

A demand-driven dynamic energy budget model

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Idea and background

5 Almost all dynamic energy budget (DEB) models (e.g. Kooijman and Metz 1984, Gurney et al. 1990, Kooijman 1993, Persson et al. 1998, Kooijman 2000, Lika and Nisbet 2000) are based on the idea that food availability determines individual food intake and the subsequent availability of energy for energy consuming processes. These models hence share a supply-driven principle of individual energetics, in which food acquisition is always the limiting process rate in the energy budget, determining the rate of growth and reproduction. The models do not incorporate a feedback of energy demands on individual food intake. As a consequence, these models give rise to indeterminate, food-dependent growth of individual organisms with asymptotic sizes that vary with food availability. Even though this type of individual growth is perhaps most common there are many groups of species, mainly terrestrial and marine vertebrates, for which growth is much more controlled by genetics and much less by the environment. Here I develop a DEB model that accounts for determinate growth in body size. Determinate growth implies that energy demands are fixed, independent of current food availability and have to be covered. On the one hand these fixed demands require that energy reserves are needed to cover demands in case of food scarcity. On the other hand, the fixed demands require that food acquisition rate has to be limited by other factors than food density under conditions of ample food supply. Otherwise, such conditions may initiate a run-away process of fat build-up. I will model this limitation of food intake rate by making it dependent on the current body condition of the individual. I assume that regulation of individual energetics is such that a target body condition is aimed for.

Schematic representation of the dynamic energy budget

25 Figure 1 provides a schematic overview over the energy budget of an individual organism. Individual organisms are represented by two measures of individual body size, structural mass S and energy reserves E . Growth in structural mass is assumed to be determinate and is directly related to individual age. I assume the relationship between individual length and age to follow the vonBertalanffy growth equation. Individual length is assumed proportional to the cubic root of structural mass $S^{1/3}$. Costs for maintenance are assumed proportional to total body mass, which is the sum of structural mass and energy reserves. Energy investment in reproduction only occurs after the individual has reached a specific size threshold. However, because of the constant relationship between age and size this is equivalent with an age threshold. The juvenile delay between birth and the onset of reproduction is therefore constant. The amount of energy invested into reproduction I assume to be a function of both

body condition and individual structural mass. Reserve dynamics can either be anabolic, when energy intake through foraging exceeds total energy demands for growth maintenance and reproduction, or catabolic, when energy intake is smaller than the total energy demands. For the sake of simplicity the conversion efficiency between energy and reserves is assumed identical for anabolic and catabolic reserves dynamics, although in reality these efficiencies are likely to be different. Finally, a feedback is assumed between the reserves status (or body condition) of an individual organism and its food ingestion rate. Ingestion is assumed to increase with a decreasing ratio between energy reserves and structural mass.

Body condition

I assume that the body condition of an individual is characterized by the ratio of energy reserves over structural mass E/S . An alternative measure of body condition would be to take the ratio of energy reserves over total body weight, $E/(E+S)$. The latter measure is uniquely, but non-linearly related to the quantity E/S through a hyperbolic function, since

$$\frac{E}{E+S} = \frac{E/S}{E/S+1}.$$

Hence, changes in energy reserves translate in more rapid changes in the measure E/S than in the measure $E/(E+S)$. For this reason I have adopted the quantity E/S as the characterization of the reserves status or body condition of an individual.

Resource ingestion

I assume that resource ingestion scales with length squared and hence is proportional to $S^{2/3}$. Furthermore, resource ingestion scales with resource density following a type II functional response with attack rate α and handling/digestion time τ . A crucial assumption of the life history model is that resource ingestion is dependent on the body condition of the individual. In particular, I will assume that the attack rate is given by the following function of structural mass and energy reserves:

$$\alpha = \frac{\alpha_m}{1 + e^{\eta(E/S - \rho)}}$$

In this equation ρ represents the target value of the individual body condition. The parameter η determines how rapidly the resource ingestion responds to changes in body condition. At very low body conditions the individual attack rate will equal its maximum value α_m , while the attack rate will approach 0 at very high body conditions. In between the attack rate follows a sigmoid relationship with body condition, the steepness of which is determined by η . For very high values of η the attack rate will be maximal when the body

condition drops below its target value ρ , while the individual will stop foraging when the body condition rises above ρ .

$$\begin{aligned}
 G(R, S, E) &= \frac{\alpha_m (1 + e^{\eta(E/S - \rho)})^{-1} R}{1 + \alpha_m (1 + e^{\eta(E/S - \rho)})^{-1} \tau R} S^{2/3} \\
 &= \frac{1}{\tau} \frac{R}{(1 + e^{\eta(E/S - \rho)}) / (\alpha_m \tau) + R} S^{2/3} \\
 &= I_{\max} \frac{R}{R_h (1 + e^{\eta(E/S - \rho)}) + R} S^{2/3}
 \end{aligned}$$

- 70 In this derivation I have made the usual substitution for the maximum ingestion rate $I_{\max} = \tau^{-1}$ and the half-saturation resource density $R_h = (\alpha_m \tau)^{-1}$. The latter parameter now represents, however, a minimum value as larger body conditions will translate into a larger effective half-saturation resource density.

Assimilation

- 75 I will assume a constant assimilation efficiency ε of ingested resource. Hence, the energy assimilation rate follows:

$$I(R, S, E) = \varepsilon I_{\max} \frac{R}{R_h (1 + e^{\eta(E/S - \rho)}) + R} S^{2/3}$$

Maintenance

- 80 Energy requirements for maintenance are assumed to be proportional to total body weight, i.e.

$$C_M(S, E) = \sigma_M (S + E)$$

In this equation σ_M is the proportionality factor.

Growth in structural mass

- 85 Growth in individual length, which is assumed proportional to the cubic root of structural mass, is assumed to follow the vonBertalanffy growth equation. Hence, the relationship between age and structural mass can be described by:

$$S^{1/3}(a) = S_m^{1/3} - (S_m^{1/3} - S_b^{1/3}) e^{-\gamma a}$$

Or equivalently

$$S(a) = \left(S_m^{1/3} - \left(S_m^{1/3} - S_b^{1/3} \right) e^{-\gamma a} \right)^3$$

90 The change in structural mass per unit time equals:

$$\begin{aligned} \frac{dS}{da} &= 3 \left(S_m^{1/3} - \left(S_m^{1/3} - S_b^{1/3} \right) e^{-\gamma a} \right)^2 \cdot \gamma \left(S_m^{1/3} - S_b^{1/3} \right) e^{-\gamma a} \\ &= 3\gamma S^{2/3}(a) \left(S_m^{1/3} - S_b^{1/3} \right) e^{-\gamma a} \\ &= 3\gamma S^{2/3}(a) \left(S_m^{1/3} - S^{1/3}(a) \right) \\ &= 3\gamma \left(S_m^{1/3} S^{2/3}(a) - S(a) \right) \end{aligned}$$

The energetic costs for growth in structural mass are assumed proportional to this growth rate in structural mass:

$$C_G(S) = 3\sigma_G \gamma \left(S_m^{1/3} S^{2/3} - S \right)$$

95 In which σ_G is a proportionality constant, representing the energy requirements for 1 unit increase in structural mass.

Fecundity and reproductive costs

Since well-fed organisms can be assumed to have higher fecundity than poorly fed ones and larger individuals can be expected to have a higher fecundity than smaller ones, I will assume
 100 that fecundity is an increasing function of both individual body condition and individual structural mass. I will assume that fecundity scales with $S^{2/3}$, which resembles the scaling of maximum ingestion rate with structural mass. With this assumption I follow the DEB models developed by Kooijman (1993, Kooijman 2000) that I want to use as comparison for the DEB model developed here. For the dependence on body condition I adopt the most simple
 105 dependence and assume that fecundity is proportional to E/S . These assumptions result in the following expression for fecundity as a function of structural mass and body condition:

$$b(E) = \beta E / S^{1/3}$$

However, I will assume that only individuals with a structural mass larger than S_j are reproducing. Because of the constant relationship between age and size this implies that the
 110 juvenile delay between birth and the onset of reproduction is constant.

The energetic costs of reproduction are proportional to the fecundity and the size at birth of the individual organism:

$$C_R(E) = \sigma_R(1 + \rho)S_b b(E)$$

115 In which σ_R is a proportionality constant, representing the energy requirements for the production of unit mass.

Dynamics of energy reserves

120 Because growth in structural mass is determinate and hence an explicit function of individual age, the only i -state variable that follows an ordinary differential equation is the amount of energy reserves of an individual. Changes in energy reserves equal the balance between energy acquisition and all energy-demanding processes:

$$\frac{dE}{da} = \sigma_E (I(R, S, E) - C_M(S, E) - C_G(S) - C_R(S, E))$$

In this equation σ_E represents a conversion efficiency that converts stored reserves into energy available for life-supporting processes.

Starvation mortality

125 In addition to size-independent background mortality individuals are assumed to experience additional mortality due to starvation, when their body condition drops below a threshold level ρ_s . Moreover, death through starvation is guaranteed when an individual has depleted all its energy reserves. Following Persson et al. (1998) I assume starvation mortality to be described by the following function:

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$$d_s(S, E) = \mu_s \max(\rho_s S / E - 1, 0)$$

Resource re-growth

I will investigate model dynamics with both semi-chemostat resource dynamics:

$$P(R) = r(R_{\max} - R)$$

And logistic resource dynamics:

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$$P(R) = r R \left(1 - \frac{R}{R_{\max}} \right) = r \frac{R}{R_{\max}} (R_{\max} - R)$$

In case of logistic resource dynamics I will take a default parameter value for r that is 4 times larger than the corresponding parameter value for semi-chemostat resource dynamics. By doing so, the maximum productivity of the resource is in both cases identical. For semi-

140 chemostat resource dynamics maximum productivity equals rR_{\max} and is reached for $R = 0$,
while for logistic resource dynamics maximum productivity is reached at $R = R_{\max} / 2$ and
equals $rR_{\max} / 4$.

Population equations

Let $c(t, a)$ denote the density of consumers at time t with age a and let $E(t, a)$ denote the amount of energy reserves of these consumers at that time. The population dynamics can then
 145 be described by the following set of 2 partial differential equations for $c(t, a)$ and $E(t, a)$, respectively, and 1 ordinary differential equation for the resource dynamics (De Roos 1997).

$$\frac{\partial c(t, a)}{\partial t} + \frac{\partial c(t, a)}{\partial a} = -(\mu_b + d_s(S, E))c(t, a)$$

$$c(t, 0) = \int_{A_j}^{\infty} b(S, E) c(t, a) da$$

$$\frac{\partial E(t, a)}{\partial t} + \frac{\partial E(t, a)}{\partial a} = \sigma_E (I(R, S, E) - C_M(S, E) - C_G(S) - C_R(S, E))$$

$$E(t, 0) = \rho S_b$$

$$\frac{dR}{dt} = P(R) - \int_0^{\infty} G(R, S, E) c(t, a) da$$

In these equations I have written S instead of $S(a)$ and E instead of $E(t, a)$ to shorten the notation, whenever these variables occur as function arguments. The boundary condition for
 150 $E(t, 0)$ implies that I assume individual to be born with the target body condition. Finally, the quantity A_j in these equations represents the age at maturation of the consumers, which is given by:

$$A_j = \frac{1}{\gamma} \ln \left(\frac{S_m^{1/3} - S_b^{1/3}}{S_m^{1/3} - S_j^{1/3}} \right)$$

Parameterization

155 To parameterize the model I will follow as much as possible the consumer-resource
interaction that is described in De Roos & Persson (2002), which model I will use for
comparison. The consumer-resource model studied in De Roos & Persson (2002) is based on
the Kooijman-Metz (1984) DEB model. The population dynamic consequences of this model
160 have been analyzed in detail in De Roos et al. (1990). De Roos & Persson (2002) use as
default parameters for their consumer-resource model: $\ell_b = 7$ mm, $\ell_j = 110$ mm, $\ell_m = 300$
mm, $I_m = 1.0 \cdot 10^{-4}$ g/day/mm², $R_h = 1.5 \cdot 10^{-5}$ g/L, $r_m = 0.003$ /day/mm², $\gamma = 0.006$ /day,
 $\mu = 0.01$ /day, $\beta = 9.01 \cdot 10^{-6}$ g/mm³, $r = 0.1$ /day and $K = 0.0003$ g/L. These parameters can be
used directly to derive default values for R_h , γ , μ_b , r and K .

The parameters ρ , ρ_s and μ_s are not part of the model studied by De Roos & Persson
165 (2002). These I take from the parameter set presented by Van de Wolfshaar et al. (2006) for
roach (*Rutilus rutilus*). In particular I assume $\rho = 0.7$. De Roos & Persson (2002) assume
that individual biomass is related to individual length following $\beta \ell^3$. I will assume that
individual biomass in this respect is identical to the sum of structural mass and energy
reserves for an individual with a target body condition. Then structural mass equals
170 $S = \beta \ell^3 / (1 + \rho)$ or equivalently:

$$S^{1/3} = \sqrt[3]{\beta / (1 + \rho)} \ell$$

This identity yields estimates for the parameters S_b , S_j and S_m . For the latter parameter I
have assumed that the maximum length reached by a consumer equals 178 mm.

The maximum ingestion rate in the model of De Roos & Persson (2002) scales with ℓ^2 with
175 proportionality constant $I_m = 1.0 \cdot 10^{-4}$ g/day/mm². Since,

$$\ell^2 = (\beta / (1 + \rho))^{-2/3} S^{2/3}$$

multiplying this proportionality constant by $(\beta / (1 + \rho))^{-2/3}$ yields an estimate of the
parameter I_{\max} in the model presented here. Similarly, the maximum fecundity in the model
of De Roos & Persson (2002) scales with ℓ^2 with proportionality constant
180 $r_m = 0.003$ /day/mm². Multiplying the proportionality constant by $(\beta / (1 + \rho))^{-2/3}$ yields the
following scaling relationship for maximum fecundity with structural mass in the model
presented here:

$$0.003 \cdot (\beta / (1 + \rho))^{-2/3} S^{2/3} \approx 9.88 S^{2/3}$$

Assuming that this maximum fecundity in the model presented here is reached by an
185 individual with a target body condition, we derive $\beta \rho \approx 9.88$ and hence $\beta \approx 14.1$. (Notice

the parameter β has a different interpretation in the model presented here and the model studied by De Roos & Persson (2002)).

The remaining parameters, ε , η , σ_M , σ_G , σ_E and σ_R , are not part of the model studied by De Roos & Persson (2002). Their values I derive from the parameterization of the Kooijman-Metz model for the interaction between perch (*Perca fluviatilis*), roach, macro-invertebrates and zooplankton (see directory programs/Pcr/KMprmz for program code and default CVF files with parameters). This model I have investigated and analyzed, but never published about. Parameter values in the Kooijman-Metz perch-roach model are derived from the models studied by Persson et al. (1998), De Roos et al. (2001) and Claessen et al. (2000).
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Default value for the assimilation efficiency is $\varepsilon = 0.65$. In the Kooijman-Metz perch-roach model maintenance scales with cubed length, following $\zeta \ell^3$ with $\zeta = 1.67 \cdot 10^{-7}$. I had taken $\beta \ell^3$ equal to individual biomass, which equals $S + E$ for an individual with standard body condition. Therefore, an estimate for σ_M can be derived from $\zeta / \beta = 0.0186$. I hence assume $\sigma_M = 0.02$. In the Kooijman-Metz perch-roach model no further overhead costs are assumed for growth or reserve dynamics. This is the same for the models studied by Persson et al. (1998), De Roos et al. (2001) and Claessen et al. (2000): all energy that is available after assimilation can be used directly for growth in body mass, if it is not used for maintenance. There are no additional “costs for growth”, nor are there costs associated with storing energy as reversible mass or energy reserves and converting them later on to usable energy for life-supporting processes. To stay in line with these models I therefore assume that both σ_G and σ_E equal 1. For the parameter σ_R , representing the overhead costs for the production of offspring I adopt the value of 2.0. This is also in line with the models studied by Persson et al. (1998), De Roos et al. (2001) and Claessen et al. (2000) and represents the additional costs associated with producing male offspring. As for growth and energy conversion, there are no additional overhead costs assumed for producing offspring.

The remaining parameter η determines the steepness in the feeding response (the individual attack rate) as a function of individual body condition. For this parameter I have assumed a default value of 20.0. This value translates into an attack rate that is only 10% of the maximum attack rate when the body condition increases to 0.8, while the attack rate reaches 90% of the maximum attack rate when the body condition drops to 0.6. For the target body condition $\rho = 0.7$ the attack rate is always 50% of its maximum. The graph below shows the dependence of the relative attack rate (scaled to a maximum value of 1) as a function of body condition for $\eta = 20$ and $\rho = 0.7$. Because at the target body condition the attack rate is always 50% of the maximum, I should double the value of the maximum attack rate, which in the model formulation presented here means that I have to decrease the value of R_h by a factor of 2. Hence, the default value for the half-saturation constant equals $R_h = 0.75 \cdot 10^{-5}$.
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Table 1: Variables and equations describing the individual life history model.

Model variables	Unit	
Resource density:	$\text{g}\cdot\text{L}^{-1}$	R
Age:	d	a
Energy reserves:	g	E
Structural mass:	g	$S(a) = \left(S_m^{1/3} - \left(S_m^{1/3} - S_b^{1/3}\right)e^{-\gamma a}\right)^3$
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Model equations		
Resource ingestion:	$G(R, S, E) = I_{\max} \frac{R}{R_h \left(1 + e^{\eta(E/S - \rho)}\right) + R} S^{2/3}$	
Resource assimilation:	$I(R, S, E) = \varepsilon I_{\max} \frac{R}{R_h \left(1 + e^{\eta(E/S - \rho)}\right) + R} S^{2/3}$	
Metabolic costs:	$C_M(S, E) = \sigma_M (S + E)$	
Growth costs:	$C_G(S) = 3\sigma_G \gamma \left(S_m^{1/3} S^{2/3} - S\right)$	
Fecundity:	$b(E) = \begin{cases} \beta E / S^{1/3} & \text{for } S(a) > S_j \\ 0 & \text{otherwise} \end{cases}$	
Reproduction costs:	$C_R(E) = \sigma_R (1 + \rho) S_b b(E)$	
Starvation mortality:	$d_s(S, E) = \mu_s \max(\rho_s S / E - 1, 0)$	

Table 2: Model parameters with default values.

Parameter	Unit	Value	Description
S_b	g	0.002	Structural mass at birth
S_j	g	7	Structural mass at maturation
S_m	g	30	Maximum structural mass
γ	d ⁻¹	0.006	Growth rate in structural mass
I_{\max}	g · g ^{-2/3} · d ⁻¹	0.33	Scalar constant in maximum grazing rate
R_h	g · L ⁻¹	0.75 · 10 ⁻⁵	Half saturation constant in grazing rate
ρ	-	0.7	Target body condition
η	-	20.0	Steepness in satiation scaling of intake rate
ε	g · g ⁻¹	0.65	Resource assimilation efficiency
σ_M	d ⁻¹	0.02	Scalar constant in metabolic costs
σ_G	g · g ⁻¹	1.0	Per unit biomass cost of structural mass growth
σ_R	g · g ⁻¹	2.0	Per unit biomass cost of reproduction
σ_E	g · g ⁻¹	1.0	Energy-reserves conversion efficiency
β	g ⁻¹ · d ⁻¹	14.0	Constant relating fecundity to energy reserves
μ_b	d ⁻¹	0.01	Background daily mortality
μ_s	d ⁻¹	0.2	Scalar constant in starvation mortality
ρ_s	-	0.2	Body condition where starvation starts
r	d ⁻¹	0.1 / 0.4	Resource re-growth rate
R_{\max}	g · L ⁻¹	0.0003	Maximum resource density

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