Supplements for: Parameterising a generic model for the dynamic energy budget of Antarctic krill, *Euphausia superba*

T. Jager*, E. Ravagnan†

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Supplement 1 Model description

Supplement 1.1 Basic model

The basic DEBkiss model is schematically depicted in Figure S1, showing the mass fluxes J_* (in dry weight per unit of time). This model has been published in the open literature [2], but an extended version of that paper is available as a freely-downloadable e-book from http://www.debtox.info/book_debkiss.php. The e-book contains more explanation, more derivations, and more possible extensions of the basic model described here.

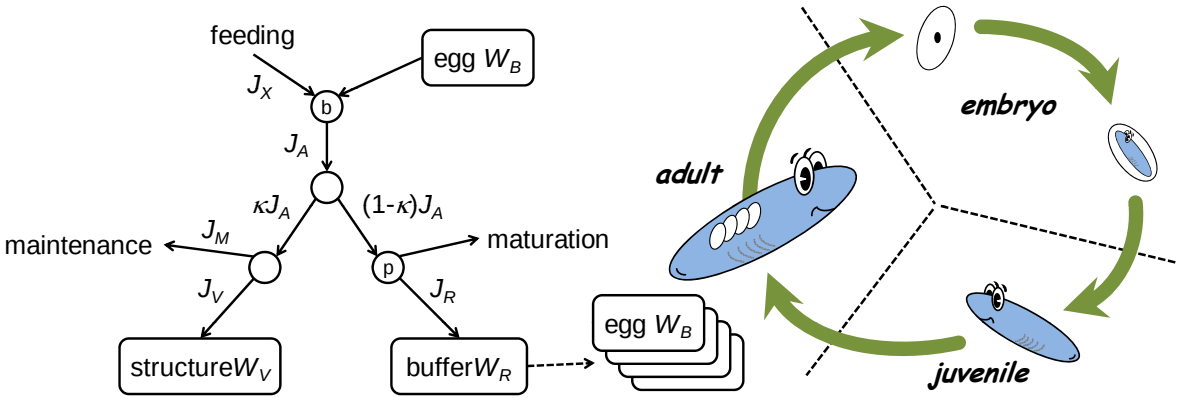

Figure S1: Schematic diagram of the energy flows and life cycle of a DEBkiss animal. The parameter symbols are explained in Table S1. The nodes b and p denote switches at birth (start of feeding; embryo to juvenile) and puberty (start of investment in the reproduction buffer; juvenile to adult). The other nodes represent a split of the assimilation fluxes.

*Dept. of Theoretical Biology, VU University, Amsterdam, The Netherlands
†IRIS Environment, International Research Institute of Stavanger, Randaberg, Norway

Table S1: Explanation of symbols, with dimensions given in mass (m for body, m_a for assimilates, and m_f for food), body length (l), numbers (#), time (t). Suggested values for the yields (apart from y_{AV}) based on the typical values in [3].

Symbol	Explanation	Dimension	Sugg. value
	Primary parameters		
f	Scaled functional response	f	–
J^a_{Am}	Maximum area-specific assimilation rate	$m_a/(l^2t)$	–
J^v_M	Volume-specific maintenance costs	$m_a/(l^3t)$	–
W_{B0}	Assimilates in a single freshly-laid egg	m_a	–
L_p	Volumetric lenght at puberty	l	–
y_{AV}	Yield of assimilates on structure (starvation)	m_a/m	0.8 mg/mg (dwt)
y_{AX}	Yield of assimilates on food	m_a/m_f	0.8 mg/mg (dwt)
y_{BA}	Yield of egg buffer on assimilates	m_a/m_a	0.95 mg/mg (dwt)
y_{VA}	Yield of structure on assimilates (growth)	m/m_a	0.8 mg/mg (dwt)
κ	Fraction of assimilation flux for soma	–	0.8
	Conversions		
d_V	Dry-weight density of structure	m/l^3	
δ_M	Shape correction coefficient	–	
	Fluxes and states		
J_A	Mass flux for assimilation	m_a/t	
J_M	Mass flux for maintenance	m_a/t	
J_R	Mass flux to reproduction buffer	m_a/t	
J_V	Mass flux for structure	m/t	
J_X	Mass flux of food	m_f/t	
W_B	Mass of assimilates buffer in egg	m_a	
W_R	Mass of reproduction buffer in adult	m_a	
W_V	Mass of structural body	m	
	Other output		
L	Volumetric body length	l	
L_w	Physical body length	l	
ΔR	Number of eggs in a clutch	#	
W_w	Physical body weight (total)	m	

The model departs from a set of assumptions, which lead to the model equations. The symbols, with their dimensions, are explained in Table S1. The first section of the table shows the primary parameters: parameters that are directly linked to a metabolic process, and that do not themselves depend on other parameters. Regarding notation, we use superscripts to indicate volume- or surface-area-specific parameters. Therefore, J_M^v is the volume-specific costs for maintenance, and J_{Am}^a is the area-specific assimilation rate at maximum food.

Assumptions 1: There are three types of biomass: food, assimilates and structural body components. Each type has a constant composition. They can be converted in each other with a certain constant efficiency. The state variables of the organism are the masses of the structural body, the reproduction buffer for adults, and the egg buffer used by the developing embryo. Total body mass is the sum of structure and reproduction buffer in adults, and the sum of structure and egg buffer for eggs. The reproduction and egg buffer consist of assimilates.

The 'currency' that we are going to follow in the model is mass as dry weight (e.g., in grammes). However, we can substitute mass for energy: because we assume that each type of biomass has a strictly constant composition, the conversions between mass and energy are also constant.

The total weight of the animal is the sum of structure and buffer ($W_w = W_V + W_R$), just like the total weight of an egg ($W_w = W_V + W_B$). For some processes, we need to have access to the structural volume (L^3) of the animal. We can assume a constant density for structure (d_V):

$$L^3 = \frac{W_V}{d_V} \tag{S1}$$

We can talk about L as the 'volumetric structural length' of the animal. If the structural biomass W_V is compressed into a cube, this will be the length of a side of that cube.

In many cases, we measure body size of an animal as some physical length measure, such as the total length in krill. As long as the organism does not change in shape during growth, we can translate structural weight to some physical length (L_w) and vice versa using a constant correction factor δ_M:

$$L_w = \frac{L}{\delta_M} \tag{S2}$$

Assumptions 2: The animal has three life stages: an embryo that does not feed but utilises the egg buffer, a juvenile that feeds but does not reproduce, and an adult that feeds and invests into a reproduction buffer. The embryo starts with an egg buffer of assimilates and negligible structural mass. The first transition (birth) is triggered by the depletion of the egg buffer, and the second transition (puberty) by reaching a critical structural body weight.

The differential equations for the egg buffer W_B, structural body mass W_V, and reproduction buffer W_R are given by (see Fig. S1):

$$\frac{\mathrm{d}}{\mathrm{d}t}W_B = -J_A \quad \text{until } W_B = 0, \text{ with } W_B(0) = W_{B0} \tag{S3}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}W_V = J_V \quad \text{with } W_V(0) \approx 0 \tag{S4}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}W_R = J_R \quad \text{with } W_R(0) = 0 \tag{S5}$$

Note that $t = 0$ marks the start of development in the egg.

Assumptions 3: The maximum assimilation rate is proportional to the surface area of the animal. The entire process of food searching and handling is condensed into a scaled function response (f).

Assumptions 4: Food is instantly translated into assimilates that are directly used to fuel metabolic processes. Embryos assimilate their egg buffer at the maximum rate for their structural size.

Feeding involves the transport of resources from the environment to the organism across a surface area (e.g., the area of the gut, or the area of the feeding appendages in filter feeders). As long as the organism does not change in shape (isomorphy), all surface areas scale with body volume to the power 2/3 (and thus L^2). The assimilation flux J_A is thus given by:

$$J_A = f J_{Am}^a L^2 \quad (\text{if } W_B > 0 \text{ then } f = 1) \tag{S6}$$

where f is the scaled functional response, which is the actual feeding rate at a certain food level divided by the maximum feeding rate for its current size. The scaled response f is thus between 0 (no food) and 1 (*ad libitum* food). The maximum specific assimilation rate (J_{Am}^a) is used as the primary parameter. The feeding rate (J_X) is derived from the assimilation flux using the yield of assimilates on food (y_{AX}):

$$J_X = \frac{J_A}{y_{AX}} \quad (\text{if } W_B > 0 \text{ then } J_X = 0) \tag{S7}$$

Here, we do not follow feeding explicitly and use f as a primary model parameter. The assimilates are directly used in metabolism, and we thus do not consider any storage other than the reproduction buffer.

Assumptions 5: The flow of assimilates is split into a constant fraction κ for maintenance and structural growth (the soma), and $1 - \kappa$ for maturation and reproduction. From the κ flow, maintenance costs are paid first. Only structural biomass requires maintenance, which is proportional to its volume. The remainder of this flow is used for growth (with certain efficiency).

A constant κ has convenient properties, which compare favourably to other possible allocation rules [4]. A constant κ, together with the assumptions for assimilation and maintenance, leads to the commonly-observed von Bertalanffy growth curve in constant environments.

Maintenance is the, rather abstract, lump sum of all the processes needed to maintain the body's integrity. Assimilate buffers are assumed not to require maintenance, which is supported by the almost-complete lack of respiration in freshly-laid eggs. The flux for structural growth (J_V) can thus be specified as:

$$J_V = y_{VA}(\kappa J_A - J_M) \quad \text{with } J_M = J_M^v L^3 \tag{S8}$$

where J_M^v is the volume-specific maintenance cost, and y_{VA} is the yield of structural biomass on assimilates.

Assumptions 6: For adults, the $1-\kappa$ flow is used to fill the reproduction buffer. For embryos and juveniles, all of the assimilates in this flux are burnt to increase complexity of the organism (maturation). At spawning events, the contents of the reproduction buffer are converted into eggs. The part of the buffer that was insufficient to create a single egg remains in the buffer. Transformation of buffer to egg comes with a certain (generally high) efficiency.

Before reaching 'puberty', the $1-\kappa$ flux is used for the maturation process (which in this model definition is not associated with the build-up of biomass), which abruptly stops at puberty, when the flux is switched to the reproduction buffer. The flux into the reproduction buffer (J_R) can thus be specified as:

$$J_R = (1-\kappa)J_A \quad (\text{if } L < L_p \text{ then } J_R = 0) \tag{S9}$$

where L_p is the volumetric length at puberty. The trigger for spawning is not specified here, as this is highly species-specific. Spawning leads to a clutch of offspring ΔR, and a reset of the reproduction buffer W_R:

$$\Delta R = \text{floor}\left(\frac{y_{BA} W_R}{W_{B0}}\right) \tag{S10}$$

$$W_R = W_R - \frac{\Delta R W_{B0}}{y_{BA}} \tag{S11}$$

where y_{BA} is the yield for the conversion of reproduction buffer to eggs. The 'floor' function for the spawning events means rounding to the nearest integer less than the value between brackets.

Assumptions 7: If feeding is insufficient to pay somatic maintenance costs, the organism first diverts energy from the 1-κ flux of assimilates and from the reproduction buffer. If that is insufficient, structure is converted into assimilates to pay maintenance.

We need assumptions to deal with the situation of starvation, as varying food levels are common in the field, and because our animal does not have a storage of assimilates (other than the reproduction buffer). The first stage of starvation occurs when the allocated flux to the soma is insufficient to pay maintenance ($\kappa J_A < J_M$), but the total assimilation flux *is* enough ($J_A > J_M$), or there is still something in the reproduction buffer ($W_R > 0$):

$$J_V = 0 \tag{S12}$$
$$J_R = J_A - J_M \quad (\text{if } L < L_p \text{ then } J_R = 0) \tag{S13}$$

For juveniles, this means that energy is diverted from the flux to maturation, as long as $J_A > J_M$ (maturation itself is not followed as a state variable). In the second stage of starvation, the reproduction buffer is empty ($W_R = 0$) and the total assimilation flux is insufficient to pay maintenance ($J_A \leq J_M$):

$$J_V = (J_A - J_M)/y_{AV} \tag{S14}$$
$$J_R = 0 \tag{S15}$$

where y_{AV} is the yield of assimilates (to pay maintenance) on structure. The maximum rates of feeding, assimilation and maintenance depend on structural size, so when the animal shrinks, these rates will decrease too. Clearly, shrinking under starvation cannot continue indefinitely. If situations of prolonged starvation are analysed, it makes sense to set a limit to shrinking, e.g., to a fraction of the maximum size that the individual has reached.

Supplement 1.2 Adaptations for krill

For krill, we introduce a specific value for the functional response before birth (embryo and non-feeding larval stages) to accommodate the slower development than predicted from the parameterisation on the juveniles/adults. In Eq. S6, the condition after the expression for J_A is modified to: if $W_B > 0$ then $f = f_B$. This introduces the parameter f_B as the scaled functional response for feeding on the egg buffer W_B.

At 'puberty' ($L = L_p$), the investment in maturity is switched to the reproduction buffer. In krill, we position this point at the moult from the last furcilia stage to the first juvenile stage. However, even though the juveniles will build up a reproduction buffer, they are not able to produce gametes. Therefore, we can refer to them as 'sub-adults'. In Table S2, we provide an overview of the stages in krill and their interpretation in a DEB context.

Supplement 1.3 Respiration flux

Respiration can be taken proportional to the total flux of assimilates that is dissipated. The dissipation flux is the sum of the assimilates used for maintenance (J_M) and maturation

Table S2: Stages in the krill life cycle, their corresponding stage in DEB terminology, and explanation of the defining properties of the stage.

Krill stage	DEB stage	Explanation
egg, nauplii	embryo	non feeding, assimilation from egg buffer
calyptopis, furcilia	juvenile	feeding, no investment in repro buffer
juvenile	sub-adult	investment in repro buffer, but no gametes
adult	adult	investment in repro buffer, gamete production

(J_H), plus the overheads for growth, reproduction and feeding. Introducing an additional subscript 'o' to specify overheads, the total dissipation flux is given by:

$$J_D = J_M + J_H + J_{Vo} + J_{Ro} + J_{Xo} \tag{S16}$$

Here, we only consider two extreme scenarios; a minimum in which only maintenance costs contribute, and a maximum in which the entire flux of assimilates that is not fixed in structure is burnt:

$$J_D = J_A - J_V \tag{S17}$$

The maximum respiration flux thus represents embryos and juveniles up to the point where the investment into the reproduction buffer starts. From that point, we use:

$$J_D = J_A - J_V - J_R \tag{S18}$$

The feeding overheads J_{X0} (also referred to as the heat increment of feeding) are ignored here, as in practice, respiration is determined in animals that have been starved for a while to allow this component to be ignored.

Respiration is often expressed as volume of oxygen used. To convert this to grammes of carbon, we need the respiratory quotient (F_{RQ}) which is the moles of CO_2 (and thus also the moles of C) eliminated per mole of O_2 taken up (which depends on which substrate is burned, e.g., lipids or protein). Furtermore, we need the molar mass of O_2 (32 g/mol) and C (12 g/mol), and the density of oxygen (1.429 g/l at 0°C and 1.331 g/l at 20°C).

$$\begin{aligned} F_{RQ}[\text{mol } O_2] &= [\text{mol C}] && \text{(S19)} \\ F_{RQ}[\text{g } O_2]/32 &= [\text{g C}]/12 && \text{(S20)} \\ F_{RQ}[\text{l } O_2] \times 1.429/32 &= [\text{g C}]/12 && \text{(S21)} \\ F_{RQ} \times 12 \times 1.429/32 &= [\text{g C}]/[\text{l } O_2] && \text{(S22)} \end{aligned}$$

Table S3 provides the conversions from oxygen to carbon for various scenarios. To link the respiration losses in grammes of carbon per day to the value of J_D (which are in mg dry weight per day), we additionally need the carbon content of biomass for the species (0.4 mg C per mg dwt is a reasonable default).

Table S3: Conversion factors from l O_2 to g C for various substrates burnt. Source for the respiratory quotients: http://en.wikipedia.org/wiki/Respiratory_quotient.

Substrate	Resp. quotient	g C / l O_2 (0°C)	g C / l O_2 (20°C)
Carbohydrates	1	0.54	0.50
Protein	0.8-0.9	0.43-0.48	0.40-0.45
Fat	0.7	0.38	0.35

Supplement 1.4 Changes in temperature

We can assume that all rate constants (with a dimension that includes 'per time') scale in the same way with temperature. We can use the Arrhenius relationship to scale from a reference temperature T^* to the actual temperature T (both in Kelvin). All physiological rate constants have to be multiplied by:

$$F_T = \exp\left(\frac{T_A}{T^*} - \frac{T_A}{T}\right) \tag{S23}$$

where T_A is the Arrhenius temperature in Kelvin. Lika and co-workers [3] suggest a value of 8000 K as typical value.

Supplement 1.5 Instantaneous growth rate

The DEBkiss model specifies growth in dry weight (Eq. S4), whch we can convert (using the chain rule for differentation) to growth on volumetric length basis:

$$\frac{\mathrm{d}}{\mathrm{d}t}W_V = \frac{\mathrm{d}}{\mathrm{d}t}(d_V L^3) = 3 d_V L^2 \frac{\mathrm{d}}{\mathrm{d}t}L \tag{S24}$$

Considering that $L = L_w \delta_M$, we can convert this to an equation for growth in physical length:

$$\frac{\mathrm{d}}{\mathrm{d}t}W_V = 3 d_V L^2 \delta_M \frac{\mathrm{d}}{\mathrm{d}t}L_w \tag{S25}$$

As $\frac{\mathrm{d}}{\mathrm{d}t}W_V = J_V$ we can derive an expression for the instantaneous growth in physical length:

$$\frac{\mathrm{d}}{\mathrm{d}t}L_w = \frac{J_V}{3 d_V L^2 \delta_M} \tag{S26}$$

Supplement 2 Estimate of storage build up

From the data of Hagen et al. [1], we can roughly calculate the size of the lipid storage over time in different classes. These authors report body dry mass and lipid mass for field-sampled animals caught in winter/spring, summer and autumn. To use these data, we need to make a series of assumptions:

1. The animals in winter/spring have no storage, so their lipid mass (around 10% of dwt) represents structural lipids. This is supported by the observation that the larval stages had a similar lipid percentage.

2. In the animals in summer and autumn, the same fraction of the lipids is structural lipids as in the winter/spring animals. Higher lipid fractions thus represent additional storage lipids.

3. Even though the sampling dates were in different years (not from the same cohort), they are representative for the general pattern in a cohort over the season.

4. Each mg dry weight of assimilates is used to make 0.5 mg dry weight of lipids (as the carbon content of lipids is roughly two times higher than that of structural biomass). This factor of 2 is supported by the data of Meyer et al [5], who measured both lipids and carbon content.

5. The water content of lipids is negligible, so the measured lipid mass is dry mass.

6. Animals invest the full $1-\kappa$ flux into the storage and nothing in maturation.

7. The animals experience a temperature of 0°C.

As we have an estimate for the structural dry weight of the animals, we can make assumptions about the food availability. We only have 3 measurements over time, with roughly 3 months in between. We fit a different constant value of f in the first 3 months than in the second 3 months (see Table S4). All other parameters are set to the values in Table 2 in the main text. The resulting values for f are smaller than 1 for juveniles, which indicates that feeding conditions for this class were less than optimal. For the adults, f is closer to one, and the same values were used for both males and females.

Table S4: Estimated values for f in the interpretation of data on lipid storage.

	f period 1	f period 2
juveniles	0.48	0.59
adults (male and female)	0.98	0.83

With f determined by the reported body weights at different time points, we can predict the build up of the lipid storage. The measured data for the lipid content are rather close to the predictions (Figure S2), especially given our crude set of assumptions. We can interpret this in two different ways:

1. Our parameterisation (especially the value for κ) is realistic and animals here did not invest in maturity or in spawning.

2. Next to storage, juveniles also invest in maturity and adults might have used energy for spawning activities, and we thus need a lower value of κ to have a flux $1-\kappa$ that is large enough to fulfil both needs (and perhaps also some additional maintenance processes in the $1-\kappa$ branch).

To investigate Option 2, we also used the alternative parameterisation with a low value for κ (Table S5 in Supplement 3) for the same analysis. This leads to a severe overprediction of the observed lipid content (Figure S3), but leaves a lot of room to use the $1 - \kappa$ flux for additional purposes (maturation, maturity maintenance, spawning). The adults would need to spend a large amount of energy on spawning activities, and the juveniles would need a large investment in maturation (which would likely show up in the respiration measurements).

With the current set of data, no firm conclusions on lipid storage or the value of κ can be drawn. Nevertheless, the predicted storage build up lies in the same order of magnitude as that observed in the field data, with reasonable values of κ. A value of $\kappa = 0.8$ may be too high, as there will be no energy left for spawning activities, but 0.4 is probably too low, as it would lead to large respiration losses in juveniles (which is inconsistent with the measured respiration rates, see Supplement 3).

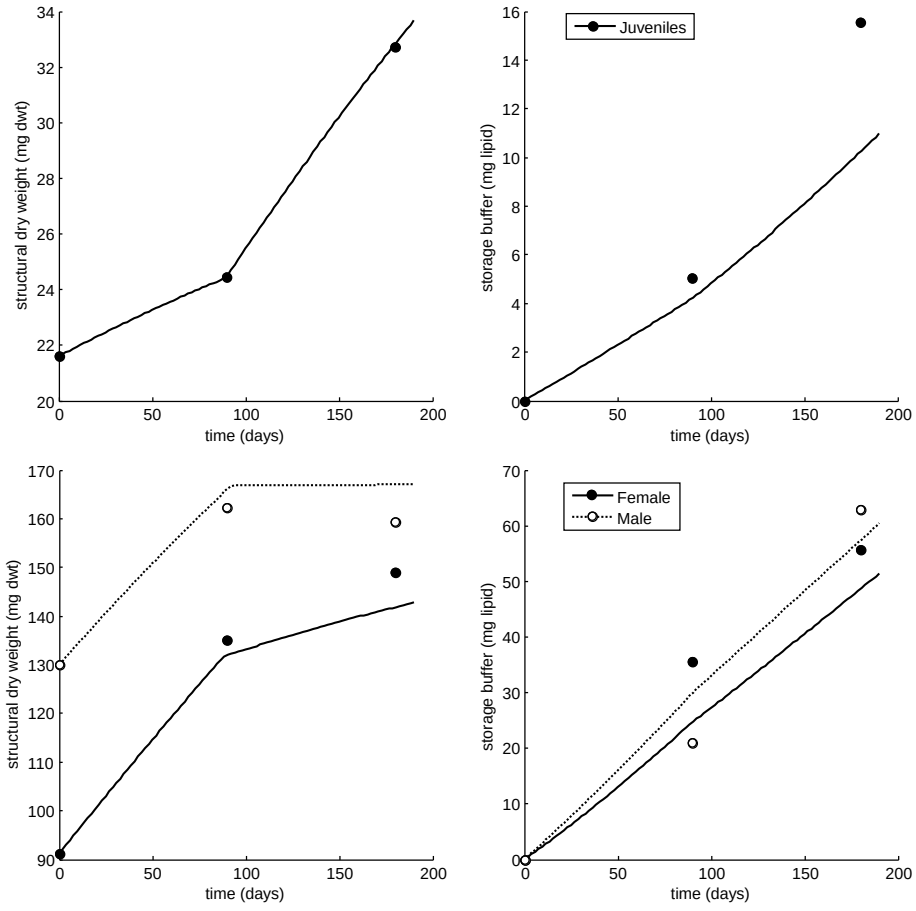

Figure S2: Estimates of structural dry weight and lipid storage from field data, with model predictions based on the parameterisation in Table 2 of the main text. The apparent food availability was fitted to match the observed structural growth (two values of f, Table S4).

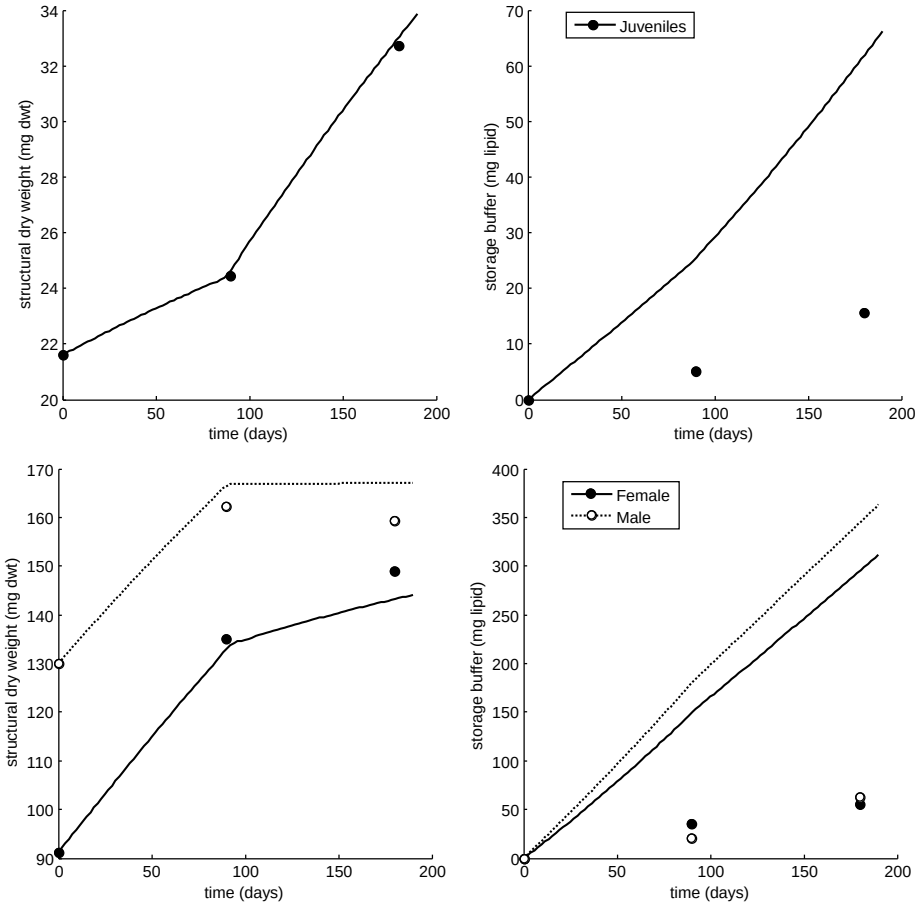

Figure S3: Estimates of structural dry weight and lipid storage from field data, with model predictions based on the alternative parameterisation with $\kappa = 0.4$. The apparent food availability was fitted to match the observed structural growth (two values of f, Table S4).

Supplement 3 Alternative parameterisation

Here, we present an alternative parameterisation based on a low value of κ of 0.4. The fit to the growth curves for juveniles/adults is exactly the same, the specific maintenance rate is unaffected by the choice of κ, but the specific assimilation rate is doubled (Table S5). The fit for the embryonic period (not shown) is slightly different as a low value of κ implies that a greater part of the egg buffer is burnt instead of fixed in structural biomass (leading to a smaller body size at 'birth').

Table S5: Alternative parameterisation for a low value of κ.

Symbol	Explanation	Value	Unit
J^a_{Am}	Maximum area-specific assimilation rate	0.087	mg/(mm^2 d)
J^v_M	Volume-specific maintenance costs	0.0032	mg/(mm^3 d)
κ	Fraction of assimilation flux for soma	0.4	–

For ingestion, the prediction are now twice as high (Figure S4). This implies that the

prediction for $f = 1$ is now closer to the highest reported values. Still, the prediction for adults (a ration of som 10%) is roughly a factor of 2 lower than the highest reported rates.

For respiration, the minimum prediction is unaffected by the re-parameterisation (Figure S4), as the specific maintenance rate stays the same. The only difference lies in the respiration rates before 'puberty' (here: the transition from furcilia to juvenile). With a low value for κ, maturation is a very large flux, and since this flux is burnt it leads to high respiration rates. Even using the low f for furcilia, the reported respiration rates for this stage are much lower than the predictions.

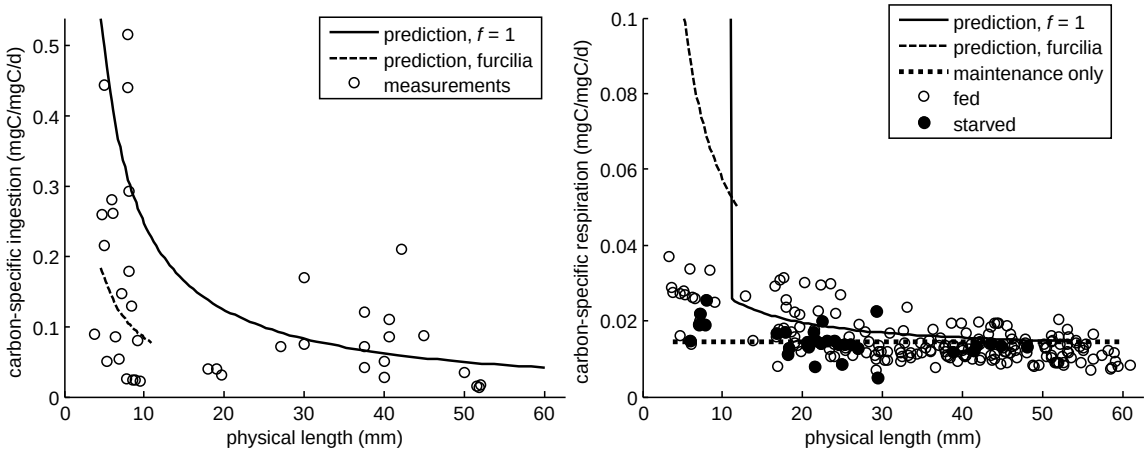

Figure S4: Prediction for ingestion and respiration rates, as in the main text, but here based on $\kappa = 0.4$.

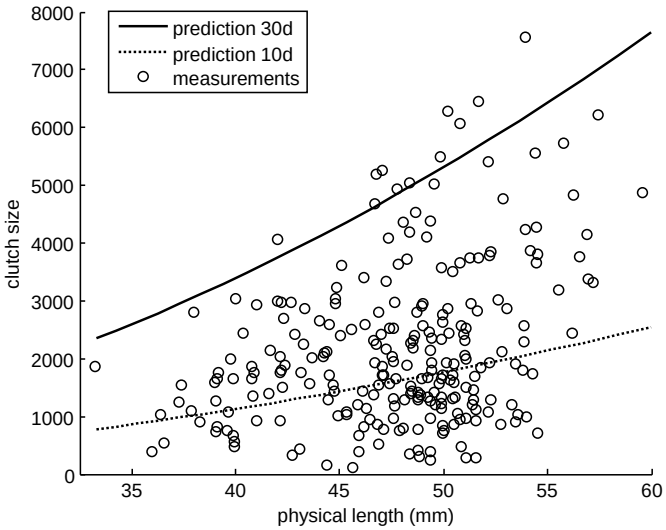

Figure S5: Prediction for clutch sizes, as in the main text, but here based on $\kappa = 0.4$.

Figure S5 shows the predictions for the clutch sizes at different build-up time of the reproduction buffer. With this parameterisation, 30 days of *ad libitum* feeding suffices to

produce the largest observed clutch sizes, and around 10 days from the most common clutch sizes. In contrast, the parameterisation in the main text would require 150 days for the largest clutches. A clutch build up time of 10 days is close to the 6.7 days predicted by Ross and Quetin [6]. Clearly, the value of κ is closely related to the potential number of spawning events within a season, and the range 0.4 and 0.8 covers the most extreme standpoints in this matter.

Decreasing κ from 0.8 to 0.4 increases the investment in the $1-\kappa$ branch by a factor of 3 (from 0.2 to 0.6). Coupled to the fact that J^a_{Am} increases by a factor of 2 (see Table S5) this implies an increased investment in storage/reproduction by a factor of 6 for a given length. Therefore, a sixfold increase in fecundity will, perhaps counter-intuitively, be accompanied by only a twofold increase in ingestion rates.

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