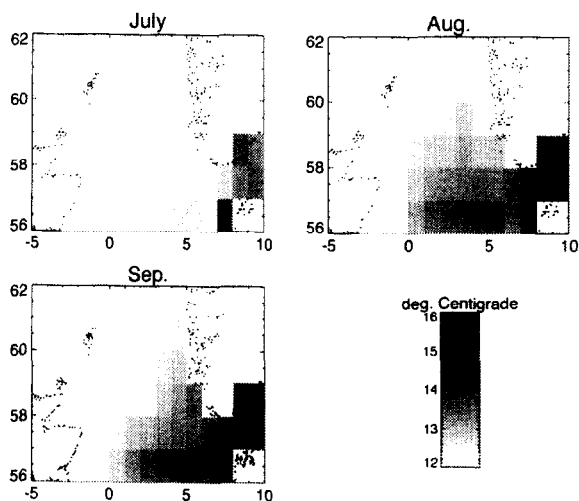


Fig. 4. Temperature data as Fig. 3 but with the scale truncated at T_{thres} to indicate seasonal and spatial distribution of temperature-related mortality in the model.

3. Model description

3.1. Hydrodynamic transport

Daily exchange coefficients between the $1^\circ \times 1^\circ$ boxes (Fig. 1) were derived from hindcast semi-baroclinic simulations of the circulation of the North Sea (Pohlmann, 1996; Pätsch and Radach, 1997). Of the 39 years of transport coefficients that are available (1955 to 1993) 1992 was selected, a year for which there are spatially-detailed depth-resolved cruise data for *C. finmarchicus*.

3.2. The biological model

3.2.1. *C. finmarchicus* population dynamics

We consider a population of individuals distinguished only by their weight. If, at time t , an individual of carbon weight w has a growth rate $\gamma(w, t)$ and a *per capita* mortality rate $\delta(w, t)$, then the time development of the population carbon weight distribution, $f(w, t)$ is described by the McKendrick von Foerster equation:

$$\frac{\partial f}{\partial t} + \frac{\partial(\gamma f)}{\partial w} + \delta f = 0.$$

Numerical realisation of this equation requires us to represent the continuous distribution, $f(w, t)$, by a discrete set of values $f_i(t)$ which we space along

the weight axis at intervals $\Delta w_i = w_{i+1} - w_i$. Using up-wind difference discretisation, and recasting our representation in terms of the number of individuals in the i th weight class, $N_i(t) \approx f_i(t) \Delta w_i$, our dynamic equation becomes:

$$\frac{dN_i}{dt} = \left[\frac{\gamma_{i-1}}{\Delta w_{i-1}} \right] N_{i-1} - \left[\frac{\gamma_i}{\Delta w_i} \right] N_i - \delta_i N_i$$

$$1 < i < q.$$

where we define $\delta_i(t) \equiv \delta(w_i, t)$. This describes the dynamics of all weight classes except the first ($i = 1$) and last ($i = q$). If $R(t)$ represents the total rate of recruitment of newborns to the population, and all newborns are recruited with the same weight (w_R), then the dynamics of the weight class covering the range w_R to $w_R + \Delta w_i$ (which we choose to number $i = 1$) are described by:

$$\frac{dN_1}{dt} = R - \left[\frac{\gamma_1}{\Delta w_1} \right] N_1 - \delta_1 N_1.$$

We now assume that individuals in only the q th weight class are adult, and that adult individuals spend all assimilate on reproduction rather than growth. This immediately implies that the population dynamics of the adult population are given by:

$$\frac{dN_q}{dt} = \left[\frac{\gamma_{q-1}}{\Delta w_{q-1}} \right] N_{q-1} - \delta_q N_q,$$

and that the rate of recruitment of newborns to the population is:

$$R(t) = \beta(t) N_q(t)$$

where $\beta(t)$ represents the per capita fecundity of an average adult at time t .

The weight intervals increase with class number i , $\Delta w_i \propto s^i$, with the scaling factor s (Table 1) chosen to give a reasonable spacing in terms of the instars, and time spent in each instar, of *C. finmarchicus*.

3.2.2. Individual dynamics

The individual model is similar to that described by Heath et al. (1997) but we describe it in full here for completeness and to indicate clearly its differences. The uptake rate of an individual of carbon weight w feeding on phytoplankton distributed at (carbon) density P , is defined as $U(w, P)$. We assume that the functional response, $U(w, P)$, follows

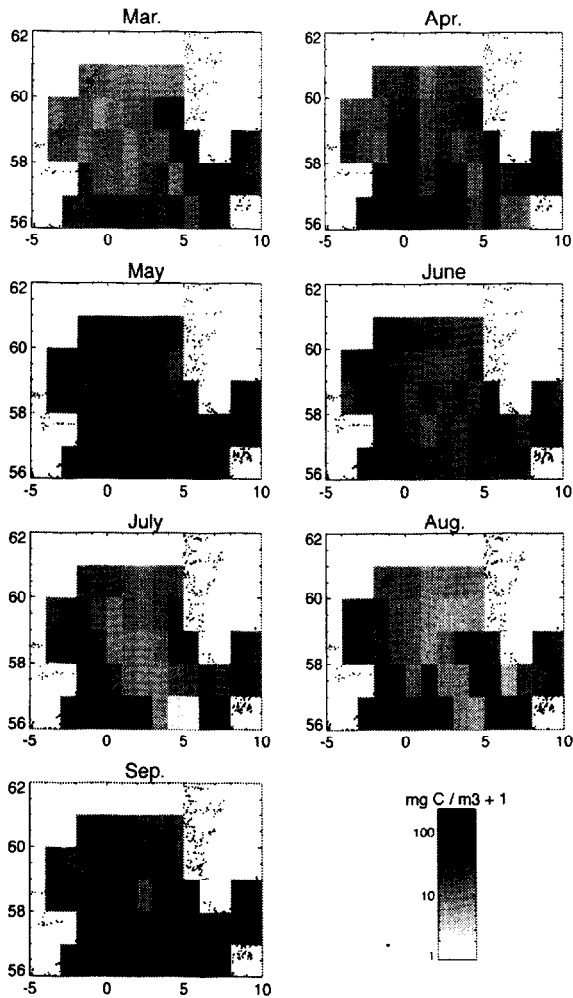


Fig. 2. Chlorophyll forcing for the zooplankton model: monthly arithmetic mean data aggregated over 1960 to 1995 for the upper 30 m of the water column.

scheme (Baretta et al., 1995). Boxes 1 and 41 were treated in this way also as many of the samples in those areas were taken in Sullom Voe and the Firth of Forth respectively, neither of which are typical of their respective $1^\circ \times 1^\circ$ areas. Data were very sparse below 30 m so we applied a conversion factor to upper 30-m densities, derived on a monthly basis from comparison of upper and lower chlorophyll densities over a wider area (boxes 2 and 12 of the 15-box scheme). The conversion factor is near-unity from January to March, and varies between 0.79 and 0.25 from April to December. Finally, we converted chlorophyll weight to carbon weight by multiplying by 30.0 and interpolated linearly between monthly

values. The upper 30-m layer data are shown in Fig. 2.

2.3. Temperature

The temperature time-series is resolved to daily values for each box of the model area, and is one of the results of a baroclinic hydrodynamic model (Pohlmann, 1996) aggregated over the years 1982 to 1992. Fig. 3 shows the upper 30 m temperatures at month mid-points over the model area. Fig. 4 shows the same data with the colour scale truncated to indicate the months and areas in which temperature-dependent mortality applies (see Section 3).

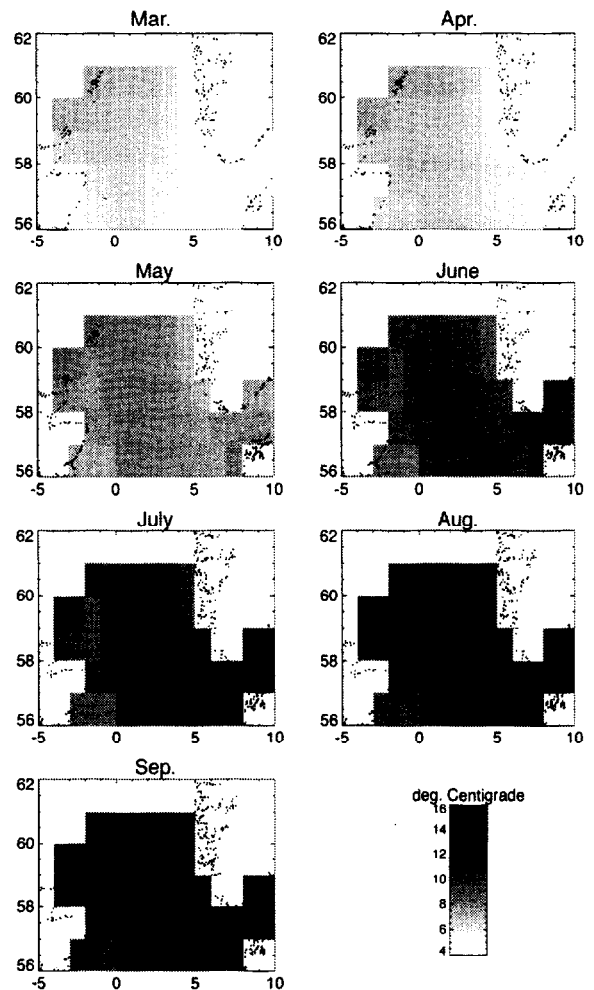


Fig. 3. Monthly mid-point plots of the daily temperature forcing (upper 30 m).

Table 1
Parameters of the zooplankton model

Parameter	Symbol	Value	Units	Notes
Max. uptake rate coefficient	a	0.075	mg C ^(1-b) d ⁻¹	fitted, see text
Max. uptake rate exponent	b	0.7	–	Carlotti and Radach (1996); Van Den Bosch and Gabriel (1994)
Half saturation	c	25.0	mg C m ⁻³	e.g. Henderson and Steele (1995)
Absorption efficiency minus SDA	ε	0.6	–	Heath et al. (1997)
Temperature response	Q_{10}	2.0	–	Marshall (1973)
Ref. temperature of Q_{10}	T_{ref}	10.0	°C	
Egg weight	w_1	0.2×10^{-3}	mg C	Hay et al. (1991)
Adult weight	w_q	58×10^{-3}	mg C	Hay et al. (1991)
Scaling of weight intervals	s	1.6	–	adjusted according to instar weights in Hay et al. (1991) and instar durations in Thompson (1982)
Number of weight classes	q	20	–	adjusted to give numerical dispersion approximating to individual variability in growth
Background mortality	δ_0	0.02	d ⁻¹	assumed
High-temp. mortality threshold	T_{thres}	12.0	°C	assumed
High-temp. mortality maximum	T_{max}	18.0	°C	assumed
Basal costs coefficient	d	0.0116	mg C ^(1-g) d ⁻¹	derived from Marshall (1973)
Basal costs exponent	g	0.65	–	derived from Marshall (1973)

With these parameters (assuming $T = T_{\text{ref}}$), ingestion rates range from 48 to 9% d⁻¹ (smallest class to largest class) at half saturation food concentration, with corresponding growth rates from 21 to 5% d⁻¹. At near-saturation (400 mg C m⁻³), ingestion rates range from 91 to 17% d⁻¹, growth rates from 59 to 21% d⁻¹ (cf. Fransz et al., 1991a).

a standard Michaelis-Menten form with the maximum uptake rate allometrically related to individual weight, a weight-independent half-saturation (for detailed discussion see Van Den Bosch and Gabriel, 1994) and a conventional Q_{10} response to temperature T :

$$U(w, P) = \frac{aw^b F}{c + F} \times Q_{10}^{\left(\frac{T - T_{\text{ref}}}{10.0}\right)}.$$

If we now write the absorption efficiency minus specific dynamic action as ε and basal metabolic costs (subject to the same Q_{10} response to temperature T) as $M(w, T)$ then the net assimilation is:

$$A(w, P) = \varepsilon U(w, P) - M(w, T),$$

where

$$M(w, T) = dw^g Q_{10}^{\left(\frac{T - T_{\text{ref}}}{10.0}\right)}.$$

For adult individuals, all net assimilate goes into offspring, while for non-adults it is used for growth. However, before we can write down sensible forms for the growth rate, γ_i , or the adult fecundity β , we

must recognise that in times of low food availability, A will be negative. Clearly negative offspring are impossible, and within this formalism, negative growth presents serious technical and conceptual difficulties. Thus, employing the notation $x^+ \equiv \max(x, 0)$, we write:

$$\beta = \frac{A(w_q, P)^+}{w_1}, \quad \gamma_i = \begin{cases} A(w_i, P)^+ & \text{if } i < q \\ 0 & i = q \end{cases}.$$

To allow the zooplankton model to operate within a nutrient-based ecosystem model we keep careful account of nutrient balance between the zooplankton population and its environment. In periods when net assimilate is negative for any weight class, the animals are respiring more carbon than they are ingesting. If exclusion of the possibility of weight loss is not to cause a (potentially serious) failure of nutrient conservation, we must arrange to reproduce the resulting nutrient flows in a technically acceptable way. Our solution to this problem relies on the fact that in this situation excess mortality would be

expected to operate. We therefore choose to impose excess mortality at just the rate required to balance the nutrient books, in any weight class where the net assimilate is negative. Additionally, we impose a high-temperature mortality term on the basis of laboratory observations of *C. finmarchicus*, since we cannot rule out the possibility that the transport scheme may advect individuals into southerly and easterly regions of the North Sea. This takes the form of a linear increase in mortality above a threshold temperature. Thus the total mortality of weight class i is:

$$\delta_i(t) = \delta_0 + \frac{1}{w_i} [-A(w_i, P)]^+ + \left[\frac{T - T_{\text{thres}}}{T_{\text{max}} - T_{\text{thres}}} \right]^+.$$

3.2.3. Unstructured zooplankton model

The ERSEM unstructured, bulk-biomass model for omnivorous mesozooplankton (Broekhuizen et al., 1995) was adapted to allow comparison with the structured model. The unstructured model has fixed quotients of N : C and P : C, and growth may be limited by any of those three nutrients depending upon the (dynamic) quotients of their food; this feature was removed, so that it could be forced by the phytoplankton food (carbon) time series described here. The carnivorous mesozooplankton group described by Broekhuizen et al. (1995) was replaced by an increase in the per capita background mortality rate for the omnivores.

3.3. Implementation and numerical methods

The structured population model was coded initially using NAG library Runge–Kutta 4th order numerics (Dew and Walsh, 1981), then was recoded using the SESAME simulation environment (Ruudij et al., 1995) to allow coupling to the ERSEM hydrodynamical scheme, and in principle the planktonic system of ERSEM. The SESAME implementation used rectilinear integration with adaptive time-stepping, the results of which were tested against those of the initial version. Simulations were started mid-March, day 75, with initial adult class densities in each model rectangle set according to the results of the *C. finmarchicus* CPR analysis. Similarly, concentrations of adults at the north and northwestern boundaries were implemented, with linear interpolation between monthly values, from the CPR analysis.

CPR ‘accepted numbers’ were converted to densities (m^{-3}) by multiplying by 10.0, after considerable experimentation.

4. Results

4.1. Testing in zero-dimensional form

The model was subjected to a limited allometric and demographic test, and sensitivity analysis, by running it with the forcing for box 12 of the model area (Fig. 1). This $1^\circ \times 1^\circ$ area is centred on 59.5°N , 0.5°E and thus overlaps with the Fladen Experiment (FLEX) box. The forcing data and results, of the structured model and the unstructured model for comparison, are given in Fig. 5. Understanding the behaviour for this area in isolation was an important first step; only with this understanding, and some adjustment of the parameters, could we begin to obtain acceptable results in the spatially resolved form. The main points of this zero-dimensional test of the structured model are presented below.

Starting in mid-March (day 75) with 10 individuals m^{-3} in the adult class only, there is immediate reproduction which results in a low but sustained density of eggs; this first generation can be seen developing through the naupliar and copepodite stages, and determines the shape of the increase in adults starting on day 110. The second generation begins as a gradual increase in egg density starting around day 120, with food concentrations still well above the half-saturation level c . It is this gradual increase which determines the major peak in naupliar, CI and CIII densities; the sharp peak in egg density around day 170, just *after* the major peak in the other classes, is of minor significance since food concentration is declining towards its minimum at this stage, resulting in minimal growth of those eggs through to nauplii. Both the adult numbers and total biomass over all classes peak in mid-June, 60 days after the chlorophyll peak. Further activity in the autumn (with no seasonal migration rules to mimic the summer descent) is largely dependent on summer adult densities and the half-saturation constant relative to the autumn food density.

The data for this area, and previous attempts to model those data, are discussed later. The features that we concentrate on in general terms here are the

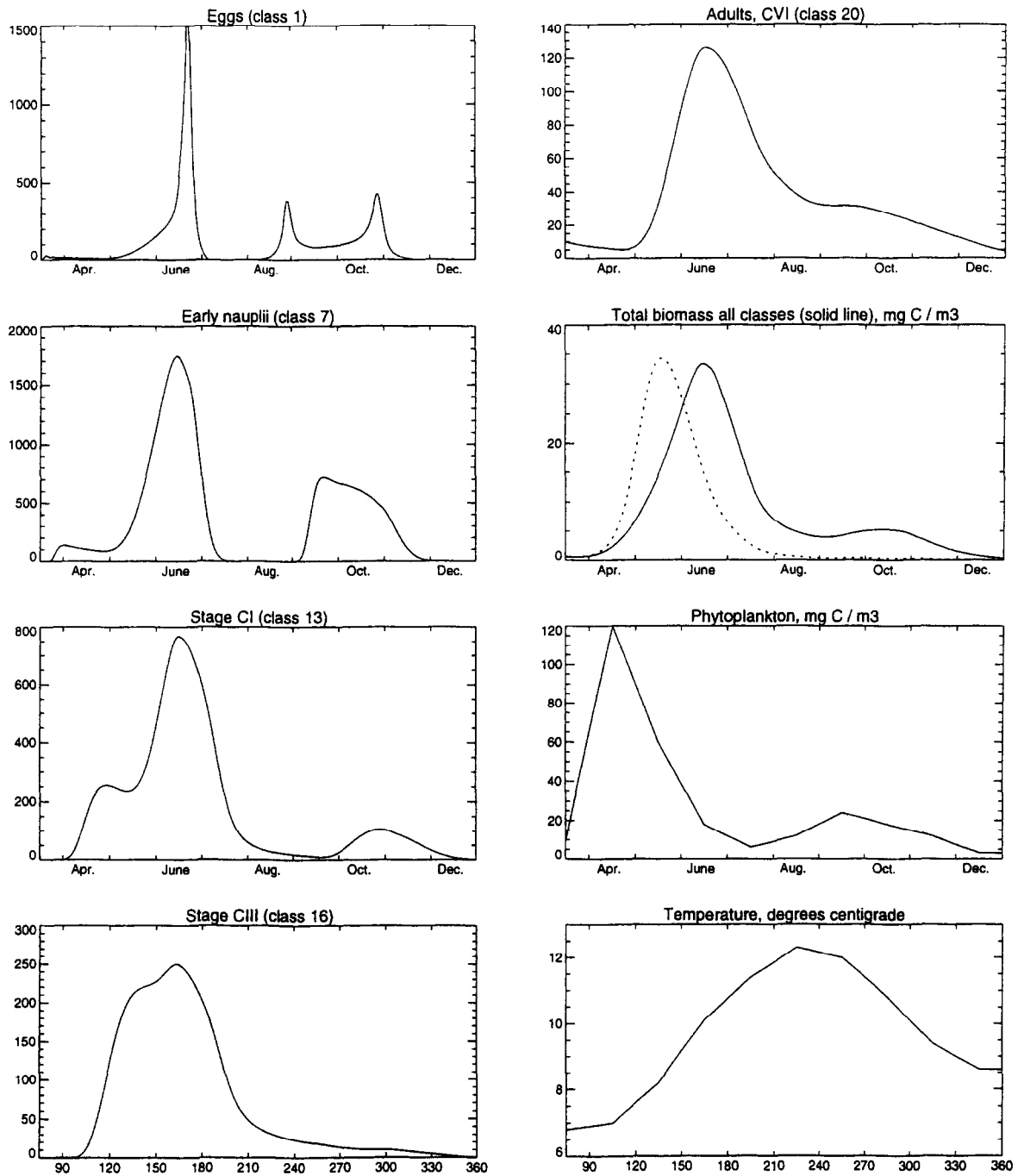


Fig. 5. Stage succession, total biomass and forcing data for the model run in isolation (box 12). Numerical abundances per m^3 are given for individual classes of the model, plotted against day of the year starting in mid-March (NB one month is taken to be 30 days). The dotted line on the plot of total biomass is that of the ERSEM unstructured omnivorous mesozooplankton model. See text for details.

generation time, the fate of the second generation, the delay between food and zooplankton dynamics, and the potential for an autumn response. With this parameterization (Table 1) the first generation reaches the adult class after 40 days. The modal first generation time is considerably greater (50–60 days), due to numerical dispersion which we have controlled to approximate individual variability in growth rate. The predator–prey delay in this particular model run is due largely to the first generation; the second generation can be seen merging with the first and is almost indistinguishable by the time the adult class is reached.

The sensitivity to the maximum uptake rate exponent b and the half-saturation c was investigated, with the proviso that the maximum uptake rate coefficient a was rescaled for each run to give reasonable numerical and total carbon densities. Varying the exponent b between 0.85 and 0.5 changes the generation time by ± 10 to 20 days and alters the balance between the first and second generation densities. A half saturation c as high as 50 mg C m^{-3} eliminates the autumn response whilst continuing to give plausible spring dynamics, with reduced success of the second generation relative to that in Fig. 5. As the food concentration is forced, the magnitude of these responses scales linearly with initial adult density.

The performance of the unstructured zooplankton model under the same forcing (total biomass shown as dotted line, Fig. 5) reveals two major differences to the structured model result. Firstly, the delay between maximum food and zooplankton concentrations is much shorter (one month rather than two) and is inconsistent with the data (Fig. 6; Thompson, 1982; Krause and Trahms, 1983; Fransz et al., 1991a). Secondly this rapid response is not sustained over the summer. Whilst it would be possible to adjust the search volume parameters to generate a response to the September/October food concentrations, the model does not give realistic summer (low food) densities with any reasonable parameterization; the response of the unstructured model is always too fast and short-lived because of the absence of any representation of development. The magnitude of the maximum zooplankton concentration in the spring varies with the mortality rate which is applied, but its timing does not vary substantially. These unstructured-model results are

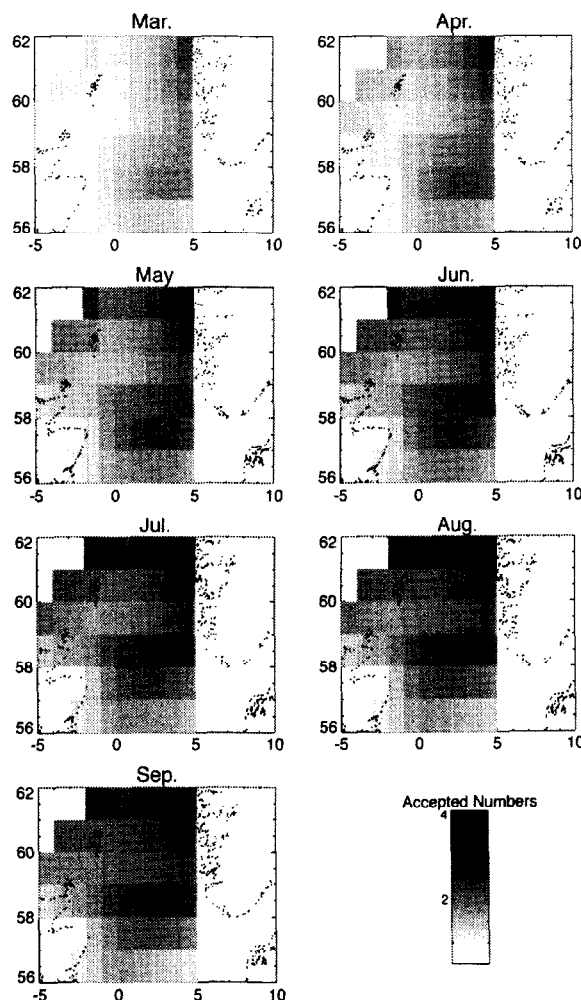


Fig. 6. *C. finmarchicus* copepodite V/VI space–time distribution: results for 1992 of the CPR data analysis interpolated for the $1^\circ \times 1^\circ$ grid.

robust to variation in the uptake, defecation and metabolic cost parameters over the ranges that are found in the literature: the overly-fast spring response and low summer concentration are robust features of modelling the system in terms of bulk-biomass.

4.2. Northern North Sea

The result of the analysis of CPR *C. finmarchicus* V/VI data is shown in Fig. 6. Although the results are plotted to only 5°E , beyond this there is simply a gradual decrease in abundance towards 10°E into the Skagerrak and towards the Danish west coast.

Similarly, the concentrations north of the maximum shown at 61.5°N 4.5°E decrease gradually to the northern extent of our CPR dataset, 64°N. The analysis shows the maximum densities to be in June and July, although the plots from April through to September are all very similar with concentrations over 1.5 ‘accepted numbers’ as far west as 1°W over virtually the full range of latitude of our area. The highest concentrations (4, ‘accepted numbers’) occur in the far northeast of our area, at 61.5°N 4.5°E, extending southwest over Viking and Bergen Banks. A second concentration (2.5, ‘accepted numbers’) occurs southeast of the Fladen Ground which is relatively restricted during April, extends northeastwards towards southern Norway during May to July, and ends as a diffuse band (58.5°N) running due east from the Fladen Ground in August and September.

The results of using the transport scheme to describe passive propagation of initial and boundary concentrations taken from the CPR results is shown in Fig. 7. The initial distribution disperses markedly in the first three months, whilst the increasing concentrations at the boundary can be seen entering the model area from May onwards. Significant inflow is evident only after April, despite the boundary concentrations increasing towards their prolonged maximum between March and April. The maximum densities at the eastern extreme of the northern boundary (3°E to 5°E) appear to have no influence, as would be expected in this net outflow region.

Fig. 8 shows the dynamics of the adult class of the *C. finmarchicus* model in spatially resolved form but without hydrodynamic transport. Although box 12 for example (see also Fig. 5) shows significant numbers of the first generation becoming adult in May, maximum densities are generally reached later, in June and July, notably off the southwestern Norwegian coast. There are features of the distribution which are far from accurate, in particular the lack of activity in the central region (0° to 5°E, 57°N to 59°N) and the overprediction off the Scottish and (not shown) English coasts. This overprediction, to several times the maximum observed densities, occurs in regions where there are consistent high summer densities of chlorophyll (4 to 6 months >40 mg C m⁻³ in the forcing data) and no high-temperature mortality (Fig. 3).

The overprediction in certain regions is less ex-

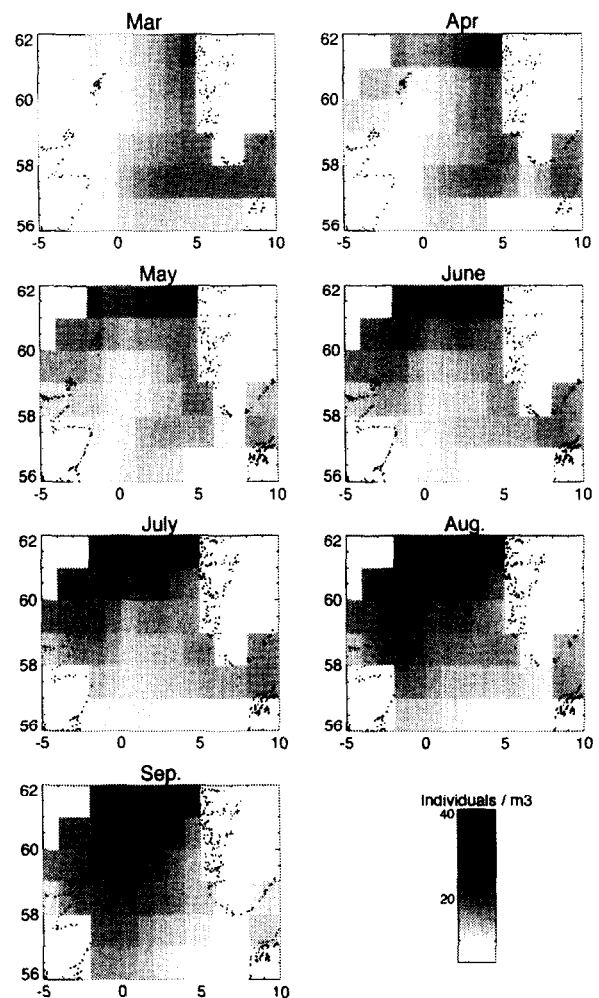


Fig. 7. Upper 30 m layer passive tracer propagation of the initial space-time distribution and north/northwest boundary time-series shown in Fig. 6, using 1992 of the hydrodynamic scheme. The greyscale is equivalent to that of Fig. 6, since ‘accepted numbers’ were multiplied by 10.0 to estimate density per m³ (see text). Initial conditions east of 5°E were set by extrapolation and the Skagerrak boundary (10°E) reflects concentrations immediately inside the model area.

treme in the model run with 1992 hydrodynamic transport (Fig. 9). Again, maximum densities are reached in June and July (except off the Scottish coast which is described separately, below), with a broadly similar distribution to the model run without transport. The major difference in distribution is the influence of the boundary conditions, which appears to be at its most significant in July and August. The overprediction off the Scottish coast is more

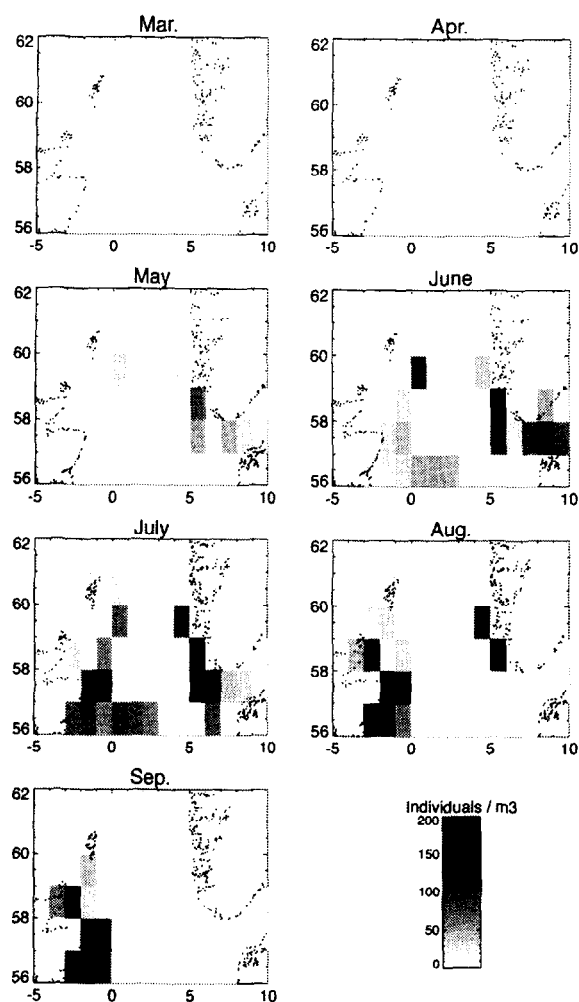


Fig. 8. Density of adults in the zooplankton model (upper 30 m) without hydrodynamic transport between boxes. Initial conditions (mid-March) were set from the CPR data analysis (Fig. 6). Boxes 26, 36, 29, 30, 41 and 42 overshoot the maximum value of the scale.

widespread in this model run with transport, due to (limited) dispersion to the east.

The total-population dynamics with and without hydrodynamic transport are shown for a few boxes in Fig. 10, to illustrate boundary influence and the effect of dispersion. Box 2, on the northern boundary, has an increased maximum density (July) with transport, due to inflow from the boundary region. Boxes 16 and 36 (and many more within the model area) have very much lower densities when the transport between boxes is active. Box 20 (immediately southwest of box 12, Fig. 5) peaks at the end of July, without transport. With transport this box shows an

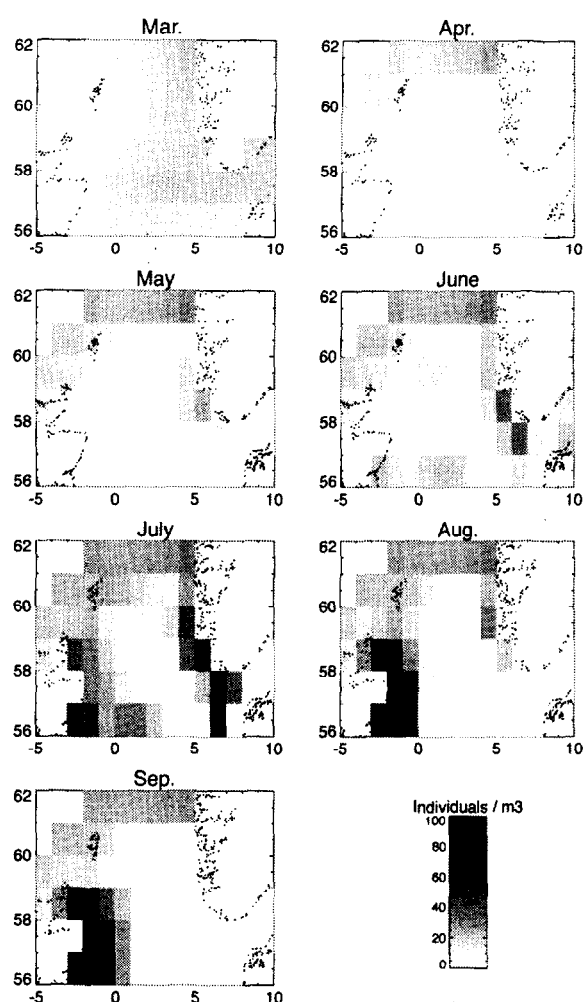


Fig. 9. Density of adults for the zooplankton model (upper 30 m) forced by 1992 hydrodynamic transport, with initial and north/northwestern boundary conditions from the CPR data analysis (Fig. 6). Note the more restricted scale relative to Fig. 8, and that boxes off the Scottish coast overshoot this scale.

autumn peak, due purely to dispersion of the erroneous overprediction off the Scottish coast. The sharp decline in August in boxes 16, 20 and 36 is due partly to high-temperature mortality.

5. Discussion

The testing of our structured model in isolation (box 12, overlapping with FLEX '76) indicates a reasonably accurate performance in the context of the consistency of available data. FLEX '76 was an early attempt at very detailed observation of plankton dy-

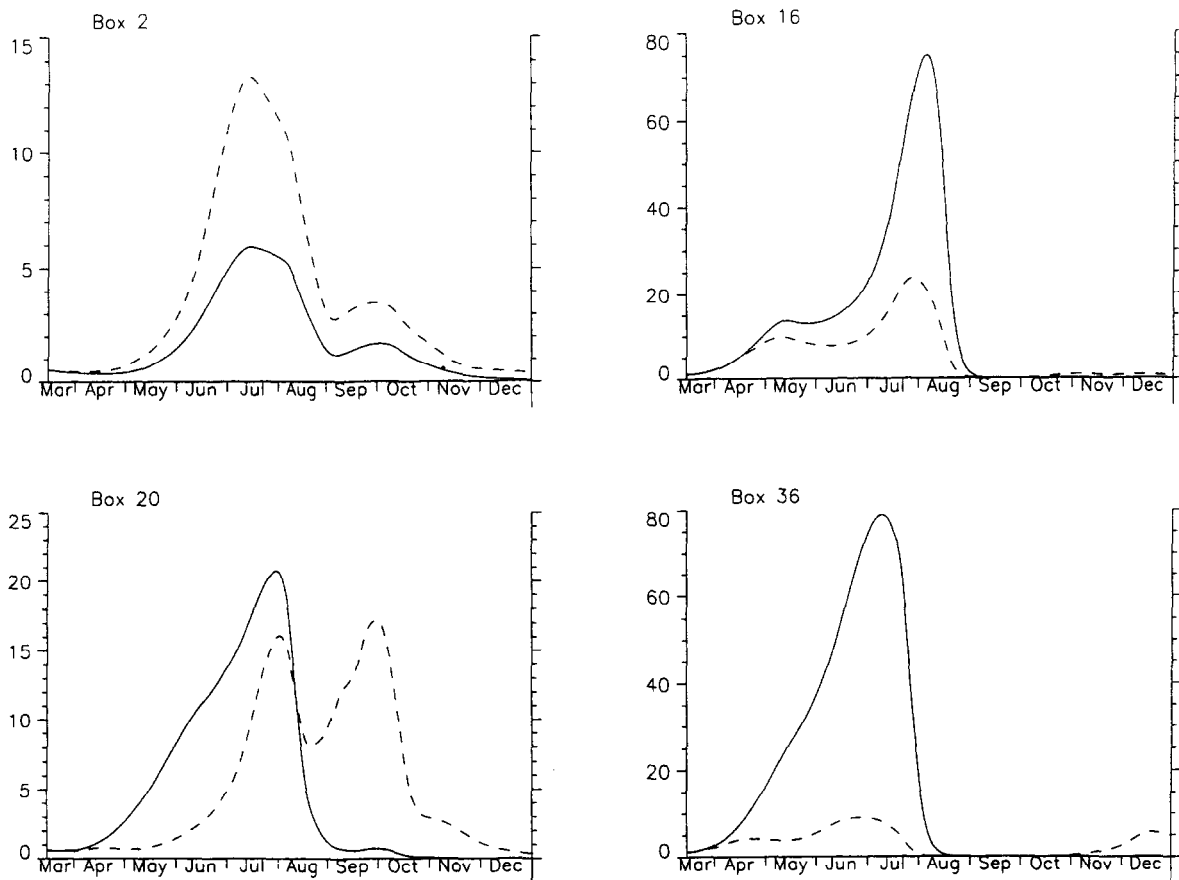


Fig. 10. Total zooplankton biomass (mg C m^{-3}) predicted by the model for different spatial boxes, without transport (solid line) and with 1992 transport (dashed line).

namics over the spring bloom period (end of March to mid-June; Krause and Trahms, 1983). That study covered almost the whole of the first generation of *C. finmarchicus*, estimating the time taken as 38 days not including the egg stage. Laboratory studies on *Calanus* sp. saturated with phytoplankton food at similar temperature indicate a generation time 2 to 3 weeks longer (Thompson, 1982). The spring generation times predicted by our model are intermediate between those observed during FLEX '76 and those observed in the laboratory. This is a feature of the structured model that is moderately sensitive to uptake and metabolic costs allometry, the parameters of which are imprecisely known. The unstructured model, in contrast, generates a relatively short delay between maximum food and zooplankton concentra-

tions (30 days), due to the lack of any representation of developmental stages.

Whilst FLEX '76 provided a detailed picture of succession between instars, it is clear that there was significant residual transport past the fixed central station (Fransz and Tijssen, 1983). The subsequent REFLEX '83 programme followed a drifting drogue from late April to late May over about 40 miles, northwards past the FLEX '76 central station. Thus the drift of the upper mixed layer was studied, with depth-resolved sampling of all life stages of *C. finmarchicus* (Fransz and Diel, 1985). In principle data such as these would be ideal for comparison against structured population models, but unfortunately cohort development from a peak of egg density around 6 May is unclear in the time-series. The study does

provide valuable data on development rates however, indicating that algal type rather than quantity as a significant determinant. An earlier *Calanus* patch-tracking study off the northeast coast of England (mid-March to early June 1954; Cushing and Tun-gate, 1963) does show coherent stage-succession but is restricted to the copepodite stages. Alternatives to drift-studies, for model–data comparisons which are essentially free of the complications of advection, are fjordic studies such as that of Aksnes and Magnesen (1983).

The temperature dependence of *C. finmarchicus* physiology and behaviour is likely to be an important determinant of seasonal dynamics. The Q_{10} response adopted here is commonly used, and has been measured precisely in the laboratory. The uncertainty lies in the response of this particular species to high temperature, relative to that of the congeneric *C. helgolandicus*. We need to know not only how physiological rates relate to temperature in these two species but also whether the stress of high temperature on *C. finmarchicus* results in increased mortality rates (cf. Tande, 1988 who observed mortality associated with a sharp temperature decrease in the laboratory). The crude assumption of linearly increasing mortality above a threshold temperature (12°C) has little effect on the dynamics on the Fladen Ground area, but has a major effect in other areas (e.g., Fig. 10).

Physiological stress due to temperature, or unfavourable competition with *C. helgolandicus*, may in fact be avoided by vertical descent through the summer (c.f. the observations of Williams, 1985 in the Celtic Sea). Whilst recent work (Backhaus et al., 1994; Anonymous, 1996) has provided mechanistic understanding of the invasion of the North Sea from deep overwintering areas, the cues for this (Miller et al., 1991) and the timing of descent in the summer/autumn remain unclear. Indeed, we do not yet know what proportion of the spring/summer stock in the northern North Sea is transported out to the overwintering grounds from which it originated. In late May of FLEX '76 Williams and Lindley (1980) observed a bimodal depth distribution of stages V/VI, with 50% of the adult biomass below 50 m. In mid-July of 1975 *C. finmarchicus* was shown to be generally deeper than 30 m at the Fladen Ground (water bottle samples, Krause and

Radach, 1989). Additionally, *C. finmarchicus* have been observed at deep overwintering depth in the southern Norwegian Sea in August [400–700 m observed by LHPR (Krause, 1978 cited in Krause and Radach, 1989); see also Østvedt (1955), observations to 2000 m using Nansen closing nets). These spatial-point observations at different times using different methods provide fragmentary evidence on the timing of descent from the surface waters. There are other data which enable the mapping of depth-distribution over large areas of the northern North Sea. Transects between 59°N and 62°N in late May 1994, for example, show the highest densities of *C. finmarchicus* to be concentrated in the upper 20 m layer, and to a lesser extent the 20–50 m layer, generally coinciding with the chlorophyll-maximum (Madden, 1997). The ZISCH project total zooplankton biomass data for a similar period in 1986 enable an approximate comparison between depth layers which shows, to the north of 56°N, higher densities to be more widespread in the upper 20 m than the 20–60 m layer (Krause and Martens, 1990 quasi-synoptic survey over a 6 week period, with *C. finmarchicus* qualitatively ranked as the dominant species over the northern North Sea).

The delay between food and zooplankton biomass maxima in our FLEX area simulation is 2 to 4 weeks greater than those of Henderson and Steele (1995) and Carlotti and Radach (1996). Whilst FLEX '76 showed the development of the first generation of *C. finmarchicus*, the time-series is of insufficient duration to determine population dynamics over the summer. Similarly, the northern North Sea data for 1961 to 1970 (held at the Marine Laboratory, Aberdeen) are too unevenly collected to characterise the total zooplankton seasonal response in a statistically robust way, due to very sparse sampling from May onwards relative to April. As such, the bimonthly means plotted by Adams (1987) over the whole year are potentially misleading. From the CPR it is clear that there are substantial densities of *C. finmarchicus* V/VI remaining near the surface in July and August (Fig. 6; see also Planque and Fromentin, 1996 fig. 3).

The approach of modelling the density of individuals in fixed weight classes is relatively simple (c.f. Carlotti and Radach, 1996; Miller and Tande, 1993), and it is this feature which allows easy adaptation to spatially resolved form. It is capable, however, of re-

producing the nature of the zooplankton population response observed during FLEX '76 in a way that would not be possible with a bulk biomass model (e.g. Broekhuizen et al., 1995). Although the classes of the model do not correspond directly to instars, comparison to stage-resolved data is possible by assuming a particular weight-at-stage relationship. The number of weight classes was chosen after sensitivity analysis, to control the numerical dispersion inherent in this type of model (Miller and Tande, 1993; see also VanSickle, 1977). Rather than suffering from unrealistic numerical dispersion (Miller and Tande, 1993) we contend that this type of model controls dispersion to a degree which is consistent with the variability in growth rate between individuals. Indeed, a useful increase in realism (compared to non-dispersive model structures in which all individuals are considered identical) may be gained by optimising the fit of model results to detailed individual-level observations of development rates, by tuning the number of classes in the model.

The passive tracer result appears to indicate, at first sight, the potential for northern inflow to drive *C. finmarchicus* spring dynamics. The lack of significant inflow between 0° and 2°E is in sharp contrast to observations of the development of the first generation of *C. finmarchicus* during early April 1992 (Fig. 11). This cannot be interpreted as evidence against inflow driving the spring population dynamics of 1992, however, for a number of reasons. Firstly, the CPR analysis involves a degree of smoothing over years, such that the features of our particular year may not be well represented; this depends on the interannual persistence of those features, something which is only now beginning to emerge as more years of detailed cruise data are collected. The relatively patchy and coarse sampling of the CPR may also dictate against such fine patterns appearing in our forcing data. Further, it is unclear whether a transport scheme resolved to $1^\circ \times 1^\circ$ boxes is sufficiently accurate to reproduce inflow dynamics at this scale; in due course a test of this should be possible by comparison of these results against those of our current work on Lagrangian particle tracking through hydrodynamic model flowfields. Finally there is the possibility that the mid-March initial concentrations may, in reality, be due to inflow before the start-point of the simulation.

The seasonal influence of the boundary conditions on the scale of the northern North Sea generally should be indicated with some reliability by such passive tracer experimentation. The one result shown here (Fig. 7) indicates concentrations advancing continuously inward (from the northwest) through the summer, which represents the propagation according to our hydrodynamic scheme in the absence of population dynamics. Properly assessing this seasonal influence would require time series of inflow rates across different boundary regions (which we have, from our hydrodynamic scheme). It would also require the accurate characterisation of *C. finmarchicus* densities at the boundary. It is the seasonal accuracy of this CPR-derived cycle which we now discuss.

Variation in sampling efficiency of the CPR has been recognised for some time (Robertson, 1968; Hays, 1994), but as yet there has been no *seasonal* comparison against directed, accurate plankton sampling. Fig. 6 shows a very broad dome-shaped response through the summer, the shape of which is almost certainly distorted by seasonal variation in sampling efficiency. This complicates the assessment of a model which predicts the timing and amplitude of that response. Our rescaling of CPR 'accepted numbers' from the statistical analysis, to obtain initial and boundary concentrations, was based on comparison against directed sampling during April 1992 (Fig. 11) and *a posteriori* examination of model results. The former indicated that the CPR-derived *Calanus* densities were considerably lower, by as much as a factor of 20, than those estimated from directed sampling.

The near-surface sampling of the CPR presents another significant limitation in the context of assessing seasonal patterns. A consideration of the depth distribution of *C. finmarchicus* during the early-April 1992 survey of the NW North Sea (in which the main concentrations were in the upper 15 m layer; Madden, 1996) indicates that the CPR gives a good measure of population density at that time of the year. The situation in late May 1994 was essentially similar, with *C. finmarchicus* concentrated in the surface waters and likely to be sampled effectively by the CPR (as discussed earlier; Madden, 1997). During the summer towards autumn however the CPR will inevitably undersample *C. finmarchicus* due to vertical descent. For the Celtic Sea, Williams (1985)

has shown that *C. finmarchicus* is largely restricted to colder water below the strong thermocline (ca. 8.5°C, cf. 16–18°C at the surface) during July and August. As discussed earlier, Krause and Radach (1989) report *C. finmarchicus* to be predominantly below 30 m during July at the Fladen Ground. Detailed data on this descent over the northern North Sea more generally (perhaps from further analysis of the ZISCH May–June survey, Krause and Martens, 1990) would be very valuable to elucidate this lesser-known part of the species' phenology, and to quantify the sampling efficacy of the CPR.

The results of the structured model in spatially resolved form fail to reproduce some of the major features of the *C. finmarchicus* distribution in the northern North Sea. A prerequisite of improving these results is a more sophisticated treatment of the phytoplankton data. As forcing we used data which were available, that is, interpolated monthly arithmetic means. Re-analysis which takes into account the highly skewed distributions, and addresses the problem of gaps in the dataset in a more robust way, would result in improved forcing for the model. It would also provide a more ideal comparison for the results of a nutrient–phytoplankton (–zooplankton) model which could replace the time-series forcing used here.

Our attempts to start model runs several months before spring phytoplankton bloom were frustrated by lack of knowledge of the biology during that phase. Simulation from mid-March onwards is an essentially similar approach to that of Carlotti and Radach (1996), who held densities constant over the early months, and to that of Henderson and Steele (1995). This period of emergence from overwintering is one of the subjects of our current work: field surveys of overwintering and spring-emergence densities that are closely coupled with Lagrangian particle tracking through hydrodynamic model flow-fields. These field data enable parameterization of the timing and speed of ascent from deep overwintering, thus yielding testable predictions and general understanding of spring near-surface distributions.

Our conclusion is that it is not yet possible to explain the spatial dimension of seasonal dynamics in terms of the present zooplankton model. Further development at the substrate level of the model is principally what is required to be able to approach

the target dataset. That dataset itself requires more thorough evaluation, in particular of its seasonal accuracy. Further, a more detailed understanding is needed of *C. finmarchicus* physiology and mortality rates in the early months of the year to be able to determine the sensitivity of in situ dynamics to the flow into the North Sea.

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