Modelling shellfish growth with dynamic energy budget models: an application for cockles and mussels in the Oosterschelde (southwest Netherlands)

T. A. Troost^{1,*}, J. W. M. Wijsman², S. Saraiva^{3,4} and V. Freitas³

¹Deltares, PO Box 177, 2600 MH Delft, The Netherlands

²Wageningen IMARES, PO Box 77, 4400 AB Yerseke, The Netherlands

³Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, The Netherlands

⁴Environment and Energy Section, Instituto Superior Técnico, Av. Rovisco Pais, 1, 1049-001 Lisboa, Portugal

Dynamic energy budget models for growth of individual cockles (*Cerastoderma edule*) and mussels (*Mytilus edulis*) are adjusted and calibrated to the Oosterschelde by formulating and parametrizing their functional responses using an extensive set of field observations. The resulting model predictions fit the observations satisfactorily. Results indicate that food quality and the importance of detritus as a food source are site-specific as well as species-specific. Despite these differences in their calibrated parameter values, both species show a very similar functional response. Compared with other systems, however, the functional responses of mussels in the present study are clearly higher than those of mussels in other systems. This may be explained by the absence of intra-specific competition in the measurement set-up that was used, and therefore supports the idea that the generally small functional response of *M. edulis* is caused by intra-specific competition.

Keywords: functional response; *Mytilus edulis*; *Cerastoderma edule*; Oosterschelde; dynamic energy budget

1. INTRODUCTION

In shallow water and coastal ecosystems, shellfish can have a significant influence on ecosystem functioning. Dense shellfish beds can filter several cubic metres of water per hour. The Oosterschelde in the southwest of the Netherlands has large stocks of mussels (*Mytilus edulis*), cockles (*Cerastoderma edule*) and oysters (*Crassostrea gigas*), and it is estimated that the total volume of the Oosterschelde is processed by shellfish every 4–5 days. The large filtration capacity of shellfish can influence the light regime in the system. In addition, dense shellfish populations may have major effects on the internal nutrient cycling of the system. As such, shellfish may greatly affect the system's carrying capacity.

To be able to answer questions with regard to the carrying capacity or water quality of a system, integrated ecosystem models are required, which should include growth models for the shellfish that are present in the system. Various of such shellfish models already exist, two of these we mention here in particular because they have been calibrated specifically for cockles and mussels in the Oosterschelde: COCO (Rueda *et al.* 2005) and EMMY (Scholten & Smaal 1999). These models resulted in a good fit between

simulated values and observations, provided much information on physiological processes and raised several issues on food selection, spawning and regulation of assimilation efficiency. However, they also have some setbacks, which hampers the incorporation of these models into the ecosystem models. First of all, the models are of the so-called net production type, meaning that maintenance costs are first subtracted from the assimilates, before the allocation to other metabolic processes occurs. This type of model is relatively complex and parameter-intensive, and has some generality issues (Kooijman 2000). Furthermore, both COCO and EMMY were calibrated by adjusting a large number of parameters, which makes them very species- and system-specific, and their results difficult to compare with those of other systems and/or species.

In this paper, we develop models for growth of individual mussels and cockles in the Oosterschelde that are as simple and general as possible. Therefore, we chose to use models based on the dynamic energy budget (DEB) theory. DEB models have a structure that is based on first principles and physiological rules, which makes them applicable to basically all animals and life stages, and at the same time requires a relatively small number of parameters. Note that the basic DEB model structure is flexible and can be extended to incorporate any species-specific characteristic that may be required for specific applications.

Our starting points are the existing DEB models for growth of individual shellfish. These are general

* Author for correspondence (tineke.troost@deltares.nl).

One contribution of 14 to a Theme Issue 'Developments in dynamic energy budget theory and its applications'.

DEB models that are adjusted to shellfish growth by incorporating filter-feeding and spawning-related processes. Recently, various DEB models for shellfish growth have been developed and described in detail (Bacher & Gangnery 2006; Pouvreau *et al.* 2006; Rosland *et al.* 2009; Wijsman *et al.* 2009). Also, a lot of effort is given to the estimation of the DEB parameters (Van der Meer 2006; Van der Veer *et al.* 2006). The present study uses as much as possible the existing knowledge and experience described in the literature.

However, none of the models mentioned above has been developed for cockles or mussels in the Oosterschelde. Adjusting them to these species and this system is done by formulating and calibrating the functional response of each of these species using Oosterschelde data on environmental conditions and individual growth curves. Also different from the studies mentioned above, is that we include more detail in the functional response function, which enables us to investigate the relative importance of various food sources. In addition, we study the variability of the functional response within the system, by considering four sections in our system with different food conditions as is permitted by our extensive dataset. Furthermore, by modelling two species in the same system, we aim to study interspecific differences in the functional responses, and compare these results with those of similar models for cockles and mussels in other systems.

2. MATERIAL AND METHODS

(a) *Description of a general dynamic energy budget model*

Dynamic energy budget theory is used to describe the energetic processes of an individual organism, determining the rates at which the organism assimilates and uses energy for maintenance, growth and reproduction as a function of the state of the organism and of its environment (Kooijman 2000). An individual organism state is represented by three state variables: structural volume (V , cm³), reserves (E , Joule) and reproductive buffer (E_{ER} , Joule). Organisms take up food from their environment, of which a fraction is released as faeces. Assimilated energy is incorporated into a reserve pool from which it is used for maintenance, growth, development and reproduction following the so-called κ -allocation rule. A fixed proportion (κ) of energy from the reserves is allocated to somatic maintenance and growth and the remaining fraction ($1 - \kappa$) is spent on maturity maintenance, development and reproduction. Juveniles use the available energy for developing reproductive organs, while adults use it for gamete production and spawning. The transition from juvenile to adult is assumed to occur at a fixed size (V_p). The dynamics of the reserves are calculated as the balance between the assimilation flux and the mobilization flux, and the dynamics of the structural volume (growth) are based on the κ -fraction of the mobilization flux and somatic maintenance. A more detailed description, including the full equations, is given by Sousa *et al.* (2010).

The length (L , cm) of the organism can be calculated from the structural volume using the shape coefficient (δ_M),

$$L = \frac{V^{1/3}}{\delta_M}.$$

In addition, the ash-free dry weight, AFDW (g) can be obtained by converting and summing the state variables V , E and E_{ER} ,

$$\text{AFDW} = \Psi_{\text{AFDW_WW}} \rho V + \frac{E + E_{ER}}{\Psi_{E_AFDW}},$$

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

Furthermore, it is assumed that all physiological rates are affected by temperature in the same way. This temperature effect is based on an Arrhenius type relation, which describes the rates at ambient temperature, $k(T)$, as follows:

$$k(T) = k_1 e^{(T_A/T_1 - T_A/T)} \times \frac{1 + e^{(T_{AL}/T_1 - T_{AL}/T_L)} + e^{(T_{AH}/T_H - T_{AH}/T_1)}}{1 + e^{(T_{AL}/T - T_{AL}/T_L)} + e^{(T_{AH}/T_H - T_{AH}/T)}},$$

where T is the absolute temperature (K), T_{AL} and T_{AH} are the Arrhenius temperatures (K) for the rate of decrease at, respectively, the lower (T_L) and upper (T_H) boundaries, T_1 is the reference temperature (293 K), T_A is the Arrhenius temperature and k_1 is the rate at the reference temperature.

(b) *Shellfish-specific modelling aspects*

The DEB models for cockle and mussel are based on the standard DEB model which is briefly described above. Specific for shellfish is that they filter food from the water column. Pseudofaeces formation (i.e. rejection of non-edible particles), known to be significant in systems with high seston concentrations, is not modelled explicitly. This does not affect the results of this study, as the pseudofaeces production and availability do not affect shellfish growth (pseudofaeces cannot be used as a food source by the shellfish). The negative effects of inedible particles on the functional response rate, however, are taken into account, as is described in §2b(i). Note that the process of pseudofaeces production will become essential when the DEB model is incorporated into an ecosystem model, as discussed in §5.

Also specific for shellfish is their spawning behaviour. Spawning events occur when enough energy is allocated into the gonads (Gonado-Somatic Index, $\text{GSI} > \text{Thresh}_{\text{GSI}}$) and when the water temperature is above a threshold value ($\text{Thresh}_{\text{Temp}}$). The gonads are released from the buffer at a rate of 2% per day until the temperature drops below the threshold value or the $\text{GSI} < 0.0001$. A 2% per day gonad-release corresponds to a period of about one month during which half of the gonads are released.

(i) *Functional response function*

The relation between food uptake and food density is described by a scaled hyperbolic functional response

f proposed by Kooijman (2006), in which the negative effects of inorganic particles concentration on the bivalve filtration rate are taken into account

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

in which

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

where X is the available density of food, and Y is the concentration of inorganic matter, which is calculated as the total particulate matter minus the particulate organic matter ($Y = \text{TPM} - \text{POM}$). X_K and Y_K are the half-saturation constants for food and inorganic particles, respectively. The value of f varies from 0 (no food uptake) to 1 (*ad libitum* food conditions). When the available amount of food equals $K'(Y)$, the food uptake rate is half the maximum uptake rate. The response curve corresponds to the type II response curve of Holling (1959). When the amount of inorganic particles in the water column increases, the f value decreases, simulating the negative influence of these particles in the filtration capacity of the bivalve.

In the formulation of the functional response, the available density of food is defined as a single variable (X). In reality, it is a function of the concentration of the various food items, the quality of the food and the food acquisition rate. The food acquisition rate, in turn, depends on factors such as filtration rate, selection efficiency, inundation, and so on. In many shellfish DEB models, the available amount of food is simplified by using the chlorophyll a (Chl a) concentration as a proxy. In the present model, X is described by a function of both the Chl a concentration ($\mu\text{g l}^{-1}$) and the detritus concentration (mg l^{-1}). Detritus (defined in this study as particulate organic matter, POM) consists of a range of components of which a fraction can be used by the bivalve as food. By incorporating detritus in the formulation, its importance as a food source for shellfish can be investigated. The unit of X is in Chl- a equivalents ($\mu\text{g l}^{-1}$) and it is computed as

$$X = \text{Chl } a + \alpha_{\text{Det}} \text{POM},$$

where Chl a and POM are the measured Chl a and detritus concentrations (mg l^{-1}), and α_{Det} is the relative contribution of detritus to food in Chl- a equivalents ($\mu\text{g Chl } a \text{ mg POM}^{-1}$).

(ii) Parameter values

The primary DEB parameters for cockle and mussel are largely based on the publications of Van der Veer *et al.* (2006) and Rosland *et al.* (2009). They are summarized in table 1. Additional parameters are either derived from literature or based on calibration. Some clear differences exist between the parameter values of cockles and mussels, such as in the maximum volume-specific ingestion rate. This could arise from differences in the life styles of cockles and mussels (buried versus bed-forming) and the adaptations this requires with regard to feeding apparatus. Other differences, such as those in κ , are more difficult to understand or interpret, but may point to different

reproduction or allocation strategies, as observed in other bivalve species (Cardoso *et al.* 2009).

(iii) Model calibration

The parameter α_{Det} and the half-saturation constant, X_K , are the free-fitted parameters of the model. The values of the parameters are species-specific and might vary both in time and space. In this study, however, we assume these parameters to be constant during the considered time period. Some variation in space is taken into account in the cockle model, by considering four different sections within the Oosterschelde. The half-saturation constant for inorganic particles, Y_K , was not free-fitted as its calibration turned out to be problematic; instead its value was set to values found in the literature.

The model was calibrated against the field observations (L and AFDW) by minimizing the weighted sum of squared residuals using the following formulation, in which Mod and Obs represent the model results and observations for length and ash-free dry weight variables:

$$\text{SSR}_{\text{Total}} = \sum_{\text{Obs}} \frac{(\text{Mod}_L - \text{Obs}_L)^2}{\text{avg}(\text{Obs}_L)^2} + \sum_{\text{Obs}} \frac{(\text{Mod}_{\text{AFDW}} - \text{Obs}_{\text{AFDW}})^2}{\text{avg}(\text{Obs}_{\text{AFDW}})^2}.$$

The model was calibrated for the two parameters simultaneously, which was done within the FEMME environment (Soetaert *et al.* 2002), using the directional iterative Levenberg–Marquardt method. X_K was allowed to vary between 0 and 100, and α_{Det} to range between 0 and 10.

(iv) Cockle

The model for cockle was calibrated using an extensive dataset on cockle growth in the Oosterschelde (figure 1). From 1992 to 2007, 18 locations were sampled for cockles on a regular (three to five times per year) basis. At each location, the age of the cockles was determined from the growth rings on the shell. For each year class, the number of cockles was counted and the fresh weight and the average shell length were determined. Since 1998, the ash-free dry weight of the cockles has been determined as well. Details on the sampling programme are described in Wijsman *et al.* (2009).

For the calibration, the Oosterschelde was divided into four compartments (West, Central, North and East), as these are known to have distinct environmental conditions. Their differences in temperature and food density are included in the model explicitly as forcing functions, but other differences may be relevant as well. For instance, differences in light conditions could well lead to differences in species composition and thus in food quality. Such quality-related differences can be studied by calibrating the value of X_K for each compartment separately. Additionally, we have also calibrated the model for all compartments at the same time.

For each age class, the cockle data (length, fresh weight and AFDW) were averaged per compartment and per month. This resulted in average growth curves of cockle cohorts within each compartment. Also, average growth curves for the Oosterschelde

Table 1. Parameter values used in the cockle and mussel model.

parameter	unit	description	cockle	references	mussel	references
<i>DEB parameters</i>						
T_A	K	Arrhenius temperature	5800	Van der Veer <i>et al.</i> (2006)	5800	Van der Veer <i>et al.</i> (2006)
$\{J_{EAm}\}$	$J d^{-1} cm^{-2}$	maximum specific ingestion rate	91.5	Van der Veer <i>et al.</i> (2006)	273	Rosland <i>et al.</i> (2009)
$[J_{EM}]$	$J cm^{-3} d^{-1}$	volume-specific maintenance costs	24	Van der Veer <i>et al.</i> (2006)	30.7	this study
m_{Em}	$J cm^{-3}$	maximum storage density	2115	Van der Veer <i>et al.</i> (2006)	2190	Van der Veer <i>et al.</i> (2006)
$1/y_{VE}$	$J cm^{-3}$	volume-specific costs of growth	1900	Van der Veer <i>et al.</i> (2006)	1900	Van der Veer <i>et al.</i> (2006)
κ	—	fraction of pC spent on maintenance plus growth	0.80	Van der Veer <i>et al.</i> (2006)	0.45	Rosland <i>et al.</i> (2009)
κ_R	—	fraction of reproduction energy fixed in eggs	0.80	Van der Veer <i>et al.</i> (2006)	0.8	this study
$1/y_{EX}$	—	assimilation efficiency	0.76	Rueda <i>et al.</i> (2005)	0.75	Van der Veer <i>et al.</i> (2006)
δ_M	—	shape coefficient	0.381	Van der Veer <i>et al.</i> (2006)	0.26	Rosland <i>et al.</i> (2009) and Van der Veer <i>et al.</i> (2006), average value
L_p	cm	length at juvenile $\rightarrow$ adult transition	2.08	Van der Veer <i>et al.</i> (2006)	1.2	Van der Veer <i>et al.</i> (2006)
<i>additional parameters</i>						
T_L	K	lower boundary of tolerance range	278	Van der Veer <i>et al.</i> (2006)	275	Van der Veer <i>et al.</i> (2006)
T_H	K	upper boundary of tolerance range	306	Van der Veer <i>et al.</i> (2006)	296	Van der Veer <i>et al.</i> (2006)
T_{AL}	K	Arrhenius temperature for rate of decrease at lower boundary	51 154	Van der Veer <i>et al.</i> (2006)	45 430	Van der Veer <i>et al.</i> (2006)
T_{AH}	K	Arrhenius temperature for rate of decrease at upper boundary	47 126	Van der Veer <i>et al.</i> (2006)	31 376	Van der Veer <i>et al.</i> (2006)
Thresh _{GSI}	—	gonado-somatic index triggering spawning	0.0034	Rueda <i>et al.</i> (2005)	0.28	Van der Veer <i>et al.</i> (2006)
Thresh _{Temp}	$^{\circ}C$	temperature threshold triggering spawning	15.84	Rueda <i>et al.</i> (2005)	15	Honkoop & van der Meer (1998)
r_S	d^{-1}	relative spawning rate	0.02	this study	0.02	this study
ρ	$g cm^{-3}$	specific mass of body structure	1.0	this study	0.8 (medium); 0.9 (small and large)	this study
Ψ_{AFDW_WW}	$g_{AFDW} g_{WW}^{-1}$	gram ash-free dry weight per gram wet weight	0.12	Van der Veer <i>et al.</i> (2006)	0.046	Ricciardi & Bourget (1998)
Ψ_{E_AFDW}	$J g_{AFDW}^{-1}$	energy content of reserves (ash-free dry mass)	17 500	Brody (1945)	17 500	Brody (1945)
Y_K	$mg l^{-1}$	half-saturation constant for sediments	100	Prins <i>et al.</i> (1991)	117	Kooijman (2006)

as a whole were calculated. Note that the used dataset includes the dataset used by Rueda *et al.* (2005), which however considered only the western compartment and covered a shorter period of time.

Water quality data (water temperature, Chl *a*, TPM and POM) were derived from the existing datasets of Rijkswaterstaat, NIOO-CEME and Wageningen

IMARES. Like the cockle data, the water quality data were aggregated by averaging all the data from 1993 to 2007 per month and per compartment. This resulted in average seasonal patterns of water quality parameters per compartment. Also, environmental conditions were calculated for the Oosterschelde as a whole (figure 2). For the calibration runs that cover

Figure 1. Map of the Oosterschelde indicating the four compartments and the location Kijkuit. Scale bar, 0–12 km.

Figure 2. Food concentrations and temperatures in an average year in the four compartments of the Oosterschelde. Filled circles, West; filled squares, Central; open circles, North; open triangles, East.

Figure 3. Time series of (a) food concentrations and (b) temperatures at Kijkuit (eastern compartment of the Oosterschelde). (a) Thick lines, Chl *a* ($\mu\text{g l}^{-1}$); thin lines, POM (mg l^{-1}); dotted lines, inorganic material (mg l^{-1}).

a simulation period of several years, these average conditions were simply repeated.

Although the averaging procedure described above led to a loss of information on interannual variability, it resulted in more complete growth curves for all age classes in each of the compartments. Besides, the variation between years seems to be of the same order of magnitude as the variation between compartments, both for the growth curves and for the environmental data.

Initial values for cockle length (and thus structural volume) were derived from the field observations. Initial energy content of the reproductive buffer was set to 0 J and initial energy content of the reserves was derived iteratively by trial and error in order to obtain a good approximation of the initial data value for total weight.

(v) Mussel

The model for mussels was calibrated using data from EU project Keyzones, where batches of mussels of three size classes (<30 mm, 30–40 mm and 40–50 mm) were stocked at Kijkuit (figure 1), located in the eastern compartment of the Oosterschelde. Sampling was carried out between December 2005 and June 2007 with frequent (almost monthly) measurements of the mussels' length and weight.

The model was calibrated using the medium-sized mussels (30–40 mm). Model validation was then done by comparing the model results (using the parameters set obtained in the calibration) with the observed values of the small and large size classes.

Water samples were taken at the time of each sampling, for analysis of TPM, POM and Chl *a* concentration (figure 3). More information concerning the experimental set-up and results obtained can be found in Wijsman *et al.* (2007). In order to obtain a complete dataset of environmental variables during

the entire period of the experiment, these measurements were combined with data from the Lodijkse Gat monitoring station.

Initial conditions for the mussels were obtained using a spin-up run of the model starting from new-born individuals and assuming optimal food conditions ($f=1$). For each size class, the model was run until the initial length of the mussels in the size-class was reached. The mussel density, ρ , was then derived for each size class separately, by setting the predicted initial weight (i.e. the sum of the weights of structure, reserves and reproduction buffer) equal to the observed initial weights. Since this approach differs somewhat from the one used for cockles, the resulting densities also differ, but these differences are not large and are not likely to have a large effect on the calibration results.

3. RESULTS

(a) Cockle

The calibrated values of the half-saturation constant for food (X_K , $\mu\text{g Chl } a \text{ l}^{-1}$) and the detritus contribution to food (α_{Det} , $\mu\text{g Chl } a \text{ mg}^{-1} \text{ POM}$) resulting for each of the Oosterschelde compartments are presented in table 2.

Fitted growth curves for the total Oosterschelde are shown in figure 4. Growth curves for each of the compartments can be found in Wijsman *et al.* (2009). In general, there is a relatively good agreement between the modelled length and the observations. Yet, in most of the compartments, as well as for the Oosterschelde as a whole, there is an overestimation of the cockle length in the first year.

Also, the model describes quite well the general trend in AFDW. However, the variation in the modelled AFDWs is less pronounced than in the observed data. In theory, the model should be capable of reproducing fluctuations owing to reproduction and

Table 2. Calibrated parameter values and goodness-of-fit for cockle and mussel models. Relative difference is computed as $\text{average}(\text{abs}(\text{Model} - \text{Observation})/\text{Observation}) \times 100\%$.

		calibrated parameter value		weighted sum of squared residuals			relative difference (%)	
		X_K	α_{Det}	L	AFDW	total	L	AFDW
cockles	West	2.05	0	0.39	3.29	3.68	0.80	9.67
	Central	1.86	0.03	0.40	5.69	6.09	0.80	16.3
	North	4.04	0	0.51	5.57	6.08	1.13	16.9
	East	6.40	1.38	0.71	10.62	11.33	1.51	33.2
	total	2.74	0.10	0.43	6.95	7.39	0.83	19.9
mussels (Kijkuit (East))	medium	2.23	0	0.62	3.11	3.73	1.6	10.3
	small ^a	—	—	—	—	—	4.4	44.3
	large ^a	—	—	—	—	—	2.9	61.8

^aData used for comparison and not used for calibration.

Figure 4. Fitted growth curves for (b) weight and (a) length of cockles, compared with observations (open circles).

spawning. Therefore, the deviation between predictions and observations might rather be caused by the averaging of the environmental data, which damps down the peak in chlorophyll concentration and may thus result in an underestimation of the modelled increase of energy reserves.

The functional response as predicted by the model for an average year is shown in figure 5. Its values range from 0.2 to 0.8 showing a strong increase in spring and a decrease towards winter.

(b) Mussel

Figure 6 represents the model results and observations for medium-sized mussels obtained after calibration of the half-saturation constant for food (X_K , $\mu\text{g Chl } a\text{ l}^{-1}$) and the detritus contribution to food (α_{Det} , $\mu\text{g Chl } a\text{ mg}^{-1}\text{ POM}$; see also table 2). The resulting model fit is quite good. Calibration results in a value of $\alpha_{\text{Det}} = 0$.

The period between March and July was identified as the main growing season for mussels (figure 6).

Figure 5. Cockle functional responses for the Oosterschelde as a whole.

During this period, the relatively high availability of food and the increase of water temperature create favourable conditions for the growth of mussels, also leading to an increase in the total body weight. After July, despite the high temperature values, the total body weight of the mussels decreases and growth seems to stop. This may be related to a lower food availability caused by the low chlorophyll concentrations found in the water column during this period. The food concentrations in this (eastern) part of the Oosterschelde are often low and make this area not very suitable for mussel production in general, which is also why commercial mussel beds are absent in this area. Furthermore, 2006 was a particularly bad year for mussel growth in the Oosterschelde as is reflected in the low flesh content of the mussels at the auction that year (Wijsman *et al.* 2007).

In this particular case, the bad food conditions may have been worsened by the presence of fouling organisms (mainly the tunicate *Ciona intestinalis*). This fouling may have reduced the water flow through the

Figure 6. Fitted growth curves for (b) weight and (a) length of medium-sized (30–40 mm) mussels at Kijkuit, compared with observations (open circles).

Figure 7. Model predictions (solid line) and observations of (a, c) weight and length for small (<30 mm) and (b, d) large (40–50 mm) mussels at Kijkuit. The used model was calibrated on medium-sized mussels. Dotted lines show additional model results, that were obtained with a 10 per cent increase in the contribution of detritus to food ($\alpha_{\text{Det}} = 0.1$).

baskets and/or which may have competed with the mussels for the available food, as previously identified and discussed by Wijsman *et al.* (2007). However, since the fouling was mechanically removed from the baskets, and since the current velocities at the Kijkuit location are high, we assume that the reduced water flow owing to fouling has played a minor role.

The two other size classes included in the experiment (small and large) were used for validation of

the calibrated model. Model predictions compared with length and weight observations are shown in figure 7. The predicted and observed mussel lengths are very similar, following the same pattern over the time period. However, some differences can be found in terms of total mussel weight. For the small size class, the model seems to underestimate the total weight, whereas for the large size class, the model seems to give overestimations. The functional response

Figure 8. Predicted functional response for mussels in the Oosterschelde during the experimental period.

predicted by the model for the experimental period (figure 8) shows significant oscillations, with high values in springtime and a more or less gradual decrease over time.

4. DISCUSSION

(a) *Within-system variation of the functional response*

In general, the calibrated models for shellfish growth performed well and showed a relatively good agreement between the modelled and observed shellfish lengths, for both species. The agreement between modelled and observed weights, however, is not as good. Several factors can contribute to this difference. The total weight is the sum of the amount of reserves, structure and reproduction buffer in the organism and it depends not only on the good prediction of the relative proportions between those compartments but also on various conversion factors, that convert energy into ash-free dry mass. From the length results it is possible to conclude that the amount of structure in the organism was well predicted and the main differences between model and observations should be explained by differences in reserves and/or reproduction buffer. In terms of the reproduction cycle, the model assumes that a threshold of gonado-somatic ratio and temperature are needed for promoting spawning in the organism. The threshold values used in this study were found in the literature but no detailed calibration or validation was possible owing to the lack of information. Differences in those values could very well lead to significant differences in the total weight of the organism.

Differences between the various compartments in the fitted values of the saturation constant, X_K , suggest that food quality varies within the system. Based on the cockle results (table 2), it may be concluded that the quality of the food in the west and central compartments is better than in the eastern and northern compartments, which could be explained by the

smaller residence times in those sections caused by their proximity to the estuary's mouth.

Results further indicate that the contribution of detritus to the cockle food is not significant ($\alpha_{\text{Det}} \approx 0$) in most compartments of the Oosterschelde (table 2). Only in the eastern compartment is its contribution large ($\alpha_{\text{Det}} = 1.38$). In this part of the Oosterschelde, the chlorophyll concentrations are very low and thus the food conditions are poor. Apparently, the cockles in this compartment can only grow if they use a substantial amount of detritus as a food source.

The measured mussels, however, are also located in the eastern compartment and, having a small value of α_{Det} , do not seem to use detritus as a food source. This parameter is thus not only site-specific, but also species-specific. Interestingly, this finding contrasts with the results of stomach content analysis showing that the various bivalve species rely on the same food sources (Kamermans 1994). In order to further investigate this issue, a simple sensitivity analysis was carried out by running the mussel model with a value of $\alpha_{\text{Det}} = 0.1$. The results are shown in figure 7 as dotted curves. As expected, the increase of detritus contribution to the mussel food has a positive effect on its length and weight, because it corresponds to an increase in food availability. As a result, this leads to an increased deviation between model results and observed data. However, for the small-sized mussels between July and October, the model results seem to show better agreement when considering the increased contribution of detritus. This suggests that in some cases detritus may indeed contribute to the food of mussels.

Despite the differences in calibrated values of their parameters, both species show a very similar trend in functional response, with a peak in the beginning of the main growing season followed by a gradual decrease towards the winter. Both curves cover the same range from 0.2 to 0.8. The functional response of the mussels shows larger oscillations, which is probably caused by the fact that the mussels were simulated for one specific year, while the cockles were simulated over an average year, in which such variations were damped down.

(b) *Across-system comparison*

In the present paper, species-specific functional response curves were used to derive growth curves for the two species, which requires substantial information on the prevailing food conditions. In most studies, however, this type of information is not available. Several authors have stressed the difficulty in a direct evaluation of the food conditions for bivalves in the field owing to its variability and seasonality. Also, assessing the food's nutritional quality is not straightforward (Kooijman 2000), although important for the growth performance. Often, the Chl *a* concentration is used as a proxy for food availability, as in the present study. This option implicitly assumes a constant relation between the amount of pigment and biomass of the cell, which is known to be variable (Lorena *et al.* 2010) and to have seasonal changes (Ren & Schiel 2008). The problem of choosing appropriate food quantifiers for modelling

ingestion has been stated previously (Pouvreau *et al.* 2006; Bourlès *et al.* 2009; Ren 2009; Rosland *et al.* 2009), as well as the dependence of X_K on food composition and quality. The calibrated value of X_K has been described as a 'Pandora's box' (S. Pouvreau 2009, personal communication), since it is not only species-specific, but also site-specific, and which thus provides a way to overcome these uncertainties in food quantity and food quality.

However, for the purpose of comparing different populations from the point of view of energy utilization, the overall scaled functional response is more important than the used food quantifiers, since it captures the energy that is actually assimilated independently of the food source. DEB theory offers the possibility of deriving the scaled functional response from observed growth and reproduction patterns under the temperature conditions experienced (Kooijman 2000). This has already been applied to compare food conditions for several bivalve species and different habitats from the Dutch Wadden Sea (Cardoso *et al.* 2006) although assuming constant food conditions over the lifespan of the species.

More recently, another approach has been used involving a *dynamic* reconstruction of the scaled functional response using reverse modelling for various bivalve populations across the NE Atlantic coast (Freitas *et al.* 2009). Results from that study showed that, across systems, *C. edule* experienced better food conditions when compared with other bivalve species, and that *M. edulis* presented the lowest food conditions in all the areas analysed. One of the explanations provided was that mussels live in dense beds and experience high intra-specific competition. In the present study, however, the mussels were held in baskets that were hanging in the water column, where they did not experience much competition. Therefore, they provide a nice opportunity to test this hypothesis. Although the results of the two studies cannot be directly compared because of the different resolution in the functional response variation (seasonal versus annual), and because, for mussels, different parameter values have been used to model ingestion and assimilation, the present study does indeed show a much higher functional response for *M. edulis*, with a very similar range and pattern as that of *C. edule*. This result therefore supports the idea that the generally small functional response of *M. edulis* is caused by intra-specific competition.

When comparing the functional responses of *C. edule* in the Oosterschelde to those in other systems, the main difference lies with the covered range (0.2–0.8), which is larger in the Oosterschelde than in any other system. This is probably because of site-specific differences in seasonality of food quantity or quality, but further research at this level is required.

5. RECOMMENDATIONS

The presented models for individual growth of mussels and cockles in the Oosterschelde satisfactorily fit the observations. Still, many possibilities exist to improve the results. These include a fine-tuning of the parameter values, and an optimization of the calibration

method. Currently, however, the largest challenge lies in incorporating these models in an ecosystem model, which was (as mentioned in the introduction) the main driver for this study.

However, before the presented models can be incorporated in an ecosystem model for the Oosterschelde, various additional steps have to be taken. These include a scaling-up from the individual growth models to population models, which requires the handling of different age and/or size classes, as well as additional formulations for mortality, larval transport and recruitment. Furthermore, the feedback of the bivalves on their environment should be fully taken into account. This implies that food preference and selection, as well as pseudofaeces production, can no longer be ignored as was done in the present study.

Not many applications are currently available where DEB shellfish models have been incorporated into an ecosystem model. A nice example, though, is that of Maar *et al.* (2009), which modelled blue mussel growth in the Nysted offshore wind farm in Denmark. However, the study of Maar and co-workers considers only one cohort of shellfish individuals, and thus ignores embryonic and larval stages, as well as recruitment and settlement. Furthermore, pseudofaeces production is not taken into account either. Therefore, this study acts as a nice 'stepping stone' towards the incorporation of shellfish models into ecosystem models, but to be able to model the full Oosterschelde system, including its extensive (wild and cultured) shellfish populations, these issues cannot be ignored.

Part of the presented work has been done within the project 'Deltakennis', which is carried out by Deltares and Wageningen IMARES, by order of the Dutch government. Additional finance was provided by the KB programme of the ministry of LNV (KB-04-001-059). The water quality and mussel growth measurements were done within the EU project Keyzones (COOP-CT-2004-512664). Contribution from Sofia Saraiva was supported by Fundação para a Ciência e a Tecnologia, Portugal (SFRH/BD/44448/2008). Dick van Oevelen and Karline Soetaert (NIOO-CEME) are thanked for their help with the set-up of the DEB model within the FEMME environment.

REFERENCES

- Bacher, C. & Gangnery, A. 2006 Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. *J. Sea Res.* **56**, 140–155. (doi:10.1016/j.seares.2006.03.004)
- Bourlès, Y., Alunno-Bruscia, M., Pouvreau, S., Tollu, G., Leguay, D., Arnaud, C., Goulletquer, P. & Kooijman, S. A. L. M. 2009 Modelling growth and reproduction of the Pacific oyster *Crassostrea gigas*: advances in the oyster-DEB model through application to a coastal pond. *J. Sea Res.* **62**, 62–71. (doi:10.1016/j.seares.2009.03.002)
- Brody, S. 1945 *Bioenergetics and growth*. New York, NY: Hafner Publishing.
- Cardoso, J. F. M. F., Witte, J. I. J. & Van der Veer, H. W. 2006 Intra- and interspecies comparison of energy flow in bivalve species in Dutch coastal waters by means of the dynamic energy budget (DEB) theory. *J. Sea Res.* **56**, 182–197. (doi:10.1016/j.seares.2006.03.011)

- Cardoso, J. F. M. F., Witte, J. I. J. & Van der Veer, H. W. 2009 Differential reproductive strategies of two bivalves in the Dutch Wadden Sea. *Est. Coast. Shelf Sci.* **84**, 37–44. (doi:10.1016/j.ecss.2009.05.026)
- Freitas, V., Cardoso, J. F. M. F., Santos, S., Campos, J., Drent, J., Saraiva, S., Witte, J. I. J., Kooijman, S. A. L. M. & Van der Veer, H. W. 2009 Reconstruction of food conditions for Northeast Atlantic bivalve species based on dynamic energy budgets. *J. Sea Res.* **62**, 75–82. (doi:10.1016/j.seares.2009.07.004)
- Holling, C. S. 1959 The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can. Entomol.* **91**, 293–320. (doi:10.4039/Ent91293-5)
- Honkoop, P. J. C. & Van der Meer, J. 1998 Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea. *J. Exp. Mar. Biol. Ecol.* **220**, 227–246. (doi:10.1016/S0022-0981(97)00107-X)
- Kamermans, P. 1994 Similarity in food source and timing of feeding in deposit-feeding and suspension-feeding bivalves. *Mar. Ecol. Prog. Ser.* **104**, 63–75. (doi:10.3354/meps104063)
- Kooijman, S. A. L. M. 2000 *Dynamic energy and mass budgets in biological systems*. Cambridge, UK: Cambridge University Press.
- Kooijman, S. A. L. M. 2006 Pseudo-faeces production in bivalves. *J. Sea Res.* **56**, 103–106. (doi:10.1016/j.seares.2006.03.003)
- Lorena, A., Marques, G. M., Kooijman, S. A. L. M. & Sousa, T. 2010 Stylized facts in microalgal growth: interpretation in a dynamic energy budget context. *Phil. Trans. R. Soc. B* **365**, 3509–3521. (doi:10.1098/rstb.2010.0101)
- Maar, M., Bolding, K., Kjerulf Petersen, J., Hansen, J. L. S. & Timmermann, K. 2009 Local effects of blue mussels around turbine foundations in an ecosystem model of Nysted off-shore wind farm, Denmark. *J. Sea Res.* **62**, 159–174. (doi:10.1016/j.seares.2009.01.008)
- Pouvreau, S., Bourles, Y., Lefevre, S., Gangnery, A. & Alunno-Bruscia, M. 2006 Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions. *J. Sea Res.* **56**, 156–167. (doi:10.1016/j.seares.2006.03.007)
- Prins, T. C., Smaal, A. C. & Pouwer, A. 1991 Selective ingestion of phytoplankton by the bivalves *Mytilus edulis* (L.) and *Cerastoderma edule* (L.). *Hydrobiol. Bull.* **25**, 93–100. (doi:10.1007/BF02259595)
- Ren, J. S. 2009 Effect of food quality on energy uptake. *J. Sea Res.* **62**, 72–74. (doi:10.1016/j.seares.2008.11.002)
- Ren, J. S. & Schiel, D. R. 2008 A dynamic energy budget model: parameterization and application to the Pacific oyster *Crassostrea gigas* in New Zealand waters. *J. Exp. Mar. Biol. Ecol.* **361**, 42–48. (doi:10.1016/j.jembe.2008.04.012)
- Ricciardi, A. & Bourget, E. 1998 Weight-to-weight conversion factors for marine benthic macroinvertebrates. *Mar. Ecol. Prog. Ser.* **163**, 245–251. (doi:10.3354/meps163245)
- Rosland, R., Strand, Ø., Alunno-Bruscia, M., Bacher, C. & Strohmeier, T. 2009 Applying dynamic energy budget (DEB) theory to simulate growth and bio-energetics of blue mussels under low seston conditions. *J. Sea Res.* **62**, 49–61. (doi:10.1016/j.seares.2009.02.007)
- Rueda, J. L., Smaal, A. C. & Scholten, H. 2005 A growth model of the cockle (*Cerastoderma edule* L.) tested in the Oosterschelde estuary (The Netherlands). *J. Sea Res.* **54**, 276–298. (doi:10.1016/j.seares.2005.06.001)
- Scholten, H. & Smaal, A. C. 1999 The ecophysiological response of mussels (*Mytilus edulis*) in mesocosms to a range of inorganic nutrient loads: simulations with the model EMMY. *Aquat. Ecol.* **33**, 83–100. (doi:10.1023/A:1009995823741)
- Soetaert, K., De Clippele, V. & Herman, P. M. J. 2002 FEMME, a flexible environment for mathematically modelling of the environment. *Ecol. Modell.* **151**, 177–193. (doi:10.1016/S0304-3800(01)00469-0)
- Sousa, T., Domingos, T., Poggiale, J.-C. & Kooijman, S. A. L. M. 2010 Dynamic energy budget theory restores coherence in biology. *Phil. Trans. R. Soc. B* **365**, 3413–3428. (doi:10.1098/rstb.2010.0166)
- Van Der Meer, J. 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. 2006 The estimation of DEB parameters for various Northeast Atlantic bivalve species. *J. Sea Res.* **56**, 107–124.
- Wijsman, J. W. M., Smaal, A. C. & Brummelhuis, E. B. M. 2007 Growth of cultivated mussels and oysters in the Oosterschelde estuary. Report/EU project on keyzones COOP-CT-2004-512664. See www.keyzones.org.
- Wijsman, J. W. M., Brummelhuis, E. B. M. & Smaal, A. C. 2009 DEB model for cockles (*Cerastoderma edule*) in the Oosterschelde. Report/IMARES C048/09, IMARES, Yerseke.