DEB model description:
'std'

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1 Introduction

The 'std' model belongs to the class of s-models. s-models assume isomorphy throughout the full life cycle.

2 std model description

Before reading further, note that all of the symbols used herein are defined in the DEB notation document.

The AmP collection contains 11 related DEB models. All models are variations on the standard ('std') model which is specified as follows, where the environmental variables, temperature $T(t)$ and food density $X(t)$, can change in time t. All models handle environmental variables in the same way:

Effect of temperature on any rate $\dot{k}$:

Basic: $\frac{\dot{k}(T)}{\dot{k}(T_{\text{ref}})} = \exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right)$

Extended: $\frac{\dot{k}(T)}{\dot{k}(T_{\text{ref}})} = \exp\left(\frac{T_A}{T_{\text{ref}}} - \frac{T_A}{T}\right) \frac{1+\exp\left(\frac{T_{AL}}{T_{\text{ref}}} - \frac{T_{AL}}{T_L}\right)_+ + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{\text{ref}}}\right)_+}{1+\exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)_+ + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)_+}$

Effect of food on assimilation:

if $E_H < E_H^b$, $\dot{p}_X = 0$, else $\dot{p}_X = f\{\dot{p}_{Xm}\}L^2$ with $f = \frac{X}{K+X}$ and $K = \frac{\{\dot{J}_{Xm}\}}{\{\dot{F}_m\}}$ and $\{\dot{p}_{Xm}\} = \{\dot{p}_{Am}\}/\kappa_X$

2.0.1 std model

The std-model follows from the assumptions as listed in Table 1.

Within the family of DEB models, the std-model can be seen as a canonical form.

Main characteristics:

- 1 type of food X, 1 type of structure V, 1 type of reserve E, 1 type of feces P
- 4 minerals (carbon dioxide C, water H, dioxygen O, N-waste N); O is not limiting
- 3 life stages (embryo, juvenile, adult) triggered by maturity thresholds
  - birth is defined as start of assimilation via food uptake
  - puberty as end of maturation and start of allocation to reproduction
- If mobilisation is not fast enough to cover maturity and/or somatic maintenance, rejuvenation and/or some shrinking can occur, but only after use of the reproduction buffer
- The reproduction buffer is continuously converted to a spawning buffer, which is instantaneously converted to exported eggs, if the spawning buffer exceeds a density threshold

Table 1: The assumptions that specify the standard DEB model quantitatively. (This is a copy of Table 2.4 from (**?**))
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1. The amounts of reserve, structure and maturity are the state variables of the individual; reserve and structure have a constant composition (strong homeostasis) and maturity represents information.
2. Substrate (food) uptake is initiated (birth) and allocation to maturity is redirected to reproduction (puberty) if maturity reaches certain threshold values.
3. Food is converted into reserve and reserve is mobilised at a rate that depends on the state variables only to fuel all other metabolic processes.
4. The embryonic stage has initially a negligibly small amount of structure and maturity (but a substantial amount of reserve). The reserve density at birth equals that of the mother at egg formation (maternal effect). Foetuses develop in the same way as embryos in eggs, but at a rate unrestricted by reserve availability.
5. The feeding rate is proportional to the surface area of the individual and the food–handling time is independent of food density.
6. The reserve density *at constant food density* does not depend on the amount of structure (weak homeostasis).
7. Somatic maintenance is proportional to structural volume, but some components (osmosis in aquatic organisms, heating in endotherms) are proportional to structural surface area.
8. Maturity maintenance is proportional to the level of maturity
9. A fixed fraction of mobilised reserves is allocated to somatic maintenance plus growth, the rest to maturity maintenance plus maturation or reproduction (the κ-rule).
10. The individual does not change in shape during growth (isomorphism). This assumption applies to the standard DEB model only.

Parameters:

Temperature: T_A, T_L, T_H, T_{AL}, T_{AH}

Hazard: $\ddot{h}_a$, s_G, δ_L, $\dot{h}_J$, $\dot{h}_0$, $\dot{h}_0^e$

Life stage: E_H^b, E_H^p

Core: $\{\dot{F}_m\}$, $\{\dot{p}_{Am}\}$, $[\dot{p}_M]$, $\{\dot{p}_T\}$, $\dot{k}_J$, $\dot{k}'_J$, $\dot{v}$, $[E_G]$, κ, κ_X, κ_P, κ_R, $[E_R^s]$

Chemical: $[M_V]$, $d_\mathcal{O} = \begin{pmatrix} d_X & d_V & d_E & d_P \end{pmatrix}$, $\mu_\mathcal{O} = \begin{pmatrix} \mu_X & \mu_V & \mu_E & \mu_P \end{pmatrix}$, $n_\mathcal{M}$, $n_\mathcal{O}^d$,
where the chemical coefficients for minerals and (dry) organic compounds are

$$n_\mathcal{M} = \begin{pmatrix} 1 & 0 & 0 & n_{CN} \\ 0 & 2 & 0 & n_{HN} \\ 2 & 1 & 2 & n_{ON} \\ 0 & 0 & 0 & n_{NN} \end{pmatrix} \text{ and } n_\mathcal{O}^d = \begin{pmatrix} 1 & 1 & 1 & 1 \\ n_{HX}^d & n_{HV}^d & n_{HE}^d & n_{HP}^d \\ n_{OX}^d & n_{OV}^d & n_{OE}^d & n_{OP}^d \\ n_{NX}^d & n_{NV}^d & n_{NE}^d & n_{NP}^d \end{pmatrix}.$$

If the N-waste is ammonia, we have $n_{CN} = 0$, $n_{HN} = 3$, $n_{ON} = 0$, $n_{NN} = 1$.

Help quantities (for the specification of changes in state):

wet/dry mass: The chemical coefficients of wet organic mass $n_{*_1 *_2}^w$ relate to that of dry mass $n_{*_1 *_2}^d$ for $*_1 \in \{H, O\}$ and $*_2 \in \{X, V, E, P\}$ as $n_{H*_2}^w = 2x_{*_2} + n_{H*_2}^d$ and $n_{O*_2}^w = x_{*_2} + n_{O*_2}^d$, while $n_{C*_2}^w = n_{C*_2}^d$ and $n_{N*_2}^w = n_{N*_2}^d$, where $x_{*_2} = \frac{1 - d_{*_2}^d / d_{*_2}^w}{18}$, while $d_{*_2}^w \simeq 1\,\text{g/cm}^3$.

mass fluxes: $\dot{J}_\mathcal{O} = \begin{pmatrix} \dot{J}_X & \dot{J}_V & (\dot{J}_E + \dot{J}_{E_R}) & \dot{J}_P \end{pmatrix}$ relate to energy fluxes $\dot{p} = \begin{pmatrix} \dot{p}_A & \dot{p}_D & \dot{p}_G \end{pmatrix}$, as

$$\dot{J}_\mathcal{O} = \eta_\mathcal{O} \dot{p} \text{ with } \eta_\mathcal{O} = \begin{pmatrix} -\frac{1}{\kappa_X \mu_X} & 0 & 0 \\ 0 & 0 & \frac{\kappa_G}{\mu_V} \\ \frac{1}{\mu_E} & -\frac{1}{\mu_E} & -\frac{1}{\mu_E} \\ \frac{\kappa_P}{\kappa_X \mu_P} & 0 & 0 \end{pmatrix} \text{ and } \kappa_G = \mu_V \frac{[M_V]}{[E_G]}$$

assimilation: $\dot{p}_A = \kappa_X \dot{p}_X$

somatic maintenance: $\dot{p}_S = [\dot{p}_S]L^3$. If $E_H < E_H^b$, $[\dot{p}_S] = [\dot{p}_M]$, else $[\dot{p}_S] = [\dot{p}_M] + \{\dot{p}_T\}/L$

maturity maintenance: if $(1-\kappa)\dot{p}_C > \dot{k}_J E_H$ (no rejuvenation), $\dot{p}_J = \dot{k}_J E_H$, else $\dot{p}_J = \dot{k}'_J E_H$

mobilization: $\dot{p}_C = E(\dot{v}/L - \dot{r})$. If $[E] \geq \frac{[\dot{p}_S]L}{\dot{v}\kappa}$ (no shrinking), $\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_S]/\kappa}{[E]+[E_G]/\kappa}$, else if $E_R > 0$, $\dot{r} = 0$, or if $E_R \leq 0$, $\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_S]/\kappa}{[E]+[E_G]\kappa_G/\kappa}$ (shrinking)

growth: $\dot{p}_G = \kappa \dot{p}_C - \dot{p}_S$, but if $\kappa \dot{p}_C < \dot{p}_S$ and $E_R > 0$: $\dot{p}_G = 0$

maturation/reproduction: $\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J$, but if $(1-\kappa)\dot{p}_C < \dot{p}_J$ and $E_R > 0$: $\dot{p}_R = 0$

dissipation: if $E_H < E_H^p$, $\dot{p}_D = \dot{p}_S + \dot{p}_J + \dot{p}_R$, else $\dot{p}_D = \dot{p}_S + \dot{p}_J + (1-\kappa_R)\dot{p}_R$

Initial states: $L(0) = 0$, $E_H(0) = 0$, $E_R(0) = 0$, $\ddot{q}(0) = 0$, $\dot{h}_A(0) = 0$ and $E(0) = E_0$ such that $[E](a_b)$ equals that of mother at egg production

Changes in state:

structure: $\frac{d}{dt}L = L\dot{r}/3$. So, initial change is $\frac{d}{dt}L(0) = \dot{v}/3$

reserve: If $E_H < E_H^b$ (embryo), $\frac{d}{dt}[E] = -[E]\dot{v}/L$, else $\frac{d}{dt}[E] = (\{\dot{p}_{Am}\}f - [E]\dot{v})/L$

maturity: If $E_H < E_H^p$ (embryo or juvenile), $\frac{d}{dt}E_H = \dot{p}_R$, else $\frac{d}{dt}E_H = 0$. However, if $\dot{p}_J < 0$ and $E_R = 0$ (rejuvenation), $\frac{d}{dt}E_H = \dot{p}'_J$ with $\dot{p}'_J = \min(0, \dot{p}_J \dot{k}'_J/\dot{k}_J)$

buffer: If $E_H = E_H^p$ (adult), $\frac{d}{dt}E_R = \dot{p}_R - \dot{p}'_J - \dot{p}'_G$, else $(E_H < E_H^p)$ $\frac{d}{dt}E_R = 0$. If adult and $E_R > 0$, $\dot{p}'_G = \max(0, [\dot{p}_S]L^3 - \kappa\dot{p}_C)$, else $(E_R \leq 0)$ $\dot{p}'_J = 0$ and $\dot{p}'_G = 0$. The buffer is partitioned as $E_R = E_R^0 + E_R^1$, where E_R^0 converts, for positive E_R^0, to E_R^1 at rate $\dot{p}_R^{\max} = \frac{1-\kappa}{\kappa} L^3 \frac{[E_G]\dot{v}/L + [\dot{p}_S]}{1+g} - \dot{p}_J$ and $g = \frac{[E_G]\dot{v}}{\kappa\{\dot{p}_{Am}\}}$.

hazard: $\dot{h} = \dot{h}_A + \dot{h}_X + \dot{h}_B + \dot{h}_P$

- aging: $\frac{d}{dt}\ddot{q} = (\ddot{q}\frac{L^3}{L_m^3}s_G + \ddot{h}_a)e(\frac{\dot{v}}{L} - \dot{r}) - \dot{r}\ddot{q}$; $\quad \frac{d}{dt}\dot{h}_A = \ddot{q} - \dot{r}\dot{h}_A$
- starving (food): If $E_H < E_H^b$, $\dot{h}_X = 0$, else if $\dot{p}_C < \frac{\dot{k}_J E_H}{1-\kappa}$, $\dot{h}_X = \dot{h}_J(1 - \frac{\dot{p}_C(1-\kappa)}{\dot{k}_J E_H})$.
  Let L_0 be the length at which $\dot{r} = 0$ for the last time.
  If $L = \delta_L L_0$, $h_X\, dt = \infty$ (instant death due to shrinking)
- accidental (background): If $E_H < E_H^b$, $\dot{h}_B = \dot{h}_B^{0b}$, else $\dot{h}_B = \dot{h}_B^{bi}$; both constant
- thinning (predation): If $E_H \geq E_H^b$, $\dot{h}_P = \frac{2}{3}\dot{r}$, else $\dot{h}_P = 0$

Input/output fluxes:

food: $\dot{J}_X = \frac{\dot{p}_A}{\kappa_X \mu_X}$

feces: $\dot{J}_P = \frac{\kappa_P \dot{p}_A}{\kappa_X \mu_P}$

eggs: If $E_R^1 = [E_R^s]L^3$: $\dot{R}\, dt = \kappa_R [E_R^s]L^3/E_0$ eggs are produced and E_R^1 is set to 0

minerals: $\dot{J}_{\mathcal{M}} = -n_{\mathcal{M}}^{-1} n_{\mathcal{O}}^{w} \dot{J}_{\mathcal{O}}$, where $\dot{J}_{\mathcal{M}} = (\ \dot{J}_C \quad \dot{J}_H \quad \dot{J}_O \quad \dot{J}_N\ )$

heat: $\dot{p}_{T+} = -\mu_{\mathcal{O}}^T \dot{J}_{\mathcal{O}}$

death: at death, $[M_V]L^3$ moles of structure and $(E + E_R)/\mu_E$ moles of reserve become available in the environment