An energetic model of the greenshell mussel *Perna canaliculus*

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Introduction

This preliminary DEB model aims to be used as one component of a carrying capacity model of mussel culture ecosystems under programme of "sustainability of cultured, enhanced and wild shellfisheries". This programme is undertaken by NIWA to investigate processes which determine the suitability and stocking level of coastal embayments for mussel aquaculture. The following is only the basic structure of the DEB model.

Model descriptions

The model is developed on the basis of the dynamic energy/mass budget theory and some functional descriptions of feeding and energetics were based experimental studies on the greenshell mussel. The model consists of two major parts: energy allocation and acquisition.

ENERGY ALLOCATION

Reserve dynamics

Following Kooijman (2000), assimilated energy (A) from food is first incorporated into the storage, from which it utilised at a rate C to maintenance, growth, development and reproduction. The dynamic of storage is then described by

$$dE/dt = A - C \qquad (1)$$

The utilisation rate of the storage depends on energy density [E] and conductance (υ), biovolume (V) and growth of an organism.

$$C = [E]\cdot\left(\upsilon\cdot V^{2/3} - \frac{d}{dt}V\right) \qquad (2)$$

while the biovolume growth of an organism follows:

$$\frac{d}{dt}V = \frac{\upsilon}{e+g}\cdot\left(e\cdot V^{2/3} - V / V_m^{1/3}\right) \qquad (3)$$

[note that I've tried to use growth data of the mussel (2 data sets, each contains 10-month growth recordings including length, dry flesh weight, food & temperature), but failed to obtain values of the parameters in equation 3, which forces me to find alternatives in obtaining biovolume growth as the following equations 4-6. Any sugestions why? Does any one have a program in estimating parameters of above equation 3?]

In practice however, to estimate these growth parameters needs comprehensive growth and environmental datasets which are usually not available. Alternatively, for the purpose of the present modelling excise, I would like to make simplification for the biovolume growth based on field observations of molluscs. At constant food density, the growth of an organism is assumed to be the von Bertalanffy type.

$$\frac{d}{dt}V = 3\cdot\gamma_B\cdot\left(V^{2/3}\cdot V_m^{1/3} - V\right) \qquad (4)$$

The condition of constant or abundant food, however, does not always occur in natural environment, because the observed growth rate of many bivalves including *P. canaliculus*e varied between ecosystems. Since food density affects both the von Bertalanffy growth rate and the ultimate volume, the equation 4 could not adequately describe dynamics of volumetric growth at varying food density. In natural environmental conditions, the equation 4 can be modified by introducing the effect of food term, as

$$\frac{d}{dt}V = 3\cdot\gamma_B\cdot\left(f\cdot V^{2/3}\cdot V_m^{1/3} - V\right)_+ \qquad (5)$$

where *f* is a type 2 functional response of food density (F) as

$$f = \frac{F}{F+F_h} \qquad (6)$$

Allocation

Following DEB theory, *k-rule* is used in energy allocation.

$_+$ The expression $(x)_+$ is defined as: $[x]_+=x$ for $x>0$, $[x]_+=0$ otherwise.

The conversion of storage into growth, development and reproduction involves in energy investment for catabolism and synthesis and therefore part of the energy is lost as dissipating heat during growth for production of new biomass. The overhead costs are incorporated into the model through introduction of conversion efficiencies: λ_g for structural growth, λ_d for development and λ_r for reproduction. Following the rule, the energy dynamic for growth will be

$$dE_C /dt = \lambda_g \cdot \ (k\ C\text{-}ME) \tag{7}$$

where ME is the heat dissipating resulted from excretion of carbon dioxide for maintenance and ammonia.

The overhead cost for growth would be

$$OH_G = (1\text{-}\lambda_g)\cdot \ (k\ C\text{-}ME) \tag{8}$$

The structural materials of a bivalve are made up of shell and flesh, so the energy available for growth would be partitioned between the two components. From aquaculture point of view, I am particularly interested in the variation in flesh weight of a mussel in a farming ecosystem. For this purpose, I may separately calculate the energy for shell and flesh structural growth through introducing a partitioning coefficient (λ_{gf}). The energy dynamic for flesh structural growth can be calculated by

$$dE_{CF} /dt =\lambda_{gf}\cdot \ \ \lambda_g\cdot \ (k\ C\text{-}ME) \tag{9}$$

According to the '*k-rule*', the energy spent on development in the juvenile equals to energy spent on reproduction in the adult. A transition length between the juvenile and adult was defined as L_p. For simplicity, it was assumed that no energy is spent on reproduction when $L<L_p$ and no energy is spent on development when $L>L_p$. Therefore, the energy dynamics for development (E_D) and reproduction (E_R) will be

$$dE_D / dt = \begin{cases} \lambda_d \cdot (1-k)\cdot C : if \ L < L_p \\ 0 : otherwise \end{cases} \tag{10}$$

$$dE_R / dt = \begin{cases} \lambda_r \cdot (1-k)\cdot C{:}if\, L > L_p \\ 0 : otherwise \end{cases} \tag{11}$$

Overhead costs from reserves to development or reproduction would be respectively:

$$OH_D = \begin{cases} (1-\lambda_d)\cdot (1-k)\cdot C : if \ L < L_p \\ 0 : otherwise \end{cases} \tag{12}$$

$$OH_R = \begin{cases} (1-\lambda_r)\cdot(1-k)\cdot C : if\ L > L_p \\ 0 : otherwise \end{cases} \tag{13}$$

ENERGY AQUISITION

Clearance

A mussel obtains its food by filtration from the water column and the filtration rate (mg time^{-1}) depends on clearance rate (l time^{-1}) and availability of food particles (mg l^{-1}). Based on experimental data, total actual clearance rate (CR) is usually determined by three factors: body size, temperature and particle concentration.

$$CR = CR_B \cdot\ CR_T \cdot\ CR_S \tag{14}$$

where CR_B, CR_T and CR_S are respectively effect of body size, temperature and particle concentration on clearance rate. At optimal temperature and low particle concentration, the equation 14 would be: $CR \cong CR_B$

Since surface areas determine food acquisition processes of an organism, at constant and optimal food density, the maximum clearance rate of a mussel is described to be proportional to its surface area (A_S).

$$CR_B = \partial \cdot\ A_S \tag{15}$$

Temperature (T) effect on clearance rate was described as a dome-shaped curve.

$$CR_T = CR_{coef} - CR_{td} \cdot\ (T - T_{opt})^2 \tag{16}$$

The effect of particle concentration (S) on clearance rate was modelled as a function of two components. The first component is a saturating function of the seston concentration used to represent the saturating effect of particles clogging the filtering apparatus. This term was described as a simple Type-2 hyperbolic functional response. The pumping rate was described as a simple exponential decline as the particle concentration increases to represent a control mechanism by which the mussel reduces feeding in response to high particle loads.

$$CR_S = \frac{S}{S + S_{HF}} \cdot e^{-p_c \cdot S} \tag{17}$$

Filtration (FR)

Filtration was calculated as a product of total actual clearance and particle concentration:

$$FR = CR \cdot\ S \tag{18}$$

Ingestion (IR)

Ingestion of organic particles is estimated as a function of filtration, food content and selective ingestion of organic particles, as

$$IR = \mu \cdot FR \cdot \left(\frac{F}{S}\right)^{\frac{S}{S+S_{HFS}}} \qquad (19)$$

Digestion (D)

Digestion is proportional to ingestion, as

$$D = De \cdot IR \qquad (20)$$

Overhead cost for feeding (OH_F)

Heat loss has been recorded to increase linearly with feeding rate in a few bivalves. Similarly, the overhead cost for feeding in this mussel is described to be proportional to ingestion rate, as

$$OH_F = \rho \cdot IR \qquad (21)$$

ENERGY EXPENDITURE

Maintenance (M)

An organism requires energy to maintain alive. This part of energy does not include overhead costs associated with the production processes of structural material growth, development and reproduction and ingestion (Kooijman 2000). Maintenance processes would result in excretion of carbon dioxide and therefore heat loss. The heat loss can be measured directly using calorimeter, which would be proportional to its biovolume.

$$M = [M] \cdot V \qquad (22)$$

The volume-specific cost of maintenance, *[M]*, is a temperature-dependent coefficient and increases with temperature within the range of tolerance.
(note that the following functional response is based on total oxygen consumption rate which of course includes growth, reproduction and feeding costs. I am not with 100% sure whether the maintenance has the same functional response. I do not have maintenance data. Any suggestions & information ??)

$$[M] = \psi + \beta \cdot T^{\sigma} \qquad (23)$$

Excretion (Excr)

Physiological processes would result in excretion of ammonia. According to experimental data of other bivalves, the ammonia excretion rate is proportional to the sum of overhead costs and maintenance, as

$$Excr = \eta \cdot (OH_G + OH_D + OH_R + OH_F + M) \qquad (24)$$

The sum of maintenance and ammonia excretion gives total energy expenditure, as:

$$ME = M + Excr \qquad (25)$$

Parameterisation and Simulations

To be completed

Discussion

The DEB model is used to simulate the growth of the greenshell mussel *Perna canaliculus* by integrating physiological processes of the mussel to changing environment. The ultimate purpose of the model, once verified, is to be integrated into a larger ecosystem model to investigate the behaviour of mussel farming ecosystems.

Allocation rule

In developing the DEB model, I was faced with choices between two energy allocation rules, neither of which has convincingly been tested. There are two conceptual models (DEB/reserve pool and production models), represented by Kooijman (1986) and Paloheimo et al. (1982), which differ in the partitioning rules of assimilation from food. The DEB model assumes that assimilation first enters a reserve pool from which it utilised at a rate of *C* to maintenance, growth, development and reproduction. The utilisation rate depends on storage of reserves. The production model however, assumes that assimilation is immediately allocated into maintenance and the rest is partitioned into growth, storage of reserves and reproduction. This model has rapid and irreversible allocation of assimilation to production processes. The storage is not available for structural growth and reproduction but is available for maintenance. The major differences of the model outcomes will be that DEB model predicts that the growth continue under starvation whilst the production model predicts that the growth immediately cease when assimilation is less than maintenance.

It is difficult to make direct comparison between the two types of models, because parameterisation is the main obstacle and assumptions are always required to obtain parameter values. Therefore, there might be uncertainties in some of parameter values, particularly these free fitting ones. I chose to use DEB allocation rule in the present model. The assumption of the allocation rule seems consistent with laboratory observations that the blue mussel *M. edulis* was able to grow at absence of food.

Although it is impossible to prove advantage of this allocation rule from available datasets of the greenshell mussel, other growth studies suggest that such an assumption is probably reasonable for this mussel (not shown, these data will be used for model calibration). The length of the mussel increased continuously during a period of one-year growth study, but the flesh weight hardly increased particularly at the first few months of the experiment (NIWA unpublished data). Although comprehensive records of environmental variables were not available, the data imply that food supply was low particularly during the first few months of the experiment. The growth of the mussel in length would be predicted by DEB model, but the predicted trajectory would be deviated from observations by the production model because most of the assimilation was possibly used to meet maintenance demands so that growth would cease under its allocation rule.

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