Clearance rate regulation in mussels: Adding the effect of seston level to a model of internal state-based regulation

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ABSTRACT

We tested a model of clearance rate regulation that specifies that clearance rate is driven by the density of energy reserves and is modulated by factors such as biochemical signalling and seston concentration (Fréchette, M. 2012. A model of clearance rate regulation in mussels. J. Sea Res. 73:32–40). Mussels were fed natural seston at high and low concentrations for 71 days to manipulate the density of energy reserves ("position effect"). Clearance rate of each group was assayed in a two-level repeated-measures design experiment, within and among days. The effect of position and its interactions was not significant. It is likely that the low seston level treatment was too mild to generate phenotypic flexibility in clearance rate. The effect of time, however, was significant at all scales. Seston variability allowed examining the functional response of mean clearance rate to seston level. Short-term clearance rate was bounded by seston concentration at very low and high seston concentration. Between concentration extremes, however, short-term clearance rate was not regulated by actual seston concentration. On some occasions hysteresis dominated the functional response, implying delayed regulation, presumably in response to gut fullness. Hourly-averaged mean clearance rate exhibited a clearly-defined non monotonous response to seston level. Therefore we modified the initial model formulation in order to include the effect of low seston level. We found an excellent fit between the modified model and the data. Therefore, in spite of appearing erratic at intermediate seston level, short-term clearance rate patterns are embedded within a well-defined functional response. Understanding these patterns apparently requires that seston level, its temporal variability and the dynamics of gut fullness be taken into account.

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1. Introduction

Food ingestion in suspension feeders typically increases with food concentration. Beyond this general pattern, variability in the relationship between feeding rate and food availability has led to the recognition of various types of feeding responses (reviewed in Gentleman et al., 2003). Type I model occurs in cases where ingestion increases linearly from the origin and reaches a maximum constant rate above a critical food level. Both segments are linear. Type I model appears to be mostly restricted to suspension feeders (Jeschke et al., 2004). Type II model occurs in cases where ingestion increases following a hyperbolic (i.e., Michaelis–Menten) relationship (e.g., marine planktonic ciliates; Verity, 1991). Type III model occurs in cases where the relationship is sigmoidal (e.g., Daphnia; Sarnelle and Wilson, 2008). Various Type III sub-categories may be recognised, depending on the actual shape of the sigmoid or depending on whether the relationship goes through the origin or not. Type IV model, where ingestion is inhibited at food concentrations beyond saturating levels, and alternative models are discussed in Gentleman et al. (2003) and in Jeschke et al. (2004).

In Dynamic Energy Budget (DEB) theory, food ingestion per gill unit (Table 1) surface per day ($\{\dot{p}_X\}$, J cm^{-2} d^{-1}) by bivalves is assumed to follow a Type II model (Kooijman, 2010) and is written

$$\{\dot{p}_X\} = \{\dot{p}_{Xm}\}\frac{X}{X_K + X} \tag{1}$$

where $\{\dot{p}_{Xm}\}$ (J cm^{-2} d^{-1}) is maximum food ingestion per gill unit surface per day, X (J L^{-1}) is (single-resource) food concentration in the water and X_K (J L^{-1}) is the half-saturation constant of Holling's Type II model. The term $\frac{X}{X_K+X}$ depicts the scaled functional response of food ingestion to food concentration. Feeding behaviour may instead be studied in terms of clearance rate ($\{\dot{C}_R\}$, L cm^{-2} d^{-1}), which is obtained by dividing ingestion rate by the concentration of food at the output of the mussel chamber (Hildreth and Crisp, 1976; Northby, 1976). The value of X_K is assumed to be constant for a given environmental setting and has been used to calibrate computer simulations of cultured bivalves for specific sites or local conditions (e.g., Alunno-Bruscia et al., 2011; Ren and Schiel, 2008; Rosland et al., 2009). It follows that for a given situation the relationship between clearance rate and food availability is assumed to be a fixed function of food availability.

Table 1
List of symbols in this paper.

Definition	Symbol	Units	Value	Source
Food ingestion per gill unit surface	$\{\dot{p}_X\}$	J cm^{-2} d^{-1}		
Maximum ingestion rate per gill unit surface	$\{\dot{p}_{Xm}\}$	J cm^{-2} d^{-1}		
Food concentration in water	X	J L^{-1}		
Half-saturation constant	X_K	J L^{-1}		
Clearance rate per gill unit surface	$\{\dot{C}_R\}$	L cm^{-2} d^{-1}		
Maximum clearance rate	$\{\dot{C}_{Rm}\}$	L cm^{-2} d^{-1}		
Concentration of ith particle type	X_i	mg L^{-1}		
Intensity of jth clearance rate modulator	X_j	Depend on the nature of factor		
Parameter	k_0	cm^3 J^{-1}		
Parameter for the jth modulator	g_j	L mg^{-1}		
Parameter for the ith particle type	g_i	L mg^{-1}		
Reserve energy density	$[E]$	J cm^{-3}		
Overall mean chamber clearance rate	$\dot{C}_{Rc}$	L d^{-1}		
Nominal flow rate in tanks	f_c	L d^{-1}		
Depletion coefficient (single tank)	f_d			
Shell length	ℓ	cm		
Number of mussels per tank	N_c			
Total gill surface area per tank	$S_{b,c}$	cm^2		
Chlorophyll a concentration at the outflow of control tanks	X_{1c}	µg L^{-1}		
Chlorophyll a concentration at the outflow of mussel tanks	X_{1m}	µg L^{-1}		
Log-transformed clearance rate data	$\{\dot{C}_R\}_{tr}$			
Volumetric concentration of seston	X_v	cm^3 L^{-1}		
Parameter	k_1	L^{1+p} cm^{-2-3p} d^{-1}	$1.3433 \cdot 10^{14}$	Present study
Parameter	k_2	L^q cm^{-3p}	$3.5622 \cdot 10^{14}$	Present study
Parameter	p		4.6125	Present study
Parameter	q		5.2663	Present study
Volumetric concentration of seston at which clearance rate is maximum	X_{vm}	cm^3 L^{-1}		
Total individual mussel mass	m	g		
Energy reserves	E	J		
Structural volume	V	cm^3		
Energy content of reproductive compartment	E_R	J		
Energy of spawning compartment	E_S	J		
Individual gill surface area	S_b	cm^2		
Overall mean clearance rate per gill unit surface	$\{\dot{C}_{Rc}\}_m$	L cm^{-2} d^{-1}		
Error clearance rate	$\{\dot{C}_R\}_e$	L cm^{-2} d^{-1}		

A central tenet in DEB theory is that animal activity is fuelled by the energy reserves compartment (Kooijman, 2010). Therefore it may be argued that feeding modules based on the dependence of $\{\dot{C}_R\}$ on actual food concentration as in a Holling's functional model (hereafter HFM) are based on the incorrect assumption that feeding rate is independent of animal internal state, in particular its energy reserves. Such models fail to account for latent effects in clearance rate and phenotypic flexibility in clearance rate regulation, for instance. To address these issues, an internal-state based feeding module (hereafter ISFM-1) was developed (Fréchette, 2012a). ISFM-1 assumes that clearance rate is regulated by a set of factors, as opposed to food concentration only. Clearance rate increases with internal energy reserves density ($[E]$, J cm^{-3}), and is modulated by a number of agents such as particle load (X_i, mg L^{-1}; subscript i denotes particle type) on the one hand, and clearance rate-independent factors on the other hand (X_j; dimensions vary according to the nature of the agent), such that

$$\{\dot{C}_R\} = \frac{\left(\{\dot{C}_{Rm}\} - \sum g_j X_j\right) \cdot \left(1 - e^{-k_0\left(1 + \sum g_i X_i\right)[E]}\right)}{1 + \sum g_i X_i} \qquad (2)$$

where $\{\dot{C}_R\}$ (L cm^{-2} d^{-1}) is clearance rate per unit gill surface, $\{\dot{C}_{Rm}\}$ (L cm^{-2} d^{-1}) is maximum clearance rate per unit gill surface and k_0, g_i and g_j are adjusted parameters. Examples of clearance rate-independent factors are hypoxia and low-salinity stress (Wang et al., 2011) and negative effects of current speed (Newell et al., 2001). DEB simulations with ISFM-1 were able to depict transient latent effects and site-related physiological flexibility in clearance rate, and to

alleviate problems in model calibration such that depth-related effects on growth prediction appeared negligible (Fréchette, 2012a). Furthermore, with ISFM-1 the type of functional response of clearance rate varied among seasons. The overall pattern closely mimicked that actually observed by Strohmeier et al. (2009) in a low seston environment. In summary, clearance rates and individual growth dynamics were consistent with the literature when modelled with ISFM-1 but not with HFM (Fréchette, 2012a). In the simulations above it was assumed that seston concentration had negligible effect on clearance rate and only the effect of energy availability was modelled.

Here we report an assessment of the ability of ISFM-1 to explain clearance rate variability of blue mussels (*Mytilus* spp.) grown in two feeding environments. Mussels were kept in growth chambers fixed in series for more than two months and fed natural seston. This provided an upstream–downstream gradient in food level. We tested whether the depletion gradient would elicit parallel variability in clearance rate, as expected with ISFM-1. Finally, we analysed short-term and hourly-averaged clearance rate patterns and extended the model depicted in Eq. (2) in order to include the effect of low food availability.

2. Methods

We conducted the experiment at the Maurice-Lamontagne Institute (IML), located on the south shore of the St. Lawrence Estuary. Seawater was pumped directly from the nearby Estuary and the mussels were fed unsupplemented natural seston. Studies made in near-by locations indicate that this is a low-seston environment except on windy days (Demers et al., 1987; Fréchette and Bourget, 1985; Fréchette and Grant, 1991; Therriault and Levasseur, 1985).