Using stable isotope enriched food pulses to deduce or verify DEB parameters

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Introduction

Any paper normally kicks off with an introduction on how important the respective topic is the world of science. Of course, I should do same. However, the potential audience of this essay is very likely to be interested in organisms and their energy management and I have therefore decided to refrain from this obligation and immediately step to the essence of writing this essay: deepening one's understanding of the Dynamic Energy Budget (DEB) theory, which is more than challenging enough.

Bas Kooijman believes that there are elementary rules of energy management that are similar across all organisms and this has lead him to build the DEB theory {Kooijman, 2000 #599}. These elementary assumptions are translated into mathematical equations that either describe the growth of an organism in terms of energy, length or mass. In his book there are a substantial amount of figures in which the DEB equations fit the observations convincingly well. From these fits the underlying governing DEB-parameter are deduced.

In our institute we study mass dynamics by tracing the fate of food sources that are enriched in their isotope composition, through the food web. The initial use of stable isotopes was aimed at qualitatively distinguishing food sources of organisms in field situations (eg. Fry, 1999 #189) and trying to estimate their trophic position {Minagawa, 1984 #188}. In more recent years the use of stable isotope tracer studies have provided valuable information on the element dynamics ranging from whole ecosystem studies (Hall, 1998 #185; Tank, 2000 #167), more confined field studies (Middelburg, 2000 #122) to mesocosm studies (Norrman, 1995 #357; Moodley, 2000 #123). These tracer studies bear resemblance with more common radioisotope studies, but the main advantage lies in the possibility of field application and the lack of legal restrictions. The basic essential compounds treated in the DEB theory are C, H, O and N, for which carbon (^{12}C – ^{13C}), nitrogen (^{14}N – ^{15}N) and oxygen (^{16}O – ^{18}O) stable isotopes exist.

Building upon the valuable quantitative information the isotope tracer studies have generated on mass dynamics in a variety of biological systems, it is tempting to speculate on the potentials in a DEB context. For example, suppose that at one point in the Von Bartalanffy growth curve, one supplies an animal with a food pulse that is strongly enriched in one particular isotope: after an initial loss in the assimilation step there is enrichment of the reserve compounds and, after again some losses, subsequent incorporation into structural compounds. Hence, besides the growth curve additional dynamical

information is available, which might allow additional DEB-parameters to be estimated from the same experimental setting.

In this essay I explore the possibility of extracting additional DEB-parameters from an experimental setting in which a Von Bartalanffy growth curve is measured by giving an enriched food pulses. In the discussion some additional possibilities will be briefly described. I realize that this analysis is neither complete nor exhaustive, but implementation of the DEB-isotope model took more effort than expected and therefore the subsequent section is limited due to time constraints. Although the eventual aim should be a practical experimental design, I leave that translation for the creative experimenter, amongst others because practical problems are highly case study dependent.

Theoretical background

DEB theory

This section will contain nothing new for the DEB diehards among us. Nevertheless, a brief introduction into some of the basic DEB equations is required for understanding the analysis offered here, especially as the stable isotope equations have to be plugged in later on. For simplicity, I will only talk about ectothermic isomorphs.

DEB treats an organism as consisting of two state variables, namely a generalized compound reserve and a generalized compounds structure. With generalized compound it is meant that its composition doesn't change over time (i.e. strong homeostasis assumption). Assimilated food adds up to reserve's, which are expressed as a reserve density (i.e. reserve energy per structural energy). The use of reserves does not directly depend on food intake, but only on the reserve density. Although the basic unit of DEB is **energy**, a link with stable isotopes requires **mass** equations. Hence, the DEB mass equations, expressed in carbon units, are used in this essay. The dynamics of the reserve density is given by

$$\frac{d}{dt} m_E = y_{EX} \{\dot{J}_{XAm}\} M_V^{-1/3} [M_V]^{2/3} \left(f - \frac{m_E}{m_{Em}} \right) \quad (1)$$

This reserve density equation based on energy follows from the absolute description of reserve energy E, which is given by

$$\frac{d}{dt} E = p_A - p_C \quad (2)$$

where $\dot{p}_A$ is the assimilated energy per unit of time (assimilation power) and $\dot{p}_C$ is the energy spent on catabolic processes per unit of time (i.e. catabolic power). Using the conversions $E = M_E \mu_E$, $\{p_{Am}\} = \mu_{AX} \{J_{XAm}\}$, $\dot{v} = y_{EX} \frac{\{J_{XAm}\}}{[M_{Em}]}$ and $V = \frac{M_V}{[M_V]}$ this becomes in mass units

$$\frac{d}{dt} M_E = \frac{\mu_{AX}}{\mu_E} f \{J_{XAm}\} M_V^{2/3} [M_V]^{-2/3} - m_e [M_V] \left(y_{EX} \frac{\{J_{XAm}\}}{[M_{Em}]} M_V^{2/3} [M_V]^{-2/3} - \frac{d}{dt} M_V [M_V]^{-1} \right) \tag{3}$$

The other state variable is structure, as derived in chapter 3 of {Kooijman, 2000 #599} its differential equation follows directly from the assumptions underlying the DEB theory (note that heating drops from the equation)

$$\frac{d}{dt} M_V = \underbrace{M_V \frac{y_{EX} \{J_{XAm}\} M_V^{-1/3} [M_V]^{-2/3} \frac{m_E}{m_{Em}}}{m_E + y_{EV}/\kappa}}_{\text{growth + somatic maintenance}} - \underbrace{M_V \frac{j_{EM}/\kappa}{m_E + y_{EV}/\kappa}}_{\text{somatic maintenance}} \tag{4}$$

Not all catabolic power is possible candidate for growth. More specifically a fixed κ-fraction of the catabolic power is used primarily for somatic maintenance and the remaining part is used for structural growth. The $1-\kappa$ fraction is spent on development and reproduction. In equation 4 the terms are explicitly separated into the total amount of energy spent on growth and maintenance and the sole maintenance term. All costs are paid directly from the reserve material.

Stable isotope notation

It is instructive here to introduce some definitions on stable isotope notation. The isotope ratio is always given by the ratio of the heavy isotope over the light isotope

$$\mathrm{R} = \frac{^{\text{heavy}}\,\text{Isotope}}{^{\text{light}}\,\text{Isotope}} \tag{5}$$

the fraction is given by

$$\mathrm{F} = \frac{^{\text{heavy}}\,\text{Isotope}}{^{\text{light}}\,\text{Isotope} + ^{\text{heavy}}\,\text{Isotope}} \tag{6}$$

with the pro-mille deviation from a reference material given by the delta notation

$$\delta^{\text{heavy}}\text{Isotope} = \left(\frac{R_{sample} - R_{reference}}{R_{reference}} \right) \cdot 1000 = \left(\frac{R_{sample}}{R_{reference}} - 1 \right) \cdot 1000 \qquad (7)$$

Hence, $\delta^{\text{heavy}}\text{Isotope}$ indicates the pro-mille deviation of the ratio of $^{\text{heavy}}$ Isotope over $^{\text{light}}$ Isotope in a sample from the reference material. In nature the lighter isotope always dominates over the heavier isotope and I will therefore refer to them as abundant and rare isotopes, respectively.

Embedding stable isotopes into DEB

The basic equations underlying DEB and the stable isotope notation are now present; the next step is to link them. It is assumed that the rare isotopes are instantly diluted into the destination pool.

Hence, the whole isotope model is given by the reserve density

$$\frac{d}{dt} m_E = y_{EX} \{\dot{J}_{XAm}\} M_V^{-1/3} [M_V]^{2/3} \left(f - \frac{m_E}{m_{Em}} \right) \qquad (8)$$

the structural dynamics

$$\frac{d}{dt} M_V = M_V \frac{y_{EX} \{\dot{J}_{XAm}\} M_V^{-1/3} [M_V]^{-2/3} \frac{m_E}{m_{Em}}}{m_E + y_{EV}/\kappa} - M_V \frac{j_{EM}/\kappa}{m_E + y_{EV}/\kappa} \qquad (9)$$

the rare isotope dynamics in reserves

$$\frac{d}{dt} MI_E = F_X \frac{\mu_{AX}}{\mu_E} f \{\dot{J}_{XAm}\} M_V^{2/3} [M_V]^{-2/3} - F_V m_e [M_V] \left(y_{EX} \frac{\{\dot{J}_{XAm}\}}{[M_{Em}]} M_V^{2/3} [M_V]^{-2/3} - \frac{d}{dt} M_V [M_V]^{-1} \right) \qquad (10)$$

and the rare isotope dynamics in structural mass

$$\frac{d}{dt} MI_V = F_E M_V \frac{y_{EX} \{\dot{J}_{XAm}\} M_V^{-1/3} [M_V]^{-2/3} \frac{m_E}{m_{Em}}}{m_E + y_{EV}/\kappa} - \left((1 - k_V) F_E M_V + k_V F_V M_V \right) \frac{j_{EM}/\kappa}{m_E + y_{EV}/\kappa} \qquad (11)$$

MI_E and MI_V is the mass of the rare isotope in reserve and structure, respectively. F stands for the fraction of the rare isotope (see equation 6), the subscript refers to the respective compound, following standard DEB notation. The parameter k_v is equation 11 is the fraction of maintenance that is directly

used for turnover of structures. The fraction $1-k_v$ is used for maintenance without affecting the structural isotope value, whereas the k_v fraction of maintenance is used for turnover of structural compounds and thereby influences the structural isotope value. The implication is that when k_v amounts to zero, that part of an enriched food pulse that gets embedded in structural mass is destined to remain in structure. If k_v is only slightly higher than zero, this implies that the isotope value of structure will eventually return to the isotope value of the non-enriched food.

Because of the isotope equations, the whole system governing the dynamics of the organism has changed from 2 to 4 equations. However, also one additional assumption is required: the isotopes dilute instantly into the destination pool. Also the additional parameter k_V is needed to describe the isotopes dynamics.

Implications

In the next steps, I attempt to determine what information can be gained from the 4 equation system compared to the 2 equation system and suggest some other roads for exploration.

To illustrate the dynamics of the DEB-isotope model a simulation was run (Fig. 1). From the simulation it is clear that the reserves converge more swiftly towards the isotope value of the enriched food pulse, whereas the lag in structure is larger. This situation is to be expected in all organisms, since the reserves are the entry stage for any food compounds. In the standard DEB equations, the reserve density remains constant through the growth curve and its value is fixed by the parameters f and m_{Em}. In the DEB-isotope model however, the turnover time of the reserves can be estimated from the rate of appearance and disappearance of the relative amount of rare isotope. The combination of the two estimates fixes the reserve dynamics more strongly.

In fact, similar reasoning holds true for the structures. Although from the growth curve several compound parameters can be estimated, again the turnover time can be estimated from the increase of the rare isotopes in response to the enriched food pulse. Moreover, k_v can be estimated from the difference between the rate of appearance and disappearance rate of the rare isotope. More specifically, a skewness towards a higher rate of increase in the rare isotope compared to the abundant isotope points towards k_V being smaller than one.

Other possible applications

Although crucial in DEB, reserve density remains a rather illusive state variable whose value is only to be determined by indirect measurements. In the DEB model, any assimilated compound initially enters the reserves before being available for other destinations. Moreover, the strong homeostasis assumption and partitionability implies that all reserve compounds have similar kinetics (page 84 in {Kooijman, 2000 #599}. From the above an interesting case can be deduced. Suppose one collects an organism from the field and after a short acclimatization period one supplies the organism with an excessive food pulse that consists of only the (in nature) rare isotope (Fig. 2). The result is that the abundant isotope value follows the curve of a depletion of reserves, whereas from the rare isotope dynamics the rate and maximum amount of reserves can be estimated. The depletion curve of the abundant isotope allows that the field value of reserve density can be estimated. From the dynamics of the rare isotopes in the reserves the maximum reserve density can be estimated. And from the combined dynamics one is able to estimate the turnover of the reserves. Of course, the above case can only be applied is one is able to designate a particular compound that solely (or at least mainly) belongs to the reserves.

The latter remark leads to another interesting application. From the pulse of enriched food one might be able to single out the contribution of different compounds to reserves. It is technically possible to separate an organism into different lipids, amino acids and carbohydrates. As the initial and maximal enrichment will be found in the compounds belonging to the reserves, isotope data on these compounds may thereby aid in recognizing the composition.

Conclusions

In general, it is true that the quality of fitted parameter increases with the number of data points. Hence, it can be expected that the error margin associated with a fitted parameter will be smaller when also isotope data are available. Although, the increase in fitting power might be substantial, the true power of the use of isotopes lies in the additional compound parameters that can be estimated from the use of isotope enriched food sources. I think I have shown that the possibilities are plentiful.

Figures

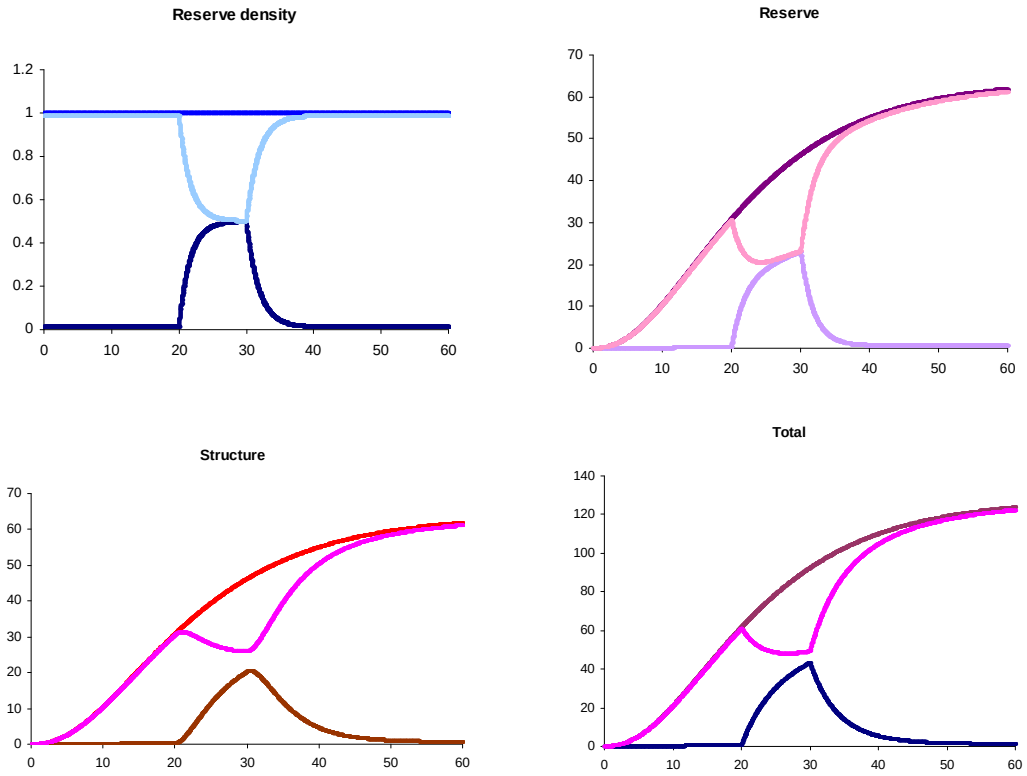

Fig. 1. Dynamics of the DEB-isotope model. The x-axis is in days and the y-axis in carbon mass. The upper constant line in the 'reserve density' figure is reserve density, the line with the dip is the ratio of the abundant isotope over total structure and the line with the bump is the ration of the rare isotope over total structure. For the remaining figures holds that the upper line is always the sum of the abundant and rare isotope, the line showing a dip is the abundant isotope and the line with the bump is the rare isotope. Parameter settings: k_V is 1, $\{\dot{J}_{XAm}\}$ is 2, m_{Em} is 1, $[M_V]$ is 1, y_{EV} is 1, y_{EX} is 1, κ is 0.8 and $\dot{k}_M$ is 0.4, $M_{V,t=0}$ is 0.01. During the whole virtual experiment the scaled food density was 1, with $F_x = 0.011$. However, between $t = 20$ and $t = 30$ the organism was fed enriched food with $F_X = 0.50$.

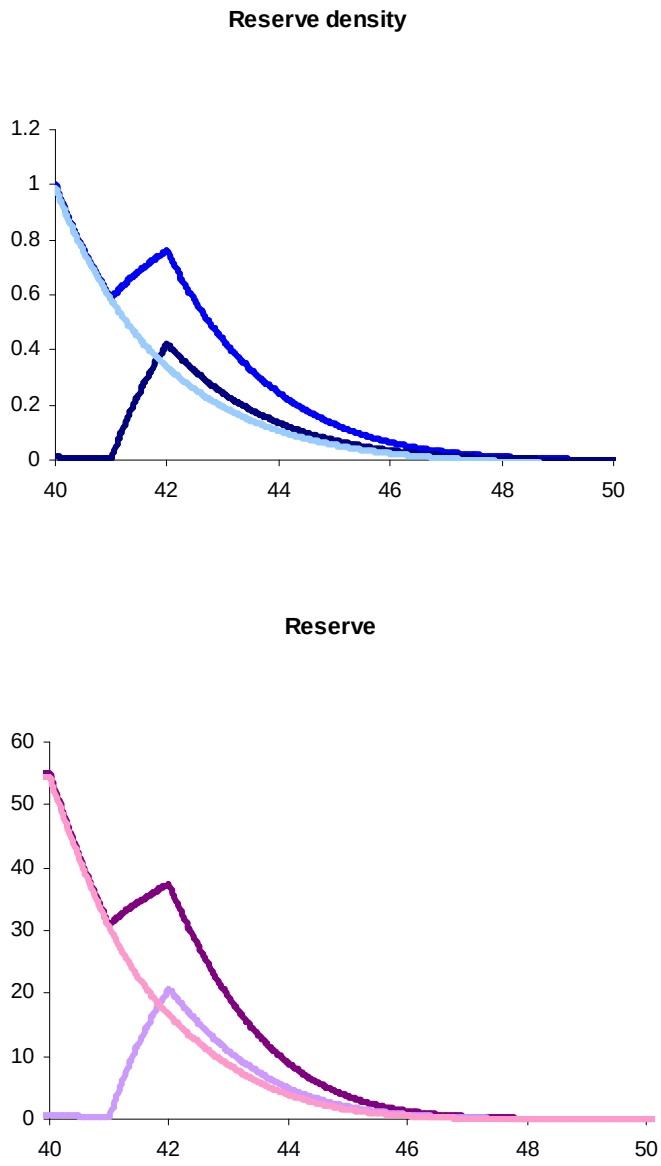

Fig 2. Dynamics of a field collected animal that was supposed to be feeding at a scaled feeding response of 1 prior to collection. Between $t = 41$ and $t = 42$ the organism was given a food pulse with $F_X = 1$. In the 'reserve density' figure the steadily decreasing line corresponds to the ratio of the abundant isotope over the total structural mass. The top irregular line is the reserve density and the lower irregular line the ratio of the rare isotope over the total structural mass. In the 'reserve' figure the steadily decreasing line is the amount of abundant isotope in the reserves, the top irregular line corresponds to the total amount of reserves and the lower irregular line is the amount of rare isotope is the reserves. Other parameters as in figure 1.