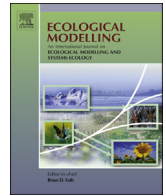




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Dynamic energy budgets in population ecotoxicology: Applications and outlook

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ABSTRACT

Most of the experimental testing in ecotoxicology takes place at the individual level, but the protection goals for environmental risk assessment are at the population level (or higher). Population modelling can fill this gap, but only models on a mechanistic basis allow for extrapolation beyond the conditions in the experimental tests. The life-history traits of individuals form the basis of population dynamics, and population modelling thus requires a proper understanding of the individual's behaviour. The dynamic energy budget (DEB) theory offers a flexible platform for the development of models at the individual level. Linking DEB models to population models can thus provide a mechanistic basis for extrapolation. Here, we provide a conceptual overview of DEB theory, with emphasis on its applications in ecotoxicology. Furthermore, we briefly review the applications in which a DEB-based individual model has been linked to structured population dynamics. Finally, we discuss some of the most important areas for further research in this context.

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1. Introduction

Environmental risk assessment aims to predict the impacts of anthropogenic stressors on populations and communities. However, most of the experimental testing takes place at the individual level. Laboratory testing usually comprises exposure to a constant concentration of a single toxicant, for a pre-defined period of time, under controlled environmental conditions, with ad libitum food supply. In the environment, however, multiple stress is the norm, exposure concentrations vary in time and space, and environmental conditions fluctuate. This huge gap between the simplified conditions of the toxicity tests and the complexity of the field situation can only be covered in an ecologically-relevant way by using population models to extrapolate from individual-level traits to population responses. However, due attention should be given to the extrapolation of traits from the experimental test to the same traits under the environmental conditions experienced in the field. This requires mechanistic models at the individual level.

Models at the individual level can be of great assistance in designing toxicity tests, interpreting the individual's response to stress, and to extrapolate that response to untested conditions (Ashauer and Escher, 2010; Jager et al., 2006). For a model to be useful at the individual level, it should explain life-history traits (feeding, survival, growth and reproduction) over the life cycle of the organism, as a function of the environment (e.g., food availability, temperature), and the presence of stressors (e.g., toxicants). The model should allow educated extrapolation from the response in controlled environments (e.g., laboratory toxicity tests) to field conditions, where populations are to be protected. The model should be as generic as possible regarding the species, chemicals, and environmental conditions that it can cover; we simply cannot build a dedicated model for each combination. Finally, the model output should allow its coupling to population models of different levels of complexity (e.g., matrix models or individual-based models), since the most appropriate population-level strategy may well depend on the risk-assessment question.

What strategy should we apply to develop mechanistic models at the individual level? Clearly, modelling every individual process at the molecular level is unlikely to yield practically-useful models. Processes at this level are also rather specific for each stressor, and each species. Fortunately, we can invoke some general biological principles to structure our modelling efforts. Every living organism

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takes up resources from its environment, and uses these resources to build and maintain their own bodies, and to create offspring. In doing so, they must adhere to the conservation laws for mass and energy. Models that operate on these principles are generally called energy budgets. A number of bioenergetic approaches have been proposed in ecology (see discussion in Sibly et al., 2013; Van der Meer, 2006), but the best-tested and most extensive framework in this field is the dynamic energy budget (DEB) theory (Kooijman, 2001; Nisbet et al., 2000; Sousa et al., 2010). At this moment, methods based on DEB theory are the only energy-budget models that have been systematically applied in ecotoxicology, and the only ones that have been included in international risk-assessment guidance for their relevance in analysing ecotoxicity data (ISO, 2006; OECD, 2006). Therefore, we limit ourselves here to a discussion of DEB-based methods.

In this paper, we provide a conceptual overview of DEB theory, and show how it has been applied to ecotoxicological questions. Subsequently, we provide a short review of the applications of DEB theory that address the effects of chemical stressors at the population level (focussing on structured population models), and highlight areas for further research.

2. Theoretical background

2.1. Energy budgets for the individual

Before we can consider toxic effects, we first have to look closer at the general biology of the organism. Toxicant effects are deviations from the situation without toxicants, and therefore, we first need a quantitative model for the unstressed behaviour before we can interpret toxicant effects. As stated in the introduction, all living organisms take up resources from the environment, and use these resources to maintain their bodies, grow, develop, and reproduce. When a stressor decreases the investment in a trait such as reproduction, we have consider where that energy went: was it never assimilated in the first place (e.g., an effect on the feeding rate), or was it used for other purposes (e.g., to increase the maintenance costs to counteract damage by the toxicant). An energy-budget model can thus be used to quantitatively test various hypotheses for the metabolic mechanism underlying the response to stressors (Alda Álvarez et al., 2006), accounting for the causal links between all traits. Identifying the affected process is essential to extrapolate the individual's response to the toxicant from the laboratory setting to the environment (e.g., with time-varying food or toxicant levels).

Every living organism has an energy budget, but different species follow different acquisition and allocation rules. In the remainder of this review, we will focus on animals, as these organisms form, metabolically speaking, a rather homogeneous group. All of them feed on other organisms to obtain their energy and building blocks, which places similar constraints on metabolic organisation. This similarity is for example supported by the observation that growth curves for a wide range of animals are well described by the same curve as long as conditions are constant; the von Bertalanffy growth curve (Kooijman, 2010). In the DEB animal framework, species differ mainly in their parameter values, and only to a lesser extent in model structure (which reflects the metabolic organisation). The level of the energy budget thus presents a relatively species- and stressor-independent platform that can be adapted to any focal species to interpret stressor effects over the life cycle.

The standard animal DEB model, as presented in Sousa et al. (2010), is the simplest complete DEB model (Fig. 1). It deals with an animal that feeds on one food source (with constant composition), does not change in shape (isomorphy), and reproduces via eggs.

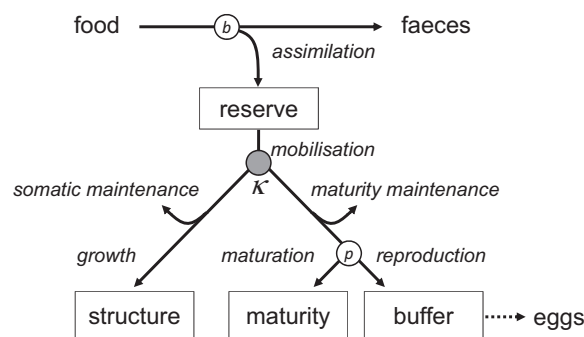


Fig. 1. Schematic representation of the standard DEB model for animals. The nodes 'b' and 'p' denote switches at birth (start of feeding) and puberty (start of investment in reproduction), respectively. The mobilisation flux is continuously split (grey circle), with a fraction κ allocated to the soma.

Biomass is divided into structure (which requires maintenance) and reserve (which can fuel metabolic processes). The state variable, 'maturity', specifies the developmental status of the individual and hence determines the start of investment into reproduction (maturity does not have associated mass in DEB but is quantified by the amount energy invested in it). Feeding rate is proportional to a surface area of the individual, and thus scales with structural volume to the power $2/3$. Food is assimilated into the reserve compartment, from which reserve is mobilised to yield energy and building blocks. A fixed fraction κ of the mobilisation flux is channelled to the soma (somatic maintenance and structural growth). The remaining fraction $1 - \kappa$ is used for maturation (in juveniles), maturity maintenance (whole life cycle), and reproduction (in adults). Maintenance costs need to be paid from the mobilised reserve first. Somatic maintenance cost is proportional to the volume of structure, whereas maturity maintenance is proportional to the actual level of maturity. The continuous investment in reproduction is first collected in a buffer, from which clutches of eggs are produced. This particular organisation of the metabolic processes is the only one that can match a full set of general empirical patterns observed in animals (Lika and Kooijman, 2011).

The standard model can be extended in various ways, but it may already be too complex and data hungry for practical applications in ecotoxicology, so simplifications of the standard model are extensively used. In Table 1 we group several of the simplifications in three categories, providing their main features and a reference (where more details on the model are provided). In the 'no maturity' models, the state variable for maturity is removed; the transition from juvenile to adult takes place at a fixed size. Furthermore, primary DEB parameters (with a direct link to metabolic processes) are usually combined into easy-to-interpret compound parameters such as maximum body size. The reserve compartment is included, but is often simplified to a situation of steady state (assuming rapid dynamics of the reserve compartment). The 'no maturity, no reserve' category contains the earliest application of a DEB model to ecotoxicology. Compared to the previous category, it is further simplified by the complete absence of the reserve compartment. Apart from these three categories, a range of DEB-inspired approaches have been used, which include more descriptive elements (e.g., Ducrot et al., 2010; Péry et al., 2002). For reviewing model approaches, we will however stick to the models that fall into one of the three categories of Table 1.

It must be stressed that there is one DEB theory (Kooijman, 2010), but a range of different DEB models can be derived from it. The most appropriate model obviously depends on the purpose for which it is to be used: more complex versions can include more biological realism, but use more parameters, which places higher

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