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D2.10 Sub -model copepod structured population model including user guide

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1. Model description

1.1. State variables to resolve the copepod life cycle

The model consists of ten state variables with biomass (Z) and abundance (N) for each of five model stages, grouping stages to: eggs, nauplii (NI-NVI), two copepodite stages (CI-CIII and CIV-CV) and adults (CVI). The basic approach for each model stage consists of the following equations:

$$\begin{aligned} \frac{d}{dt}Z_i &= T_{i-1,j} \cdot Z_{i-1} + g_i \cdot Z_i - (\mu_i + l_i) \cdot Z_i - T_{i,j+1} \cdot Z_i \\ \frac{d}{dt}N_i &= T_{i-1,j} \cdot N_{i-1} - \mu_i \cdot N_i - T_{i,j+1} \cdot N_i \end{aligned}$$

with rates of transfer $T_{i,j+1}$ from stage i to the next, grazing g_i , mortality μ_i and losses l_i .

Stage-specific processes control the metabolism of a 'mean individual' using the mean individual mass for each stage i , defined as stage biomass divided by the number of individuals (Z_i/N_i). Thus, simulated abundances and biomasses are connected as functions of time.

Fennel (2001) formulated stage-resolved equations for each state variable by employing the concept of critical masses of Carlotti and Sciandra (1989), which defines a specific stage by a mass m within the values $X_{i-1} < m \leq X_i$. Thus, these critical masses X_i had to be defined for each stage. Although it is known that body weight and carbon content vary seasonally and geographically (Krause *et al.*, 2003), we tabulated stage-dependent dry weights from available literature and found a range of 2-5 times the minimal stage weights. Among others, three references (Hay *et al.*, 1988; Hay *et al.*, 1991; Klein Breteler *et al.*, 1982) contain estimates of dry weights for all stages. We derived mean and extreme values from these literature data which were used for the weight depending functions of ingestion and transfer.

A conceptual model diagram of the copepod life cycle is shown in Figure 1 including growth processes and the influence of the environment. Growth is characterised by increase of weight and stage development, which can be expressed by stage durations. Physiological processes consist of two categories: first, processes affecting abundance, i.e. hatching, moulting and reproduction, which are controlled by weight, and mortality. Second, processes affecting only biomass. These determine stagespecific weights through gain (ingestion) and loss (respiration, excretion and egestion) of matter. Ingestion itself is influenced by weight and depends on the environmental food supply and forms the population's source of biomass. Temperature, directly or indirectly, influences several developmental processes. The overview in Figure 1 illustrates the steps of model process parameterisation.

1.2. Process parameterisation

In the following subsections the parameterisations were described. For a better comparison the process formulas, parameter tables and resulting diagrams were presented together in one figure in Stegert *et al.* (2007).

1.2.1. Ingestion

The formula for the ingestion rate, abbreviated as g_i , (Stegert *et al.* – Fig. 2) describes the amount of ingested food per day in relation to the available food $f1(F)$, temperature $f2(T)$ and body mass $f3(W)$ multiplied by the stage-specific maximum ingestion rate $P1$.

Fennel (2001) formulated the food dependence of ingestion $f1(F)$ using a modified Ivlev formula. Half-saturations occur at food levels of 100-200 $\mu\text{g C l}^{-1}$ for the different stages (Stegert *et al.* – Fig. 2). In a study on the functional response of *P. elongatus* Harris and Paffenhöfer (1976) reported, that 80% of

the maximum ingestion was reached at 100 µg C l⁻¹ for adults. Thus, for the present model food dependence was raised for lower concentrations. Among various available functions (Gentleman *et al.*, 2003) the common Michaelis-Menten function was used sharpened by the power factor P3.

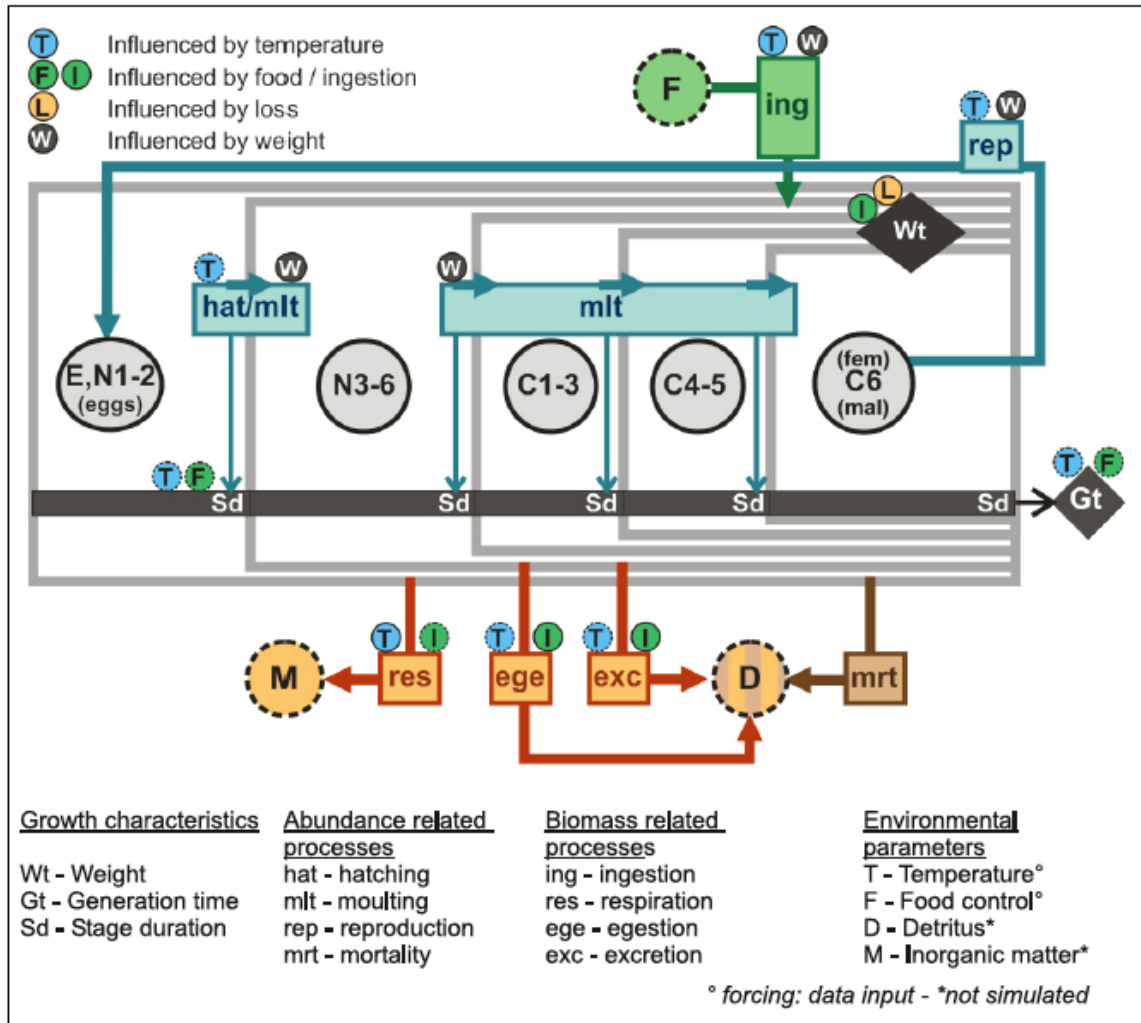


Figure 1: Interaction diagram of the model copepod life cycle adapted to *Pseudocalanus elongatus*. Development characteristics of state variables (thick circles) are connected to internal physiology (white boxes) and external environment (dashed circles) using growth characteristics of individual weight, stage duration and generation time (dark boxes). Material fluxes denoted by thick arrows.

Half-saturation coefficient P2 was fixed to 20 µg C l⁻¹ for the NIII-NVI group and equal to 50 µg C l⁻¹ for the copepodites and adults. These values have partly been fitted to obtain realistic simulated developmental durations compared to laboratory data.

The influence of temperature on ingestion rates $f_2(T)$ was implemented by Fennel by an Eppley function representing a Q10-value of 1.9 (Stegert *et al.* – Fig. 3). As the temperature impact in the laboratory data for *P. elongatus* is much higher, a Q10 of 2.58 was included, aligned to the temperature range of 5 to 15°C. Additionally, a parabolic threshold function realises a decrease at higher temperatures as a result of physiological depression (Corkett and McLaren, 1978). So, ingestion follows an exponential curve up to the reference temperature of 15°C, reaches its maximum at 18.5°C and decreases for temperatures above.

To represent inhibition of ingestion due to limited body volume by the cuticle of copepods, which do not moult, we followed the concept presented in Carlotti and Sciandra (1989). Fennel (2001) used a Fermi filter function which is maximum at low stage mean masses and decreased sigmoidally for higher masses (Stegert *et al.* – Fig. 4). The 50% level of ingestion was reached, when individuals obtained the critical weight X_i . In our parameterisation we used a parabolic function allowing individuals to feed at maximum rate up to the critical weight X_{ti} , and then decreasing for higher weights down to zero at X_{gi} , the maximum values presented in Stegert *et al.* - Appendix, which is hardly reached. Thus, the

shape of the curves is different between the models and the critical masses were derived from measurements for *P. elongatus*.

1.2.2. Losses

The ingested food is processed in growth, respiration, excretion, egestion, moulting and reproduction. Thus, g_i is partly used for growth and metabolism of the animal ($g_i \cdot AE$) and partly egested as faecal pellets ($g_i \cdot (1-AE)$), where AE is the assimilation efficiency. For the losses Fennel assumed constant quotas of ingested food: 35% as egestion (corresponding to an assimilation efficiency of 65%), 10% as excretion and 10% by respiration, and about 15% for the moulting process, in total 70%. Thus, for nauplii and copepodite stages the remaining 30% of ingested food were used for growth whereas for adult females a higher amount is invested for egg production (see 'Reproduction') and less goes to growth (see Table 1).

Beside the direct impact of feeding on loss due to active metabolism, there are evidently losses through basal respiration when the copepods do not feed (Carlotti and Sciandra, 1989). To realise this fact, the respiration losses were divided into active and basal metabolism. Thus, the total loss, l_i , is given by:

$$l_i = (1 - AE) \cdot g_i + (R_A \cdot g_i + R_B \cdot Q^{(T-T_{r1})/10})$$

with AE of 0.65 to keep the egestion at 0.35. RA and RB are coefficients for active and basal metabolism and the Q10 value (Q) assumed to be the same as for ingestion (Table 1).

1.2.3. Transfer

An essential consequence of growth is transfer to the next stage through moulting. Fennel introduced the Fermi function to realise a smooth transfer to the next stage representing faster and slower development of some individuals. When transfer is coupled with the grazing function both Fermi functions were combined, which leads to a double threshold giving just a small 'moulting window' of low rates (Stegert et al. – Fig. 5). As no reference gives information on direct relationship between grazing and stage transfer this is left out in our formula. The Fermi function f_6 is of sigmoidal type which starts at zero and becomes positive for positive mean body masses and a proportion of these individuals moulted very early to the next stage.

To enable a certain response time for moulting, in our model a different sigmoidal function was used. Transfer is now inhibited before the subsequent stage reference weight R_{ti} (see Table 1) is reached and a rate of 50% is assigned at the critical moulting weight X_{ti} .

1.2.4. The non-feeding group

The first two naupliar stages (NI/NII) do not feed (Corkett and McLaren, 1978) and should be separated from the older nauplii. To avoid the introduction of an additional state variable for this group, in our model the non-feeding naupliar stages were combined with the state variable for eggs.

The nauplii comprise stages NIII-NVI only. Thus, development within the first stage includes hatching and transfer from eggs to NII. Due to respiration losses a reduced mean body weight was assumed during this development. The transfer

(T_{nf}) is defined by the weight-depending function as described for the other stages but with an increasing rate at decreasing weight (Stegert et al. – Fig. 6). For the reference value R_{tnf} , when transfer is initiated, the mean egg mass of 0.14 $\mu\text{g C}$ and for the critical moulting mass X_{tnf} the minimum body weight of NII with 0.10 $\mu\text{g C}$ were used (see Stegert et al. - Appendix).

Respiration rates are difficult to obtain experimentally. Therefore we calculated the loss term depending on temperature for this stage group by the same formula as for the other model stages –

except that there are no ingestion terms (i.e. $gnf = 0$). Thus, development time is related to temperature by the impact of embryonic metabolism (Stegert et al. – Fig. 6).

1.2.5. Reproduction

The reproduction rate (R) describes the amount of biomass, which female adults provide for reproduction when reaching the maturation mass Rta (Stegert et al. – Fig. 7). In the model this was expressed as a transfer from adults to eggs. Fennel assumed, that 30% ($P8$) of growth was transferred into egg biomass, i.e. 6% of ingestion, resulting in an egg production rate (EPR) of <1 egg fem-1 d-1. Due to the dependence on ingestion the EPR is related to food and temperature. For *Pseudocalanus elongatus* rates of 2.3 eggs fem-1 d-1 at 8.4°C (Corkett and McLaren, 1978) and 3-5 eggs fem-1 d-1 at 15°C (Mauchline, 1998) were reported. We followed the approach of Carlotti and Sciandra (1989) and assumed a maximum biomass of 0.8 µg C fem-1 d-1 ($P8$) allocated to eggs, which is related to the mean weight $Wa = Za/Na$. As not all females are reproductive (Halsband and Hirche, 2001), we considered 30% ($P9$) of adults laying eggs, i.e. 70% being males or non-productive females. This results in a rate of 2.8 eggs fem-1 d-1 at a mean weight of Xta and up to 5 eggs fem-1 d-1 at the maximum mass Xga (Stegert et al. – Fig. 7).

1.2.6. Mortality

Mortality involves age and disease related death and predation by planktivorous fish, jelly fish, chaetognaths and others. Fennel chose constant mortality rates. Highest mortality rate was set for eggs (0.2 d-1) and decreased to adults (0.01 d-1). In contrast to broadcast spawners (like *Calanus finmarchicus*) egg mortality of sac spawners is not higher compared to the other stages (Eiane and Ohman, 2004). As mortality rates have only a slight effect on stage durations (see 'Sensitivity Analysis') identical rates for all stages of $\mu_i = 0.03$ d-1 were chosen, which is nearly the mean rate for 5-15°C experiments by Klein Breteler *et al.* (1995). Life-time of adults was confined by adding the sigmoidal function $f4$ of transfer: $\mu_a = 0.03 + 0.1 \cdot f4$. The factor of 0.1 ensures a maximum rate of 0.13 d-1, which corresponds to maximum mortality rates of adults presented by Ohman *et al.* (2002).

1.3. Species specific model parameters

The species-specific life cycle processes of growth, transfer and reproduction were parameterized according to data cited for *Pseudocalanus elongatus* in the North Sea. Table 1 synthesizes the different qualities of parameter values. Three types of parameters were discerned:

- Parameters with robust values taken from published studies. This includes weights at different stages and derived reference and critical values, which come from compilation of observed data. Among the processes, egg production and hatching are examples of well investigated species-specific estimates.
- Parameters derived from general information on copepods by reasonable assumption but for which tuning was necessary. For the ingestion and metabolic loss processes missing parameter values were derived from general specifications for *Pseudocalanus sp.* For the temperature dependent ingestion no process data were available and therefore parameter values were calculated by fitting simulated development to stage durations from the laboratory experiments.

Parameters defining shapes of function, as the power parameters. These are almost impossible to test with data, but for which several parts of the stage abundance and the growth curves within stages give a qualitative check, as the initial start value of the curve or the queue of laggards.

Table 1 Species-specific parameter values for *Pseudocalanus elongatus* in the model and their grade of sensitivity.

| Parameter name | Sig. | Fct. | E-NII | NIII-VI | CI-III | CIV-V | CVI | test | sensitivity |
|-------------------------|----------|---------------|-------|---------|--------|-------|-------|------|--|
| Maximum ingestion rate | P_1 | f_1 | - | 1.00 | 0.60 | 0.50 | 0.30 | yes | very sensitive |
| Half saturation | P_2 | f_1 | - | 20.00 | 50.00 | 50.00 | 50.00 | yes | sensible |
| Power coefficient | P_3 | f_1 | - | 1.15 | 1.40 | 1.40 | 1.40 | yes | not sensitive |
| Q10-parameter ingestion | P_4 | f_2 | 3.60 | 2.58 | 2.58 | 2.58 | 2.58 | yes | sensible |
| Power coefficient | P_5 | f_2 | - | 1.50 | 1.50 | 1.50 | 1.50 | - | curve fitted to data |
| Slope factor | P_6 | f_2 | - | 0.70 | 0.70 | 0.70 | 0.70 | - | curve fitted to data |
| Reference temperature | T_{r1} | f_2, l_i | 10.00 | 10.00 | 10.00 | 10.00 | 10.00 | - | reference value |
| Reference temperature | T_{r2} | f_2 | - | 15.00 | 15.00 | 15.00 | 15.00 | - | reference value |
| Assimilation efficiency | AE | l_i | - | 0.65 | 0.65 | 0.65 | 0.55 | yes | very sensitive |
| Active Metabolism | R_A | l_i | - | 0.40 | 0.33 | 0.33 | 0.28 | yes | very sensitive |
| Basal Metabolism | R_B | l_i | 0.07 | 0.05 | 0.02 | 0.02 | 0.02 | yes | not sensitive |
| Q10-parameter loss | Q | l_i | 3.60 | 2.58 | 2.58 | 2.58 | 2.58 | yes | not sensitive |
| Reference mass | Rf_i | f_4 | 0.14 | 0.50 | 1.80 | 4.30 | 7.50 | yes | considered as robust, not sensitive |
| Critical moulting mass | Xf_i | f_3 | - | 0.70 | 2.40 | 5.40 | 8.60 | - | considered as robust |
| Critical ingestion mass | Xg_i | f_3, f_4 | - | 0.80 | 2.70 | 6.00 | 9.60 | - | considered as robust |
| Slope factor | P_7 | f_4, T_{nf} | 6.00 | 4.00 | 4.00 | 4.00 | 4.00 | - | considered as robust |
| Maximum biomass | P_8 | R | - | - | - | - | 0.80 | - | considered as robust |
| Reproductive females | P_9 | R | - | - | - | - | 0.30 | - | curve fitted to data |
| Mortality | μ_i | - | 0.03 | 0.03 | 0.03 | 0.03 | 0.03 | yes | not sensitive |

2. Implementation to ECOHAM

For the zooplankton analysis we used the three-dimensional ecosystem model ECOHAM3 (Ecological Model, Hamburg), which calculates the cycles of carbon, nitrogen and oxygen on the Northwest European Continental Shelf with a horizontal resolution of 20 km (Stegert et al., 2009).

For the investigation of *Pseudocalanus elongatus* we implemented the model population in competition to the rest zooplankton as illustrated in Figure 2. The state variables (circles) are connected by arrows symbolizing fluxes of matter which are numbered. Numbers are explained in the legend of the ECOHAM User Guide (Pätsch et al., 2009). The population was described by ten state variables representing the naupliar and copepodite stage groups of eggs-N2 (i.e. non-feeders), N3-6, C1-3, C4-5 and adults each in terms of abundance and biomass. Development of *P. elongatus* was described by the change in mean individual weight through gain (ingestion) and loss (respiration, excretion and egestion) of matter. Stage transfer was implemented by a sigmoidal function allowing a statistical scattering of moulting around the critical weight. Population dynamics of *Pseudocalanus* in the North Sea were parameterised by the zero-dimensional case scenarios in laboratory culture experiments (Stegert et al., 2007). When the process equations were adopted for the three-dimensional environment, some parameter values were changed to fit the population abundance to the reported annual development. A reduction of the Q10 (2.0 instead of 2.58) and reduced ingestion at higher temperatures adapted the population to the earlier and colder season. Low February values resulted from the parameterisation of overwintering, which was realised by limiting reproduction in winter so that individuals were summed in the model stage group for adults.

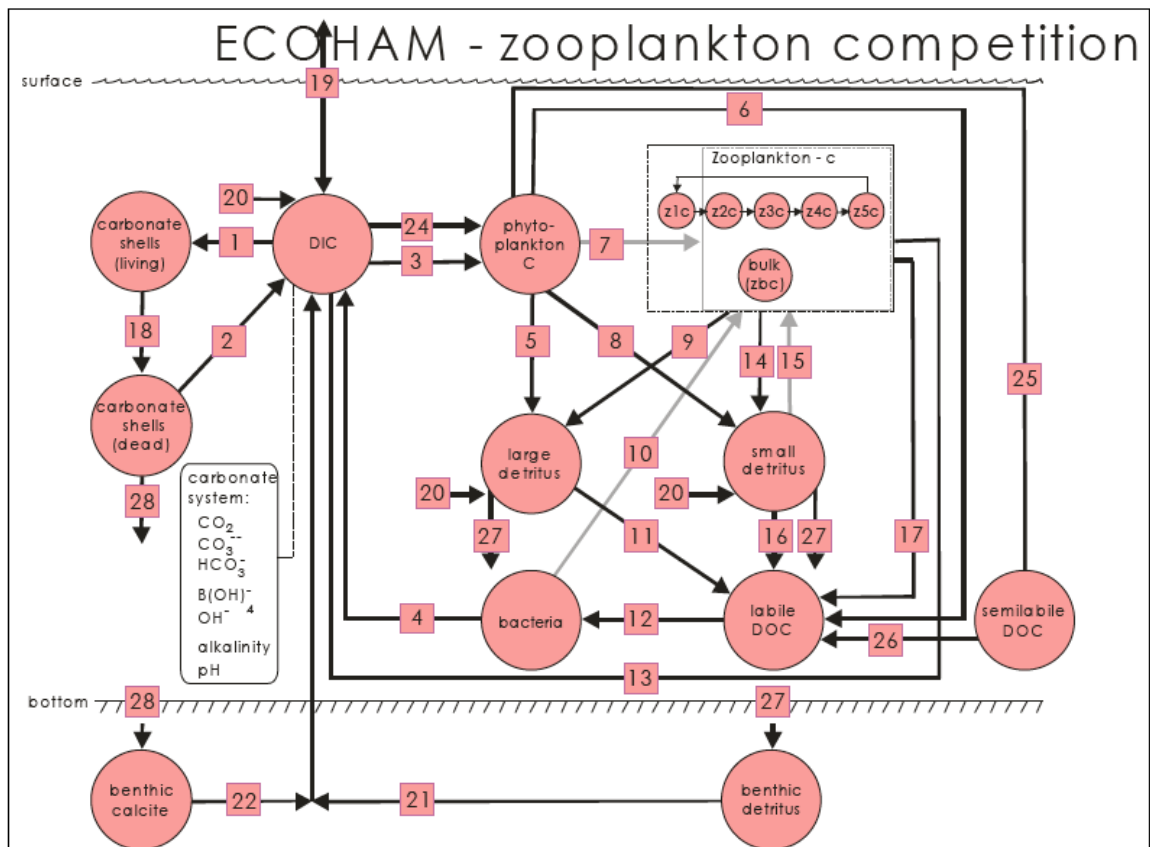


Figure 2 Diagram of the carbon cycle with structured zooplankton.

The population competed for existing food with the bulk zooplankton variable. This bulk variable represented the rest of the total zooplankton biomass, though its dynamics was parameterised towards generic copepod behaviour as this group constitutes the largest part of zooplankton in the North Sea (Fransz et al., 1991). Major differences compared to the population involve a lower Q10 of 1.0 for ingestion.

First, the model was applied to the northern North Sea (Moll and Stegert, 2007) without any other zooplankton. Then, we added in detail the necessary model state variables for the additional bulk zooplankton, with emphasis on grazing and food competition formulations given in Kreuz (2006). The zooplankton population in ECOHAM3 consists of the same five model stage groups for *Pseudocalanus elongatus* represented by the stage-structured abundance ($\text{PeA}(i)$, $i=1, \dots, 5$) and the biomass in terms of nitrogen and carbon ($\text{PeN}(i)$, $\text{PeC}(i)$, $i=1, \dots, 5$). And we included the rest of the zooplankton community as one state variable, called "bulk zooplankton" in terms of nitrogen and carbon biomass (ZN, ZC) as close as possible to the basic NPZD - ecosystem model description by Pätzsch and Kühn (2008).

$$\begin{aligned} \frac{\partial Pe_N(i)}{\partial t} = & AE_N \cdot (I_{PhyN}(i) + I_{BacN}(i) + I_{DetN}(i)) - ML_N^{Pe}(i) - MO_N^{Pe}(i) + TR_N(i-1) - TR_N(i) \\ & - \left(\frac{\partial}{\partial x} \left(A_H \frac{\partial Pe_N(i)}{\partial x} \right) + u \frac{\partial Pe_N(i)}{\partial x} + \frac{\partial}{\partial y} \left(A_H \frac{\partial Pe_N(i)}{\partial y} \right) + v \frac{\partial Pe_N(i)}{\partial y} + \frac{\partial}{\partial z} \left(A_M \frac{\partial Pe_N(i)}{\partial z} \right) + w \frac{\partial Pe_N(i)}{\partial z} \right) \end{aligned} \quad \text{Eq (1)}$$

$$\begin{aligned} \frac{\partial Pe_C(i)}{\partial t} = & AE_C \cdot (I_{PhyC}(i) + I_{BacC}(i) + I_{DetC}(i)) - ML_C^{Pe}(i) - MO_C^{Pe}(i) + TR_C(i-1) - TR_C(i) \\ & - \left(\frac{\partial}{\partial x} \left(A_H \frac{\partial Pe_C(i)}{\partial x} \right) + u \frac{\partial Pe_C(i)}{\partial x} + \frac{\partial}{\partial y} \left(A_H \frac{\partial Pe_C(i)}{\partial y} \right) + v \frac{\partial Pe_C(i)}{\partial y} + \frac{\partial}{\partial z} \left(A_M \frac{\partial Pe_C(i)}{\partial z} \right) + w \frac{\partial Pe_C(i)}{\partial z} \right) \end{aligned} \quad \text{Eq (2)}$$

$$\begin{aligned} \frac{\partial Pe_A(i)}{\partial t} = & -MO_A^{Pe}(i) + TR_A(i-1) - TR_A(i) \\ & - \left(\frac{\partial}{\partial x} \left(A_H \frac{\partial Pe_A(i)}{\partial x} \right) + u \frac{\partial Pe_A(i)}{\partial x} + \frac{\partial}{\partial y} \left(A_H \frac{\partial Pe_A(i)}{\partial y} \right) + v \frac{\partial Pe_A(i)}{\partial y} + \frac{\partial}{\partial z} \left(A_M \frac{\partial Pe_A(i)}{\partial z} \right) + w \frac{\partial Pe_A(i)}{\partial z} \right) \end{aligned} \quad \text{Eq (3)}$$

$$\begin{aligned} \frac{\partial Z_N}{\partial t} = & AE_N \cdot (G_{PhyN} + G_{BacN} + G_{DetN}) - ML_N - MO_N \\ & - \left(\frac{\partial}{\partial x} \left(A_H \frac{\partial Z_N}{\partial x} \right) + u \frac{\partial Z_N}{\partial x} + \frac{\partial}{\partial y} \left(A_H \frac{\partial Z_N}{\partial y} \right) + v \frac{\partial Z_N}{\partial y} + \frac{\partial}{\partial z} \left(A_M \frac{\partial Z_N}{\partial z} \right) + w \frac{\partial Z_N}{\partial z} \right) \end{aligned} \quad \text{Eq (4)}$$

$$\begin{aligned} \frac{\partial Z_C}{\partial t} = & AE_C \cdot (G_{PhyC} + G_{BacC} + G_{DetC}) - ML_C - MO_C \\ & - \left(\frac{\partial}{\partial x} \left(A_H \frac{\partial Z_C}{\partial x} \right) + u \frac{\partial Z_C}{\partial x} + \frac{\partial}{\partial y} \left(A_H \frac{\partial Z_C}{\partial y} \right) + v \frac{\partial Z_C}{\partial y} + \frac{\partial}{\partial z} \left(A_M \frac{\partial Z_C}{\partial z} \right) + w \frac{\partial Z_C}{\partial z} \right) \end{aligned} \quad \text{Eq (5)}$$

The sum of the five population state variables (Pe(i)) represents the total biomass of the population in terms of carbon and nitrogen, respectively.

C:N ratios and process formulations

The model uses fixed C:N ratios (mol C : mol N) for the biological state variables phytoplankton (C:NPhy=6.625), zooplankton (C:NZoo=5), and bacteria (C:NBac=4), and variable C:N ratios for the state variables detritus and dissolved organic matter.

The amount of food (phytoplankton, bacteria and detritus) ingested by the bulk zooplankton and by the population is assimilated with the same efficiency AEC=0.65, as calculated for carbon by Anderson (1994). The grazing/ingestion parameterization depends on the available food in terms of nitrogen (fFN), the temperature relation (fT), and the maximum ingestion rate ($gmax$) for bulk zooplankton. The stage-specific maximum ingestion rates ($Imax(i)$) decrease with increasing weight. Finally, according to the carbon:nitrogen ratio, the total grazed/ingested amount of nitrogen is converted to carbon units.

The bulk grazing food-limitation is expressed by a modified Michaelis-Menten formula with a halfsaturation value ($K3=1$ mmol N m⁻³). For the population a modification to a single-prey Sigmoidal (Holling Type 3) function was chosen, which is sharpened by using a power exponent of 2. Halfsaturation constants range from 20 µg C l⁻¹ (1.7 mmol C m⁻³) for the nauplii group to 50 µg C l⁻¹ (4.2 mmol C m⁻³) for the copepodites and adults. These values were adjusted to obtain realistic developmental durations. The influence of temperature on ingestion rates was implemented by an Eppley function with a Q10in-value of 2.0 for the temperature range of 5-15°C. A parabolic function realises an ingestion rate decrease at higher temperatures as a result of physiological depression using a temperature offset at $To=22^\circ\text{C}$. Additionally, ingestion rates depend on the body weight (fW) using a reference weight, for which ingestion ends. The ingested food is partitioned into growth and metabolic losses of respiration, excretion, egestion and additionally for the population in moulting and reproduction on one hand and growth on the other one.

Total losses were parameterized for the bulk zooplankton (MLN and MLC) using a Michaelis-Menten approach and the half-saturation constant K_6 . A coarse loss term within the bulk zooplankton is contrasting a more explicit formulation of metabolic losses (MLN μ_e , MLC μ_e) and mortality (MOA μ_e) for the population (eq. 2 and 3). Besides the direct impact of feeding on loss due to active metabolism for the population, there are also losses due to basic respiration when the copepods do not feed. Accordingly, the respiration losses were divided into active and basic metabolism. Active metabolism is related to ingestion, thus the same Q_{10} -values as for ingestion (Q_{10in}) were assumed. Routine metabolism is a function of temperature with a higher Q_{10} -value (Q_{10ml}). Contrasting the universal loss term including mortality for bulk zooplankton, within the population an explicit formulation of mortality (MOA μ_e) was applied and stage-dependent mortality rates ($\mu_{MO(i)}$) were considered. For comparison, the explicit values of the bulk loss (μ_2) and population stage mortality (μ_{MO}) rates were opposed by equivalents derived for population loss values ($\mu_{2(i)^*}$) and bulk mortality (μ_{MO^*}).

Finally, all fluxes from the population to other compartments, processes number 13, 17, 9 and 14) within eq. 1-2 and 4-5 were determined. To prevent that any flux goes negative, each flux get checked and if necessary the time step loop is iterated with half the time step until the flux is positive otherwise the program stops.

The model system was set up using forcing and boundary conditions of the years 2003-2004 which are summarized in Figure 3. Reanalysis data from the National Centers for Environmental Prediction (NCEP) were used for the meteorological forcing (i.e. air temperature, cloud coverage, humidity, pressure, radiation and wind speed) to run a HAMSOM application for these years providing the necessary hydrodynamic forcing for ECOHAM3. Initial and boundary data were derived from the World Ocean Atlas 2001 for the biogeochemical module. A two year spin-up for 2003 with the population initiated by an overwintering stock of adults of 300 Ind m^{-3} corresponding to 0.3 mg N m^{-3} was made previous to the consecutive simulation of the years 2003 and 2004.

Two North Sea positions were selected for further analysing the 3D simulation. One site is located in the northern North Sea (FLEX, 58° 55' N, 0° 30' E; depth 135 m) dominated by North Atlantic water masses with strong wind-induced (winter) mixing and the development a seasonal thermocline during Apr-Oct. The other site is a station in the southern North Sea (GLOBEC-Germany station #32 (GG32), 54° 40' N, 7° 00' E; depth 38 m) with variable river plume fronts and strong horizontal gradients due to (vertical) tidal mixing. An additional station known as Helgoland Reede has a long tradition in plankton observation.

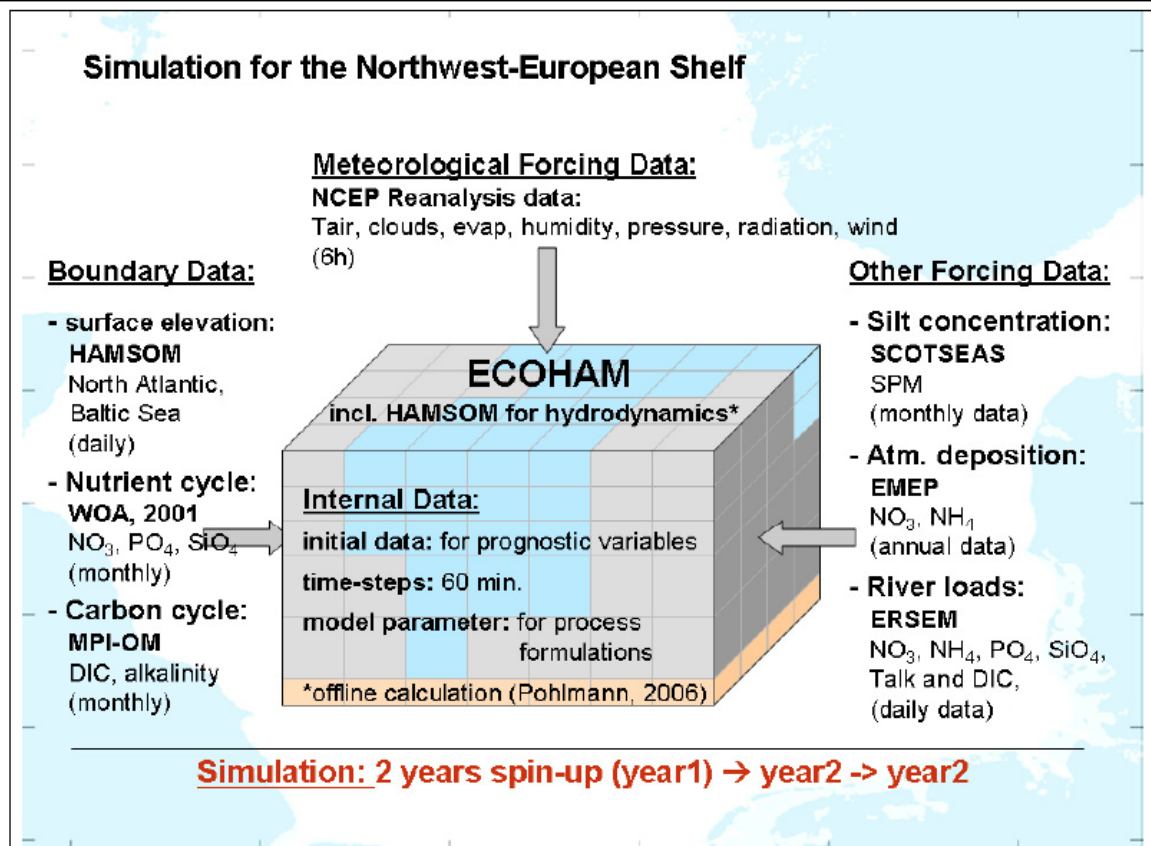


Figure 3 Initial, boundary and forcing data necessary for the three-dimensional ECOHAM runs applied to the North Sea simulation.

3. Model Code

The code is in MATLAB and open to sharing and can be downloaded from the Model Library on the MEECE Project website (www.meece.eu) or requested from Andreas Moll (andreas.moll@zmaw.de) at the University of Hamburg, see overview at the Appendix.

Brief outline of Model: The structured copepod population sub-model is parameterized for *Pseudocalanus elongatus* at five stage groups. The zero-dimensional version is for parameterization according to laboratory data. A three-dimensional version simulates the annual cycle and regional differences of the North Sea zooplankton. The name of the ecosystem model is ECOHAM (ECOsystem model, HAMBurg) which is a lower food web functional-type model that was developed in the Institute of Oceanography, Hamburg within German BMBF funded projects. It is related to NPZD type models, but includes the microbial loop, (partly) variable C:N stoichiometry, and a simple description of benthic biochemical processes. The zooplankton population model (parameterized) for *Pseudocalanus elongatus* has been coupled to ECOHAM. The hydrodynamic, biogeochemical and ecosystem modules include several refinements necessary to correctly represent the key processes of temperate shelf ecosystems, like the North Sea.

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Parameterization: The file system "PROCOPE5*.m" contains several Matlab routine that calculates zero-dimensional (0D) laboratory culture studies. A data set from Klein Breteler et al. (1995) was used, which includes estimates at temperatures of 5, 10, 15 and 20 °C each at food concentrations of <70, ~100 and >200 µg C l⁻¹. Simulations at each scenario showed the effectiveness in terms of stage duration. Results of the Matlab run (here run R07) were stored in a file "PROCOPE5_R07.log/dat for print out and plot analysis as a pure text file.

The biological functions were chosen particularly and formulated to get realistic characteristics of growth and development under conditions of temperature and food reported for the North Sea (Stegert

et al., 2007). Parameter values for weight, hatching and assimilation were taken from the literature, employing robust values from various published studies and parameters derived from similar species. The influence of temperature on feeding and basal respiration and the half-saturation of ingestion were obtained indirectly by successive fitting of developmental times and stage durations observed. Several plot routines exist.

Implementation in ECOHAM: The three-dimensional ecosystem model for the North Sea (ECOHAM) includes competition between one structured copepod population and the rest of the zooplankton biomass within the carbon, nitrogen and oxygen cycles of the lower trophic ecosystem (Pätsch et al., 2009). Outputs are values for ten state variables representing the naupliar and copepodite stage groups of eggs-N2 (i.e. non-feeders), N3-6, C1-3, C4-5, and adults each in terms of abundance and biomass. The species-specific (critical moulting) weights were determined from laboratory data and from GLOBEC-Germany cruise data in the German Bight. Additional output is the bulk zooplankton biomass, and thus the ratio of population biomass to total biomass. A comparison of simulated total zooplankton biomass and stage-resolved abundances with copepod counts at several stations in the German Bight during the GLOBEC-Germany project from February to October 2004 give Stegert et al. (2009). Code developed by IfM, based on a cooperation between Andreas Moll, Christoph Stegert, Markus Kreuz and Francois Carlotti.

Statement of Use: It is strongly recommended that you contact the originator of this document (Andreas Moll, andreas.moll@zmaw.de) before using the code provide, so that additional support (by selection of existing code also in FORTRAN subroutines) can be provided as required (for a best fit to the intended application).

Klein Breteler, W.C.M., Gonzales, S.R. and Schogt, N., 1995. Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Marine Ecology Progress Series*, 119: 99-110.

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4. Appendix A: Overview on Matlab code for the (0D) laboratory studie

```

PROCOPE5_R07_multi.m
%=====
% initialization & start - file for PROCOPE5.m
%=====

PROCOPE5pres.m
% Main programm for rearing tank experiment
% Pseudocalanus dynamics with five stages
%=====
% ---- Definitions ----
% please see inside m-file
%=====

Subroutines:
ode_outputfun.m
sub_fermi_FENNEL.m
sub_fermi_PROCOPE.m
sub_grazPC_FENNEL.m
sub_grazPC_PROCOPE_MM3.m
sub_grazPC_sigmoidal.m
sub_hatchPC_FENNEL.m
sub_hatchPC_PROCOPE.m
sub_metLossPC.m
sub_mortPC.m
sub_parabolic_PROCOPE.m
sub_reprodPC_CARLOTTI.m
sub_sigmoidal_PROCOPE.m
sub_sun_d.m
sub_transPC_FENNEL.m
sub_transPC_PROCOPE.m

PLOTTING:
clip_figures.m
clip_stagedur.m
plot_abundance.m
plot_biomass.m
plot_development.m
plot_egestion.m
plot_forcing.m
plot_grazfun2_test.m
plot_growth.m
plot_ingestion.m
plot_losses.m
plot_meanmass.m
plot_mortality.m
plot_reproduction.m
plot_stageduration.m
plot_stagefrequencies.m
plot_transfer.m
suptitle.m

File for output named by run number:
PROCOPE5_R07_multi.log
PROCOPE5_R07_multi.dat

```

5. Appendix B: Output file for the laboratory studie

MODEL-RUN: 04-Jun-2008 13:38:08

INITIALISATION FILE

```
=====
PROCOPE5_R07_multi
INCLUDE SUBFUNCTIONS
=====
```

```
C.grazfun1 : sub_grazPC PROCOPE MM3
C.grazfun2 : sub_parabolic_PROCOPE
C.transfun : sub_transPC_PROCOPE
C.hatchfun : sub_transPC_PROCOPE
C.reprofun : sub_reprodPC_CARLOTTI
C.Mlossfun : sub_metLossPC
C.mortfun  : sub_mortPCa
```

INITIAL SETTINGS

```
=====
first day : 0
last day  : 80
t-resolution : auto (ode23-resolution)
C.SwitchE : 0 => no egg laying
C.SwitchT : 0 => transfer uncoupled
C.SwitchV : NaN => default (latest) version
```

forcing data:

```
-----
water temp. [°C] : 20
Phytoplankton [µgC/l] : 221.00
```

functional parameters:

```
-----
C.PA - accuracy/relevancy [%/totN] of graph.display : 0.010
C.GE - to check grazing efficiency experimentally : 1.000
C.RT - reference Temperature for parametrisations [°C] : 10.000
```

constants:

```
-----
C.PC(1) - p-fun.: %-added to crit. mass (-> max mass) : 2.000
C.EC(1) - female-percent. of adultes for reproduction : 0.500
C.EC(2) - loss of weight in %-bodymass per egg laid : 0.800
```

stage dependent constants & coefficients for function formulation

```
-----
          %eggs %naup %cop1 %cop2 %adul
C.rMt = [ 0.14 0.50 1.80 4.30 7.50 ]; %transfer reference mass [µgC]
C.cMt = [ 0.10 0.70 2.40 5.40 8.60 ]; %transfer critical mass [µgC]
C.rMg = [ NaN 0.70 2.40 5.40 8.60 ]; %growth/ingestion reference mass [µgC]
C.cMg = [ NaN 0.80 2.70 6.00 9.60 ]; %growth/ingestion critical mass [µgC]
C.IDX = [ 2 6 9 11 12 ]; %Stage Index (number of last stage in group)
C.IR = [ NaN 1.0000 0.6000 0.5000 0.3000 ]; %ingestion: rates at T=Tref [as % of body mass]
C.IQ = [ NaN 2.58 2.58 2.58 2.58 ]; %ingestion: ingestion Q10-factor
C.IE = [ NaN 1.15 1.40 1.40 1.40 ]; %ingestion: ingestion-function exponent)
C.RP = [ NaN 30.00 60.00 60.00 60.00 ]; %ingestion @MM: reference phc-concentration [µgC/l]
C.TO = [ NaN 15.00 15.00 15.00 15.00 ]; %ingestion @HY: Temp.offset/fit for reducing ingestion
C.Ic1 = [ NaN 1.40 1.40 1.40 1.40 ]; %ingestion @HY: constant for ingestion reducing hyperbola
C.Ic2 = [ NaN -0.12 -0.12 -0.12 -0.12 ]; %ingestion @HY: constant for ingestion reducing
hyperbola
C.MLa = [ NaN 0.40 0.33 0.33 0.28 ]; %metabolic loss: activity metabolism [%-ingestion rate]
C.MLb = [ 0.07 0.05 0.02 0.02 0.02 ]; %metabolic loss: basic metabolism [%-of body mass] at
10°C
C.MLQ = [ 3.60 2.58 2.58 2.58 2.58 ]; %metabolic loss: Q10-factor (for basic metabolism)
C.AE = [ NaN 0.65 0.65 0.65 0.65 ]; %egestion: assimilation efficiency [%-ingestion rate]
C.MR = [ 0.0300 0.0300 0.0300 0.0300 0.0300 ]; %mortality: rate constants
C.IE = [ 6.00 4.00 4.00 4.00 4.00 ]; %transfer: transfer-function exponent)
C.mP = [ NaN NaN NaN NaN NaN ]; %min. phc [µgC/l] -> switch off grazing
C.mA = [ NaN 0.00 0.00 0.00 0.00 ]; %min. abund. [ind/l] -> switch off transfer
C.mT = [ NaN NaN NaN NaN NaN ]; %min. temp. [°C] -> switch off transfer
C.mB = [ NaN 0.00 0.00 0.00 0.00 ]; %min. biomass [µgC/l] -> switch off mortality
```

initial state vector

```
-----
[ 1 2 3 4 5 % column
```

```
Z0 = [ z1c;      z2c;      z3c;      z4c;      z5c;      ... % biomass
Z0 = [ 1.40e-001; 0.00e+000; 0.00e+000; 0.00e+000; 0.00e+000; ... % [µgC/l]
      6          7          8          9          10          % column
      i1c;      i2c;      i3c;      i4c;      i5c ];      % abundance
      1.00e+000; 0.00e+000; 0.00e+000; 0.00e+000; 0.00e+000 ]; % [ind/l]
```

=====

FUNCTION OUTPUT

=====

| TIME | z1c | z2c | z3c | z4c | z5c | i1c | i2c | i3c | i4c |
|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| i5c | phc_z1c | phc_z2c | phc_z3c | phc_z4c | phc_z5c | z1c_z2c | z2c_z3c | z3c_z4c | z4c_z5c |
| z5c_z1c | z1c_dic | z2c_dic | z3c_dic | z4c_dic | z5c_dic | z1c_doc | z2c_doc | z3c_doc | z4c_doc |
| z5c_doc | z1c_dXc | z2c_dXc | z3c_dXc | z4c_dXc | z5c_dXc | graz_f1 | graz_f1 | graz_f1 | graz_f1 |
| graz_f1 | graz_f2 | graz_f2 | graz_f2 | graz_f2 | graz_f2 | trans | trans | trans | trans |
| trans | egg/fem | T | phc | | | | | | |

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