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# Body-size scaling relationships in bivalve species: A comparison of field data with predictions by the Dynamic Energy Budget (DEB) theory

Joana F.M.F. Cardoso [a,*], Henk W. van der Veer [a], Sebastiaan A.L.M. Kooijman [b]

[a] Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg Texel, The Netherlands
[b] Free University, Department of Theoretical Biology, De Boelelaan 1087, 1081 HV Amsterdam, The Netherlands

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## Abstract

In this paper, we apply the Dynamic Energy Budget (DEB) theory to bivalve species (1) to provide basic body-size scaling relationships that can be used to predict species characteristics when basic information is lacking, and (2) to analyse the discrepancy between DEB predictions based on energetic constraints and field observations, in order to identify potentially important factors in life history strategy of bivalves. Body-size scaling relationships were identified for size at first reproduction, Von Bertalanffy growth parameter, and egg and larval development time in relation to egg and larval volume and temperature conditions. Due to their small egg volume, bivalve species are characterised by a relatively short pelagic larval stage. The main discrepancy between field observations and DEB predictions was in the relationship between egg and larval volume and adult body volume. In bivalves, the characteristics of the early life stages are not related to body size of the species. Since the minimum size of settling larvae is always larger than 125 μm, it is suggested that successful settlement might be the key factor. Settlement size or volume of the fragile larvae must be in balance with the sediment composition, i.e. similar to or larger than that of the sediment grain size.

*Keywords:* Body size; Dynamic Energy Budget; Bivalve; Von Bertalanffy; Egg; Larva; Development; Growth; Recruitment

## 1. Introduction

The benthic community of estuarine coastal systems is characterised by a mosaic of species, including a variety of bivalves (for a general overview see: Ketchum, 1983; Mathieson and Nienhuis, 1991). In the western Dutch Wadden Sea, various bivalve species account for most of the biomass (Beukema, 1976). Although the maximum age of the various species is about the same (Tebble, 1966), they differ with respect to growth and reproduction. For instance, their maximum length differs by more than a factor of 10 (Tebble, 1966; Carriker and Gaffney, 1996; Poppe and Goto, 1993). Despite these large differences, annual spatfall and subsequent recruitment of all species is successful (Beukema et al., 2001; Van der Meer et al., 2001) indicating that different life history strategies can be adopted successfully in these fluctuating estuarine environments.

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* Corresponding author.
*E-mail address:* joanafcardoso@portugalmail.com (J.F.M.F. Cardoso).

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Any analysis of life history strategies in terms of the trade-off between growth and reproduction requires a general framework to compare the energetics of the different species in a systematic way. The Dynamic Energy Budget (DEB) theory (Kooijman, 1993, 2000) offers this general framework. DEB models can be used in various ways. First of all, various aspects in the life history and energetics of different species can be captured in a single model whereby differences between species are reflected in differences in parameter values only. Van der Veer et al. (2006) provide estimates of the various DEB parameters and a comparison of sets for a number of abundant bivalve species in Dutch coastal waters. Based on these, Cardoso et al. (2006) applies the DEB model to analyse the intra- and interspecies comparison of the energy flow in bivalve species in Dutch coastal waters.

A second application of the DEB theory is the prediction of various body-size scaling relationships. Such relationships have already been under study and under debate for decades since the pioneering work of Kleiber (1932) on the scaling of metabolic rate with body size. Thus numerous empirical relationships of biological rates as simple functions of body size and other variables have been established (for an overview see Peters, 1983). Although this descriptive ecology has proved to be valuable, it has been criticised for seeking post-hoc explanations of observed patterns without experimental tests of hypotheses (Blackburn and Gaston, 1999). The DEB theory of Kooijman (1993, 2000), based on surface- and volume-related processes can be considered as a clear response to this criticism. However, the DEB theory has so far not been recognised as such. Despite the fact that it was introduced in the late 1980s, recent literature is still suggesting that we lack a general theory on body-size scaling relationships based on first principles (e.g. Blackburn and Gaston, 1999; Brown et al., 2004; Harte, 2004). To our knowledge, the DEB theory is the only theory that is based on a set of general assumptions regarding food uptake, storage and utilisation that predicts many types of intra- and interspecific scaling relationships (Kooijman, 2000). In this paper, we develop the predictions of the DEB theory for bivalves with the aims of:

(1) providing basic body-size scaling relationships that can be applied to predict species characteristics in case basic information is lacking;
(2) analysing the discrepancy between DEB predictions based on energetic constraints and field observations to identify potentially important factors in life history strategy of bivalves.

## 2. DEB model predictions

A conceptual introduction of the DEB theory can be found in Kooijman (2001), and a full description is given in Kooijman (2000). The DEB theory describes the energy flow through an animal (Fig. 1) and also changes therein in environments with varying food densities and temperatures. In the model, three life stages (embryos, which neither feed nor reproduce; juveniles, which feed but do not reproduce; adults which both feed and reproduce) and three main body components (structural biovolume or somatic tissue; stored energy reserves; and gonads and/or stored energy reserves allocated to reproduction) are distinguished. Five equations with a small number of parameters (Table 1) can fully determine feeding, growth, survival and reproductive behaviour (see Kooijman, 2000).

The DEB theory implies interspecific body-size scaling relationships via a classification of its parameters into intensive parameters (which do not depend on the body size of the organism) and extensive parameters (which do depend on body size). In the DEB theory, size is measured in terms of volume. However, since literature data on volume is scarce, the volumetric length (i.e. the cubic root of the volume) is used to quantify body size.

Some of the volume- and growth-related relationships are temperature dependent and need to be corrected for temperature differences before a comparison between species can be made. Therefore, we corrected for differences in temperature using the Arrhenius relationship, which is an alternative to the $Q_{10}$ (for details see Kooijman, 1993, 2000). The predictions of various

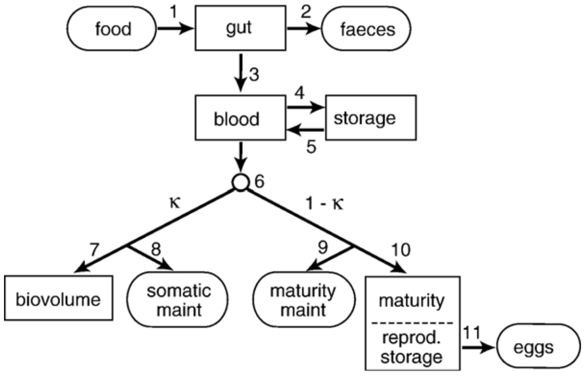

Fig. 1. Energy flow through an organism in the DEB model, after Van Haren (1995). Rates: 1 ingestion (uptake), 2 defecation, 3 assimilation, 4 demobilisation of energy into reserves, 5 mobilisation of energy from reserves, 6 utilisation, 7 growth, 8 somatic maintenance, 9 maturation maintenance, 10 maturation, 11 reproduction. The rounded boxes indicate sources or sinks; the rectangles indicate state variables.