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About the DEB-course

First of all, I want to thank Bas Kooijman for the opportunity "to learn in progress" with this interactive course. I had a real interest in reading of book even if I didn't always understand all the mathematical subtlety.

In practice, although the time shift due to my location didn't permit real time exchanges, I followed with interest and tried to contribute actively to the discussion board.
The course organisation and assignments based on the book progression was fine. Nevertheless, the weeks flewby very fast and it was not always easy assimilate the material each week (*maybe also because I worked alone*).
This year we worked in one group, with three local discussion groups. Unfortunately I didn't really see the result of group's discussions and interactions with others on black board.
I had an interesting work in the redaction of my essay with an approach in a transversal way (from the first chapter to the last one). It is nevertheless a first step and I must progress with my comprehension and my questioning.

Introduction

The subject of my PhD research deals with the modelling of growth and dispersal of the pearl oyster (*Pinctada margaritifera*) larvae into a Polynesian lagoon. The practical application of this coupled model (biological and physical) is to better understand the processes and extract the principal influence factors who define the spat collecting success.

Like several bivalve species, the pearl oyster has a pelagic life stage. During this period in open water, which goes from egg (with an external fecundation) to the seed oyster (defined as the first fixed stage, after metamorphosis), the oyster undergoes a great number of physiological modifications.
Indeed, the embryonic stage is characterised by a lecitotrophic behaviour ; the oyster takes its energy from egg's reserves. This stage is followed by a mixotrophic transition with the acquisition of the food uptake capacity ; larva continues to use its vitellins reserves and begins to feed itself. Finally, larva takes all its energy by feeding.
These upheavals are accompanied by a strong modification in morphology. During the 20 days of the larval phase, the oysters pass from 50µm (at the gastrula stage) to close to 250µm (before fixing).
Several parameters are likely to influence the larval development *e.g.* internal factors like the optimal temperature range or the amount of energy fixed into the egg and available at birth or external factors like temperature or food availability (quantity and quality).

So, I'm going to place the pearl oyster larvae development into the Dynamic Energetic Budget theory context in order to evaluate its capacity to allow us to reach our goals. Thus, I'm going to present the model design, the parameters estimation and the integration of the influencing factors.

From theory

In our case, the DEB theory application to the pearl oyster larvae (*PO* in the following paragraphs) is done (i) to simulate the growth during the pelagic phase (*in a first time*) (ii) and to evaluate the consequences of environmental factors on larval physiology and *in fine* on their development success.
We will consider the standard DEB model, with 1 reserve and 1 structure (*however, the distinction between the reserves of egg and the reserves acquired at initiation of ingestion is an open question (?)*). Moreover, *PO* are ectotherms organisms (so the costs for heating $\dot{p}_T = 0$, Kooijman, 2000, see{92}) and are isomorphs (see {25}).

Three states variables are identified to describe organisms : the structural volume V, the amount of energy in reserves E and the amount of energy invested into maturation E_H.

The descriptor usually used in the case of larvae growth is it (large) length of shell.
Then, we'll used the shape parameter (δ_M) to extract this length *L* (cm) from the physical volume V_w (cm^3), such as (see {23}) :

$$V_w = (\delta_M L)^3 \quad (1)$$

where $V_w = W_w/d_{Vw}$ with W_w (g) the wet flesh weight and d_{Vw} ($g.cm^{-3}$) the specific density (close to 1 $g.cm^{-3}$).

The structural volume V (cm^3) is extracted from the volume-specific costs for structure $[E_G]$ ($J.cm^{-3}$) via the energy allocated to growth (see {94}) :

$$\frac{dV}{dt} = \frac{(\kappa [\dot{p}_C] V - [\dot{p}_M] V)}{[E_G]} = \frac{\dot{p}_G}{[E_G]} \quad (2)$$

where, $[\dot{p}_C]$ ($J.cm^{-3}$) is the volume-specific catabolic power, κ the fraction of catabolic power spent on maintenance plus growth and $[\dot{p}_M]$ ($J.cm^{-3}$) the volume-specific somatic maintenance costs.

The larval development follows the embryonic stage. It presents morphological and behavioural characteristics associated with a pelagic life and the acquisition of final characters. From an energetic point of view, the larval phase is integrated into the juvenile stage with food intake and no reproduction ; « *A larva is a morphologically defined stage, rather than an energy defined one* » {60}.

That results in a dynamic of the reserves E {83} :

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

where $\dot{p}_A$ is the assimilation rate and $\dot{p}_C$ the catabolic power (or utilization rate), such as :

$$\dot{p}_A = \{\dot{p}_{Am}\} f V^{2/3} \text{ with } f = \left(\frac{X}{X + X_K} \right) \quad (4)$$

and (from eq. 3.44 {111})

$$\dot{p}_C = \frac{[E][E_G]}{[E_G]+\kappa[E]}\left(\frac{\{\dot{p}_{Am}\}V^{2/3}}{[E_m]}+[\dot{p}_M]V\right) \quad (5)$$

where, $\{\dot{p}_{Am}\}$(J.cm^{-2}) is the maximum surface-area-specific assimilation rate, linked to the maximum surface-area-specific ingestion rate $\{\dot{J}_{Xm}\}$ (J.cm^{-2}) via the assimilation efficiency *ae* (dimensionless) such as : $ae = \{p_{Am}\}/\{J_{Xm}\}$. f is the scaled functional response (dimensionless), X the substrate density, X_K the saturation coefficient (same dimension as X), $[E]$ (J.cm^{-3}) the reserve energy density such as $[E] = E / V$ and $[E_m]$ (J.cm^{-3}) the maximum reserve energy density.

The transition from embryo to juvenile and from juvenile to adult occurs if the cumulative investment to increase the state of maturity exceeds specified amount. Two boundary are then define : V_b and V_p, which respectively describe the structural volume at birth and structural volume at puberty {111}.
The amount of energy allocated to maturation in a juvenile is :

$$(1-\kappa)\,\dot{p}_C = \dot{p}_R + \dot{p}j \quad (6)$$

Where $\dot{p}_R$ is the maturity growth {123} and $\dot{p}_j$ the energy flow to maintain a certain degree of maturity, with :

$$\dot{p}_R = \frac{1-\kappa}{\kappa}[E_G]\frac{dV}{dt} \quad (7)$$

and,

$$\dot{p}j = \min\{V, V_p\}[\dot{p}_M]\frac{1-\kappa}{\kappa} \quad (8)$$

The initial state of egg and the embryo-juvenile transition are not very clear to me. Nevertheless, the initial reserves of egg E_0 depends (according to {107}) to the reserve energy at birth E_b and to the energy allocated for growth via L_b ; « *E_0 is not consider to be a free parameter* » {97}. *What is, in this context, the « maternal effect » described in KooySous2007 which is defined as :* $[E_b] = [E_{mother}]$ *at egg formation?*

Two variables are included as forcing in the DEB theory :

→ the first is the body **temperature** which acted on all the physiological rates {53}. In our case of an ectotherm organism, this temperature will be the environmental one. According to the Arrhenius relation (eq. 2.20 {53}) and the Sharpe proposition (eq. 2.21 {57}), the temperature affects physiological rate such as :

$$\dot{k}(T) = \dot{k}_1 \exp\left\{\frac{T_A}{T_1}-\frac{T_A}{T}\right\}\left(1+\exp\left\{\frac{T_{AL}}{T}-\frac{T_{AL}}{T_L}\right\}+\exp\left\{\frac{T_{AH}}{T_H}-\frac{T_{AH}}{T}\right\}\right)^{-1} \quad (9)$$

where $\dot{k}(T)$ is the temperature coefficient, $\dot{k}_1$ the value of a physiological reaction rate at the chosen reference temperature T_1 (°K), T_A (°K) the Arrhenius temperature and T (°K) the absolute temperature. T_L (°K) and T_H (°K) relate to the lower and the upper boundaries of the tolerance range and T_{AL} (°K) and T_{AH} (°K) are the Arrhenius temperatures for the rate of decrease at both boundaries.

This temperature coefficient is applied on two process into the model : the assimilation rate $\dot{p}_A$ and the maintenance rate $\dot{p}_M$.

→ The second variable is the **trophic resource** who define the amount of energy available for the ingestion process via the functional response *f* (eq. 4).

These nine equations seem to resume the principal fluxes which define the energy state of our larvae. They contain the primary parameters summarized in the Table 1.

symbol	unit	description	Process
$\{\dot{J}_{Xm}\}$	J.cm^{-2}.time^{-1}	surface-area-specific max ingestion rate	Feeding
X_K	Substrate concentration	Saturation coefficient of substrate X	Feeding
ae	-	Assimilation efficiency	Assimilation
$[\dot{p}_M]$	J.cm^{-3}.time^{-1}	Volume-specific somatic maintenance rate	Turnover / activity
$[E_m]$	J.cm^{-3}	Maximum energy density	mobilisation
$[E_G]$	J.cm^{-3}	Volume-specific costs for structure	Growth
V_b	cm^{-3}	Structural volume at birth	Life history
V_p	cm^{-3}	Structural volume at puberty	Life history
κ	-	fraction of catabolic power energy spent on maintenance plus growth	Allocation
δ	-	Shape coefficient	Measures relation
T_A	°K	Arrhenius temperature	Regulation
T_L	°K	Low boundary temperature	Regulation
T_H	°K	High boundary temperature	Regulation
T_{AL}	°K	Arrhenius temp for low boundary	Regulation
T_{AH}	°K	Arrhenius temp for high boundary	Regulation

Table 1. Primary parameters of the standard DEB model for the pearl oyster larva. (*maybe the parameters linked to the Sharpe proposition are not to be considered like primary parameters?*)

Parameters estimation

Some parameters can be estimated directly (or indirectly) via experimental measurements. They are presented in the following paragraphs.

This is a first approach which needs to be supplemented, mainly with new developments like the “practical guide for the estimation of Dynamic Energy Budget parameters” from KooySous, 2007.

The three parameters $[E_m]$, $[E_G]$ and κ seem more difficult to measure directly, mainly with larvae. Thus, the practical guide of KooySous2007 should give some keys to obtain parameters via compound parameters and from quantities easy to measure. *I won’t develop this point here*.

Measures relation

The shape parameter can be extract from the relation (see eq. (1)) :

$$\delta = \frac{\sqrt[3]{W_w \cdot d_w}}{L} \qquad (10)$$

As the wet weight W_w is difficult to estimate due to the proportion of external water around larvae, the dry weight seems to be a good descriptor with a standard water content estimation.

Feeding

Three parameters define the food uptake : $\{\dot{J}_{Xm}\}$, X_K and ae.
The maximum surface-specific ingestion rate $\{\dot{J}_{Xm}\}$ can be obtained from measurements of the feeding rate at several food densities (KooySous2007). The saturation coefficient X_K can thus be obtained by the same way via the functional response *f*.
The maximum surface-specific ingestion rate is considered as a parameter that depends on the composition of the diet {75}. Moreover, in some species, the developing juvenile takes a sequence of type of food or size of food particles {60}. That could happen with the *PO* larvae, which present some morphological development mainly in their feeding functions. Thus, several food types need to be tested in parallel to the several densities.

The assimilation efficiency *ae* seems to be difficult to estimate for the larvae. Indeed, the measurement of the faeces production is fastidious with the larvae. So, this measurement could be made on older oyster and apply to the larvae. (*But we can't be sure that this assimilation efficiency is the same for different stages and different food quality (i.e. different algae).*)

Turnover – activity

The volume-specific maintenance rate $[\dot{p}_M]$ can be estimated from starvation experiments, as is explained for several bivalves species in Van Der Veer et al, 2006. It seems to be relatively constant at 24 $J.cm^{-3}.d^{-1}$ at 20°C for the five species studied in this paper.

Regulation

The Arrhenius temperature can be obtained via the measurement of a physiological rate $\dot{k}$ at different temperatures. The plot $\ln\dot{k} = f\left(T^{-1}\right)$ give a slope equal to T_A (see fig. 2.17 {55}).
Thus, a physiological rate easy to measure has to be chosen (e.g. growth or ingestion rate).
Moreover, the temperature range needs to be large in order to extract the boundary parameters : T_L, T_H, T_{AL}, and T_{AH}.

Life history

If the simulation begins at egg stage, the mean energy content of an egg E_0 can be measured indirectly via the egg diameter (and a mean energy content) or directly with calorimetric measurement.
The volume at birth V_b can be obtained by the measurement of length at hatching and via the shape relation.
The volume at puberty V_p can be obtained by cytology and observation of the first maturation.

In situ behaviour

The feeding behaviour appears like the main factor influencing the larval development *in situ*. Consequently, we need to identify precisely the trophic resources.
Larval feeding behaviour corresponds to a several substrates with parallel processing (see {162}), where the larva feeds on different algae (and others) with no competition for access to the same carriers. Thus :

$$j_X = \sum_{i=1}^{n} j_i \quad (11)$$

with :

$$j_i = j_{im}\left(1+\frac{X_i}{X_{Ki}}\right)^{-1} \quad (12)$$

where j_X is the total amount of substrate uptake, j_i the amount of substrate *i* uptake, j_{im} the maximum specific uptake rate of substrate *i*, X_i the substrate *i* concentration and X_{Ki} the saturation coefficient of substrate *i*.
Thus, the specific uptake rates need to be obtained for the various algae identified as main trophic resources.
In their pelagic stage, the larvae can swim in the water column. Thus, they can have a specific behaviour potentially linked to the phytoplankton distribution (mainly in a vertical dimension but also in horizontal dimension).
With our goal to couple the larval development to their distribution, it thus appears interesting to understand the feeding behaviour of the *PO* larvae.

Spawning seems to occur all the year, but spat fall appears more abundant during inter-season (observations made in one atoll lagoon). We need thus to identify the main factor influencing the development success.
The prolonged starvation seems to be a potential factor of no development and death. The boundaries conditions followed by death can be evaluated through the DEB parameters according to the no growth threshold $e = l$ (see {227}). The minimum food density is also exposed in {274}.
Critical temperature condition can be an other factor preventing development. It can also be a potential factor influencing larval dispersal in the water column (in case of temperature layers). Thus, the optimum temperature range, extracted from $\dot{k}(T)$, should be an interesting information.
Finally, some other factors like the initial amount of energy into the egg should be studied as a parameter determining the viability of the larva

The last paragraph of this essay is about the species comparison.
In some Polynesian lagoons with pearl production, two oyster species of the same genus are present : *Pinctada margaritifera* (exploited for the pearl) and *Pinctada maculata* (not exploited). The specie *P. maculata* seems to compete for the space with *P. margaritifera* on the commercial collectors.
A comparison between the two species seems thus interesting in order to better understand the potential interactions, mainly according to the forcing variables (i.e. trophic resources via the functional responses and temperature via $\dot{k}(T)$).

Literature

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