

Pseudo-faeces production in bivalves

S.A.L.M. Kooijman

Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands

Available online 30 March 2006

Abstract

Many filter feeders produce pseudo-faeces from selected particles that are filtered; pseudo-faeces does not pass the gut. Food intake can be limited by the filtering (acquisition) as well as the digestion (processing) rate. Its dynamics can be analysed in a straightforward way in the context of the Dynamic Energy Budget (DEB) theory using the closed hand-shaking protocol of Synthesizing Units. The model reveals how food intake depends on the relative size of the filtering and digestion machinery, which can be used to model differentiated growth of these structures if allocation is linked to their relative workload. It turns out that non-digestible particles modify the apparent half-saturation coefficient, which makes that estimates for this coefficient can be used to quantify the mean silt load in a given habitat.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Synthesizing Units; DEB theory; Pseudo-faeces; Half-saturation coefficient; Differentiated growth; Filtering rate; Digestion rate; Food intake

1. Introduction

The half-saturation constant of the Pacific oyster turns out to be site-specific (Pouvreau et al., 2006-this issue). Discussions with these authors have led to the hypothesis that site-specific silt load (turbidity) might be one of the possible explanations for the differences among half-saturation constants. This short note will demonstrate that silt and other particles that bivalves select for pseudo-faeces production do indeed affect the half-saturation constant. This does not ‘prove’ that variations in turbidity is the main cause of the observed variation in half-saturation coefficients, but it motivates further investigations in this direction.

The aim is to find expressions for the feeding and filtering rates, where food and silt compete for access

to the acquisition machinery of the bivalve, in a way that is consistent with the standard DEB model (Kooijman, 2000). For food X that is present in density X , this standard model specifies that in the absence of silt, food intake can be written as $J_X = \{J_{Xm}\}fV^{2/3}$ with scaled functional response $f = X/(X + K)$. This model has two parameters, the half-saturation constant K and the maximum surface area-specific food uptake rate $\{J_{Xm}\}$, and contains one state variable, viz. structural volume V , which changes in time as long as the individual is not fully grown.

2. Acquisition and digestion

We partition feeding into acquisition A with N_A functional units and digestion D with N_D functional units. The numbers N_* are proportional to the surface area of the individual; an acquisition unit might be a filtering hair, and a digestion unit a site in the gut wall at which absorption occurs. Non-digestible

E-mail address: bas@bio.vu.nl.

particles Y (here called silt particles, but possibly including other particles as well) are present in density Y . Food is passed from the acquisition units to the digestion units by channelling using a closed hand-shaking protocol (so no acquired food is spoiled) and silt is excreted as pseudo-faeces and not passed to the digestion units.

The concept of Synthesising Units (SU) (Kooijman, 1998) is very suitable for modelling functional responses, as will be illustrated. SUs are generalised enzymes that turn arriving substrate fluxes into product fluxes via SU-substrate complexes. The kinetics has much in common with classic enzyme kinetics, which is based on substrate concentrations, however. We follow (Kooijman and Segel, 2005) for closed handshaking, and include pseudo-faeces production. This means that food is only passed from the acquisition units to the digestion units if the latter are ready for acceptance.

Let θ^A be the fraction of acquisition units that is not bound to food or silt, θ_X^A the fraction that is bound to food, and θ_X^D the fraction of digestion units that is bound to food. For $1 = \theta^A + \theta_X^A + \theta_Y^A$ and $1 = \theta^D + \theta_X^D$, the changes in the fractions of A and D are

$$\frac{d}{dt}\theta^A = (\theta_X^D - \theta_X^A)k_X + \theta_Y^A k_Y - \theta^A(b_X X + b_Y Y)$$

$$\frac{d}{dt}\theta_Y^A = \theta^A b_Y Y - \theta_Y^A k_Y$$

$$\frac{d}{dt}\theta^D = \theta_X^D k_D - (\theta_X^D - \theta_X^A)k_X N_A / N_D$$

where b_X and b_Y are the affinities of X and Y ; k_X^{-1} and k_Y^{-1} are the mean handling times of X and Y by the acquisition machinery, and k_D^{-1} is the mean handling time of X by the digestion machinery. The steady state fractions are

$$\theta^{A*} = k_X k_Y k_D N_D / \Theta$$

$$\theta_X^{A*} = k_Y b_X X (k_X N_A - k_D N_D) / \Theta$$

$$\theta_Y^{A*} = k_X k_D N_D b_Y Y / \Theta$$

$$\theta_X^{D*} = k_X k_Y N_A b_X X / \Theta$$

$$\Theta = k_X k_Y N_A b_X X + k_D N_D (k_X k_Y - k_Y b_X X + k_X b_Y Y).$$

3. Feeding and pseudo-faeces production

The time-scale separation argument links (pseudo)-faeces production to the fractions of bounded SUs in pseudo-steady state. The feeding and pseudo-faeces production rates are

$$J_X = N_A \theta^{A*} b_X X = N_D \theta_X^{D*} k_D \\ = \frac{k_X k_Y k_D N_A N_D b_X X}{k_X k_Y k_D N_D + (k_X N_A - k_D N_D) k_Y b_X X + k_D N_D k_X b_Y Y}$$

$$J_Y = N_A \theta^{A*} b_Y Y = N_A \theta_Y^{A*} k_Y \\ = \frac{k_X k_Y k_D N_A N_D b_Y Y}{k_X k_Y k_D N_D + (k_X N_A - k_D N_D) k_Y b_X X + k_D N_D k_X b_Y Y}$$

Testing the consistency of this model with the standard DEB model will yield suggestions for further simplification. In the absence of silt, so $Y=0$, we have

$$J_X = \frac{k_X k_D N_A N_D b_X X}{k_X k_D N_D + (k_X N_A - k_D N_D) b_X X} = \frac{\{J_{Xm}\} V^{2/3} X}{K + X}$$

for $\{J_{Xm}\} V^{2/3} = \frac{k_X k_D N_A N_D}{k_X N_A - k_D N_D}$ and $K = \frac{k_X k_D N_D}{(k_X N_A - k_D N_D) b_X}$. The conclusion must be that the model is DEB-consistent for $N_A, N_D \propto V^{2/3}$ (so the number of acquisition and digestion units must be proportional to the surface area of the structure); the half-saturation coefficient K is then independent of structural volume V and the maximum food uptake equals $J_{Xm} \propto V^{2/3}$.

4. Reparametrisation

To remove parameters that are difficult to measure from the behaviour of individuals, we introduce the silt saturation coefficient $K_Y = k_Y / b_Y$ and relative affinity $\delta_{YX} = b_Y / b_X$. Substitution gives the ingestion rates for food and silt particles

$$J_X = \frac{\{J_{Xm}\} V^{2/3} X}{K'(Y) + X} \text{ with } K'(Y) = K(1 + Y/K_Y)$$

$$J_Y = \delta_{YX} J_X Y / X$$

If no selection in acquisition occurs, we have $\delta_{YX}=1$, which means that this model for how silt affects food uptake has one extra (compound) parameter K_Y which is inverse to the product of the mean handling time of a silt particle, k_Y^{-1} , and its affinity, b_Y ; its dimension is silt density. Faeces production is proportional to food consumption; the conversion depends on food quality

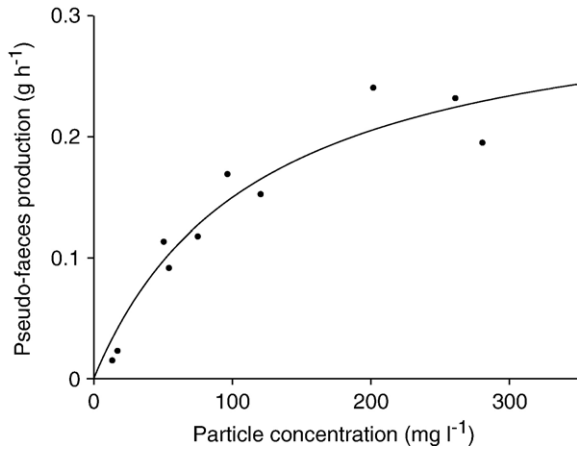


Fig. 1. Pseudo-faeces production for a 7 cm *Mytilus edulis*. Data from Widdows et al. (1979). The fitted curve assumes that food X and silt Y covary, so Y/X is constant. The result is that pseudo-faeces production amounts to $J_Y = J_{Ym}X/(K'_Y + X)$, with $J_{Ym} = \alpha J_{Xm}Y/X$ and $K'_Y = \alpha K$ for $\alpha = (Y/K_Y + 1)^{-1}$, while X is treated as the measured particle concentration. The parameter estimates are $J_{Ym} = 0.325$ g/h and $K' = 117$ mg/l.

parameters. Pseudo-faeces production equals silt consumption J_Y ; mucus production might also have a contribution to pseudo-faeces production, depending on the choice of quantifiers.

Fig. 1 illustrates that this model for pseudo-faeces production matches experimental data for *Mytilus edulis*.

The filtering rate of an individual that completely clears the filtered water equals $F(X, Y) = J_X/X = J_Y/Y$ for

$\delta_{YX} = 1$. The maximum filtering rate is at $X=0$, $Y=0$, so

$$F_m = F(0, 0) = \frac{J_{Xm}}{K} = \frac{k_X k_D N_A N_D}{k_X N_A - k_D N_D} \frac{(k_X N_A - k_D N_D) b_X}{k_X k_D N_D} = N_A b_X$$

$$F(X, Y) = \frac{\{F_m\} V^{2/3}}{1 + Y/K_Y + X/K}$$

for $\{F_m\} = F_m/V^{2/3}$. The implicit assumption is that the individual is parsimonious; it does not filter faster than necessary. Notice that if X and Y covary, so Y/X remains constant, this model for filtering rate has two parameters only, since $Y/K_Y + X/K = X(K_Y^{-1}Y/X + K^{-1}) = X/K''$ and K'' is constant.

5. Apparent saturation coefficient

Notice that if food density X varies at constant silt density Y , the apparent half-saturation coefficient $K'(Y) = K(1 + Y/K_Y)$ is constant, and the standard DEB formulation applies, but its value depends on the constant silt density Y . Suppose that Y is site-specific, then K' is linear in the silt density Y . We can invert the argument and obtain $Y = K_Y(K'/K - 1)$, where K is the minimum among K' 's if there is a “clean” site in the set of measurements. If measurements of (mean) silt densities Y are available, we can test the relationship between K' and Y , and arrive at an estimate for silt saturation coefficient $K_Y = Y/(K'/K - 1)$.

6. Differential growth of velum and gut

We might have chosen to model silt and food as substitutable substrates for a single type of SUs, where the conversion efficiency from silt to reserve equals zero. Using the closed handshaking formalism, however, we now have an expression for how feeding depends on the sizes of the acquisition and the digestion machinery. Macoma larvae show differential growth in velum versus gut, depending on the food level. The allocation can be linked to relative work-load, (see Philippart et al., 2006). The present model quantifies the effect of differential growth on food uptake if we link the numbers of functional units N_A and N_D , to the masses of the food acquisition and digestion machinery. Changes in N_A/N_D affect both $\{J_{Xm}\}$ and K .

The relative workload of the acquisition and digestion machinery equals in absence of silt

$$F/F_m = \frac{k_X K_D N_D}{k_X k_D N_D + (k_X N_A - k_D N_D) b_X X} = 1 - f = \kappa_A$$

$$J_X/J_{Xm} = \frac{(k_X N_A - k_D N_D) b_X X}{k_X k_D N_D + (k_X N_A - k_D N_D) b_X X} \equiv f = \kappa_D$$

Let us now partition structure V into three contributions: acquisition machinery, V_A , digestion machinery, V_D , and the rest, V_G ; so $V = V_A + V_D + V_G$. The only extra step that is necessary to arrive at a model for differentiated growth is to link the volumes of the acquisition and digestion machineries, V_A and V_D , to the number functional units, N_A and N_D ,

e.g. $N_A = (n_A V_A)^{2/3}$ and $N_D = (n_D V_D)^{2/3}$. This choice makes that if V_D/V_A remains constant, the standard DEB model applies. We now incorporate an allocation based on relative work load, which has as consequence that V_A/V_D will depend on (mean) food density.

Assuming that the costs of structure and its somatic maintenance are independent of the type of structure, the κ -rule of the standard DEB model can be generalised for $\kappa_A = 1 - \kappa_D$ as

$$\left. \begin{aligned} \kappa \kappa_X \kappa_A \dot{p}_C &= [E_G] \frac{d}{dt} V_A + [\dot{p}_M] V_A \\ \kappa \kappa_X \kappa_D \dot{p}_C &= [E_G] \frac{d}{dt} V_D + [\dot{p}_M] V_D \\ \kappa (1 - \kappa_X) \dot{p}_C &= [E_G] \frac{d}{dt} V_G + [\dot{p}_M] V_G \end{aligned} \right\} \kappa \dot{p}_C = [E_G] \frac{d}{dt} V + [\dot{p}_M] V$$

where κ_X is the fraction of the catabolic power that is allocated to the assimilation machinery; the fraction $1 - \kappa$ of the catabolic power is allocated to maturity maintenance plus maturation (or reproduction in adults). The standard DEB model specifies that the catabolic rate and the scaled reserve dynamics equal

$$\dot{p}_C = [E] \left(\dot{V} V^{2/3} - \frac{d}{dt} V \right) \text{ and } \frac{d}{dt} [E] = y_{EX} J_X - v [E] V^{-1/3}$$

Substitution gives for $e = [E]/[E_m]$

$$\frac{d}{dt} V = \frac{\dot{V} e V^{2/3} - \dot{k}_M g V}{e + g} \text{ and } \frac{\kappa \dot{p}_C}{[E_G]} = \frac{e}{e + g} \left(\dot{V} V^{2/3} + \dot{k}_M V \right)$$

with maintenance rate coefficient $\dot{k}_M = [\dot{p}_M]/[E_G]$ and investment ratio $g = [E_G]/\kappa [E_m]$.

Using the catabolic power just obtained and dividing by $[E_G]$ we arrive at

$$\begin{aligned} \frac{d}{dt} V_A &= \kappa_A \kappa_A \frac{e}{e + g} \left(\dot{V} V^{2/3} + \dot{k}_M V \right) - \dot{k}_M V_A \\ \frac{d}{dt} V_D &= \kappa_A \kappa_D \frac{e}{e + g} \left(\dot{V} V^{2/3} + \dot{k}_M V \right) - \dot{k}_M V_D \\ \frac{d}{dt} V_G &= (1 - \kappa_A) \frac{e}{e + g} \left(\dot{V} V^{2/3} + \dot{k}_M V \right) - \dot{k}_M V_G \end{aligned}$$

Together with given volumes at birth, V_{Ab} , V_{Db} and V_{Gb} , and the expression for $(d/dt)e$, these equations fully determine growth of body parts. As long as the fractions κ are constant, this is still the standard DEB model if $V_{Ab} = \kappa_X \kappa_A V_b$ and $V_{Db} = \kappa_X \kappa_D V_b$, which makes that $V_A = \kappa_X \kappa_A V$ and $V_D = \kappa_X \kappa_D V$ at any time. We can now deviate from this standard by allowing that κ_A (and so $\kappa_D = 1 - \kappa_A$) is no longer constant, but can vary in time, depending on the feeding conditions (where food density X varies in time); fractions κ_X and κ are kept constant.

References

- Kooijman, S.A.L.M., 1998. The synthesizing unit as model for the stoichiometric fusion and branching of metabolic fluxes. *Biophys. Chem.* 73, 179–188.
- Kooijman, S.A.L.M., 2000. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press.
- Kooijman, S.A.L.M., Segel, L.A., 2005. How growth affects the fate of cellular substrates. *Bull. Math. Biol.* 67, 57–77.
- Philippart, C.J.M., Bos, O.G., Gontikaki, E., Kooijman, S.A.L.M., 2006. Consequences of phenotypic plasticity of feeding organs for age and size at metamorphosis. *Ecol.* (submitted).
- Pouvreau, S., Bourles, Y., Lefevre, S., Gangery, A., Alunno-Bruscia, M., 2006. Application of a dynamic energy budget model to the pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. *J. Sea Res.* 56, 156–167 doi:10.1016/j.seares.2006.03.007 (this issue).
- Widdows, J., Fieth, P., Worrall, C.M., 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.* 50, 195–207.