Estimating the effect of phenotypic flexibility in feeding morphology on cockle growth (*Cerastoderma edule*) under different environmental conditions

Master thesis by Vera Rullens

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Abstract

Dynamic Energy Budget (DEB) models are often used to describe growth in bivalve species. Ingestion rate determines the amount of energy assimilated and therefore the amount of energy allocated to growth, maintenance, and reproduction. Gills and palps are involved in the ingestion of food as their size determines clearance rate and selection efficiency. In bivalves, gills create a water current from which particles are filtered and palps sort these particles into edible and non-edible. Gill and palp sizes are phenotypically flexible and depend on environmental conditions. So far, variation in gill and palp size has not been incorporated in DEB models, even though they could greatly affect the amount of energy assimilated. Therefore, this research aims at linking environmental conditions to variation in gill and palp size in cockles (*Cerastoderma edule*) and incorporates this into a standard DEB model to estimate growth for cockles that adjusted their feeding apparatus to optimize food intake. Data on variation in feeding morphology has been collected under different conditions in the Dutch Wadden Sea. DEB models were applied to three different sites to compare variation in growth under different environmental conditions with and without flexibility in the feeding morphology. Results indicate that variation in gill size is mostly explained by shell length and exposure time while variation in palp size relates to shell length, median grain size, exposure time and density. Model estimates for cockle growth show a reduced growth under low Chlorophyll a and high Suspended Particulate Matter concentrations. In addition, it is beneficial for cockles to adjust their palp size, as this result in increased growth, while adjusting gill size seem to negatively affect growth. Therefore, it is concluded that flexibility in feeding morphology influences the growth of cockles and should not be ignored when modelling bivalve growth.

1. Introduction

In the Wadden Sea, the common cockle (*Cerastoderma edule*) is one of the key species inhabiting the tidal flats. With ca. 16% of the total zoobenthic biomass, cockles make up a large fraction of the biomass in the ecosystem (Beukema 1976; Beukema & Dekker 2006). Cockles are an important part of the Wadden Sea ecosystem as they form an important food source for many bird species (Beukema et al. 1993). However, density-independent mortality and the lack of a stock-recruitment relationship suggest that bird predation does not regulate bivalve dynamics (van der Meer 1997; van der Meer et al. 2001). Population dynamics of cockles are mostly controlled by recruitment and (mass) mortality. Mortality is high for all age classes, so rapid growth in the early life stages is considered the best growth strategy for cockles, as relatively few cockles survive beyond their third year (Seed & Brown 1978). Growth rate and numbers during the growing season determine, by definition, the yearly cockle production (Beukema & Dekker 2006). Therefore, understanding growth under varying conditions will provide valuable insight in bivalve ecology.

Varying environmental conditions like temperature and food availability can affect growth by altering the energy available for physiological processes (Cardoso et al. 2006). To understand the impact of variation in energy availability on the growth of cockles, a general framework is needed. The Dynamic Energy Budget (DEB) theory provides such a framework, describing the flow of energy in an individual, where energy is allocated to reproduction, maintenance or growth (Kooijman 2010). A known fraction (κ) of the total energy is allocated to somatic maintenance and growth while the remaining fraction ($1 - \kappa$) is allocated to maturity and reproduction. Applying DEB theory to model the growth of cockles gives the opportunity to simulate growth under natural environmental conditions and food availability.

Food intake determines the amount of energy assimilated to reserves, and therefore the amount that can be allocated to growth (Kooijman 2010). As cockles are suspension feeding bivalves, food is obtained by filtering water over the gills, after which it is transported to the labial palps where selection between edible and non-edible particles takes place (Honkoop et al. 2003). Edible particles are ingested while the non-edible particles are discarded as pseudofaeces (Kiorboe & Mohlenberg 1981). The size of the gills and palps is flexible and relates to environmental conditions (Theisen 1982; Essink et al. 1989; Barillé et al. 2000). Particle collection and selection capacity increases with increasing gill and palp size respectively (Honkoop et al. 2003). Gill and palp size relates to the particle concentration and the quantity and quality of the food in the water respectively and can be adjusted to fit a specific set of environmental conditions (Payne et al. 1995a; Payne et al. 1995b; Honkoop et al. 2003).

Cockles can adjust the size of the gills and palps to local food conditions to optimize their food intake (Essink et al. 1989). Structural adaptations can be explained by control of the ingestion rate, which depends on the clearance rate and selection efficiency. Reducing gill area will decrease the clearance rate and therefore limit ingestion rate. Small gill size is suggested to be advantageous under high particle concentrations as it avoids clogging of the gills with sediment and saturation of other feeding processes (Hawkins et al. 1990) and therefore allows for continued processing of particles. On the other hand, having large gills is beneficial when food is scarce or when feeding periods are short (Worrall et al. 1983; Franz 1993). Suspended Particulate Matter (SPM) is the key driver for palp size, as the selection efficiency increases with increasing palp size. Under low SPM concentrations, it is not necessary to increase palp size, while for high SPM concentrations an increase in palp size increases the amount of high-quality organic particles taken up (Nelson 1960; Kiorboe & Mohlenberg 1981). So there is a trade-off between the positive and negative effects of varying organ size, as well as the energetic costs involved in frequently adapting gill and palp size.

Changes in gill and palp size affect energy uptake by variation in the amount and quality of the food taken up. Under poor food conditions (low quantity and quality of organic particles) the total energy assimilated will be smaller, resulting in reduced growth (Honkoop et al. 2003). Silt-rich environments are considered poor conditions as the resuspension of silt by wind- and tide-induced erosion will lead to relatively low organic matter content in the suspended matter in relation to the amount of silt (De Jonge & van Beusekom 1995). It is expected that not only food availability but also feeding time and cockle density can affect the growth of cockles (Jensen 1992). Assuming cockles to feed when inundated, a longer inundation time will allow for a higher food uptake and therefore growth (Franz 1993). When cockle densities are high, relatively less food will be available per individual, resulting in reduced growth (Honkoop et al. 2003).

Even though both gill and palp sizes are flexible, they do not necessarily change simultaneously or to an equal extent. Both Honkoop et al. (2003) and Dutertre et al. (2009) state that it is mostly palp size that is adjusted under high turbidity conditions compared to less marked changes in gill size. However, feeding morphology of bivalves is described as the log-transformed ratio between gill ash-free dry mass (AFDM) and palp ash-free dry mass (AFDM). Using this ratio in gill and palp size does not allow distinguishing between variations in either gill or palp size, which could arguable differ.

Therefore, it is preferred to work with gill and palp size separately to observe variations in size due to changes in (environmental) conditions (Honkoop et al. 2003).

Furthermore, gill and palp sizes are related to the organisms' size. Small individuals will have smaller organs than large individuals, which should be taken into account when explaining variation in organ size. The general formula describing the scaling of biological variables to size is $Y = Y_0M^b$ where Y is the biological variable, Y_0 the normalization constant, M the body mass and b the allometric scaling component (Filguiera et al. 2008). For bivalves, the relation between shell length and dry weight to gill and palp area are expressed in this form, where gills and palps are related closely to Length^2 (among others: Kiorboe & Mohlenberg 1981; Jones et al. 1991; Filguiera et al. 2008). Not only is length an important explanatory variable in explaining organ size, the influence of length is also important for DEB theory, as energetics for acquisition processes are related to surface area (Kooijman 2010). For this research, ash-free dry mass is used as a measure of gill and palp size rather than area. As is confirmed by Honkoop et al. (2003), there is a significant relationship between the mass of gills and surface area and it is preferred to work with mass. However, the relation between mass and shell length is not reported in literature. Therefore, gill and palp mass will be related to shell length as $\text{Organ weight} = a{\cdot}\text{Length}^b$ for which a and b are estimated, consistent to the general formula.

The aim of this thesis is to estimate growth of cockles under different environmental conditions and relate this to variation in feeding morphology observed in the field. This thesis comprises of two sections: first, gill and palp size of cockles are related to environmental conditions. This will answer the question whether or not variation in gill and palp size is observed in the field and how the variation can be explained. Second, the growth of cockles is modelled using a basic DEB model for cockles from the Oosterschelde which will be adjusted to include optimization of food uptake based on changes in feeding morphology. These models will then be used to predict growth of cockles under different conditions in the Wadden Sea to examine differences in expected growth for basic DEB models and to assess the importance of adaptations in feeding morphology on predicted growth.

2. Material and Methods

2.1. Study sites

All data collected for this study is obtained from the Dutch part of the Wadden Sea. The Wadden Sea (52°57′–55°37′N, 4°44′–8°12′E) is a shallow sea along the Dutch, German and Danish coast and is characterized by a semidiurnal tide, resulting in intertidal sandbanks and mudflats that form a habitat for many marine species and birds. Data on cockle morphology are collected from the tidal flats surrounding Texel from three different sites during the summer of 2015 (table 1, figure 1a). The sites have different characteristics (median grain size (MGS), exposure time and cockle density) and therefore allow studying the relation to the size of the gills and palps of the cockles. For the second part of the study, cockle growth is modelled for varying environmental conditions. This model is based on data from the Oosterschelde, where data on cockle sizes and environmental parameters are available (Troost et al. 2010). Three sites have been chosen in the Dutch part of the Wadden Sea that represents different sets of conditions (table 2, figure 1b) to simulate the growth of cockles using the model described for the Oosterschelde.

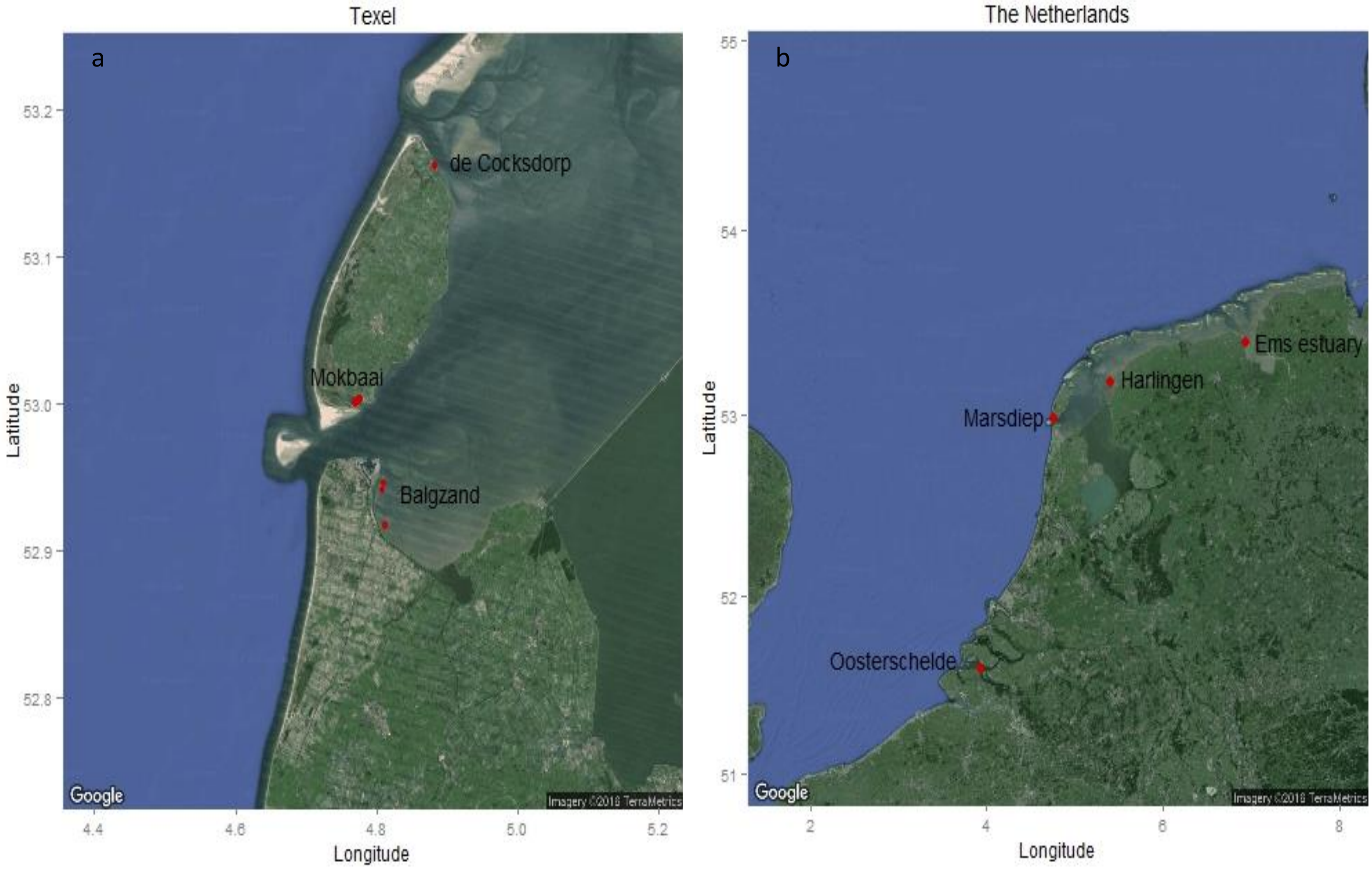

Figure 1 a) Map with locations used for cockle morphology: (i.e. Balgzand, de Cocksdorp and Mokbaai) and b) Map with locations used for DEB model simulations (i.e. Oosterschelde, Marsdiep, Harlingen and Ems estuary) (Kahle & Wickham, 2013).

Table 1 Timeline for data collection on feeding morphology in the Wadden Sea. Sampling date and number of cockles are represented per sampling date and location. Mokbaai 1 is used for within location comparison while data for De Cocksdorp, Balgzand and Mokbaai 2 are used for between location comparisons.

	Location	Sampling round 1	Sampling round 2	Sampling round 3
Within location comparison	Mokbaai 1	29-6-2015 (N=23)	2-8-2015 (N=10)	27-8-2015 (N=11)
Between location comparison	De Cocksdorp	1-7-2015 (N=26)		
	Mokbaai 2		29-7-2015 & 30-7-2015 (N=80)	
	Balgzand			2-9-2015 & 8-9-2015 (N=63)

Table 2 Sources of environmental data used for DEB model input where SST is the sea surface temperature (°C), chlorophyll a is the concentration of chlorophyll in the water (µg l^{-1}) and SPM is the suspended particulate matter concentration (mg l^{-1}). For each location, the station and years used to collect the data from the Rijkswaterstaat database (Rijkswaterstaat 2015b) are shown.

Location	SST (°C)	Chlorophyll a	SPM	Years	Source
Oosterschelde	Oosterschelde west	Oosterschelde west	Oosterschelde west	1993-2007	Troost et al. 2010
Marsdiep	Den Helder	Marsdiep Noord	Marsdiep Noord	1988-1995	Rijkswaterstaat 2015b
Harlingen	Harlingen	Harlingen havenmond west	Harlingen havenmond west	1988-1995	Rijkswaterstaat 2015b
Ems estuary	Delfzijl	Bocht van Wattum	Bocht van Wattum	1988-1995	Rijkswaterstaat 2015b

2.2 Feeding morphology

2.2.1. Field conditions

For each sampling date and location, coordinates were marked and used to determine altitude relative to mean sea level based on the bathymetry data from Deltares (2014). Altitude was used to calculate exposure time based on predicted tidal curves for the date the samples were taken. Predicted tidal curves are obtained from Rijkswaterstaat (2015a) for station Den Helder (Mokbaai and Balgzand) and Texel Noordzee (de Cocksdorp). Exposure time is expressed as a fraction, where 1 represents being completely exposed and 0 being completely inundated during a tidal cycle.

To measure sediment grain size, samples for each location were taken from the top 5 mm of the sediment. A cut of syringe was pressed into the sediment and pulled vacuum by closing of the top with a plunger. The top 5 mm is chosen as this layer could affect particle uptake by cockles due to resuspension of silt and microphytobenthos (De Jonge & van Beusekom 1995). Samples are analyzed with a Coulter LS320, where fresh sediment samples are added to the Aqueous Liquid Module (obscuration between 7 and 13%) (Beckman Coulter 2011). Data on both silt content (%) (particles smaller than 63 µm) and median grain size were obtained from these measurements (Blott & Pye 2001) as it remained unclear whether or not they would have the same effect on gill and palp size prior to the experiment.

Cockles are collected from the tidal flat by hand-picking them from a 0.25 m^2 frame placed arbitrarily on the tidal flat, except for the sampling of the Mokbaai on 29-7-2015 and 30-7-2015 when samples were taken in a 4x4 sampling point grid in an area of 250 by 250 meter. The number of cockles was counted and converted to density (individuals m^{-2}).

2.2.2. Bivalve feeding morphology

Prior to dissection, cockles are sedated in a 50 gl^{-1} $MgCl_2$ solution for 16 hours to avoid damaging organs while opening the cockle during dissection (Suquet et al. 2009). Length of the cockle was determined by measuring the length along the anterior-posterior axis and age by counting age rings on the shell. During dissection, distinction was made between gills, palps, and gonads. The foot was removed for isotope analysis and was corrected for in total weight. To do so, 57 cockles of different sizes from multiple locations were dissected to correlate foot ash-free dry mass (AFDM) to remaining soft tissue. This way the weight of the foot can be back-calculated from the soft tissue weight for all cockles to obtain total weight. Gills, palps, gonads, foot and rest materials were placed in platinum crucibles to dry for three days at 60°C. After cooling down in a desiccator, weight was determined to the nearest 0.1 mg. The organs were incinerated at 560°C for 5 hours to determine ash weight. Again, after cooling the weight of the organs was measured to the nearest 0.1 mg. Ash-free dry mass (AFDM) is used as a measure of biomass and is determined by subtracting the ash weight from the dry weight.

2.2.3. Within and between location comparison

To explain the variation in gill and palp size between cockles, combinations of physiological and environmental variables are used as explanatory variables. As length of the cockle has an obvious influence on the size of the gills and palps, length is considered the most influential explanatory variable and is therefore included in every model. Length is known to influence gill and palp size by $a*L^b$ (Kiorboe & Mohlenberg 1981; Jones et al. 1992). Data exploration (as explained in Zuur et al. (2010)) resulted in dropping age and silt content as explanatory variables due to covariance with length and median grain size & exposure time respectively. Each of the variables (length, Median Grain Size (MGS), cockle density and exposure time) was examined individually and in different combinations of variables.

As not all locations could be visited every sampling round due to logistical issues, it was decided to only resample one side of the Mokbaai for every sampling round. With this data, a within location comparison of the gill and palp size can be done for the Mokbaai on three different sampling dates. Generalized Linear Models (GLMs) were used to model the effect of combinations of explanatory variables on the variation in gill and palp size (table 3). The main reason to do this is to determine the effect of sampling date on gill and palp size. If sampling date has a significant effect on gill and palp size, this has to be accounted for in the between location comparison as locations are sampled during different sampling rounds. Between location comparison is based on the same principal as the within location comparison. Here, Generalized Additive Models (GAMs) are used to model the effect of multiple explanatory variables on the gill and palp size (see table 4 for all combinations) (Zuur 2012). Here sampling date is not included as an explanatory variable, but location is.

Model selection for both within and between location comparison is based on the Akaike Information Criterion (AIC value), where the model with the lowest AIC value is considered to have the best fit (Akaike 1973; Burnham & Anderson 2004). However, it has to be kept in mind that models with an AIC difference ($\Delta AIC = AIC - AIC_{min}$) smaller than two still have substantial support and cannot be rejected (Burnham & Anderson 2004). If models have $\Delta AIC < 2$, 1 parameter difference and essentially the same log likelihood value as the best model, the larger model is no longer supported (Burnham & Anderson 2003). Instead, the smaller model will be chosen as the best model.

Table 3. Within location comparison: overview of the combination of variables to explain the variation in gill and palp size as modelled with GLMs. The ‘Variables’ column indicates the number of variables used to explain gill or palp size.

Model	Variables	Explanatory variable
1	0	1
2	1	$a \cdot Length^b$
3	2	$a \cdot Length^b$ + Density
4	2	$a \cdot Length^b$ + MGS
5	2	$a \cdot Length^b$ + Exposure time
6	2	$a \cdot Length^b$ + Sampling date
7	3	$a \cdot Length^b$ + Density + MGS
8	3	$a \cdot Length^b$ + Density + Exposure time
9	3	$a \cdot Length^b$ + MGS + Exposure time
10	3	$a \cdot Length^b$ + Density + Sampling date
11	3	$a \cdot Length^b$ + MGS + Sampling date
12	3	$a \cdot Length^b$ + Exposure time + Sampling date
13	4	$a \cdot Length^b$ + Density + MGS + Exposure time
14	4	$a \cdot Length^b$ + Density + MGS + Sampling date
15	4	$a \cdot Length^b$ + Density + Exposure time + Sampling date
16	4	$a \cdot Length^b$ + MGS + Exposure time + Sampling date
17	5	$a \cdot Length^b$ + Density + MGS + Exposure time + Sampling date

Table 4. Between location comparison: overview of the combination of variables to explain the variation in gill and palp size modelled with GAMs, where s represent variables smoothed and f represent variables added as a factor. The 'Variables' column indicates the number of variables used to explain gill or palp size.

Model	Variables	Explanatory variable
1	0	1
2	1	$a \cdot Length^b$
3	2	$a \cdot Length^b$ + s(Density)
4	2	$a \cdot Length^b$ + s(MGS)
5	2	$a \cdot Length^b$ + s(Exposure time)
6	2	$a \cdot Length^b$ + f(Location)
7	3	$a \cdot Length^b$ + s(Density) + s(MGS)
8	3	$a \cdot Length^b$ + s(Density) + s(Exposure time)
9	3	$a \cdot Length^b$ + s(MGS) + s(Exposure time)
10	3	$a \cdot Length^b$ + s(Density) + f (Location)
11	3	$a \cdot Length^b$ + s(MGS) + f (Location)
12	3	$a \cdot Length^b$ + s(Exposure time) + f (Location)
13	4	$a \cdot Length^b$ + s(Density) + s(MGS) + s(Exposure time)
14	4	$a \cdot Length^b$ + s(Density) + s(MGS) + f (Location)
15	4	$a \cdot Length^b$ + s(Density) + s(Exposure time) + f (Location)
16	4	$a \cdot Length^b$ + s(MGS) + s(Exposure time) + f (Location)
17	5	$a \cdot Length^b$ + s(Density) + s(MGS) + s(Exposure time) + f(Location)

2.3. DEB model for cockles

2.3.1. DEB theory

Energetic processes of individual organisms can be described by the Dynamic Energy Budget (DEB) theory, which determines the rate at which an organism assimilates and utilizes energy (Kooijman 2010). Energy is allocated to somatic maintenance, growth, and reproduction as a function of state of the environment and organism. Environmental state comprises of temperature (T, K), food availability (Chlorophyll a, µg l^{-1}) and inorganic matter (SPM, mg l^{-1}), while organism state is represented as structural volume (V, cm^3) and reserves (E, Joule) (Kooijman 2010). Food is ingested and either discarded as (pseudo)faeces or assimilated as energy to the reserves. From the reserves, energy is allocated in a fixed fraction (κ) to somatic maintenance and growth, while the remaining fraction (1-κ) is allocated to development, reproduction and maturity maintenance (Kooijman 2010). Reserves form a balance between the assimilation flux and mobilization flux and structural volume depends on the energy allocated to growth (mobilization flux – somatic maintenance flux). Structural volume is related to the length of an organism (L, cm), based on the shape coefficient δ_M.

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

2.3.1.1. Temperature

Environmental conditions can greatly affect the energy uptake and physiological rates. The rates of physiological processes at the organismal scale are dependent on temperature, described by an Arrhenius type of relation. Here, physiological rates are described at ambient temperatures as:

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

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

2.3.1.2. Functional response

Food availability and inorganic matter concentration are linked to ingestion rate ($\dot{J}_X$) and is described by a hyperbolic functional response (Type II Holling response curve). The scaled functional response, (f) represents the intake rate of a consumer as a function of food density. In a type II response curve, a decelerating intake rate is caused by a limited food processing capacity of the consumer (Holling 1959). The scaled functional response is given by:

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

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

where X and Y are the food and SPM concentrations respectively and X_K and Y_K are their half saturation coefficients (Kooijman 2006).

2.3.1.3. Cockle specific parameters

Many of the parameters required for the DEB model have been estimated before and are obtained mostly from van der Veer et al. (2006). The used parameters are summarized in table 5.

Table 5 Original parameter values used in the cockle DEB model. Values are obtained from van der Veer et al. (2006) (1) and Troost et al. 2010 (2)

Parameter	**Unit**	**Description**	**Value**	**Reference**
T_A	K	Arrhenius temperature	5800	1
T_L	K	Lower boundary of tolerance range	278	1
T_H	K	Upper boundary of tolerance range	306	1
T_{AL}	K	Arrhenius temperature at lower boundary	51154	1
T_{AH}	K	Arrhenius temperature at upper boundary	47126	1
p_{Am}	$J\ d^{-1}\ cm^{-2}$	Maximum surface area specific assimilation rate	68.6	1
p_M	$J\ d^{-1}\ cm^{-3}$	Volume specific somatic maintenance costs	24	1
ec	$cm\ d^{-1}$	Energy conductance	0.032	1
E_G	$J\ cm^{-3}$	Volume specific cost of structural volume	1900	1
κ	-	Fraction of mobilized reserves allocated to soma	0.8	1
δ_M	-	Shape coefficient	0.381	1
X_K	$\mu g\ Chla\ l^{-1}$	Half saturation coefficient for food	2.74	2
Y_K	$mg\ l^{-1}$	Half saturation coefficient for sediments	100	2

2.3.2. DEB model

As a basic DEB model, the model from Gerla & Soetaert (2014) for blue mussels is modified by implementing the parameter values (table 5) for cockles in R (R Core Team 2015). The initial model was adapted by incorporating the temperature function and functional response as described above. The model was run for data on cockle length over time, obtained from Troost et al. (2010) using the environmental conditions in the Oosterschelde estuary. The model described by Gerla & Soetaert (2014) is slightly different from the model described by Troost et al. (2010) as it does not incorporate Particulate Organic Matter (POM) in the model. Therefore, the model by Gerla & Soetaert will not give the same result as the DEB model output from Troost.

By re-estimating the parameters for cockles the DEB model is fitted to the data on cockle size from Troost et al. (2010). In general, parameter estimates are used as described in van der Veer et al. (2006), who estimated DEB parameters for several North Atlantic bivalve species. However, these parameters have been estimated indirectly and can contain large standard errors. Therefore, the results are uncertain, which allowed us to slightly vary the parameters estimates and half saturation coefficients to increase the fit of the model substantially. From a sensitivity analysis (as described in Soetaert & Petzoldt (2010)) the model turned out to be most sensitive to variation in the parameters p_{AM}, p_M, E_G, X_K, and Y_K. Based on a model cost analysis, these parameters are fitted to the data to obtain a set of parameters which results in the best fit (lowest 'model costs') (Soetaert & Petzoldt 2010). The fitted model is hereafter referred to as the 0-model and will form the basic model from which alterations are made.

The 0-model has been extended to incorporate the effect of varying gill and palp size. Three extra situations have been modelled, where either the influence of palps, gills or both gills and palps have been added. Organ size is not modelled explicitly; instead, the possibility to optimize half saturation constants depending on the organic and inorganic matter in the water is used. Inorganic matter affects K'(Y) as the uptake efficiency of organic particles is depressed with increasing inorganic matter. The half-saturation coefficient for inorganic matter determines the degree of this trend (Ren 2009). Palp sorting efficiency will cause variation in Y_K as the negative influence of inorganic particles will be reduced when sorting capacity increases. Considering a linear increase in Y_K with increasing inorganic matter concentration, $Y_K = a*Y + b$, where a and b are estimated. For gills, an increase in particle loads can lead to a decrease in gill area and therefore filtration capacity. This causes a linear increase in X_K with a decreasing gill size (Alunno-Bruscia et al. 2011). As shown in Alunno-Bruscia et al. (2011) $X_K = c*X + d$, where c and d are estimated for the Oosterschelde data. The combination of both gills and palps incorporate the changes in both X_K and Y_K. All parameters (0-model) are kept constant for the models where gill and/or palp size are adjusted to compare between model outputs. The values for a, b, c and d are estimated to fit the models to the Oosterschelde data.

2.3.3. Model simulations

The model parameters, as fitted for the Oosterschelde data are used to model growth of cockles under different environmental conditions represented by three locations in the Wadden Sea. As can be seen in table 2, monthly data is available for eight years (1988-1995). To get some insight into the conditions at a site, the data is averaged for these eight years to exclude year specific extremes. Then, a cyclic spline GAM model is fit to the data to obtain environmental data per day. For each location, the four models are run (0-model, Palp model, Gill model and Gill & Palp model) based on the environmental data to compare length (after six years of growth) for cockles between and within location considering different adaptation abilities. To run the model for 6 years, the environmental data is repeated six times to avoid variation in growth due to (yearly) varying environmental conditions.

3. Results

3.1. Feeding morphology

3.1.1 Variation in gill and palp size

The first step to determine the effect of environmental conditions on the gill and palp size is to establish whether actual variation in organ weight is observed. To do so, gill and palp size are corrected for the size of the organism, which is shown in figure 2, where the weight of the gills and palps is plotted against length and the line represents the function Organ weight = $a \cdot \text{Length}^b$. The value for a and b are estimated and are 1.4 and 2.33 for gill size and 0.51 and 3.33 for palp size. To compare the variation in organ size, the data on gill and palp weight is corrected for length, as can be seen in figure 3. For both gills and palps, variation in organ size can be observed between and within locations. Gill weight is significantly different between the Mokbaai and Balgzand (anova: $p<0.05$) and palp weight is significantly different between all three locations (anova: $p<0.05$).

3.1.2 Within location comparison

To examine the effect of sampling date on gill and palp size, the North-East side of the Mokbaai has been sampled during all sampling rounds. When comparing the 5 variables (length, density, MGS, exposure time and sampling date) used to explain the variation in gill and palp size, the effect of sampling date can be examined. The AIC values per model can be found in table 6 (model numbers correspond to table 3). Model 10 is the model that explains most variation in gill size and includes length, density and sampling date. Length is significant in explaining gill size variation and density is not significant ($p>0.05$) (table 7). Furthermore, gill size is significantly higher for cockles collected in the Mokbaai on 2-8-2015 (2nd sampling round) than cockles collected on 29-6-2015.

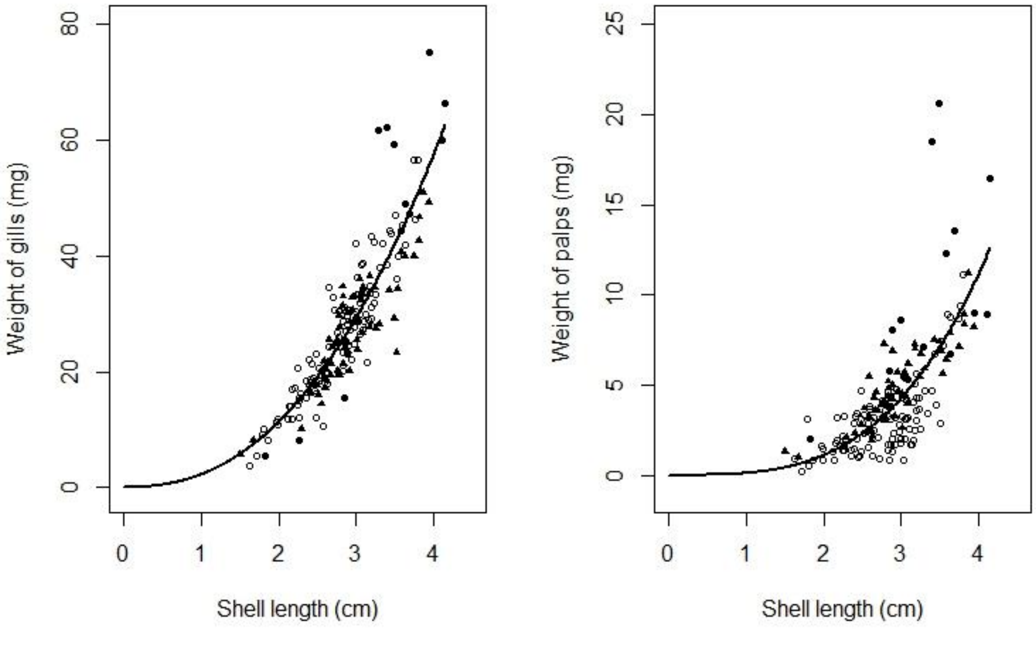

Figure 2 Correlation between shell length (cm) and the weight of the organs (gills and palps) (mg). The fitted line represents the function Organ weight = $a*\text{Length}^b$, where a = 1.4 & b = 2.33 for gill weight and a = 0.051 & b = 3.33 for palp weight. ○ Location = Mokbaai, ● Location = De Cocksdorp and ▲ Location = Balgzand

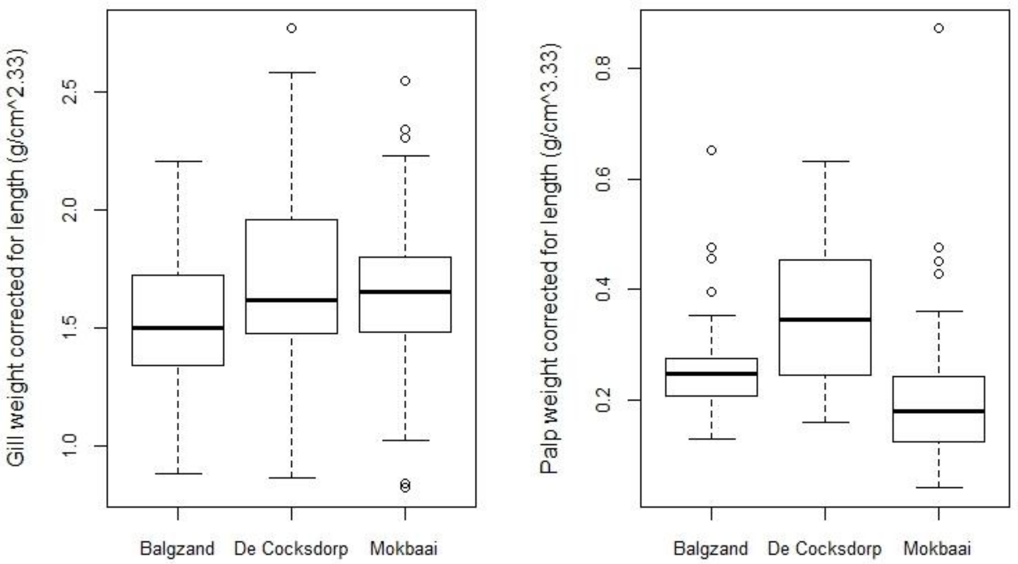

Figure 3 Variation in gill and palp size per location. Weight of gills and palps are corrected for Length ($a \cdot L^b$), to compensate for their effect on the size of the organs. The boxplots show variation in gill and palp size within locations and between locations. The Mokbaai is significantly different from Balgzand for gill weight ($p<0.05$) and all three locations are significantly different for palp weight ($p<0.05$).

Table 6 GLM model results for the within location comparison. Model numbers correspond to table 3, indicating the explanatory variables in the model. The table represents the degrees of freedom (Df), log Likelihood value, AIC value and the Δ AIC value per model for gills and palps. The Δ AIC value of 0.000 represents the best model and is model 10 for gills and model 5 for palps (dark grey). Models with ΔAIC<2 are colored light grey; however they don't fit the best model criteria.

	Gill				Palp			
Model	**Df**	**Log Likelihood**	**AIC**	**Δ AIC**	**Df**	**Log Likelihood**	**AIC**	**ΔAIC**
1	2.00	-118.33	240.67	68.39	2.00	-71.26	146.52	78.15
2	3.00	-84.87	175.75	3.46	3.00	-33.10	72.20	3.83
3	4.00	-83.39	174.78	2.50	4.00	-32.57	73.14	4.76
4	4.00	-84.72	177.44	5.16	4.00	-33.03	74.06	5.69
5	4.00	-84.40	176.81	4.52	4.00	-30.19	68.37	0.00
6	5.00	-81.97	173.94	1.65	5.00	-30.94	71.88	3.50
7	5.00	-83.30	176.61	4.33	5.00	-32.53	75.05	6.68
8	5.00	-83.12	176.24	3.96	5.00	-29.93	69.86	1.49
9	5.00	-84.31	178.62	6.34	5.00	-30.19	70.37	2.00
10	6.00	-80.14	172.28	0.00	6.00	-30.90	73.81	5.43
11	6.00	-81.91	175.81	3.53	6.00	-30.94	73.87	5.50
12	6.00	-81.91	175.82	3.54	6.00	-28.82	69.65	1.27
13	6.00	-83.06	178.13	5.85	6.00	-29.93	71.86	3.49
14	7.00	-80.09	174.19	1.91	7.00	-30.90	75.80	7.43
15	7.00	-80.12	174.23	1.95	7.00	-28.74	71.47	3.10
16	7.00	-81.85	177.69	5.41	7.00	-28.82	71.65	3.27
17	8.00	-80.07	176.14	3.85	8.00	-28.74	73.47	5.10

Table 7 Generalized Linear Model results from the within location comparison: model summaries indicating significance of the environmental variables in explaining the variation in gill and palp size respectively. Sampling date is compared to 29-6-2015 and shows whether there is a (significant) difference between the first sampling data and the second/third. Significance indicator: $p<0.1$. $p<0.05$ *, $p<0.01$ **, $p<0.001$ ***

	Environmental variables	**p-value**		**Environmental variables**	**p-value**
Gills (model 10)	$1.4 \cdot \text{Length}^{2.33}$	<0.001 ***	Palps (model 5)	$0.51 \cdot \text{Length}^{3.33}$	<0.001 ***
	Density	0.0853 .		Exposure time	0.0236 *
	Sampling date				
	- 02-08-2015	0.0255 *			
	- 27-08-2015	0.5701			

This implies that for the between location comparison it has to be taken into account that gill size might be overestimated for the data collected in the 2nd sampling round. The best palp model is model 5 that includes length and exposure time, where length and density both have a significant effect on palp size (table 7). For palp size, sampling date is not included in the model and is therefore assumed not to significantly affect the palp size. For the between location comparison this implies that different sampling times will not affect the size of the palps.

3.1.2 Between location comparison

Three different locations have been sampled (figure 1) to be able to relate the effect of different (environmental) conditions on the size of the gills and palps. As can be seen in figure 4, the variables used in the GAM models vary among the different locations. For de Cocksdorp larger cockles are found, compared to Balgzand and Mokbaai ($p<0.01$). Median grain size is significantly different among the three locations ($p<0.001$), where Balgzand shows low MGS while the Mokbaai shows the highest values. Density is relatively low for Balgzand and de Cocksdorp while the Mokbaai shows a large variation in densities and is significantly higher ($p<0.001$). Finally, Balgzand shows a large range in exposure time, compared to the other locations. However, only de Cocksdorp and Mokbaai differ significantly from one another ($p<0.05$).

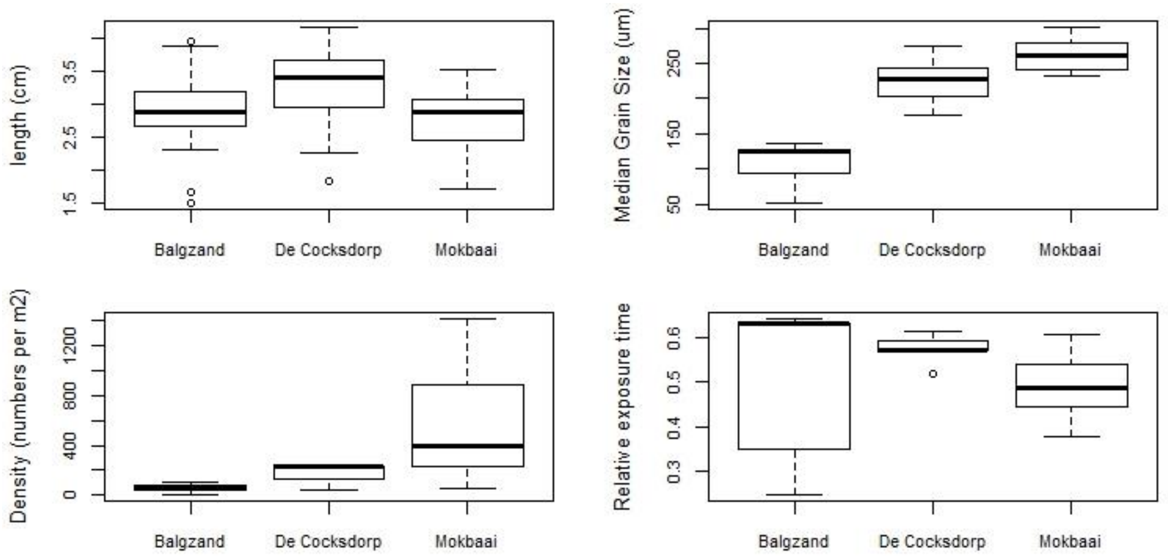

Figure 4 Variation in explanatory variables (shell length, MGS, density and exposure time) between locations. For shell length, De Cocksdorp has significantly larger cockles than the other locations ($p<0.01$). For MGS, all locations are significantly different in terms of grain size with the finest sediment in Balgzand ($p<0.001$). The Mokbaai has significantly higher densities than Balgzand and De Cocksdorp ($p<0.001$). For exposure time, De Cocksdorp and the Mokbaai differ significantly ($p<0.05$).

Combinations of explanatory parameters are used in Generalized Additive Models to examine their combined effect on gill or palp size. As can be seen in table 8, model 5 gives the best fit for gill size and explains 82.4% of the deviance (table 9). Here the best model is the one with Δ AIC = 0 as no other model fits the best model criteria (as explained in the methods). The model includes length and exposure as explanatory variables, which are both highly significant. For palp size, the best model is model 13 (table 8), explaining 53.7% of the deviance. The model with the smallest AIC value is 17; however, as there is only one parameter difference and the log likelihood value is similar, model 13 is preferred over model 17. The explanatory variables for model 13 are length, density, MGS and exposure time, which are all significant in explaining palp weight on the size of the palps (table 9).

Plotting the model outcomes provides a visual interpretation of the effect of explanatory variables on the gill and palp size. Figure 5 shows the effect the variables in the gill model have on the size of the gills. Length has a positive linear effect on gill size and exposure time has a non-linear positive effect on gill size. For exposure time the general trend is positive, however, the slope varies and even shows a small negative effect between 0.42 – 0.55, after which is shows another peak. For palp size, figure 6 shows the model output for the four explanatory variables. Again for length, palp size shows a positive linear increase with increasing length. Median Grain Size and density show a negative influence on palp size and exposure time has again a positive effect on gill size.

Table 8 GAM model results for the between location comparison. Model numbers correspond to table 4, indicating the explanatory variables in the model. The table represents the degrees of freedom (Df), log Likelihood value, AIC value and the Δ AIC value per model for gills and palps. The Δ AIC value of 0.000 represents the best model and is model 5 for gills, for palps the model with Δ AIC = 0 is not the best model, as model 13 has a Δ AIC<2, a similar log-likelihood and 1 parameter less and is therefore considered better in explaining variation in palp size (dark grey). Models with Δ AIC < 2 are colored light grey; however they don't fit the best model criteria.

	Gill				Palp			
Model	**Df**	**Log Likelihood**	**AIC**	**Δ AIC**	**Df**	**Log Likelihood**	**AIC**	**ΔAIC**
1	2.00	-608.93	1221.85	252.11	2.00	-399.08	802.16	117.42
2	3.00	-494.83	995.66	25.92	2.00	-347.53	699.07	14.33
3	6.26	-488.65	989.83	20.08	2.92	-341.56	688.96	4.22
4	5.42	-483.47	977.77	8.03	2.81	-345.11	695.84	11.10
5	10.52	-474.35	969.74	0.00	2.82	-345.24	696.10	11.37
6	5.00	-486.09	982.18	12.44	2.00	-347.53	699.07	14.33
7	7.99	-480.91	977.79	8.05	3.00	-341.03	688.05	3.31
8	6.85	-481.04	975.78	6.03	2.95	-340.76	687.43	2.69
9	8.33	-477.90	972.46	2.72	3.83	-340.42	688.49	3.76
10	7.83	-484.43	984.53	14.78	2.95	-340.69	687.27	2.54
11	8.74	-477.63	972.74	2.99	2.87	-344.73	695.20	10.46
12	6.00	-482.44	976.87	7.13	2.82	-345.18	696.00	11.27
13	9.36	-477.77	974.26	4.52	3.77	-339.06	685.68	0.94
14	11.44	-475.34	973.56	3.82	3.00	-340.23	686.46	1.72
15	8.63	-478.99	975.24	5.49	2.97	-339.95	685.83	1.09
16	10.14	-475.70	971.68	1.93	3.78	-339.69	686.94	2.20
17	13.01	-473.59	973.21	3.46	3.79	-338.58	684.74	0.00

Table 9 Generalized Linear Model results from the between location comparison: model summaries indicating the significance of the environmental variables in explaining the variation in gill and palp size respectively. The explanatory variables in the models are printed with the p-value showing their significance (significance indicator: p<0.1 . p<0.05 *, p<0.01 **, p<0.001 ***). The adjusted R^2 value and explained deviance are shown to indicate the fit of the model.

	Explanatory variables	**p-value**	**R^2 adj.**	**Deviance explained**
Gill (model 5)	$1.4 \cdot \text{Length}^{2.33}$ Exposure time	<0.001 *** < 0.001 ***	0.814	82.4%
Palp (model 13)	$0.51 \cdot \text{Length}^{3.33}$ Density MGS Exposure time	<0.001 *** <0.001 *** 0.00457 ** 0.00886 **	0.531	53.7%

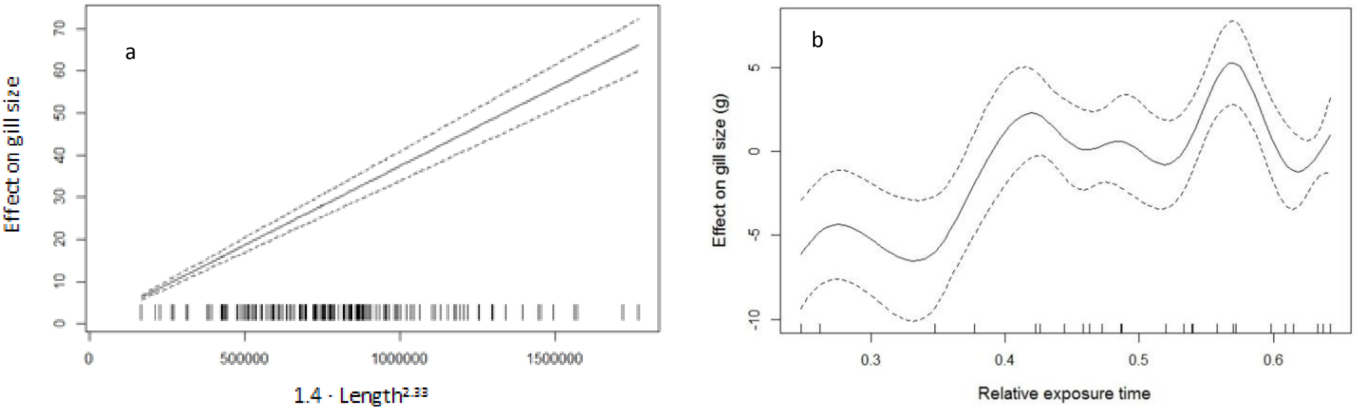

Figure 5 Generalized additive model derived effects for gill size (model 5) of (a) 1.4·Length$^{2.33}$, (b) Relative exposure time with the standard error confidence belt (dashed line). The y-axis represents the normalized effect of the variable on the gill size and the rug plot on the x-axis shows the distribution of the observations.

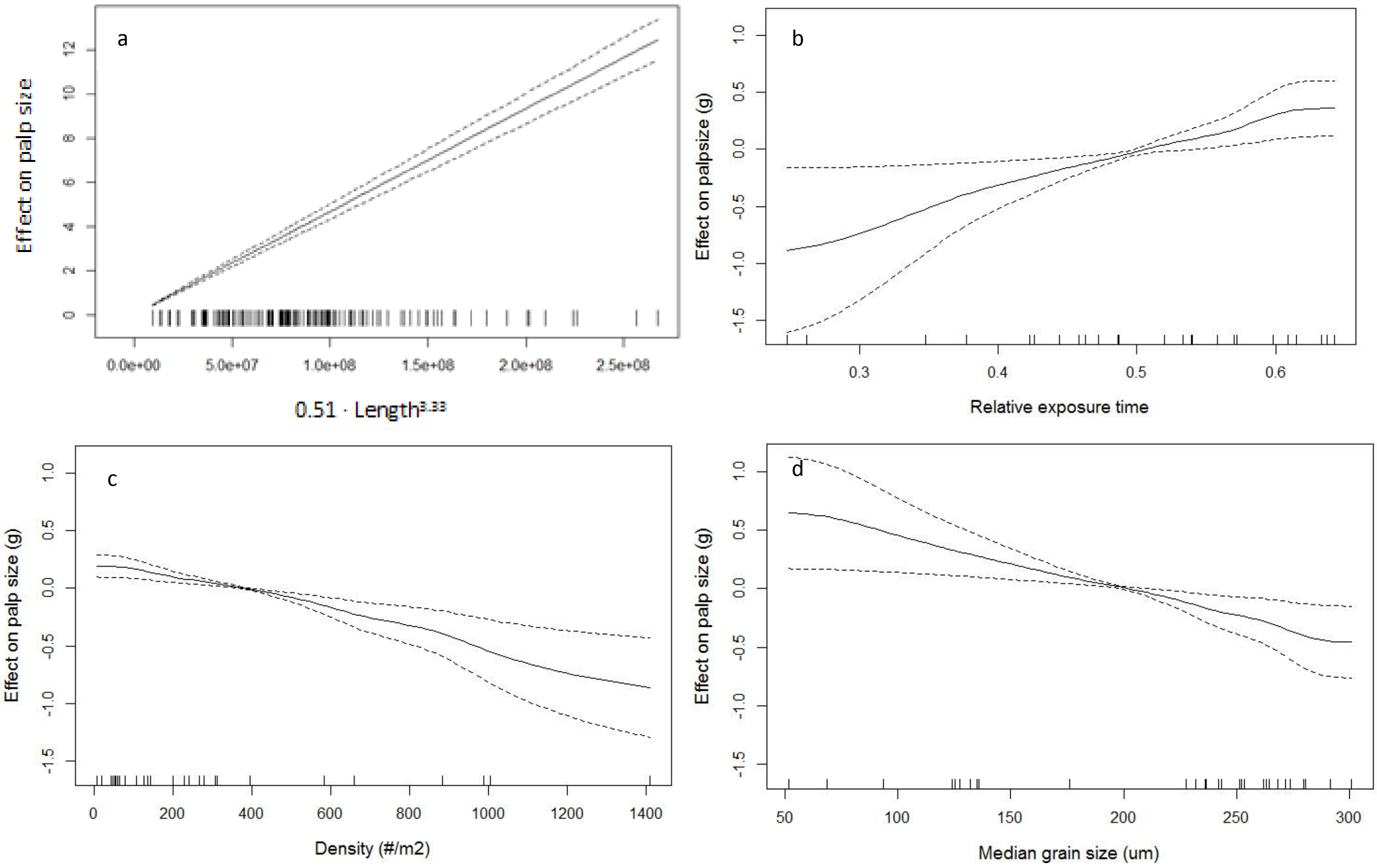

Figure 6 Generalized additive model derived effects for palp size (model 13) of (a) 0.51·Length$^{3.33}$, (b) Relative exposure time, (c) Density and (d) Median Grain Size with the standard error confidence belt (dashed line). The y-axis represents the normalized effect of the variable on the palp size and the rug plot on the x-axis shows the distribution of the observations.

3.2. DEB model

3.2.1 Environmental data

To run the DEB models, environmental data is required as an input for temperature, Chlorophyll a (X) and SPM (Y) in the model. As explained in the material and methods, data is obtained from the Rijkswaterstaat database (Rijkswaterstaat 2015b), which is averaged per year and then modelled to obtain daily data. Figure 7 shows the data on temperature, Chlorophyll and SPM concentration for the four locations used for DEB modelling. Temperature shows a similar trend over time, with differences in the extremes in summer and winter between the locations. The Oosterschelde is a few degrees warmer than the Wadden Sea sampling locations in summer. Chlorophyll concentrations are all showing the seasonal pattern (spring and autumn peaks), the ranges are however different per location. The Oosterschelde has relatively low concentrations while especially Harlingen has high chlorophyll a concentrations. For SPM the variation in ranges is even bigger, where again the Oosterschelde has low values and the Ems estuary has very high SPM values and strong variation over the year.

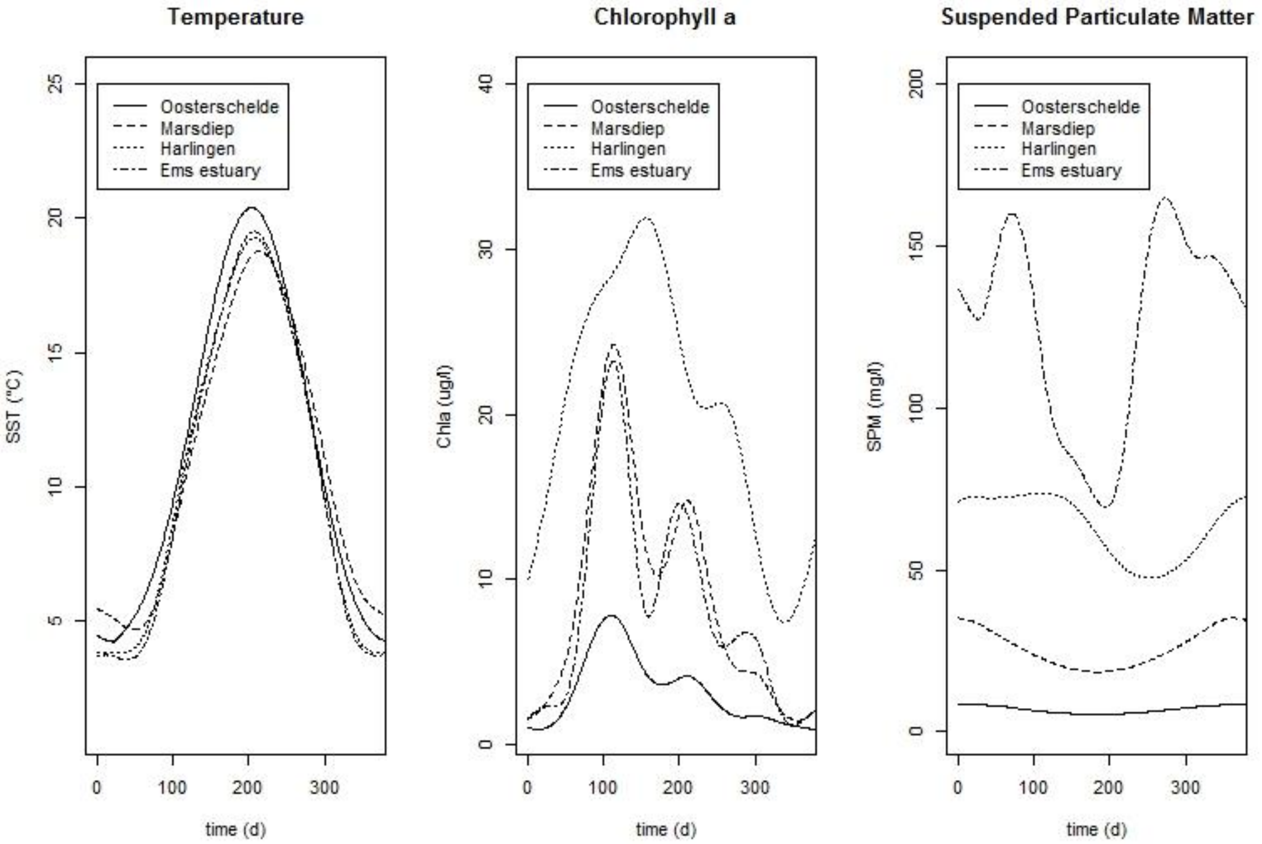

Figure 7 Yearly averaged environmental data on a) Temperature (°C), b) Chlorophyll a concentration (µg/l) and c) Suspended Particulate Matter concentration (mg/l) for the Oosterschelde (Troost et al. 2010), Marsdiep, Harlingen and Ems estuary (Rijkswaterstaat 2015b) as a smoothed yearly average calculated over data from 1988-1995.

3.2.2 Parameter estimates

The basic DEB model is used to model the growth of cockles based on the data available in Troost et al. (2010) for the Oosterschelde. Figure 8 shows the predicted growth of cockles based on the conditions in the Oosterschelde (dashed line). When comparing the predicted line with the observed values, the model fit is low. To fit the model to the data obtained from Troost et al. (2010), parameter values are fitted. Small variations in the parameter estimates for the 0-model create a better model fit (table 10). Especially after one year the fit of the model gets better, however, the first year shows an underestimate in the beginning compared to the data points and an over fit at the end of the first year. For the models where gills and palps are optimized, the parameters (except for X_K and Y_K) are kept constant to compare between models. For the palp model, gill model and gill & palp model Y_K (a and b) and/or X_K (c and d) are estimated to fit the cockle growth data (table 10, figure 9).

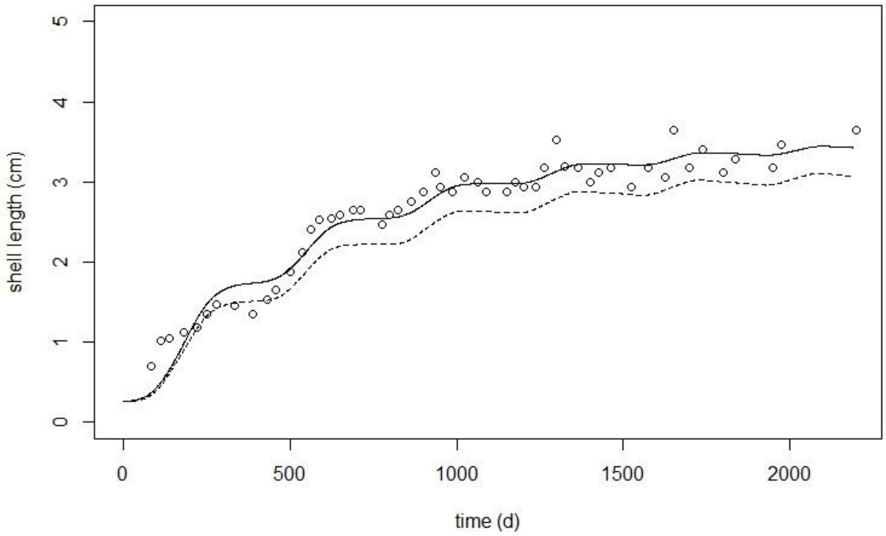

Figure 8 DEB estimates based on the original DEB model from Gerla & Soetaert (2014) (adapted for temperature and functional response as described in the Material and Methods), based on data obtained from (Troost et al. 2010). The solid line represents the 0-model and the dashed line the original model.

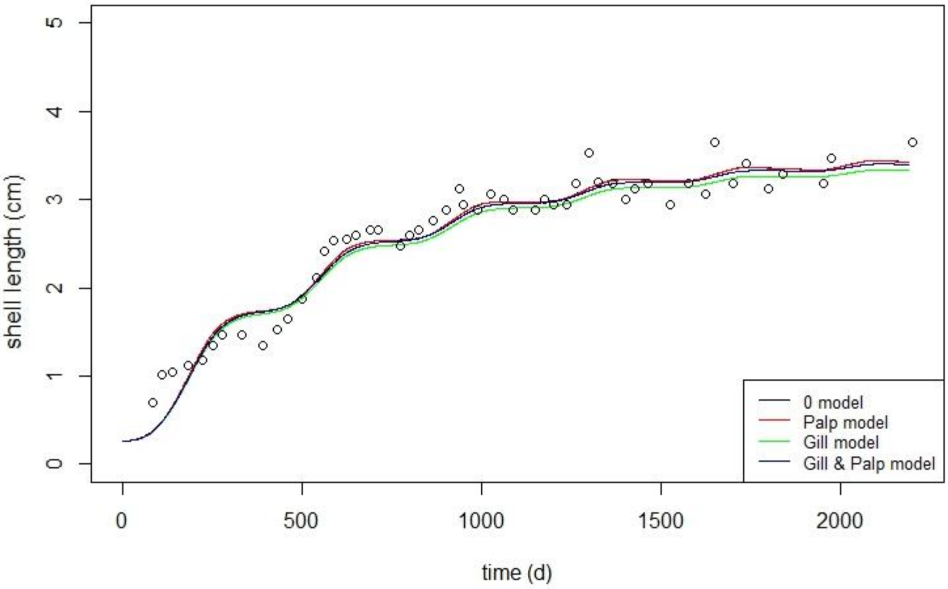

Figure 9 DEB estimates for the four models (0-mode, palp model, gill model and gill & palp model) fitted to the data from the Oosterschelde (Troost et al. 2010). 0 model: black line, palp model: red line, gill model: green line, gill & palp model: blue line.

Table 10 Parameter estimates for the cockle DEB model for different models. Original model: model based on original parameters; 0-model: parameters estimated; Palp model: a and b estimated; Gill model: c and d; Gill & Palp model: a, b, c and d. For every model, the bold parameters are estimated, while the others were fixed.

Parameter	Original	0-model	Palp model	Gill model	Gill & Palp model
p_{Am}	68.6	**65.18**	65.18	65.18	65.18
p_M	24	**28.64**	28.64	28.64	28.64
ec	0.032	0.032	0.032	0.032	0.032
E_G	1900	**1927.79**	1927.79	1927.79	1927.79
κ	0.8	0.8	0.8	0.8	0.8
δ_M	0.381	0.381	0.381	0.381	0.381
X_K	2.74	**1.033**	1.033	-	-
Y_K	100	**79.74**	-	79.74	-
a	-	-	**0.95**	-	**0.85**
b	-	-	**71.1**	-	**120.2**
c	-	-	-	**0.21**	**0.18**
d	-	-	-	**0.48**	**0.52**

3.2.3 Cockle growth predictions

Estimates for cockle growth under different environmental conditions are modelled for the environmental data for the Marsdiep, Harlingen, and Ems estuary, based on the estimated parameters (figure 10). Between locations comparison (0-model) shows that the conditions in the Ems estuary would result in the least growth over time (3.54 cm after six years (table 11)). Marsdiep and Harlingen both show larger shell length (3.89 and 4.19 cm after six years) than the Ems estuary, with the highest estimated growth for Harlingen. When comparing the different models within a site, the gill model and gill & palp model will always result in smaller cockles after six years, while the palp model shows an increased shell length compared to the 0-model (table 11). Adjusting to SPM concentrations results in the largest increase in shell length between models (7.6%) in the Ems estuary (compared to the 0-model).

Table 11 Length of the cockle after six years (cm) and the difference in length after 6 years by the models where gills and/or palps are adapted as a percentage of the 0-model length. Positive values, therefore, represent an increase in length, while negative values represent a decrease in length compared to no adaptations.

Location	0-model (cm)	Gill model (cm, %)	Palp model (cm, %)	Gill & Palp model (cm, %)
Marsdiep	3.89	3.41 (- 12.3)	3.91 (+ 0,5)	3.57 (- 8,2)
Harlingen	4.19	3.29 (- 21.5)	4.24 (+ 1,2)	3.60 (- 14,1)
Ems Estuary	3.54	2.83 (- 20.1)	3.81 (+ 7,6)	3.36 (- 11,8)

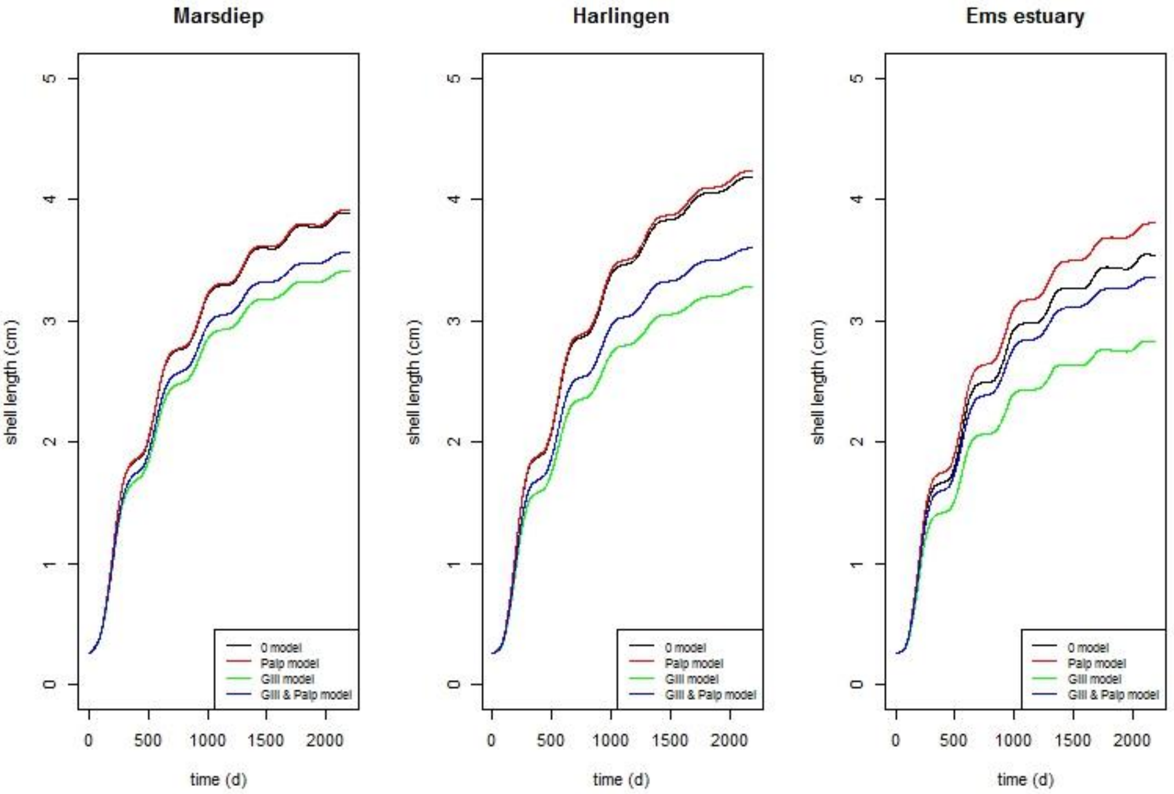

Figure 10 Cockle growth estimates based on DEB model simulations for three locations in the Wadden Sea (Marsdiep, Harlingen, and Ems estuary) representing different combinations of environmental conditions. Growth is estimated by calculating shell length over six years. 0 model: black line, palp model: red line, gill model: green line, gill & palp model: blue line.

4. Discussion

4.1 Feeding morphology

Time constraints prohibited sampling all locations each round, therefore, only the North-East side of the Mokbaai was sampled repeatedly so it could later be checked whether or not sampling date had a significant effect on the gill and palp size. This is confirmed by the results which show that for the repeated measurements in the Mokbaai, the model including the sampling date could not be rejected for the gill model compared to the model without a time component. This complicates a between location comparison, as they were sampled at different dates and are thus influenced by temporal variations in the gill size. As gill size only increases from the first sampling date for cockles sampled in the Mokbaai on 2-8-2015, gill size for this location is possibly overestimated. As sampling date is not included in the palp model we can assume that palp size did not vary with sampling time for the other locations, which allows for a between location comparison.

Variation in gill and palp size is observed for cockles within and between locations. When comparing the variation in gill and palp size (corrected for length), palps show more variation in size between locations than the gills. This is in line with previous observations that palp size, in particular, varies with the amount of particles in the water, while gill area showed no clear relation with turbidity for oysters (Honkoop et al. 2003; Dutertre et al. 2009). The dependence of gill and palp size on length is the reason why length is used for every model input and is not smoothed. Within location comparison shows that gill size depends mostly on length, density and sampling date while palp size relates to length and exposure time. The effect of MGS on organ sizes within one location could not be tested as the range in MGS for each separate site was very small and would therefore not be able to explain variation in gill and palp size.

When comparing the between location model outcome, both gill and palp size are strongly influenced by length, as was expected. Exposure time is in the model explaining gill size as well and has a significant non-linear positive effect. As examined in the within location analysis, gill size for cockles sampled in the second sampling round (the Mokbaai) could be overestimated due to temporal variation in gill size. However, location is not included in the best model and therefore it is assumed that variation in gill size is not explained by location differences. If the overestimated gill size would matter, an effect of location was expected where the Mokbaai would have a significant positive effect on gill size; this however, is not the case.

For palp size, the remaining variation is explained by variation in median grain size, exposure time and density, which all have a significant effect on palp size. Many articles state the influence of suspended matter on the size of the palps (Essink et al. 1989; Payne et al. 1995a; Payne et al. 1995b; Barillé et al. 2000; Dutertre et al. 2009). Silt can consolidate when unperturbed for a while. When consolidated, silt is very hard to erode. Resuspension of the sediment by wind- and tide-erosion causes an increase in inorganic particles in the water (De Jonge & van Beusekom 1995). Larger palps are expected under high inorganic particle concentrations in the water. The results indicate a decreasing trend in palp size under increasing median grain size, which is in line with our expectations.

A negative influence of density is observed on palp size. This does not correspond to the findings of (Honkoop et al. 2003) that density does not have a significant effect on gill and palp size, as well as the Gill-to-palp mass ratio in *Crassostrea gigas* and *Saccostrea glomerata*. Negative effects of density on cockle growth due to limited food availability are only present at extremely high densities of over 600 individuals m^{-2} (Beukema & Dekker 2015). These high densities are only observed in the Mokbaai, where food might be limiting under densities found in this study (maximum observed density is 1408 individuals per m^{2}), here adaptation of gill and/or palp size might be required. Exposure time is present in both the gill and palp model, where it shows an increasing trend with increasing exposure time. This is in line with Franz (1993), stating that a longer inundation time will allow for a higher food uptake and less pumping is needed compared to cockles under short inundations time that need to collect all their food in a shorter time window, resulting in more pumping and larger gills.

4.2 DEB model

By re-estimating the parameters for the DEB model, the model estimates are fitted to the data on shell length. Variation in p_{Am}, p_M and E_G are small while the half saturation coefficients show a strong variation compared to the original values. This can be explained by the difference in the models used. Troost et al. (2010) incorporated POM as part of the food source and the inorganic matter in the functional response, resulting in different X_K and Y_K values compared to a model without POM. When adjusting the parameters, the fit of the model closely resembles the fit of the model of Troost. The new parameters are fixed and form the 0-model from where adjustments to include gill and/or palp variation are made.

Model outcomes between the three locations used in the DEB model show differences in maximum cockle length. When comparing the 0-models of the different locations, variation in maximum length after six years varies among the locations. Under conditions in the Ems estuary, the cockles will be smallest (35.4 mm) as the Ems estuary is characterized by low chlorophyll a concentrations (on average 8.7 µg/l) and high SPM concentrations (on average 124.9 mg/l). Cockles from Harlingen are largest after six years (41.9 mm) and cockles in the Mokbaai are in-between the Ems estuary and Harlingen in terms of size (38.9 mm).

Comparing the model results to the results published in (Wijsman & Smaal 2011), who compared DEB models for cockles in different compartments of the Oosterschelde, shows that the locations with low algae concentrations (Northern and Eastern part of the Oosterschelde) present the smallest growth. Cardoso et al. (2006) modelled growth under set food conditions (f = 0.7 and f=1.0) for cockles (intertidal). After 6 years, the maximal growth observed is 3.8 and 4.8 cm respectively, which are well in line with the range observed in this study. Under a varying functional response, Freitas et al. (2009) modeled the growth for cockles in the Wadden Sea (Balgzand) and observed a maximum length of about 4.5 cm after 6 years. Both studies by Cardoso et al. (2006) and Freitas et al. (2009) do not incorporate the negative effect of inorganic matter and might therefor result in a slightly higher maximum shell length.

Within location comparison of differences between models always result in the least growth under the gill models, even less than for the 0-model. The palp models, on the other hand, seem to result in similar or larger growth compared to the 0-model under Wadden Sea conditions. In table 11 the effect of the palp size is expressed as an increase compared to the 0-model (%) and shows that this is highest for the Ems estuary. With increasing SPM concentrations, the difference between the 0-model and palp model increases. These results suggest that changing palp size is beneficial for growth, especially under high SPM concentrations. However, changing gill and gill & palp size results in reduced growth and would therefore not be beneficial to the bivalves, which is in line with the lower variation in gill size (after correction for shell length) that was found in the feeding morphology data.

So far phenotypic flexibility in feeding morphology has not been included in DEB models. However, the results of this study suggest that adjusting palp size is beneficial for cockles under limiting environmental conditions. When not taking food uptake optimization into account the cockles under poor conditions are predicted to show less growth as was the case in this study for the 0-model. However, most of the variation in shell length is compensated for when the cockles are allowed to adjust their feeding morphology. An increase of 3 mm is observed for cockles in the Ems estuary adjusting their palp size, which brings them back in about the same size range as the cockles from the Marsdiep. Including adjustment to high SPM concentrations will, therefore, result in more realistic models and should be incorporated when modelling bivalve growth. Further research on model validation will show whether the model results including optimized food uptake actually result in more realistic values by comparing the predicted growth to observations in the field. Shell length observations of cockles from different locations on the tidal flat can validate the model and can be done based on data available from the synoptic intertidal benthic sampling program (SIBES) (Bijleveld et al. 2012; Compton et al. 2013). If this is the case, DEB models including actual variation in gill and/or palp size as a compartment in the model would be an improvement of the DEB model for bivalves. Being able to model cockle growth as realistic as possible provides valuable insight for understanding bivalve ecology, which results in better understanding of the Wadden Sea ecosystem.

5. Conclusion

Overall, it can be concluded that variation in gill and palp size (corrected for shell length) is observed within and between different locations in the Dutch Wadden Sea. The remaining variation in gill size is best explained by the effect of exposure time. For palp size, the remaining variation is explained by cockle density, median grain size and exposure time. Variation in environmental conditions causes not only variation in gill and palp size, but also in growth. When considering the effect this variation in feeding morphology has on the growth of cockles, it turns out that adjusting the palp size results in increased shell length, especially for cockles under high SPM concentrations. It, however, is not effective to invest energy in adjusting gill size as it will cause reduced growth compared to no adaptations. Therefore, it is concluded that flexibility in feeding morphology influences growth of cockles and should not be ignored when modelling the growth of bivalves.

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7. References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Second Int. Symp. Inf. Theory pp. 267-281.

Alunno-Bruscia, M., Bourlès, Y., Maurer, D., Robert, S., Mazurié, J., Gangnery, A., Goulletquer, P. & Pouvreau, S. 2011. A single bio-energetics growth and reproduction model for the oyster *Crassostrea gigas* in six Atlantic ecosystems. *Journal of Sea Research,* vol. 66, no. 4, pp. 340-348.

Barillé, L., Haure, J., Cognie, B. & Leroy, A. 2000. Variations in pallial organs and eulatero-frontal cirri in response to high particulate matter concentrations in the oyster *Crassostrea gigas*. *Canadian Journal of Fisheries and Aquatic Sciences,* vol. 57, no. 4, pp. 837-843.

Beckman Coulter, I. 2011. LS 13 320 Laser Diffraction Particle Size Analyzer Instructions For Use PN B05577AB.

Beukema, J.J. 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Netherlands Journal of Sea Research,* vol. 10, no. 2, pp. 236-261.

Beukema, J.J. & Dekker, R., 2006. Annual cockle Cerastoderma edule production in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: How predictable is this food source for birds? *Netherlands Journal of Sea Research,* vol. 31, pp. 319-330.

Beukema, J.J. & Dekker, R. 2015. Density dependence of growth and production in a Wadden Sea population of the cockle *Cerastoderma edule*. *MEPS,* vol. 538, pp. 157-167.

Beukema, J.J. Essink, K. Michaelis, H. & Zwarts, L. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Netherlands Journal of Sea Research,* vol. 31, no. 4, pp. 319-330.

Bijleveld, A.I., van Gils, J.A., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W. & Piersma, T. 2012. Designing a benthic monitoring programme with multiple conflicting objectives. *Methods in Ecology and Evolution,* vol. 3, no. 3, pp. 526-536.

Blott, S.J. & Pye, K. 2001. GRADISTAT: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms,* vol. 26, no. 11, pp. 1237-1248.

Burnham, K.P. & Anderson, D.R. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological methods & research,* vol. 33, no. 2, pp. 261-304.

Cardoso, J.F.M.F, Witte, J.I. & 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. *Journal of Sea Research,* vol. 56, no. 2, pp. 182-197.

Compton, T.J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D. & van der Meer, J. van der Veer, H.W., Piersma, T., 2013. Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *Journal of Sea Research,* vol. 82, pp. 103-116.

De Jonge, V.N. & Van Beusekom, J.E.E. 1995. Wind-and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. *Limnology and Oceanography,* vol. 40, no. 4, pp. 776-778.

Deltares 2014. Dataset documentation vaklodingen. Available: https://publicwiki.deltares.nl/display/OET/Dataset+documentation+Vaklodingen [2015, 10/1]

Dutertre, M., Barillé, L., Beninger, P.G., Rosa, P. & Gruet, Y. 2009. Variations in the pallial organ sizes of the invasive oyster, *Crassostrea gigas*, along an extreme turbidity gradient. *Estuarine, Coastal and Shelf Science,* vol. 85, no. 3, pp. 431-436.

Essink, K., Tydeman, P. & Koning, F.D. 1989. On the adaptation of the mussel *Mytilus edulis* L. to different environmental suspended matter concentrations, in 21st European Marine Biological Symposium. Polish Academy of Sciences, Institute of Oceanology, Gdansk, pp. 41-51.

Filgueira, R., Labarta, U. & Fernández-Reiriz, M.J. 2008. Effect of condition index on allometric relationships of clearance rate in *Mytilus galloprovincialis* Lamarck, 1819. *Rev.Biol.Mar.Oceanogr,* vol. 43, no. 2, pp. 391-398.

Franz, D.R. 1993. Allometry of shell and body weight in relation to shore level in the intertidal bivalve *Geukensia demissa* (Bivalvia: Mytilidae). *Journal of experimental marine biology and ecology,* vol. 174, no. 2, pp. 193-207.

Freitas, V., Cardoso, J.F.M.F, Santos, S., Campos, J., Drent, J., Saraiva, S., Witte, J.I., 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. *Journal of Sea Research,* vol. 62, no. 2, pp. 75-82.

Gerla, D. & Soetaert, K.E.R. 2014. Dynamic Energy Budget (DEB) model of *Mytilus edulis*. Available: http://www.rforscience.com/modelling/musseldeb/" \t "_blank [2015, 5/1].

Hawkins, A.J.S., Navarro, E. & Iglesias, J.I.P. 1990. Comparative allometries of gut-passage time, gut content and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. *Marine Biology,* vol. 105, no. 2, pp. 197-204.

Holling C. S. 1959. Some Characteristics of Simple Types of Predation and Parasitism. *The Canadian Entomologist*, 91, pp 385-398.

Honkoop, P.J.C., Bayne, B.L. & Drent, J. 2003. Flexibility of size of gills and palps in the Sydney rock oyster *Saccostrea glomerata* (Gould, 1850) and the Pacific oyster *Crassostrea gigas* (Thunberg, 1793). *Journal of experimental marine biology and ecology,* vol. 282, no. 1, pp. 113-133.

Jensen, K.T. 1992. Dynamics and growth of the cockle, *Cerastoderma edule*, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. *Netherlands journal of sea research,* vol. 28, no. 4, pp. 335-345.

Jones, H.D., Richards, O.G. & Southern, T.A. 1992. Gill dimensions, water pumping rate and body size in the mussel *Mytilus edulis* L. *Journal of experimental marine biology and ecology,* vol. 155, no. 2, pp. 213-237.

Kahle, D. & Wickham, H. 2013. ggmap: Spatial Visualization with ggplot2. The R Journal, 5(1), 144-161. Available: http://journal.r-project.org/archive/2013-1/kahle-wickham.pdf

Kiorboe, T. & Mohlenberg, F. 1981. Particle selection in suspension-feeding bivalves. *Marine Ecology Progress Series,* vol. 5, pp. 291-296.

Kooijman, S.A.L.M. 2010. Dynamic energy budget theory for metabolic organization. Cambridge university press.

Kooijman, S.A.L.M. 2006. Pseudo-faeces production in bivalves. *Journal of Sea Research,* vol. 56, no. 2, pp. 103-106.

Nelson, T.C. 1960. The feeding mechanism of the oyster. II. On the gills and palps of *Ostrea edulis, Crassostrea virginica* and *C. angulata*. *Journal of Morphology,* vol. 107, no. 2, pp. 163-203.

Payne, B.S., Miller, A.C., Hubertz, E.D. & Lei, J. 1995a. Adaptive variation in palp and gill size of the zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*). *Canadian Journal of Fisheries and Aquatic Sciences,* vol. 52, no. 5, pp. 1130-1134.

Payne, B.S., Miller, A.C. & Lei, J. 1995b. Palp to gill area ratio of bivalves: a sensitive indicator of elevated suspended solids. *Regulated Rivers: Research & Management,* vol. 11, no. 2, pp. 193-200.

R Core Team 2015, R: a language and environment for statistical computing, Vienna, Austria.

Ren, J.S. 2009. Effect of food quality on energy uptake. *Journal of Sea Research,* vol. 62, no. 2, pp. 72-74.

Rijkswaterstaat 2015a. Getij informatie. Available: getwij.rws.nl [2015, 10/28].

Rijkswaterstaat 2015b. Waterbase . Available: live.waterbase.nl [2016, 1/11].

Seed, R. & Brown, R.A. 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *The Journal of Animal Ecology,* pp. 283-292.

Soetaert, K.E.R. & Petzoldt, T. 2010. Inverse modelling, sensitivity and monte carlo analysis in R using package FME. *Journal of Statistical Software,* vol. 33.

Suquet, M., De Kermoysan, G., Araya, R.G., Queau, I., Lebrun, L., Le Souchu, P. & Mingant, C. 2009. Anesthesia in Pacific oyster, *Crassostrea gigas*. *Aquatic Living Resources,* vol. 22, no. 01, pp. 29-34.

Theisen, B.F. 1982. Variation in size of gills, labial palps, and adductor muscle in *Mytilus edulis* L.(Bivalvia) from Danish waters. *Ophelia,* vol. 21, no. 1, pp. 49-63.

Troost, T.A., Wijsman, J.W.M., Saraiva, S. & Freitas, V. 2010. Modelling shellfish growth with dynamic energy budget models: an application for cockles and mussels in the Oosterschelde (southwest Netherlands). *Philosophical transactions of the Royal Society of London.Series B, Biological sciences,* vol. 365, no. 1557, pp. 3567-3577.

Van der Meer, J. 1997. A handful of feathers. Natural Sciences. Rijksuniversiteit Groningen, Groningen.

Van Der Meer, J. Beukema, J. J. & Dekker, R. 2001. Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. Journal of Animal Ecology, 70(1), 159-169.

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. *Journal of Sea Research,* vol. 56, no. 2, pp. 107-124.

Wijsman, J.W.M. & Smaal, A.C. 2011. Growth of cockles (*Cerastoderma edule*) in the Oosterschelde described by a Dynamic Energy Budget model. *Journal of Sea Research,* vol. 66, no. 4, pp. 372-380.

Worrall, C.M. Widdows, J. & Lowe, D.M. 1983. Physiological ecology of three populations of the bivalve *Scrobicularia plana*. *Marine Ecology Progress Series,* vol. 12.

Zuur, A.F. 2012, A beginner's guide to Generalized Additive Models with R, Highland Statistics Ltd.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution,* vol. 1, no. 1, pp. 3-14.