

VU Research Portal

Linking Individual-based Models and Dynamic Energy Budget Theory: Lessons for Ecology and Ecotoxicology

Martin, B.

2013

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

Martin, B. (2013). *Linking Individual-based Models and Dynamic Energy Budget Theory: Lessons for Ecology and Ecotoxicology*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam].

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Summary

Understanding how the structure and dynamics of populations emerge is one of the fundamental challenges in ecology. As the influence of individual variation, local interactions, and adaptive behaviour on population dynamics have become more appreciated, individual-based models (IBMs) are playing an increasing role in both basic and applied disciplines. IBMs represent individual organisms as unique entities that differ from each other and change over their life cycle. Individuals are characterized by a set of state variables and attributes that are chosen according to the problem addressed with the model. Individuals behave as autonomous entities according to behavioural rules. They interact with each other and their abiotic environment, including habitat structure and environmental drivers such as temperature, humidity, or disturbances. Population dynamics emerge from these interactions.

IBMs have been shown to be powerful and flexible tools. However, they have also been criticized for often being based on ad hoc assumptions and representations of individual dynamics and behaviour. This makes the development of IBMs inefficient and the field of individual-based modelling incoherent. To facilitate re-usability of IBMs and their elements, and to facilitate distilling general insights from specific IBMs, it is desirable to base IBMs more on standardized and well-tested approaches for individual behaviour.

Dynamic Energy Budget (DEB) theory is such an approach. It has been developed with the goal of understanding the dynamics of biological systems, from cells to ecosystems, via a balance approach for mass and energy. As in IBMs, in DEB theory individuals are considered the key unit of interest for understanding dynamic systems at higher levels of organisation. Focusing on the individual is motivated by the fact that mass and energy balances are easier to calculate for individuals than for higher or lower levels of biological complexity. DEB theory provides a quantitative framework for modelling the acquisition and use of resources for organisms over the entire life cycle. It thereby generates a quantitative explanation for the time patterns of life-history traits such as growth, maturity, and reproduction in dynamic environments.

Thus, the use of IBMs in combination with DEB theory has the potential to strengthen the field of population ecology. Because DEB theory provides a generic framework for modelling the life-history of an individual, the same

modelling framework can be used for all species. This increases the generality of model results, as the differences in the behaviour of models of different species can be ascribed to differences in parameter values, rather than to differences in any part of the model structure. IBMs, in turn, allow those working with DEB theory at the individual level to test the consequences of individual-level processes at the population level via simulations.

Despite the great potential of Dynamic Energy Budget theory as the foundation for IBMs, their use together has been limited. To facilitate their combination, I developed a framework for using DEB theory in connection with IBMs: DEB-IBM. DEB-IBM is an accessible implementation of DEB in which a user can enter the DEB parameters of a species and evaluate their dynamics at the population level under various resource conditions. More importantly however, users can adapt the code to address specific research question, for example, how the distribution of resources over space alters the stability of populations in time, or how stressors, such as pesticides alter the dynamics of populations.

Using the DEB-IBM framework I tested the ability of the DEB theory to predict population-level dynamics from the properties of individuals. I used *Daphnia magna* as a model species, where data at the individual level was available to parameterise the model, and population-level predictions were compared against independent data from controlled population experiments.

I found that DEB theory successfully predicted population growth rates and peak densities of experimental *Daphnia* populations in multiple experimental settings, but failed to capture the decline phase, when the available food per *Daphnia* was low. Thus, the analysis revealed that correctly representing resource-dependent mortality is critical for linking individual and population levels. The fact that the standard DEB model was unable to capture patterns of resource-dependent mortality reflects the fact that most work on individuals has been conducted under relatively favourable food conditions. Further assumptions on food-dependent mortality of juveniles were needed to capture the population dynamics after the initial population peak. Specifically, the assumption that juveniles were more vulnerable to resource dependent mortality than adults. The resulting model then predicted, without further calibration, characteristic switches between small- and large-amplitude cycles, which have been observed for *Daphnia* populations. I conclude that cross-level tests help detecting gaps in current individual-level theories and ultimately will lead to theory development and the establishment of a generic basis for individual-based models and ecology.

In addition to theoretical explorations, I tested the potential of DEB theory combined with IBMs to extrapolate effects of chemical stress from the individual to the population level. For this I used information at the individual level on the effect of 3,4-dichloroaniline on *Daphnia*. The individual data suggested direct effects on reproduction but no significant effects on growth. Assuming such direct effects on reproduction, the model was able to accurately predict the population response to increasing concentrations of 3,4-dichloroaniline. Interestingly, the model was able to make extrapolations to environmental conditions not included in the parameterization process. Specifically, in the 21-day *Daphnia* reproduction test, *Daphnia* are fed *ad libitum* however, in the population experiments the food amount of food per *Daphnia* fluctuated dramatically. This highlights a significant benefit of using well-constructed, process-based models: the ability to extrapolate to untested scenarios.

In addition to showing the potential for linking individual and population levels, our result also highlight several shortcomings of current standard risk assessment tests. The practice of measuring chemical effects on reproduction without concurrently measuring body size is insufficient to predict population level effects. This is because stress on many physiological processes can result in a reduction in reproduction (reduced feeding, increased maintenance costs, mortality of embryos, etc.). However, these processes can have very different effects at the population level. With limited extra effort, standard tests at the individual level could deliver data that could considerably improve the applicability and precision of extrapolation to the population level. Specifically, the measurement of a toxicants effect on growth in addition to reproduction, and presenting and analysing data over time as opposed to relying on a single number to represent the toxicity at the end of the test (such as NOEC or EC50).

In conclusion, this thesis shows the potential of DEB and IBMs in combination to help illuminate the links between individual and population levels in both basic and applied contexts. The advantage of using a generic approach is that the lessons learned are directly transferable to other species.