The dynamic energy budget theory: Essay

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I work with model DEB for my Master 2 Internship and I study the dynamic of *Pelagia noctiluca* in Mediterranean Sea, I use DEB model to quantify the biologic part link in the growth in response with the environmental changes and we introduce environmental forcing obtained with the software Ichthyop (NetCDF format). I introduced too more measures in the my-data and predict script to compare prediction with other real data. Model for *Pelagia noctiluca* is abj, it's mean is existing acceleration phenomenon during metamorphosis.

The first week of the DEB-télécourse we discuss about difference between weak and strong homeostasis:

- Weak homeostasis is based on constant chemical compositions of generalized compounds in constant environment.

- Strong homeostasis each pool has constant chemical composition independent of environment. Pool can be considered as set of entities with the same kinetics for example and not just as lipids.

Standards models describe isomorph organisms with one reserve and one structure, isomorphism is when the organism can be considered as a sphere and surface-area is proportional with (volume)^1/3.

First, food is assimilated by the organism. Energy flux will be allocated from reserve to the structure, its maintenance and to maturity or reproduction material and their maintenance.

-**<u>Dynamic of reserves</u>:** Working on relative reserve compared to the structure (reserve density), not on absolute reserve. (E = reserve, E_H is maturity's reserve and E_R is reproduction's reserve).

$$\frac{dE}{dt} = \dot{p}A - \dot{p}C$$

$$\frac{dEH}{dt} = (1 - ꝁ)(\dot{p}A - \dot{p}J) = \dot{p}R \text{ if } E_H < E_H^P \text{ else } \frac{dEH}{dt} = 0$$

$$\frac{dER}{dt} = ꝁ_R \dot{p}R \text{ if } E_H < E_H^P \text{ else } \frac{dER}{dt} = 0$$

With ṗA assimilation flux, ṗC is mobilisation flux, ṗJ is maintenance maturity,
ꝁ is the part allocated from reserve to structure and its maintenance.

<u>-Dynamic of structure</u>: Energy storage into reserve is catabolic flux and these flux is divided into 2 parts: somatic growth and reproduction material. Proportion of growth represents this ꝁ (kappa), which is constant. It's the kappa-rule.

$$\frac{dV}{dt} = \frac{\dot{p_G}}{EG}$$

With $\dot{p_G}$ energy's flux allocated to growth and EG is the cost of one structurally unity.

The standard model describes too metabolic switches and it defines three stages:

-Embryo stage: there is no assimilation and reserve is E_0 , initial energy into eggs gave by the mother.

-Juvenile stage: Start with the birth it's the beginning of assimilation, growth and somatic maintenance.

-Adult stage: It's the start of puberty and reproduction, there is no maturation but maintenance of this maturity.

Temperature affect metabolic flux, it's existing à correction factor:

$$c(T) = \exp((\frac{TA}{T1} - \frac{TA}{T}))$$

With T_A = Arrhenius temperature = 11270 Kelvin

$T_1 = T_{ref}$ = 293 kelvin

DEB theory describes Energy budget only when it is in the organism. Terms with brackets correspond to volumetric amounts, those between accolades correspond to surface-area specific amount. Those with a dot are rate (per time).

The somatic maintenance depends on volume and surface-area: [PS] = [PM] + {PT}/L. Level of maturation EH is link to the level of food consumed. Higher is this maturity and more energy it needs to maintain it (maturity maintenance flux depends on maturity). As long as EH is lower than E_{Hp} (level of maturity at puberty) there is no reproduction but still maturation and as soon as $E_H > E_{Hp}$ allocation to the reproduction starts and EH stays constant, equal to the threshold value. The reproduction is not always used, the energy to reproduction is stocked into a buffer.

The mobilization of reserve is associated to growth and reproduction, a proportion kappa is allocated to growth and somatic maintenance.

In order to simplify the model as much as possible and get a model which can be used to compare any species, adimensionalization is performed:

e = [E]/[E_m] where E_m is the highest value that E can take

The unitary cost of growth, it represents the same thing than $[E_G]$, cost of synthesis of a structure but without dimension.

$g=[E_G]/k*[E_m]$: if g is close to 0, the cost for growth (in energy) is low. If the maximal energy density [Em] is allocated (with the kappa rule) to growth, then g=1. Then g is between 0 and 1.

$k_M = [P_M] /[E_G]$ is the ratio between the volume specific maintenance rate and volume specific growth cost.

Von Bertalanffy growth curves are very common. In DEB theory, the VB model results from the DEB model with the hypothesis that food is constant. The ultimate length is Linf different from L_m used in DEB theory excepted for f=1. The link with DEB theory is made when we use the growth rate rb whose depends on k_M, f and g, it represents the speed at which one individual reaches adult maximal size. Higher the organism is and longer it takes to reaches adulthood. If f=1, $L_i = L_m$ and if f is small $L_i = L_m/2$.

At birth the initial quantity of reserve depend on E0 gave by the mother (maternal effect). The initial length at birth is call L_b.

At Embryo stage, there is no gain of resource but the initial resource is used to the development and the growth but it seems negligible. The birth is the start of assimilation.

DEB parameters are not measurable directly, thus they are estimated in such a way that DEB theory matches with measurable quantities.

The transport of food is make through a surface-area, that the reason why it's depend on length.

The functional scale response (Holling) f is food quantity per individual per time and depends on prey density X. In DEB theory f is an arbitrary choice because it's need a study behavioral to estimate it. Flux of assimilation depends on f.

Formula 3.10 is matter statement of accounts: It's equal to zero because of elements conservation law.

$$0 = ns * Jsk + np * Jpk$$

Where J_{sk} is a matrix of mineral matter consumed (N, C, O, H) it's represents the flow associated to the structure, reserve and assimilation and np is matrix of elements in the compartment of the organism in mol. It gives relations between composition of compounds with C, H, O and N and compounds expressed in X, V and E (or E_R).

We can calculate the masse of structures produced for example thanks to this matrix.

Biosynthesis from enzymes and synthesis units:
Θ ** = free enzyme, Θ can be associated to A or B (elements) and form an enzymatic complex.

A and B are complementary substrates to be active and to make product there needs to be link together to Θ.
The enzyme can start with A first and then B or reverse (parallel substrates). In DEB theory: bending rate = b and dissociation rate = k.

Concept of rejection unit: In this concept, the dissociation rates k is infinite so the enzyme is not efficient.

Concept of synthesizing unit: In this concept, k is close to 0 and in the DEB theory, k is considered equaled to 0. This hypothesis simplifies the calculations.

In equation 3.29, we have the sum of the different proportions the different states of the enzyme (or SU) Θ. This sum is equal to 1:

$$1 = \Theta^{**} + \Theta^{*A} + \Theta^{*B} + \Theta^{AB}$$

In equation 3.30: we have the variation by unit of time of the free enzyme. The negative terms correspond to binding processes with the enzyme. b_A and b_B are the binding rates between compound A or B with Θ. X_a and X_b are the concentrations of A or B. The positive terms correspond to the dissociation. In this case, Θ is released so the term is positive. Same rules for equations 3.31 and 3.32.

It is commonly assumed that enzymatic reactions are very fast in regards to growth dynamics, thus the dynamics are set to equilibrium; the equations 3.29 and 3.30 are then equal to zero. The advantage is that the computer can easily do the calculations for this linear system.

There are different kinds of substrate: complementary, parallel …

In case of inhibition pattern (figure 3.8) enzyme Θ is free: When it meet substrate S1, it links to S1 and form an enzymatic complex Θ^{S1} and produced product. If Θ meet S2 it free S1 and links to S2 so S2 inhibit S1's produce.

It's the same thing with reserve and structure in case of starvation, reserve inhibit the structure to "pay" maintenance, but it's depends on organism because reproduction can be inhibiting instead of structure. It's too kappa-rule.

The univariate model: In case of f or T varying there are consequences to considered. (Sometimes light can be considered as food).

Shape variation: There is three sort of shape considered in DEB theory, in the standard model we study isomorphism:

-Isomorphism: Organism is considered as a ball and growth in three direction: $S = V^{2/3}$

-V0-Morphisme: Surface is proportional to volume puissance 0, surface-area varying in function of volume. In this case contact surface with food is constant, there are more cells but same access to resources: $S = V^0$

-V1-Morphisme: Surface is proportional to volume puissance 1. Surface of contact with resources increase with volume: $S = V^1$

$M(V)$ is shape function we used it to get the model for V0 and V1-morphs from the model for isomorphs, we must multiply j_{Am} an υ (energy conductance) by the shape function.

During life cycle of an organism it's possible to have isomorphism then V1-morphisme, it's the acceleration phenomenon and it can occurs during metamorphosis or other stage of the organism.

Energie	Embryo $0 < l <= l_b$	juvenile naissance $l_b < l <= l_j$	juvenile metamorphose $l_j < l <= l_p$	adulte $l_p < l <= 1$
Assimilation, $\dot{p}_A$	0	$fl^2 \frac{l}{l_b}$	$fl^2 \frac{l_j}{l_b}$	$fl^2 \frac{l_j}{l_b}$
Maintenance somatique, $\dot{p}_S$	κl^3	κl^3	κl^3	κl^3
Maintenance de la maturité, $\dot{p}_J$,	ku_H	ku_H	ku_H	ku_H^p
Mobilisation, $\dot{p}_C$	$el^2 \frac{g+l}{g+e}$	$el^2 \frac{gl/l_b+l}{g+e}$	$el^2 \frac{gl_j/l_b+l}{g+e}$	$el^2 \frac{gl_j/l_b+l}{g+e}$

Exemple of consequence of shape variation during growth of *Pelagia noctiluca:* "Embryo" and "juvenile naissance" is isomorphism and "juvenile metamorphose" and "adulte" is V1-Morphs. lj/lb is the shape coefficient. All the terms are divided by $p_{Am}*L_m^2$.