Dynamic Energy Budget (DEB) model Blue mussels *(Mytilus edulis)*

Technical report INNOPRO project

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Research report C009/19

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Contents

Summary

A Dynamic Energy Budget (DEB) model is a generic model that describes the energy flow in organisms focusing on food assimilation and utilization for maintenance, growth and reproduction. The parametrization of this model is species-specific and presently a large dataset exists DEB parameters for many species including the DEB parameters for the blue mussel (*Mytilus edulis*). However, the application of the present DEB parameters for *Mytilus edulis* resulted in an underestimation of the growth of this species. Therefore, we have decided to re-estimate the DEB parameters for *Mytilus edulis* using new and relevant data.

In this technical report, a new estimation for the DEB parameters of *Mytilus edulis* is presented. The parameter estimation has been done with the Add_My_Pet module of Kooijman. The parameter estimation resulted in a more realistic description of the growth and development of *Mytilus edulis.*

The newly estimated parameters are summarised in the following table:

Symbol	*Description*	*Units*	*Value*
z	Zoom factor relative to reference L_m=1cm	-	1.056
$\{\dot{F}_m\}$	Maximum specific searching rate*	l d^{-1} cm^{-2}	105.6
$\{\dot{p}_{Am}\}$	Surface specific maximum assimilation rate	J m^{-2} d^{-1}	314.9
κ_X	Fraction of food energy fixed in reserve*	-	0.8
κ_P	Fraction of food energy fixed to faeces*	-	0.15
$\dot{v}$	Energy conductance	cm d^{-1}	0.0197
κ	Allocation fraction to growth and somatic maintenance	-	0.6496
κ_R	Fraction of reproduction energy fixed in reserve*	-	0.95
$[\dot{p}_M]$	Volume specific somatic maintenance	J d^{-1} cm^{-3}	81.98
$\{\dot{p}_T\}$	Surface specific somatic maintenance*	J d^{-1} cm^{-2}	0
k_J	Maturity maintenance rate	d^{-1}	1.581e-02
$[E_G]$	Volume specific cost for structure	J cm^{-3}	2333
E_H^b	Maturation threshold for feeding (birth)	J	1.55e-06
E_H^j	Maturation threshold for metamorphosis	J	1.55e-06
E_H^p	Maturation threshold for reproduction (puberty)	J	39.67
h_a	Weibull aging acceleration	d^{-1}	4.191e-09
s_G	Gompertz stress coefficient*	-	0.0001
K_Y	Half saturation coefficient for inorganic matter	mg l^{-1}	0.2375
X_K	Half saturation coefficient for food*	µg Chla l^{-1}	2
T_{ref}	Reference temperature*	K	293.15
T_A	Arrhenius temperature*	K	7022
T_{AH}	Arrhenius temp. for rate of decrease at upper boundary*	K	31376
T_{AL}	Arrhenius temp. for rate of decrease at lower boundary*	K	45430
T_H	Lower boundary of tolerance range*	K	296
T_L	Upper boundary of tolerance Range*	K	275
δ_M	Shape coefficient	-	0.231

*Parameter not estimated in the present study

The results of the DEB model with the newly estimated parameters are compared with the results of the previously estimated parameters.

In a next step, the DEB model for *Mytilus edulis* will be included in the ecosystem model of the Oosterschelde to describe the growth and development of mussels at commercial culture plots. This model will be developed within the INNOPRO project.

1 Introduction

1.1 Background

The bottom culture of mussels in the Netherlands takes place at leased sublittoral culture plots in the Wadden Sea and in the Oosterschelde. The culture cycle starts with seed mussels fished from natural beds in the Wadden Sea or collected with Seed Mussel Collectors (SMCs). The seed mussels are seeded on the culture plots, and when the mussels are consumption size (ca 6 cm) they are harvested and sold at the auction in Yerseke. On average the culture cycle is about 2 years. During this period the mussels are susceptible to storms, predation, suffocation and food-shortage. On average 1 kg of seed mussels yield a production of 1.6 kg consumption mussels. The survival of mussels during the culture cycle is only 10%. Since the costs of the seed mussels become higher and higher, the mussel farmers need to increase the production efficiency.

The project "INNOvatie en Rendementsverbetering mossel PROductie (INNOPRO)" focusses on the improvement of the production efficiency of the bottom culture of mussels by (i) realising the same production with less seed mussel resources (ii) increasing the production efficiency (volume and quality) using culture measures, and (iii) developing a simulation model that can be used by mussel farmers to gain insight in the important processes so they can increase the production efficiency.

Growth and development at the culture plots is depending on food conditions (phytoplankton, detritus, suspended solids) and water temperature. Mussels are poikilothermic animals and physiological processes (e.g. food uptake, respiration) are influenced by temperature (Dennis et al., 1999). Within the range between the upper and the lower tolerated temperature, the rates of the physiological processes increase with water temperature (Freitas et al., 2010). Food uptake in terms of Energy (J) is depending on the maximum uptake capacity and the availability and quality of the food in the water. The maximum uptake capacity of the mussel is depending on the size of the gills and the surface area of the gastrointestinal tract. The availability and quality of the food is depending on environmental conditions such as:

- Concentration of phytoplankton in the water: The higher the concentration, the more food there is potentially available.
- Type of algae: The energetic value for mussels varies with algal species but also seasonally.
- Size of the algae: The filtering efficiency of the gills is less for small algae (< 3-5 µm) such as picoplankton.
- The amount of inorganic material in the water. At higher concentration of inorganic suspended solids, the food intake is less because more pseudofaeces is produced.
- Current velocity: Current velocity transports algae to the mussels. At high mussel densities such as at culture plots, high current velocities can prevent local food depletion.

From culture practice it is known that there is a large spatial variation in growth and quality of the mussels at the culture plots that can partly be related to environmental conditions. Within the INNOPRO project a model tool will be developed that can be used by mussel farmers to simulate and eventually predict the production efficiency at their culture plot. The core of this model tool is a dynamic water quality model. This water quality model will describe the nutrient cycling (N) within different state variables, including inorganic nutrients, phytoplankton, zooplankton, mussels and detritus. This model will be developed and parameterised for the Oosterschelde.

The culture mussels within this model will be described by the DEB (Dynamic Energy Budget) theory (Kooijman, 2010). DEB is a generic model that describes the growth and development of organisms through their life cycle as a function of the environmental conditions food (calculated by the water quality model) and temperature. The species specific DEB parameters are presently available for more than 1000 species, including the blue mussel (*Mytilus edulis*) (e.g. Saraiva et al., 2011).

1.2 Problem definition

The application of the DEB parameters for blue mussels as estimated by Saraiva et al. (2011) result in an underestimation of growth of mussels within the Wadden Sea and the Oosterschelde in comparison to field observations of mussels at commercial mussel plots. This is partly due to bias in the data that are used to estimate the parameters. Also the model fit by Saraiva et al. (2011) was not satisfactory for all data.

1.3 Goal

Within the INNOPRO project it is decided to re-estimate the DEB parameters for *Mytilus edulis*. In this technical report the results of this new parameter estimation is presented and the procedure for the parameter estimation is documented. The new DEB parameters will be used as input for the DEB model as part of the water quality model for the Oosterschelde.

1.4 Approach

The parameter estimation is done using the Add_My_Pet software (Kooijman, 2009; Lika et al., 2011b; Marques et al., 2018) within Matlab. Starting point were the scripts that have been developed by Saraiva in 2010 for the parameter estimation of *Mytilus edulis*. Biased data are replaced by more recent and relevant data. The results of the new DEB parameters are compared with the DEB parameters estimated by Saraiva using the DEB model in relation to the data.

1.5 Acknowledgements

This project has received funding from the European Union, through the European Maritime and Fisheries Fund (EMFF) and from the Producers' Organization of the Dutch mussel culture (POM).

2 Estimating DEB parameters for *Mytilus edulis*

2.1 DEB theory

A Dynamic Energy Budget (DEB) model (Kooijman, 1986; Kooijman, 2000; Kooijman, 2010) describes the individual growth, energy dynamics and reproduction as a function of environmental conditions such as temperature and food. The DEB theory is a generic theory that can be applied to different species and life stages by using species specific parameters (Kooijman, 2001). A more detailed overview of the theory behind the DEB model is given in Annex 1. One of the main advantages of a DEB model is that it is based on a generic theory, meaning that the same model structure can be applied to different species, where only parameter values differ (Saraiva et al., 2012). The parameters used in a DEB model are often abstract and not easy to measure directly. In Annex 2 an overview and explanation of the DEB parameters is given. At present the DEB parameters of more than 1000 species are available from the Add_My_Pet website (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/index.html).

2.2 Method

The simplicity and generality of DEB theory comes at a cost, however, in that its formulation involves a high level of abstraction. For example, total body mass is abstracted into the concepts of "reserve" and "structure", which are primary state variables but cannot be directly observed or measured. In order to estimate the primary DEB parameters (Table 4 and Table 5 in Annex 2) for a specific species, field observations need to be translated to state variables that are modelled by DEB by using formulations from the DEB theory.

The Add_My_Pet routine (Kooijman, 2009; Marques et al., 2018) allows to estimate the species specific DEB parameters simultaneously using the co-variation method (Lika et al., 2011a). The co-variation method is an iterative optimisation routine based on the Nelder-Meads simplex algorithms. The method is computing-intensive, but relatively stable. Optimization is based on the minimization of the weighted squared residuals between model and observations. The mean relative error (MRE) was estimated by:

$$MRE = \sqrt{\frac{\sum_{i=1}^{n} \sum_{j=1}^{m_i} \beta_{ij} (\frac{Y_{ij} - \hat{Y}_{ij}}{Y_{ij}})^2}{\sum_{i=1}^{n} \sum_{\mathrm{j=1}}^{\mathrm{m_i}} \beta_{ij}}}$$

Where n is the number of datasets. Each zero-variate data value is one data set. m_i is the number of data in dataset i. Y_{ij} and $\hat{Y}_{ij}$ are the observations and model predictions of the j^{th} data point in dataset i. β_{ij} is the weight coefficient of the j^{th} data point in dataset i.

The goodness of fit (GOF) of the model is calculated from the MRE by

$$GOF = 10 \cdot (1 - MRE)$$

The DEB parameters for the blue mussel (*Mytilus edulis*) have been estimated by Sofia Saraiva in 2010. However, some of the data that are used in this estimation are biased and dated. Moreover, the model fit is not satisfactory for all data. For example in Figure 1, it can be seen that both the wet weight and the oxygen consumption as a function of shell length is underestimated by the DEB model using the parameters estimated by Saraiva. The length at age measurements that are used by Saraiva

come from Rodhouse et al. (1984)(Figure 2). The DEB model gives an acceptable fit through the data, however, the data are based on very slow growing mussels from Killary Harbor (Ireland). It takes 5 to 8 year for the mussels to reach a shell length of 4 cm. Data from culture plots in the Oosterschelde and the Wadden Sea show that the size of 4 cm can already be reached after one year at good conditions. For the present study, a new estimation of the DEB parameters is made using newer and more relevant data.

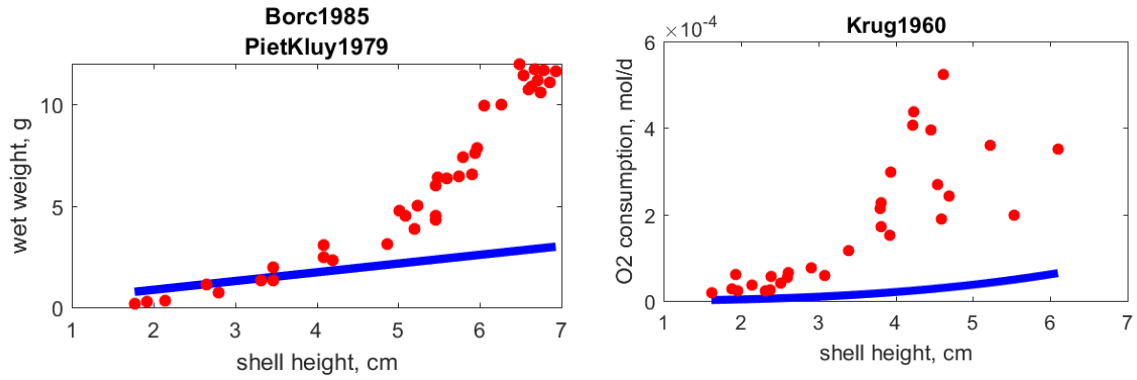

Figure 1: Relation between shell length (cm) and wet weight (g) (left panel) and shell length (cm) and oxygen consumption (mole d^{-1}) (right panel). Blue line is the model estimation by the DEB model using the DEB parameters estimated by Saraiva. Red dots are the measurements. Data are from Borchardt (1985), Pieters et al. (1979)

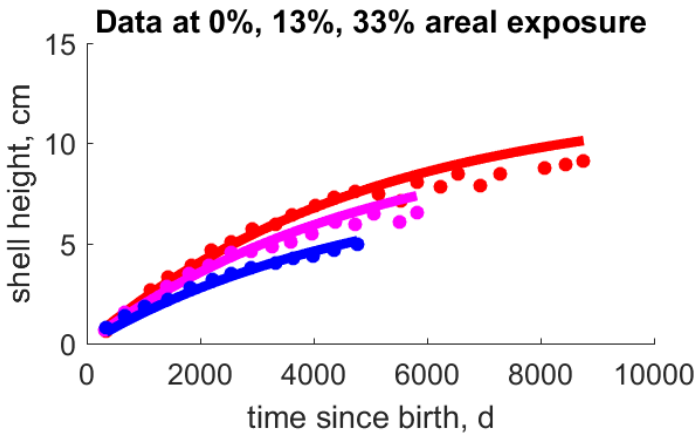

Figure 2: Length (cm) at age (d) data for mussels used for the parameter estimation by Saraiva. Data are derived from Rodhouse et al. (1984).

In the present study, the add-my-pet procedure is run under Matlab version R2016b (9.1.0.441655). The add-my-pet makes use of four different files (Marques et al., 2018):

- **run_Mytilus_edulis.m**: contains the settings for the optimization procedure
- **mydata_Mytilus_edulis.m**: contains the data to fit the model (zero-variate and univariate data), including the references. This file also contains the weight coefficients for all data values.
- **pars_mytilus_edulis.m**: contains the initial values for the parameter at the start of the optimization procedure. Parameters can be included and excluded in the calibration procedure.
- **predict_Mytilus_edulis.m**: contains code to relate the observed data to the model results. The formulations are based on the DEB theory.

2.3 Data used in parameter estimation

To estimate the DEB parameters, observed data and measurements are needed. In the Add_My_Pet procedure, two types of data are used: (1) zero-variate data and (2) uni-variate data. The user has the possibility to give weight factors to all zero- and uni-variate data based on the quality and the uncertainty of the data. In the optimization procedure, more emphasis is paid to a good fit of the data with the higher weight factors. The data can also be supplemented with pseudo-data. Pseudo-data are typical values for a generic animal (Kooijman, 2010) and the weight coefficients for pseudo-data are set an order of magnitude smaller than that for zero- and uni-variate data to make sure that if zero- and uni-variate data determine parameters well, pseudo-data hardly contribute.

2.3.1 Zero-variate data

Zero-variate data are 0-dimensional data such as maximum length, age at puberty, etc. In Table 1, an overview is given on the zero-variate data that are used in this study to estimate the DEB parameters for *Mytilus edulis*.

The trochophore larvae develops between 5 and 24 hours after fertilization (Newell, 1989). This larvae can migrate in the water column using the cillia at their velum. From the moment that the larvae have developed the shell valves, they are called D-larvae. The D-larvae of a mussel is about 120 µm and has a weight of about 236 ng (Sprung, 1984). After about one year, or at a size of about 1.2 cm the mussels are able to reproduce (Van Der Veer et al., 2006). Based on growth rings in the shells, Theisen (1973) showed that mussels can reach an age of 24 year. The maximum size is estimated at 15 cm (Van Der Veer et al., 2006). The flesh wet weight at puberty and ultimate length ($W_{w,p}$ and $W_{w,m}$, respectively) are derived from the shell lengths using the relation from Van Haren and Kooijman (1993).

$$W_w = 0.03692 \cdot (L_w)^3$$

The gonado-somatic index (GSI) is defined as the ration between the weight (g AFDW) of the gonads and the total weight of the mussel (g AFDW). For blue mussels the GSI is estimated at 0.2 (Cardoso et al., 2007). Reproduction is derived from Honkoop and Van Der Meer (1998), who estimate that one mussel can produce 1 – 2 million eggs per spawning. The eggs have a diameter of about 72 µm (Honkoop and Van Der Meer, 1998).

Table 1: Zero-variate data for *Mytilus edulis* used in the parameter estimation.

Symbol	Unit	Value	Description	Reference
a_b	d	0.2	Age at birth	(Newell, 1989)
a_p	d	365	Age at puberty	(Newell, 1989)
$a_\dagger$	d	8760	Age at death (life span)	(Theisen, 1973)
$L_{w,b}$	cm	0.012	physical length at birth	(Sprung, 1984)
$L_{w,p}$	cm	1.2	physical length at puberty	(Van Der Veer et al., 2006)
$L_{w,m}$	cm	15	Ultimate physical length	(Van Der Veer et al., 2006)
$W_{w,b}$	g	2.36e-7	Wet weight at birth	(Sprung, 1984)
$W_{w,m}$	g	124.6	Ultimate wet weight: $W_{w,m} = 0.03692 \cdot (L_{w,m})^3$	(Van Haren and Kooijman, 1993)
$\dot{R}_m$	# d^{-1}	8.219e4	Maximum reproduction rate	(Honkoop and Van Der Meer, 1998)
GSI	-	0.67	Gonado Somatic index	(Cardoso et al., 2007)

2.3.2 Uni-variate data

For uni-variate data there is a relationship between two variables. The data can be derived from field observations and from lab experiments. In the parameter estimation different types of uni-variate data are used:

- Length-weight data
- Length at age data
- Oxygen consumption
- Ingestion rate, faeces and pseudo-faeces production

2.3.2.1 Length-weight data

In general an allometric relation exists between the shell length and the weight of a mussel. Rosland et al. (2009) have measured the shell length and dry flesh weight for a number (99) of mussels at low food conditions (Figure 3).

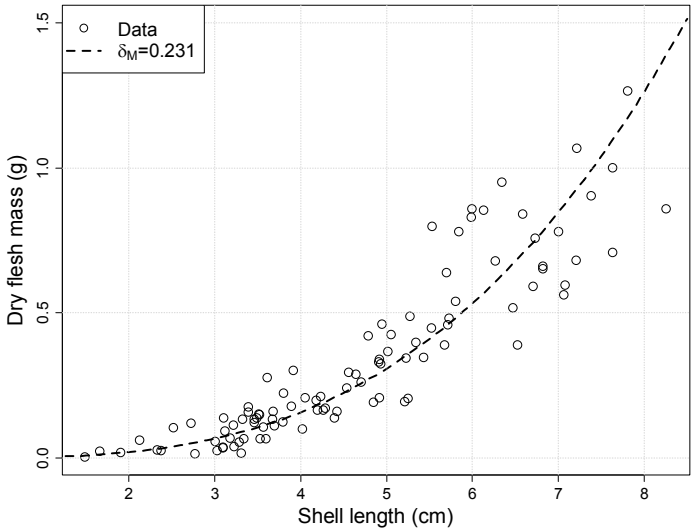

Figure 3: Length (cm) weight (dry flesh, g) data for mussels collected from Flødevigen (Norway) at low food conditions (Rosland et al., 2009). The broken line indicates the results of the linear regression resulting in a shape factor of 0.231.

In DEB formulation

In general, the relation between dry between dry weight (W_d) and physical length (L_w) can be described by:

$$W_d = (\delta_M \cdot L_w)^3 \cdot d_V \cdot (1 + f * w)$$

Where δ_M is the shape factor, d_V the specific density of structural volume, f is the functional response and w represents the contribution of reserves to the total biomass. Length-weight data at low food conditions ($f \approx 0$), are often used to estimate the shape factor. Since the mussels in Flødevigen are grown at low food conditions, a value of 0.2 is used for the functional response (f). The parameter w represents the contribution of reserves to the total biomass and is calculated by:

$$w = \frac{[E_M] \cdot w_E \cdot d_V}{w_V \cdot d_E}$$

In this relation $[E_M]$ is the maximum energy density (J cm^{-3}), w_V and w_E are the molecular weights of structural biomass and reserves (both 23.9 g mole^{-1}). The parameters d_V and d_E are specific density of structural volume and reserves, respectively (both 0.09 g DW cm^{-3}).

2.3.2.2 Length at age data

De Mesel et al. (2009) measured length at age data for mussels at commercial culture plots in the Wadden Sea for the years 2007 and 2008 (Figure 4). The age of the mussels is estimated based on information on the year that the mussels are fished from the natural seed beds and assuming that the mussels were born on Julian day 100 (10th April) in that year. A Von Bertalanffy growth curve is fitted through the data. The data show a clear seasonal pattern, caused by fluctuations in temperature and food availability (De Mesel et al., 2009). Another dataset for mussels at culture plots in the Wadden Sea is presented by (Capelle, 2017) (Figure 5). The main difference with the data from De Mesel et al. (2009) is that the latter has relative many data of mussels with an age of more than 2 years. Those older mussels are the slower growing individuals sampled at culture plots where food conditions are sub-optimal. The fastest growing mussels have already been harvested after two years. This can also be seen in the Von Bertalanffy growth curves and the predicted ultimate physical length by these curves. The VBGF curve through the data of De Mesel et al. (2009) predict an ultimate physical length of 7.2 cm, while the predicted ultimate physical length based on the data of Capelle (2017) is 14.6 cm.

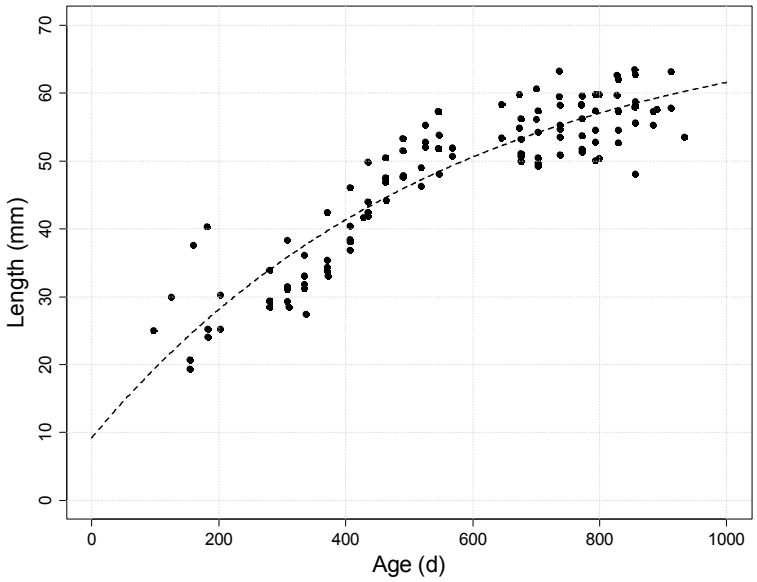

Figure 4: Length (mm) as a function of age (d) for mussels at commercial culture plots in the Wadden Sea (De Mesel et al., 2009). The broken line represents the Von Bertalanffy growth function fitted through the data.

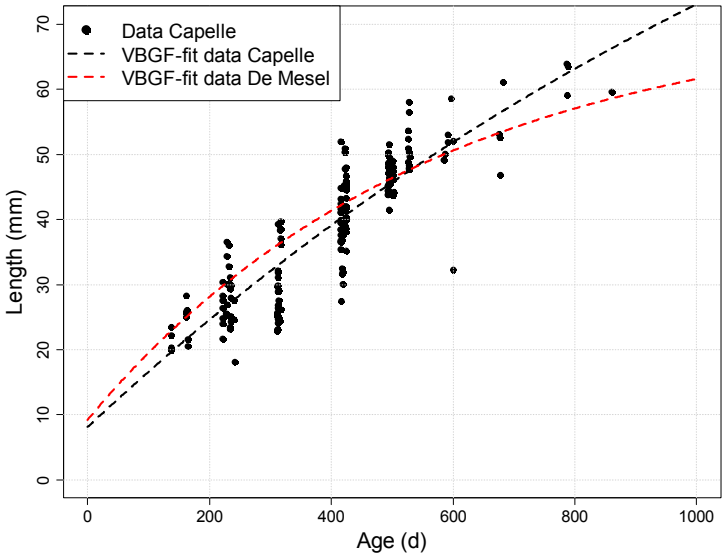

Figure 5: Length (mm) as a function of age (d) for mussels at commercial culture plots in the Wadden Sea (Capelle, 2017). The black broken line represents the Von Bertalanffy growth function fitted through the data. The red broken line represents the Von Bertalanffy growth function fitted through the data of De Mesel et al. (2009) (Figure 4).

In DEB formulation

The length of a mussel as function of age can be described by the Von Bertalanffy growth curve:

$$L(t) = L_\infty - (L_\infty - L_b) \cdot e^{(-\dot{r}_B \cdot t)}$$

Where $L(t)$ is the structural length (cm) at an age of t days. L_∞ is the maximum structural length (cm), L_b is the structural length at birth and $\dot{r}_B$ is the Von Bertalanffy growth rate (d^{-1}). According to the DEB theory, this parameter can be calculated by:

$$\dot{r}_B = \dot{k}_M \frac{g}{3 \cdot (f+g)}$$

Where $\dot{k}_M$ is the somatic maintenance rate coefficient (d^{-1}) that can be calculated from the ratio between somatic maintenance rate $[\dot{p}_M]$ (J cm^{-3} d^{-1}) and the volume-specific costs of structure $[E_G]$ (J cm^{-3}).

$$\dot{k}_M = \frac{[\dot{p}_M]}{[E_G]}$$

The parameter g is the energy investment ratio, that can be calculated by $[E_G]$, κ and the maximum energy density $[E_m]$:

$$g = \frac{[E_G]}{\kappa \cdot [E_m]}$$

The physical length at age ($L_w(t)$) can be calculated from the structural length at age ($L(t)$) using the shape coefficient (δ_M):

$$L_w(t) = \frac{L(t)}{\delta_M}$$

2.3.2.3 Oxygen consumption

Jansen et al. (2009) measured the oxygen consumption of mussels at different temperatures (10, 17, 24 and 27 °C) (Figure 6). Since the optimum temperature for mussels is below 23°C (Van Der Veer et

al., 2006), the data at 24 and 27°C are not used in the present study. The size of the mussels in the experiments was between 2.5 and 4.0 cm (average 3.74 cm). The average dry weight of the mussels was 0.25 g. The oxygen consumption rate in mg g^{-1} d^{-1} is converted to mole O_2 d^{-1} by:

$$j_O[mol\ O_2 d^{-1}] = j_O[mg\ O_2 gdw^{-1} h^{-1}] \cdot \frac{24 \cdot 0.25}{31.998 \cdot 1000}$$

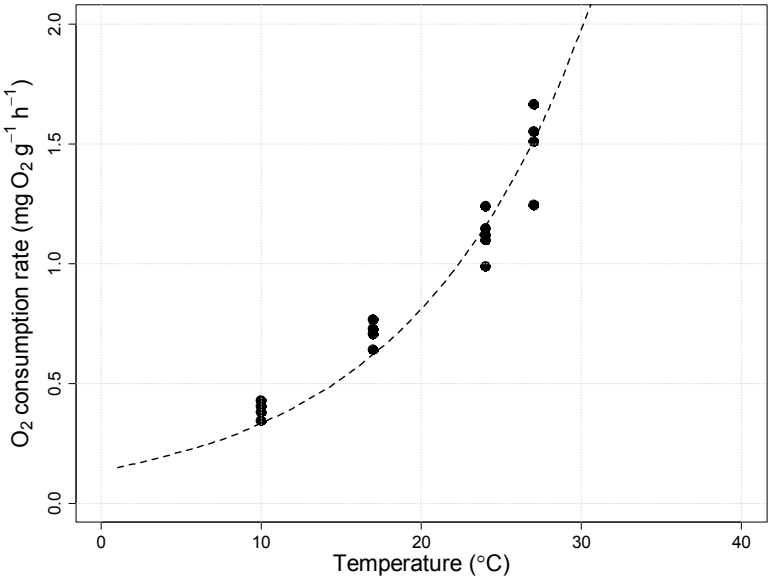

Figure 6: Oxygen consumption rate (mg O_2 g^{-1} h^{-1}) as a function of temperature. The dotted line represents the relation $0.0258*e^{0.089*T}$. Data from Jansen et al. (2009).

Van Haren and Kooijman (1993) use data from (Kruger, 1960) on oxygen consumption of mussels as a function of shell length (Figure 7). This figure shows that the oxygen consumption increases with the size of the mussels. Oxygen consumption in cm^{-3} h^{-1} is converted to mole O_2 d^{-1} by:

$$j_O[mol\ O_2 d^{-1}] = j_O[cm^3\ O_2\ h^{-1}] \cdot \frac{24}{22400}$$

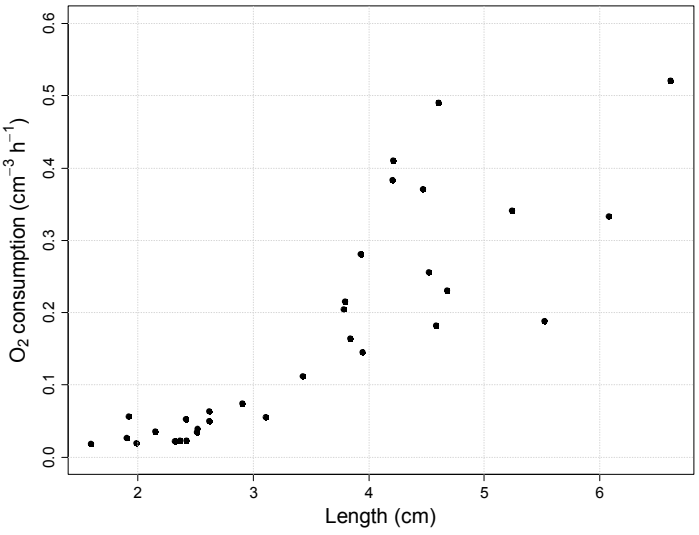

Figure 7: Oxygen consumption of mussels (cm^{-3} h^{-1}) as a function of shell length. Data from Kruger (1960) in Van Haren and Kooijman (1993).

A third dataset is from Van Haren and Kooijman (1993) using the data from (Bayne et al., 1987; Bayne et al., 1989). The oxygen consumption rate increases with ingestion rate. The ingestion rate in mg POM h^{-1} is converted to C-mole d^{-1} by multiplication with 24/(12*1000).

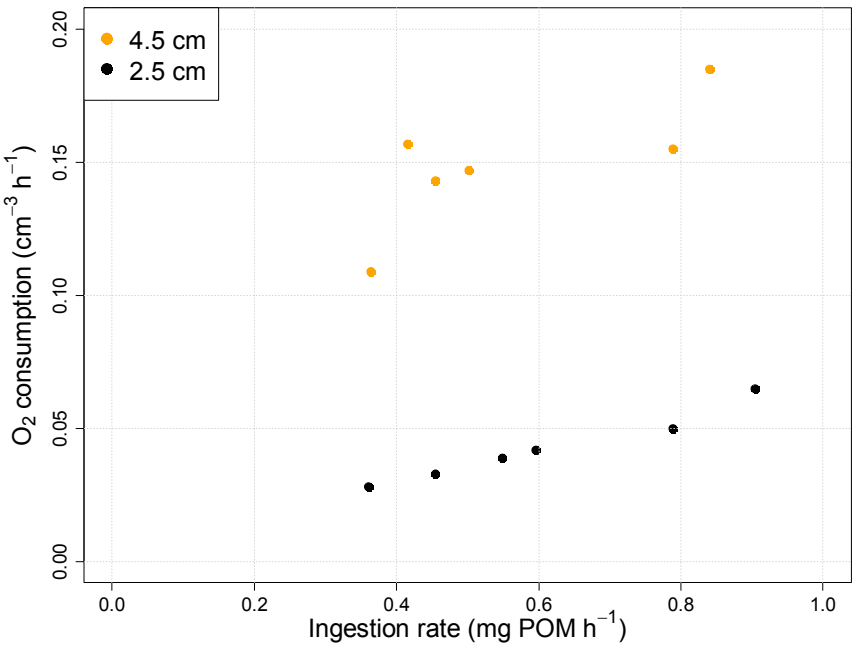

Figure 8: Oxygen consumption of mussels (cm^{-3} h^{-1}) as a function of ingestion rate (mg POM h^{-1}) for mussels of 2.5 cm and 4.5 cm. Van Haren and Kooijman (1993) based on data from Bayne et al. (1987); Bayne et al. (1989).

In DEB formulation

To calculate the oxygen consumption as a function of length, ingestion rate and temperature, the mass balance of the elements (*C*, *H*, *N* and *O*) is used. In DEB, a distinction is made between the mineral fractions (CO_2, H_2O, O_2 and NH_3) and the organic fractions (food, structural volume, reserves and faeces) of the elements. Due to the conservation of mass, the following mass balance can be made:

$$0 = \underbrace{n_M \cdot j_M}_{mineral\ fluxes} + \underbrace{n_O \cdot j_O}_{organic\ fluxes}$$

Where $n_M \cdot j_M$ is a vector with the mineral fluxes of the elements *C*, *H*, *O* and *N* in mole d^{-1} and $n_O \cdot j_O$ is a vector with the organic fluxes of the elements.

In matrix notation this relation can be written as:

$$\begin{pmatrix}0\\0\\0\\0\end{pmatrix} = \underbrace{\underbrace{\begin{pmatrix}1&0&0&0\\0&2&0&3\\2&1&2&0\\0&0&0&1\end{pmatrix}}_{n_M} \cdot \underbrace{\begin{pmatrix}j_C\\j_H\\j_O\\j_N\end{pmatrix}}_{j_M}}_{mineral\ fluxes} + \underbrace{\underbrace{\begin{pmatrix}1&1&1&1\\1.8&1.8&1.8&1.8\\0.5&0.5&0.5&0.5\\0.15&0.15&0.15&0.15\end{pmatrix}}_{n_O} \cdot \underbrace{\begin{pmatrix}j_X\\j_V\\j_E+j_{E_R}\\j_P\end{pmatrix}}_{j_O}}_{organic\ fluxes}$$

The matrix n_M represents the chemical composition of the mineral fractions CO_2, H_2O, O_2 and NH_3 (columns) in terms of the elements *C*, *H*, *O* and *N* (rows). Matrix n_O represents the chemical composition of the organic fractions organic fractions (food, structural volume, reserves and faeces) in the columns in terms of the elements *C*, *H*, *O* and *N* (rows). In this case all organic fractions have the same mineral composition: mole *C*:mole *H*:mole *O*:mole *N* = 1:1.8:0.5:0.15.

The vector (j_O) represents the organic fluxes in terms of C-mole d^{-1}. j_X is the flux of food, j_V is the flux structural volume (V) $j_E + j_{E_R}$ is the flux van reserves (E) and reproduction (R). j_P is the flux of faeces.

$$j_O = \begin{pmatrix} j_X \\ j_V \\ j_E + j_{E_R} \\ j_P \end{pmatrix}$$

The vector j_M represents the fluxes of the mineral fractions (CO_2, H_2O, O_2 and NH_3, respectively) in units of mole d^{-1}. The third element of this vector is negative (consumption) and represents the respiration rate (mole O_2 d^{-1}).

$$j_M = \begin{pmatrix} j_C \\ j_H \\ j_O \\ j_N \end{pmatrix}$$

The vector with the mineral fluxes (j_M) can be derived by rewriting the function:

$$j_M = -\left(n_M{}^{-1} \cdot n_O \cdot j_O\right)$$

Where is $n_M{}^{-1}$ is the inverse of matrix n_M

$$\underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 2 & 0 & 3 \\ 2 & 1 & 2 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{n_M} \cdot \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & -1.5 \\ -1 & -0.25 & 0.5 & 0.75 \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{n_M{}^{-1}} = \underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{I}$$

Vector j_O can be derived from the three major fluxes from the energy balance within DEB, and stored in the vector $\dot{p} = \begin{pmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{pmatrix}$

- Assimilation ($\dot{p}_A$, J d^{-1})
- Loss to respiration and reproduction ($\dot{p}_D$, J d^{-1})
- Growth ($\dot{p}_G$, J d^{-1})

$$\underbrace{j_O = \begin{pmatrix} j_X \\ j_V \\ j_E + j_{E_R} \\ j_P \end{pmatrix}}_{j_O} = \underbrace{\begin{pmatrix} -\eta_{XA} & 0 & 0 \\ 0 & 0 & \eta_{VG} \\ \bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} \\ \eta_{PA} & 0 & 0 \end{pmatrix}}_{\eta_O} \cdot \underbrace{\begin{pmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{pmatrix}}_{\dot{p}}$$

The matrix η_O translates the energy fluxes from $\dot{p}$ in J d^{-1} into fluxes in mole C d^{-1}. This matrix is composed of various parameters. The parameter η_{XA} (C-mole J^{-1}) couples mass flux (X) to the energy flux (A). The change in food (j_X, mole C d^{-1}) is calculated from the assimilation flux ($\dot{p}_A$, J d^{-1}) by:

$$\dot{\mathrm{J}}_\mathrm{X} = -\eta_{\mathrm{XA}} \cdot \dot{\mathrm{p}}_\mathrm{A}$$

The assimilation flux is first stored in reserves: $\dot{\mathrm{p}}_\mathrm{A}/\bar{\mu}_\mathrm{E}$ (C-mole d^{-1}) with $\bar{\mu}_\mathrm{E}$ is the chemical potential of reserves (J C-mole^{-1}).The reserves are used for respiration and gonad production ($\dot{\mathrm{p}}_\mathrm{D}/\bar{\mu}_\mathrm{E}$) and growth ($\dot{\mathrm{p}}_\mathrm{G}/\bar{\mu}_\mathrm{E}$).

Once the powers ($\dot{p}_A$, $\dot{p}_D$ and $\dot{p}_G$, J d^{-1}) are calculated by DEB, the fluxes of the mineral components (CO_2, H_2O, O_2 and NH_3) can be calculated by:

$$\underbrace{\begin{pmatrix} j_C \\ j_H \\ j_O \\ j_N \end{pmatrix}}_{j_M} = -\underbrace{\begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 0.5 & 0 & -1.5 \\ -1 & -0.25 & 0.5 & 0.75 \\ 0 & 0 & 0 & 1 \end{pmatrix}}_{n_M{}^{-1}} \cdot \underbrace{\begin{pmatrix} -\eta_{XA} & 0 & 0 \\ 0 & 0 & \eta_{VG} \\ \bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} \\ \eta_{PA} & 0 & 0 \end{pmatrix}}_{\eta_O} \cdot \underbrace{\begin{pmatrix} -\eta_{XA} & 0 & 0 \\ 0 & 0 & \eta_{VG} \\ \bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} & -\bar{\mu}_E{}^{-1} \\ \eta_{PA} & 0 & 0 \end{pmatrix}}_{\eta_O} \cdot \underbrace{\begin{pmatrix} \dot{p}_A \\ \dot{p}_D \\ \dot{p}_G \end{pmatrix}}_{\dot{p}}}_{j_O}$$

The third element (j_O) in the vector $\dot{j}_M$ is the oxygen consumption (mole O_2 d^{-1}) required for the model parametrization.

2.3.2.4 Ingestion rate, faeces and pseudo-faeces production

Prins et al. (1991) present data on Chl-a ingestion rate (µg Chl-a h^{-1}), Chl-a production in faeces (µg Chl-a h^{-1}) and pseudo-faeces production (mg DW h^{-1}) as a function of suspended matter concentration (mg DW l^{-1}) (Figure 9). The experiments were done with mussels of an average size 6.0 cm and an average ash-free-dry weight of 1.13 g.

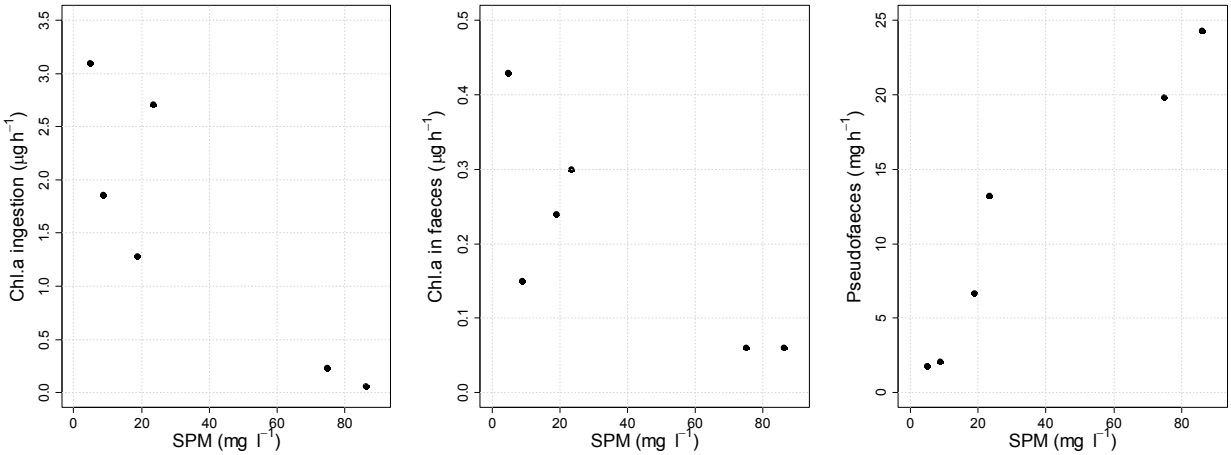

Figure 9: Chl-a ingestion rate, Chl-a in faeces and pseudo-faeces production as a function of SPM concentration. Data are from (Prins et al., 1991). Experiments were done with mussels with a shell length of 57-64 mm and an ash free dry weight of 1.13 g.

In DEB formulation

The relation between food uptake and food density in DEB, the functional response, is often described by a hyperbolic (Monod-type) function (Kooijman, 2006; Troost et al., 2010).

$$f = \frac{X}{K'(Y) + X}$$

With

$$K'(Y) = K\left(1 + \frac{Y}{K_Y}\right)$$

In these functions Y is the concentration of inorganic particles (mg l^{-1}) and X is the food concentration (C-mole l^{-1}). In the experiments the average chlorophyll-a concentration was 6.2 µg l^{-1}. Assuming a Carbon:Chlorophyll ratio of 30 (Cloern et al., 1995), the food concentration in C-mole l^{-1} can be calculated from the Chlorophyll-a concentration by:

$$X = \frac{\mathrm{Chla} \cdot 30}{12 \cdot 10^6}$$

The half saturation coefficient for food uptake $K'(Y)$ (C-mole l^{-1}) decreases with increasing concentration of inorganic matter (Y, mg l^{-1}), with the parameter K_Y (mg l^{-1}) being the half saturation constant for inorganic matter. The parameter K (C-mole l^{-1}) can be calculated from the surface area specific maximum ingestion rate $\{\dot{j}_{XAm}\}$ (C-mole cm^{-2} d^{-1}) and the maximum specific searching rate $\{\dot{F}_m\}$ (l cm^{-2} d^{-1}):

$$K = \frac{\{\dot{j}_{XAm}\}}{\{\dot{F}_m\}}$$

The ingestion rate $\dot{J}_X$ (C-mole d^{-1}) is calculated by:

$$\dot{J}_X = \{\dot{J}_{XAm}\} \cdot L^2 \cdot f$$

The faeces production rate $\dot{J}_P$ (C-mole d^{-1}) is calculated from the ingestion rate using the faecation efficiency of food to faeces (K_P, -).

$$\dot{J}_P = K_P \cdot \dot{J}_X$$

The fluxes in C-mole d^{-1} are converted to µg Chl-a h^{-1} by multiplying with the factor $\frac{12 \cdot 10^6}{30 \cdot 24}$ to express them in the same units as used in Prins et al. (1991).

Filter feeders filter food particles from the water column using their gills. The clearance rate $\dot{C}R$ is the volume of water filtered per unit of time (l d^{-1}). The clearance rate depends on the size of the gills ($\sim L^2$, cm^{-2}) and the maximum surface specific searching rate $\{\dot{F}_m\}$ (l cm^{-2} d^{-1}):

$$\dot{C}R = \{\dot{F}_m\} \cdot L^2$$

The filtration rate ($\dot{F}$), mg d^{-1}) is the clearance rate multiplied by the concentration suspended particles ($X + Y$) both in mg l^{-1}.

$$\dot{F} = CR \cdot (X \cdot w_X \cdot 1000 + Y)$$

The food concentration in C-mole l^{-1} is converted to mg dw l^{-1}. Assuming a ratio between the elements C:H:O:N of 1:1.8:0.5:0.15, the weight of a mole food is 23.9 g (w_X).

The rate of pseudo-faeces production is calculated from the difference between the filtration rate and the total (food and inorganic particles) ingestion rate, where it is assumed that the ratio between food and inorganic particles of ingestion is the same as the ratio between food and inorganic particles in the environment.

3 Results

3.1 Model fit

The DEB parameters were estimated by fitting the DEB model to the data described in paragraph 2.3. The overall goodness of fit was 6.07 (MRE = 0.393). In Table 2 a comparison is given between the measured data and the model predictions. The comparisons for the univariate data is given in Figure 10 to Figure 16. Overall the model fit is quite satisfactory. As can be seen from Table 2, the estimated age at puberty (ca 60 days) is less than the observed value (365 days). In the model, a constant temperature value (10°C) and *ad libitum* food conditions ($f = 1$) are assumed. This might result in an earlier age at puberty compared to the field conditions with varying food and temperature. Because the discrepancy in temperature regime, the weight factor for this data item is set to 0.1 in order to get a good fit for the other data. Ultimate length is underestimated by the model (10.8 cm versus an observed value of 15 cm), while physical length at birth is underestimated. This could also be the result of the use of a constant temperature (10°C) in the model while in the field the temperature fluctuates due to seasonal changes. The length versus weight data (Figure 10) is fitted *a-priori* to the fitting using the covariation method since basically one parameter, the shape coefficient (δ_M.), determines the curve. In order to fit the length at age data correctly, the weight factors were set to 10 for these data, which resulted in a good fit (Figure 11). For the data of Capelle (2017), a higher value for the functional response was assumed ($f = 0.9$) than for the slightly slower growing mussels in the data of de De Mesel et al. (2009) ($f = 0.7$).Also a higher weight factor (3) was applied to the oxygen consumption versus shell length data (Figure 12) resulting in a good model fit. The other data on oxygen consumption (Figure 13 and Figure 14) were slightly overestimated by the model, which might indicate an overestimation of the maintenance rates. Data on ingestion rate (Figure 15) and faeces production (Figure 16) as a function of total particulate matter concentration gave a good fit.

Table 2: Zero-variate data for *Mytilus edulis* used in the parameter estimation. The model prediction is presented in the fifth column.

Symbol	Unit	Description	Observation	Model prediction	Weight factor	Relative error
a_b	d	Age at birth	0.2	0. 1755	1	0.1225
a_p	d	Age at puberty	365	59.1	0.1	0.8381
$a_\dagger$	d	Age at death (life span)	8760	8823	1	0.007224
$L_{w,b}$	cm	physical length at birth	0.012	4.639e-3	1	0.6134
$L_{w,p}$	cm	physical length at puberty	1.2	1.271	1	0.05943
$L_{w,m}$	cm	Ultimate physical length	15	10.8	1	0.2798
$W_{w,m}$	g	Ultimate wet weight	124.6	135.5	1	0.08751
GSI	-	Gonado Somatic index	0.67	0.6062	1	0.09067
LW		Length-weight data			0*	0.3037
Lt_1		Length at age data de Mesel			10	0.08333
Lt_2		Length at age data Capelle			10	0.1045
O_2_L		O_2 cons vs shell length			3	0.3506
O_2_T		O_2 cons vs temperature			1	0.171
$O_2\_\dot{j}_X$		O_2 cons vs ingestion rate			1	2.065/0.6923
$\dot{j}_X\_TPM$		Ingestion rate versus TPM			1	0.3316
$\dot{j}_P\_TPM$		Faeces production versus TPM			1	0.4741

*Length-weight data are fitted prior to the covariation procedure by adjusting the shape coefficient δ_M.

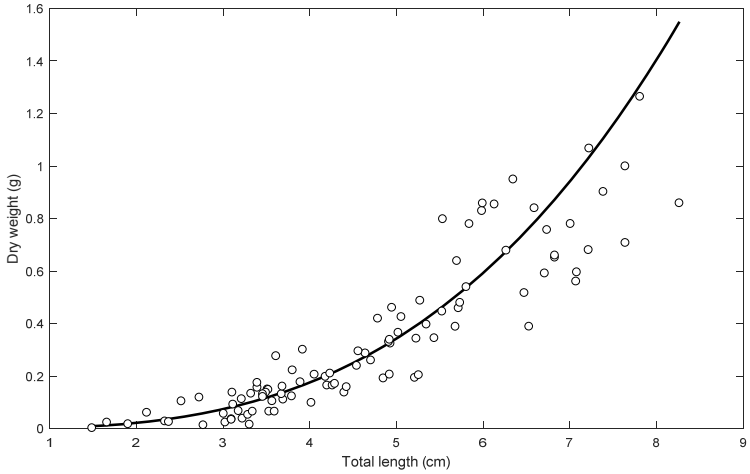

Figure 10: Data (dots) and model results (line) for the length-weight data. Data are from Rosland et al. (2009)

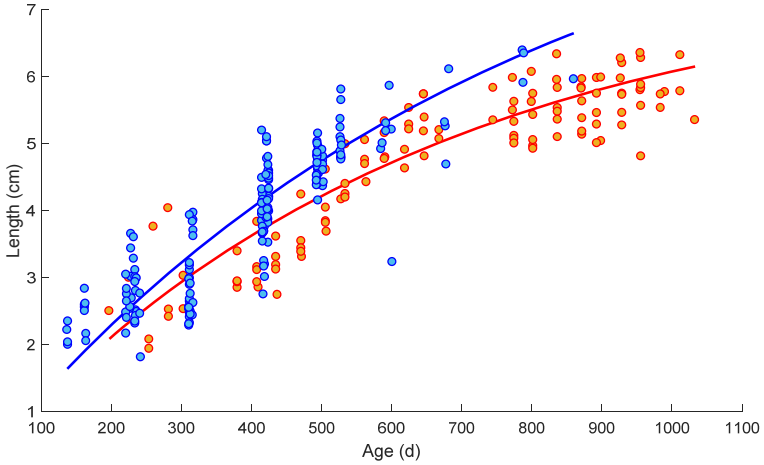

Figure 11: Data (dots) and model results (lines) for the length-weight data. In blue model fit for data from Capelle (2017) assuming $f = 0.9$ and in red model fit for data from De Mesel et al. (2009), assuming $f = 0.7$. All other parameters where kept identical.

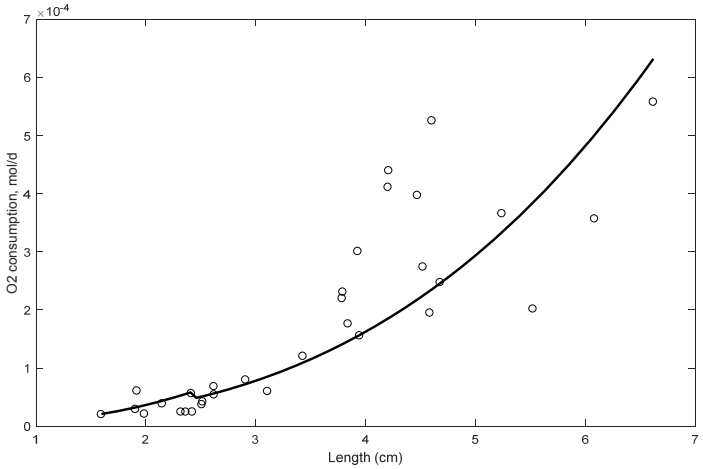

Figure 12: Data (dots) and model results (line) for oxygen consumption rate as a function of shell length. Data from Kruger (1960) in Van Haren and Kooijman (1993).

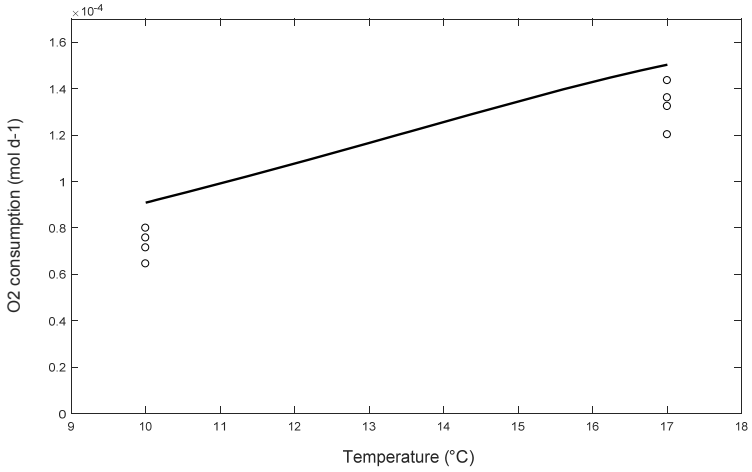

Figure 13: Data (dots) and model results (line) for oxygen consumption rate (mole d^{-1}) as a function of temperature. Data from Jansen et al. (2009). Only data for temperatures below 20°C are used.

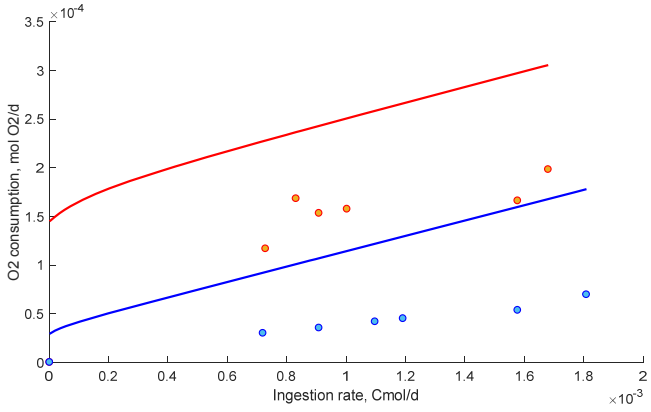

Figure 14: Data (dots) and model results (lines) for oxygen consumption of mussels (mole O_2 d^{-1}) as a function of ingestion rate (C-mole d^{-1}) for mussels of 2.5 cm (blue) and 4.5 cm (red). Data from Van Haren and Kooijman (1993) based on data from Bayne et al. (1987); Bayne et al. (1989).

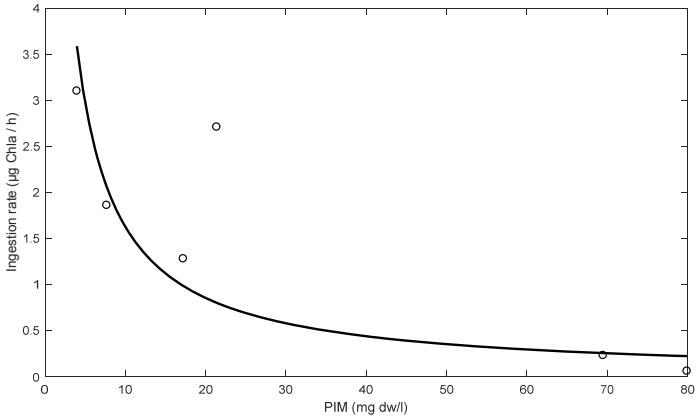

Figure 15: Data (dots) and model results (line) for the ingestion rate (µg Chla h^{-1}) as a function of the particulate inorganic matter concentration of the water (PIM, mg dw l^{-1}). Data are from Prins et al. (1991).

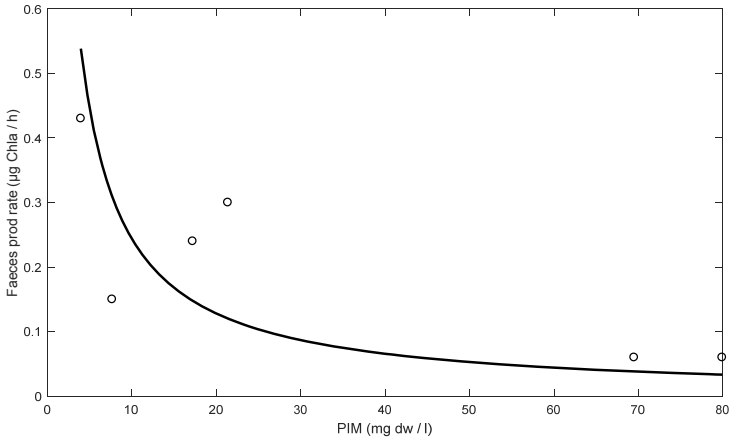

Figure 16: Data (dots) and model results (line) for the faeces production rate (µg Chla h^{-1}) as a function of the particulate inorganic matter concentration of the water (PIM, mg dw l^{-1}). Data are from Prins et al. (1991).

3.2 Estimated parameter values

The estimated primary DEB parameters for *Mytilus edulis* are presented in Table 3, together with the parameter estimations of Saraiva as derived from the Add_My_Pet collection. As can be seen from this table, the value of the surface specific maximum assimilation rate has increased with a factor of more than 30. Also the somatic and maturity maintenance rate parameters have increased compared to the Saraiva values reported.

Table 3: Estimated DEB parameters for *Mytilus edulis*. The column Saraiva represents the parameters estimated by Saraiva and retrieved from the Add_My_Pet collection in January 2018. The last column represents the parameters estimated in this study. The parameters indicated with * are not calibrated in this study.

Symbol	*Description*	*Units*	*Value*	
			Saraiva	*This study*
z	Zoom factor relative to reference L_m=1cm	-	4.0561	1.056
$\{\dot{F}_m\}$	Maximum specific searching rate*	l d^{-1} cm^{-2}	105.6	105.6
$\{\dot{p}_{Am}\}$	Surface specific maximum assimilation rate	J m^{-2} d^{-1}	9.13762	314.9
κ_X	Fraction of food energy fixed in reserve*	-	0.9485	0.8
κ_P	Fraction of food energy fixed to faeces*	-	0.0493	0.15
$\dot{v}$	Energy conductance	cm d^{-1}	0.052206	0.0197
κ	Allocation fraction to growth and somatic maintenance	-	0.9968	0.6496
κ_R	Fraction of reproduction energy fixed in reserve*	-	0.95	0.95
$[\dot{p}_M]$	Volume specific somatic maintenance	J d^{-1} cm^{-3}	2.2456	81.98
$\{\dot{p}_T\}$	Surface specific somatic maintenance*	J d^{-1} cm^{-2}	0	0
k_J	Maturity maintenance rate	d^{-1}	9.565e-05	1.581e-2
$[E_G]$	Volume specific cost for structure	J cm^{-3}	2348	2333
E_H^b	Maturation threshold for feeding (birth)	J	2.156e-07	1.55e-06
E_H^j	Maturation threshold for metamorphosis	J	3.693e-07	1.55e-06
E_H^p	Maturation threshold for reproduction (puberty)	J	0.533	39.67
h_a	Weibull aging acceleration	d^{-1}	2.574e-09	4.191e-09
s_G	Gompertz stress coefficient*	-	0.0001	0.0001
K_Y	Half saturation coefficient for inorganic matter	mg l^{-1}	1.6399	0.2375
X_K	Half saturation coefficient for food*	µg Chla l^{-1}		2

Symbol	*Description*	*Units*	*Value*	
			Saraiva	*This study*
T_{ref}	Reference temperature*	K	293.15	293.15
T_A	Arrhenius temperature*	K	7022	7022
T_{AH}	Arrhenius temp. for rate of decrease at upper boundary*	K	31376	31376
T_{AL}	Arrhenius temp. for rate of decrease at lower boundary*	K	45430	45430
T_H	Lower boundary of tolerance range*	K	296	296
T_L	Upper boundary of tolerance Range*	K	275	275
δ_M	Shape coefficient	-	0.39706	0.231

*Fixed parameter in this study

3.3 Model performance

The DEB model with the newly estimated parameters was compared to the model with the parameters estimated by Saraiva (Table 3). The models were run for 9 years, using seasonally varying environmental conditions (temperature and Chl-a concentration) (Figure 17). The environmental data are yearly repetitions of a typical year in the Oosterschelde. The temperature varies between 3 °C in the winter period to 23 °C in the summer. The chlorophyll-a concentration varies between 0.5 µg Chl-a l^{-1} in the winter period to maximum concentrations of about 14 µg Chl l^{-1} in spring. The functional response variable (*f*), follows directly from the Chl-a concentration and varies between 0.3 in the winter to 0.9 in spring.

In Figure 18, it can be seen that the length of the mussels is much better estimated using the new DEB parameters. After two summers, the mussels reach a shell length of about 5.5 cm while using the model with the old DEB parameters the mussels reach a shell length of only 3.2 cm. The lower value of the shape factor (0.231 versus 0.39, see Table 3), however, result on average in slightly lower values in the simulations with the new DEB parameters. The amount of reserves (and thus also wet weight) is much less with the old DEB parameters. It can be seen that the reserves decrease during the wintertime due to the reduced food conditions.

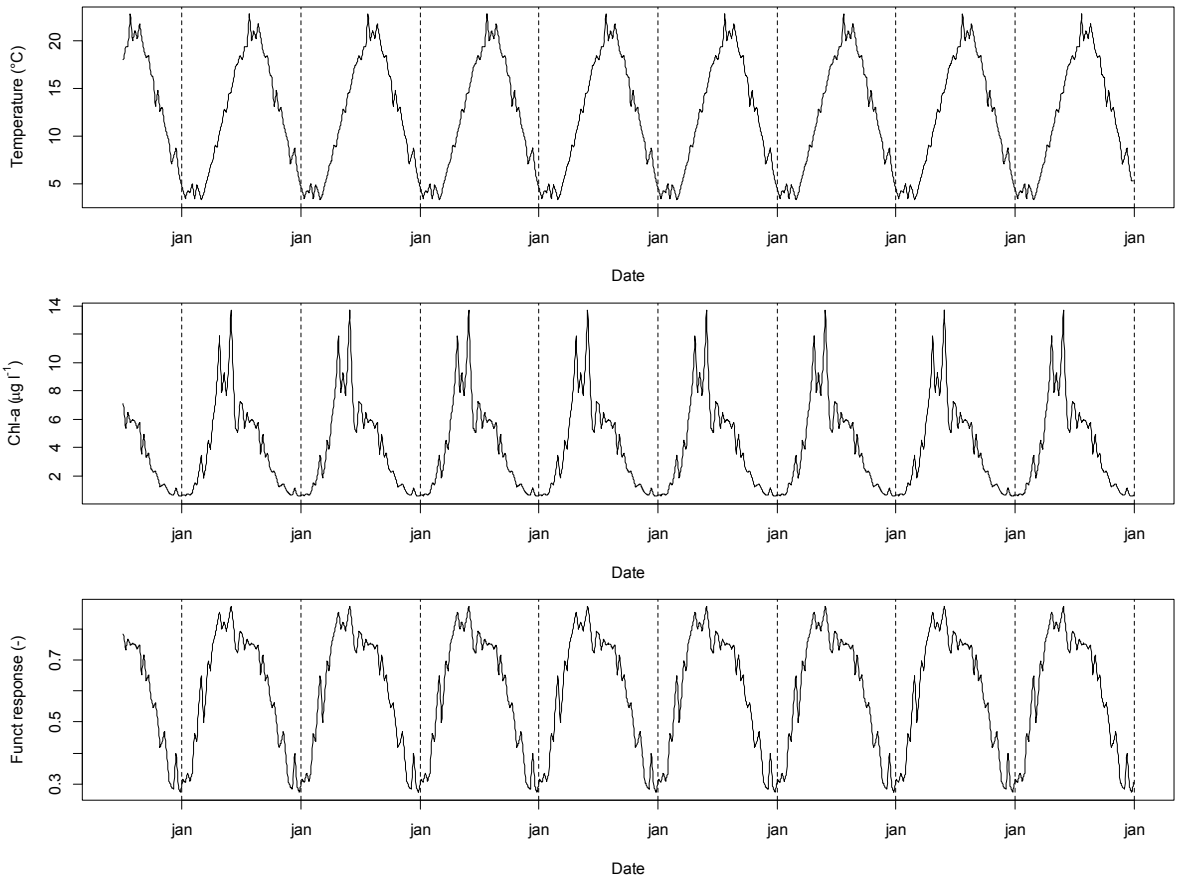

Figure 17: Forcing functions of temperature (°C) and chlorophyll-a concentration (µg Chl l^{-1}) used for model simulations. Data represent a typical year in the Oosterschelde (period 1993 – 2007) which is repeated 9 years. The functional response is calculated from Chl-a concentration.

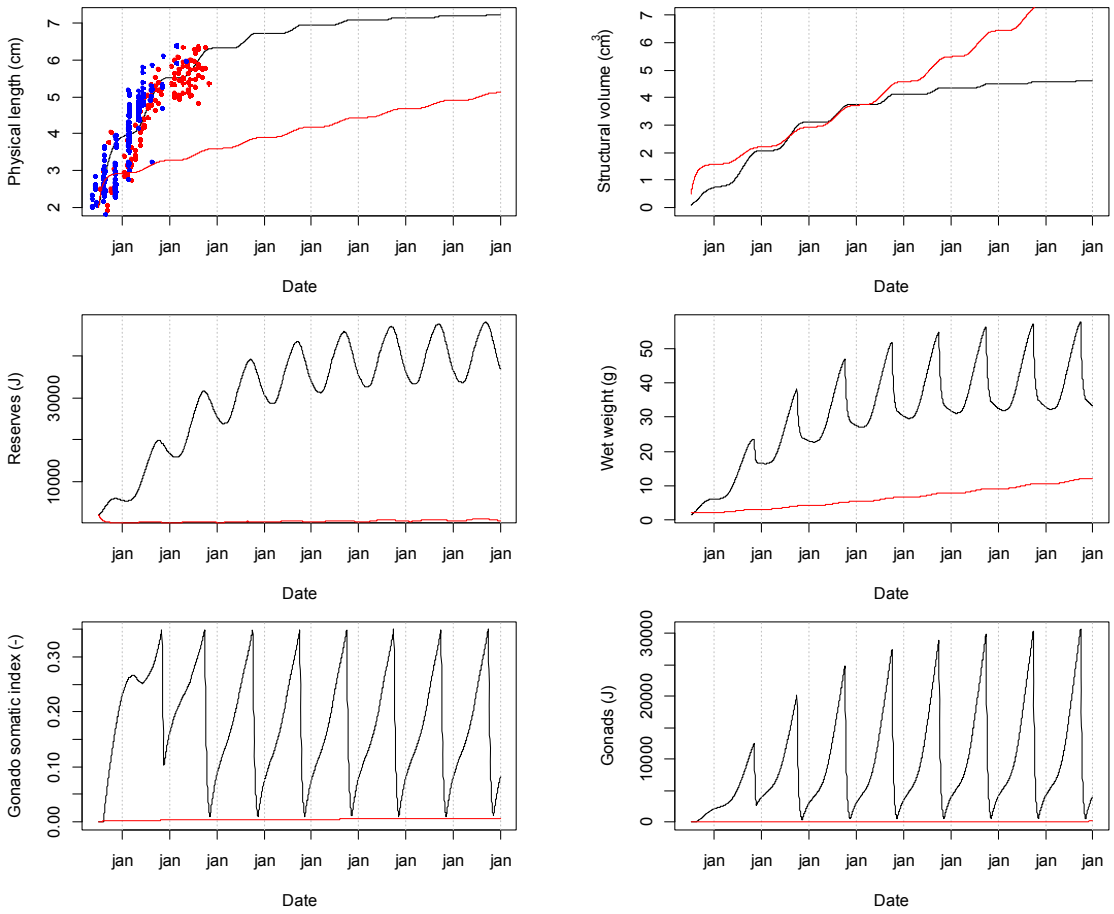

Figure 18: Model output for some selected variables. Red lines are the results of the DEB model with the parameters from Saraiva and black lines represent the results of the model simulations with the newly estimated parameters. Red and blue dots indicate measured values from De Mesel et al. (2009) and Capelle (2017), respectively.

4 Conclusions

The DEB parameters that have been estimated by Saraiva result in an underestimation of the growth for *Mytilus edulis*. This is mainly caused by the use of biased length-at-age data of slow growing mussels from Killary Harbor (Ireland). These mussels reached a shell length of 4 cm after 5 to 8 years, while the cultured mussels in the Wadden See (the Netherlands) can already reach a shell length of 4 cm after 1 year under good conditions.

New DEB parameters have been estimated for *Mytilus edulis* using growth data from commercial culture plots in the Wadden Sea. The DEB model with the newly estimated parameters showed a more realistic growth of the mussels in the area of application (culture plots in the Oosterschelde and Wadden Sea). The new DEB parameters differ from the previous estimated parameters from Saraiva in a higher assimilation rate, a lower energy conductance, a higher somatic maintenance rate and a lower kappa.

The growth and development of mussels is well described by the DEB model with the newly estimated parameters. The model can be included as a module into the Oosterschelde model (Carrasco de la Cruz, 2018) to replace the present shellfish module based on carrying capacity. This will allow to simulate growth and quality of the mussels during the season, which are important variables for shellfish farmers.

5 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. This certificate is valid until 15 December 2021. The organisation has been certified since 27 February 2001. The certification was issued by DNV GL.

Furthermore, the chemical laboratory at IJmuiden has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2021 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation. The chemical laboratory at IJmuiden has thus demonstrated its ability to provide valid results according a technically competent manner and to work according to the ISO 17025 standard. The scope (L097) of de accredited analytical methods can be found at the website of the Council for Accreditation (www.rva.nl).

On the basis of this accreditation, the quality characteristic Q is awarded to the results of those components which are incorporated in the scope, provided they comply with all quality requirements. The quality characteristic Q is stated in the tables with the results. If, the quality characteristic Q is not mentioned, the reason why is explained.

The quality of the test methods is ensured in various ways. The accuracy of the analysis is regularly assessed by participation in inter-laboratory performance studies including those organized by QUASIMEME. If no inter-laboratory study is available, a second-level control is performed. In addition, a first-level control is performed for each series of measurements.
In addition to the line controls the following general quality controls are carried out:

- Blank research.
- Recovery.
- Internal standard
- Injection standard.
- Sensitivity.

The above controls are described in Wageningen Marine Research working instruction ISW 2.10.2.105. If desired, information regarding the performance characteristics of the analytical methods is available at the chemical laboratory at IJmuiden.

If the quality cannot be guaranteed, appropriate measures are taken.

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Justification

Report C009/19
Project Number: 4311400011

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

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Annex 1 Dynamic Energy Budget model

General structure

A Dynamic Energy Budget (DEB) model (Kooijman, 1986; Kooijman, 2000) describes growth, energy dynamics and reproduction as a function of environmental conditions such as temperature and food. The DEB theory is a generic theory that can be applied to different species and life stages by using species specific parameters (Kooijman, 2001). An individual organism is described by four state variables: structural body volume (V, cm^3), reserves (E, J), maturity (E_H, J) and reproduction (E_R, J) (Figure 19). The reserves are often quantified as energy density ($[\mathrm{E}] = {}^{\mathrm{E}}/_{\mathrm{V}}$, J cm^{-3}). Filterfeeding bivalves like the blue mussel (*Mytilus edulis*) filter food from the water column with their gills. A fraction of the filtered food is assimilated, the rest is released as faeces and pseudo-faeces. The assimilated energy is incorporated into a reserve pool (E) from which it is used for maintenance, growth, development and reproduction. A fixed fraction (κ) of the mobilization energy flux from reserves is utilized for growth and somatic maintenance, but maintenance is given first priority under energy limitation. The remaining energy flux from the reserve pool ($1-\kappa$) is spent on maturation and reproduction in juveniles and adults, respectively, including maintenance of these components.

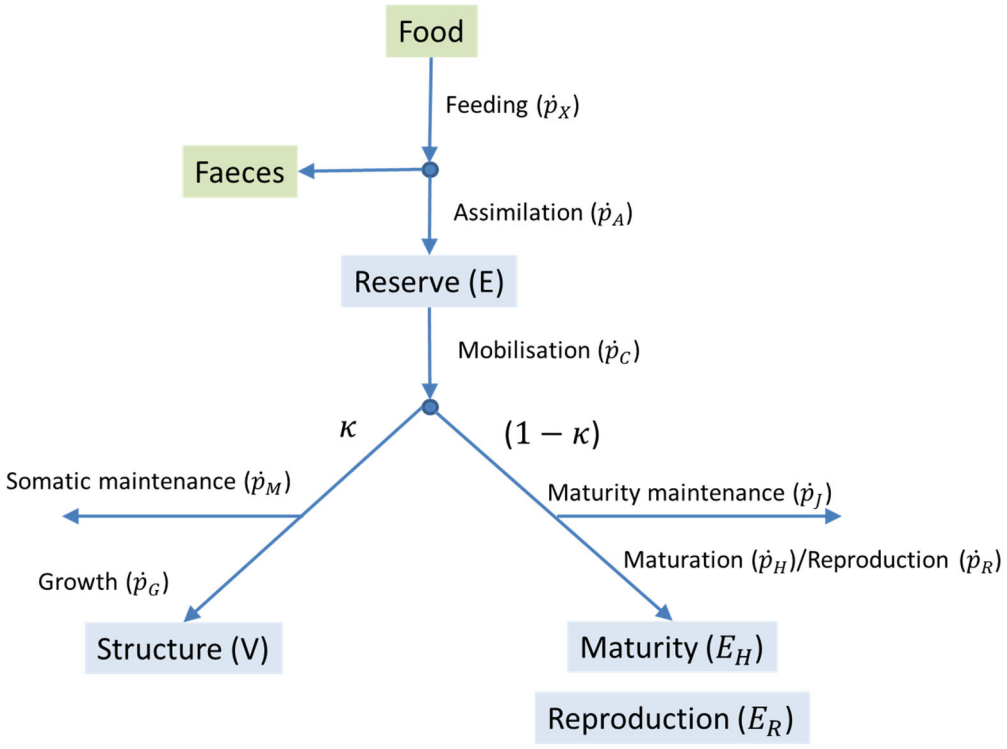

Figure 19: Schematic presentation of the DEB model

Temperature

All physiological rates depend on temperature according to the Arrhenius relation with an upper and lower boundary of the tolerance range (Kooijman, 2000; Van Der Veer et al., 2006).

$$\dot{k}(T) = \dot{k}_{ref} \cdot e^{\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right)} \cdot \frac{\left(1 + e^{\left(\frac{T_{AL}}{T_{ref}} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{ref}}\right)}\right)}{\left(1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}\right)}$$

Where $\dot{k}_T$ is the value of the physiological rate at ambient temperature, $\dot{k}_{ref}$ is the physiological rate at reference temperature, T is the absolute temperature, T_{ref} is the reference temperature (293 K), T_A is the Arrhenius temperature (K), T_{AL} and T_{AH} are the Arrhenius temperatures for the rate of decrease at respectively the lower (T_L) and the upper (T_H) boundaries.

Shape coefficient

The DEB model assumes isomorphy, which means that the shape does not change during growth. The volumetric structural length (L) can be calculated from the structural volume by:

$$L = V^{\frac{1}{3}}$$

The shape coefficient δ_M is defined as volume$^{1/3}$ length^{-1}, so the physical volume is given by:

$$V_w = (\delta_M \cdot L_w)^3$$

Where V_w and L_w are physical volume and physical length respectively. The shape coefficient can be used to convert shape-specific length measurements to volumetric structural length:

$$L = \delta_M \cdot L_w$$

Functional response

The relation between food uptake and food density is described by a scaled hyperbolic functional response *f* (Figure 20). At increased concentration of inorganic particles, a part of the filtered material is excreted as pseudo-faeces (Wijsman et al., 2012). The functional response is defined by:

$$f = \frac{X}{K'(Y) + X}$$

Where X is the food concentration *X* is the food concentration, expressed in (µg chl-a l^{-1}), K′$_Y$ is the half saturation constant (µg chl-a l^{-1}). In the present application the food concentration *X* is multiplied by the food correction factor (ψ).

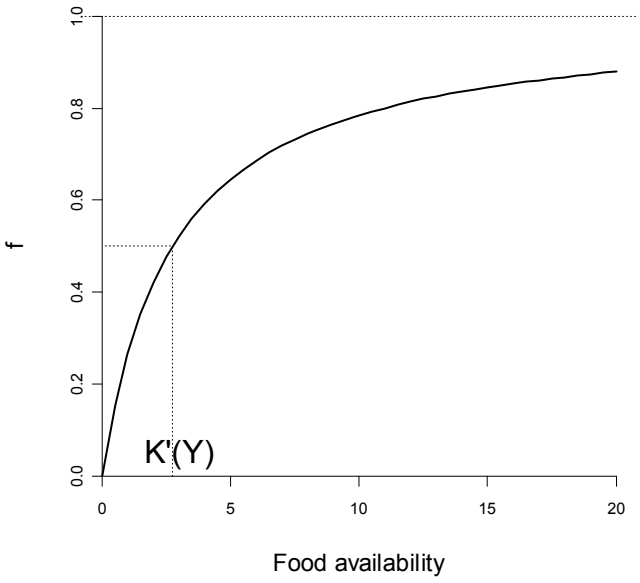

Figure 20: Functional response relation. At finite food availability, the relative food uptake is maximum (f=1). When the food ability is K'(Y), the food uptake rate is half the maximum uptake rate (f=0.5).

Assimilation

In DEB models, energy ingestion rate ($\dot{p}_I$, J d^{-1}) is proportional to the surface-specific maximum ingestion rate ($\{\dot{j}_{XAm}\}$, J d^{-1} cm^{-2}), the scaled functional response *f* and the surface area of the structural volume ($V^{2/3}$, cm^2).

$$\dot{p}_I = \{\dot{j}_{XAm}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T)$$

Only a fraction of the ingested food is assimilated, the rest is lost. DEB assumes that assimilation efficiency of food is independent of the feeding rate. The assimilation rate is calculated by
$\dot{p}_A = \{\dot{p}_{Am}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T)$

where $\{\dot{p}_{Am}\}$ is the surface area specific maximum assimilation rate (J d^{-1} cm^{-2}).
The ratio $\{\dot{j}_{XAm}\}/\{\dot{p}_{Am}\}$ gives the conversion efficiency of the ingested food into assimilated energy and is known as assimilation efficiency (AE).

The assimilated energy is stored in the reserve pool (E). The dynamics of the reserve pool is written by:

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$$

Where $\dot{p}_A$ is the assimilation rate (J d^{-1}) and $\dot{p}_C$ is the utilization rate (J d^{-1}).

Growth and somatic maintenance

The utilization rate ($\dot{p}_C$, J d^{-1}) is the rate at which the energy is utilized from the reserves. A fixed proportion (κ) of utilized energy is spent on growth plus maintenance. The rest (1-κ) goes to development (juveniles) or to reproduction (adults) and the maintenance related to the reproduction.

$$\dot{p}_C = \left(\frac{[E]}{\kappa \cdot [E] + [E_G]}\right) \cdot \left(\frac{\{\dot{p}_{Am}\} \cdot [E_G]}{[E_m]} \cdot V^{\frac{2}{3}} + [\dot{p}_M] \cdot V\right)$$

where [E] corresponds to the energy density of the organism (J cm^{-3}), $[E_G]$ is the volume specific costs for of structure (J cm^{-3}) and $[E_m]$ is the maximum energy density of the reserve compartment. The parameter $[\dot{p}_M]$ is the volumetric cost of maintenance (J cm^{-3} d^{-1}).

The energy flow required for maintenance is

$$\dot{p}_M = [\dot{p}_M] \cdot V$$

The dynamics of the structural volume can be derived according to the κ-rule by:

$$\frac{dV}{dt} = GR = \frac{\kappa \cdot \dot{p}_C - [\dot{p}_M] \cdot V}{[E_G]}$$

Where GR is the growth rate of structural biomass. When energy required for maintenance $\dot{p}_M$ is higher than the energy available for growth and maintenance ($\kappa \cdot \dot{p}_C$) the energy for maintenance is paid by energy in the reproduction buffer R. When energy in the reproduction buffer is depleted, maintenance can be paid by the structural volume and the organism shrinks.

Maturity and reproduction

DEB describes the maturation and reproduction though different developmental stages of the organism. During the juvenile stage, energy is used to develop reproductive organs which increases the level of maturation (E_H) of the organism. When the organism reaches a certain maturity level (E_H^p), the reproductive organs are fully developed and the organism reaches the adult stage. From that moment on, it allocates the energy that is used for the reproductive flux to gametes (eggs and sperm)production (E_R). Gonads also requires maintenance which is proportional to the level of maturity ($\dot{k}_J \cdot E_H^p$). A fixed proportion (1- κ) of the utilized energy ($\dot{p}_C$) goes to the gonads, either to, maturity development (juveniles), reproduction (adults) or maintenance. The energy allocation to reproduction equals:

$$\dot{p}_R = (1 - \kappa) \cdot \dot{p}_C - \dot{k}_J \cdot E_H^p$$

Where $\dot{k}_J$ is the maturity maintenance rate coefficient (d^{-1}) and $E_H^p$is the maturation threshold for reproduction (puberty).

Spawning

Spawning occurs when enough energy is allocated to the gonads and when the water temperature is above a threshold value. The gonads are released from the buffer with a specific rate until the temperature drops below the threshold value (10°C), all gonads are released.

Acceleration

The model allows for metabolic acceleration (Kooijman, 2014; Lika et al., 2014; Zimmer et al., 2014). It is assumed that species change their shape during early juvenile period. After this period of metabolic acceleration they reach their adult shape and the growth becomes isomorphic. During metabolic acceleration, the surface to volume ratio is altered and this has consequences to the DEB parameters that have length in their dimensions, specifically the parameters parameters $\{\dot{p}_{Am}\}$ and $\dot{v}$. In the DEB model these parameters are multiplied with the shape correction function $\mathcal{M}(L)$.

$\mathcal{M}(L) = \frac{L_b}{L_b} = 1$ if $E_H < E_H^b$ (embryo)
$\mathcal{M}(L) = \frac{L}{L_b}$ if $E_H^b < E_H < E_H^j$ (early juvenile)
$\mathcal{M}(L) = \frac{L_j}{L_b}$ if $E_H > E_H^j$ (late juvenile and adult)

Annex 2 DEB parameters

Primary DEB parameters

A powerful aspect of Kooijman's DEB theory is that differences between species can be captured in the same model using a different set of parameter values only. However, estimation of these parameters is complicated. The parameters are often cryptic and cannot be estimated in a direct way (Van Der Meer, 2006).

A DEB model consists of primary and compound parameters. The primary parameters are most intimately connected to a single underlying process, while compound parameters typically depend on several underlying processes. The compound parameters can be derived from the primary parameters using the formulations of the DEB theory. The primary DEB parameters can be split into the core parameters and auxiliary parameters (Lika et al., 2011a). Core DEB parameters directly control the state variables (except the defecation efficiency) and are linked to the concepts of the standard DEB model. The core DEB parameters are described in Table 4. Auxiliary parameters primarily converts various measurements and quantify the effect of temperature on the rates. The auxiliary parameters are listed in Table 5.

Core DEB parameters

Table 4: Core DEB parameters

Parameter	Unit	Description
z	-	Zoom factor
$\{\dot{F}_m\}$	l d^{-1} cm^{-2}	Maximum surface area-specific filtration rate
κ_X	-	Digestion efficiency
κ_X^p	-	Faecation efficiency
$\dot{v}$	cm d^{-1}	Energy conductance
κ	-	Allocation fraction to soma
κ_R	-	Reproduction efficiency
$[\dot{p}_M]$	J d^{-1} cm^{-3}	Volume-specific somatic maintenance
$\{\dot{p}_T\}$	J d^{-1} cm^{-2}	Surface-specific somatic maintenance
$\dot{k}_J$	d^{-1}	Maturity maintenance rate coefficient
$[E_G]$	J cm^{-3}	Specific cost for structure
E_H^b	J	Maturity at birth
E_H^p	J	Maturity at puberty
$\dot{h}_a$	d^{-2}	Weibull ageing acceleration
s_G	-	Gompertz stress coefficient

Zoom factor
The zoom factor (z,-) is developed to improve comparability of parameter values, length parameters are standardized such that the maximum structural volumetric length L_m^{ref} equals 1 cm $z = L_m/L_m^{ref}$. The zoom factor z is subsequently used to arrive at other values of the maximum structural volumetric length. The zoom factor in combination with the shape coefficient (δ_M,-) controls the length-weight relationship.

Maximum surface specific filtration rate
The maximum surface specific filtration rate ($\{\dot{F}_m\}$, l d^{-1} cm^{-2}) controls the food intake if the food is not abundant and has no effect when food is abundant. A low value means a dramatic drop in food intake when lowering food abundance. The actual filtration rate is a function of the gill size (cm^2), and thus of the size of the animal.

Digestion efficiency and faecating efficiency
The parameters digestion efficiency (κ_X,-) and faecating efficiency (κ_X^p,-) are parameters indicating the fraction of the energy in the food that is fixed in reserves and ends up in faeces, respectively. The parameters are not necessary reciprocal of each other. The sum of κ_X and κ_X^p is less than 1.

Energy conductance
The energy conductance velocity ($\dot{v}$, cm d^{-1}) controls the mobilization of the reserves.

Allocation fraction to soma
The parameter kappa (κ, -) controls the allocation of the mobilized reserves to somatic maintenance and growth. The remainder ($1-\kappa$) is allocated to maturity maintenance and maturation of reproduction. High values result in rapid growth to a large size, long development times and low reproduction

Reproduction efficiency
The reproduction efficiency (κ_R, -) controls the reserve allocated to reproduction that is fixed in the reserve of offspring. The rest ($1-\kappa_R$, -) is used as reproduction overhead.

Volume-specific somatic maintenance
The volume-specific somatic maintenance costs ($[\dot{p}_M]$, J d^{-1} cm^{-3}) are the costs for maintenance of the structural body volume. The energy is used for processes as the maintenance of the concentration gradients across membranes and the turnover of structural body proteins.

Surface-specific somatic maintenance
Surface-specific somatic maintenance costs ($\{\dot{p}_T\}$, J d^{-1} cm^{-2}) are the maintenance costs related to the surface area of individuals such as osmoregulation and heat loss.

Maturity maintenance rate coefficient
The maturity maintenance rate coefficient ($\dot{k}_J$, d^{-1}) also controls the sink of reserve. This parameter can be compared with the somatic maintenance coefficient ($\dot{k}_M$, d^{-1}), which is the ratio of the costs of somatic maintenance $[\dot{p}_M]$, and the specific costs for structure $[E_G]$. A high value delays development and reduces the ultimate length, the von Bertalanffy growth rate does not depend on this rate.

Specific costs for structure
The volume specific costs for structure ($[E_G]$, J cm^{-3}) control the conversion of reserve to structure. This parameter gives the amount of energy that is required to synthesise a unit of volume of structure. This includes the energy content of the tissue plus the overhead costs of the anabolic machinery. A high value reduces the growth rate, but not the ultimate size, and decreases the size at birth and puberty.

Maturity at birth
The maturity at birth (E_H^b, J) controls the timing of birth and the moment that assimilation is switched on.

Maturity at puberty
The maturity at puberty (E_H^p, J) is the maturity threshold at puberty and controls the timing of puberty. At this moment the investment into maturation is redirected to reproduction.

Weibull aging acceleration
The Weibull aging acceleration parameter ($\dot{h}_a$, d^{-2}) controls the mean life span in a way that is hardly dependent on food density. This is because the increased respiration is cancelled out by dilution by growth. Increasing values reduce the mean life span and the survival probabilities at birth and puberty.

Gompertz stress coefficient
The Gompertz stress coefficient (s_G, -) also has an effect on the mean life span depending on food density.

Table 5: Auxiliary DEB parameters, temperature and scaling parameters

Parameter	Unit	Description
δ_M	-	Shape coefficient
d_0	g cm^{-3}	Specific densities
μ_0	J mole^{-1}	Chemical potentials organic materials
μ_M	J mole^{-1}	Chemical potentials inorganic materials
η_0	-	Chemical indices
w_0	g mole^{-1}	Molecular weights
T_{ref}	K	Reference temperature
T_A	K	Arrhenius temperature
T_L	K	Lower boundary temperature tolerance range
T_H	K	Upper boundary temperature tolerance range
T_{AL}	K	Parameter that controls the rate around lower border of temperature tolerance
T_{AH}	K	Parameter that controls the rate around upper border of temperature tolerance

Shape coefficient

The shape coefficient (δ_M,-) converts the physical length (L_w) to the volumetric structural length (L).
$L = \delta_M \cdot L_w$

Structural volume (V) can be calculated from the structural length (L) using the shape factor by:
$V = L^3$
Consequently the structural volume can be calculated from the physical length (L_w) by
$V = (\delta_M \cdot L_w)^3$

In combination with the zoom factor, the shape factor controls the length-weight relationship.

Specific densities

The specific densities, $d_0 = (d_X \quad d_V \quad d_E \quad d_P)$ convert volumes to grams for food (*X*), structure (*V*) reserve (*E*) and faeces (*P*).

Chemical potentials

The chemical potentials of the organic components, $\mu_0 = (\mu_X \quad \mu_V \quad \mu_E \quad \mu_P)$ convert moles to energy for food (*X*), structure (*V*) reserve (*E*) and faeces (*P*). The parameter $\mu_M = (\mu_C \quad \mu_H \quad \mu_O \quad \mu_N)$ converts moles to energy for carbon dioxide (*C*), hydrogen (*H*), dioxygen (*O*) and nitrogen waste (*N*).

Chemical indices

The chemical indices $\eta_0 = (\eta_X \quad \eta_V \quad \eta_E \quad \eta_P)$ relate the frequency of the chemical elements (C,H,O and N) to C (in the rows) for organic compounds food (*X*) structure (*V*), reserve (*E*) and faeces (*P*). This matrix controls the chemical composition and so the production of CO_2 and O_2.

The same accounts for the mineral compounds, $\eta_M = (\eta_C \quad \eta_H \quad \eta_O \quad \eta_N)$ for respectively carbon dioxide (*C*), water (*H*), dioxygen (*O*) and nitrogen waste (*N*).

Molecular weights

These are the molecular weights of carbon, hydrogen, oxygen and nitrogen: $w_0 = (w_C \quad w_H \quad w_O \quad w_N)$.

Reference temperature

The reference temperature (T_{ref}) is the temperature for which the rates and times are given.

Arrhenius temperature

The Arrhenius temperature (T_A) controls the effect of temperature on the rates, similar to a Q_{10} value. An increase in the value increases the effect of temperature.

Temperature tolerance range
Lower (T_L) and upper (T_L) boundary temperatures between which Arrhenius relationship applies.

Arrhenius temperatures for transitions
Parameters that control the rate around the borders (Lower border: T_{AL}; upper border: T_{AH}) of the tolerance.

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