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ACCEPTED MANUSCRIPT

Challenges for Dynamic Energy Budget theory

Comment on "Physics of metabolic organization" by Marko Jusup et al.

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Jusup et al. [1] provide a comprehensive review of Dynamic Energy Budget (DEB) theory – a theory of metabolic organization that has its roots in a model by S.A.L.M Kooijman [2] and has evolved over three decades into a remarkable general theory whose use appears to be growing exponentially. The definitive text on DEB theory [3] is a challenging (though exceptionally rewarding) read, and previous reviews (e.g. [4, 5]) have provided focused summaries of some of its main themes, targeted at specific groups of readers. The strong case for a further review is well captured in the abstract: *"Hitherto, the foundations were more accessible to physicists or mathematicians, and the applications to biologists, causing a dichotomy in what always should have been a single body of work."* In response to this need, Jusup et al provide a review that combines a lucid, rigorous exposition of the core components of DEB theory with a diverse collection of DEB applications. They also highlight some recent advances, notably the rapidly growing on-line database of DEB model parameters (451 species on 15 August 2016 according to [1], now, just a few months later, over 500 species).

In the hope that Jusup et al. inspire interest in the core DEB concepts and that their review encourages new advances in DEB theory, this commentary suggests three themes that may represent productive directions for new research. The first is narrow and may appear somewhat technical, though it has wide implications; the other two suggest routes for making connection with other rapidly advancing areas of theory in biology. Achieving tighter synthesis with overlapping sub-disciplines is an exciting prospect as DEB theory has so much to offer, but there are intellectual hurdles to be overcome if we are to move from its current state as a niche specialism to wider recognition as part of fundamental biology.

1. Rates of energy mobilization

One of the most original parts of DEB theory is its approach to calculating expressions for rate processes *within* an organism. Prior to Kooijman's development of DEB theory, a number of researchers (e.g. [6]) were working with compartmental models of organism growth and reproduction using schemes similar to Fig.1 in [1] but with different organization of the boxes and arrows, and with no explicit incorporation of energy reserves. With reserves included as an abstract variable, there is no "natural" mechanistic way of choosing an expression for rate of mobilization of energy or elemental matter from the abstract "reserve" compartment (Fig.1 in [1]). Kooijman adopted a top-down approach using what amounts to reverse engineering - the mobilization flux was assumed to take the only form consistent with a pre-specified set of requirements. The challenge is to identify the requirements; they must be sufficiently restrictive to yield a problem with a unique solution but general enough to be a component of general

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