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Application of a bioenergetic growth model to larvae of the pearl oyster *Pinctada margaritifera* L.

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ABSTRACT

We applied, for the first time, a dynamic energy budget (DEB) growth model to the larval phase in the pearl oyster *Pinctada margaritifera var. cumingii* (Linnaeus, 1758) to evaluate the impact of spatio-temporal variation in the atoll lagoon environment on its capacity for development. The specific parameters of the model, which represent ingestion, temperature effect and the relationship between length and biovolume of the larvae, were determined from experiments or taken from the literature. The interpretation of the values of these parameters allowed us to identify the underlying adaptive character trait: *P. margaritifera* larvae have a good capacity to exploit low food concentrations and a narrow range of thermal tolerance restricted to hydrobiological conditions found in the tropical oligotrophic waters of its distribution zone. Growth simulations show a good fit with the observations made on reared larvae under different conditions: fed on either cultured algae or natural plankton, and with growth data from a natural cohort. Finally, a first application of the model to a pearl-culture lagoon reveals the predominant effect of the vertical structure of trophic resources in determining spatial variation in larval growth.

1. Introduction

Pearl culture has a major economic and social role in French Polynesia (83 million euros in exports and about 5000 jobs). This activity is based on the production of a single species: the black-lipped pearl oyster (*Pinctada margaritifera cumingii*, Linnaeus 1758). The supply of juvenile oysters for the farms is spread across thirty pearl-growing islands and atolls. This supply depends entirely on natural collection on artificial substrates, made on only about fifteen atolls. This collection is performed by trial and error and the spatio-temporal variation in yield of spat on collectors is very high (Brié, 1999), meaning that local demand is not always satisfied. Combined with an overall increase in pearl culture, this demand for spat has led to significant transfers of oysters between islands, with some negative consequences: mixing of populations, which can cause a decrease in their genetic diversity (Arnaud-Haond et al., 2003), dissemination of invasive epibiota, and the risk of pathogen transmission. To increase spat collection yields in the pearl oyster industry and counter spatio-temporal variation in settlement, it appears necessary to improve our understanding of the factors that affect the success of larval development and, ultimately, settlement.

Apart from the genetically induced 'internal' parameters such as capacity for nutrition or metabolic processes (Pace et al., 2006), growth and survival of bivalve larvae depend on complex interaction between physiology, environmental conditions and food availability (Doroudi et al., 1999; Eckman, 1996; Hofmann et al., 2004; Powell et al., 2002). The variability of environmental parameters and notably food availability can affect development, metamorphosis success and survival — especially through the slowing of growth, which can increase predation risks (Hofmann et al., 2004). It appears very difficult to examine larval survival and development *in situ*, firstly, because the dispersive nature of the pelagic larval stage necessitates a huge sampling effort (Levin, 1992; Scheltema, 1986) and, secondly, due to the difficulty in identifying species (Garland and Zimmer, 2002). Growth models, therefore, represent an interesting alternative for studying the effect of environmental parameters on the development and survival of bivalve larvae, allowing us to identify the best periods and areas of larval settlement (Dekshenieks et al., 1993; Hofmann et al., 2004; Powell et al., 2004).

The dynamic energy budget (DEB) model has been developed and applied to adult growth in numerous bivalve species (Bacher and Gangnery, 2006; Bourlès et al., 2009; Casas and Bacher, 2006; Pouvreau et al., 2006; Rosland et al., 2009; van der Veer et al., 2006; Van Haren and Kooijman, 1993). This generic model describes energy fluxes in an organism, from energy acquisition to its use in growth, maintenance, development and reproduction, depending on two forcing variables: temperature and food concentration. The work of Rico-Villa et al. (2009) recently established a model describing growth of the Pacific oyster *Crassostrea gigas* (Thunberg, 1793) larval phase on the basis of DEB modelling.

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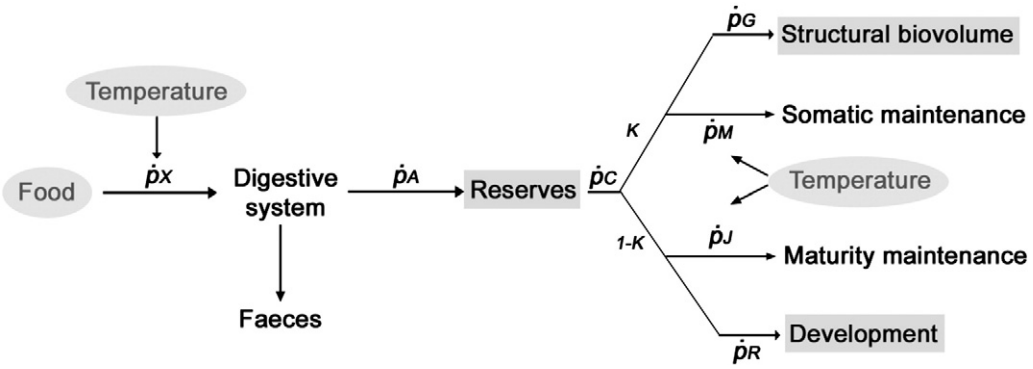

Fig. 1. Schematic representation of energy allocation according to DEB theory for larvae of *P. margaritifera*. State variables are shown on a rectangular grey background and forcing variables are circled.

In that context, the objective of our present study was, therefore, to calibrate and validate, for the first time, a DEB model for the larval phase of the pearl oyster *P. margaritifera* so as to evaluate the impact of spatio-temporal variation in the lagoon environment on larval development capacities. The model was based on that of Rico-Villa et al. (2009), using experiments to measure and define the specific parameters of *P. margaritifera* larvae, notably the ingestion function and the shape relationship between length to volume. Finally, after a validation step, the model was applied under different food and temperature conditions recorded in the Ahe pearl farming atoll (Tuamotu archipelago), and the impact on simulated larval growth performances was evaluated.

2. Material and methods

After a description of the main principles of energy acquisition and allocation, and their formulation in the DEB model, we will give the methods used to obtain values for specific parameters. Finally, we will present the larval growth data used to validate the model and the forcing variables (temperature and food) used for the application of the model.

2.1. DEB model design for pearl oyster larvae

The dynamic energy budget model (DEB) used in this study was developed based on DEB theory (Kooijman, 2000), applied to the larval stage according to Rico-Villa et al., (2009). A full description of the processes in the model can be found for the adult stage in Pouvreau et al. (2006) and for the larval stage in the aforementioned study of Rico-Villa et al. (2009). Briefly, the DEB model distinguishes three life stages: 1) the embryo, which does not eat or reproduce; 2) the juvenile, which eats but does not reproduce; and 3) the adult, which eats and reproduces. The larval stage, from D-larvae onwards, corresponds to the DEB juvenile life stage. The DEB model aims to describe the growth dynamics of larvae according to different equations representing the dynamics of three state variables (Fig. 1, Table 1): the growth of structural biovolume (somatic tissues) E_V, the dynamic of energy reserves E, and the dynamic of energy allocated to development to reach adulthood E_R, which corresponds to the extra energy needed to achieve complexity, such as the development of the eye spot, foot or gills. Parameters of the DEB model for the larval stage in *P. margaritifera* are listed in Table 2.

2.2. Protocols for measuring specific parameters

The experiments were conducted at the Ifremer centre, Tahiti. Larvae were obtained after stimulating the genitors by thermal shock (Southgate and Beer, 1997). After fertilisation, the trochophore larvae were recovered and placed in 150-l rearing tanks. Tank water was renewed every two days and larvae fed daily with an algal mixture composed of cultured *Isochrisis affinis galbana*, *Chaetoceros sp. jonquieri* and *Chaetoceros gracilis* in a variable proportion depending on the stage of larval development.

2.2.1. Determination of the shape coefficient δ_M

The value of the shape coefficient δ_M was determined from measurements of larval shell length and dry flesh mass, transformed into fresh mass by considering flesh water content to be 80% and converted into structural volume considering a density assumed not to be too different from 1 g cm^{-3}. Mean length was measured by image analysis on a batch of over 30 individual larvae (IMAQ Vision Builder 6, Nat. Instrument Corporation software). Ash-free dry flesh mass, corresponding to the mass or organic material, was obtained by the difference between the total dry weight of a sample of larvae

Table 1
Equations describing the energy fluxes in the DEB model. X corresponds to the food concentration (Chl a, μg l^{-1}) and T to the water temperature (K). See Table 2 for the parameter description.

Flux description	Equation
Ingestion	$\dot{p}_X = \mu_X \cdot \{\dot{J}_{Xm}\} \cdot \left(\frac{X}{X + X_k}\right) \cdot V^{2/3} \cdot \dot{k}(T)$
Assimilation	$\dot{p}_A = \kappa_A \cdot \dot{p}_X$
Catabolic flux	$\dot{p}_C = \frac{E/V}{[E_G] + \kappa E/V} \left(\frac{[E_G] \cdot \{\dot{p}_{Am}\} \cdot V^{2/3}}{[E_m]} + [\dot{p}_M] \cdot V \right)$
Energy allocated to structural biovolume	$\dot{p}_G = \kappa \cdot \dot{p}_C - \dot{p}_M$
Maintenance of structural biovolume	$\dot{p}_M = [\dot{p}_M] \cdot V \cdot \dot{k}(T)$
Energy allocated to development	$\dot{p}_R = (1-\kappa) \cdot \dot{p}_C - \dot{p}_J$
Maintenance of reproductive structures	$\dot{p}_J = min(V, V_p) \cdot [\dot{p}_M] \cdot \left(\frac{1-\kappa}{\kappa}\right) \cdot \dot{k}(T)$
Effect of the temperature	$\dot{k}(T) = exp\left\{\frac{T_A}{T_1} - \frac{T_A}{T}\right\} \cdot \left(1 + exp\left\{\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right\} + exp\left\{\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right\}\right)^{-1}$
Conversion of physical length (L) into structural volume (V)	$V = (\delta_M L)^3$