The estimation of Dynamic Energy Budget (DEB) parameters for *Crassostrea gigas* larvae

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1. Introduction.

The major commercial marine bivalve in French aquaculture is the Pacific oyster, *Crassostrea gigas*. Traditionally, bivalve culture relies on juvenile collection from the natural environment but due to the high year-to-year variation in spatfall recruitment the spat production in hatcheries is increasing recently. In this context, a better understanding of the biology of *C. gigas* larvae is required suggesting that the larval stage is critical for hatchery management. The growth and the survival of oyster larvae is determined by complex interactions between larval physiology and environmental conditions. Among the variety of factors, temperature and food density are considered as primary environmental factors affecting the physiological processes of bivalve larvae.

To study quantitatively the interaction of these environmental factors on larval growth, a numerical model is an useful tool. The Dynamic Energy Budget (DEB) theory developed by Kooijman (2000) offers a quantitative description of the energy flow through an individual organisms (micro-organisms, plants and animals) from food uptake to the allocation of energy on physiological functions as maintenance, growth, development and reproduction. In addition, DEB theory has a considerable power based on simple assumptions to describe energy flows through organisms and the flow changes in environments in which food densities and temperature vary. In this context, we aim to apply the DEB theory to model growth of *Crassostrea gigas* larval stage. The first step in building an energetic allocation model is the estimation of the DEB parameters values. In this paper, we introduce principles of DEB theory applied in oyster larvae experimentations under environmental laboratory conditions for assessing energetic parameters. This study is the first step in the construction of a larval growth DEB model for *Crassostrea gigas*.

2. Concepts and DEB model formulation

The structure and functional processes of the DEB model are represented in Figure 1 and described below.

According to Kooijman (2000) an organism ingests food at a rate dependent on its size and the food density. Energy is extracted from food and stored directly as reserves. This energy is directed towards growth and maintenance (as absolute priority) of structural cells, corresponding to a fixed proportion of utilisation energy. The remaining fraction of energy is allocated to development and reproduction.

The ingestion rate $\dot{J}x$ (µm^3 d^{-1}) is proportional to the biosurface of a larvae ($V^{2/3}$, µm^2) and depends hyperbolically on available food density X (phytoplankton) in the environment (expressed in µm^3 µl^{-1} in this paper) following a type-II Holling function response:

$$\dot{J}_X = \{\dot{J}_{Xm}\} \cdot f \cdot V^{2/3} \qquad \text{with } f = \left(\frac{X}{X+X_K}\right) \tag{1}$$

where f is the scaled functional response, which can vary between 0 and 1 (dimensionless), $\{\dot{J}_{Xm}\}$ is the maximum ingestion rate per unit of biosurface (expressed in µm^3 d^{-1} µm^{-2}) and X_K is the half saturation coefficient or Michaelis-Menten constant (µm^3 µl^{-1}).

Therefore the ingested food is converted into energy reserves with a constant assimilation efficiency and consequently the total energy input can be described as the assimilation rate, $\dot{p}_A$:

$$\dot{p}_A = \{\dot{p}_{Am}\} \cdot \left(\frac{X}{X+X_K}\right) V^{2/3} \tag{2}$$

where $\{\dot{p}_{Am}\}$ is the maximum surface-area-specific assimilation rate expressed in J d^{-1} µm^{-2}.

The assimilated energy flows into a storage compartment (Figure 1). From this reserve pool, the energy is mobilised by the somatic tissues at a rate called the catabolic power or utilisation rate, $\dot{p}_C$.

The parameter κ corresponds to a fixed fraction of utilisation rate spent on maintenance of somatic tissue, as priority, and structural growth; the rest (1 - κ) goes to development (for embryos and juveniles) and maturity maintenance or reproduction (for adults).

In this context, Kooijman (2000, chapter 2) defines a larva like a morphologically defined stage. If the larva feeds, it is treated as a juvenile; if not, it is considered to be an embryo. Oyster larva feeding occurs from D-stage to settlement, so, larva is treated as a juvenile in DEB terms. In addition, the DEB model is simplified for juvenile stage in comparison with the adult stage because reproduction is absent.

Maintenance costs are mainly scaled with volume. Somatic maintenance has priority over growth, hence it ceases when the fraction κ of the mobilised reserve is equal to, or lower than, somatic maintenance demands. $[E_G]$ denotes the volume-specific costs for structural growth (J μm^{-3}). On the other hand, the somatic maintenance costs ($\dot{p}_M$, J d^{-1}) is expressed as:

$$\dot{p}_M = [\dot{p}_M] \cdot V \tag{3}$$

where $[\dot{p}_M]$ denotes the volume-specific maintenance rate (J μm^{-3} d^{-1}) and V the body volume (μm^{-3}). Maintenance costs correspond to all processes necessary to 'stay alive', i.e. for a oyster larvae it consists of the immune system, the concentration gradients across membranes, the osmo-regulation and a mucociliary activity (Strathmann, 1979).

DEB theory states that for larvae a fixed proportion (1 – κ) is used for developing reproductive organs and regulation systems called development costs ($\dot{p}_J$, J d^{-1}) related to the transition from juvenile (larva) to adult and can be defined as:

$$\dot{p}_j = [\dot{p}_j] \cdot V \tag{4}$$

where $[\dot{p}_j]$ denotes the volume-specific development rate (J μm^{-3} d^{-1}) and V the body volume (μm^{-3}). In addition, for a larvae (considered as a juvenile), the energy spent on somatic maintenance $\dot{p}_M$ and the development costs $\dot{p}_J$ can be combined, because both can be taken to be proportional to volume and can be referred to as maintenance costs M (J μm^{-3} d^{-1}) in the present study.

Physiological rates (ingestion and growth) depend on the body temperature. This relation is usually well described by a Arrhenius-type equation within a species-specific tolerance range for a low and high temperatures (Kooijman, 2000). In DEB, this dependency can be expressed as:

$$\dot{k}(T) = \dot{k}_1 \cdot \exp\left\{\frac{T_A}{T_1} - \frac{T_A}{T}\right\} \tag{5}$$

where $\dot{k}(T)$ is the value of the physiological rate that depends upon an ambient temperature T (in Kelvin), $\dot{k}_1$ is the value of the physiological rate at a reference temperature T_1, and T_A is the so-called Arrhenius temperature (in Kelvin).

Table 1. List of DEB parameters determined in this study with symbol and unit.

Parameters	Symbols	Units
Primary parameters		
Arrhenius temperature	T_A	K
Maximum surface area-specific ingestion rate	$\{\dot{J}_{Xm}\}$	μm^3 d^{-1} μm^{-2}
Maximum surface area-specific assimilation rate	$\{\dot{p}_{Am}\}$	J d^{-1} μm^{-2}
Half saturation coefficient	X_K	μm^3 μl^{-1}
Shape coefficient	δm	-
Fraction of catabolic power energy spent on maintenance plus growth	κ	-
Volume-specific costs for structure	$[E_G]$	J μm^{-3}
Volume-specific maintenance rate	$[\dot{p}_M]$	J μm^{-3} d^{-1}
Volume-specific costs for development	$[\dot{p}_j]$	J d^{-1}
Compound parameters		
Energy conductance	$\dot{v}$	μm d^{-1}
Maintenance rate constant	$\dot{k}_M$	d^{-1}
Investment radio	g	-

Figure 1. Schematic representation of the energy flow through an organism in its larval stage in the DEB model (Kooijman, 2000). Rates: 1 ingestion, 2 defecation, 3 assimilation, 4 utilisation, 5 growth, 6 maintenance, 7 maturity, 8 reproduction. State variables are grey.