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Too much food may cause reduced growth of blue mussels (*Mytilus edulis*) – Test of hypothesis and new 'high Chl *a* BEG-model'

Poul S. Larsen[a,*], Florian Lüskow[b], Hans Ulrik Riisgård[b]

[a] DTU Mechanical Engineering, Fluid Mechanics, Technical University of Denmark, Building 403, DK-2800 Kgs. Lyngby, Denmark
[b] Marine Biological Research Centre, University of Southern Denmark, Hindsholmvej 11, DK-5300, Kerteminde, Denmark

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ABSTRACT

Growth of the blue mussel (*Mytilus edulis*) is closely related to the biomass of phytoplankton (expressed as concentration of chlorophyll *a*, Chl *a*), but the effect of too much food in eutrophicated areas has so far been overlooked. The hypothesis addressed in the present study suggests that high Chl *a* concentrations (> about 8 μg Chl $a\,l^{-1}$) result in reduced growth because mussels are not evolutionarily adapted to utilize such high phytoplankton concentrations and to physiologically regulate the amount of ingested food in such a way that the growth rate remains high and constant. We first make a comparison of literature values for actually measured weight-specific growth rates (μ, % d^{-1}) of small (20 to 25 mm) *M. edulis*, either grown in controlled laboratory experiments or in net bags in Danish waters, as a function of Chl *a*. A linear increase up to about $\mu = 8.3\%\,d^{-1}$ at 8.1 μg Chl $a\,l^{-1}$ fits the "standard BEG-model" after which a marked decrease takes place, and this supports the hypothesis. A "high Chl *a* BEG-model", applicable to newly settled post-metamorphic and small juvenile (non-spawning) mussels in eutrophicated Danish and other temperate waters, is developed and tested, and new data from a case study in which the growth of mussels in net bags was measured along a Chl *a* gradient are presented. Finally, we discuss the phenomenon of reduced growth of mussels in eutrophicated areas *versus* a possible impact of low salinity. It is concluded that it is difficult to separate the effect of salinity from the effect of Chl *a*, but the present study shows that too much food may cause reduced growth of mussels in eutrophicated marine areas regardless of high or moderate salinity above about 10 psu.

1. Introduction

Filter feeding in *Mytilus edulis* is a secondary adaptation where the gills have become greatly enlarged to become mainly feeding structures that pump and filter water at rates evolutionarily adapted to the prevailing (low) concentration of phytoplankton in the sea (Jørgensen, 1966, 1990; Famme and Kofoed, 1980; Jørgensen et al., 1986; Gosling, 2015). Thus, the gills in mussels are much larger than needed for respiration. But the large gills are expensive to maintain and about 20% of the total metabolic output is used for maintaining the feeding structures, irrespective of whether or not the water-pumping lateral cilia are actively beating (Riisgård and Larsen, 1995). According to the hypothesis of 'minimal scaling' the energy cost for maintaining the structures of a filter-pump can only be justified when this part of the organism is minimally dimensioned, and for that reason continuously filtering the ambient water (Jørgensen, 1975, 1990; Riisgård, 2001). Because *M. edulis* is adapted to low phytoplankton concentrations it tends to be continuously filter-feeding at inherent rates when the food concentration is above a certain lower trigger level of about 0.5 to 0.9 μg Chl $a\,l^{-1}$ (Pascoe et al., 2009; Riisgård et al., 2011). Therefore, both the 'standard' BioEnergetic Growth model (BEG) (Riisgård et al., 2012) and the "modified BEG-model" (Larsen et al., 2014; Larsen and Riisgård, 2016) are based on the presumption that *M. edulis* is continuously exploiting its filtration rate capacity when the Chl *a* concentration is above the lower trigger level. Only in eutrophicated waters may phytoplankton levels reach concentrations above which *M. edulis* reduces its filtration rate by valve closing ('saturation reduction'). Thus, under optimal conditions, *M. edulis* tends to filter the ambient water at a maximum rate, but under sub-optimal conditions, including very low or very high phytoplankton concentrations, the filtration rate becomes reduced (Riisgård, 2001; Riisgård et al., 2011).

Mussels save energy during starvation periods by partly closing their valves and thereby reducing the water transport through the mantle cavity so that the oxygen uptake and thus the metabolism is reduced, resulting in reduced body-weight loss (Famme, 1980; Jørgensen et al., 1986; Riisgård and Larsen, 2015; Tang and Riisgård, 2016). The weight-specific growth rate of *Mytilus edulis* was found by Riisgård et al. (2013) to strongly decrease above the saturation level

* Corresponding author.
E-mail address: psl@mek.dtu.dk (P.S. Larsen).

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(C_{sat} = about 7.5 to 8.8 μg Chl $a\,l^{-1}$) clearly indicating that the growth potential was not being exploited. The reason is likely to be due to partial valve-closure and reduced oxygen uptake, because optimal growth seems to depend on unrestrained oxygen uptake, although production of pseudofaeces from the overloaded gills and excretion of undigested algae may also restrict the ability of *M. edulis* to grow (Riisgård et al., 2013). Thus, the phenomenon of reduced growth seems to be that *M. edulis* is not evolutionarily adapted to utilize (very) high phytoplankton concentrations and to physiologically regulate the amount of ingested food in such a way that the growth rate remains high and constant. Numerous growth rate measurements have over the years been made on *M. edulis*, and many environmental factors have been suggested to affect the actual growth, but the effect of too much food seems so far to have been overlooked as emphasised by Riisgård et al. (2013).

In laboratory experiments Riisgård et al. (2013) measured the filtration and growth rates of 22 to 35 mm shell length *M. edulis* at different algal concentrations maintained either below or above the limit of incipient saturation concentration (C_{sat} ≈ 6500 *Rhodomonas salina* cells ml^{-1}, equivalent to about 8.1 μg Chl $a\,l^{-1}$, Clausen and Riisgård, 1996), which is in agreement with Riisgård et al. (2011, Fig. 5 therein). From a constant and high filtration rate (F) measured below C_{sat} the filtration rate decreased above C_{sat} to about 10% of the former maximum value. Further, the measured weight-specific growth rates (μ) decreased sharply above C_{sat} from a maximal value of about 9.5% d^{-1} to about 1.5% d^{-1} (Riisgård et al., 2013, Fig. 4 therein), but below C_{sat} the μ-values increased linearly with increasing algal concentration (C) in good agreement with the "standard BEG-model" presented by Riisgård et al. (2012, Eq. 18 therein). The functional response of *M. edulis* described by Riisgård et al. (2013, Fig. 3 therein) resembled a Type I in terms of gross ingestion ($I = F \times C$), but with rapid decrease instead of a constant maintained level above C_{sat} in terms of net (or actual) ingestion (= gross ingestion − pseudofaeces). The physiological implications of this response are not obvious because it is only seen above C_{sat} and then as reduced filtration rate along with production of pseudofaeces (Riisgård et al., 2011). As pointed out by Riisgård et al. (2013, Table 5 therein) the naturally occurring phytoplankton biomass (expressed as Chl a) in coastal and open waters (excluding heavily eutrophic areas) is generally below C_{sat} and therefore mussels tend to feed at optimal rates provided the Chl a concentration is above the lower trigger level where the mussels close their valves and reduce or cease filtering. In heavily eutrophicated marine areas the Chl a concentrations may exceed C_{sat} and the consequence of this for the growth of mussels seems so far to have been overlooked.

The hypothesis addressed in the present study suggests that high Chl a concentrations (> about 8 μg Chl $a\,l^{-1}$) result in reduced growth because mussels are not evolutionarily adapted to utilize such high phytoplankton concentrations. The value of about 8 μg l^{-1} is the mean between 6 and 10 μg l^{-1}, equivalent to the range 5000–8000 *Rhodomonas* cells ml^{-1} found in the controlled feeding experiments by Riisgård et al. (2011, Fig. 5 therein).

Here, we first (Section 2) compare with published values for actually measured weight-specific growth rates of blue mussels in field and laboratory exposed to various Chl a concentrations, including very high values as recently presented by e.g. Maar et al. (2015) and Landes et al. (2015) who correlated reduced growth with low salinity. Next (Section 3), we present a "high Chl a BEG-model" for mussel growth at extremely high Chl a concentrations. Then (Section 4), we present a case study in which the growth of mussels has been measured along a Chl a gradient and finally (Section 5), we discuss the phenomenon of reduced growth of mussels in eutrophicated areas *versus* a possible impact of low salinity.

2. Literature values of actual growth *versus* Chl *a* concentration

Fig. 1 shows the weight-specific growth rate of juvenile (20 to 25 mm shell length) *Mytilus edulis* as a function of Chl a measured in a number of studies conducted in temperate (8 to 20 °C, 8.5 to 29.9 psu) Danish waters or in controlled laboratory experiments (10 to 15 °C). It can be seen that the linear increase up to about μ_{max} = 8.3% d^{-1} at C_{sat} = 8.1 μg Chl $a\,l^{-1}$ fits the "standard BEG-model" after which a marked decrease takes place. However, in two cases where the mussels were fed algal cells in the laboratory they were also offered suspended inorganic particles (i.e. silt) and this resulted in even higher growth rates of 9.7 and 9.1% d^{-1} at 15.1 and 17.0 μg Chl $a\,l^{-1}$, respectively (Clausen and Riisgård, 1996, Table 4 therein). In general, the pattern supports the hypothesis that very high Chl a concentrations (> about 8 μg Chl $a\,l^{-1}$) result in reduced growth and a "high Chl a BEG-model" for this phenomenon is presented in the next section. However, variations in salinity have also been suggested to be an important factor for reduced growth (e.g. Maar et al., 2015). This aspect is further treated in Section 5.

3. 'High Chl *a* BEG-model'

3.1. Model development

The 'modified BEG-model' (Larsen et al., 2014, Eq. 5 therein) is given by

$$(dW/dt)_{mod}(\text{mg d}^{-1}) = c_1 W(\text{mg})^{0.66},\ C < C_{sat}, \quad (1)$$

where

$$c_1 = 0.1047 \times m_1 \times (0.871 \times m_2 \times n_2 \times C \times AE/0.80–0.986 \times m_3 \times n_3). \quad (2)$$

Coefficients m_1, m_2, m_3, n_2, and n_3, listed in Table 1, account for reduced filtration rate at low values of C (< 1 μg Chl $a\,l^{-1}$) and the temperature dependence of filtration rate and respiration above about 8 °C. When these coefficients are equal to 1.0 Eqs. (1) and (2) reduce to the "standard BEG-model", or in terms of μ(% d^{-1}) = $W^{-1}dW/dt$, to (Riisgård et al., 2012, Eq. 18 therein).

$$\mu_{Std} = (0.871 \times C \times AE/0.80 - 0.986)W^{-0.34}, \quad (3)$$

which for a given W(g) suggest the linear increase of μ with increasing $C < C_{sat}$ as shown by data in Fig. 1. However, above C_{sat} (= 8.1 μg Chl $a\,l^{-1}$ ≈ 6500 *Rhodomonas salina* cells ml^{-1}) the data suggest an exponential (or hyperbolic) decrease of μ with increasing C to a low level of about $\mu_\infty \approx 1.5\%\,d^{-1}$. More detailed data (Riisgård et al., 2013, Fig. 3 therein) show a similar decrease of the filtration rate F with increasing C while the gross ingestion rate $I = F \times C$ remains nearly constant which confirms consistently the trends. Since the two terms in the bracket of Eq. (3) represent assimilated food (A) and respiration, respectively, it is concluded the assimilation efficiency $AE = A/I$ must decrease with increasing C above C_{sat} which in turn appears to be consistent with the observed increasing production of pseudofaeces. This suggests a "high Chl a BEG-model" for C > C_{sat} of the form

$$\mu_{Hi\text{-}Chl} = (0.871 \times m_4–0.986)W^{-0.34}, \quad (4)$$

or in terms of form and units of Eq. (1),

$$(dW/dt)_{Hi\text{-}Chl}(\text{mg d}^{-1}) = 0.1047 \times (0.871 \times m_4 - 0.986)W(\text{mg})^{0.66},\ C > C_{sat}, \quad (5)$$

where

$$m_4(=C \times AE/0.80) = C_{sat}E + C_\infty(1–E);\quad E = \exp[-(C - C_{sat})/C_{ref}]. \quad (6)$$

Here, constants are determined to approximately match data at saturation of Fig. 1 to Eq. (3) such that C_{sat} = 8.1 μg Chl $a\,l^{-1}$ for mussels of shell length L = 25 mm corresponding to W (g) = 2.15 × 10^{-6} $L(\text{mm})^{3.40}$ = 0.122 g (according to Larsen et al., 2013, Fig. 8 therein), which gives $\mu_{sat} \approx 12\%\,d^{-1}$. Constants for