Dynamic Energy Budget (DEB) parameters for *Ensis directus*

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Summary

In this report a Dynamic Energy Budget (DEB) model for razor clams (*Ensis directus*) is presented. A DEB model is a generic model describing growth and development of individual organisms as a function of environmental conditions. The DEB model for *Ensis directus* is based on the standard DEB model. The species specific primary DEB parameters are estimated with the Add_my_pet procedure, using literature data and the results of laboratory experiments with *Ensis directus*. The performance of the model is demonstrated by theoretical model experiments with varying environmental conditions.

In following projects, the model will be used to predict and quantify the effects of sand mining on the shellfish community in the Dutch coastal zone. For this purpose the functional response of the model should be adapted so that the combined effect of changing phytoplankton and suspended sediment concentration on the uptake rate can be simulated.

1 Introduction

1.1 Background

Yearly, large amounts of sand are dredged from the Dutch part of the North sea. Possible ecosystem effects of sand mining can be divided into direct and indirect effects. Direct effects are mostly related to the removal of benthic organisms. Indirect effects are caused by increased concentrations of suspended inorganic particles in the water column, which reduces light conditions. An increased Suspended Particulate Matter (SPM) concentration is especially effecting ecological processes (primary production and feeding) in the water column, but it may, directly or indirectly, also affect ecological processes that take place at the bottom (feeding).

Primary production (PP) in the North Sea is governed by light and nutrients. As a result, turbidity may lead to a decrease in primary production. When primary production decreases, less food is available to primary consumers, such as zooplankton and zoobenthos.

Moreover, inorganic particles could have an effect on food uptake rate of filterfeeding bivalves since at high concentrations of inorganic particles the filtered material is removed in the form of pseudofaeces (Prins et al., 1991). Also a decrease of the organic to inorganic ratio of the particles can decrease the food quality. It takes extra energy to extract useful particles (algae), because the proportion of useful particles decreases at higher SPM levels. The extra energy it takes to filter SPM out of the water can result in a decrease of the energy that is available for somatic growth. In a previous study by Witbaard and Kamermans (2009) the effect of SPM on filtration activity of *Ensis directus* has been investigated. In general, the decreased food uptake may lead to a reduced growth of filter feeders. The filtering speed (l h^{-1}) of filter feeders shows an optimum curve with SPM concentrations. Research into the filtering capacity of Blue Mussels (*Mytilus edulis*) has shown that an average Mussel of 3 centimetres of length, reaches the maximum filtering speed at a SPM concentration of 125 mg l^{-1}. When SPM concentration is 225 mg l^{-1}, filtering capacity has decreased to about 30% and at a suspended solids concentration of 250 mg l^{-1} filtering will be ceased (Widdows et al., 1979). Filtering rate (l h^{-1}) is not the same as energy uptake rate (J h^{-1}). Energy uptake rate could be derived from filtration rate if food concentration and production rate of faeces and pseudo faeces is known.

1.2 Research question

Large amount of sand is dredged from the North Sea for construction purposes and for coastal protection. In the period 1992 to 1996 on average a yearly amount of 20 million m^3 was dredged from the Dutch part of the North sea. At present, the amount has already increased to more than 30 million $m^{3.}$. Part of this sand is used for coastal protection. On average 10.8 million m^3 of sand was yearly nourished in the Dutch coastal between 2001 and 2010 (Figure 1). It is expected that in the future the demand for sand from the Dutch part of the North Sea will increase to an amount ranging from 33 million m^3 $year^{-1}$ (NWP) to 110 million m^3 $year^{-1}$ (Deltacommissie, maximum scenario) due to sea level rise and the need for coastal protection.

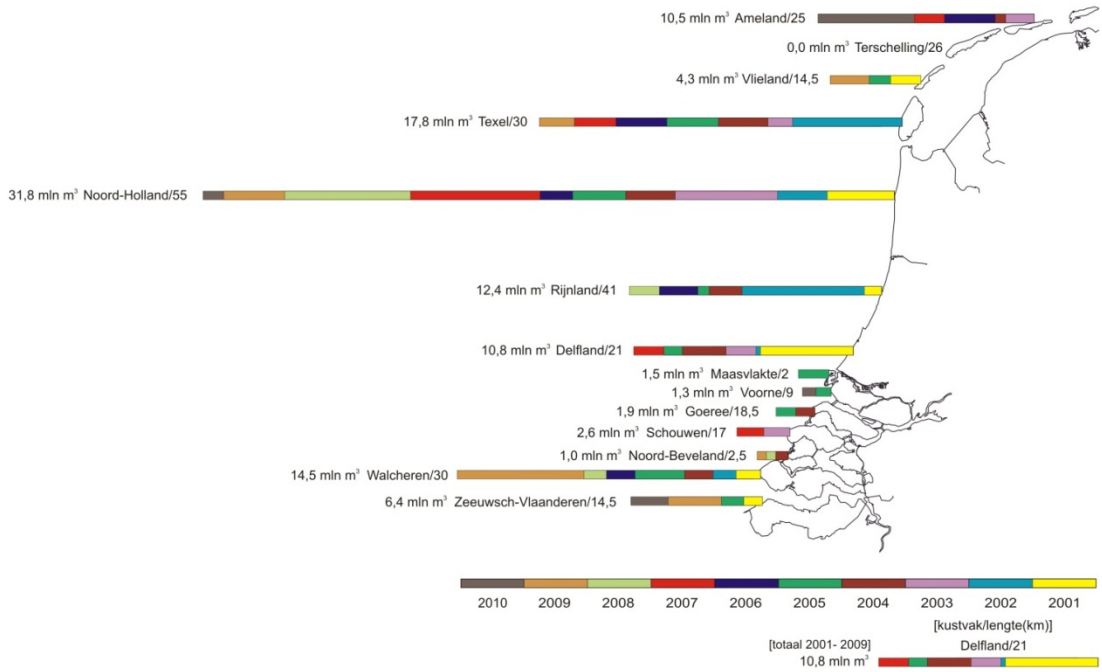

Figure 1: Total nourishment volumes per year along the Dutch coast (2001 to 2010).

For the Environmental Impact Assessment (MER) it is important to quantify the effect of sand mining on the functioning of the ecosystem. A Monitoring and Evaluation programme was proposed by a collaboration of RWS and LaMER (a foundation of water constructors). The research questions of the Monitoring and Evaluation programme are:

1. What are the effects of reduced food conditions on growth of razor clams (*Ensis directus*)
2. When does food limitation occur as a result of these changed conditions?

The approach taken is the development and use of a DEB (Dynamic Energy Budget) model for *Ensis directus*. The model will be integrated into a water quality model.

The Ministry of Infrastructure and the Environment has chosen *Ensis directus* as a model species for the benthic community. This exotic species is by far the most dominant shellfish species in the Dutch coastal zone. In 2010 the total amount of *Ensis directus* in the Dutch coastal zone was estimated to be 479 million kg (Goudswaard et al., 2010). A physiological model for *Ensis directus* (DEB) will be coupled to a water quality model (Delft-3D GEM). With the water quality model the effect of sand mining on suspended solid concentrations and algae concentration and composition will be calculated. The effect on growth and performance of *Ensis directus* will be evaluated with a Dynamic Energy Budget (DEB) model (Kooijman, 1986, 2010). The DEB model is a generic physiologic model that simulates growth and development in relation to environmental conditions. Growth, however, is not the only process that influences the dynamics of a shellfish population. Mortality and recruitment are also important processes which are not explicitly modelled by a DEB model.

The purpose of the present study is to develop a DEB model and estimate specific DEB parameters for *Ensis directus*.

1.3 Approach

This report presents the DEB model for *Ensis directus*. The specific DEB parameters for *Ensis directus* are estimated with the Add_my_pet routine developed by Kooijman (2009). The data used for parameter fitting are derived from a literature research (Cardoso et al., 2011) and laboratory experiments (Kamermans et al., 2011) that were part of the present project and additional measurements with *Ensis directus* by Kamermans and Dedert (2011). Validation of the model with field observations in the Dutch coastal zone is not part of this study and will be done in a follow-up of this project. In the present study, no specific attention was paid to the formulation of the functional response and the effect of suspended sediment on the functional response (e.g. Wijsman and Smaal, 2011). In general suspended sediment will have a negative effect on the uptake rate of filterfeeding bivalves. The inorganic particles will be excreted in the form of pseudofaeces. In order to quantify the effect of sand mining on the shellfish community, the effect of suspended sediment on the physiology of *Ensis directus*, this process should be included in the functional response.

1.4 Set-up of the report

In chapter 2 a general overview of the generic Dynamic Energy Budget model is given. General formulations are given and the functional response is introduced. In chapter 3 the DEB parameters are described. The parameter estimation using the Add_my_pet routine is presented in chapter 4. In this chapter the method is described and an overview of literature data and lab experiments are given. The resulting primary DEB parameters are presented in this chapter in
Table 5. Also the results of the model are compared with the data in this chapter. In order to study the performance of the model, theoretical model simulations have been run with constant and varying environmental conditions (temperature and phytoplankton concentration). The results are presented in chapter 5. Finally in chapter 6, concluding remarks are given on the results of this study which can be useful in the application of the results in future projects.

2 The Dynamic Energy Budget (DEB) model

2.1 General structure

A Dynamic Energy Budget (DEB) model (Kooijman, 1986, 2010) 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 three state variables: structural body volume (V, cm^3), reserves (E, Joule) and reproduction buffer (R, Joule) (Figure 2). The reserves are often quantified as energy density ($[E] = E/V$, J cm^{-3}). Filterfeeding bivalves like *Ensis* 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 feaces. 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.

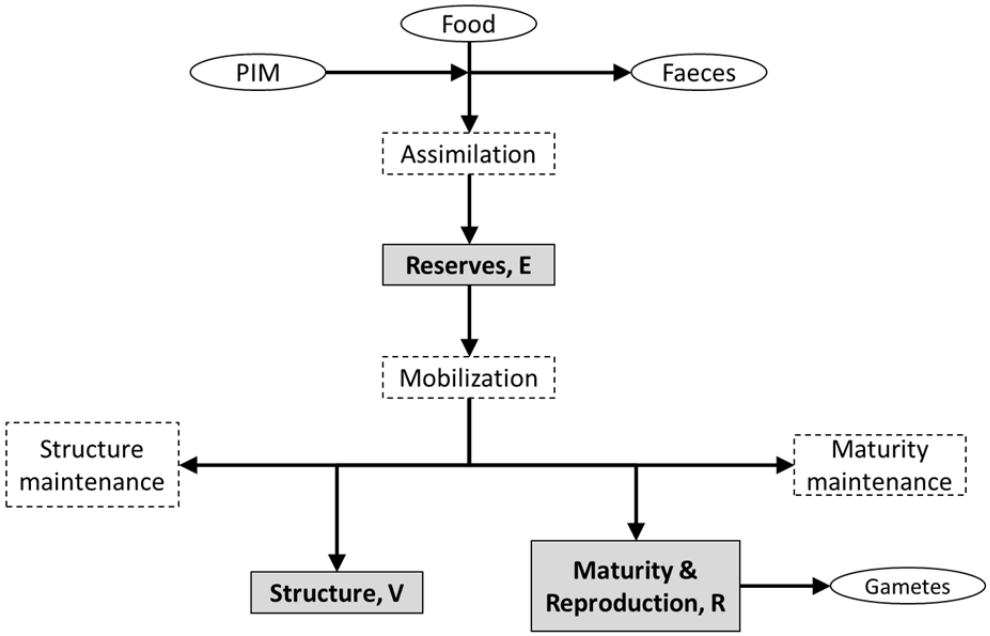

Figure 2: Schematic presentation of the DEB model.

2.2 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).

$$\dot{k}(T) = \dot{k}_1 \cdot e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)} \cdot \frac{\left(1 + e^{\left(\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_1}\right)}\right)}{\left(1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}\right)}$$

Length can be calculated from structural volume through the shape coefficient (δ_m).

$$L = \cdot \frac{V^{1/3}}{\delta_m}$$

2.3 Functional response

The relation between food uptake and food density is described by a scaled hyperbolic functional response *f* (Figure 3). At increased concentration of inorganic particles, a part of the filtered material is excreted as pseudo-faeces (e.g.Kooijman, 2006).

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

with $K'(Y) = X_K\left(1 + \frac{Y}{Y_K}\right)$

X is the food concentration, expressed in (µg chl-a l^{-1}), X_K is the half saturation constant (µg chl-a l^{-1}). *Y* is the concentration of particulate inorganic matter (TPM-POM) expressed in mg l^{-1} and Y_K is the saturation constant for particulate inorganic matter (mg l^{-1}). If the amount of suspended sediment in the water increases, the variable *K'(Y)* increases and more food is needed in order to reach the same value for the functional response *f*.

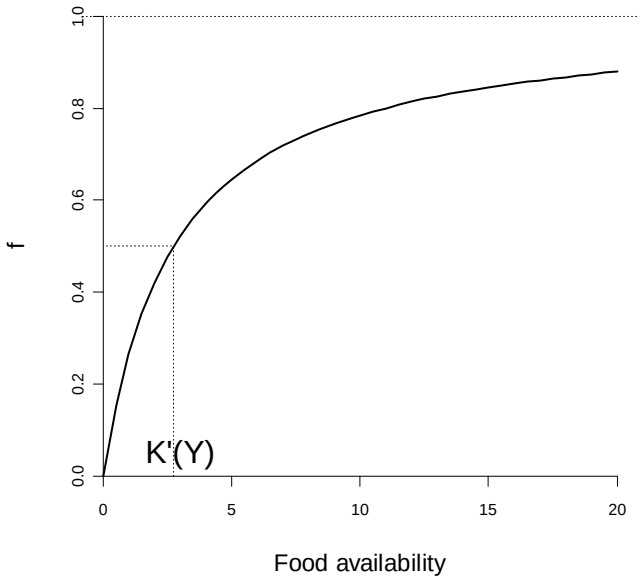

Figure 3: Functional response relation. At infinite food availability, the relative food uptake rate is maximum (f=1). When food availability is K'(Y), the food uptake rate is half the maximum uptake rate (f=0.5).

In this study, food (X) is composed both of chl-a and particulate organic matter (POM). POM is composed of a living fraction (mainly phytoplankton) and a non-living part (detritus). The detritus part consists of a range of various components with different digestibility. Only a fraction can be used by the razor clams as food. The quality of seston as a food source depends on the composition of the edible fraction, the phytoplankton fraction and the labile detritus. The contribution of POM to X is scaled by a scaling factor α (µg chl-a mg^{-1} POM).

$$X = Chla + \alpha \cdot POM$$

The value of f varies from 0 (no food uptake) to 1 (maximum food uptake). When the available amount of food equals X_K, food uptake rate is half the maximal uptake rate. A typical vale for Y_K is for bivalves (cockles and mussels) is about 100 mg l^{-1} (Prins et al., 1991; Rueda et al., 2006).

2.4 Assimilation

In standard DEB models, energy ingestion rate (p_I, J d^{-1}) is proportional to the maximum specific energy ingestion rate ($\{J_{Xm}\}$, J d^{-1} cm^{-2}), the scaled functional response f and the surface area ($V^{2/3}$, cm^2).

$$p_I = \{J_{Xm}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T)$$

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

$$p_A = \{p_{Am}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T)$$

where $\{p_{Am}\}$ is the maximum surface-area specific assimilation rate (J d^{-1} cm^{-2}).
The ratio $\{J_{Xm}\}/\{p_{Am}\}$ 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:

$$\frac{dE}{dt} = p_A - p_C$$

2.5 Growth and somatic maintenance

The utilization rate (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.

$$p_C = \left(\frac{[E]}{\kappa\cdot[E]+[E_G]}\right)\cdot\left(\frac{\{p_{Am}\}\cdot[E_G]}{[E_m]}\cdot V^{\frac{2}{3}} + [p_M]\cdot V\right)$$

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

The energy flow required for maintenance is

$$p_M = [p_M]\cdot V$$

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

$$\frac{dV}{dt} = GR = \frac{\kappa\cdot p_c - [p_M]\cdot V}{[E_G]}$$

Where GR is the growth rate of structural biomass. When energy required for maintenance [p_M] is higher than the energy available for growth and maintenance ($\kappa\, p_C$) 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.

2.6 Maturity and reproduction

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

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

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

2.7 Spawning

Spawning events occur when enough energy is allocated in the gonads and when the water temperature is above a threshold value. The gonads are released from the buffer with a specific rate of 2% per day until the temperature drops below the threshold value or all the gonads are released.

2.8 Conversions

The body mass in terms of ash-free dry weight (g), can be obtained by summing-up the ash-free dry weight of the state variables V, E and R.

$$AFDW = \psi_{AFDW\_WW} \cdot \rho \cdot V + \frac{(E+R)}{[\mu_E]}$$

where AFDW is the ash-free dry weight (g), ρ is the density of the flesh (1 g cm^{-3}), μ_E is the energy content of the reserves in ash-free dry mass (J g^{-1}) and Ψ_{AFDW_WW} is the conversion factor from wet weight to AFDW (g AFDW g Wet $weight^{-1}$).

The AFDW can be converted into wet weight using the relation

$$WW = \frac{AFDW}{\psi_{AFDW\_WW}}$$

3 DEB Parameters

3.1 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., 2011). 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 1. Auxiliary parameters primarily converts various measurements and quantify the effect of temperature on the rates. The auxiliary parameters are listed in Table 2.

3.2 Core DEB parameters

Table 1: 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	-	Faecating efficiency
$\dot{\upsilon}$	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
$\ddot{h}_a$	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 ($\dot{\upsilon}$,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 osmo-regulation 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 and of structure. 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 ($\ddot{h}_a$, 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.

3.3 Auxiliary parameters

Table 2: Auxiliary parameters and temperature and scaling parameters

Parameter	Unit	Description
δ_M	-	Shape coefficient
d_o	g cm^{-3}	Specific densities
μ_o	J mol^{-1}	Chemical potentials organic materials
μ_M	J mol^{-1}	Chemical potentials inorganic materials
η_o	-	Chemical indices
w_o	g mol^{-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 to volumetric structural length. Structural volume (V) can be calculated from the length (L) using the shape factor by:

$$V = (\delta_M L)^3$$

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

Specific densities
The specific densities, $d_o = \begin{pmatrix} d_X & d_V & d_E & d_P \end{pmatrix}$ convert volumes to grams for food (*X*), structure (*V*) reserve (*E*) and faeces (*P*).

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

Chemical indices
The chemical indices $\eta_o = \begin{pmatrix} \eta_X & \eta_V & \eta_E & \eta_P \end{pmatrix}$ 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, $\eta_M = \begin{pmatrix} \eta_C & \eta_H & \eta_O & \eta_N \end{pmatrix}$ 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: $w_o = \begin{pmatrix} w_C & w_H & w_O & w_N \end{pmatrix}$.

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 increase the effect of temperature.

Temperature tolerance range
Lower (T_L) and upper (T_U) 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.

4 Parameter estimation

4.1 Method

The primary DEB parameters Table 1 and Table 2 are often rather cryptic and usually not easy to measure. Using the formulations within the DEB model, however, many physiological quantities can be written as functions of the primary DEB parameters. In this way DEB parameters can be estimated by fitting model results to observations.

The Add_my_pet routine (Kooijman, 2009) is developed by Kooijman to collect the primary DEB parameters of various animal species, based on the covariation method (Lika et al., 2011). In this method, the primary DEB parameters are estimated by an iterative fitting routine called Nelder Mead's simplex method. This method is computationally intensive but relative robust. The method uses the weighted least squares criterion.

In this study, the add-my-pet procedure is run under Matlab (version 7.11.0.584).

The Add-my-pet makes use of two different files:

- Mydata_Ensis_directus.m: Data, weight coefficients, initial values
- Predict_Ensis_directus.m: Matlab code to relate the data to primary DEB parameters.

Both matlab files can be found in the Add_my_pet library (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/mydata/index.php)

4.2 Data used in parameter estimation

Measured and literature data can be used for the fitting routine (real data). This data can be zero-dimensional (e.g. ultimate length, size at puberty) or univariate (e.g. growth curve). The real data are supplemented with pseudo-data, which are typical values for a generalised animal (Kooijman, 2010). Weighting coefficients can be applied to the data in order to force the fitting. The procedure results in a set of DEB parameters with the best fit where the weighted sums of squared deviations between model predictions and observations is minimized.

4.2.1 Zero-variate data

Zero variate data refer to single numbers (zero dimensional; e.g. maximum length, age at puberty), whereas uni-variate data are one-dimensional (e.g. length versus age; length versus weight). The zero-variate data (Table 3) for *Ensis directus* are derived from the literature study that was part of the present study.

Table 3: Zero-variate data used in the parameter estimation

Symbol	Unit	value	Description
L_0	cm	0.0067	Egg diameter
a_b	d	5	Age at birth at temperature 291 °K
L_b	cm	0.0136	Length at birth at temperature 291 °K
a_j	d	15.5	Age at settlement
L_j	cm	0.045	Length at settlement at temperature 291°K
a_p	d	492	Age at puberty
L_p	cm	4.841	Length at puberty at temperature 285°K
W_d^p	g AFDW	0.08622	Weight at puberty
L_{730}	cm	8.0	Physical length at 730 days at temperature 285°K
L_{1825}	cm	15.0	Physical length at 1825 days at temperature 285°K
$L_{w\infty}$	cm	17.1	Maximum physical length at temperature 285°K
$W_{d\infty}$	g AFDW	1.831	Ultimate weight
GSI_m	-	0.025	Maximum gonado-somatic index
a_m	d	2555	Mean maximum life span
CR_∞	$dm^3\ h^{-1}$	5.2	Maximum clearance rate at temperature 285°K

Birth and settlement

During spawning, the eggs of *Ensis directus* are about 64-70 µm (Kenchington et al., 1998) (L_0 = 0.0067 cm). During spawning, eggs and sperm are released into the water where fertilization occurs. In an experimental set-up at 18°C, the early veliger stage, known as the D-larva stage because of the characteristic "D" shape of the shell valves was reached after 5 days (a_b = 5 d) (Kenchington et al., 1998). The larvae have at that moment an average size of 136 µm (L_b = 0.0136 cm). Settlement takes place after about 15 days (a_j = 15 d), when the larva reached the pediveliger stage at a size of about 245 µm (L_j = 0.0245 cm) (Kenchington et al., 1998)

Age and size at puberty

Sexual maturation is reached after one year. Data from Cardoso show that the youngest individuals with developing gonads were 492 days old (a_p =294 d), had a shell length of 4.841 cm (L_p =4.841 cm) and an ash-free dry weight of 0.08622 g (W_d^p =0.08622 g) (Cardoso et al., 2011). Assuming a AFDW/DW ratio of 0.83 (Ricciardi and Bourget, 1998), the dry weight size at puberty is 0.101 g DW.

Length at age

Ensis directus reaches a size of about 80 mm in two years (L_{730} = 8 cm) and after 5 years it is about 150 mm (L_{1825} = 15 cm) (Cardoso et al., 2011). The maximum age reported in literature for *Ensis directus* was 7 years (a_m =2555 days) (Armonies and Reise, 1999). The maximum size reported in Europe was 18.6 cm in the German waters. Maximum observed size was 17.1 cm in the intertidal of the western Wadden Sea ($L_{w\infty}$ = 17.1 cm), however, the species can reach more than 20 cm in the western Atlantic coast (Kenchington et al., 1998). The largest size of *Ensis directus* in the data from Cardoso was

1.831 g AFDW ($W_{d\infty}$ =1.831 g). Assuming a AFDW/DW ratio of 0.83 (Ricciardi and Bourget, 1998), the ultimate weight is 2.206 g DW

Reproduction

There are not many data on reproduction of *Ensis directus* (Cardoso et al., 2007a; Cardoso et al., 2009; Cardoso et al., 2007b). In general the gonadosomatic ratio of *Ensis directus* is very low. Just before the spawning period, only 2.5% of the body mass of *Ensis directus* consisted of gonads.(Cardoso et al., 2009) (GSI_m =0.025).

Clearance rate

Filter feeders such as *Ensis directus* filter food particles from the water column with their gills. There is hardly any information on filtration rate of *Ensis directus* or other razor clams. Witbaard and Kamermans (2009) measured the filtration rate of Ensis directus under different algal concentrations and silt content in the water. Filtration rate varied between 0.4 and 5.3 l h^{-1} (CR_∞ = 5.3 l h^{-1}).

4.2.2 Uni-variate data

Uni-variate data are data that relate dependent data (response variable) to a single type of independent data (explanatory variable). The relations come both from literature as from field observations and lab-experiments. In the Add_My_pet, four types of uni-variate data are used

- Length at age data
- Length-weight data
- Oxygen consumption as a function of shell length
- Clearance rate as a function of shell length

Length at age data

Length at age data for *Ensis directus* are derived from animals collected monthly in a subtidal area of the western Dutch Wadden Sea (53° 10′ N, 5° 22′ E), from November 2001 to January 2003 (Cardoso et al., 2011) (Figure 4). Individuals were randomly collected with a 'Reineck' box corer (0.06 m^2) in an area of 1–2 km^2 at a water depth of about 2.5 m. In the laboratory, shell length of each individual was measured to the nearest 0.01 mm total length (range: 8.5–141.0 mm) and age was determined by analysing the external shell year marks. It is assumed that the individuals are born at Julian day 189, which corresponds to the beginning of June, which fits with the settlement period described by Beukema and Dekker (1995) and Cardoso et al.(2009).

Length-weight data

In this study the length-weight relationship was determined from data of *E. directus* that has been retrieved from the IMARES database (Figure 5). A total of 780 individuals collected in various cruises were selected for analysis. From each individual, shell length (mm) and fresh weight (g) was measured (Cardoso et al., 2011). The largest individual from the dataset was 14.1 cm.

Oxygen consumption as a function of shell length

The results of the oxygen consumption rates were derived from incubation experiments that were done in the framework of the present study (Kamermans et al., 2011). Small clams were put in plastic 60-ml centrifuge tubes and left undisturbed for 10 to 20 minutes. The big clams where put in plastic 1-liter containers and left undisturbed for 1 to 2 hours. The data presented are averaged values of 6 to 24 measurements (Figure 6).

Clearance rate as a function of shell length

Clearance rates were measured in experimental flow-through systems (Kamermans et al., 2011) (Figure 7). Clearance rates was calculated from the difference between the concentration of algal cells in the incoming and outflowing water.

$$CR = \frac{[cells_{in}] - [cells_{out}]}{[cells_{out}]} \times Q$$

Where *CR* = clearance rate (l h^{-1}), *Q* = flow rate (l h^{-1}); [$cells_{in}$] is the concentration of algal cells in the incoming water (# cells l^{-1}) and [$cells_{out}$] is the concentration of algal cells in the outflowing water (# cells l^{-1}). The clearance rates were measured 5 to 10 times per animal. The data in Figure 7 show the averaged values of these replicates.

The experiments showed that it is not easy to measure clearance rates with *Ensis directus*. The razor clams are easily disturbed which lead to lower clearance rates. The clearance rates of the measurements in 2010 were low and there was no clear increase with body size. The razor clams were derived from a growth experiment and they were in poor condition which resulted in low clearance rates (Kamermans et al., 2011). In 2011, the clearance rate experiments were repeated with fresh razor clams and varying algae concentrations (6 µg l^{-1} and 15 µg l^{-1}) and suspended sediment concentrations (0, 50, 150 and 300 mg l^{-1}). Highest clearance rates were found at low food concentrations (6 µg Chl-a l^{-1}) and without suspended sediment concentrations (0 mg l^{-1}). Therefore these data were used in the parameter fitting. Three datapoints were not used in the model fitting (open dots in Figure 7). Those clams might have been disturbed and did not filter at their maximum rate.

4.2.3 Pseudo data

The pseudo data include primary DEB parameters from a standard DEB organism (Table 4, Table 8.1 of Kooijman 2010). The pseudo data supplement the real data, if necessary, to provide enough information for all parameters to be estimated.

Table 4: Pseudo data uses in the Add_my_pet routine. Pseudo data derived from Table 8.1 of Kooijman 2010).

Symbol	Value	Unit	Description
$\dot{v}$	0.02	cm d^{-1}	Energy conductance
κ	0.8	-	Allocation fraction to soma
κ_R	0.95	-	Reproduction efficiency
$[\dot{p}_M]$	18	J d^{-1} cm^{-3}	Volume specific somatic maintenance costs
$[\dot{p}_T]$	0	J d^{-1} cm^{-2}	Surface specific somatic maintenance costs
$\dot{k}_J$	0.002	d^{-1}	Maturity maintenance rate coefficient
$[E_G]$	2800	J cm^{-3}	Specific costs for structure

4.2.4 Conversion data

Specific density (g cm^{-3}) for food, structure reserve and faeces:

$$d_o = (0.1 \quad 0.1 \quad 0.1 \quad 0.1)$$

Chemical potential (J mol^{-1}) for organic components (Food, Structure, Reserves and Faeces)

$$\mu_o = (525000 \quad 472745 \quad 474400 \quad 480000)$$

Chemical indices to relate the frequency of the chemical elements (C, H, O and N, rows) to the organic compounds (food, structure, reserves and faeces, columns). All data in the matrix are relative to the carbon content. The first column shows that the food is composed of 1.00 C/C, 1.80 H/C, 0.50 O/C and 0.20 N/C.

$$\eta_o = \begin{pmatrix} 1.00 & 1.00 & 1.00 & 1.00 \\ 1.80 & 1.78 & 1.79 & 1.80 \\ 0.50 & 0.48 & 0.53 & 0.50 \\ 0.20 & 0.15 & 0.14 & 0.15 \end{pmatrix}$$

The molecular weights of elements C, H, O and N (g mol^{-1}) of food, structure, reserves and faeces.

$$w_o = \begin{pmatrix} 12 & 1 & 16 & 14 \end{pmatrix} \cdot \eta_0$$

4.2.5 Weight coefficients

Weight coefficients can be used to quantify the "quality" and variation of the data. The higher the weight factor, the more effect a difference between model and measurement has to the total sum of squares. All pseudo data have a low weight coefficient during the fitting procedure. As a consequence, the pseudo data have not much influence on the calculation of the weighted least squares. The weight coefficient of CR_∞ was set to zero. The weight coefficients of L_{1825} and $L_{w\infty}$ were multiplied by 100 and the weight coefficient of the uni variate data were multiplied by 10.

4.3 Results

The primary DE B parameters for *Ensis directus* are given in Table 5. The parameters z, $\{\dot{F}_m\}$, $\dot{\upsilon}$, $[\dot{p}_M]$, $\dot{k}_J$, $[E_G]$, E_H^b, E_H^p and $\ddot{h}_a$ were free-fitted. The other parameters were fixed (grey in Table 5).

Table 5: Primary DEB parameters Ensis directus. Parameters that were fixed in the calibration procedure are marked as grey-shaded rows.

Parameter	Value	Unit	Description
z	3.397	-	Zoom factor
$\{\dot{F}_m\}$	35.62	l d^{-1} cm^{-2}	Maximum surface-area-specific filtration rate
κ_X	0.8	-	Digestion efficiency
$\dot{\upsilon}$	0.07684	cm d^{-1}	Energy conductance
κ	0.9731	-	Allocation fraction to soma
κ_R	0.95	-	Reproduction efficiency
$[\dot{p}_M]$	31.03	J d^{-1} cm^{-3}	Volume-specific somatic maintenance
$\{\dot{p}_T\}$	0	J d^{-1} cm^{-2}	Surface-specific somatic maintenance
$\dot{k}_J$	2.262x10^{-3}	d^{-1}	Maturity maintenance rate coefficient
$[E_G]$	2372	J cm^{-3}	Specific cost for structure
E_H^b	5.65x10^{-4}	J	Maturity at birth
E_H^j	6.92x10^{-4}	J	Maturity at metamorphosis
E_H^p	60.11	J	Maturity at puberty
$\ddot{h}_a$	6.35x10^{-8}	d^{-2}	Weibull ageing acceleration
s_G	1.0x10^{-4}	-	Gompertz stress coefficient

The correspondence of the model with the uni-variate data is presented in Table 6. The pseudo data are in the lower part of the table. As can be seen from the table, most of the parameters are quite well fitted. The model underestimates the ages at birth, settlement and puberty and overestimates the length at birth and puberty. The length at age data are relatively well modelled although the ultimate length is lower than the maximum length observed in the field. The weight value for the maximum clearance rate was set to zero.

Table 6: Univeriate data Ensis directus. Pseudo data are presented in the grey-shaded rows. The observed value is given in the fourth column and the modeled value is in the last column.

Symbol	Unit	Description	Data	Model
a_b	d	age at birth	5	1.207
L_b	cm	physical length at birth	0.0136	0.1002
a_j	d	age at settlement	15.5	2.167
L_j	cm	physical length at settlement	0.045	0.1071
a_p	d	age at puberty	492	212.7
L_p	cm	physical length at puberty	4.841	4.308
W_d^p	g	AFDW at puberty	0.08622	0.1017
L_{730}	cm	physical length at 730 d	8	10.07
L_{1825}	cm	physical length at 1825 d	15	13.56
$L_{w\infty}$	cm	ultimate physical length	17.1	14.22
$W_{d\infty}$	g	ultimate AFDW	1.831	3.657

Symbol	Unit	Description	Data	Model
GSI_m	-	gonado-somatic index	0.025	0.06383
a_m	d	life span	2555	2555
CR_∞	l h^{-1}	maximum clearance rate	5.3	7.055
$\dot{\nu}$	cm d^{-1}	energy conductance	0.02	0.07684
κ	-	allocation fraction to soma	0.8	0.9731
κ_R	-	reproduction efficiency	0.95	0.95
$[\dot{p}_M]$	J $d^{-1}.cm^{-3}$	vol-spec som maint	18	31.03
$[\dot{p}_T]$	J $d^{-1}.cm^{-2}$	surf-spec som maint	0	0
$\dot{k}_J$	d^{-1}	maturity maint rate coefficient	0.002	0.002262
κ_G	-	growth efficiency	0.8	0.8818

4.3.1 Length at age

From Figure 4 it can be seen that there is a large variation in length measurements at a certain age. This is partly due to the errors in age determination (in terms of days) and the variation in the field as a function in environmental conditions. The model fits the data very well. The resulting growth curve increased to a maximum length of 14.2 cm. The largest razor clams in the data are 14 cm as well.

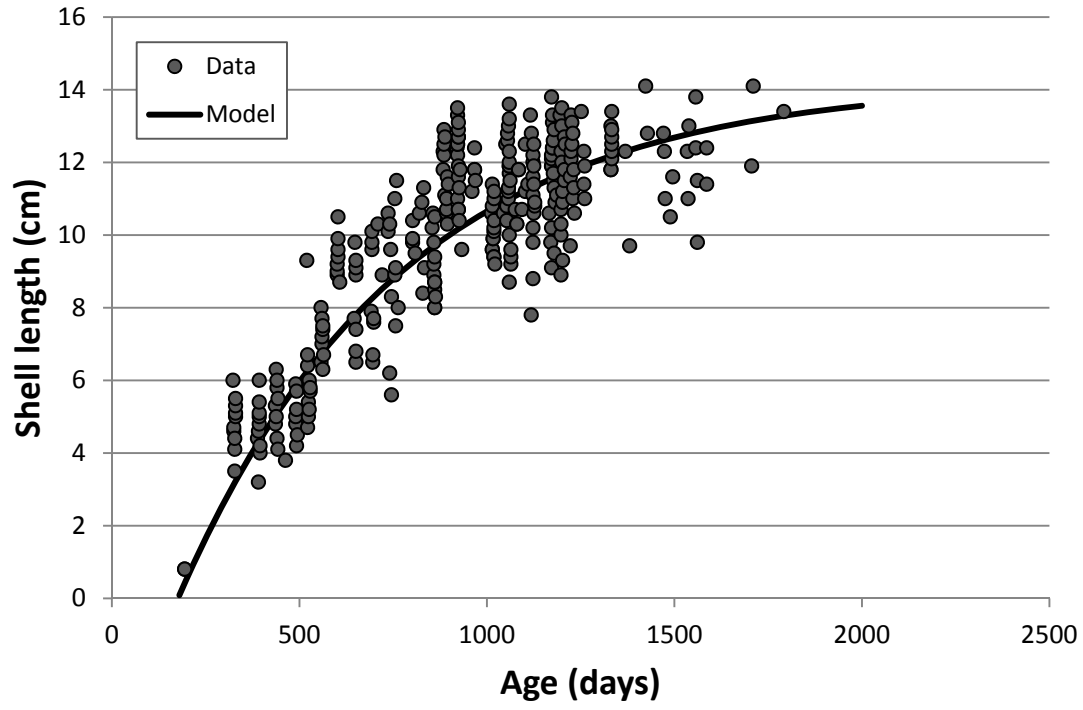

Figure 4: Shell length (cm) as a function of age (days since January 1st of the year of birth). Dots indicate data (Cardoso et al., 2011) and the solid line represents the results of the fitted model. The data are derived from the Wadden Sea

4.3.2 Length-weight relation

The model results for fresh weight as a function of shell length are presented in Figure 5 together with the observations. The corresponding shape factor (δ_M) is 0.2043. Also for these data there is a good correspondence between model and observations.

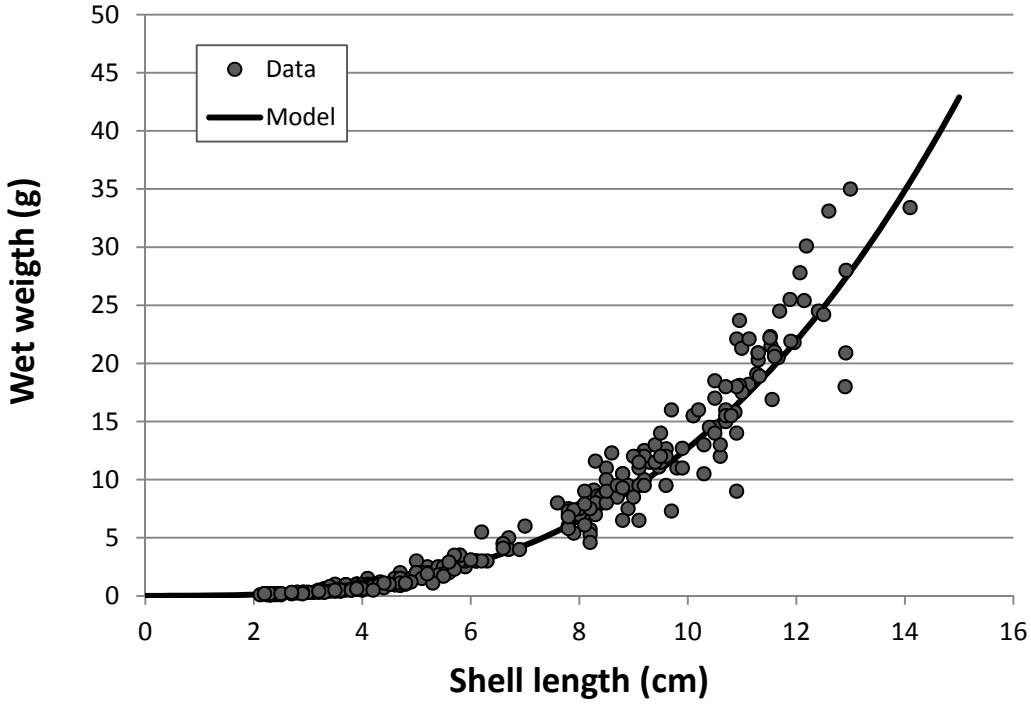

Figure 5: Ensis directus fresh wet weight (g) as a function of shell length (cm). Dots indicate data derived from the IMARES database (780 individuals). The solid line represents the results of the fitted model.

4.3.3 Oxygen consumption as function of shell length

The modelled oxygen consumption rate is slightly lower than measured in the lab experiments (Figure 6). The oxygen consumption rate of razor clams with a shell length of 11 cm is underestimated by 30%. At smaller shell sizes the differences are less.

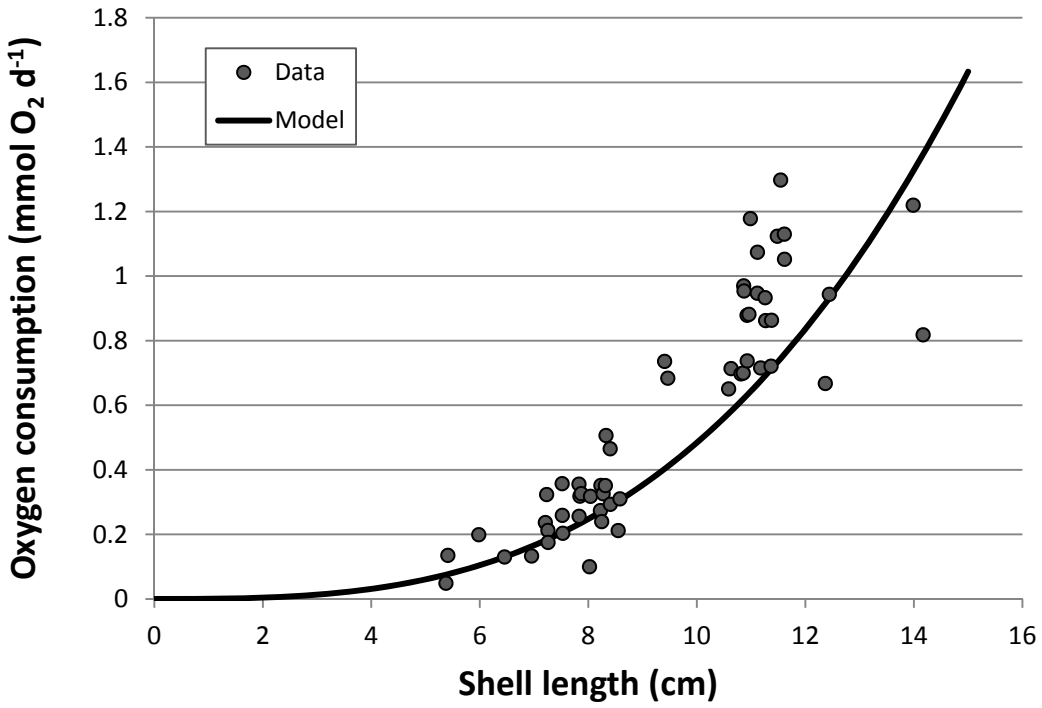

Figure 6: Oxygen consumption (mmol O_2 d^{-1}) of Ensis directus as a function of shell length (cm). Dots are the results of the lab experiments (Kamermans et al., 2011). The solid line represents the results of the fitted model.

4.3.4 Clearance rate as a function of shell length

The model was fitted with the clearance rate data from 2011 (Figure 7). The data from 2010 were very low (triangles in Figure 7) and it is assumed that the clams did not filter optimally due to the poor condition after the growth experiment of almost 3 months . The data from 2011 show higher clearance rates indicating that these razor clams had a better condition. The clams used in the 2011 experiment were fresh and were not previously used in a growth experiment. Only three measurements (indicated by open dots in Figure 7) show low clearance rates and they were not used in the parameter estimation. This resulted in a good fit between modelled data and observations.

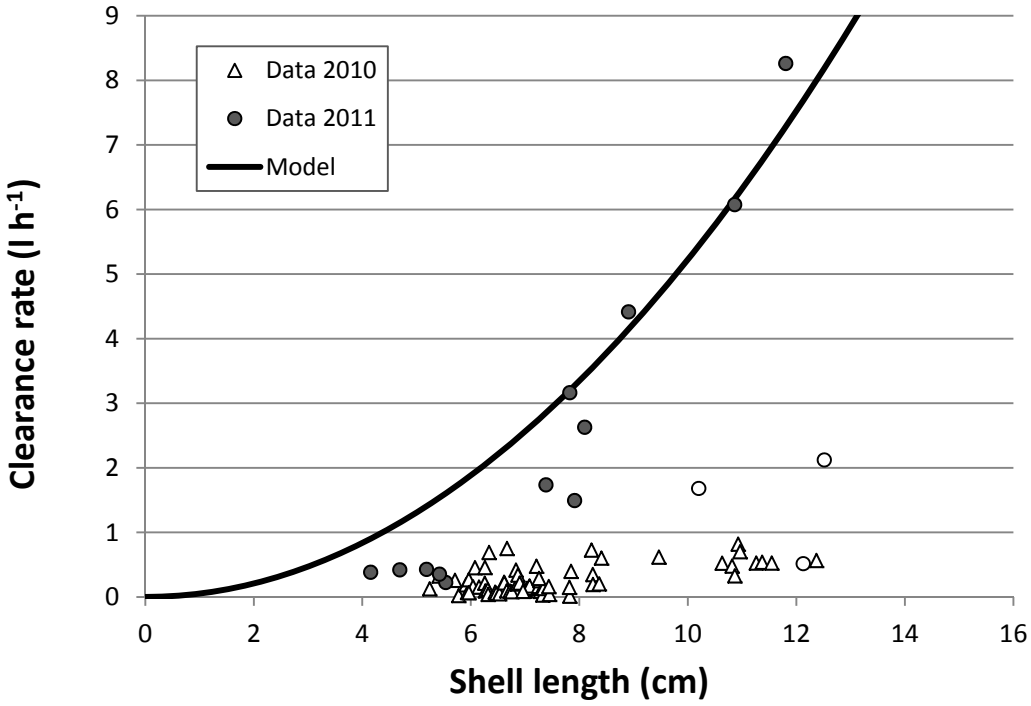

Figure 7: Clearance rate (l h^{-1}) of Ensis directus as a function of shell length (cm). Open triangles are the results of the lab experiments from 2010 (Kamermans et al., 2011). Dots are the results of the lab experiments in 2011 (data Kamermans). The open dots and the triangles are not used in the model fitting. The solid line represents the results of the fitted model using part (black dots) of the 2011 data.

5 Model simulations

In order to visualise the performance of the model with the fitted parameters for *Ensis directus*, various experimental model simulations have been executed with the standard DEB model and the primary DEB parameters for *Ensis directus* (last column of Table 6). The models were run in R, using the package FME. All simulations started with recruitment at day = 180. The parameters for the functional response were set to $\alpha = 0$ (detritus is not used as a food source) and $X_K = 0.75$ µg Chla l^{-1}. Suspended sediment was not taken into account. It is assumed that spawning occurs when the water temperature is above 18.4 ºC and when the gonado-somatic index is higher than 0.06383 (Table 6).

Three different type of model simulations were run with the standard model. The simulations differed from each other in the forcing functions (water temperature and Chlorophyll-a concentration):

A. Constant temperature and food conditions. Temperature was set to 12.5 ºC and Chlorophyll-a concentration was kept constant at 1, 2 and 10 µg l^{-1}.
B. Variable temperature and constant food conditions. A seasonal varying water temperature was used, ranging between 3 and 23 ºC and the Chlorophyll-a concentration was kept constant at 1, 2 and 10 µg l^{-1}.
C. Variable temperature and variable food conditions. A seasonal varying water temperature was used, ranging between 3 and 23 ºC. For the standard simulation, the Chlorophyll-a concentration varied seasonally between 0.5 and 14 µg l^{-1} (average 4.1 µg l^{-1}). In the alternative simulations, the Chlorophyll-a concentrations from the standard simulations were multiplied with 2 and 0.5, respectively.

5.1 A: Constant food and constant temperature

In Figure 8, the forcing functions for exercise A are given. Temperature was kept constant and the same for all simulations. Chlorophyll-a concentration was kept constant, but varied between the different simulations (1, 2 and 10 µg Chl-a l^{-1}, respectively). The third panel represents the resulting functional response. It can be seen from this figure that the variation of Chl-a at the low concentrations have more effect on the functional response (f) that at the higher concentrations. This is due to the form of the functional response (monod-type).

The model results (Figure 9) show that the differences in food conditions is reflected in the growth and ultimate length of the shellfish. At a constant food level of 10 µg Chl-a l^{-1}, the maximum size is about 15 cm, while at 1 µg Chl-a l^{-1} the razor clams stay below 10 cm. These differences are even more pronounced in the body mass (AFDW). This is because at low food conditions less energy is stored in reserves and gonads. Reproduction does not occur since the temperature threshold of 18.4 ºC is not reached.

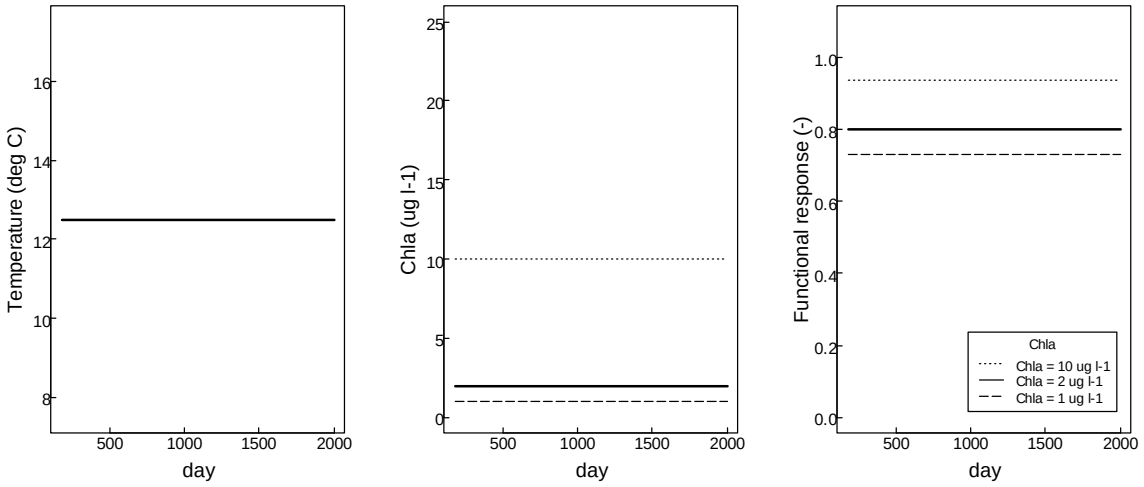

Figure 8: Forcing functions and functional response for model simulation A. Constant temperature (12.5 °C) and constant Chlorophyll-a levels (1, 2 and 10 µg l^{-1})

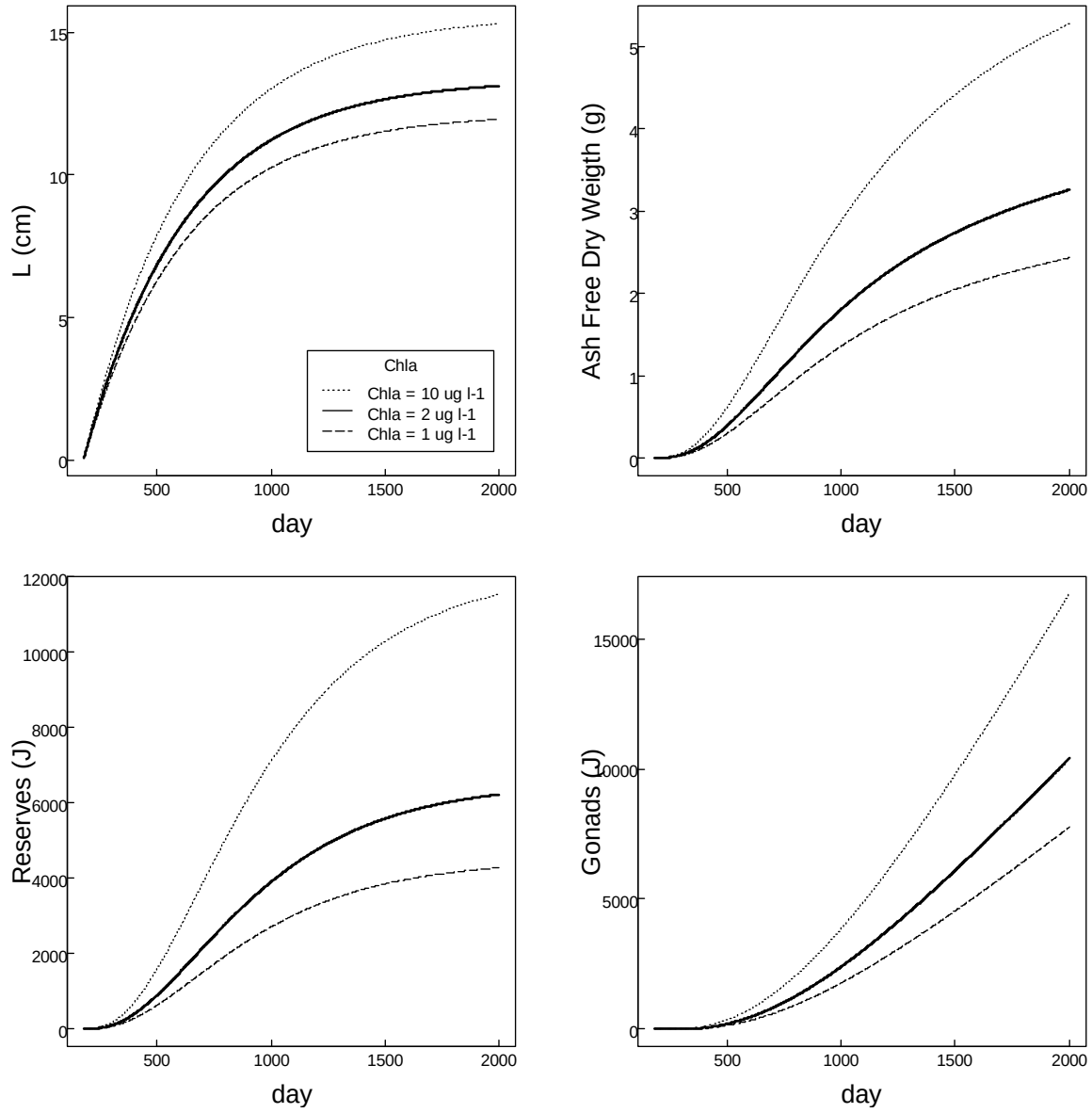

Figure 9: Total length (cm), Ash-free dry weigth (g), Energy content of reserves (J) and energy content of gonads (J) for the three different constant Chlorophyll-a levels (1, 2 and 10 µg l^{-1})

5.2 B: Constant food and variable temperature

In Figure 10, the forcing functions for exercise B are given. The water temperature varied seasonally, with minimum values of 3 ºC and maximum values of 23 ºC. The same temperature forcing was repeated for 5 years. Chlorophyll-a concentration was kept constant, but varied between the different simulations (1, 2 and 10 µg Chl-a l^{-1}, respectively). Since the functional response is not depending on the water temperature, the values are the same as in Figure 8

The model results (Figure 11) show that the seasonal pattern in temperature is reflected in the growth of the razor clams. Growth is high during the summer time and stagnates at cold temperatures in the winter. Reproduction takes place in the early summer of the second year, when the water temperature exceeds 18.4 ºC. The weight loss of spawning is also reflected in the AFDW. Spawning only occurs once a

year. As in the simulations with constant temperature there is a clear effect of food concentration on the growth of the razor clams.

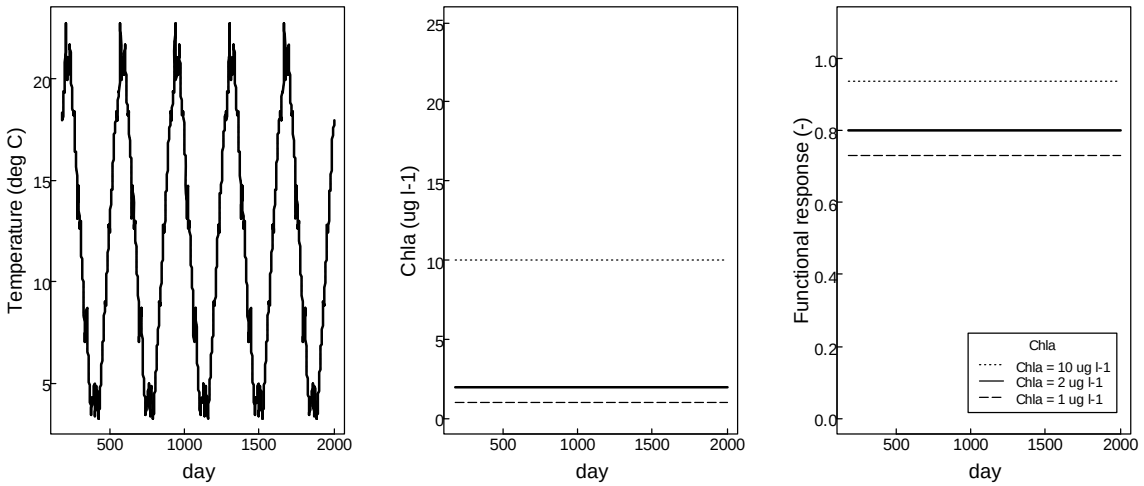

Figure 10: Forcing functions and functional response for model simulation B. Seasonal varying temperatures and constant Chlorophyll-a levels (1, 2 and 10 µg l^{-1})

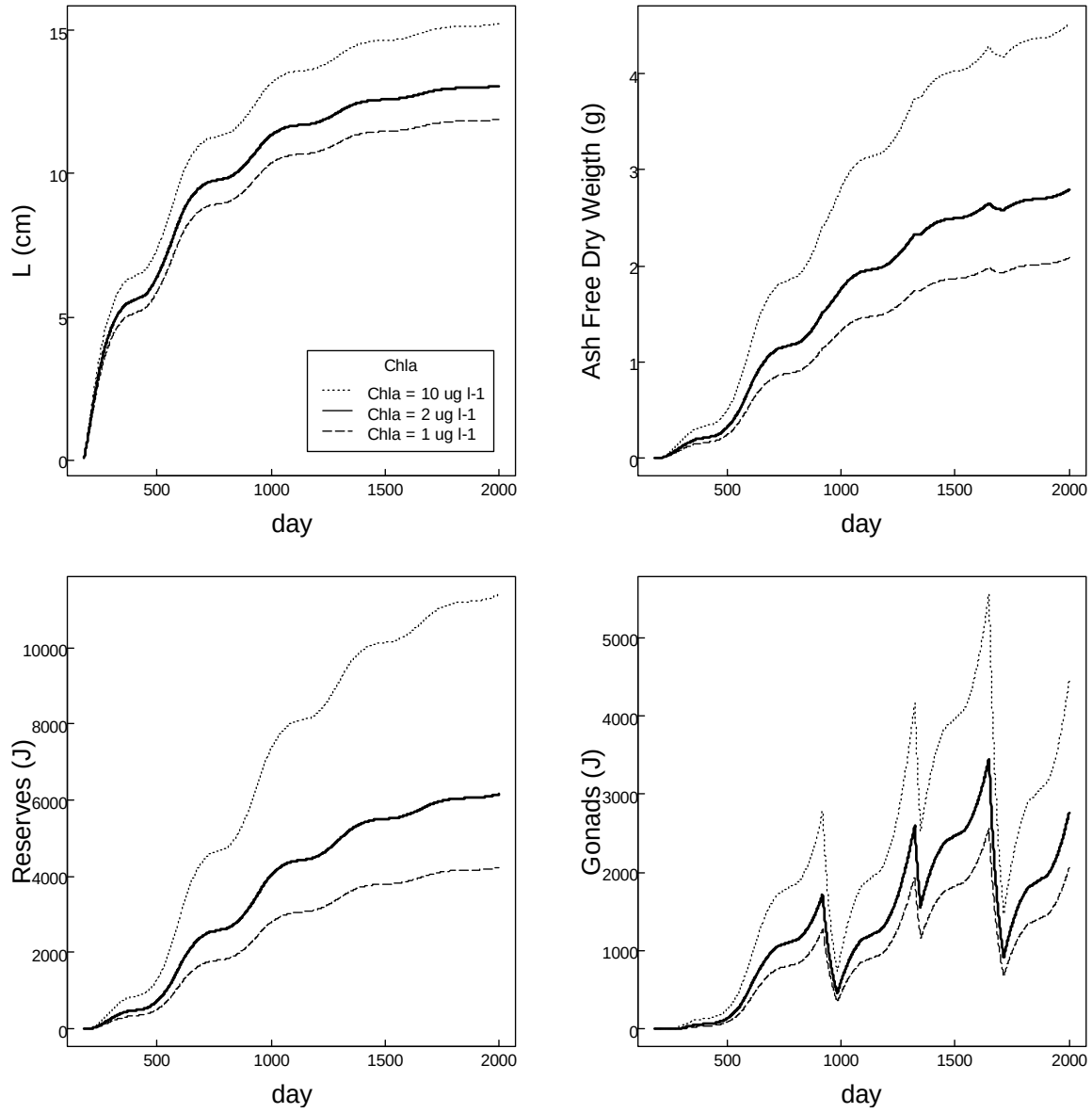

Figure 11: Total length (cm), Ash-free dry weigth (g), Energy content of reserves (J) and energy content of gonads (J) for the three different constant Chlorophyll-a levels (1, 2 and 10 µg l^{-1}) and seasonal varying temperatures.

5.3 C: Variable food and variable temperature

In Figure 12, the forcing functions for exercise C are given. The water temperature varied seasonally, with minimum values of 3 ºC and maximum values of 23 ºC. Besides the water temperature, also the Chlorophyll-a concentrations varied seasonally. For the standard situation, the Chlorophyll-a concentration varied between 0.5 µg l^{-1} in the winter and 14 µg l^{-1} in spring. In the alternative simulations, the chlorophyll-a concentrations were multiplied by 0.5 and 2 respectively. The seasonal varying temperature and Chlorophyll-a forcings were repeated for 5 years. As a result of the varying Chlorophyll-a concentrations, the functional response also showed a seasonal pattern. During late autumn and winter, the functional response reaches values of less than 3.

The model results (Figure 13) show that the seasonal pattern both temperature and chlorophyll-a is reflected in the differences the growth of the razor clams. Growth is high during the summer time and stagnates at cold temperatures in the winter. As can be seen from the figures, the simulations with the low food concentrations (Chla*0.5) stops at day 705. Due to the low food conditions and the low amount of energy reserves, there is not enough energy for maintenance. Initially some energy from the gonads is used for maintenance, but when the reproduction buffer is depleted, the razor clam dies and the simulation is stopped. The varying food conditions has a clear effect on the energy content of the reserve buffer. During winter time, the energy of the reserve buffer decreases. This is also reflected in the ash-free dry weight of the razor clams. The effect of increasing the Chlorophyll-a concentrations with a factor 2 does not have much effect on the growth of the razor clams since the functional response at the standard run is already close to 1.

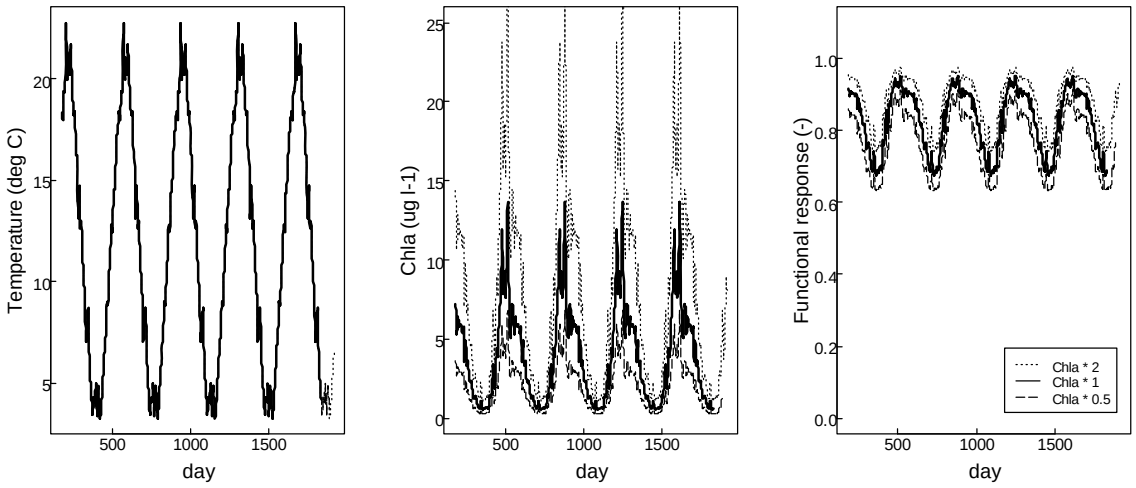

Figure 12: Forcing functions and functional response for model simulation C. Seasonal varying temperatures and Chlorophyll-a levels. Solid line represents standard concentrations, dotted line represents the standard concentrations multiplied by 2 and broken line represents the standard concentrations multiplied by 0.5.

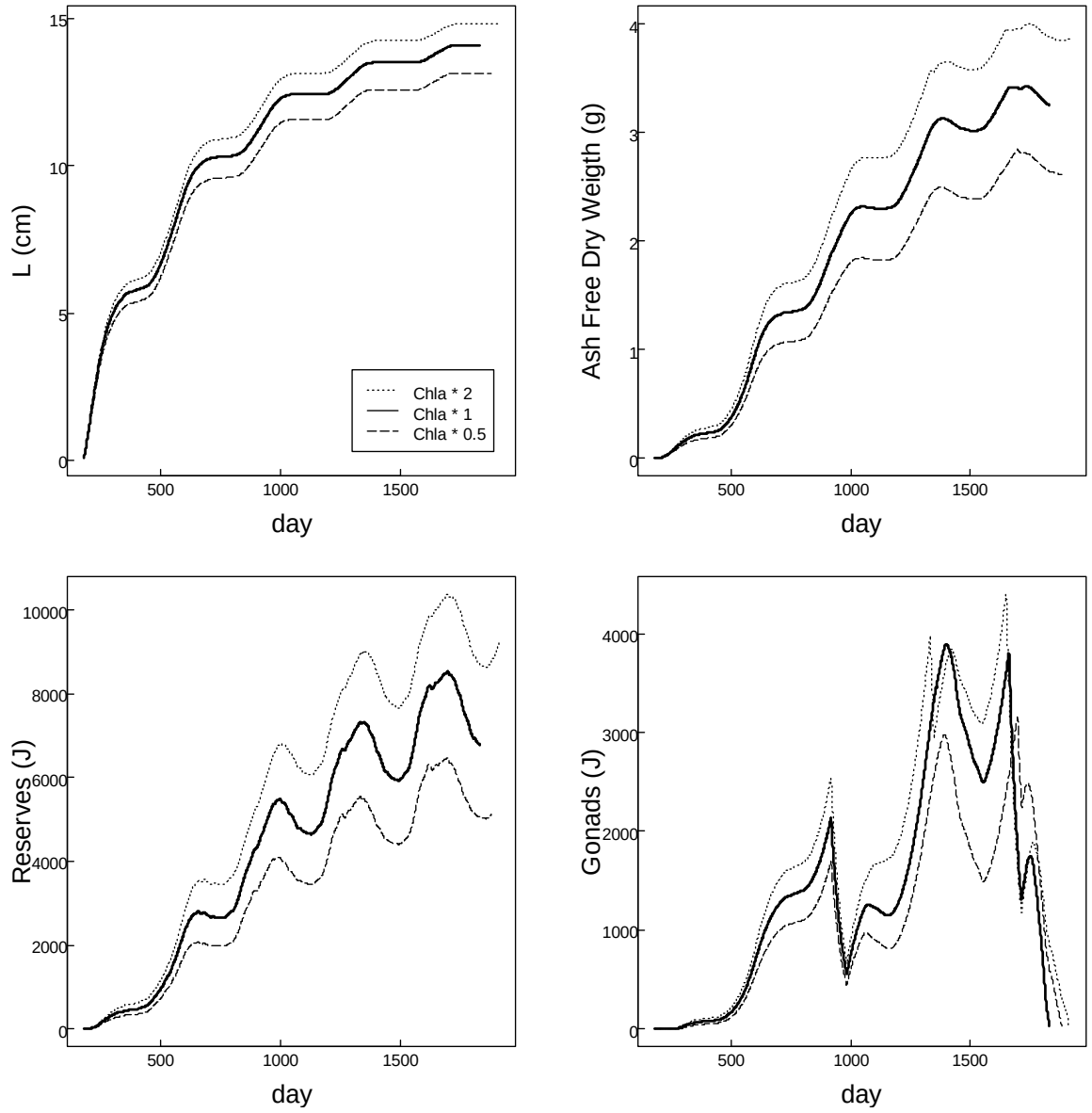

Figure 13: Total length (cm), Ash-free dry weigth (g), Energy content of reserves (J) and energy content of gonads (J) for the simulations with seasonal varying temperatures and Chlorophyll-a levels. Solid line represents standard chlorophyll concentrations, dotted line represents the standard concentrations multiplied by 2 and broken line represents the standard concentrations multiplied by 0.5.

6 Concluding remarks

The primary goal of the present study is to estimate the specific DEB parameters for *Ensis directus*. In a follow-up of this study, the model will be used to simulate the effect of changes in phytoplankton and suspended sediment concentration on the growth and development of *Ensis directus* as a model species for the benthic community. However, in order to do so, the standard model needs to be extended. In the present model the parameters of the functional response (X_K, Y_K and α) are not calibrated. Also the lab experiments that were done in the context of this project were not aimed to study the effect of suspended sediment concentration on the physiology of *Ensis directus*. In 2011, additional laboratory experiments have been done with *Ensis* at varying suspended sediment concentrations (Pauline Kamermans, IMARES). These data can be used to improve the formulation and parameter estimation of the functional response.

Validation of the model with field observations was not part of the scope of the present project. In the framework of the Environmental Impact Assessment of the sand mining in the North Sea, a monitoring campaign is carried out where the growth and development of *Ensis directus* is measured together with environmental conditions (sea water temperature, phytoplankton concentration, suspended sediment concentration). These data can be used to calibrate the functional response parameters of *Ensis directus* and/or to validate the DEB model.

Ensis directus will be used as a model species to estimate the effect of sand mining in the North Sea on the shellfish community in the coastal area. *Ensis directus* is presently by far the most dominant shellfish species in the Dutch coastal zone and is a food source for birds and fish. However, other shellfish species (e.g. *Donax vittatus*, *Spisula subtruncata*) might react differently on changes in abiotic conditions due to sand mining. Moreover, the DEB model is a physiologic model that simulates the growth and development of a species in reaction to the environmental conditions. Mortality and recruitment, which are not explicit output of the model, are also important processes that influence the total stock of razor clams. The effect of sand mining on these processes should also be quantified.

The Add_my_pet routine estimates the DEB parameters iteratively on the basis of the minimization of the weighted sum of squared deviations between predicted and observed values. The user can give weights to the data based on the "quality" of the data, the variation of the data and importance of the data. If the weight factor is higher, the model will be forced to fit better to the specific data. This gives flexibility to the user but could introduces arbitrariness. Therefore it is important to indicate the weight coefficients that have been used in the parameter fitting.

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8 Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2012. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

References

Armonies, W., Reise, K., 1999. On the population development of the introduced razor clam Ensis americanus near the island of Sylt (North Sea). Helgoländer Meeresuntersuchungen 52, 291-300.

Beukema, J.J., Dekker, R., 1995. Dynamics and growth of a recent invader into European coastal waters: The American razor clam, Ensis directus. Journal of the Marine Biological Association of the United Kingdom 75, 351-362.

Cardoso, J.F.M.F., Langlet, D., Loff, J.F., Martins, A.R., Witte, J.I., Santos, P.T., Van der Veer, H.W., 2007a. Spatial variability in growth and reproduction of the Pacific oyster Crassostrea gigas (Thunberg, 1793) along the west European coast. J. Sea Res. 57, 303-315.

Cardoso, J.F.M.F., Wijsman, J.W.M., Nieuwland, G., Van der Meer, J., Witbaard, R., Van der Veer, H.W., 2011. Determination of growth and Dynamic Energy Budget (DEB) parameters for Ensis directus (L.). Royal NIOZp.

Cardoso, J.F.M.F., Witte, J.I., van der Veer, H.W., 2009. Reproductive investment of the American razor clam Ensis americanus in the Dutch Wadden Sea. J. Sea Res. 62, 295-298.

Cardoso, J.F.M.F., Witte, J.I.J., Van der Veer, H.W., 2007b. Growth and reproduction of the bivalve Spisula subtruncata (da Costa) in Dutch coastal waters. J. Sea Res. 57, 316-324.

Goudswaard, P.C., Perdon, K.J., Kesteloo, J.J., Jol, J., Van Zweeden, C., Hartog, E., Jansen, J.M.J., Troost, K., 2010. Schelpdieren in de Nederlandse kustwateren, een kwantitatieve en kwalitatieve bestandsopname in 2010. IMARES, Yerseke, 66 p.

Holling, C.S., 1959. The components of predation as revealed by a study of small mammal predation of the European sawfly. Can. Ent. 91, 293-320.

Kamermans, P., Brummelhuis, E., Wijsman, J.W.M., 2011. First pioneering laboratory experiments on filtration, respiration and growth of the razor clam (Ensis directus, Conrad) at different food concentrations, p.

Kenchington, E., Duggan, R., Riddel, T., 1998. Early life history characteristics of the razor clam (Ensis directus) and the Moonsnails (Euspira spp.) with applications to fisheries and aquaculture. Canadian Technical Report of Fisheries and Aquatic Sciences 2223, 1-32.

Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. Journal of Theoretical Biology 121, 269-282.

Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budgets in Biological Systems. Cambridge University Press, Great Britain.

Kooijman, S.A.L.M., 2001. Quantitative aspects of metabolic organisation: a discussion of concepts. Philosophical Transactions of the Royal Society of London 356, 331-349.

Kooijman, S.A.L.M., 2006. Pseudo-faeces production in bivalves. J. Sea Res. 56, 103-106.

Kooijman, S.A.L.M., 2009. Add my pet. VU, Amsterdam, 24 p.

Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organisation, 3 ed. Cambridge university Press, Cambridge.

Lika, D., Freitas, V., Van der Veer, H.W., Van der Meer, J., Wijsman, J.W.M., Pecqerie, L., Kearney, M.R., Kooijman, S.A.L.M., 2011. Capturing species diversity with the parameters of the standard DEB model: the covariation method of estimation. J. Sea Res.

Prins, T.C., Smaal, A.C., Pouwer, A., 1991. Selective ingestion of phytoplankton by the bivalves Mytilus edulis L. and Cerastoderma edule (L.). Hydrobiological Bulletin 25, 93-100.

Ricciardi, A., Bourget, E., 1998. Weight-to-weight conversion factors for marine benthic invertebrates. Marine Ecology Progress Series 163, 245-251.

Rueda, J.L., Smaal, A.C., Scholten, H., 2006. A growth model of the cockle (Cerastoderma edule L.) tested in the Oosterschelde estuary (The Netherlands). J. Sea Res.

Van Der Meer, J.R., 2006. An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation. J. Sea Res. 56, 85-102.

Van Der Veer, H.W., Cardoso, J.F.M.F., Van Der Meer, J.R., 2006. The estimation of DEB parameters for various Northeast Atlantic bivalve species. J. Sea Res. 56, 107-124.

Widdows, J., Fieth, P., Worrall, C.M., 1979. Relationships between seston, available food and feeding-activity in the common mussel Mytilus edulis. Mar. Biol. 50, 195-207.

Wijsman, J.W.M., Smaal, A.C., 2011. Growth of cockles (Cerastoderma edule) in the Oosterschelde described by a Dynamic Energy Budget model. J. Sea Res.

Witbaard, R., Kamermans, P., 2009. De bruikbaarheid van de klepstandmonitor op Ensis directus ten behoeve van de monitoring van aan zand suppletie gerelateerde effecten. . NIOZ, Texelp.

Justification

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The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department Delta of IMARES.

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