frontiers

Supplementary Material

Quantifying the roles of food intake and stored lipid for growth and development throughout the life cycle of a high-latitude copepod, and consequences for ocean carbon sequestration
(Frontiers in Marine Science)

Thomas R. Anderson, Dag O. Hessen, Wendy C. Gentleman, Andrew Yool and Daniel J. Mayor

1 Supplementary Appendix 1. Model equations

A description of the model assumptions and parameterisation is provided in the main text. Here, we provide the model equations. There are four state variables: structural biomass, Z_S, storage lipid, Z_L, gonad biomass, Z_G, and egg biomass, Z_E (all with units μmol C per individual). Z_G and Z_E are for accounting purposes only, i.e., they store cumulative production of gonad and eggs, without loss terms. Structural biomass is assumed to have a fixed C:N ratio, θ_{ZS}, while lipid contains only C. Each of the different model Phases has its own rules for how Z_S and Z_L are produced and subsequently used for maintenance, growth, gonad development and egg production (Figure 2, main text). Equations are therefore presented for each Phase in turn, for these two state variables. A table of model parameters is provided in the main text (Table 1). A listing of model variables is presented at the end of this appendix (Table S1.1).

Phase 1: Egg development and early naupliar stages

The model simulation starts with the spawning of an egg on a specified day of year, D_{start}. Phase 1 follows the development of this egg through to the end of stage NII, noting that no feeding occurs during this period. For simplicity in terms of model functionality and evaluation, we assume that egg biomass is structure only, with a C:N θ_{egg} = 5.8. As such, this Phase (only) does not conform to parameter θ_{ZS} which is the fixed C:N in structural biomass (4.9) that applies from Phase 2 onwards in the simulation.

The start and end points for Phase 1 are Z_{egg} = 0.025 μmol C and Z_1 = 0.021 μmol C. If the duration of Phase 1 at reference temperature (T_{ref} = 10°C) is 7 d (parameter ($L_{1,Tref}$), then the rate of attenuation of biomass (N), k_1, is:

$$k_1 = \frac{-\ln(Z_1/Z_{egg})}{L_{1,Tref}} \quad \text{(S1.1)}$$

The resulting value of k_1 with these settings is 0.025 d^{-1}. Temperature dependence is calculated according to a Q_{10} relationship:

$$k_{1(T)} = Q_D^{\frac{T-T_{ref}}{10}} \quad \text{(S1.2)}$$

where $Q_D = 2$ is the Q_{10} of development rate during Phase 1. The differential equation for the rate of change of Z_S during Phase 1 is:

$$\frac{dZ_S}{dt} = k_{1(T)}Z_S - \Phi_{12}(Z_S, t) \quad \text{(S1.3)}$$

The only loss term is the transfer of the individual from Phase 1 to Phase 2, Φ_{12}, which occurs as an instantaneous loss (single model timestep) when Z_S reaches Z_1.

Phase 2: Feeding without lipid storage

This Phase represents naupliar stages 3-6 plus copepodite stages 1-2 in *Calanus finmarchicus*. The animal is now feeding, producing structural biomass as growth, but is not yet laying down lipid reserves. The differential equation for Z_S is:

$$\frac{dZ_S}{dt} = G_S(\Gamma_T, F_t, \tau_T, \xi_T, \eta)Z_S - m(\psi, Z_S, Z_{Smax}) - \Phi_{23}(Z_S, Z_2) \quad \text{(S1.4)}$$

where the terms are structural growth, mortality and transfer to Phase 3. The first of these, structural growth, depends on the functional response as influenced by temperature, Γ_T, the available food at time t, F_t, and metabolic losses, namely biomass turnover, other basal metabolism and specific dynamic action (SDA), parameters τ_T, ξ_T and η, respectively.

The seasonal cycle of prey fields – diatoms (P_d; mmol C m^{-3}), non-diatoms (P_n), microzooplankton (Z_{mi}) and detritus (D_C) – are taken as mixed layer averages from the MEDUSA ecosystem model (Yool et al., 2013), as a "climatology" based on simulations for the years 2000-2009. Feeding is calculated using a multiple-prey Sigmoidal (Holling III) multiple prey functional response (Gentleman et al., 2003; Anderson et al., 2010). For example, feeding on diatoms (I_{Pd}, μmol C ind^{-1} d^{-1}) is calculated as follows:

$$I_{Pd} = \frac{g_T \omega_{Pd} P_d^2 Z_S}{k_g^2 + \omega_{Pd} P_d^2 + \omega_{Pn} P_n^2 + \omega_{Zmi} Z_{mi}^2 + \omega_D D_C^2} \quad \text{(S1.5)}$$

where g_T is the temperature-dependent (Q_{10} parameter Q_g) maximum feeding rate (d^{-1}) applied to all food types, k_g is the half saturation constant for this measure of total food (mmol C m^{-3}) and ω_X are the prey preference parameters (preferences are given by ω_X multiplied by prey density). The corresponding N intake for the different prey items are calculated by dividing by the fixed C:N ratios in phytoplankton (diatoms and non-diatoms; $\theta_P = 6.625$) and microzooplankton ($\theta_{Zmi} = 5.5$) and the variable ratio in detritus (D_N and D_C are separate inputs within the off-line MEDUSA forcing). Organisms process food in terms of biomolecules. Metabolic stoichiometry operates by dividing organic C into protein and non-protein based on a fixed C:N ratio of the former, θ_V. Total intakes of protein and non-protein C, I_V and I_H (μmol C ind^{-1} d^{-1}) are then:

$$I_V = \frac{\theta_V}{\theta_f} I_{TC} \quad \text{(S1.6)}$$

$$I_H = \frac{\theta_f - \theta_V}{\theta_f} I_{TC} \quad \text{(S1.7)}$$

where I_{TC} is total intake of C and θ_f is food C:N ratio. A fixed fraction of intake, ϕ, is lost as "messy feeding". The remainder is ingested by the copepod and is subjected to absorption efficiencies for protein and non-protein C, β_V and β_H. Absorbed substrates are used for metabolism and growth using metabolic stoichiometry, as described in the main text. The reader is referred to Anderson et al. (2020, 2021) where a full description and equations of metabolic stoichiometry can be found (see also Appendix 2).

Starvation occurs if there is insufficient food to meet the metabolic costs of biomass turnover, other basal metabolism and specific dynamic action (SDA). In that case, structural biomass is used as a source of substrate to meet the shortfall resulting in decreasing body weight. Death is assumed to occur when structural biomass, Z_S, decreases below a specified carcass fraction, $\psi = 0.3$, of the previously highest achieved Z_S, Z_{Smax}. Thus, for example, if an animal reaches a structural biomass $Z_S = 2.0$ μmol C, it will subsequently die of starvation if its biomass subsequently decreases to 0.6 μmol C.: function $m(\psi, Z_S, Z_{Smax})$ in Eq. S4; as with transfer between Phases, this process occurs instantaneously on a single model timestep). Finally, Φ_{23}, represents transfer from Phase 2 to Phase 3, which takes place when the copepod reaches its maximum Phase 2 biomass, $Z_2 = 0.7$ μmol C.

Phase 3: Feeding with lipid storage

Phase 3 represents copepodite stages CIII to CV. Progression within this Phase is the same as in Phase 2 with one major exception: the animal now lays down lipid reserves. The differential equation for the rate of change of structure, Z_S, is:

$$\frac{dZ_S}{dt} = G_S(\Gamma_T, F_t, \tau_T, \xi_T, \eta, \omega)Z_S - m(\psi, Z_S, Z_{Smax}) - \Phi_{34}(Z_S, Z_{3max}) \quad \text{(S1.8)}$$

The non-protein fraction of C intake is subdivided into lipid and carbohydrate (fraction $\omega = 0.5$ to lipid) in Phase 3. This lipid is prioritised for the accumulation of lipid storage (Z_S) throughout Phase 3 whereas, once maintenance costs have been met, protein and carbohydrate are prioritised for structural growth until the maximum structural biomass for Phase 3 (Z_{3S}) is reached. The usual sequence of events during Phase 3 is then as follows. Assuming that food is adequate (sufficient to meet the costs of maintenance plus extra for growth), the copepod initially grows fast, laying down structural biomass at a rate faster than lipid reserves because lipid is only a relatively minor fraction of overall food C. This continues until $Z_{3S} = 6.5$ μmol C is reached. Thereafter, protein and carbohydrate contribute to the lipid reserve, less the costs of maintenance. Lipid is synthesised with an efficiency $\gamma_L = 0.75$, with the remainder lost as respiration. Mortality is calculated as for Phase 2 (second term in Eq. S8). Transfer to Phase 4 occurs when the individual copepod reaches its maximum size in terms of both structure and storage, Z_{3max} (μmol N), which is calculated as:

$$Z_{3max} = \frac{\theta_{Z3} Z_{3S}}{\theta_{ZS}} \quad \text{(S1.9)}$$

where θ_{Z3} is the C:N ratio of a CV individual at maturity, i.e., when at maximum size for both structure and lipid. The maximum lipid biomass, Z_{3L}, is then calculated by difference:

$$Z_{3L} = Z_{3max} - Z_{3S} \quad \text{(S1.10)}$$

The differential equation for lipid, Z_L, mirrors that for structure:

$$\frac{dZ_L}{dt} = G_L(\Gamma_T, F_t, \tau_T, \xi_T, \eta, \omega)Z_L - m(\psi, Z_S, Z_{Smax}) - \Phi_{34}(Z_S, Z_{3max}) \quad \text{(S1.11)}$$

where G_L is the growth in the storage lipid pool (μmol C ind^{-1} d^{-1}).

Phases 4 and 5: Diapause and gonad development

The diapausing model animal no longer has access to food and exhibits reduced metabolic rate, both intrinsically and because of the lower temperature in deep waters. Diapause lasts until a specified day of year in the second year, D_{exit}, with gonad maturation taking place for a specified period prior to emergence in surface waters, L_{gonad} (d). Differential equations for Z_S and Z_L are:

$$\frac{dZ_S}{dt} = -M_S(\tau_{dia,T}, \xi_{dia,T}, Z_S, Z_L)Z_S - \Omega_S(\tau_{gonad,T}, \xi_{gonad,T}, Z_S, Z_L) - m(\psi, Z_S, Z_{Smax}) - \Phi_{45}(Z_S, D_{exit}) \quad \text{(S1.12)}$$

M_S represents metabolic losses, namely biomass turnover and other basal metabolism. These are temperature dependent (same Q_{10} relationship for surface waters), with values at temperature T_{ref} = 10°C of $\tau_{dia,Tref}$ = 0.0003 d^{-1} and $\xi_{dia,Tref}$ = 0.0016 d^{-1}. Without food, the animal uses lipid reserves for energy and structural biomass as a source of protein for biomass turnover. Z_S therefore decreases with time. As with previous Phases, if structural biomass declines below the carcass weight, the animal is assumed to die (the third term in Eq. S1.12). Exit from diapause occurs on day D_{exit} (fourth term in Eq. S1.12).

Gonad development represents the replacement of “ordinary” structural biomass with gonad tissue. For accounting purposes, it is represented as a state variable, Z_G, in the model code:

$$\frac{dZ_G}{dt} = \Omega_S(\tau_{gonad,T}, \xi_{gonad,T}, Z_S, Z_L) \quad \text{(S1.13)}$$

This replacement process is akin to biomass turnover and is modelled as such, using parameters $\tau_{gonad,Tref}$ = 0.11 d^{-1} and $\xi_{gonad,Tref}$ = 0.055 d^{-1}. It is fueled by structural biomass (for protein) and lipid (for energy). Although new gonad tissue is produced, the net overall is a decrease in Z_S (and Z_L) because of efficiency losses.

The equation for the rate of change of lipid again mirrors that of structure:

$$\frac{dZ_L}{dt} = -M_L(\tau_{dia,T}, \xi_{dia,T}, Z_S, Z_L)Z_L - \Omega_S(\tau_{gonad,T}, \xi_{gonad,T}, Z_S, Z_L) - m(\psi, Z_S, Z_{Smax}) - \Phi_{45}(Z_S, D_{exit}) \quad \text{(S1.14)}$$

Phase 6: Reproduction

Reproduction is calculated as income egg production (G_E; fueled by food intake and lipid reserves):

$$G_E = E(\Gamma_T, F_t, \tau_T, \xi_T, \eta, \omega, Z_L) \quad \text{(S1.15)}$$

$$\frac{dZ_E}{dt} = G_E \quad \text{(S1.16)}$$

Allocation of substrates to egg production only occurs after maintenance requirements have been met, calculated using metabolic stoichiometry.

There is no further allocation to structural or lipid growth, in which case Z_S and Z_L can only remain unchanged or decline when either is used to for maintenance or reproduction:

$$\frac{dZ_S}{dt} = -M_S(\tau_T, \xi_T, Z_S, Z_L)Z_S - m(\psi, Z_S, Z_{Smax}) \quad \text{(S1.18)}$$

$$\frac{dZ_L}{dt} = -M_L(\tau_T, \xi_T, Z_S, Z_L)Z_L - m(\psi, Z_S, Z_{Smax}) \quad \text{(S1.19)}$$

The animal keeps on reproducing until it dies, at which point the model simulation ends.

Table S1.1. Model variables

variable	description	units
Z_S	structural biomass	μmol C ind^{-1}
Z_L	storage lipid biomass	μmol C ind^{-1}
Z_G	gonad biomass	μmol C ind^{-1}
Z_E	biomass of eggs produced	μmol C ind^{-1}
Z_{Smax}	maximum achieved structural biomass	μmol C ind^{-1}
Z_{3max}	maximum biomass Phase 3 (Z_S + Z_L)	μmol C ind^{-1}
Z_{3L}	maximum lipid biomass Phase 3	μmol C ind^{-1}
k_1	rate of attenuation of biomass in Phase 1	d^{-1}
G_S	growth: structural biomass	μmol C ind^{-1} d^{-1}
G_L	growth: storage lipid biomass	μmol C ind^{-1} d^{-1}
G_E	egg production: income	μmol C ind^{-1} d^{-1}
Γ	functional response	d^{-1}
P_d	food: diatoms	mmol C m^{-3}
P_n	food: non-diatoms	mmol C m^{-3}
Z_{mi}	food: microzooplankton	mmol C m^{-3}
D_C	food: detritus C	mmol C m^{-3}
I_X	intake of specific food types	μmol C ind^{-1} d^{-1}
I_{TC}	total C intake	μmol C ind^{-1} d^{-1}
I_V	intake protein	μmol C ind^{-1} d^{-1}
I_H	intake carbohydrate	μmol C ind^{-1} d^{-1}
M_S	Z_S losses due to metabolism	μmol C ind^{-1} d^{-1}
M_L	Z_L losses due to metabolism	μmol C ind^{-1} d^{-1}
Ω	gonad development	μmol C ind^{-1} d^{-1}
D_{start}	start day of year: spawning of egg	d
D_{exit}	day of year of exit from diapause (year 2)	d
m	mortality due to starvation	(instantaneous)
Φ_{ij}	transfer from Phase i to Phase j	(instantaneous)

2 Supplementary Appendix 2. Substrate use for maintenance and production

Maintenance and production (structural growth and eggs) are calculated based on Geometric Stoichiometry (GS; Anderson et al., 2020) which uses protein- and non-protein-C (nominally, carbohydrate) as currencies, and where the former has a fixed C:N ratio, θ_V. A fundamental assumption is that carbohydrate is prioritised over protein for the energetic costs of maintenance and production, namely other basal metabolism (parameter ξ) and SDA (parameter η), thereby sparing protein to meet the N requirements of biomass turnover (parameter τ) and production. The situation becomes more complex when storage lipid is introduced as an additional source of energy or C. We developed our model to include storage lipid, which fulfils the same role of carbohydrate obtained from food and thus comes into play when this is in short supply.

Given the need to prioritise substrate use, it is simplest to use a sequential approach to calculate maintenance and growth in turn. Ingested food is fist subject to absorption efficiencies β_V and β_H for protein and carbohydrate, respectively, with associated loss to faecal pellets. The resulting quantities of absorbed protein and carbohydrate, A_V and A_H, related to intake, I_V and I_H, are:

$$A_V = \beta_V I_V \quad \text{(S2.1)}$$

$$A_H = \beta_H I_H \quad \text{(S2.2)}$$

SDA is an additional loss term that is proportional to total C intake, IT_C. This cost, ηI_{TC}, can therefore also be deducted at source but there is a complication in that η (the SDA parameter) does not apply to the different ingested substrates in proportion. SDA is an energetic cost and therefore, in order to spare protein for growth, the prioritisation of substrate use is: carbohydrates, storage lipid, protein. For example, if the whole SDA cost can be met using carbohydrate, the remaining absorbed carbohydrate, $A_H^{\#}$, is:

$$A_H^{\#} = A_H - \eta I_{TC}, A_H \geq \eta I_{TC} \quad \text{(S2.3)}$$

where the superscript "#" denotes absorbed substrates or stored lipid after deductions for SDA. In the event that A_H is insufficient, lipids and then proteins are utilised, giving rise to $Z_L^{\#}$ and $A_V^{\#}$, from which maintenance and growth can subsequently be calculated, in sequence.

A table of symbols used in the following equations is provided at the end of this appendix (Table S2.1).

Maintenance

The costs of biomass turnover (τ) and other basal metabolism (ξ) must be met, where both are proportional to structural biomass (Z_S). In other words, these costs are ongoing whether or not an animal has food at its disposal, unlike SDA. Biomass turnover requires both C and N, whereas other basal metabolism is an energetic cost. A schematic of substrate use in maintenance is shown in Figure S2.1. The first step in modelling maintenance is to calculate biomass turnover. The requirement for absorbed protein in maintenance, $A_{Vm}^{\#}$, is (Anderson et al., 2020):

$$A^{\#}_{Vm} = \frac{\theta_V \tau}{k^*_N \theta_Z} \quad \text{(S2.4)}$$

Note that the rates in this section are normalised to copepod structural biomass, Z_S, and so have units mol C mol C^{-1} d^{-1}. Absorbed protein is used to meet this requirement. If this is insufficient, then structural biomass is used instead, resulting in loss in body weight of the copepod.

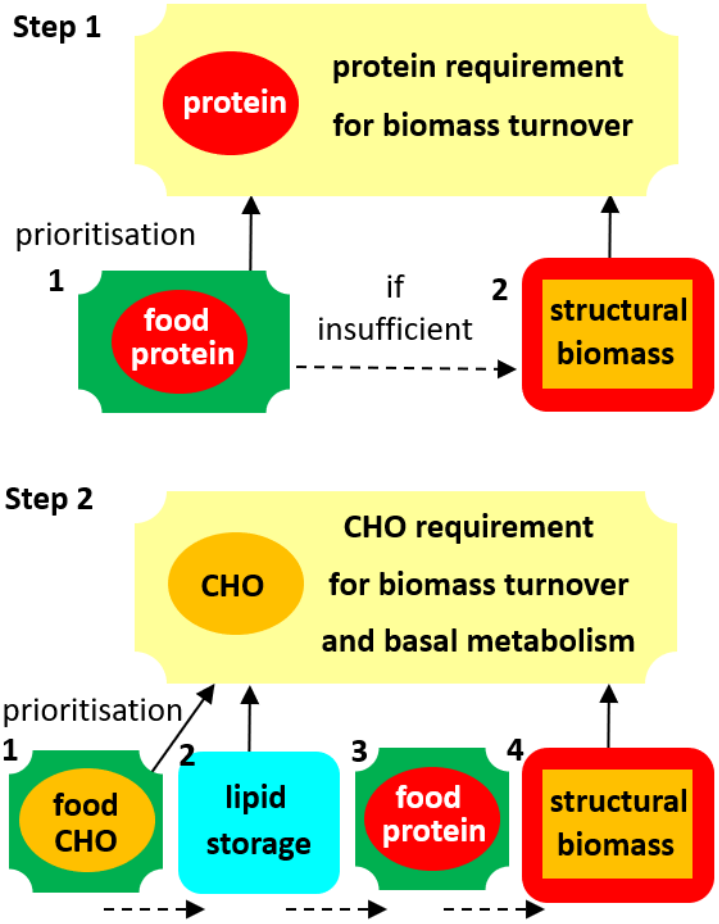

Figure S2.1. Steps and prioritisation of substrate use for maintenance in the model.

The remaining C required in maintenance, $A^{\#}_{Cm}$, is:

$$A^{\#}_{Cm} = \frac{(\theta_Z - \theta_V)\tau}{\theta_Z} + \xi \quad \text{(S2.5)}$$

The first term represents the non-protein C in biomass turnover, while ξ is other basal metabolism. As shown in Figure S2.1, the prioritisation for absorbed substrate use is carbohydrate in food, stored lipid, food protein and, as a last resort, structural biomass.

Production

The requirement for absorbed protein for production (in the absence of maintenance), $A^{\#n}_{Vprod}$ (per unit growth such that it is dimensionless), is (Anderson et al., 2020):

$$A^{\#n}_{VG} = \frac{\theta_V}{k^*_N \theta_G} \quad \text{(S2.6)}$$

where θ_G is the C:N ratio of production which can be θ_{ZS} (in the case of structural biomass) or θ_{egg} (egg production). Carbohydrate is prioritised to meet the remaining C requirement, $A^{\#n}_{Hprod}$, which is the difference between C:N ratios in biomass and protein:

$$A^{\#n}_{HG} = \frac{\theta_G - \theta_V}{\theta_G} \quad \text{(S2.7)}$$

The optimal carbohydrate to protein (H:V) ratio for use of absorbed substrate in growth, $\theta^{\#*}_{AHVG}$, is now:

$$\theta^{\#*}_{AHVG} = \frac{A^{\#n}_{HG}}{A^{\#n}_{VG}} \quad \text{(S2.8)}$$

For reference, the corresponding C:N ratio, $\theta^{\#*}_{ACNG}$, is (it is not required in the calculation of production):

$$\theta^{\#*}_{ACNG} = \theta_V\left(\theta^{\#*}_{AHVG} + 1\right) \quad \text{(S2.9)}$$

If $\theta^{\#R}_{AHV}$, is the H:V ratio of remaining (after maintenance) absorbed H and V from food ($A^{\#R}_H$ and $A^{\#R}_V$) then, ignoring storage lipid for the moment, limitation by protein (corresponding to N limitation) occurs when $\theta^{\#R}_{AHV} > \theta^{\#*}_{AHVG}$,in which case growth, G, is:

$$G = \frac{k^*_N A^{\#R}_V \theta_G}{\theta_V}, \theta^{\#R}_{AHV} \geq \theta^{\#*}_{AHVG} \quad \text{(S2.10)}$$

The potential for limitation by protein increases if remaining storage lipid, $Z^{\#R}_L$, is an additional substrate, coming into play when $\theta^{\#R}_{AHV} < \theta^{\#*}_{AHVG}$. Protein limitation then occurs when $\theta^{\#R}_{AHLV} \geq \theta^{\#*}_{AHVG}$, where $\theta^{\#R}_{AHLV}$ is the ratio of remaining carbohydrate plus lipid to protein. In this case, is also calculated using Eq. S2.10, but with the condition $\theta^{\#R}_{AHLV} \geq \theta^{\#*}_{AHVG}$.

Food quantity (or C) limitation occurs when $\theta^{\#R}_{AHLV} < \theta^{*}_{AHVG}$, in which case there is excess protein. Growth is then calculated in two steps. First, the available (limiting) carbohydrate and storage lipid are used in combination with protein at the optimal ratio, θ^{*}_{AHVG}. The amount of protein used, $A^{\#}_{AVused}$, is:

$$A^{\#}_{Vused} = \frac{A^{\#R}_H + Z^{\#R}_L}{\theta^{*}_{AHVG}} \quad \text{(S2.11)}$$

The resulting growth, G_1, is:

$$G_1 = \frac{k_N^* A_{Vused} \theta_G}{\theta_V} \quad \text{(S2.12)}$$

In the second step, remaining protein, $A_V^{\#R2}$, is now used on its own for growth without accompanying carbohydrate or lipid because they have been exhausted. If carbohydrate had been present, then each unit V would require θ_{AHVG}^* units H. Thus, if protein is used throughout, each unit protein that is assimilated into new biomass requires an additional θ_{AHVG}^* units, assuming that utilisation of C has the same efficiency in both instances. The resulting growth, G_2, is:

$$G_2 = \frac{k_N^* A_V^{\#R2} \theta_G}{\theta_V (1+\theta_{HVG}^*)} \quad \text{(S2.13)}$$

Total growth is then:

$$G = G_1 + G_2, \theta_{AHLV}^{\#R} < \theta_{AHVG}^* \quad \text{(S2.14)}$$

Table S2.1. Table of model variables used in this section, excluding those in Table S1.1

symbol	description	units
G	growth	d^{-1}
G_1, G_2	steps towards calculating G (protein-limitation)	d^{-1}
θ_G	C:N ratio of growth	mol C mol N^{-1}
A_V	absorbed protein (V)	µmol C ind^{-1} d^{-1}
A_H	absorbed carbohydrate (H)	µmol C ind^{-1} d^{-1}
$A_V^{\#}$	absorbed protein minus allocation to SDA	µmol C ind^{-1} d^{-1}
$A_H^{\#}$	absorbed carbohydrate minus allocation to SDA	µmol C ind^{-1} d^{-1}
$Z_L^{\#}$	storage lipid minus allocation to SDA	µmol C ind^{-1} d^{-1}
$A_{Vm}^{\#}$	requirement for absorbed protein in maintenance	d^{-1}
$A_{Cm}^{\#}$	remaining C required in maintenance	d^{-1}
$A_{VG}^{\#n}$	absorbed protein required for growth	mol C mol C^{-1}
$A_{HG}^{\#n}$	absorbed carbohydrate required for growth	mol C mol C^{-1}
$\theta_{AHVG}^{\#*}$	optimal H:V ratio for absorbed substrates in G	mol C mol C^{-1}
$\theta_{ACNG}^{\#*}$	optimal C:N ratio for absorbed substrates in G	mol C mol N^{-1}
$A_V^{\#R}$	remaining $A_V^{\#}$ after maintenance	d^{-1}
$A_H^{\#R}$	remaining $A_H^{\#}$ after maintenance	d^{-1}
$Z_L^{\#R}$	availability stored protein after maintenance	d^{-1}
$\theta_{AHV}^{\#R}$	ratio remaining absorbed H to V after maint.	mol C mol C^{-1}
$\theta_{AHLV}^{\#R}$	ratio remaining absorbed H+L to V after maint.	mol C mol C^{-1}
$A_{AVused}^{\#}$	absorbed protein used in calculation of G_1	d^{-1}
$A_V^{\#R2}$	remaining protein after G_1	d^{-1}

3 Supplementary Appendix 3. Functional response parameters

Assigning values to the parameters in a multiple prey functional response is non-trivial, due in part to the fact that there are rarely empirical data to support such formulations. Furthermore, the biological conceptualisation of parameters may not be congruent with their corresponding r mathematical significance. For example, in the Sigmoidal multiple-prey response that we are using (Eq. S1.5), the so-called half saturation constant for ingestion, k_g, is the half-saturation value of a preferentially-weighted measure of total food (i.e. the value of total preferentially-weighted food for which total ingestion is half the maximum rate g_T). Unless the food preference parameters are all equal to 1, this k_g is not the half-saturation value for total food. Nor is it the density of a particular food item for which ingestion of that item is $g_T/2$ because the actual half-saturation value is increased by the presence of other prey items (see denominator in Eq. S1.5).

The value of k_g in a multiple-prey functional response cannot therefore be directly compared with estimates from the literature. Gentleman et al. (2003) recommended using an implied single prey functional response to guide parameter choices for use in multiple-prey functional responses. The implied single-prey response is obtained by setting the densities of all other prey types, excluding the item in question, to zero. In the case of Eq. S1.5, setting the densities of non-diatoms, microzooplankton and detritus to zero, leaves us with an ingestion for diatoms, I_{pd}, of:

$$I_{Pd} = \frac{g_T \omega_{Pd} P_d^2 Z_S}{k_g^2 + \omega_{Pd} P_d^2} \quad \text{(S3.1)}$$

Dividing through the numerator and denominator by ω_{Pd} yields:

$$I_{Pd} = \frac{g_T P_d^2 Z_S}{\kappa^2 + P_d^2}, \;\; \kappa^2 = \frac{k_g^2}{\omega_{Pd}} \quad \text{(S3.2)}$$

which is a classic Sigmoidal Type 2 single-prey functional response for which the half-saturation constant κ is the half-saturation value equivalent to the corresponding single-preyhalf-saturation constant for a copepod ingesting a monoculture of diatoms, as might be found in the literature.

Given that we have assigned ω_{Pd} (and the other preference parameters) to match those used in MEDUSA (Yool et al., 2013), we can use those values to choose a value for k_g such that κ is consistent with single-prey studies. The literature reports half-saturation values of ~1.7 mmol C m-3 (Maps et al., 2012, Campbell et al., 2001) which, for our ω_{Pd} = 0.35, corresponds to k_g = 1 mmol C m^{-3}. Note that this value for k_g results in implied single-prey half saturation values of 1.7 for microzooplankton and 2.6 for non-diatoms and detritus.

When using the implied single-prey functional response, maximum ingestion rate, g_T, can be assumed to be identical for all prey types and is thereby comparable to values presented in the literature.

4 Supplementary Appendix 4. Sensitivity analysis on functional response parameters

Assigning values for the parameters that define functional response, namely the maximum rate, g_T (d^{-1}), and the multiple-prey half saturation constant, k_g (mmol C m^{-3}), is surprisingly difficult despite many studies on copepod grazing in the literature. We therefore undertook a sensitivity analysis on these parameters (Figure S4.1), noting that the standard values of these parameters are $g_T = 0.5$ d^{-1} and $k_g = 1.0$ mmol C m^{-3}. The simulated copepod often failed to reach lipid-replete CV (completion of Phase 3) when decreasing g_T below 0.4 d^{-1} or increasing kg above 1.2 mmol C m^{-3}, hence our chosen ranges for the sensitivity analysis of 0.4 – 1.0 d^{-1} for g_T and 0.6 – 1.2 mmol C m^{-3} for k_g.

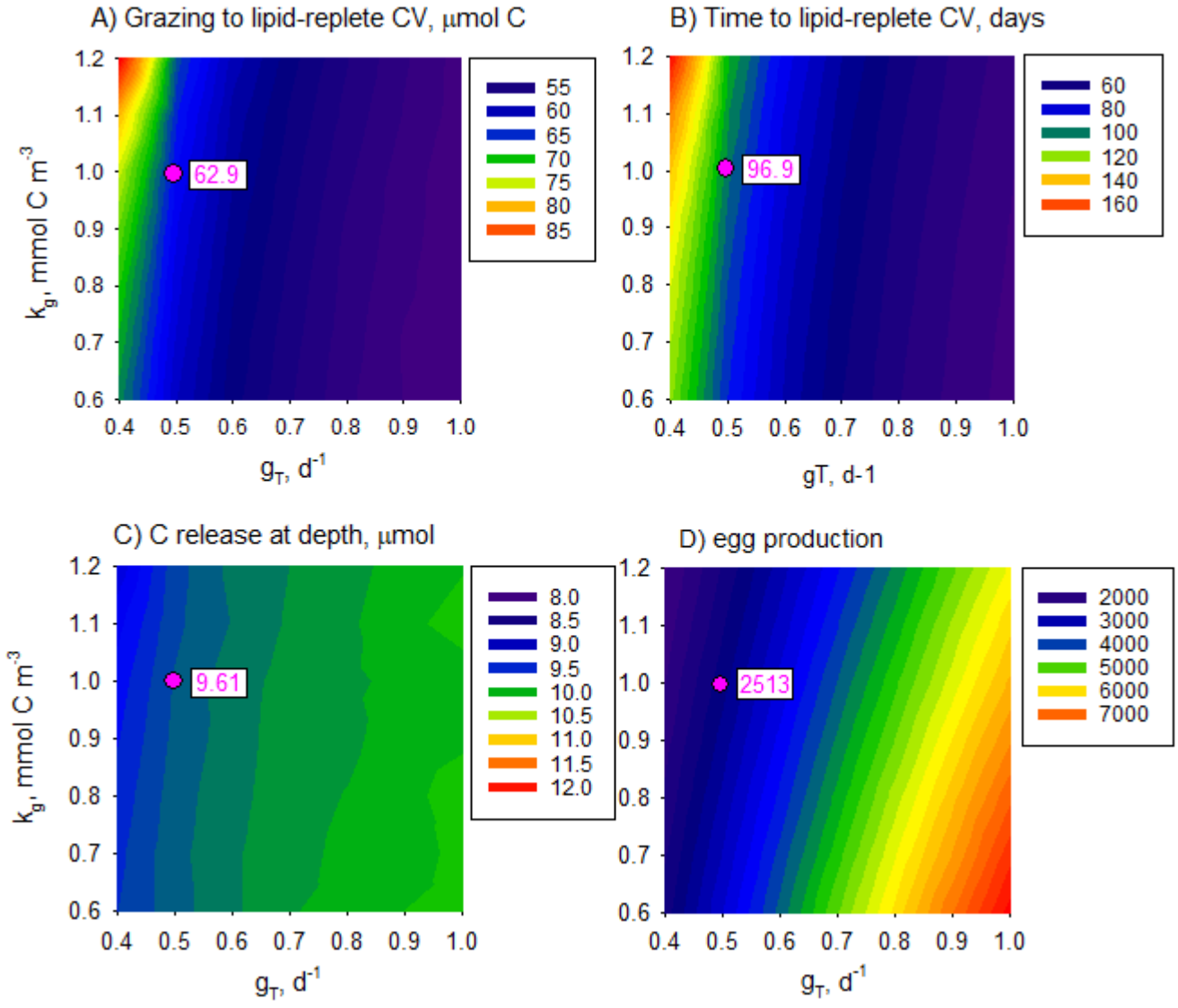

Figure S4.1. Sensitivity analysis on functional response parameters g_T (maximum grazing rate, d^{-1}) and k_g (multiple-prey half saturation constant, mmol C m^{-3}): A) food quantity grazed during development to lipid-replete CV, µmol C; B) development time to lipid-replete CV, d; C) C release via respiration at depth during Phases 4 (diapause) and 5 (gonad development), µmol C; D) egg production in year 2. The pink points signify the combination of standard parameters, accompanied by the standard simulation results.

Intake at any given point in time is reduced by either decreasing g_T or increasing k_g. Making these parameter changes means that gross growth efficiency decreases (reduced intake while having to maintain the same metabolic costs) in which case animals must consume a greater food quantity to reach lipid-repeat CV (Fig. S.4.1A) and consequently have a longer development time (Fig. S4.1B). In turn, this leads to a shorter period spent in diapause (Phase 4) and less C respired in deep water, although the effect is relatively small (Fig. S4.1C). Egg production in year 2 is driven almost entirely by food such that increasing g_T or decreasing k_g causes it to significantly increase (Fig. S4.1D). Our results highlight the need for experimental and observational studies to better quantify functional response and grazing by copepods, as influenced by food quantity.

5 Supplementary Appendix 5. Model results for Station India

Results are shown here for a model simulation carried out for Station India (60°N, 20°W) in the North Atlantic. As for the Station Mike simulation, the initial condition is an egg spawn on day 120. Results are shown in Figure S5.1.

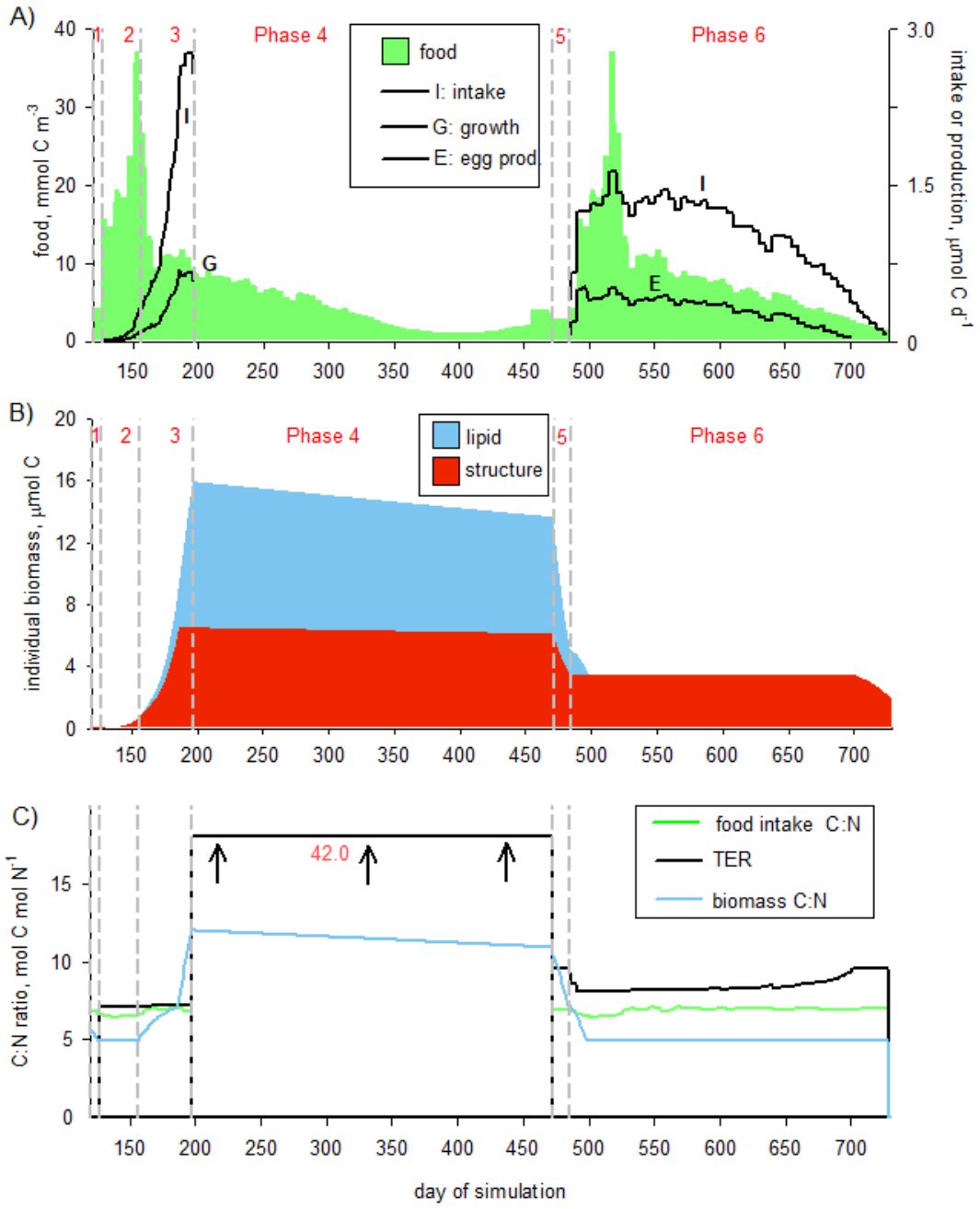

Figure S5.1. Predicted development of a *C. finmarchicus* individual throughout its life cycle at Station India. A) Intake (I), growth (G) and egg production (E), along with the concentration of available food from the MEDUSA model output (green); B) structural biomass (red) and lipid reserves (blue); C) comparison of C:N ratios for food intake (green), copepod biomass (structure + lipid; blue) and the Threshold Elemental Ratio (TER; black).

Supplementary Material

Food concentration at the peak of the bloom was 37.2 mmol C m^{-3}, substantially higher than the corresponding 19.4 mmol C m^{-3} seen at Station Mike. This extra food resulted in a shorter development time for egg through to lipid-replete CV, 77 versus 97 days, after which the animal entered diapause. The predicted duration of diapause was therefore longer, 275 days, because re-emergence was on day 120 of the second year, as in the Station Mike simulation. The losses of lipid during diapause and gonad development were 1.9 and 5.9 μmol C, respectively, with an overall loss of 7.8 μmol C. Corresponding losses of structural biomass during this period were 0.4 and 2.7 μmol C, with a combined loss of 3.1 μmol C. The predicted total CO_2 generated via respiration during these two phases is the sum of these losses, namely 10.9 μmol C. If copepod densities are 15,000-40,000 individuals m^{-2}, this translates as a C sequestration in deep waters of 2.0 – 5.2 g C m^{-2} yr^{-1}. Greater food availability led to increased egg production in year two relative to Station Mike, 2642 versus 2513, at an average of 12.3 eggs d^{-1} during the production period. The animal eventually ran out of food and died of starvation one day 728 of the simulation.

6 Supplementary references

Anderson, T. R., Gentleman, W. C., and Sinha, B. (2010). Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global general circulation model. *Prog. Oceanogr.* 87, 201–213. doi.org/10.1016/j.pocean.2010.06.003

Anderson, T. R., Raubenheimer, D., Hessen, D. O., Jensen, K., Gentleman, W. C., and Mayor, D. J. (2020). Geometric Stoichiometry: unifying concepts of animal nutrition to understand how protein-rich diets can be "too much of a good thing". *Front. Ecol. Evol.* 8, 196. doi.org/10.3389/fevo.2020.00196

Anderson, T. R., Hessen, D. O., and Mayor, D. J. (2021). Is the growth of marine copepods limited by food quantity or quality? *Limnol. Oceanogr. Lett.* 6, 127–133. doi.org/10.1002/lol2.10184

Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A., and Durbin, E. G. (2001). Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. *Mar. Ecol. Prog. Ser.* 221, 161–183. doi:10.3354/meps221161

Gentleman, W., Leising, A., Frost, B., Strom, S., and Murray, J. (2003). Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep-Sea Research II*, 50, 2847–2875. doi.org/10.1016/j.dsr2.2003.07.001

Maps, F., Runge, J. A., Leising, A., Pershing, A. J., Record, N. R., Plourde, S., and Pierson, J. J. (2012). Modelling the timing and duration of dormancy in populations of *Calanus finmarchicus* from the Northwest Atlantic shelf. *J. Plankton Res.* 34, 36–54. doi.org/10.1093/plankt/fbr088

Yool. A., Popova, E. E., and Anderson, T. R. (2013). MEDUSA-2.0: an intermediate complexity biogeochemical model of the marine carbon cycle for climate change and ocean acidification studies. *Geosci. Mod. Dev.* 6, 1767–1811. doi.org/10.5194/gmd-6-1767-2013