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Somatic growth of mussels *Mytilus edulis* in field studies compared to predictions using BEG, DEB, and SFG models

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ABSTRACT

Prediction of somatic growth of blue mussels, *Mytilus edulis*, based on the data from 2 field-growth studies of mussels in suspended net-bags in Danish waters was made by 3 models: the bioenergetic growth (BEG), the dynamic energy budget (DEB), and the scope for growth (SFG). Here, the standard BEG model has been expanded to include the temperature dependence of filtration rate and respiration and an *ad hoc* modification to ensure a smooth transition to zero ingestion as chlorophyll *a* (chl *a*) concentration approaches zero, both guided by published data. The first 21-day field study was conducted at nearly constant environmental conditions with a mean chl *a* concentration of $C = 2.7\ \mu g\ L^{-1}$, and the observed monotonous growth in the dry weight of soft parts was best predicted by DEB while BEG and SFG models produced lower growth. The second 165-day field study was affected by large variations in chl *a* and temperature, and the observed growth varied accordingly, but nevertheless, DEB and SFG predicted monotonous growth in good agreement with the mean pattern while BEG mimicked the field data in response to observed changes in chl *a* concentration and temperature. The general features of the models were that DEB produced the best average predictions, SFG mostly underestimated growth, whereas only BEG was sensitive to variations in chl *a* concentration and temperature. DEB and SFG models rely on the calibration of the half-saturation coefficient to optimize the food ingestion function term to that of observed growth, and BEG is independent of observed actual growth as its predictions solely rely on the time history of the local chl *a* concentration and temperature.

1. Introduction

The development and testing of mathematical models against field data for the prediction of mussel growth have attracted much attention because of their potential use in ecosystem and aquaculture studies (Cardoso et al., 2006; Grant and Bacher, 1998; Kitazawa et al., 2008; Lauzon-Guay et al., 2006; Ren and Ross, 2005; Riisgård et al., 2012a; Rosland et al., 2009, 2011; van der Veer et al., 2006; van Haren and Kooijman, 1993; and others). Other aspects include the coupling to dynamic ecosystem and costal ocean models (e.g. Ferreira et al., 2009) and physiological interactions coupled to a biogeochemical food-web process (e.g. Dabrowski et al., 2013). Despite much testing of models the inter-comparison experiments at one site are still relevant to prove models' usefulness and explore weaknesses and strengths of the different approaches with the ultimate goal of improving modelling capabilities. Here we confine the attention to two established models: dynamic energy budget (DEB, Kooijman, 1986) and scope for growth (SFG, Winberg, 1960), and a recent model: bioenergetic growth (BEG, Riisgård et al., 2012a). We also limit the comparative study to one nutritional environment, Danish waters with low inorganic suspended matter loads. Despite the common goal of predicting the rate of growth in terms of time evolution of dry weight of soft parts, $W(t)$, and accounting for the ingestion and metabolism of the organism at given environmental conditions, there are many differences between the 3 models although all of them are forced by temperature and chlorophyll *a* (chl *a*) concentration, which is commonly used as proxy of phytoplankton availability (Alunno-Bruscia et al., 2011; Filgueira et al., 2011; Rosland et al., 2009). In brief, DEB is a mechanistic theory based on the assumption that assimilated energy is first stored in 'reserves' which in turn are utilized to fuel other metabolic processes (Kooijman, 1986, 2010). SFG is based on an empirical energy balance, assuming assimilated energy to be immediately available for catabolism, and it uses allometric relations to extrapolate to other sizes of organisms. BEG is based on empirical allometric relations for filtration and respiration rates used in the energy budget for estimating the growth of the blue mussel, *Mytilus edulis*, at specified chl *a* concentrations in Danish waters.

The purpose of this study was to further develop the BEG-model by modifications to account for temperature and low chl *a* concentrations and to compare actual somatic growth of *M. edulis* measured in the field of Danish waters to predictions based on the 3 models, BEG, DEB

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and SFG in order to evaluate differences between these models. Spawning and end-of-life were not included in the models given the characteristics of the studied datasets, which in part were motivated by performance prediction of mussel farming in Danish waters.

Following a summary of the growth models (with further details in the Supplementary Material) Materials and methods section presents two case studies: 'triangle study' is a relatively short 21-day field growth experiment with mussels from the Central Baltic Sea and Great Belt (Denmark) in a nearly constant environment excluding any significant environmental changes; 'winter study' is an extended study with mussels from the Great Belt covering the winter and spring periods from January to June with significant changes in phytoplankton biomass (measured as chl *a* concentration) and temperature. The 'triangle study' should test the models' ability to predict the correct level of growth while the 'winter study' should test the models' response to large variations particularly in phytoplankton availability and temperature. The section Results considers experiments and model predictions while further interpretations and a summary of differences between models appear in the Discussion and Conclusions sections.

2. Growth models

2.1. Bioenergetic growth (BEG)

For clarity, in this and in the following sections, the notation of each model is that used in previous publications, as summarized in Table A5 of Supplementary Material. The growth of filter-feeding mussels is primarily dependent on the amount of food ingested, which is closely related to the filtration rate, and the energy used in metabolism, frequently measured as the oxygen uptake rate or respiration rate. The filtration rate (F, L h^{-1}) of *M. edulis* can be estimated from the dry weight of soft parts (W, g) according to the following formula (Møhlenberg and Riisgård, 1979): $F = a_1 W^{b1}$, where $a_1 = 7.45$ and $b_1 = 0.66$, and further, the respiration rate (R, μL O$_2$ h^{-1}) can be estimated according to the formula (Hamburger et al., 1983): $R = a_2 W^{b2}$, where $a_2 = 475$ and $b_2 = 0.663$. Because $b_1 \approx b_2 = 0.66$ for mussels >10 mg tissue dry weight, it has been suggested by Riisgård et al. (2012a) that the weight-specific growth rate ($\mu = (1 / W)\mathrm{d}W/\mathrm{d}t$) may be expressed as

$$\mu_{est} = aW^b, (a = 0.871 \times C - 0.986; b = -0.34) \tag{1}$$

where μ (% d^{-1}), W (g) is the dry weight of soft parts and C (μg chl a L^{-1}) is the chlorophyll *a* (chl *a*) concentration, which determine units of constants in Eq. (1). This is the standard bioenergetic growth model (BEG), which depends only on the environmental parameter of chl *a* concentration in the range of constant filtration rate (between about 1 and 6 μg chl a L^{-1}), excluding spawning, and where the first constant in a is proportional to the assimilation efficiency, originally assumed to be $AE = 0.80$.

Given the experimental data, or the predicted time history of growth $W(t)$, the weight-specific growth rates of mussels (μ, % d^{-1}) were calculated from

$$\mu = \ln(W_2/W_1)/(t_2 - t_1) \tag{2}$$

(or equivalently from the slope of the trend line in a plot of ln$W$ versus time), where indices 1 and 2 refer to the start and end of a growth period, respectively. The average value of μ obtained this way is taken to be valid at the average dry weight of soft parts defined by

$$W_{\mathrm{avg}} = (W_1 \times W_2)^{1/2} \tag{3}$$

To predict weight of soft parts versus time, $W(t)$, amounts to integrate Eq. (1) multiplied by W,

$$\mathrm{d}W/\mathrm{d}t = 0.1047 \times (0.871 \times C \times \mathrm{AE}/0.80 - 0.986) \times W^{0.66} \tag{4}$$

where units are now t (day), W (mg), and C (μg chl a L^{-1}), the constant being $(1000/1000^{0.66}) \times 0.01 = 0.1047$, and the explicit dependence on assimilation efficiency, AE, has been included. The required initial condition, $W_0 = W(t = t_0)$, is typically chosen as the first data point from an experiment to be examined.

Further, to account for low values of chl *a* concentration and varying temperature, here we introduce additional factors leading to the modified BEG model

$$\begin{aligned}(\mathrm{d}W/\mathrm{d}t)_{\mathrm{mod}} = 0.1047 &\times m_1 \\ &\times (0.871 \times m_2 \times n_2 \times C \times AE/0.80 - 0.986 \times m_3 \times n_3) \\ &\times W^{0.66}\end{aligned} \tag{5}$$

where the first 'low-C' modification (expressed by coefficients m_{i}) pertains to low chl *a* concentration, and the second 'low-T' modification (expressed by coefficients n_{i}) pertains to low temperature. Either modification is suppressed for $m_{\mathrm{i}} = 1$ and $n_{\mathrm{i}} = 1$, respectively, and the standard BEG model Eq. (4) is recovered for $m_{\mathrm{i}} = n_{\mathrm{i}} = 1$.

The low-C modification is related to the fact that Eq. (4) has been validated for $C > 1.5$ μg chl a L^{-1} while observed chl *a* concentration in 'winter study' is below this value. Introducing the coefficients $m_1 = 1.12 / [1 + (a_0 - 1)n_3 (1 - E)]$; $m_2 = 1 - E$; $m_3 = 1–0.9(1 + C / C_0)E$, with $E = \exp(-C / C_0)$, the modification ensures a smooth transition for $C \rightarrow 0$ such that filtration rate approaches zero as observed by, e.g., Rosland et al. (2009, Fig. 4), and respiration rate approaches an estimated finite value of one tenth of the normal (coefficient 0.986 in Eqs. (1) and (4) approaches 0.0986, cf. Riisgård and Larsen 2014) to reflect suggested reduced respiration when the mussel reduces the opening degree of its valves, cf. Jørgensen et al. (1986). The constant $a_0 = 1 + 0.12$, accounting for the estimated 12% respiration cost associated with growth and entering as denominator in numerical coefficients from Eq. (1) (see Riisgård et al., 2012a), is assumed to decrease smoothly to unity as $C \rightarrow 0$ and to depend on temperature as the respiration term (see below). The decay constant $C_0 \approx 0.4$ μg chl a L^{-1} has been tuned from the present 'winter study' data.

The low-T modification is related to the fact that Eq. (4) has been established for a temperature range of about 15 °C to 20 °C while observed temperature in 'winter study' is as low as 2 °C. Introducing the coefficients $n_2 = [1 + 0.0251(T - T_{\mathrm{F}})]$ and $n_3 = 1.54^{(T - T\mathrm{Q})/10}$ takes into account the effect of temperature variations on filtration according to Kittner and Riisgård (2005, Fig. 3) and on respiration by a Q_{10} factor of 1.54 based on Bayne et al. (1976), where reference temperatures according to these studies are $T_{\mathrm{F}} = 11.5$ °C and $T_{\mathrm{Q}} = 14$ °C, respectively. Note that the 12% respiration cost associated with growth now also depends on temperature by the factor n_3 in coefficient m_1. The temperature coefficient in n_2 was determined as follows. Kittner and Riisgård (2005, Fig. 3) measured the filtration rate (F) of 3 groups of 44 mm *M. edulis* seasonally acclimated to 18 ºC at 10.3, 15.6, and 20.3 ºC over a period of 23 days. The individual filtration rate of mussels in each group remained near constant, and on day 20, the filtration rates were 5.49, 5.09, and 4.20 L h^{-1} at 20.3, 15.6, and 10.2 ºC, respectively. Thus, $(1/F)\ \mathrm{d}F/\mathrm{d}T = (1/5.09)(5.49 - 4.20)/10.1 = 0.0251$ °C^{-1}.

2.2. Dynamic energy budget (DEB)

The model used in this study is based on Rosland et al. (2009). A detailed description of the model, equations, and parameters is given in Filgueira et al. (2011), Pouvreau et al. (2006), and Rosland et al. (2009). However, the feeding module is described below, given the importance of ingestion for the calibration of the model to each specific dataset. The energy ingestion rate $\dot{p}_X$ (J d^{-1}) is assumed to be proportional to the surface area (cm^2) of the mussel:

$$\dot{p}_X = \{\dot{p}_{Xm}\} T_D V^{2/3} f \tag{6}$$