Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*

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Appendix 1. Model specification

State variables

Our model is an adaptation of that described by Speirs et al. (2005), itself based on the methodology of Gurney et al. (2001). It describes a domain from 30 to 80° N and 80° W to 90° E, divided into cells measuring 0.25° N by 0.5° E, each identified by a vector address $\mathbf{x} \equiv \{N, E\}$, where N and E respectively represent the latitude and longitude of the cell centre.

At each cell location, the population is divided into 3 groups. Surface developers consist of all the developmental stages from egg to the end of C5, and inhabit the surface water at a nominal fixed depth (z_S). Diapausers are individuals in the C5 stage that are overwintering in deep water at a depth that depends on location ($z_{D,\mathbf{x}}$). Adults (C6s) are individuals in the surface layer that have completed their development and can reproduce. For the individuals apart from the adults we define a developmental index, q, which takes a value of zero for eggs and unity at the end of C5. We can then divide the surface developers into a series of n classes of equal width Δq, and the overwintering individuals into m classes of width δq. Although the egg to adult time depends on the environment (temperature and food) the relative durations of the inter-moult periods remain essentially constant. We therefore have one-to-one correspondence between the constant-width classes of the model and the observable physiological stages, as shown in Table A1. The model cells vary in area, so rather than use densities we define our state variables in terms of the total population in each cell, making the conversion to densities only during output. Thus:

$$C_{i,\mathbf{x},t} \equiv \text{No. of class } i \text{ developers in surface cell } \mathbf{x} \text{ at time } t \quad \text{(A1)}$$

$$D_{j,\mathbf{x},t} \equiv \text{No. of class } j \text{ diapausers in deep cell } \mathbf{x} \text{ at time } t \quad \text{(A2)}$$

$$A_{\mathbf{x},t} \equiv \text{No. of adults in surface cell } \mathbf{x} \text{ at time } t \quad \text{(A3)}$$

Transport updates

The physical transport of individuals from one cell to another is simulated by redistributing the contents of each cell to a set of destination cells at a set of times separated by the transport update interval Δt. Using superscript – and + to denote the system state infinitesimally before and after the update, we can write:

$$C_{i,\mathbf{x},t}^{+} = \sum_{\text{all } \mathbf{y}} \Psi_{\mathbf{x},\mathbf{y},t}^{S} \, C_{i,\mathbf{y},t}^{-} \quad \text{(A4)}$$

$$D_{j,\mathbf{x},t}^{+} = \sum_{\text{all } \mathbf{y}} \Psi_{\mathbf{x},\mathbf{y},t}^{D} \, D_{j,\mathbf{y},t}^{-} \quad \text{(A5)}$$

$$A_{\mathbf{x},t}^{+} = \sum_{\text{all } \mathbf{y}} \Psi_{\mathbf{x},\mathbf{y},t}^{S} \, A_{\mathbf{y},t}^{-} \quad \text{(A6)}$$

The transfer distributions $\Psi_{\mathbf{x},\mathbf{y},t}^{S}$ and $\Psi_{\mathbf{x},\mathbf{y},t}^{D}$ represent the proportion of individuals in the surface and deep layers of cell $\mathbf{y}$ at $t - \Delta t$ that are transported to the same layer of cell $\mathbf{x}$ by time t. Thus, using $L \in [S,D]$ to denote the layer we define:

$$\Psi_{\mathbf{x},\mathbf{y},t}^{L} \equiv \Pr\{\text{particle at } \mathbf{y} \text{ at time } t - \Delta t \text{ is at } \mathbf{x} \text{ at time } t\} \quad \text{(A7)}$$

Table A1. Stage-dependent model parameters. The upper section shows the values for surface developers. The first row defines the mapping between the stages E to C5 and 57 development classes (implying that each class has width $\Delta q = 0.01754$) by giving the last class in each stage. The dry weights of each stage are given in the second row. The next 2 rows show the food-dependent mortality thresholds and stage-dependent background mortality rates. The lower section shows diapausing C5s mapped onto 31 classes of width $\delta q = 0.00910$ together with their background mortality rate

Stage	E	N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5
Surface												
last class	2	5	8	11	14	17	20	25	30	35	41	57
w_q^C (µg)	0.50	0.33	0.49	1.0	1.5	2.1	2.8	4.2	13	23	64	170
$F_{M,q}$ (mgC/m^3)	0	0	0	8	8	8	8	8	8	8	8	8
μ_q^E (d$^{-1} \times 100$)	18.2	33.6	33.6	14.9	2.6	2.6	2.6	1.5	0.0	2	2	15
Diapause												
last class	–	–	–	–	–	–	–	–	–	–	–	31
μ_q^D (d$^{-1} \times 100$)	–	–	–	–	–	–	–	–	–	–	–	0.5

We determine this quantity by releasing N_e particles at the centre of each cell and tracking their position from $t - \Delta t$ to t, assuming that the deterministic part of velocity is given by the OCCAM model (Webb et al. 1998) and the random components correspond to a diffusion process with coefficient Φ_S or Φ_D as appropriate. The velocities provided by OCCAM are time-dependent, and so we require to do this for a complete set of Δt intervals spanning the simulated year.

Biological updates

We update the state of the surface developer population of cell $\mathbf{x}$ at a set of times $\{u_\mathbf{x}^c\}$ related to each other by the requirement that:

$$\Delta q = \int_{u_{\mathbf{x},i-1}^C}^{u_{\mathbf{x},i}^C} g_{\overline{\mathbf{x}}}^C(\tau)\,d\tau \tag{A8}$$

where $g_\mathbf{x}^C(\tau)$ represents the development rate of surface developers in cell $\mathbf{x}$ at time τ. The update process requires that we add the survivors from the last developing class ($q = 1$) to the surviving adults and then move all other survivors one class to the right either within the surface population, or by transfer into the diapausing population. The now empty first developer class receives the eggs produced by the adults surviving from the last update. To describe diapause entry we define an ancillary function $\theta_{i,\mathbf{x},t}$ which returns the fraction of individuals who transfer to the first class of the overwintering stock. In the following equations we use $B_{\mathbf{x},t}$ to denote the per capita egg production from the previous update to the one taking place at time t in cell $\mathbf{x}$. If $\xi_{\mathbf{x},t}^A$ and $\xi_{i,\mathbf{x},t}^C$ denote the respective survival of adults and surface developers then, for compactness, we can write the surviving developers and adults as: $S_{i,\mathbf{x},t}^C \equiv \xi_{i,\mathbf{x},t}^C C_{i,\mathbf{x},t}^-$ and $S_{\mathbf{x},t}^A \equiv \xi_{\mathbf{x},t}^A A_{\mathbf{x},t}^-$. Thus we have:

$$C_{i,\mathbf{x},t}^+ = \begin{cases} B_{\mathbf{x},t}S_{\mathbf{x},t}^A & i = 1 \\ (1-\theta_{i-1,\mathbf{x},t})S_{i-1,\mathbf{x},t}^C & \text{otherwise} \end{cases} \tag{A9}$$

$$D_{0,\mathbf{x},t}^+ = D_{0,\mathbf{x},t}^+ + \sum_{i=1}^{n} \theta_{i,\mathbf{x},t}S_{i,\mathbf{x},t}^C \tag{A10}$$

$$A_{\mathbf{x},t}^+ = (1-\theta_{n,\mathbf{x},t})S_{n,\mathbf{x},t}^C + S_{\mathbf{x},t}^A \tag{A11}$$

The diapausing population of cell $\mathbf{x}$ is updated, in a similar way to the surface developers, at a set of times $(u_\mathbf{x}^D)$ related to each other by the requirement that:

$$\delta q = \int_{u_{\mathbf{x},i-1}^D}^{u_{\mathbf{x},i}^D} g_{\overline{\mathbf{x}}}^D(\tau)\,d\tau \tag{A12}$$

where $g_\mathbf{x}^D(\tau)$ represents the development rate of diapausing individuals in cell $\mathbf{x}$ at time τ. The update process requires that we move survivors from all development classes but the last, one class to the right. It is assumed that individuals that have completed their diapause only appear in the surface waters when the photoperiod is sufficiently large. The last class thus accumulates surviving individuals until emergence is cued, at which point they are transferred into the adult class. To describe this we define an ancillary function $\Omega_{\mathbf{x},t}$ which returns the fraction of individuals that have completed diapause which rise to the surface. If $P_{\mathbf{x},t}$ is the hours of daylight at location $\mathbf{x}$ and time t, and

$$\Omega_{\mathbf{x},t} = \begin{cases} 1 & P_{\mathbf{x},t} > P_e \text{ and } \frac{dP_{\mathbf{x},t}}{dt} > 0 \\ 0 & \text{otherwise} \end{cases} \tag{A13}$$

Let $\xi_{j,\mathbf{x},t}$ be the survival of individuals in class j at location $\mathbf{x}$ from the last update to the one at time t, so that $S_{j,\mathbf{x},t}^D \equiv \xi_{j,\mathbf{x},t}^D D_{j,\mathbf{x},t}^-$ is the number of surviving diapausers just before the update.

Thus the diapausers are updated according to:

$$D_{j,\mathbf{x},t}^+ = \begin{cases} 0 & j = 1 \\ (1-\Omega_{\mathbf{x},t})(S_{m-1,\mathbf{x},t}^D + S_{m,\mathbf{x},t}^D) & j = m \\ S_{j,\mathbf{x},t}^D & \text{otherwise} \end{cases} \tag{A14}$$

and at the same times:

$$A_{0,\mathbf{x},t}^+ = A_{0,\mathbf{x},t}^- + \Omega_{\mathbf{x},t}D_{m,\mathbf{x},t}^+ \tag{A15}$$

Update strategy

We only expect to output state variables from the model immediately after transport updates. Our strategy for updating the biological system between transport updates is thus to scan through all the cells, updating each one until the next unprocessed operation would occur beyond the next transport update. Once all the cells are thus processed, the transport update is performed and state variables output before the process begins again. The process for updating a single cell is as follows:
(1) Collect all unprocessed updates from the adult, surface developer and diapause sequences for this cell: $\{u_\mathbf{x}^A\}$, $\{u_\mathbf{x}^S\}$.
(2) Select the subset of each sequence which falls before the next transport update;
(3) Form these into a single ordered sequence and process them in order of occurrence.

Development rates

The development rates in the surface and deep layers of cell $\mathbf{x}$ at time t are given by:

$$g_\mathbf{x}^C(t) = G_C\left(1 + \frac{T_\mathbf{x}^S(t)}{T_G}\right)^P\left(1 - \exp\left[-\frac{F_\mathbf{x}(t)}{F_G}\right]\right) \tag{A16}$$

and

$$g_\mathbf{x}^D(t) = G_D \exp\left[-\frac{T_\mathbf{x}^D(t)}{T_G^D}\right] \tag{A17}$$

where $T_\mathbf{x}^S(t)$ and $T_\mathbf{x}^D(t)$ respectively represent the *in situ* temperature in that layer of the cell at time t and $F_\mathbf{x}(t)$ represents the surface layer food concentration at the same time.

Diapause entry

We assume that at each development update a fixed fraction θ_D of all individuals with development index in the range $q_D \rightarrow q_U$ will enter diapause:

$$\theta_{q,\mathbf{x},t} = \begin{cases} \theta_D & q_D \leq q \leq q_U \\ 0 & \text{otherwise} \end{cases} \tag{A18}$$

Survival

Using u_n to denote the nth update time in $(u_\mathbf{x}^K)$, with $K \in [A, C, D]$ to denote the target population, we write:

$$\xi_{q,\mathbf{x},u_i}^K = \exp[-m_{q,\mathbf{x},u_i}^K(u_{i-1})] \tag{A19}$$

For diapausers, the total mortality rate is simply a constant background rate:

$$m_{i,\mathbf{x},t}^D = \mu^D \tag{A20}$$

For surface developers we assume that the total mortality consists of a background rate that is an increasing function of temperature, together with density-dependent and starvation terms. If $T_\mathbf{x}^S(t)$, $W_{\mathbf{x},t}$ and $F_{\mathbf{x},t}$ are respectively the surface temperature, *Calanus* biomass, and food at cell $\mathbf{x}$ and time t, we have:

$$m_{i,\mathbf{x},t}^C \;=\; \gamma(T_{\mathbf{x}}^S(t))\mu_i^C\,(1 + \phi W_{\mathbf{x},t}) + \mu_F \qquad (A21)$$

$$m_{\mathbf{x},t}^A \;=\; \gamma(T_{\mathbf{x}}^S(t))\mu^A(1 + \phi W_{\mathbf{x},t}) + \mu_F \qquad (A22)$$

where the temperature dependence is given by:

$$\gamma(T_{\mathbf{x}}^S(t)) \;=\; \gamma 0 + (1 - \gamma 0)(T/T_c)^z \qquad (A23)$$

The parameter $\gamma 0$ is the fraction of the mortality at some characteristic temperature T_c that is experienced at 0°C, and z determines the non-linearity, and hence how fast the mortality increases for temperatures above T_c.

The starvation mortality is zero above a stage dependent threshold, and varies linearly to a maximum (μ_F^{max}) below that threshold. The developer thresholds are given in Table A1 and the adult value in Table A2.

$$\mu_F(F_{\mathbf{x}}(t),F_M) \;=\; \begin{cases} 0 & \text{if } F_{\mathbf{x}}(t) > F_M \\ \mu_F^{max}\left[1 - \dfrac{F}{F_M}\right] & \text{otherwise} \end{cases} \qquad (A24)$$

The total biomass density in cell $\mathbf{x}$ is given by the sum over all developer classes of the number of individuals in each class multiplied by the dry weight of each individual plus a similar sum over the adult population, divided by the surface area of the cell ($\alpha_{\mathbf{x}}$).

$$W_{\mathbf{x},t} \;=\; \frac{1}{\alpha_{\mathbf{x}}}\left[\sum_{i-1}^n w_i^C C_{i,\mathbf{x},t} + w^A A_{\mathbf{x},t}\right] \qquad (A25)$$

Fecundity

Using u_n in the same way as the previous section, we can express the per capita egg production from over from the last update to the one occurring at time t as:

$$B_{\mathbf{x},t} \;=\; \beta_{\mathbf{x},t}(u_n - u_{n-1}) \qquad (A26)$$

where $\beta_{\mathbf{x},t}$ is the per capita egg production rate. We model this rate as a saturating function of food, but where the asymptote is linearly dependent on temperature:

$$\beta_{\mathbf{x},t} \;=\; \frac{(\alpha_1 + \alpha_2 T)F_{\mathbf{x}}(t)}{(F_h + F_{\mathbf{x}}(t))} \qquad (A27)$$

which yields a good fit to the laboratory experiments of Hirche et al. (1997) with the parameter values given in Table A2.

Parameters

Table A2 lists the parameter values used. Where published sources for parameter values exist, these are given in the final column of the table. Some parameters, such as the transport update time interval Δt, are either arbitrary or only have a weak influence on the model results. These are described as 'chosen'. For the remaining unknown parameters we carried out an extensive series of model runs and picked values that were qualitatively judged to yield the most satisfactory results. These parameters are described as 'fitted'.

Table A2. Parameter values used in the model. Inc: increment; dev.: development; temp: temperature; mort: mortality; spec: specific; wt: weight; max: maximum; min: minimum; coef: coefficient

Parameter	Symbol	Value	Units	Source
Physical environment				
Ensemble size	N_E	100	–	This study chosen
Surface layer depth	z_S	20	m	This study chosen
Deep layer depth	$z_{D,\mathbf{x}}$	100–1500	m	Heath et al. (2004)
Surface diffusion	Φ_S	100	$m^2\,s^{-1}$	Gurney et al. (2001)
Deep diffusion	Φ_D	50	$m^2\,s^{-1}$	This study chosen
Transport update inc.	Δt	7	d	Gurney et al. (2001)
Surface developers				
Dev. increment	Δ_q	0.01754	–	Campbell et al. (2001)
Dev. rate scale	G_C	6.75×10^{-3}	d^{-1}	Campbell et al. (2001)
Dev. rate power	P	2.05	–	Campbell et al. (2001)
Characteristic food	F_G	29.2	$mg\,C\,m^{-3}$	Campbell et al. (2001)
Dev. rate temp.	T_G	10.6	deg	Campbell et al. (2001)
Nominal mortality	μ_q^E	Table 1	d^{-1}	Eiane et al. (2002)
Background/nominal mortality	v	0.2	–	This study fitted
Stage spec. Dry wt	w_q^C	Table 1	µg	Lynch et al. (2001)
Starvation threshold	$F_{M,q}$	Table 1	$mg\,C\,m^{-3}$	This study fitted
Adults				
Max. fecundity at 0°C	α_1	12.86	d^{-1}	Hirche et al. (1997)
Fecundity temp. coeff.	α_1	3.218	$d^{-1}\,deg^{-2}$	Hirche et al. (1997)
Fecundity half saturation food	F_h	82.02	$mg\,C\,m^{-3}$	Hirche et al. (1997)
Adult dry weight	w^A	276	µg	Lynch et al. (2001)
Adult mortality	μ_y^A	0.01	d^{-1}	This study fitted
Starvation threshold	F_M^A	8	$mg\,C\,m^{-3}$	This study fitted
Starvation and density dependent mortality				
Max. starvation mortality	μ_F^{max}	1	d^{-1}	This study fitted
Density dependence	ϕ	3×10^{-6}	$d^{-1}m^3\,µg^{-1}$	This study fitted
Fraction background mortality at 0°C	γ_0	0.65	–	This study fitted
Characteristic temp.	T_C	8	°C	This study fitted
Temp. power coeff.	z	7	–	This study fitted
Diapausers				
Diapause entry fraction	θ_D	0.7	–	This study fitted
Min. q at diapause entry	q_D	$55\Delta q$	–	This study chosen
Max. q at diapause entry	q_D	$56\Delta q$	–	This study chosen
Diapause exit photoperiod	P_E	12	h	This study chosen
Mortality rate	μ_D	0.05	d^{-1}	This study fitted