From individual to population and from physiology to ecology

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1 Main points of the basic concepts of DEB theory

The DEB (Dynamic and Energy Budget) theory offers a new approach for the modeling of numerous living processes. The aim of the theory is to describe physiological processes independently from the considered species {1}[1]. The reference scale use for this purpose is the individual {10} and more precisely physiological level to avoid too much complexity in the model. Individual level is indeed natural because it's easy to assess mass and energy at this scale of organisation {19}. The theory is also based on underscale phenomenon like synthesizing units part {43} which deals with enzyme kinetics or thermodynamic {3,35} which deals with energy. Overscale phenomenon are also include like shape relations between area and volume {23} or temperature {53}. This approach is coupled with some important modeling considerations on the use of dimension in models {12}, on the link between testability and parameter evaluation {14} or more general {7}. Another key idea is that productions are linked to volumes and exchanges to areas.

These ideas lead to a small number of choices and assumptions used to build the DEB theory. States variables are carefully chosen {20}. Age variables are rejected because the environment can't have direct impact on them. Volume, as a size descriptor, is preferred to weight due to the multiple area relations in physiological processes {22}. On the global DEB model structure, a variable describing reserves {20} is necessary to lift influence of food fluctuation on organisms and to ensure continuous maintenance. Energetic allocation rule, the κ-rule {65,86} says that there is a fix κ part of the energy dedicated to development for juveniles and reproduction for adults while the 1-κ part is allocated to growth. This comes from previous observations in order to avoid the problem of growth continuity and allow different growth pattern. This is completed by maintenance {89} taken on each of

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[1] Number in brackets refer to the page of the book (Kooijman, 2000)

these two parts for respectively maturity and somatic work. Homeostasis hypothesis {30} explains that the reserve and the structure composition doesn't change in time (strong homeostasis) and that the global composition of the organism doesn't change any more at steady state, with no food fluctuations (weak homeostasis). This hypothesis is often useful in determining and simplifying equations in the framework of the theory. Hypothesis on the shape {25} serves the same purpose.

The key step in building the model is on the reserve equation construction which follows from weak homeostasis, partitionability and independence between the use of reserve and the availability of food {82}. A simple first-order equation is obtained to describe the reserves density dynamic {85} which is then used to construct the growth equation {94}. These equations with those deduced for development {111} and reproduction {114} constitute the core of the theory summarize in {120}.

DEB theory is at first glance a bit disconcerting by the wide range of scientific domain which are implicated, then attractive by the gap it fills between modeling and experiment and finally very impressive by its ability to explain results by general processes. And here are the three main point I would like to underline. The DEB theory has clearly melt various scientific domain in a powerful way and is therefore very useful following {8}. In the second point, this theory seems to be an answer to those who say that modeling is disconnected from experiment, and that is thanks to the carefulness given to dimensional problems and to the choice to research the good mechanism instead of the good shape. This search for generality permits the global explanation of allometric relationships {95} or of the wide variety of growth curves {2,109}. Numerous examples given along the book show the pertinence of this approach.

2 How I use the DEB theory

I applied more specifically DEB model to a study of population dynamics. The DEBf model allows this under some assumptions {122} :

- Organisms are V1-morph, their surface is proportional to their volume
- Individuals propagates through mitosis at a fixed length
- There is an homogeneous melt in the chemostat
- Only structure is digested by the predator.

The resulting differential system is shown in {343}. Parameters used here come from the estimation in (Kooi & Kooijman, 1994) on an experiment in (Dent *et al.* , 1976). Two parameters can be employed to simulate the enrichment, the dilution

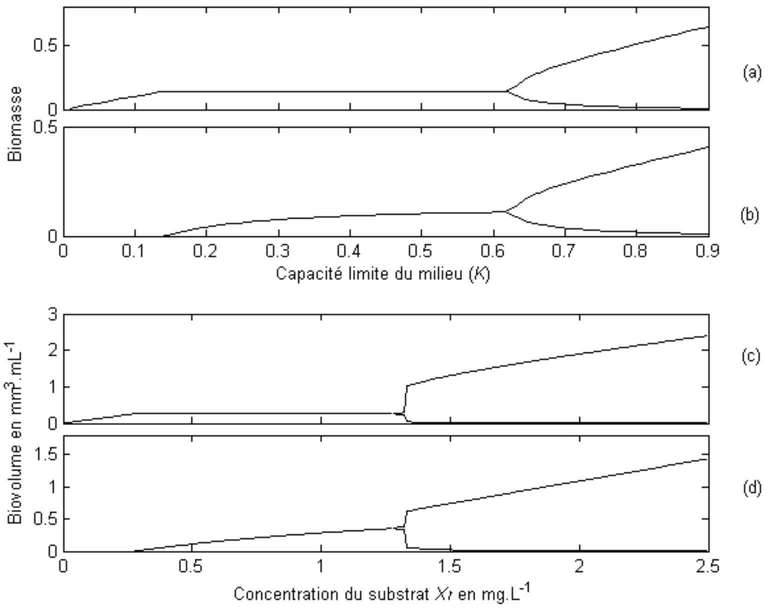

Figure 1: Comparison of the bifurcation diagrams of the R-M model for prey (a) and predators (b) with those of the DEBf model for prey (c) and predators (d)

rate $\dot{h}$ and the concentration of the nutrient X_r. The second is preferred because the first mix mortality and enrichment.

It is then possible to compare what happens in this model for a fixed dilution rate when X_r is increasing with the classical model of Rosenzweig and Mac-Arthur (1963), noted R-M. The two models follow the pattern of the paradox of enrichment (Fig. 1) first describe in (Rosenzweig, 1971). There is a similar first step from an equilibrium without predator to a stable coexistence between prey and predator. This equilibrium is then destabilised in a limit cycle represented by the minimum and the maximum reached value.

The next step is to transform this instability in term of species survival. This can be done with the concept of persistence. It defines a threshold under which the species go extinct. Using the persistence, a map of survival of the two species can be drawn for each ones of these models. For the R-M model four different areas appears, in white, the two species extinct, in light gray, only the prey survive, in gray, the extinction of the prey lead to the extinction of the predator and in black the two species coexist. This diagram shows the impact of the carrying capacity as an enrichment parameter on the persistence of species.

The second map (Fig. 3) shows the persistence of the species for the DEBf model. The boomerang shape in black is the coexistence area of the two species and the light gray areas are domains of enrichment parameters where only the prey survive. In the DEB model with this set of parameters, the predator always go extinct before

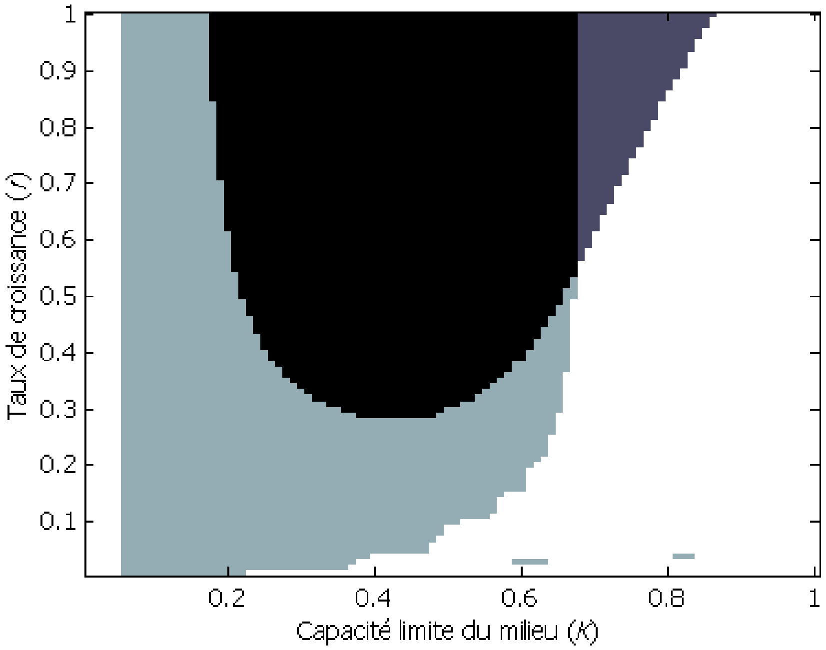

Figure 2: Survival map of the Rosenzweig - MacArthur model, in white : extinction of the prey and the predator, in light gray : the prey survive, in dark gray : the predator go extinct after the disappearance of the prey and in black : coexistence.

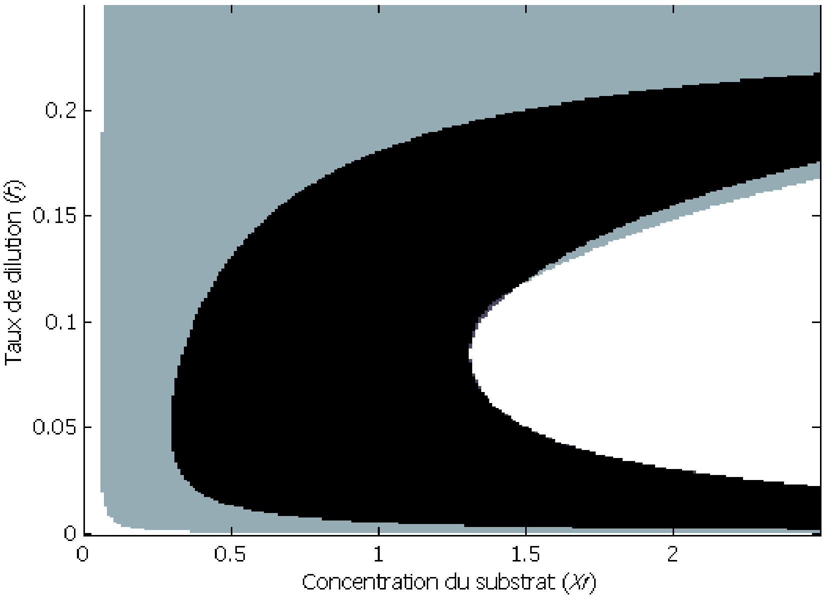

Figure 3: Survival map of the DEBf model, in white : extinction of the prey and the predator, in light gray : the prey survive and in black : coexistence.

the prey if we use the same threshold for both.

Further developments must lead to study the persistence for the same range of parameter with 3-species models. The behavior of longer food chain models is far more complex, with chaotic dynamics, so changes in the enrichment paradox pattern are possible.

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