Dynamic Energy Budget Theory for Metabolic Organisation

Dynamic Energy Budget (DEB) theory is a formal theory for the uptake and use of substrates (food, nutrients and light) by organisms and their use for maintenance, growth, maturation and propagation. It applies to all organisms (micro-organisms, animals and plants). The primary focus is at individual level, from a life cycle perspective, with many implications for sub- and supra-individual levels. The theory is based on sound chemical and physical principles, and is axiomatic in set-up to facilitate testing against data. It includes effects of temperature and chemical compounds; ageing is discussed as an effect of reactive oxygen species, with tight links to energetics. The theory also includes rules for the covariation of parameter values, better known as body size scaling and quantitative structure–activity relationships. Many well-known empirical models turn out to be special cases of DEB theory and provide empirical support. Many additional applications are illustrated using a wide variety of data and species. After 30 years of research on DEB theory, this third edition presents a fresh update. Since the second edition in 2000, some 140 papers have appeared in journals with a strong focus on DEB theory.

A lot of supporting material for this book meanwhile has been developed and is freely available, such as the software package DEBtool; one of its toolboxes contains code that generates the figures of this book: setting of data, model specification, parameter estimation, and plotting. By replacing data of your own, you have a convenient tool for applying the theory.

This edition includes a new chapter on evolutionary aspects; discusses methods to quantify entropy for living individuals; isotope dynamics; a mechanism behind reserve dynamics and toxicity of complex mixtures of compounds. An updated ageing module is now also applied to demand systems; there are new methods for parameter estimation; adaptation of substrate uptake; the use of otoliths for reconstruction of food level trajectories; the differentiated growth of body parts (such as tumours and organs) linked to their function, and many more topics are new to this edition.

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Third Edition

Dynamic Energy Budget Theory for Metabolic Organisation

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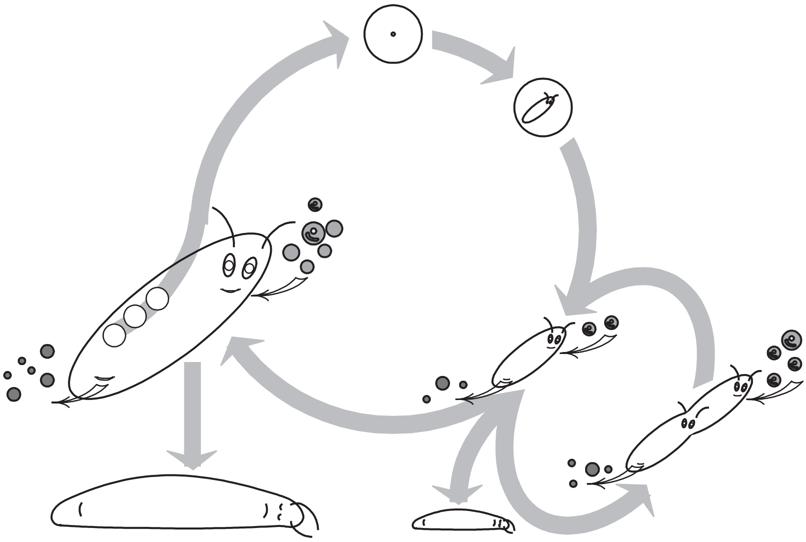

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Summary of contents

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Preface

What to expect in this book?

This book is about a formal consistent and coherent theory for the processes of substrate uptake and use by organisms, which I called the Dynamic Energy Budget (DEB) theory. Over the 30 years of research on this theory, it became well established; some 140 papers on DEB theory have appeared since the second edition in 2000. The application of the theory by the international research group AQUAdeb, http://www.ifremer.fr/aquadeb/, and of this book in the DEB tele-courses, http://www.bio.vu.nl/thb/deb/course/, urged for a new edition. This book gives a fresh update of the present state of the theory. In view of its accelerating development, this update will probably not be the last one. To accommodate all new material, I had to cut out most methodological parts of the previous edition, which is a pity because opponents of DEB theory typically seem to differ in opinion on 'details', but actually differ in opinion on the role of models in research and related methodological issues. I wrote a document on methods in theoretical biology, which also summarises the mathematics that is used in this book, see http://www.bio.vu.nl/thb/deb/.

Many empirical models, ranging from Lavoisier's model for indirect calorimetry, Kleiber's model for the respiration as function of body weight, von Bertalanffy's model for animal growth and Droop's model for nutrient-limited algal growth, turned out to be special cases of DEB models that follow from the theory. This means that DEB theory is the best tested quantitative theory in biology.

Support of this book

Although I have tried hard to avoid errors, experience tells me that they are unavoidable. A list of detected errors can be found at the DEB information page http://www.bio.vu.nl/thb/deb/, and I offer my apologies for any inconvenience. The errata, and all support material mentioned below, will frequently be updated.

I have tried to emphasise the concepts in this book, and to reduce on technicalities a section-wise summary of concepts gives an overview, skipping tests against realism. Mathematical derivations of results are important, however, especially for people who want to contribute to the further development of the theory. These derivations are collected in the comments on DEB theory, which can also be found at the DEB information

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page. These comments also give further background information and summarise the developments of the theory and its applications since this book appeared.

Software package DEBtool can be downloaded freely from the electronic DEB laboratory, http://www.bio.vu.nl/thb/deb/deblab/; the manual is included (run file *index.html* in subdirectory *manual* in a browser, such as *firefox*). DEBtool is written in Octave and in Matlab. The purpose of this package is a mix of demonstrations of what the theory can do, routines that can be used to fit DEB models to data, to calculate quantities such as the initial amount of reserve in eggs, to reconstruct food-density trajectories from observations on an individual, to run numerical simulations for plant growth, etc. Toolbox *fig* collects the files that have been used to create the figures of this book. Here you can see how the data are set, how the model is specified and how it is fitted to the data. The files give the figures in colours, and also present standard deviations of parameters that are estimated. These standard deviations are not presented in this book. If you want to apply the theory to your own data, and your application resembles one of the figures, an efficient way to do this is to go the file that produces the figure, replace the data with your own data and rerun the file.

This book is used in the international biannual DEB tele-course. Its set-up can be found on http://www.bio.vu.nl/thb/deb/course/; starting in 2009, the course will be linked to an international symposium on DEB theory, organised by previous participants of the tele-courses. The DEB information page also gives access to other material that is used and produced in this course. This includes collections quizzes, exercises and solutions, Powerpoint sheets, questions and answers, essays written by participants and, typically, later used in publications.

The book mentions many names of taxa; I have collected recent ideas on the evolutionary relationships between living organisms. This document can be found on the DEB information page.

The DEB information page also presents a number of papers that introduce DEB theory, ongoing activities, job opportunities, etc. Examples of application of DEB theory can be found in the special issues of the *Journal of Sea Research*, **56** (2006), issue 2 and **62** (2009), issue 1/2.

Set-up of this book

$$\begin{tikzcd} 1 \arrow[r] & 2 \arrow[r] & 3 \arrow[r] & 4 \arrow[r] \arrow[dl] \arrow[d] \arrow[dr] & 5 \arrow[r] & 9 \arrow[r] & 10 \arrow[r] & 11 \\ & & 6 & 7 & 8 & & & \end{tikzcd}$$

The logical structure of the chapters is indicated in the diagram (left). *A first quick glance through the section on notation and symbols, page* {494}, *saves time and annoyance.*
A glossary at {487} explains technical terms.

Chapter 1 gives introductory concepts, namely the notion of the individual, its life-stages, the various varieties of homeostasis and the effects of temperature on metabolic rates. The choice of topics is based on their relevance for the standard DEB model.

Chapter 2 specifies the standard DEB model, which represents the simplest non-degenerated model in DEB theory, so a canonical form, which uses one type of substrate (food), one reserve, one structure for an isomorph, i.e. an organism that does not change in shape during growth. It neglects all sorts of complications for educational purposes, to illustrate the basic DEB concepts in action; a summary section presents the list of assumptions from which the standard DEB model follows.

Chapter 3 discusses the relationships between energy, compounds and biomass, and presents basic concepts on metabolism. It presents the actions of synthesising units (SUs), i.e. a generalised form of enzymes that basically follow enzyme kinetics, but with an important modification: SU kinetics is based on fluxes, not on concentrations. The material in this chapter prepares for the next one.

Chapter 4 describes univariate DEB models, which have one type of substrate (food), one reserve and one structure, and starts with a discussion on changes in food density and extends the standard DEB model of Chapter 2 by accounting for changing shapes. The various chemical compounds, isotopes and energies are followed, product formation is specified and respiration is discussed in some detail. The quantification of entropy of living biomass is discussed. The parameter estimation section of Chapter 2 is now extended to include mass, energy and entropy parameters. The final section shows the use of observations on individuals to reconstruct how the food availability and temperature changed in time. This is useful e.g. to study size-dependent food selection.

Chapter 5 extends the theory to include several substrates, reserves and structural masses to increase the metabolic versatility that is found in organisms that acquire nutrients and light independently, and have to negotiate the problem of simultaneous limitation caused by stoichiometric coupling. The various ways in which substrate can take part in metabolic transformations are discussed. The processes of photosynthesis and calcification are discussed; the implications for plant development are evaluated.

Chapter 6 starts with a discussion of ageing that is caused by the effects of reactive oxygen species, which are formed as side-products of respiration, and its links with energetics. This chapter considers the uptake and effects of non-essential compounds, such as toxicants. The significance of effects of toxicants for energetics is that DEB parameter values are changed and the response to these changes reveals the metabolic organisation of individuals.

Chapter 7 extends DEB theory to include more detail for the various applications, especially if the shorter timescales need to be included to link to developments in molecular biology. The purpose of this chapter is to show how DEB theory fits into a wider context of biological research. Some parameter values turn out to change sometimes during the development of an organism and are discussed; it prepares the topic of the next chapter.

Chapter 8 analyses the intra- and inter-specific variation of parameter values among individuals. It compares the energetics of different species by studying the implications of DEB theory for the covariation of parameter values among species. The chapter shows how, for a wide variety of biological variables, body size scaling relationships can be derived from first principles rather than established empirically. This approach to body size scaling relationships is fundamentally different from that of existing studies.

Chapter 9 considers interactions between individuals and develops population consequences. The population, after its introduction as a collection of individuals, is considered as a new entity in terms of systems analysis, with its own relationships between input, output and state. These new relationships are expressed in terms of those for individuals. The coupling between mass and energy fluxes at the population level is studied and the behaviour of food chains and of canonical communities is discussed briefly.

Chapter 10 presents scenarios for the evolution of metabolic organisation and the gradual coupling and uncoupling of the dynamics of partners in symbiotic interactions; it also aims to make DEB theory biologically explicit. Apart from showing how DEB theory fits into an evolutionary context, this chapter demonstrates a key issue: two species that follow DEB rules can merge such that the merged new species again follows DEB rules. The process that life became increasingly dependent on life is discussed and illustrated with examples.

Chapter 11 places the approach taken by the DEB theory in existing eco-energetic research, and highlights some differences in concepts. A collection of well-known empirical models is presented that turn out to be special cases of DEB theory and their empirical support also supports DEB theory.

Acknowledgements

Many people have contributed to the development of the theory and to this book in different ways. I would specifically like to thank Bob Kooi and Tjalling Jager for the continuing support for this work at the Theoretical Biology Department in Amsterdam. Years of intensive discussions with Tânia Sousa, Tiago Domingo and Jean-Christophe Poggiale sharpened my mind to the extent of directing theoretical developments. The 30 Ph.D. students who have graduated on DEB-related topics also contributed a lot; it has been a real pleasure to work with them. I also want to thank people of the AQUAdeb group, and especially Marianne Alunno-Bruscia, for their work and enthusiasm, and Ifremer for supporting this group. Anna Hodson was of great help in the production of this book and Yues Descatoire created the banner on the cover.

Present behind all aspects of the 30 years of work on the theory is the critical interest of Truus Meijer, whose loving patience is unprecedented. The significance of her contribution is beyond words.