



A Dynamic Energy Budget (DEB) growth model for Pacific oyster larvae, *Crassostrea gigas*

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ABSTRACT

Dynamic Energy Budget (DEB) theory aims to quantify the energetic framework of an individual organism as a dynamic model, from the uptake of food to its utilisation in metabolic processes (maintenance, growth, development and reproduction). The purpose of the present paper is to extend the existing DEB model for adult Pacific oyster *Crassostrea gigas* to the larval life stage of this species. We present the application of generic DEB theory to oyster larvae, with the formulation of the specific assumptions based on the characteristics of this stage. The model depends on seawater temperature and food density, as forcing variables, followed throughout the whole larval development. We calculated DEB parameter values for larvae by means of laboratory experiments specifically designed to collect datasets on ingestion and growth at different levels of phytoplankton density and temperature. The DEB model developed here showed good growth simulations and provided an extensive description of the energetic needs of *C. gigas* during its larval stage. It was demonstrated that, at 27 °C, a food density of 1400 $\mu\text{m}^3 \mu\text{l}^{-1}$ must be maintained throughout larval development to maximise growth and metamorphosis success. Timing of metamorphosis decreases exponentially with increasing temperature.

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1. Introduction

Bivalve molluscs (e.g. oysters, mussels, clams and scallops) represent a significant proportion of world aquaculture production (Helm et al., 2004), in which the most important commercial marine bivalve is the Pacific oyster, *Crassostrea gigas* (FAO, 2008). Traditionally, bivalve culture in France relies on the collection of juveniles from the natural environment but, due to irregular recruitment (spatfall) and the high demand for triploid oysters, spat production in hatcheries has been increasing rapidly over the last five years. In this context, a better understanding of the biology of *C. gigas* larvae is required because the larval stage is critical for hatchery management.

The growth and survival of bivalve larvae is determined by complex interactions between their physiology and the environmental conditions. Among the diversity of influencing factors, temperature and food concentration are considered to be the primary environmental factors affecting physiological processes in oyster larvae (Robert et al., 1988; His et al., 1989; Lemos et al., 1994; Dove and O'Connor, 2007). Quantitative study of the effects of these environmental factors and their interactions on larval growth can be aided by numerical models. An existing model for *Crassostrea virginica* larvae (Deksheniaks et al., 1993) explains growth and development as function of temperature, food concentration, salinity and turbidity.

Nevertheless, this work does not examine the energetic functioning of larvae at the level of basic physiology (ingestion and maintenance processes). In *C. gigas*, a net production-type model (Bochenek et al., 2001; Powell et al., 2002; Hofmann et al., 2004) was developed to examine the biochemical influence of changes in food quality and quantity on larval development. Although this approach is more appropriate for modelling larval growth, this model lacks valid experimental measurements made for the whole larval development over a wide range of environmental factors. In addition, this model is based on the Scope for Growth concept (Bayne, 1976), which is empirically-based and free-formulated through allometric relationships (Bourles et al., 2009) and assumes that assimilated energy is immediately available for maintenance while the rest is converted into structural components (growth) or storage material (reserves) (Bochenek et al., 2001).

In the present paper, a more mechanistic energetic model is proposed based on the Dynamic Energy Budget (DEB) theory (Kooijman, 2000). The recent development of DEB theory offers a general framework for examining the bioenergetics of an organism in a systematic way. This theory describes the rates at which an individual organism assimilates energy from food uptake and stores this energy as reserves for allocation to the physiological functions of maintenance, growth, development and reproduction. In addition, DEB theory offers attractive improvements for energetic modelling based on simple assumptions that describe energy flow according to physiological processes that species have in common. This generic aspect allows different species to be compared, as the only

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interspecies difference will lie in the DEB parameter values. Most parameters can be estimated in the laboratory under controlled environmental conditions, using temperature and food density as forcing variables. Recently, practical applications of DEB theory have been validated for bioenergetics in *C. gigas* adults in natural surroundings (Bacher and Gangnery, 2006; Ren and Schiel, 2008) as well as in controlled conditions (Pouvreau et al., 2006; Bourles et al., 2009). Based on this last existing DEB model, the present study aimed to apply DEB theory to simulate growth of *C. gigas* at larval stage in the hatchery. This is the first model that would be capable of representing the energetic needs of a bivalve species throughout the whole larval life cycle. Furthermore, such model can be used to treat on a hierarchical basis the key parameters of *C. gigas* larval development and physiology, improve accordingly culture conditions in hatchery (e.g. metamorphosis delay) or knowledge of ecological requirements in surroundings (e.g. wild spat collection).

The first part of this paper presents some basic concepts of the DEB theory and assumptions made for *C. gigas* larvae. The second part consists of the estimation of DEB parameter values for oyster larvae from experimental data on ingestion and growth collected under precisely controlled conditions of phytoplankton density and temperature. The final part of the paper focuses on calibration and simulation with the larval DEB model using our own experimental datasets, and its validation based on the input of “external” data collected in our experimental facilities by means of other independent trials.

2. Materials and methods

2.1. Concepts and DEB model formulation for the larval stage

In DEB theory, an organism is partitioned into three main body components: 1) structural biovolume or somatic tissue; 2) stored energy reserve; and 3) gonads and/or stored energy reserves allocated to maturity and reproduction (Kooijman, 2000). Moreover, in the theory, three life stages are distinguished: 1) embryos, which neither feed nor reproduce; 2) juveniles, which feed but do not reproduce; and 3) adults which both feed and reproduce. DEB theory describes a larva as a juvenile because larvae feed and their resources are not yet allocated to reproduction, but to other developmental processes. Therefore, energy from food is stored directly as reserves and is then directed towards growth, development and their maintenance. The DEB model was accordingly simplified for the larval stage, compared with the adult stage (Pouvreau et al., 2006), due to the absence of reproduction.

The general framework of the DEB model for a larva is represented in Fig. 1 and main parameters of different equations of the model are given in Table 1. DEB theory is described below and the equations used were issued or adapted from the DEB model validated for adult *C. gigas* (Pouvreau et al., 2006). The notation and symbols used are from Kooijman (2000) and faithfully follow the rules: quantities that

are expressed per unit of structural biovolume have square brackets, []; quantities per unit of biosurface have braces, { }; and rates, which have dots above them, indicate the dimension over time.

According to DEB theory, a larva can be described by three state variables: the energy in the reserve, E , the structural body volume, V , and the amount of energy invested into development to reach juvenile stage, E_R . The ingestion rate, \dot{J}_X ($\mu\text{m}^3 \text{d}^{-1}$), is proportional to the biosurface of a larva, $V^{2/3}$ (μm^2), and relies on available food density, X (phytoplankton expressed in $\mu\text{m}^3 \mu\text{l}^{-1}$), in the environment:

$$\dot{J}_X = \left\{ \dot{J}_{Xm} \right\} \cdot f \cdot V^{2/3} \quad (1)$$

where $\left\{ \dot{J}_{Xm} \right\}$ is the maximum ingestion rate per unit of biosurface (expressed in $\mu\text{m}^3 \text{d}^{-1} \mu\text{m}^{-2}$), X_K is the half saturation coefficient ($\mu\text{m}^3 \mu\text{l}^{-1}$) and f is the feeding functional response, which can vary between 0 and 1 (dimensionless).

The ingested food is converted into assimilates, which are added to the reserve, E , with constant assimilation efficiency (ae , dimensionless) according to a food energy conversion (μ_X , $\text{J} \mu\text{m}^{-3}$) before allocation. Consequently the assimilation rate, \dot{p}_A , can be described in Eq. (2) as:

$$\dot{p}_A = ae \cdot \mu_X \cdot \dot{J}_X = ae \cdot \mu_X \cdot \left\{ \dot{J}_{Xm} \right\} \cdot f \cdot V^{2/3} = \left\{ \dot{p}_{Am} \right\} \cdot f \cdot V^{2/3} \quad (2)$$

where $\left\{ \dot{p}_{Am} \right\}$ is the maximum surface-area-specific assimilation rate expressed in $\text{J} \text{d}^{-1} \text{cm}^{-2}$. The assimilation efficiency was assumed to be 0.4 (Walne, 1965; Sprung, 1984) and the food energy conversion was found to be equal to $4.5 \times 10^{-9} \text{J} \mu\text{m}^{-3}$ of microalgae (Brown, 1991; Brown and Robert, 2002).

The dynamics of the energy in the reserve, E , follow the energy conservation law and can be described as:

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C \quad (3)$$

Energy is mobilised from this reserve pool to fuel the activities of organism at a rate called the catabolic power or utilisation rate, \dot{p}_C :

$$\dot{p}_C = \frac{E/V}{[E_G] + \kappa \cdot E/V} \left(\frac{[E_G] \cdot \left\{ \dot{p}_{Am} \right\} \cdot V^{2/3}}{[E_m]} + \left[\dot{p}_M \right] \cdot V \right) \quad (4)$$

An extended explanation of Eq. (4) can be found in Kooijman (2000). In summary, E/V corresponds to the energy density in an organism ($\text{J} \text{cm}^{-3}$), which may vary between 0 and the maximum energy density, $[E_m]$ ($\text{J} \text{cm}^{-3}$), according to the food density in the environment. The mobilised reserve is described by the allocation rule where the parameter κ corresponds to a fixed fraction of utilisation rate, \dot{p}_C , spent on maintenance of somatic tissue, as absolute priority, and structural growth for larvae; the rest $(1 - \kappa)$ goes to development

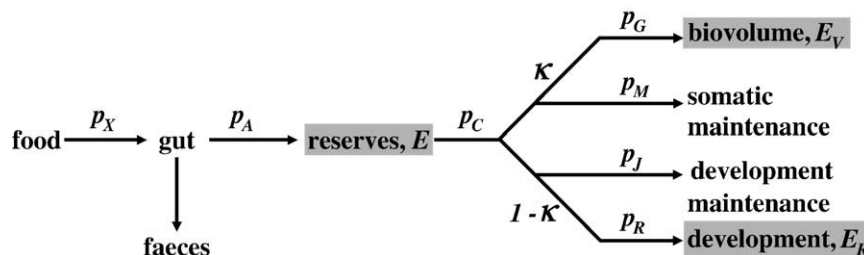


Fig. 1. Schematic representation of the energy flow through *Crassostrea gigas* larvae according to the DEB model (Kooijman, 2000). The three state variables are highlighted in grey.

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