DEB theory

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Goal

The goal of DEB theory is the study of the organization of metabolism described by the mass and energy flows inside the organisms. This theory aims to capture the quantitative aspects of the organization of metabolism at the organism level with implications for the sub and supra organismic levels (Kooijman 2000, 2001; Nisbet et al. 2000).

Principles

This theory is compatible with physics and evolution.
The physical principles considered here are:

P1 mass and energy are conserved quantities;

P2 any energy conversion process leads to dissipation;

P3 mass and energy flows depend only on intensive properties;

P4 mass and energy transport are proportional to surface areas because they occur across surfaces.

The evolutionary principles taken into account are:

E1 organisms have increased their control over their metabolism during evolution allowing for some adaptation to environmental changes in short periods;

E2 organisms inherit parent's characteristics in a sloppy way allowing for some adaptation to environmental changes across generations.

Basic concept	**Principles and assumptions**	Catabolism	Conclusion and Quizz
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Assumptions

- Individual as the basic level of metabolic organization
- Biomass has tow components: structure and reserve.
- Homeostasis
- Temperature effects

Individual as dynamic system

DEB theory unifies the commonalities between organisms as prescribed by the implications of energetics, which links different levels of biological organization (cells, organisms and populations).

DEB theory starts at the level of the individual, many organisms are unicellular which link directly sub-cellular level with individual level.

Population can be considered as a set of individuals, their dynamics follows from the behavior of individuals,
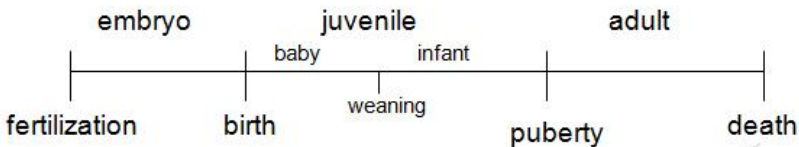
Reserve and structure

Deb theory partitions biomass into one or more reserves and one or more structures.

- to include metabolic memory : smooth out fluctuations
- to make sure that no essential type of resource is temporarily absent
- the chemical composition of the individual depends on the growth rate
- . . .

Remarque
The term reserve does not mean '"set apart for latter use'". Reserve molecules can have active metabolic function. *Ribosomal RNA, turns out to belong to the reserve.*

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Life stages

- Essential: switch points, not periods
- birth: start of feeding
- puberty: start of allocation to reproduction
- stage transition Occurs if cumulated investment into maturation exceeds a threshold

Homeostasis

Homeostasis is the ability to run metabolism independent from environmental conditions. This can obviously not be perfect, all organisms require food and/or nutrients. Homeostasis can be strong or weak :
We need 5 difference homeostasis concepts to capture the extent organisms sport homeostasis.

1. Strong homeostasis.
2. Weak homeostasis.
3. Structure homeostasis.
4. Thermal homeostasis.
5. Acquisition homeostasis

Strong homeostasis

Stoichiometric constrains, the structure volume V and the reserve energy E do not change in chemical composition and thermodynamic properties.
An organism feeds on a resource X and produces products P, also with fixed chemical compositions and constant thermodynamic properties.
Strong homeostasis has nothing to do with reserve dynamics. DEB theory assumes that the chemical composition of reserve(s) and structure(s) are constant.

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The amount of reserve(s) ans structure(s) can vary but not their chemical composition

Homeostasis key of life

Weak homeostasis

Definition : If food does not change, reserve density becomes constant even when growth continues, reserve and structure grow in harmony and biomass no longer changes in composition.

This make sense only if reserve and structure obey strong homeostasis.

The ratio of the amount of reserve and structure is constant.

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Weak homeostasis applies to the whole body not to its compounds

Structural homeostasis : Isomorphy

Is about shape, this assumption is only of the standard DEB model, but not of DEB models.

generally, The length is defined as a structural volumetric (volume of the structure) length *i.e.* $L = V^{1/3}$ et $S = V^{2/3}$.

Homeostasis key of life

Thermal homeostasis: ecto, homeo and endothermy

As heat is a side product of all uses of energy, Thermal homeostasis is maintained by keeping the heat production and thermal loss continuously in balance.

- Ectotherms : heat dissipates without increasing the body temperature above that of the environment.
- Endotherms : use energy to maintain their body temperature at a predetermined level.

Basic concept   **Principles and assumptions**   **Catabolism**   **Conclusion and Quizz**
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Homeostasis key of life

Acquisition homeostasis: supply and demand

Extreme supply or demand systems don't exist, all species represent a mixture of these extremes.

- Plants come close to the supply end of the spectrum and can adapt their metabolism to the local environment relatively well. Demand systems adapt their metabolism much less and compensate that by a high level of behavioral flexibility.
- The characterizing property of demand systems is that the use of resources (growth, reproduction) is (preprogrammed), which causes a particular need for food and growth curves that are given functions of age.

Temperature effect

I will not speak about that now, but later.

1. Arrhenius temperature.
2. Coupling of rate in a single reserve systems.
3. State can depend on temperature via rate.
4. van't Hoff coefficient.
5. Temperature tolerance range.
6. Outside the temperature tolerance range.

Basic concept **Principles and assumptions** **Catabolism** **Conclusion and Quizz**
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The Standard model

The standard model assumptions

The standard model is the simplest one, it can be considered as a canonical form or as common ancestor of other more specific models.

- One food type of constant composition and particle size that can be used to complete life cycle

- One reserve type

- One structure type : Isomorphy

- Only food is limiting, not e.g. dioxygen

Basic concept **Principles and assumptions** **Catabolism** **Conclusion and Quizz**
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The Standard model

State variables

The state of the organism is completely described by the volume of the structure V, the amount of energy in the reserve E and the accumulated energy investment into maturation E_H

We note:

- $\dot{p}$ as the energy flux.
- E is non-allocated energy.
- $\{E\} = \frac{E}{L^2}$: quantity per unit of structural surface.
- $[X] = \frac{X}{V}$: quantity per unit of structural volume.

Metabolism can be characterized by the following processes:

1. Feeding : The intake of substrates from the environment.
2. Assimilation : Generation of reserves from substrates.
3. Catabolism : The use of reserves for metabolism
   1. Reserve dynamics.
   2. Somatic and maturity maintenances.
   3. Reproduction.

Basic concept	Principles and assumptions	Catabolism	Conclusion and Quizz
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The Standard model

We will use here the standard DEB model, which considers an isomorphic organism, with one reserve and one structure. This model is assumed to be appropriate for heterotrophic unicellular organisms and animals (Kooijman 2010).
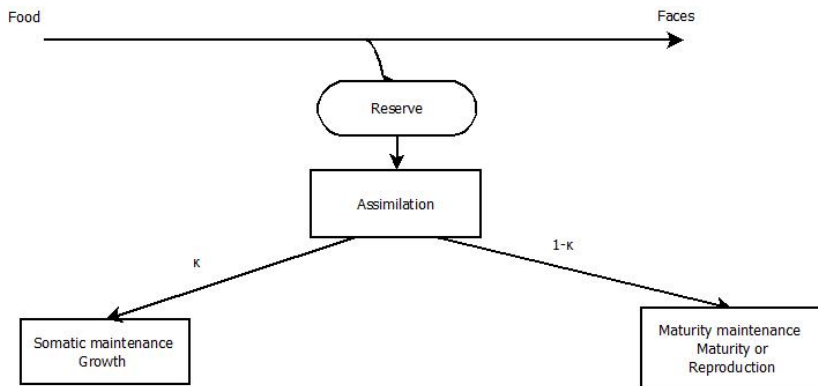

Figure : A fixed fraction (called kappa) of mobilized reserve is allocated to somatic maintenance plus growth, the rest on maturity maintenance plus maturation or reproduction.

Basic concept	Principles and assumptions	Catabolism	Conclusion and Quizz
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Feeding and assimilation

Let X be the food density, the feeding or ingestion flow rate $\dot{p}_X$ is:

$$\dot{p}_X = f(X/X_K)\dot{p}_{Xm} = f(X/X_K)\{\dot{p}_{Xm}\}L^2$$

with

- $f(x) = \frac{x}{1+x}$ Holling type II functional response. But it can be another functional response type depending on the specie.
- $\dot{p}_{Xm}$ is the maximum ingestion rate. $\dot{p}_{Xm}$ depend on volume surface so that $\{\dot{p}_{Xm}\}$ is surface and so length independent.
- L volumetric length.

the set of reactions that transform food into reserve, where $\dot{p}_A$ the rate of energy that is the input of reserve.

$$\dot{p}_A = \kappa_X\dot{p}_X = \kappa_X\{\dot{p}_{Xm}\}f(X/X_K)L^2$$

Let $\dot{p}_{Am} = \kappa_X\dot{p}_{Xm}$ the maximum assimilation rate.

Reserve dynamics

The mobilization of the reserve to fuel the organism's activities, where $\dot{p}_C$ is the energy of the mobilized rate. Thus, reserve dynamics is

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$$

Thus,

$$\frac{d[E]}{dt} = [\dot{p}_A] - [\dot{p}_C] - [E]\dot{r} \tag{1}$$

with $\dot{r} = \frac{1}{V}\frac{dV}{dt}$.

Weak homeostasis implies that $\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]}$, and thus $\dot{r} = \frac{[\dot{p}_G]}{[E_G]}$.

$\dot{r}$ stands for the specific growth rate, and can than be written as

$$\dot{r} = (\kappa[\dot{p}_c] - [\dot{p}_s])/[E_G] \tag{2}$$

With $\dot{p}_G$ the reserve flow allocated to growth and E_G the cost of growth.

$$[\dot{p}_C] = \underbrace{(1 - \kappa([E], V))[\dot{p}_C]}_{\text{Reproduction, maturity and maturity maintenance}} + \underbrace{\kappa([E], V)[\dot{p}_C]}_{\text{Growth and somatic maintenance}} \tag{3}$$

$$\kappa([E], V)[\dot{p}_C] = [\dot{p}_S] + [\dot{p}_G] \tag{4}$$

Thus

$$\frac{d[E]}{dt} = [\dot{p}_A] - [\dot{p}_C] - [E]\frac{\kappa[\dot{p}_C] - [\dot{p}_S]}{[E_G]}, \tag{5}$$

$$= [\dot{p}_A] - [\dot{p}_C](1 + \kappa\frac{[E]}{[E_G]}) + \frac{[E]}{[E_G]}[\dot{p}_S] \tag{6}$$

Remark

From homoeostasis of structural mass we have:

① *$[\dot{p}_S]$ depend on V.*

② *$[E_G]$ is independent on V.*

Consequence of strong homeostasis

- fixed yield of structure on reserve y_{VE}
- fixed density of structure. $[M_V] = \frac{M_V}{V}$, number of C-atoms per unit of structural body volume.

In another way:

$$[\dot{p}_A] = \dot{p}_A / V \tag{7}$$

$$= \frac{\{\dot{p}_{Xm}\} f(X/X_K) L^2}{V} \tag{8}$$

$$= \frac{\{\dot{p}_{Xm}\} f(X/X_K)}{L} \propto L^{-1} \tag{9}$$

Thus

$$\frac{d[E]}{dt} = [\dot{p}_A] - \frac{\dot{H}(E, \Theta)}{L} \tag{10}$$

and $\dot{H}(E, \Theta)$ do not depend on L.

Equations (1),(2) and (10) imply

$$[\dot{p}_A] - [\dot{p}_C](1 + \kappa \frac{[E]}{[E_G]}) + \frac{[E]}{[E_G]}[\dot{p}_S] = [\dot{p}_A] - \frac{\dot{H}(E,\Theta)}{L} \tag{11}$$

Thus

$$[\dot{p}_C] = \frac{\dot{H}(E,\Theta)/L + [E][\dot{p}_S]/[E_G]}{1 + \kappa[E]/E_G} \tag{12}$$

Mergeabilty and Partitionability

> **Partitionability definition**
>
> When reserve is partitioned e.g. into lipids and non-lipids maintenance and growth are partitioned as well to arrive at a situation where the partitioning remains without effects for the individual .
> Partitioning of reserve has no effect its dynamics *i.e.* the sum of the dynamics of partitioned reserves should be identical to that of the lumped one in terms of growth, maintenance, development and reproduction.
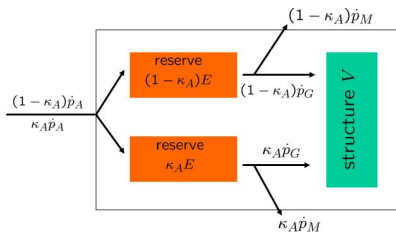

Figure : When the reserve is partitioned in tow parts, the somatic maintenace costs ans the cost for structure also need to be partitioned. Partitionning remains without effects for the individual.

Mergeabilty definition

Mergeabilty means that reserve can be added without effects on the reserve density dynamics if assimilation of the ressources to syntheisis the reserves is coupled and the total intake is constant. This is also implied by weak homeostasis; partitionable dynamics is also mergeable.

Let suppose that the reserve is divided in two A and the complementary of A. Let κ_A such that $A = \kappa E$.
By the mergability we have the following picture:

Then,

$$\kappa_A \dot{H}([E], \Theta) = \dot{H}(\kappa_A[E], \Theta), \tag{13}$$

$$\kappa(\kappa_A[E], V) = \kappa([E], V) \tag{14}$$

Thus,

1. $\dot{H}$ is a linear function of $[E]$, let note $\dot{H} = \dot{v}[E]$. Where the unity of $\dot{v}$ is $\frac{1}{time}$, is Energy "Conductance".

2. κ do not depend of $[E]$.

Substitution of $\dot{H}$ into (10) gives:

$$\frac{d[E]}{dt} = [\dot{p}_A] - [E]\dot{v}/L = (\{\dot{p}_{A_m}\}f(X/X_k) - [E]\dot{v})/L \tag{15}$$

From (15), we have:

$$[\dot{p}_C] = [\dot{p}_A] - \frac{d[E]}{dt} - [E]\dot{r} = [E](\dot{v}/L - \dot{r}) \tag{16}$$

and from (12),

$$[\dot{p}_C] = [E]\frac{[E_G]\dot{v}/L + [\dot{p}_S]}{\kappa[E] + [E_G]}. \tag{17}$$

By (2),

$$\dot{r} = \frac{[E]\dot{v}/L - [\dot{p}_S]/\kappa}{[E] + [E_G]/\kappa}. \tag{18}$$

κ rule

From mergeability and partionability concepts we have:

The kappa rule I: The κ function is independent of E, i.e. $\kappa(\lambda E, V) = \kappa(E, V)$.

The kappa rule II: In the standard model κ function, is independent of V.

This means that reproduction does not compete with growth, which is in agreement with the fact that many organisms do not stop growing after reproduction has started.

Somatic maintenance

The somatic maintenance is divided into volume maintenance $\dot{p_M}$ and surface maintenance $\dot{p_T}$.

$$[\dot{p_S}] = [\dot{p_M}] + \frac{\{\dot{p_T}\}}{L}. \tag{19}$$

$\dot{p_M}$: We suppose that maintenance costs are proportional to the volume. Strong homeostasis says that : a metazoan with twice the volume of a conspecific has twice as many cells and then will uses twice more energy.
So that $\dot{p_M}$ is linear V dependant and then $[\dot{p_M}]$ is constant.

$\dot{p_T}$: Correspond the cost of energy transfer via body surfaces *i.e.* by temperature diffusion, changing skins, moult . . . .

Basic concept	Principles and assumptions	**Catabolism**	Conclusion and Quizz
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Somatic and maturity maintenances

Let $L_T = \frac{\{\dot{p}_T\}}{[\dot{p}_S]}$ be the heating length, $V_T = L_T^3$ the heating volume and $I_T = \frac{\{\dot{p}_T\}}{[\kappa\{\dot{p}_{Am}\}]}$

$$[\dot{p}_S] = [\dot{p}_M] + \{\dot{p}_T\}/L = [\dot{p}_M](1 + \frac{L_T}{L}). \tag{20}$$

Maturation and its maintenance

DEB implementation is motivated by 4 observations

1. Contrary to age, volume at birth or puberty hardly depends on food density. So stage transitions cannot be linked to age.

2. Some species continue growing after puberty. Other species, such as birds, only reproduce well after the growth period. So stage transitions cannot be linked to size.

3. Total cumulative energy investment in development at any given size of the individual depends on food density; this can be removed by allowing for maturity maintenance.

4. No reproduction occurs at very low food densities. This demonstrates the existence of maturity maintenance

Maturation

the amount of energy invested into maturation E_H. The structure and the reserve are generalized compounds, *i.e.* mixtures of a large number of compounds that compose the biomass of the organism.

Increase of information and structure.

The sate variable E_H measure the level of maturity. Although maturity represents neither mass nor energy, it is quantified as the cumulative energy investment into maturation because an organism has to spend energy to increase its complexity (P2).

Thus life-stage events are linked with maturity, *i.e.* they occur when E_H exceeds certain thresholds. Feeding begins when $E_H = E_H^b$ and allocation to reproduction coupled to the ceasing of maturation begins when $E_H = E_H^p$. The dynamics of E_H is given by,

$$\frac{dE_H}{dt} = \dot{p}_R, E_H < E_H^p$$

where $\dot{p}_R$ is the power allocated to maturation if $E_H < E_H^p$ and the power allocated to reproduction if $E_H = E_H^p$.

Remark

1. *Other life-history events, such as cell division, metamorphosis or other stage transitions (e.g to the pupal stage), also occur at threshold values for E_H.*

2. *When $E_H^p > E_H^b$ the multicellular organisms have at least three life stages: they start as an embryo or foetus that does not feed; become juveniles when feeding starts; and reproduce as adults.*

Maturity maintenance

Collection of processes required to maintain current state of maturity Comprises maintaining defense systems (immune system) Paid from fraction $(1 - \kappa)$ branch of mobilized reserve.

The maturity maintenance is assumed to be proportional to maturity level:

$$\dot{p}_J = \dot{k}_J E_H,$$

where $\dot{k}_J$ is the maturity maintenance rate coefficient.

After maturity the maturity maintenance is equal to

$$\dot{p}_J = \dot{k}_J E_H^p,$$

Into this energy cost we have the defense systems, such as the immune system of the vertebrate.

Remark

The maturity maintenance rate coefficient, $\dot{k}_J$, is comparable to the somatic maintenance rate coefficient $\dot{k}_M$.

Basic concept	Principles and assumptions	**Catabolism**	Conclusion and Quizz
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Somatic growth

Equation (18),

$$[\dot{p}_C] = (\kappa[E_m]g\dot{v}/L + [\dot{p}_S])\frac{eg}{e+g} \tag{21}$$

Using equation (20), we obtain:

$$[\dot{p}_C] = [E_m](\dot{v}/L + \dot{k}_M(1 + \frac{L_T}{L}))\frac{eg}{e+g} \tag{22}$$

with $e = \frac{[E]}{[E_m]}$ the maximum assimilation rate and $g = \frac{E}{\kappa[E_m]}$.
In the same way, we have:

$$\dot{r} = \frac{\dot{v}e/L + (1 + \frac{L_T}{L})/L_m}{e+g}. \tag{23}$$

Moreover, the maximum length $L_m = \frac{\kappa\{\dot{P}_{Am}\}}{[\dot{p}_M]} = \frac{\dot{v}}{k_M g}$.

I recall the equation (1), the somatic growth implies increase in structure

$$\frac{dV}{dt} = \dot{r}V$$

Thus,

$$\frac{dL}{dt} = \frac{1}{3}rL \tag{24}$$

Replacing $\dot{r}$ from equation (23), we have:

$$\frac{dl}{dt} = \dot{k}_M \frac{g}{3} \frac{e - l - l_T}{e + g} \tag{25}$$

and equation (15) is equivalent to,

$$\frac{de}{dt} = (f - e)\frac{g\dot{k}_M}{l} \tag{26}$$

If f is constant then $[E] = f[E_m]$ (thus $e = f$)) We have the von Bertalanfly equation:

$$L(t) = L_\infty - (L_\infty - L_b) \exp(-t\dot{r}_B) \tag{27}$$

with $\dot{r}_B = \frac{1}{3/\dot{k}_M + 3fL_m/\dot{v}} = \frac{\dot{k}_M/3}{1+f/g}$, $L_\infty = fL_m - L_T$ and $L_b = L(0)$.

State at birth and initial amount of reserve

The state variables (E_H, E, L) evolve from $(0, E_0, O)$ at age $a = 0$ to $(E_H^b, [E_b]L_b^3, L_b)$. We have the relationship for the structural volume at birth,

$$V_b = L_b^3 = \frac{E_H^b/[Em]}{(1 - \kappa)g}$$

and

$$u_E^b = \frac{e_b l_b^3}{g}$$

State at puberty

Puberty occurs as soon as $E_H = E_H^p$, or

$$U_H = U_H^p = E_H^p / \dot{p}_{Am}$$

or with scaled maturity $u_H = u_H^p = \frac{E_H^p}{g[E_m]L_m^3}$. If $\dot{k}_j = \dot{k}_M =$ and $L_T = 0$ we have:

$$V_p = \frac{E_H^p / [E_m]}{(1 - \kappa)g}$$

Reproduction

The amount of energy allocated to maturation in a juvenile is

$$\dot{p}_R = (1 - \kappa)\dot{p}_c - \dot{k}_j E_H$$

and to reproduction in an adult is

$$\dot{p}_R = (1 - \kappa)\dot{p}_c - \dot{k}_j E_H^p$$

The amount of energy invested continuously into gametes production is accumulated in a buffer and then it is converted into eggs.

The energy rate allocated to other reproduction cost is,

$$\dot{P}_{\text{other reproduction cost}} = (1 - \kappa_R)\dot{P}_r$$

The buffer handling rules are species specific.

Homeostasis implications on reproduction

- Fixed conversion efficiency.
- Weak homeostasis : reserve density at birth equals that of mother.

Reproduction rate

Mean reproduction rate (number of offspring per time)

$$\dot{R} = \frac{(1 - \kappa_R)\dot{P}_R}{E_0}$$

$$\dot{R} = \frac{\kappa_R \dot{k}_M}{v_E^0} \left(\frac{el^2}{e+g}(g + l_T + l) - kv_H^p \right) \tag{28}$$

This formula links directly the production of gametes th the individual size.

- $v_E^0 = \frac{u_E^0}{1 - kappa}$ is the scaled initial amount of reserve of one egg, we remark then that scaled reserve is proportional to scaled volume.
- $v_H^p = \frac{u_H^b}{1 - \kappa}$ is the scaled maturity volume at puberty.
- v_0^p scaled initial maturity volume.
- l_T heating length.
- e scaled reserve density $e = \frac{[E]}{[E_m]}$
- g energy investment ratio: $g = \frac{[EG]}{\kappa[Em]}$
- $K = \frac{\dot{k}_j}{\dot{k}_M}$ maintenance ratio where $\dot{k}_j$ is maturity maintenance rate coefficient. $\dot{k}_M$ is somatic maintenance rate coefficient.

Conclusion

To describe the energetic behavior of an isomorph that feeds on a single type of food and has a single reserve and a single structure, the standard model has three state variables: structural volume V, reserve energy E and maturity, expressed in terms of cumulative energy investment, E_H.

This model is the canonical form, and other models are modified versions of the standard deb model to include dividing organisms, changing of shapes, multiple types of food, reserve and structure, adaptation, ...

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Conclusion

Questions?