Editorial

35 years of DEB research

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ABSTRACT

Research on the Dynamic Energy Budget (DEB) theory started 35 years ago. Initially much emphasis was put on the development of a consistent theory. During recent years attention was paid on parameterizing DEB models for a huge collection of species. This enables the search for patterns in parameter values in an ecological and evolutionary context. This special issue presents some of the results of this quest, among other things focusing on the development of metabolic acceleration, combined with various applications of DEB theory in fisheries, aquaculture, climate science and ecotoxicology.

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1. Introduction

Dynamic energy budget (DEB) theory aims to quantify the metabolism at the level of the individual that all organisms share and it tries to do this on the basis of simple physico-chemical principles. It wants to understand possible deviations in terms of mechanisms in an evolutionary context. This aim asks for a formalized modular set-up of the quantification of metabolism that respects the interactions of processes that constitute metabolism: feeding, maintenance, development, growth, reproduction, and aging. The way these processes are modified by environmental factors, primarily temperature and food availability, are taken into account as well. The inclusion of reserves acting as metabolic memory, the full-life cycle of individuals (embryo, juvenile, adult) and the explicit use of conservation laws (energy, chemical elements and isotopes) sets the theory apart from other approaches known to the authors. Within DEB theory the individual is considered the basic unit and its metabolism forms the basis of population and ecosystem dynamics. The steps from the individual towards the ecosystem involve interactions between individuals, physical transport, and chemical transformation of nutrients and substrates and all these issues are covered by DEB theory.

It has now been 35 years since DEB research started (in 1979) and while initially much emphasis was put on the development of a consistent theory, during recent years a lot of effort has been put in the further development of parameter estimation methods (and software), testing them on a rapidly growing number of species (Lika et al., 2011a, 2011b). This collection of species, which comes under the name of the add_my_pet collection has presently about 400 entries. Almost all larger animal phyla are represented and all chordate classes. The software package DEBtool (Matlab/Octave) that is used has now over 1000 functions. Many of these functions are becoming more robust and faster and are intensively tested. In the near future we can expect new developments in the field of parameter estimation of several species simultaneously that exploit similarities and differences between these species and the integrated use of the bijection between parameter and data spaces that has been worked out (Lika et al., 2014).

This special issue of the Journal of Sea Research (JSR) is the fifth one on DEB theory, after issue 1557 of the Philosophical Transactions of the Royal Society 365 (2010) and issues 2 of volume 56 (2006), 2–3 of volume 62 (2009) and 4 of volume 66 of JSR (2011). DEB theory is about all species, and though many papers have been written on for example micro-organisms, most applications, like the ones in this special issue, are on animals. Because of the general interest in animals, data are more easily available, specifically in the context of aquatic sciences. Animals are from a metabolic perspective also relatively simple. Many features can be understood using a single reserve and structure and most species are approximately isomorphic, which means that they do not change in shape during growth.

All applications of any quantitative theory start with the knowledge of the parameter values. The increasing size of the add_my_pet collection provides this knowledge and enables further testing of the theory and identification of ecological and evolutionary patterns in parameter values. DEB theory is uniquely poised to provide insight into the evolution of life histories because it provides physio-chemical expectations for how life history traits

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should co-vary in the absence of any particular evolutionary optimizations. Some patterns that have been detected so far are quite remarkable, such as the patterns on somatic maintenance (Kooijman, 2013), allocation fraction to soma (Kooijman and Lika, 2014b), altriciality index (Kooijman and Lika, 2014b) and supply stress (Lika et al., 2014).

2. Patterns in parameters

For specific taxa the number of species is already large enough to explore within-taxon patterns. This special issue has a study on fish classes by Kooijman and Lika (2014–this issue), and we can expect studies on mammals, birds, insects, reptiles, and jellyfish soon. Kooijman and Lika's study (2014–this issue) of the energetics of fishes represents the broadest application of DEB theory to date in comparative analyses of life history. It includes 64 fish species representing all five fish classes. Some fascinating perspectives come out of this study. One of the most striking is that, as a group, bony fish have experienced selection for many small offspring, which has had flow-on effects in terms of metabolic acceleration. In contrast, the life history characteristics of the cartilaginous fishes (sharks and rays), including size at birth and puberty, closely follow the DEB expectations for how they should scale with body size. DEB theory is uniquely able to make these inferences because of the null hypotheses it provides for the expected patterns of co-variation, and Kooijman and Lika's study will undoubtedly inspire others to take the same approach to other taxonomic groups.

3. Metabolic acceleration

Kooijman et al. (2014) previously recognized that, although many species match predictions of the standard DEB model for metabolic rates, particular taxa deviated and have a lower metabolic rate as embryo, compared to late juvenile and adult stages. These taxa include all those with larval development, but also ones with less clear larval stages. They accelerate their metabolism during the life cycle. Acceleration of metabolism is thus defined as a long-term increase of respiration, that is faster than the typical 'standard' trajectory during the life cycle of an individual, from embryo to adult. Quite a few species accelerate their metabolism during ontogeny in different ways (Kooijman et al., 2014), beyond expectations based on the standard DEB model.

In this special issue Kooijman (2014–this issue) proceeds on this earlier work. Five different types of acceleration are identified. Arguments are presented for why accelerating species have an extra slow start of metabolism and why parental care evolved in endotherms. This phenomenon of initially slower growth in larvae than in juveniles was identified by Lika et al. (2014–this issue) when they considered DEB parameters for nine Mediterranean fish species of the order of Perciformes. Their work, confronting model fits with observed larval growth data, provides strong empirical support for metabolic acceleration. Furthermore, they present a novel hypothesis on the evolutionary context behind metabolic acceleration, and find that high metabolic acceleration of demersal species is associated with summer–autumn spawning in the Mediterranean, where temperature is high and food availability is low.

Zimmer et al. (2014–this issue) present a full-life-cycle model of the pond snail *Lymnaea stagnalis*. This species is of great historical significance in DEB theory, in that it was one of the first species to which the standard DEB model was applied (Zonneveld and Kooijman, 1989) subsequent to its initial development with *Daphnia magna*. This pond snail is also of significance because of its increasing role in ecotoxicology. Zonneveld and Kooijman (1989) were able to fit the standard DEB model to a wide range of metabolic phenomena in *L. stagnalis*, including egg development, starvation sensitivity and plasticity of the life-history associated with changes in day length. However, they were unable to explain the full life cycle with one parameter set — the egg development phase required substantially different parameter values in comparison to the adult. In this study, Zimmer et al. consider the extent that

metabolic acceleration can explain this discrepancy as well as departures from von Bertalanffy, noted in a previous paper by Zimmer et al. (2012). While Zimmer et al. (2014–this issue) do find that the assumption of metabolic acceleration provides predictions that are more consistent with the energetics of *L. stagnalis*, their conclusions remain cautions given the lack of obvious shape changes in this species during its ontogeny. Zimmer et al. suggest a range of alternative explanations, including the possible influence of nutritional conditions, together with potential experiments by which to distinguish them. In doing so, they highlight the power of DEB theory as a conceptual framework through which to interpret observations on the energetics and life histories of organisms.

Augustine et al. (2014–this issue-b) studied the purple mauve stinger *Pelagia noctiluca*. The stinger is another species where metabolism accelerates several days after birth. The DEB parameter set obtained suggests that *P. noctiluca* is well adapted to survive long periods of starvation since the predicted maximum reserve capacity is extremely high, and even if food is scarce (ingestion levels only 14% of the maximum for a given size) an individual would still mature and be able to reproduce. Apparently *P. noctiluca* combines maximizing allocation to reproduction with rather extreme capabilities to survive starvation. The combination of these properties might explain why *P. noctiluca* is a rapidly growing concern to fisheries and tourism.

In a second paper by Augustine et al. (2014–this issue-a), DEB parameters of another holoplanktonic gelatinous zooplankton species, the invasive comb jelly *Mnemiopsis leidyi*, were estimated and compared to the parameters of *P. noctiluca*. Both species undergo metabolic acceleration after hatching, which confers a lot of metabolic flexibility by controlling generation time. In contrast to *P. noctiluca*, *M. leidyi* is comprised more of structure than of reserve. Moreover, *M. leidyi* shows higher turnover rates of reserve compounds and faster shrinking rates. It is suggested that the large variation in the number of size classes of *M. leidyi* that are observed in the field is related to environmental factors that affect the delay in metabolic acceleration.

A specific form of metabolic acceleration (or should it be called deceleration?) was studied by Teixeira et al. (2014–this issue), who looked at the growth of juvenile wandering albatrosses *Diomedea exulans*. Similar to other seabirds this species exhibits a growth pattern that includes a period of body mass decrease before fledging. They first parameterized the DEB standard model and then showed that a combination of a decline in food availability before fledging and a difference in locomotion effort between chicks and adults (resulting in a difference in maintenance costs) was enough to accurately predict the observed mass recession. No other differences in DEB parameters between chicks and adults were needed. They thus have very similar metabolic traits.

4. Fish, bivalves and the use of renewable resources

DEB theory already has many applications in research related to fisheries and aquaculture and this special issue contains quite a few new contributions to this lively field of research. Most of them present parameter estimation exercises for species so far not covered. Such contributions are a pre-requisite for further comparative studies, and some of them already contain preliminary comparisons. As a sideline, quite a few of the species discussed in these papers also show metabolic acceleration. Finally, these studies may well contribute to the management of these precious resources.

van der Meer and Kooijman (2014–this issue), for example, discuss the fishery on Atlantic hagfish *Myxine glutinosa*, as a typical example of a deep-sea fisheries that occur without much knowledge of the life-history characteristics of the exploited stock. There is lack of data on distribution and stock abundance, but especially knowledge on reproduction and growth is lacking. Major problems are that hagfish cannot be aged, and that they behave abnormally in captivity. Luckily DEB theory enables the estimation of maximum growth rates and age at maturity on the basis of limited information only, on among other things length