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"The Dynamic Energy Budget (DEB) model"

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The Dynamic Energy Budget (DEB) model

S.A.L.M. Kooijman, 12 sept 96

This short note introduces the Dynamic Energy Budget (DEB) model which specifies the rules for uptake and use of food for ectothermic ("cold-blooded") animals. The term 'Dynamic' refers to the change of the energy budget during the life history of an animal, see Figure 1. Three stages are distinguished: the embryo (which does not eat), the juvenile (which eats, but does not reproduce) and the adult (which eats and reproduces). With minor modifications, the model also applies to endothermic ("warm-blooded") animals and unicellulars (including bacteria) that are limited in growth by a single resource.

The diagram in Figure 2 presents the fluxes of energy through an animal, as conceived in the DEB model. Energy is extracted from food and added to the reserves, i.e. a combination of carbohydrates, lipids and proteins. Energy in the reserves is used for four destinations, which can be combined into two groups of two: growth (i.e. increase in structural biomass, mainly in the form of proteins) plus somatic maintenance (including activity, protein turnover, etc) and maturation (i.e. development, the increase in the state of maturity) plus maturity maintenance (i.e. maintaining the acquired state of maturity). Adults do not longer invest into maturation, but into reproduction. The various destinations only compete within each group. So, the animal ceases growth when the energy allocated to growth plus somatic maintenance is fully required for somatic maintenance. Under these conditions, it can continue to reproduce (if it is an adult), because reproduction is not in the same group of destinations. Likewise, reproduction ceases when the energy allocation to reproduction plus maturity maintenance is fully required for maturity maintenance.

The rules, presented as axioms in Table 1, quantify the fluxes that are shown in Figure 2. Each of these axioms can be justified mechanistically, and has been tested against experimental data for a wide variety of species. These simple rules have a myriad of implications for suborganismal organization and population dynamics. For instance, the energy costs of an egg and its incubation time follow directly from these rules. Although the rules define energy fluxes, all mass fluxes, including respiration (i.e. oxygen use or carbon

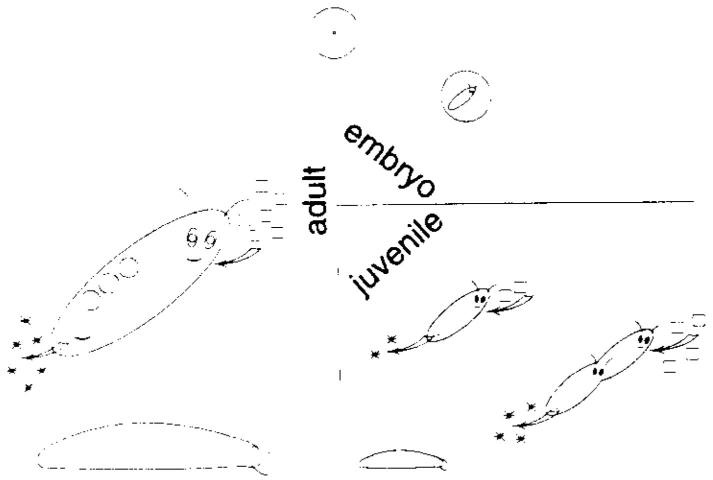


Figure 1: Dynamic Energy Budget theory quantifies the energetics as it changes during life history. The key processes are feeding, digestion, storage, maintenance, growth, development, reproduction and aging. Dividing organisms, such as microbes, are included by conceiving them as juveniles.

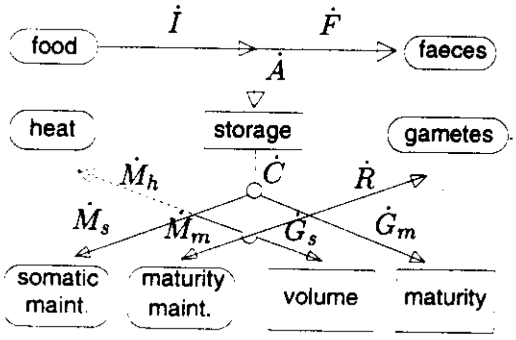


Figure 2: Energy fluxes through an animal: $\dot I$ ingestion (uptake), $\dot F$ defecation, $\dot A$ assimilation, $\dot C$ catabolic, $\dot M_s$ somatic maintenance, $\dot M_m$ maturity maintenance, $\dot M_h$ heating (endotherms), $\dot G_s$ somatic growth, $\dot G_m$ maturation, $\dot R$ reproduction. The rounded boxes indicate sources or sinks. All fluxes contribute a bit to dissipating heat, but this is not indicated in order to simplify the diagram.

dioxide production) and the rate of nitrogen waste (ammonia, urine) also follow from these rules, via the conservation law for mass. The rules give an explanation for the observed increase in respiration coupled to the feeding process (this previously poorly understood phenomenon is called the 'specific dynamic action'). It can be shown that the rules provide a theoretical basis for the widely applied method of indirect calorimetry, where measurements of oxygen use, carbon dioxide production and nitrogen waste are used to obtain the flux of dissipating heat.

The DEB model specifies the uptake and use of food by an animal as a dynamic system with three state variables (volume of structural biomass, amount of reserves and cumulated damage) and 11 parameters:

L_b	length at birth	L_p	length at puberty	K	saturation constant
$\{\dot I_m\}$	max. spec. ingestion rate	$\{\dot A_m\}$	max. spec. assim. rate	$\ddot p_a$	ageing acceleration
$[\dot M]$	spec. somatic maint. costs	$[G]$	spec. growth costs	$[E_m]$	max. spec. reserves
κ	$\frac{\text{somatic maint.+growth costs}}{\text{catabolic energy}}$	q	overhead costs of reprod.		

Although the number of parameters might seem large, it is in fact extremely small in view of the number of processes that are specified. Only a small selection of these parameters is involved in the description of any particular measured variable. If we evaluate the expression for size as a function of age, for instance, we know beforehand that parameters with energy in their dimensions will occur only as ratios, such that the dimension energy drops out. This is because energy is not involved directly in size measurements. We need to know the value of a parameter that has energy in its dimensions only if we want to describe energies.

Three compound parameters frequently appear in expressions for physiological quantities (cf Figure 3): The maintenance rate constant, $\dot m \equiv [\dot M]/[G]$ (dimension: time^{-1}); the energy conductance, $\dot v \equiv \{\dot A_m\}/[E_m]$ (dimension: length time^{-1}); the energy investment ratio, $g \equiv [G]/\kappa[E_m]$ (dimension: none).

Figure 3 presents the feeding-at-length, respiration-at-length, growth-at-age and reproduction-at-age of the waterflea *Daphnia magna* for the situation of constant food density and temperature. This species, like most other species of animal, hardly changes its shape during growth, which implies that its surface area is proportional to the squared volumetric length and its volume to the cubed length. The four relationships in Figure 3 cover the major processes of uptake and use of food. The expressions, which follow from the set of rules of Table 1, show how the (compound) parameters in the description of these relationships depend on the feeding conditions. The scaled functional response f (defined as the ratio of the ingestion rate and the maximum one for an animal of that size) is under experimental control. Length-at-age turns out to follow the von Bertalanffy growth curve. By choosing different feeding levels, the von Bertalanffy growth rate (which is a compound parameter) and the ultimate length (another compound parameter) change in a particular way. This information can be used to estimate the compound parameters ($\dot{m}$, $\dot{v}$ and g) that are involved. These compound parameters can also be estimated from data such as the specific rate of weight decrease during starvation, respiration ontogeny during the embryonic period and survival probability-at-age.

The most far reaching and spectacular implications of the rules are the inter-specific body-size-scaling relationships. These relationships give trends in parameter values as they covary over different species (bacteria to whales). The 11 parameters can be classified in two groups. One group of parameters does not depend on body size, while the other group does depend on body size in a simple and predictable way: these parameters are proportional to the volumetric length, i.e. the cubic root of the body volume. Deviations of parameter values from these trends reflect ecophysiological adaptations of that species. All physiological variables that can be written as functions of the parameters can, for this reason, also be written as functions of (maximum) body size. Many of these functions have been worked out, tested against data and found to be realistic. Among them is the respiration rate, which turns out to be a weighted sum of squared and cubic (volumetric) length. This is very similar to empirical relationships, that indicate that respiration is approximately proportional to body mass to the power 0.75. The DEB model solves the long standing problem of understanding this empirical relationship.

The intra-specific body-size-scaling relationships (where we have just one set of parameters to describe the processes of food uptake and use) are fundamentally different from inter-specific body-size-scaling relationships (where we have 'sloppy' trends in parameter values among species). Hence, the fact that respiration, as it increases during the growth of an indivudual, turns out to be a weighted sum of squared and cubic length, just like for inter-specific comparisons, is merely coincidence. The volume-specific respiration decreases with body volume during life, because of the decreasing investment into growth.

A full description of the theory can be found in:
Kooijman, S.A.L.M. 1993. *Dynamic Energy Budgets in Biological Systems. Theory and applications in ecotoxicology.* Cambridge University Press, ISBN 0-521-45223-6, 350 pp.

Table 1: Key assumptions of the DEB model that specify a dynamical system with the state variables structural body mass, reserves and cumulated damage.

- If the investment into maturation exceeds a given threshold value, the organism changes its stage, i.e. it switches from the embryonic stage to the juvenile stage by initiating the feeding process, or from the juvenile stage to the adult stage by ceasing maturation and initiating the production of gametes (eggs, sperm).
- Food uptake is proportional to surface area and depends hyperbolically on food density (i.e. Holling type II functional response).
- The specific reserve dynamics is first order, with a rate that is inversely proportional to the volumetric length.
- The allocation to somatic maintenance plus growth (i.e. increase in structural biomass) is a fixed fraction of the energy drain from the reserves, which further includes maturity maintenance plus maturation or reproduction. This rule is called the κ-rule.
- Homeostasis of structural biomass and reserves, i.e. their chemical composition does not change, despite changes in the chemical composition of the environment. Since the amount of reserves can change relative to the structural biomass, certain changes in the chemical composition of the individual as a whole are possible. The homeostasis assumption implies that the following items are constant

  food-energy conversion, although it depends on the type of food

  volume-specific maintenance costs (both somatic and maturity)

  volume-specific growth costs
- The hazard rate is proportional to the accumulated damage

  the damage production is proportional to the changed DNA

  the DNA change is proportional to the use of oxygen
- The initial conditions are given by

  The initial structural biomass is negligibly small.

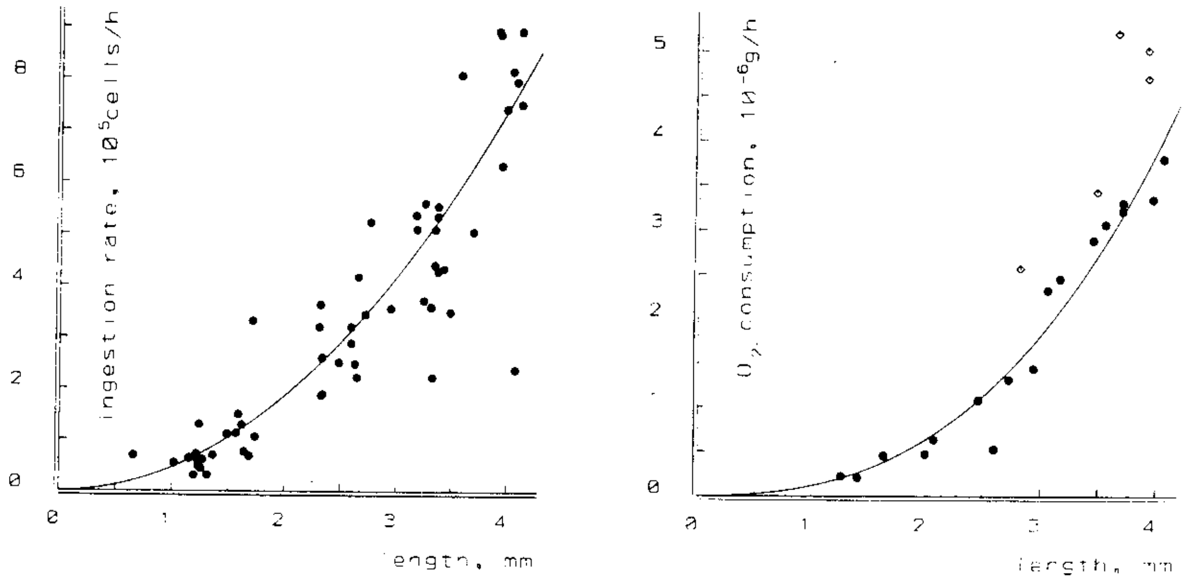
  The reserve density at birth equals that of mother at egg laying.

  The initial damage is negligibly small.

Figure 3: Investment into maturation and the κ-rule for allocation of energy from reserves solves the following puzzle: *Daphnia magna* starts to reproduce upon exceeding 2.5 mm body length. Reproduction takes about 80% of the budget. Where does this energy come from? Ingestion or respiration is not rapidly increased at this size, nor is growth reduced. The rules in Table 1 imply the expressions presented above the graphs, where L stands for body length, a for age, and the compound parameters are given in the text.

Ingestion $\propto fL^2$

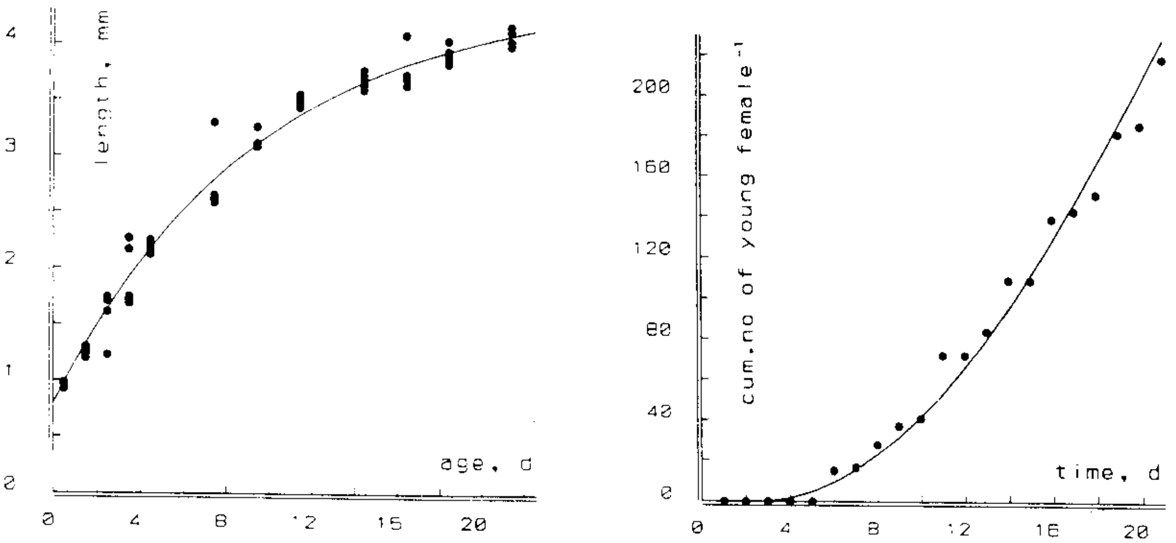
Respiration $\propto \dot{v}L^2 + \dot{m}L^3$



Growth: $\frac{d}{dt}L = \dot{\gamma}(L_\infty - L)$

$$\dot{\gamma} = \frac{\dot{m}g}{3(f+g)}; \quad L_\infty = \frac{f\dot{v}}{g\dot{m}}$$

Reproduction $\propto \dot{v}L^2 + \dot{m}L^3 - (1 + g/f)\dot{m}L_p^3$



Appendix: Publications on the DEB-model

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