

## Comment

# Is reproduction limiting growth? Comment on “Physics of metabolic organization” by Marko Jusup et al.

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Jusup et al. [1] aimed at covering the theoretical foundations of DEB theory and presenting the broadness of its applications for both physicists and biologists and they successfully do so. One of the most striking assumptions of DEB theory for biologists that is, as mentioned by the authors, at odds with an existing body of literature in fisheries sciences [2,3], is the so-called  $\kappa$ -rule. A constant allocation to growth and somatic maintenance throughout ontogeny is indeed at odds with the widely accepted limitation of growth at the onset of sexual maturity by the reproduction process.

As any striking assumption, it is likely to be questioned, and it should be questioned. But it may also prevent some readers to proceed further. This commentary aims to alleviate this legitimate skepticism i) by discussing the new understandings that can be gained by strictly applying this rule first and ii) by illustrating that DEB models can also accommodate for changes in allocation rules during ontogeny, consistently with DEB theory core assumptions.

## 1. Constant allocation to growth and somatic maintenance is an assumption of the *standard* DEB model

DEB theory states that an organism partitions its energy use in two branches: *i*) the growth and somatic maintenance branch and *ii*) the development, reproduction and maturity maintenance branch. It further states that this partition can only be a function of structural volume [1], e.g. an increasing allocation towards the development/reproduction branch as the organism grows in length.

From the body of DEB theory's assumptions, and the application of Occam's razor principle [1], the standard DEB model can be derived: The simplest allocation scheme that captures observed patterns is a constant proportion of the

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mobilized flux being allocated to the growth and somatic maintenance branch [4]. Thus, in the standard DEB model, reproduction is not limiting growth after the onset of sexual maturity.

## 2. Von Bertalanffy growth model is a special case of the standard DEB model

Many empirical models turn out to be special cases of DEB theory [5, see Table 11.1]. DEB theory states the mechanisms behind these models, and provides a better understanding of the conditions under which they can be applied. As presented by Jusup et al. [1], for the standard DEB model being equivalent to the commonly-used VB growth function (in length) the following conditions should hold throughout ontogeny: *i*) constant temperature, *ii*) constant food density, in addition to *iii*) constant food quality and *iv*) isomorphic growth, these last two conditions already being assumptions of the standard DEB model.

A single VB equation does not always simultaneously capture juvenile and adult growth. Assuming that one or more of these four conditions may not hold, while keeping the core of the standard DEB model the same, provides testable predictions and may lead to new understandings of the conditions encountered by individuals throughout ontogeny (see following section).

We argue that this approach provides a testable alternative to the new growth models proposed by Minte-Vera et al. [3], which include additional cost of reproduction after the onset of sexual maturity in order to improve model fit to both juvenile and adult growth data.

## 3. Ontogenic shifts in food requirements and habitats

If temperature, food density and/or food quality cannot be considered constant throughout ontogeny, the conditions for the von Bertalanffy growth model to apply are not fulfilled and the use of the standard DEB model should be preferred to jointly capture juvenile and adult growth.

Observing that pond snail juvenile growth was lower than predicted by a VB growth model fitted to adult data, Zimmer et al. [6] successfully showed that optimal food quality throughout ontogeny did not hold in this given experiment. Changes in food requirements between juvenile and adults is a well-known pattern. Juveniles pond snail in traditional ecotoxicology tests may be food limited if provided with the same food type as the adults, which may lead to bias interpretation of the effects of toxicants.

Pecquerie et al. [7] could not fit juvenile and adult anchovy data with a single VB growth equation but resolved this discrepancy by assuming that the vertical distribution of juveniles at the surface in late spring/summer would lead to a much higher temperature averaged over the juvenile period than the average temperature experienced by adult anchovy over a year in the Bay of Biscay, explaining fast juvenile growth compared to adults.

No assumption regarding the limitation of growth by the reproduction process was required in these studies. While attempting to apply the simplest model (i.e. the standard DEB model) to describe the observed growth pattern, both studies led to new assumptions and understandings.

## 4. Plasticity and varying $\kappa$

Organisms live in varying environmental conditions and, as mentioned above, the standard DEB model is suitable to take into account dynamic environmental conditions. But plasticity, i.e. changes in energy allocation in response to these varying conditions, can also be taken into account in more realistic, but more complex, models with changing  $\kappa$ .

We refer the reader to a study case in Kooijman [5, p. 115 and references therein] regarding pond snails that continued energy allocation to reproduction during prolonged starvation under a light:dark 16:8 cycle (summer conditions), but that ceased reproduction under a 12:12 cycle (spring/autumn conditions). Ceasing allocation to reproduction in spring or autumn may increase survival as prolonged starvation periods might be more likely. Under non-limiting food, individuals kept under a spring-type light regime also displayed a larger ultimate length, a strong indication that photoperiod can modify the energy allocation  $\kappa$  and that the reproduction process may limit growth at a seasonal scale [5].

The study by Mueller et al. [8] is also an elegant case where the authors showed that a change in  $\kappa$  between early-life and subsequent life stages could explain accelerated development in amphibians. An increase in  $\kappa$  between hatching and the onset of feeding in *Crinia Georgiana* could indeed explain how this species could develop two times

faster and metamorphoses at a smaller size than another frog species, *Pseudophryne bibronii*, while displaying similar egg and adult size. In this study, it is noteworthy that it is the development process, not reproduction, that is limiting growth; DEB theory treats these two processes similarly (i.e. with the same equation) in the juvenile and adult stages, respectively.

## 5. Concluding remarks

Constant allocation to growth and somatic maintenance throughout ontogeny is one of the key assumptions of the standard DEB model as well as a family of derived DEB models. It has been shown that constant allocation to growth captures many empirical growth and reproduction patterns [4]. It has also led some authors to propose new alternative explanations for the observed growth pattern, e.g. [6,7].

However, a  $\kappa$  varying with length is not violating DEB theory's first principles. It is a more complex situation that, we believe, should be considered once all possible alternatives regarding changes in the conditions experienced by an organism during ontogeny have been examined.

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