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A model of clearance rate regulation in mussels

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ABSTRACT

Clearance rate regulation has been modelled as an instantaneous response to food availability, independent of the internal state of the animals. This view is incompatible with latent effects during ontogeny and phenotypic flexibility in clearance rate. Internal-state regulation of clearance rate is required to account for these patterns. Here I develop a model of internal-state based regulation of clearance rate. External factors such as suspended sediments are included in the model. To assess the relative merits of instantaneous regulation and internal-state regulation, I modelled blue mussel clearance rate and growth using a DEB model. In the usual standard feeding module, feeding is governed by a Holling's Type II response to food concentration. In the internal-state feeding module, gill ciliary activity and thus clearance rate are driven by internal reserve level. Factors such as suspended sediments were not included in the simulations. The two feeding modules were compared on the basis of their ability to capture the impact of latent effects, of environmental heterogeneity in food abundance and of physiological flexibility on clearance rate and individual growth. The Holling feeding module was unable to capture the effect of any of these sources of variability. In contrast, the internal-state feeding module did so without any modification or ad hoc calibration. Latent effects, however, appeared transient. With simple annual variability in temperature and food concentration, the relationship between clearance rate and food availability predicted by the internal-state feeding module was quite similar to that observed in Norwegian fjords. I conclude that in contrast with the usual Holling feeding module, internal-state regulation of clearance rate is consistent with well-documented growth and clearance rate patterns.

1. Introduction

Clearance rate regulation is usually understood as an instantaneous response of suspension feeders to ambient seston concentration. In current Dynamic Energy Budget (DEB) theory, for instance, clearance rate regulation has been described using Michaelis–Menten kinetics (also known as a Holling's Type II functional response; Real, 1977). According to this view, clearance rate saturates in response to current high food concentration. The actual satiation mechanism may be gut fullness or a similar feedback mechanism (Kooijman, 2010, p. 263). Recent developments whereby different particle types are taken in consideration follow the same instantaneous-regulation logic (Saraiva et al., 2011a).

The above view is based on the assumption that clearance rate is regulated by external control variables, such as seston concentration and quality. Studies of clearance rate regulation have assumed external regulation, irrespective of whether they were embedded in the Scope for Growth (SFG) paradigm (e.g., Bayne and Widdows, 1978; Cranford and Hargrave, 1994; Strohmeier et al., 2009; Widdows et al., 1979) or the DEB paradigm (Saraiva et al., 2011a). Feeding activity, however, requires energy. According to DEB theory, this is fuelled by reserves (Kooijman, 2010). Therefore it must be recognised that feeding activity is driven by biochemical processes and that Michaelis–Menten or similar kinetics apply to the relationship between energy reserves and feeding activity. Consequently, variability in energy reserves provides a potential source for internal state-driven regulation of clearance rate. In contrast, environmental factors such as water viscosity (Podolsky, 1994; Riisgård and Larsen, 2007), for instance, are external and may add to internal state-driven regulation of clearance rate. Based on first principles, therefore, it appears that clearance rate regulation should result from dual influences, external and internal.

An empirical perspective leads to the same conclusion as above: Some aspects of mussel growth and clearance rate regulation appear to require internal state-driven regulation. I base this suggestion on two sets of observations. The first set of observations involves latent effects during ontogeny. Pechenik (2006) defined latent effects as characteristics that originate from a developmental phase that become apparent only during later stages. Such effects are particularly obvious in studies of the effect of stress, particularly food level, during early ontogeny. Pechenik (2006) reviewed studies spanning a large phylogenetic array and found latent effects in 38 of the 43 studies examined. More recent contributions concur with Pechenik's analysis (e.g., Chiu et al., 2007). Typically, such studies report that stress, generally low food availability, during the larval phase, results

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in reduced growth in juveniles, and survivorship may also be affected (Phillips, 2002, 2004).

Latent effects may persist, be amplified or vanish at subsequent life stages (Podolsky and Moran, 2006). They also appear to depend on the timing of stress application, as early stress has more pronounced effect than stress applied late during larval stage (Chiu et al., 2008; Phillips, 2004), in spite of the apparent ability of larvae to recover from poor feeding conditions during larval life (Ben Kheder et al., 2010; Pechenik et al., 2002). Latent effects are usually ascribed to the consequences of low energy reserves with ensuing negative effects on general individual performance (Phillips, 2002, 2004; Thiyagarajan et al., 2003), although morphological factors may be involved (Pechenik, 2006; Phillips, 2002). Reduced clearance rate has been seen as the proximal mechanism linking lower energy content and latent effects (Chiu et al., 2007; Pechenik et al., 2002).

The second set of observations concerns phenotypic flexibility of clearance rate regulation after metamorphosis. Most of these studies involve reciprocal transfers between various sites and monitoring subsequent changes in clearance rate. Worrall and Widdows (1983) transferred clams *Scrobicularia plana* between three distant sites. Depending on the origin and the receptor site, they found either partial or complete acclimatisation of clearance rate to the new sites. Widdows et al. (1984) transferred blue mussels between two sites and reported that after 7 weeks, clearance rates of transferred mussels were intermediate between those observed in mussels kept in their original site. In a similar experiment, Okumus and Stirling (1994) transferred mussels between two Scottish sea lochs and found short term differences in clearance rate, but in the long run transferred mussels eventually conformed to the rate found in mussels from the receptor site. These studies suggest that clearance rate regulation is in part dependent of internal condition of the animals. This view was further strengthened by Babarro et al. (2000a) who transferred mussel spat from the shore to a culture raft in Ría de Arousa, NW Spain. Clearance rate of shore spat was subsequently compared with clearance rate of raft spat with a single source of water. Significant differences occurred early after transferring the mussels and progressively vanished within one month when mussels were transferred in late fall (Babarro et al., 2000a). In contrast, no such differences occurred when mussels were transferred in summer (Labarta et al., 1997). This is clear evidence that internal state of spat regulated clearance rate. Internal-state driven seasonal variability in clearance rate was also implied in a study of blue mussel and sea scallop clearance rates based on indirect measurements (Cranford and Hill, 1999). Taken together, these studies show that internally-based physiological factors are involved in clearance rate regulation.

In the present study, I develop a model of an internal-state feeding module (hereafter ISFM) based on the regulation of ciliary beat frequency (CBF) and its effect on clearance rate. The model includes internal and external regulating variables. I then incorporate ISFM into a standard mussel DEB model. Finally, based on standard DEB simulations I study the ability of ISFM and of the usual Holling's Type II feeding module (hereafter HFM) to capture growth and clearance rate patterns in simple hypothetical situations that mimic actual experiments. These studies examined 1) latent effects in clearance rate and growth (Chiu et al., 2007; Phillips, 2002, 2004), 2) the effect of environmental gradients on DEB-modelled oyster growth (Ren and Schiel, 2008), and 3) flexibility of feeding behaviour (Babarro et al., 2000a; Labarta et al., 1997).

2. Clearance rate regulation: a model

Here I describe HFM used in standard DEB theory and I derive the ISFM model. I use conventional terminology and notation in DEB theory. Square brackets [ ] and braces { } denote quantities per unit structural volume and per surface area, respectively, and rates (dimensions per time) have dots.

According to HFM (e.g., Rosland et al., 2009), food ingestion ($\dot{p}_X$, J d^{-1}) is given by

$$\dot{p}_X = \{\dot{p}_{Xm}\}V^{2/3}\left(\frac{X}{X+X_K}\right) \tag{1}$$

where $\{\dot{p}_{Xm}\}$ (J cm^{-2} d^{-1}) is maximum daily ingestion rate per gill surface area, V (cm ^{3}) is structural body volume, X is food concentration, as estimated by chlorophyll *a* concentration (Chl *a*; µg L^{-1}) and X_K (µg Chl *a* L^{-1}) is the half-saturation constant of the feeding response. The effect of temperature is not included in Eq. (1), but in the simulations below all rates are corrected for temperature dependence as in usual DEB theory (Kooijman, 2010). The last term of the right-hand side of Eq. (1) accounts for the regulation of the feeding response by (food) particle concentration. Eq. (1) assumes that for an individual bivalve, food ingestion is instantaneously regulated by food concentration only. This formulation overlooks the internal state of the individuals as a determinant of feeding behaviour.

I begin the derivation of ISFM by considering that water processing by bivalve gills is driven by ciliary activity (see e.g., Jørgensen, 1990). Increased CBF entails increased force production (Teff et al., 2008), consistent with model predictions (Gueron and Levit-Gurevich, 1999). This translates into increased clearance rate (Riisgård and Larsen, 2007). CBF is modulated by factors such as neurotransmitters (Jørgensen, 1990), and the combined effects of water viscosity and temperature (Podolsky, 1994; Riisgård and Larsen, 2007). Although the complete CBF regulation machinery may be complex (Salathe, 2007), it has been shown that CBF increases directly with energy (ATP) availability in various organisms (Lieb et al., 2002; Noguchi et al., 2001; Teff et al., 2008). I assume that a similar direct relationship exists in suspension-feeding bivalve gills and that ATP availability is proportional to energy reserves of tissue mass. Therefore in the following I assume that CBF depends of energy density, $[E]$ (J cm^{-3}) in DEB terminology. To model this relationship, I begin with Newton's heat transfer equation (von Bertalanffy)

$$\frac{\partial \dot{f}_*}{\partial [E]} = k_1\left(\dot{f}_{*m} - \dot{f}_*\right) \tag{2}$$

where $\dot{f}_*$ is observed CBF (d^{-1}), $\dot{f}_{*m}$ is maximum CBF (d^{-1}) and k_1 (cm^3 J^{-1}) is a constant.

Riisgård and Larsen (2007) analysed the relationships between kinematic viscosity and CBF, and between kinematic viscosity and clearance rate at constant temperature (22 °C). Based on their results, it is clearly acceptable to assume that clearance rate increases linearly with CBF (not shown). It follows that energy density directly impacts clearance rate. Therefore, assuming that neglecting curvilinearity between CBF and clearance rate is of little consequence across the normal temperature range experienced by mussels, clearance rate per unit gill surface ($\{\dot{C}_R\}$, L cm^{-2} d^{-1}) and maximum clearance rate per unit gill surface ($\{\dot{C}_{Rm}\}$, L cm^{-2} d^{-1}) can be substituted for $\dot{f}_*$ and $\dot{f}_{*m}$, respectively. One gets

$$\frac{\partial\left\{\dot{C}_R\right\}}{\partial [E]} = k_1\left(\left\{\dot{C}_{Rm}\right\} - \left\{\dot{C}_R\right\}\right). \tag{3}$$

Clearance rate has been shown to vary in response to a number of modulating agents such as neurotransmitters (see Jørgensen, 1990) and high seston loads, inorganic (e.g., Widdows et al., 1979; Barillé et al., 2006) and organic (Møhlenberg, 1999; Riisgård, 2001; Riisgård et al., 2011). Two cases may be recognised. First, the effect of such agents may be mediated through an interaction with clearance rate itself. This is the case of high concentrations of particles in the water. The intake rate of such particles is expected to increase with clearance rate and particle concentration. This is depicted by