

# Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions

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## Abstract

The Dynamic Energy Budget (DEB) model (Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. *J. Theor. Biol.* 121, 269–282; Kooijman, S.A.L.M., 2000. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge, 424 pp.) has been adapted to describe the dynamics of growth and reproduction of the Pacific oyster (*Crassostrea gigas*) reared in different areas under conditions ranging from controlled to natural. The values of the model parameters were estimated from available physiological data and from published information. The sets of data used to validate the model came from three long-term growth experiments (>5 months) performed on Pacific oysters reared under different conditions of food and environment. The forcing variables were temperature and phytoplankton densities, the latter being assessed from in vivo fluorescence and chlorophyll-a concentration measurement. The successful validation of the model on the three data sets demonstrated its ability to capture the dynamics of the energy budget in the Pacific oyster in various environments with the same set of parameters. The only parameter that varied between simulations was the half-saturation coefficient ( $X_K$ ), because of a different diet composition between the three environments under test. The model successfully reproduced quantitatively the growth and reproduction and the timing of spawning. These first simulation data led us to propose several promising perspectives of application for this model in shellfish ecosystems.

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## 1. Introduction

Marine bivalves, and especially the Pacific oyster *Crassostrea gigas*, are economically important in

French aquaculture. Exceeding 109 million kg in 2001 (Girard et al., 2001), the production of this species has become a major industry on the French coasts. As a consequence, oysters are often dominant in terms of biomass in several shellfish areas and form an integral part of the ecosystem in which they occur. These constraints have prompted the necessity for tools to

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understand ecological processes in shellfish ecosystems and to help management of the oyster farming. Understanding of the interaction between this species and its environment could be facilitated through the development of ecological models (e.g. Héral, 1991).

The last fifteen years have seen the development of numerous energetic models that explain the growth of molluscs according to their environment, i.e. temperature and food supply. Most of them are net-production models based on the Scope for Growth concept (Bayne, 1976). They use a detailed empirical sequence of steps for nutrition and resource allocation, based on allometric relationships, and assume that assimilated energy is immediately available for maintenance, the rest is used for growth or stored as reserves (e.g. Bacher et al., 1991; Powell et al., 1992; Schneider, 1992; Raillard et al., 1993; Barillé et al., 1997; Grant and Bacher, 1998; Scholten and Smaal, 1998; Ren and Ross, 2001). Some of the models developed for bivalves are more mechanistic (Ross and Nisbet, 1990; Van Haren and Kooijman, 1993; Cardoso et al., 2001; Ren and Ross, in press). They are based on the dynamic energy budget or DEB theory proposed by Kooijman (1986) and extensively discussed in Kooijman (2000). DEB models differ from net-production models in several aspects. They assume that assimilated energy is first stored in reserves, and reserves are utilised to fuel other metabolic processes (maintenance, growth, development and reproduction). DEB models do not use empirical allometric relationships, but simply state that feeding is proportional to surface area whereas maintenance scales to structural body volume. More generally, DEB theory aims for a generic theory of energy budgets that assumes common physiological processes across species and life stages via a set of common DEB parameters, the only difference between species lying in the value of these parameters. These promising considerations led us to conduct investigations to apply the DEB model proposed by Kooijman (2000) to catch and simulate the life history (namely growth and reproduction) of *C. gigas* under different environmental conditions from controlled to natural ones.

The first problem in building such a model lies in the estimation of the DEB parameters. Most of them were previously assessed for the Pacific oyster by Van der Veer et al. (2006) independent of this study. Our contribution was aimed at checking the generic property of these parameters to determine whether their assessment of DEB parameters was sufficient to model oyster growth in various environments and for different populations. We also wondered whether the intra-specific differences are so great that the DEB parameters

need to be recalculated for each new population and/or new environment.

A second problem lies in the diversity of the sources of food (phytoplankton, protozoa, micro-zooplankton, bacterial aggregates, detrital organic matter etc.) as well as its dilution in seston by mineral particles. The exact determination of ingestion fluxes is, thus, very hazardous because of the difficulty to monitor food and ascertain its origin. Energy allocation can be prejudicially affected by this lack of information. To overcome these problems and develop a generic model for *C. gigas*, we have designed a DEB model and we have tested it on several populations of oysters reared under conditions clearly identified through daily or weekly measurements of water temperature, salinity, oxygen concentration as well as food quality and phytoplankton concentration. This paper is focused on oysters after metamorphosis, i.e. juvenile and adult stages; embryonic and larval stages are not considered.

## 2. Material and methods

### 2.1. DEB model

The dynamic energy budget model used in this study is developed on the basis of DEB theory (Kooijman, 1986, 2000) and is depicted in Fig. 1. It includes some specific extra parameters needed to model the bioenergetics of the Pacific oyster. According to Kooijman (2000), the dynamics of growth and reproduction can be fully described by three differential equations: the first one specifies the growth of the structural body volume,  $V$ , the second one describes the dynamics of the energy reserves,  $E$ , and the third one deals with the storage and use of the energy allocated to development and reproduction,  $E_R$ .

Food uptake is assumed to: (i) follow a type-II Holling function response depending on food density  $X$  (expressed in  $\mu\text{g chl-a l}^{-1}$  in this study) and (ii) be proportional to the surface area of the structural body volume ( $V$ ,  $\text{cm}^3$ ); thus, the ingestion rate  $\dot{J}_X$  ( $\text{mg d}^{-1}$ ) can be written as:

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

where  $f$  is the scaled functional response (dimensionless),  $X_k$  is the saturation coefficient or Michaelis-Menten constant ( $\mu\text{g chl-a l}^{-1}$ ) and  $\left\{ \dot{J}_{Xm} \right\}$  the area-specific maximum ingestion rate, expressed in  $\text{mg d}^{-1} \text{cm}^{-2}$ . As a first approximation, the absorption efficiency ( $ae$ , dimensionless) and the food-energy conversion

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