DEB model for cockles (*Cerastoderma edule*) in the Oosterschelde

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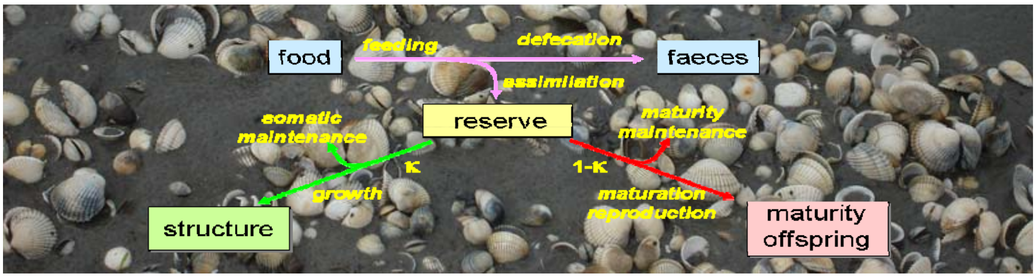

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Summary

The natural and cultured shellfish populations in the Oosterschelde are of considerable biological and economical interest. The hydromorphology of the Oosterschelde is continuously changing and adapting in response to natural anthropological and climatological changes. In view of these changes and of possible future developments in the region, questions arise with regard to the impact on the system's carrying capacity for shellfish populations. Dynamic shellfish models can help to answer these questions.

In this study, a Dynamic Energy Budget (DEB) model for cockles (*Cerastoderma edule*) in the Oosterschelde estuary is presented. The model has been developed and validated with long-time field observations in the Oosterschelde. The field observations cover the population dynamics of cockles in the intertidal areas of the Oosterschelde since 1992 as well as the environmental conditions. This dataset gives a good overview of the development of the cockle population in relation to the environmental conditions (food availability and ambient temperature). A functional response has been formulated and calibrated to translate the field measurements of food quality parameters such as chlorophyll-a, POM, POC and TPM into ingestion rate for the cockles. The model performance is validated by relating the model output to field observations. A sensitivity analysis has been applied to display the sensitivity of the model output to the parameters related to the functional response.

The standard DEB model simulates growth of cockles in the Oosterschelde quite well. However, there is a mismatch between model and data is in the underestimation in AFDW by the model during spring, where the sharp increase in cockle biomass could not be simulated. This might partly be caused by the choice to work with averaged data as well that there is no data on the quality of the food, which might vary during the season. The model can also be applied to other situations (Westerschelde, Waddensea, on-land production) and will be incorporated in ecosystem models.

1 Introduction

A dynamic energy budget (DEB) model (Kooijman 1986, 2000) describes the growth, energy dynamics and reproduction as a function of body size. The DEB theory is a generic theory that can be applied to different species and life stages by using species specific parameters (Kooijman 2001). Intraspecific variability in growth and reproduction, therefore, is caused by differences in environmental conditions (e.g. food, temperature).

In this paper, a specific DEB model for Cockles in the Oosterschelde is developed and compared with detailed field observations. In 2005 a physiological model for cockles (COCO, COckle COmputer model) was developed for the Oosterschelde (Rueda et al. 2006). This ecophysiological model also simulates individual growth and reproduction of cockles under ambient conditions. The filtration activity and the food selection and ingestion are processes that are not included explicitly within the DEB models and therefore the COCO model is used as a source for these processes.

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2 Material and methods

2.1 Cockle growth data

In order to get more insight in the factors that influence the growth and development of the cockle populations in the Oosterschelde and the Westerschelde, a monitoring campaign has been carried out at fixed locations since 1991 (Kamermans et al. 2003). In the Oosterschelde 18 locations are monitored on a regular basis (Figure 1). At each location a permanent quadrant (40×40 m) was marked with wooden poles. At each sampling event 50 random samples were taken with piston cores (86.5 cm^2) within the quadrants. All 50 samples were pooled and sieved over a 2 mm mesh size. For each cockle the age was determined from the growth rings on the shell. For each year class, the number of cockles were counted and the fresh weight and the average shell length was determined. Since 1998 the ash-free-dry weight of the cockles was determined.

From 1992 to 1994, each location was sampled 5 times per year. Since 1995 the sampling frequency was 3 times each year. The first sampling was carried out before the growing season, the second at the end of the growing season and the third after the fishing season. In February 1997 extra sampling took place after the severe winter of 1996/1997.

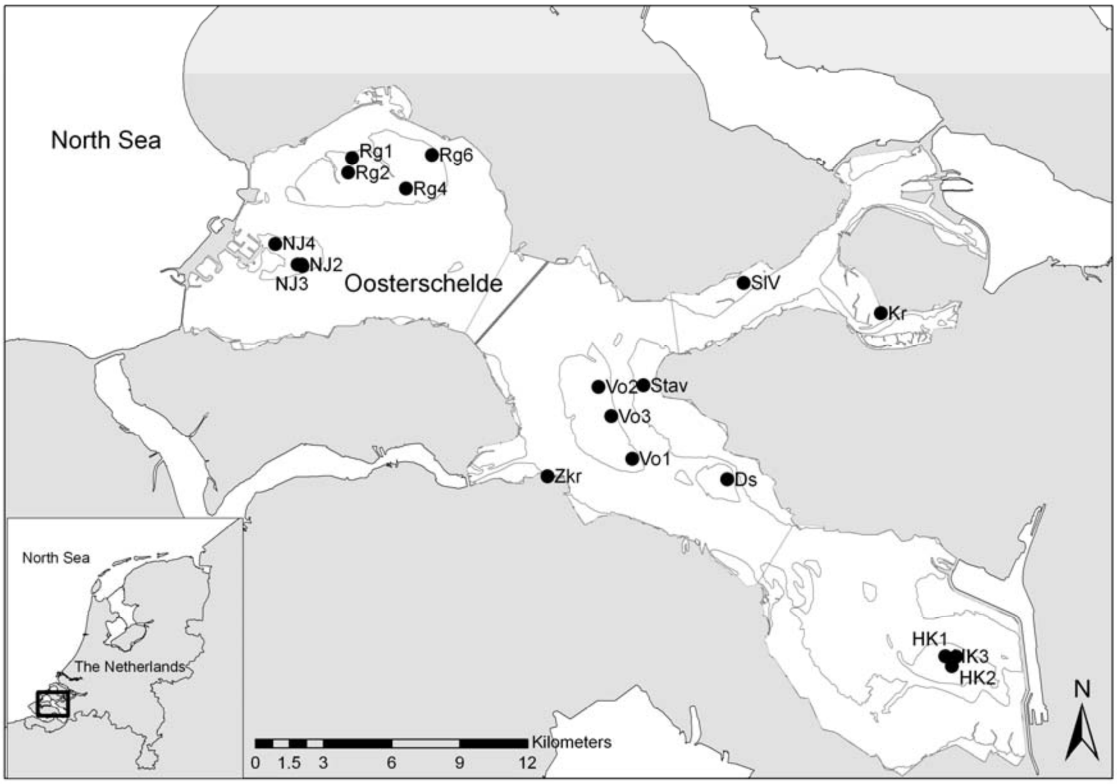

Figure 1: Overview of the Oosterschelde and the locations of the 18 permanent quadrants for cockle monitoring. NJ2, NJ3, NJ4, Rg1, Rg2, Rg4 and Rg6 are in the western part of the Oosterschelde. Vo1, Vo2, Vo3, Stav, Zkr and Ds are in the central part of the Oosterschelde. SIV and Kr are in the Northern part of the Oosterschelde and HK1, HK2 and HK3 are in the Eastern part of the Oosterschelde

2.2 Environmental data

Environmental data are derived for various locations distributed over the Oosterschelde from datasets of Rijkswaterstaat, NIOO-CEME and IMARES Yerseke. The following data were selected from the database:

- Water temperature (°C)
- Chlorophyll-a concentration (µg l^{-1})
- Total Particulate Matter (TPM) (mg l^{-1})
- Particulate Organic Carbon (POC) (mg l^{-1})
- Particulate Organic Matter (POM) (mg l^{-1})
- Particulate Organic Nitrogen (PON) (mg l^{-1})

2.3 DEB model

2.3.1 Introduction

The generic dynamic energy budget (DEB) model has been developed by Kooijman 30 years ago (Kooijman 1986, 2000). The DEB model describes the energy flow through an organism as a function of its size, its development stage and environmental conditions. An individual organism is described by the state variables structural body volume V (cm^3), Reserves E (Joule) and Reproduction (Joule) (Figure 2). The reserves can also be quantified as energy density (E/V, J cm^{-3}). The length can be calculated from the structural volume with a shape coefficient (δ_m).

$$L = \cdot \frac{V^{1/3}}{\delta_m} \qquad \text{(Eq. 1)}$$

Food is filtered by the cockles from the water column. With the palps, edible particles are selected and the rest is released in the form of pseudo faeces. The energy that is not assimilated by the cockle is released as faeces. The assimilated energy is first stored into reserves (blood, glycogen). A fixed fraction (κ) of the energy flow from the reserves is used for growth a somatic maintenance, with priority to maintenance. The rest of the energy flow from the reserves ($1-\kappa$) is spent on maturity maintenance and reproduction (gamete production and spawning). For juveniles, energy is spent on maturation. It is assumed that both the structural body and the reserves have a constant chemical composition (assumption of strong homeostasis). At constant food density, the energy reserve density (E/V) becomes constant (weak homeostasis assumption).

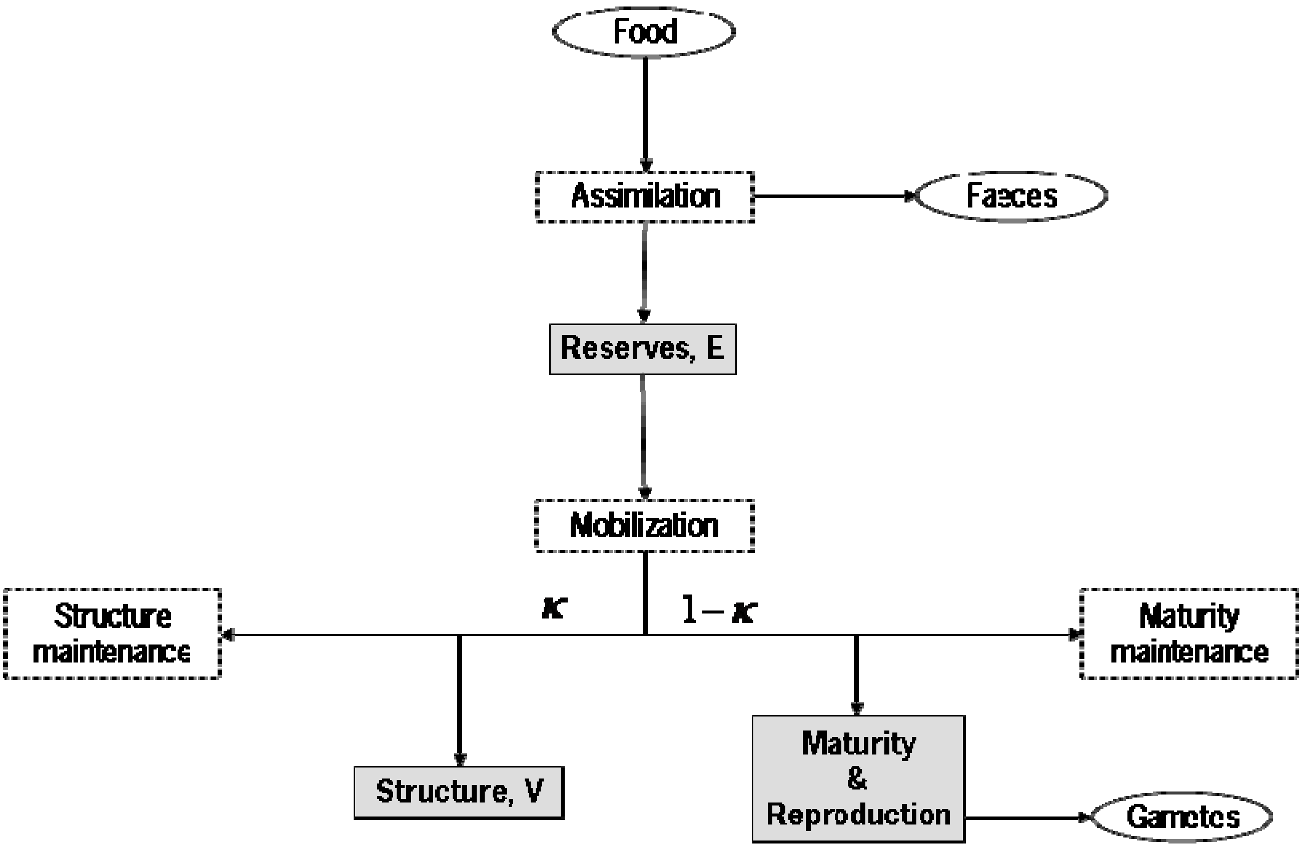

Figure 2: Schematic presentation of the DEB model for cockles.

2.3.2 Temperature

Temperature is forced to the model with a forcing function of field measurements. All physiological rates depend on the body temperature with a relation that is well described by the Arrhenius relation:

$$\dot{k}(T) = \dot{k}_1 \cdot e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)} \qquad \text{(Eq. 2)}$$

Where T is the absolute temperature (K), T_1 is the reference temperature (293 K), T_A is the Arrhenius temperature, $\dot{k}_1$ is the value of the physiological rate at the reference temperature and $\dot{k}(T)$ is the rate at ambient temperature (T).

At the lower and the upper temperature boundaries, the rates are usually lower than calculated from the Arrhenius relation. This is because at low temperatures, the physiology of the organisms changes into a resting phase and at high temperatures, the organisms approach a condition of rapid death.

$$\dot{k}(T) = \dot{k}_1 \cdot e^{\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)} \cdot \frac{\left(1 + e^{\left(\frac{T_{AL}}{T_1} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_1}\right)}\right)}{\left(1 + e^{\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right)} + e^{\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)}\right)} \qquad \text{(Eq. 3)}$$

Where 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. The estimates for the specific parameters in this relation are derived from Van der Veer et al. (2006).

As a first approximation it is assumed that all physiological rates are affected by temperature in the same way.

2.3.3 Food intake

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

$$f = \frac{X}{K'(Y) + X} \qquad \text{(Eq. 4)}$$

with $K'(Y) = X_K \left(1 + \frac{Y}{Y_K}\right)$ (Eq. 5)

X is the food concentration, expressed in (µg chl-a l^{-1}), X_K is the half saturation constant (µg chl-a l^{-1}). Y is the concentration of particulate inorganic matter (TPM-POM) expressed in mg l^{-1} and Y_K is the saturation constant for the particulate inorganic matter (mg l^{-1}).

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

$$X = Chla + \alpha \cdot POM \qquad \text{(Eq. 6)}$$

The value of f varies from 0 (no food uptake) to 1 (optimal food conditions). When the available amount of food equals X_K, the food uptake rate is half the maximal uptake rate. The response curve corresponds to the Type II response curve of Holling (1959).

The parameters α, and X_K are free-fitted parameters of the DEB model. Y_K is estimated at 100 mg l^{-1} (Prins *et al.* 1991, Rueda *et al.* 2006). It is assumed that the values of the parameters are depending on the quality of the various components. Therefore the value of the parameters might vary both in time and in space. In the present study the values of the parameters are fitted for each compartment of the Oosterschelde separately, as well for the whole Oosterschelde.

2.3.4 Assimilation

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

$$p_I = \{J_{Xm}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T) \qquad \text{(Eq. 7)}$$

Only a fraction of the ingested food is assimilated, the rest is lost. DEB assumes that the assimilation efficiency of food is independent of the feeding rate. The assimilation rate is calculated by

$$p_A = \{p_{Am}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T) \qquad \text{(Eq. 8)}$$

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

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

$$\frac{dE}{dt} = p_A - p_C \qquad \text{(Eq. 9)}$$

2.3.5 Growth and somatic maintenance

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

$$p_C = \left(\frac{[E]}{\kappa \cdot [E] + [E_G]} \right) \cdot \left(\frac{\{p_{Am}\} \cdot [E_G]}{[E_m]} \cdot V^{\frac{2}{3}} + [p_M] \cdot V \right) \qquad \text{(Eq. 10)}$$

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

The energy flow required for maintenance is

$$p_M = [p_M] \cdot V \qquad \text{(Eq. 11)}$$

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

$$\frac{dV}{dt} = GR = \frac{\kappa \cdot p_c - [p_M] \cdot V}{[E_G]} \quad \text{(Eq. 12)}$$

Where GR is the growht rate of structural biomass. When the energy required for maintenance [p_M] is higher than the energy available for growth and maintenance (κ p_C) the energy for maintenance is paid by energy in the reproduction buffer R. When the energy in the reproduction buffer is depleted, maintenance can be paid by the structural volume and the cockle shrinks.

2.3.6 Maturity and reproduction

A fixed proportion (1- κ) of the utilized energy (p_c) goes to maturity maintenance, development (juveniles) and reproduction (adults). Since the development stops at maturity, the maturity maintenance costs do not increase after maturity. Juveniles use the available energy for developing reproductive organs and regulation systems. Adults, which do not have to invest in development anymore, use the energy for reproduction and maintenance. The transition of juvenile to adult occur at fixed size (V_p).

Juveniles: Organism with a volume V smaller than V_p

Maturity maintenance costs:

$$p_J = \left(\frac{1-\kappa}{\kappa}\right) \cdot [p_M] \cdot V \quad \text{(Eq. 13)}$$

Development costs:

$$p_{dev} = \left(\frac{1-\kappa}{\kappa}\right) \cdot E_G \cdot GR \quad \text{(Eq. 14)}$$

Juveniles don't reproduce so the costs for reproduction are zero:

$$p_{rep} = 0 \quad \text{(Eq. 15)}$$

Adults are organisms with a volume V larger than V_p
Maturity maintenance costs:

$$p_{mat} = \left(\frac{1-\kappa}{\kappa}\right) \cdot p_M \cdot V_p \quad \text{(Eq. 16)}$$

Development costs:

$$p_{dev} = 0 \quad \text{(Eq. 17)}$$

Costs for reproduction:

$$p_{rep} = (1-\kappa) \cdot p_c - p_{mat} \quad \text{(Eq. 18)}$$

2.3.7 Spawning

Spawning events occur when enough energy is allocated in the gonads (Gonado Somatic Index, GSI > 0.05) and when the water temperature is above a threshold value (15.84 °C) (Hummel & Bogaards 1989). The gonads are released from the buffer with a specific rate of 2% per day until the temperature drops below the threshold value or all the gonads are released.

2.3.8 Conversions

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

$$AFDW = \psi_{AFDW\_WW} \cdot \rho \cdot V + \frac{(E+R)}{[\mu_E]} \qquad \text{(Eq. 19)}$$

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

The AFDS can be converted into wet weight using the relation

$$WW = \frac{AFDW}{\psi_{AFDW\_WW}} \qquad \text{(Eq. 20)}$$

3 Results

3.1 Cockle growth data

The cockle shell length development is plotted in Figure 3 to Figure 6 as a function of the age of the cockles. Although the year of birth of the cockles is known from the growth marks on the shells, the month of birth is not known. Therefore the age in months in the plots is relative to January in the year of birth. For each of the compartments (West, Central, North and East) the average shell length (mm) per location per age group was calculated. Samples with less than 5 cockles per age group per location are omitted. The box and whisker plots give the range of the average length at age (in months) measured at the various locations.

In month 5 to 7 of the first year, the cockles are about 10 mm long. Growth mainly takes place during Spring and early Summer. In Autumn/Winter, growth stagnates. After the second winter the cockles are close to their maximum size and the do not increase much in shell length anymore. Cockles in the Eastern part of the Oosterschelde on average are smaller than in the rest of the Oosterschelde.

There is more variation in fresh weight and the ash-free dry weight than in shell length of the cockles (Figure 8 to Figure 16).This is caused by temporarily (both seasonally and from year to year) and spatially fluctuating environmental conditions, but also reproduction of the cockles has an effect on the variation in body mass. Reproduction leads to a decrease in biomass (especially ash-free dry mass) but not to a decrease in shell length. From Figure 16 it is clear that the cockles from the Eastern part of the Oosterschelde are generally in poor condition compared to the cockles from other locations, which is caused by the low food concentration in the water. In general there is a good relation between the shell length and the fresh weight of the cockles (Figure 18). This is because a large part of the fresh cockle weight is attributed to the weight of the shell. The relation between ash-free dry weight and length has more variation due to variations in the condition of the cockles due to varying environmental conditions and reproduction (Figure 19).

3.2 Environmental data

The temperatures in the Oosterschelde show a clear sinusoidal function with highest water temperatures in August and lowest temperatures in January and February (Figure 20 to Figure 24). Lowest (and highest) temperatures are found in the eastern part of the Oosterschelde, where large intertidal flats are located and the residence times of the water is largest. The chlorophyll concentrations in the Oosterschelde show a clear peak in Spring (April, May). However, in the northern part of the Oosterschelde, the high chlorophyll concentrations are found during the whole summer period (May – August). The western part of the Oosterschelde has the highest concentrations of total particulate matter. Maximum concentrations of TPM are present in the Oosterschelde during the winter. In the northern part, where the TPM concentrations are generally low, there is no clear seasonal pattern. TPM is composed of inorganic particles and organic particles (POM). The POM concentration in the Oosterschelde is about 2 mg l^{-1}. High POM concentrations are observed in January and February in the western part of the Oosterschelde and low concentrations are observed in March and April in the northern part. A fraction of the organic matter is organic carbon and organic nitrogen. The patterns of organic carbon and organic nitrogen are similar.

3.3 Model simulations

The DEB mode for cockle was run for the various compartments of the Oosterschelde (West, Central, North and East) and for the whole Oosterschelde (Figure 1). The simulated state variables are the structural body volume V (cm^3), the energy in reserves E (Joule) and the energy allocated to development and reproduction R (Joule) (Table 1). All parameters were kept the same for all model simulations. Primary DEB parameters were mainly derived from the study of Van der Veer et al. (2006). The assimilation efficiency of the cockles is derived from Rueda et al. (2006). The parameters for the Arrhenius temperature function are derived from Van der Veer et al. (2006). Both the gonado-somatic index threshold and the temperature threshold for spawning are derived from Rueda et al. (2006). The relative decrease rate of gonads during spawning is set to 2 % per day. It is also assumed that $\rho = 1$ (1 cm^3 of fresh tissue has a mass of 1 g).

The models have been run within the Femme simulation environment (Soetaert et al. 2002), starting at 18th of May. The simulations were run for 6 years. Environmental data (Temperature, Chl-a, POM and TPM) were provided to the model as forcing functions. All available measurements from 1993 to 2007 within a compartment were averaged per week number (1 – 52). The forcing functions were repeated for the 6 years of simulation.

The initial values of shell length at the start of the simulation were derived from the field observations (Figure 3 to Figure 7). Initial values were: Western part: 0.82 cm, Central part: 0.36 cm, Northern part: 0.71 cm, Eastern part: 0.60 cm and total Oosterschelde: 0.73 cm.

Table 1. State variables used in the model

Variable	Unit	Description
V	cm^3	Structural body volume
E	J	Reserves
R	J	Energy allocated to development and reproduction

Table 2. DEB parameters used in the model

Parameter	Unit	Description	Value	Reference
T_A	K	Arrhenius temperature	5800	Van der Veer et al. (2006)
$\{J_{Xm}\}$	J d^{-1} cm^{-2}	Maximum specific energy ingestion flux	91.5	Van der Veer et al. (2006)
$[p_M]$	J cm^{-3} d^{-1}	Volume specific maintenance costs	24	Van der Veer et al. (2006)
$[E_m]$	J cm^{-3}	Maximum storage density	2115	Van der Veer et al. (2006)
$[E_g]$	J cm^{-3}	Volume specific costs of growth	1900	Van der Veer et al. (2006)
$[E_v]$	J cm^{-3}	Volume specific energy content of structural tissues	1350	Van der Veer et al. (2006)
κ	–	Fraction of catabolic flow (p_C) spent on maintenance plus growth	0.80	Van der Veer et al. (2006)
κ_R	–	Fraction of reproduction energy fixed in eggs	0.80	Van der Veer et al. (2006)
ae	–	Assimilation efficiency	0.76	Rueda et al (2006)
δ_m	–	Shape coefficient	0.381	Van der Veer et al. (2006)
L_p	cm	Length at juvenile -> adult transition	2.08	Van der Veer et al. (2006)

Table 3. Additional parameters

Parameter	Unit	Description	Value	Reference
T_L	K	Lower boundary of tolerance range	278	Van der Veer et al. (2006)
T_H	K	Upper boundary of tolerance range	306	Van der Veer et al. (2006)
T_{AL}	K	Arrhenius temperature for rate of decrease at lower boundary	51154	Van der Veer et al. (2006)
T_{AH}	K	Arrhenius temperature for rate of decrease at upper boundary	47126	Van der Veer et al. (2006)
Y_k	mg l^{-1}	saturation constant for the particulate inorganic matter	100	Prins et al. (1991)
GI	–	Gonado-somatic index triggering spawning	0.0034	Rueda et al. (2006)
T_S	°C	Temperature threshold triggering spawning	15.84	Rueda et al. (2006)
r_S	d^{-1}	Relative spawning rate	0.02	This study
ρ	g cm^{-3}	Specific mass of body structure	1	This study
Ψ_{AFDW_WW}	–	Gram ash-free dry mass per gram wet mass	0.12	Van der Veer et al. (2006)
μ_E	J g^{-1}	Energy content of reserves (ash free dry mass)	17500	Brody (1945)

3.4 Model calibration

The model is calibrated against the field observations (L and AFDW). Calibrated parameters were X_k, and α. X_k was allowed to vary between 0 and 100 and α between 0 and 10. The model was calibrated by minimizing the sum of squared residuals:

$$SSR_{Total} = \sum_{obs} \frac{(Mod_L - Obs_L)^2}{avg(Obs_L)^2} + \sum_{obs} \frac{(Mod_{AFDW} - Obs_{AFDW})^2}{avg(Obs_{AFDW})^2} \qquad \text{(Eq. 21)}$$

where SSR_{Total} = sum of squared residuals, Mod_L and Obs_L are the modeled and observed shell length (cm), Mod_{AFDW} and Obs_{AFDW} are the modeled and observed ash-free dry weight of the cockles (g).

Table 4 Calibration parameters and goodness of fit

Compartiment	Calibrated parameter value		Sum of squared residuals		
	X_k	α	L	AFDW	Total
West	2.05	0.00	0.39	3.29	3.68
Central	1.86	0.03	0.40	5.69	6.09
North	4.04	0.00	0.51	5.57	6.08
East	6.40	1.38	0.71	10.62	11.33
Total	2.74	0.10	0.43	6.95	7.39

From Table 4 it can be seen that the parameter estimates for the different compartments and the whole Oosterschelde are quite similar, especially the values for the Western part and the central part of the Oosterschelde. The worst fit was achieved in the eastern part of the Oosterschelde, where chlorophyll concentrations are lowest.

In general there is a quite good agreement between the modeled length and the observations. In the western (Figure 25), northern (Figure 27) and eastern (Figure 28) part as well as for the whole Oosterschelde (Figure 29) there is an overestimation of the cockle length in the first year. In the central part of the Oosterschelde (Figure 26) there is a good agreement between model and data on shell length for the whole simulation period. In the eastern part of the Oosterschelde the length of the cockles of 1, 2 and 3 years old are underestimated.

The general trend in ash free dry mass is described well by the model. However, the variation in ash-free dry weight over the season in the model results is less pronounced than the variation in the observed data. The data show relative high values in ash-free dry weight in the early summer with low ash-free dry weight during winter and spring. This might be caused by the averaging of the environmental data. The peak in chl-a concentration is diluted and are therefore less pronounced. This might result in a lower amount of energy in reserves.

In Figure 30 to Figure 34 the evaluation of several DEB variables are plotted. E, S and R indicate the energy allocated to reserves, structural volume and reproductive organs respectively. WW indicates the total wet weight. F is the functional response and T is the ambient water temperature.

4 Concluding remarks

This study shows that standard DEB model with the cockle-specific DEB parameters simulates growth of cockles in the Oosterschelde quite well. A clear mismatch between model and data is in the underestimation in AFDW by the model during spring. This might partly be caused by the approach that is chosen to work with averaged data on cockle growth as well in the data on food conditions. By averaging the data on food concentration, both in time and in space, the peak in chlorophyll concentrations will be lower than observed in the field. The spring peak of chlorophyll-a is very important for the growth of cockles and is reflected in a sharp increase in body weight. Simulation of a specific cohort of cockles from one locations with real environmental data might give better results.

Also, the model makes no distinction in the quality of the algae as a food source for cockles during the season. However, the algae in spring have a different composition than later in the season and also the quality as a food source for the cockles varies. This seasonal variation of quality of the food is not included in the model.

The present DEB model for cockles is more generic en less complex than the COCO model of Rueda et al. (2006). However, processes as pseudo-faeces and faeces production are not included in the present DEB model. Production of faeces and pseudo-faeces can be calculated from filtration rates using size-dependent relations in combination with the functional response.

With the model, sensitivity analyses can be performed on the specific DEB parameters. With the parameters that are most sensitive for the model performance, additional experiments can be done to get better estimations.

The cockle DEB model can be incorporated into a population dynamics model for cockles in the Oosterschelde. Data on recruitment and mortality can be estimated from the data measured in the field. Moreover, the model can be incorporated into ecosystem models where the cockles might have a role as grazers. The DEB model can also be adapted for other important grazers in the Oosterschelde like Pacific oysters and mussels. DEB parameters for these species are available. Only the data are less complete for these species.

Quality Assurance

IMARES utilises an ISO 9001:2000 certified quality management system (certificate number: 08602-2004-AQ-ROT-RvA). This certificate is valid until 15 December 2009. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2009 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation, with the last inspection being held on the 5th of October 2007.

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Justification

Rapport C048/09
Project Number: 430.42022.01

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

Approved: Dr. Ir. A.G. Brinkman
Scientist

Signature:

Date: June 5th 2009

Approved: Drs. J. Asjes
Head of department Ecology

Signature:

Date: June 5th 2009

Number of copies:	10
Number of pages	44
Number of tables:	4
Number of graphs:	34
Number of appendix attachments:	1

Appendix A. Figures

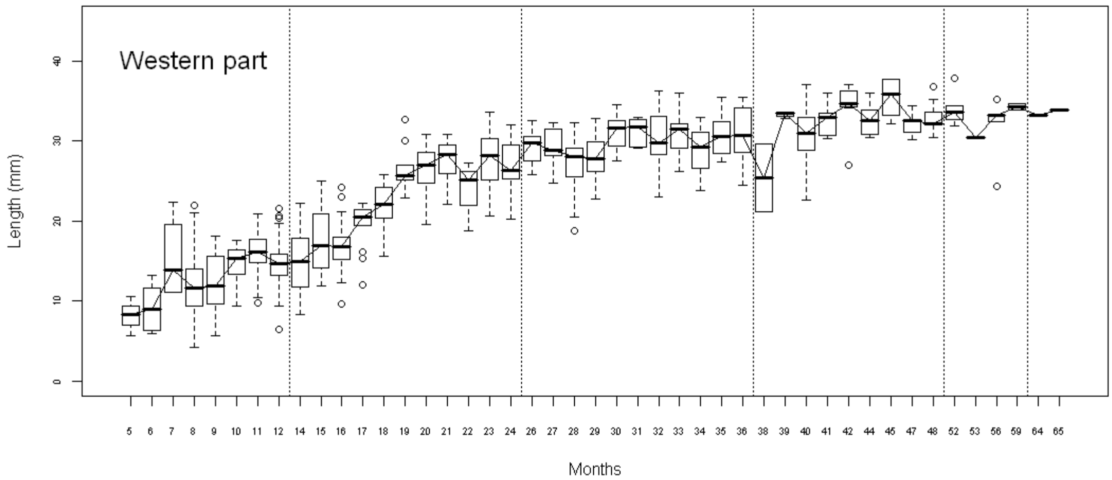


Figure 3 Evaluation of the average observed shell length (mm) of the cockles in the Western part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

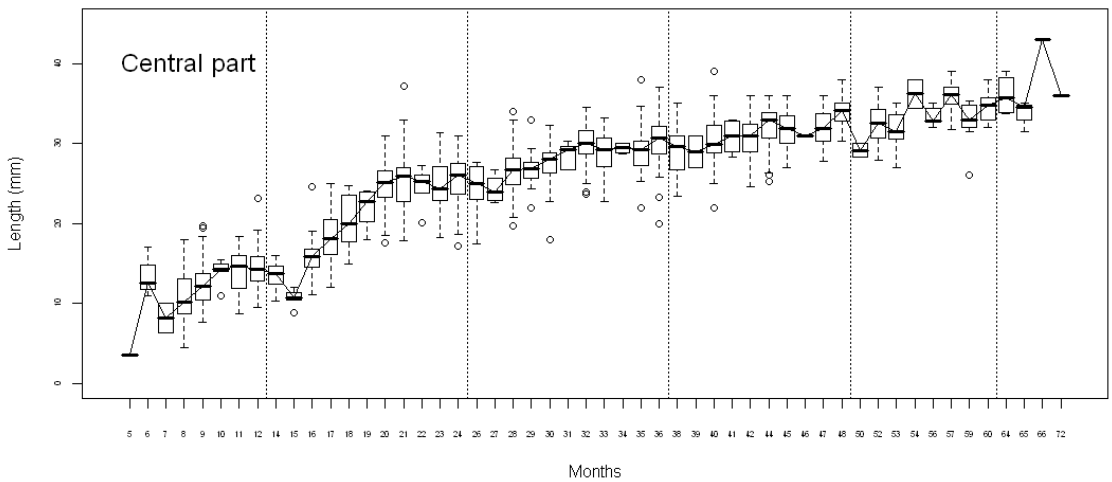


Figure 4 Evaluation of the average observed shell length (mm) of the cockles in the Central part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

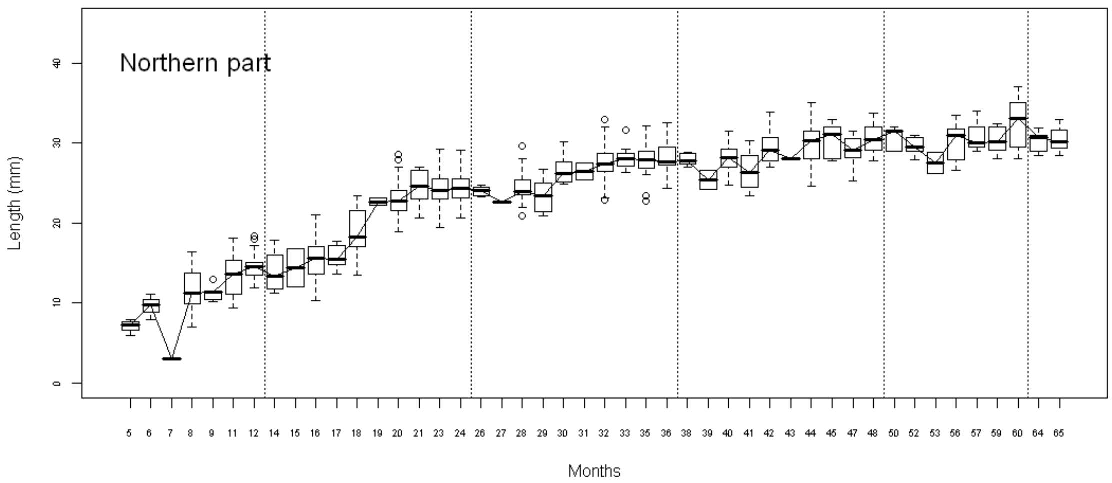


Figure 5 Evaluation of the average observed shell length (mm) of the cockles in the Northern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

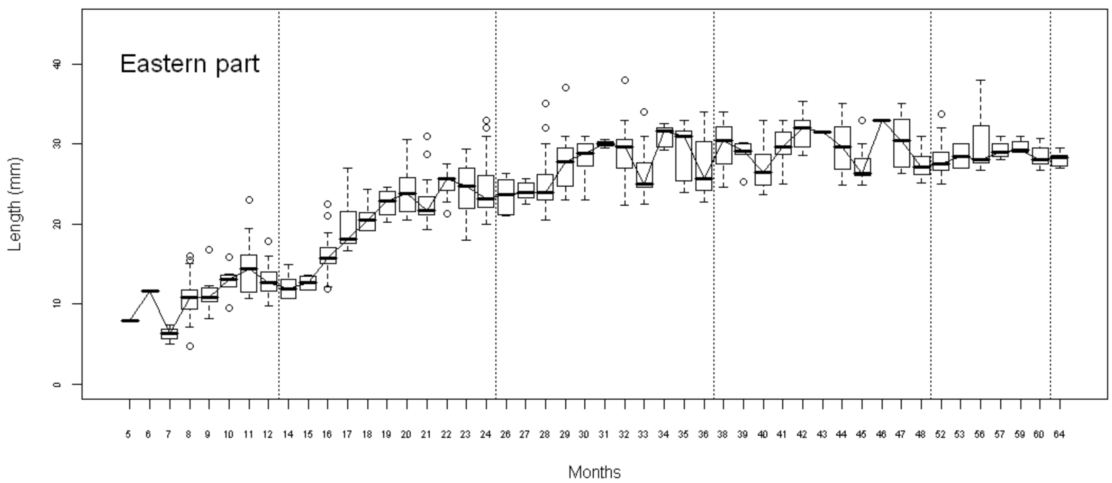


Figure 6 Evaluation of the average observed shell length (mm) of the cockles in the Eastern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

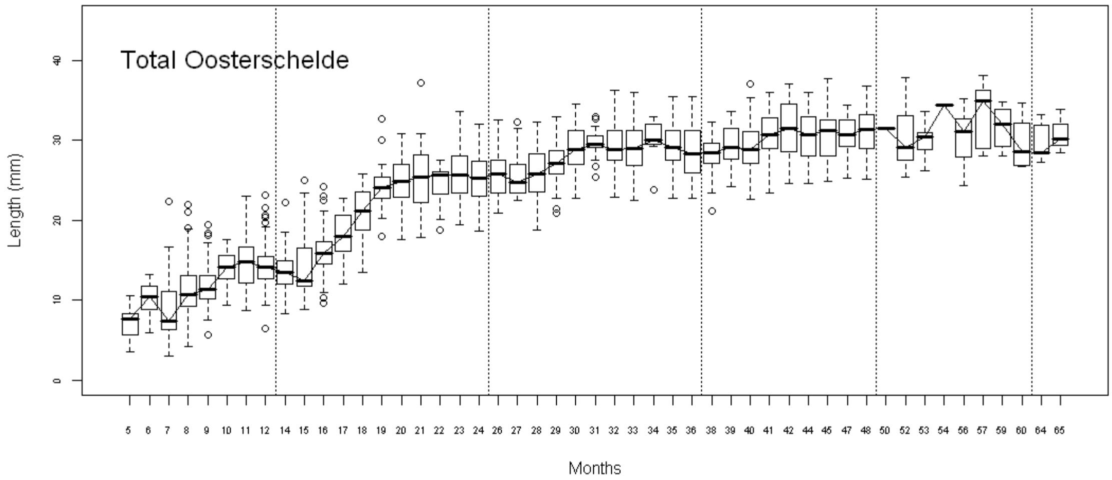


Figure 7 Evaluation of the average observed shell length (mm) of the cockles in the whole Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

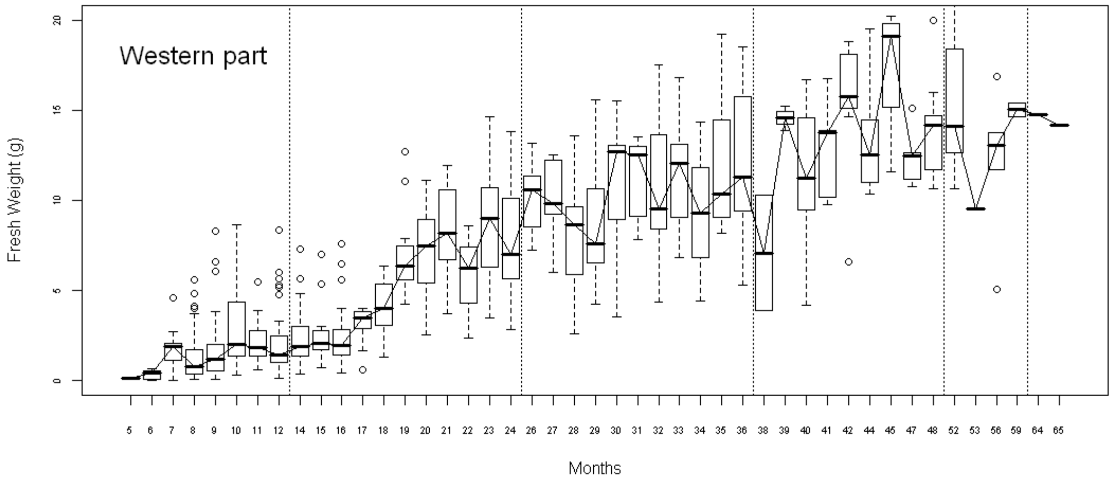


Figure 8 Evaluation of the average observed fresh weight (g) of the cockles in the Western part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

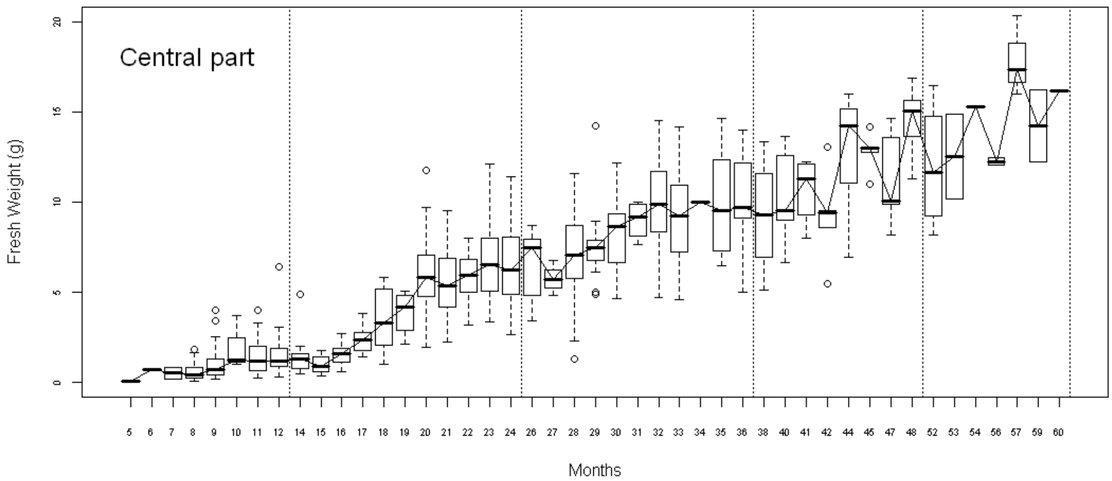


Figure 9 Evaluation of the average fresh observed weight (g) of the cockles in the Central part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

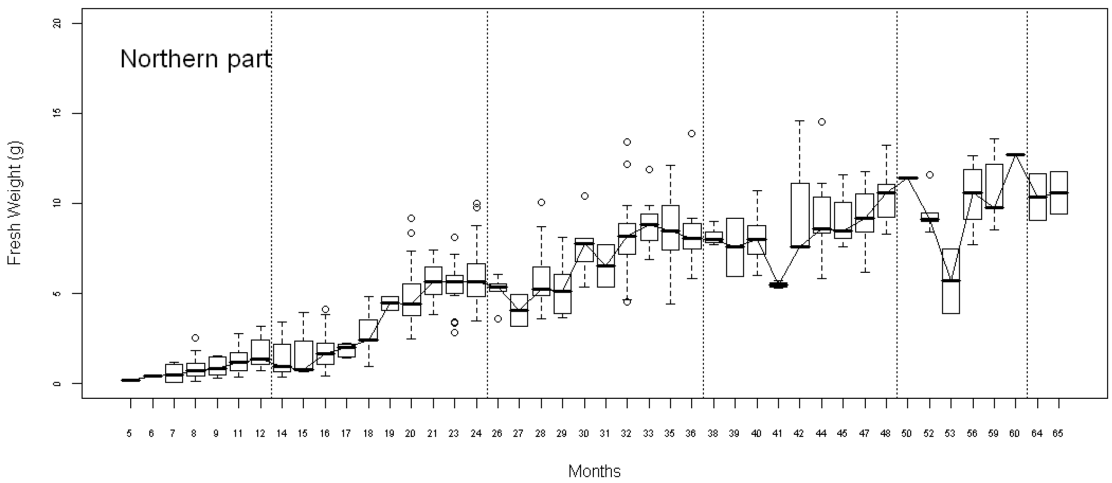


Figure 10 Evaluation of the average observed fresh weight (g) of the cockles in the Northern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

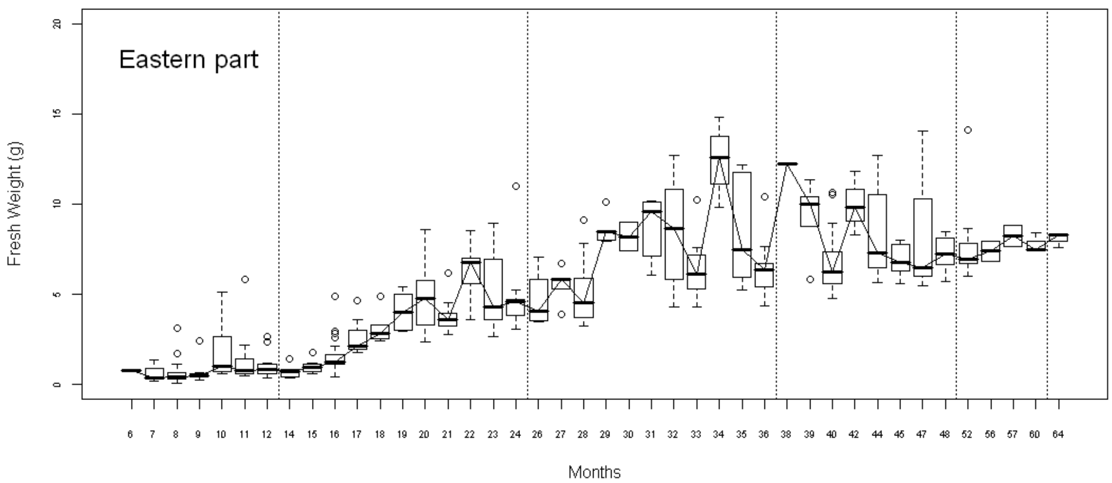


Figure 11 Evaluation of the average observed fresh weight (g) of the cockles in the Eastern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

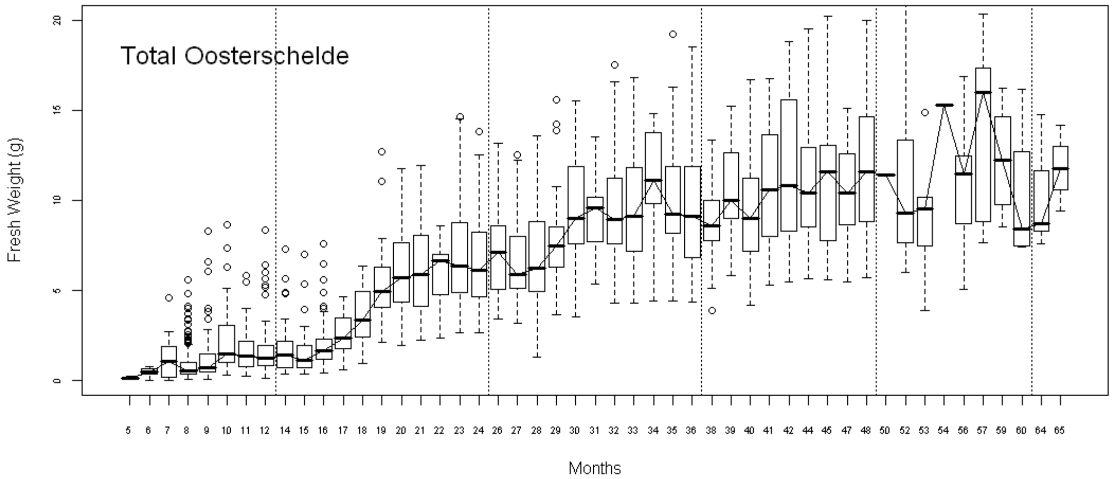


Figure 12 Evaluation of the average observed fresh weight (g) of the cockles in the whole Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

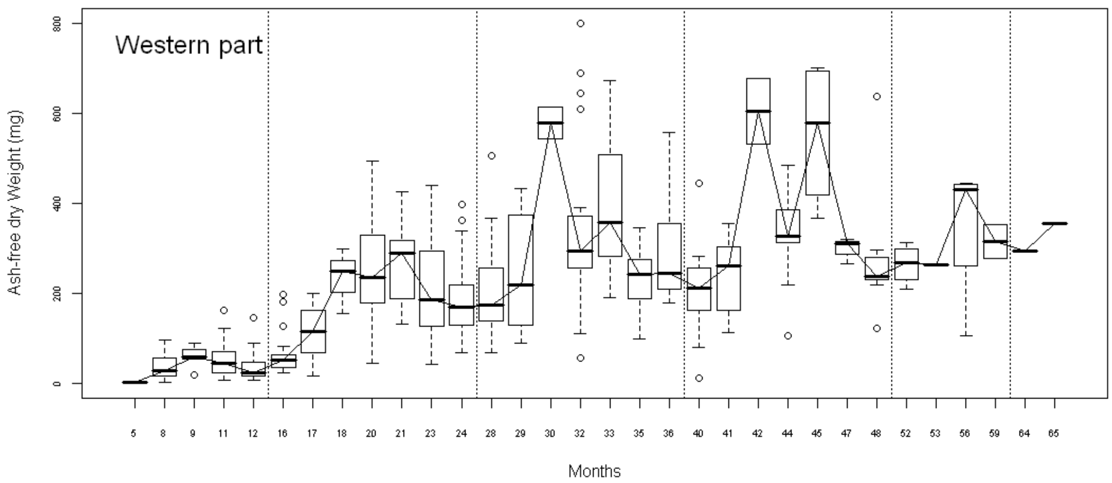


Figure 13 Evaluation of the average observed ash-free dry weight (mg) of the cockles in the Western part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

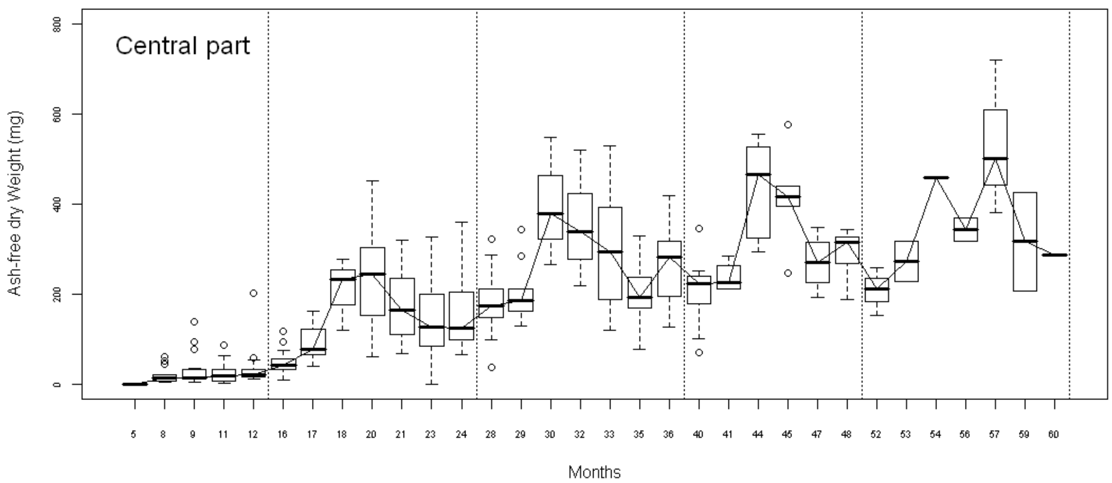


Figure 14 Evaluation of the average observed ash-free dry weight (mg) of the cockles in the Central part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

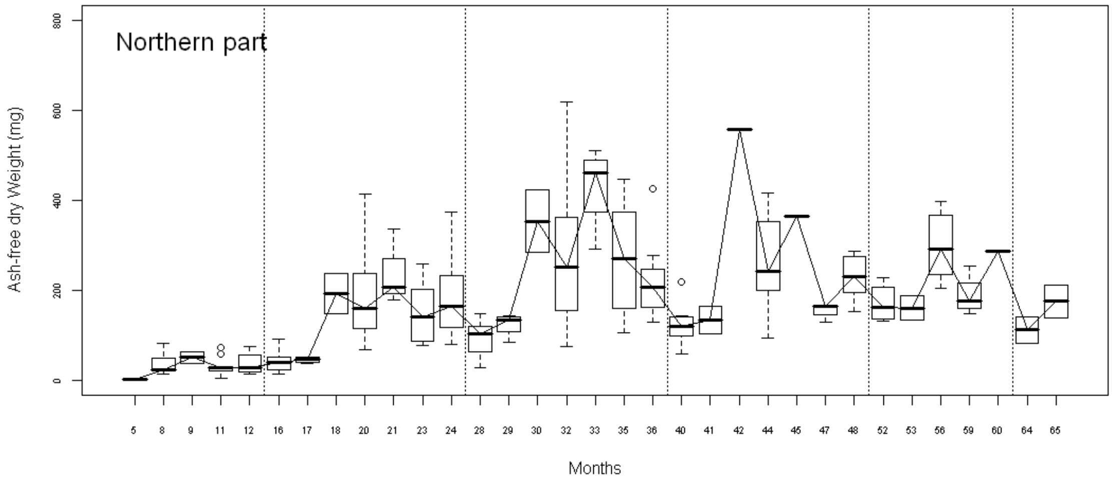


Figure 15 Evaluation of the average observed ash-free dry weight (mg) of the cockles in the Northern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

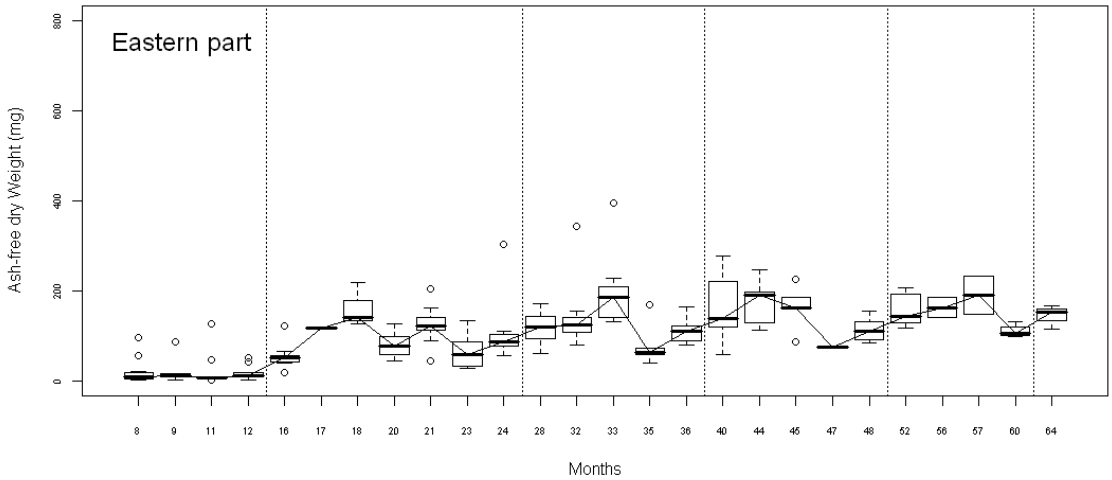


Figure 16 Evaluation of the average observed ash-free dry weight (mg) of the cockles in the Eastern part of the Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

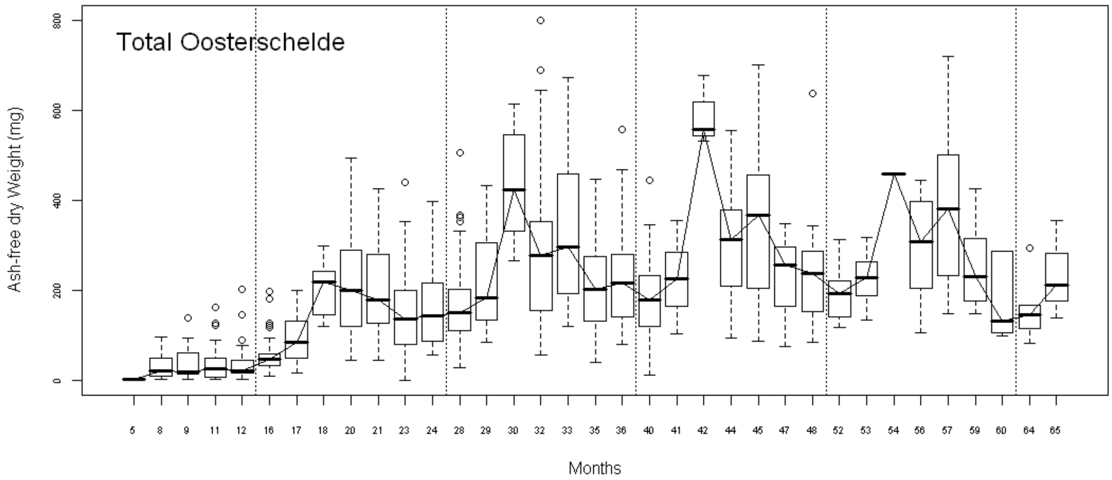


Figure 17 Evaluation of the average observed ash-free dry weight (mg) of the cockles in the total Oosterschelde as a function of age in months. Month 1 is defined as January in the year of birth. Vertical grey lines indicate end of a year.

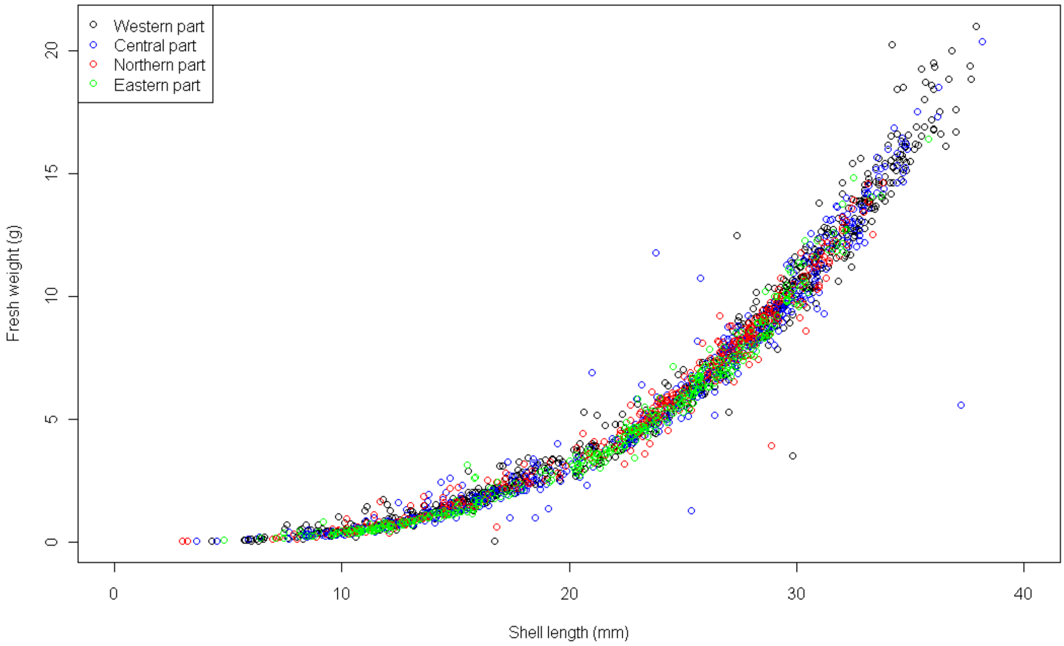


Figure 18 Average fresh weight (g) of the cockles per year class per sampling location as a function of average shell length (mm). Colors indicate the compartment where the sampling was done.

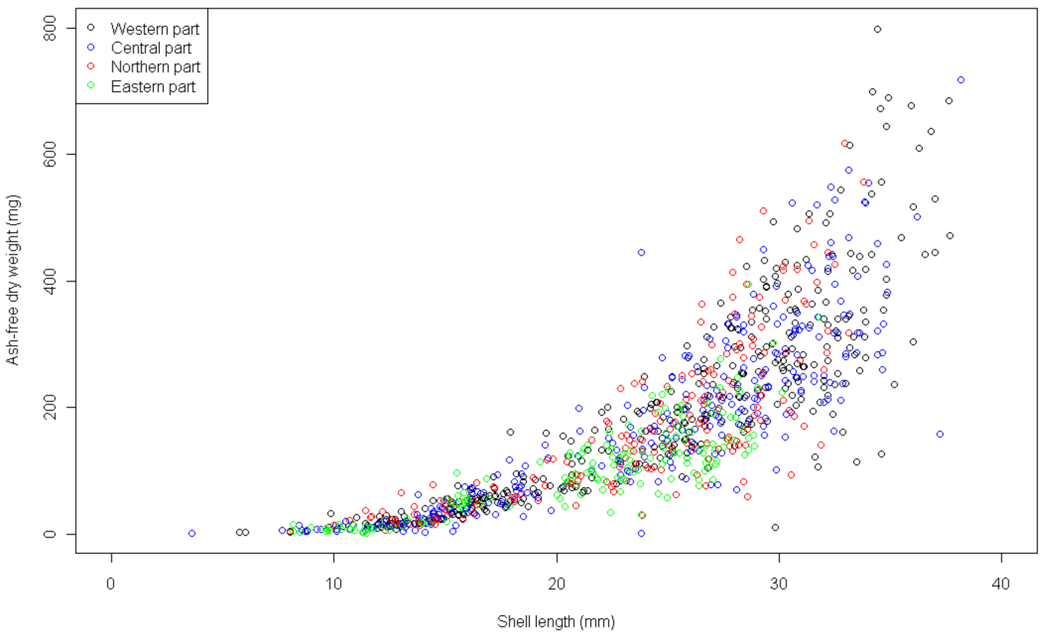


Figure 19 Average ash-free dry weight (mg) of the cockles per year class per sampling location as a function of average shell length (mm). Colors indicate the compartment where the sampling was done

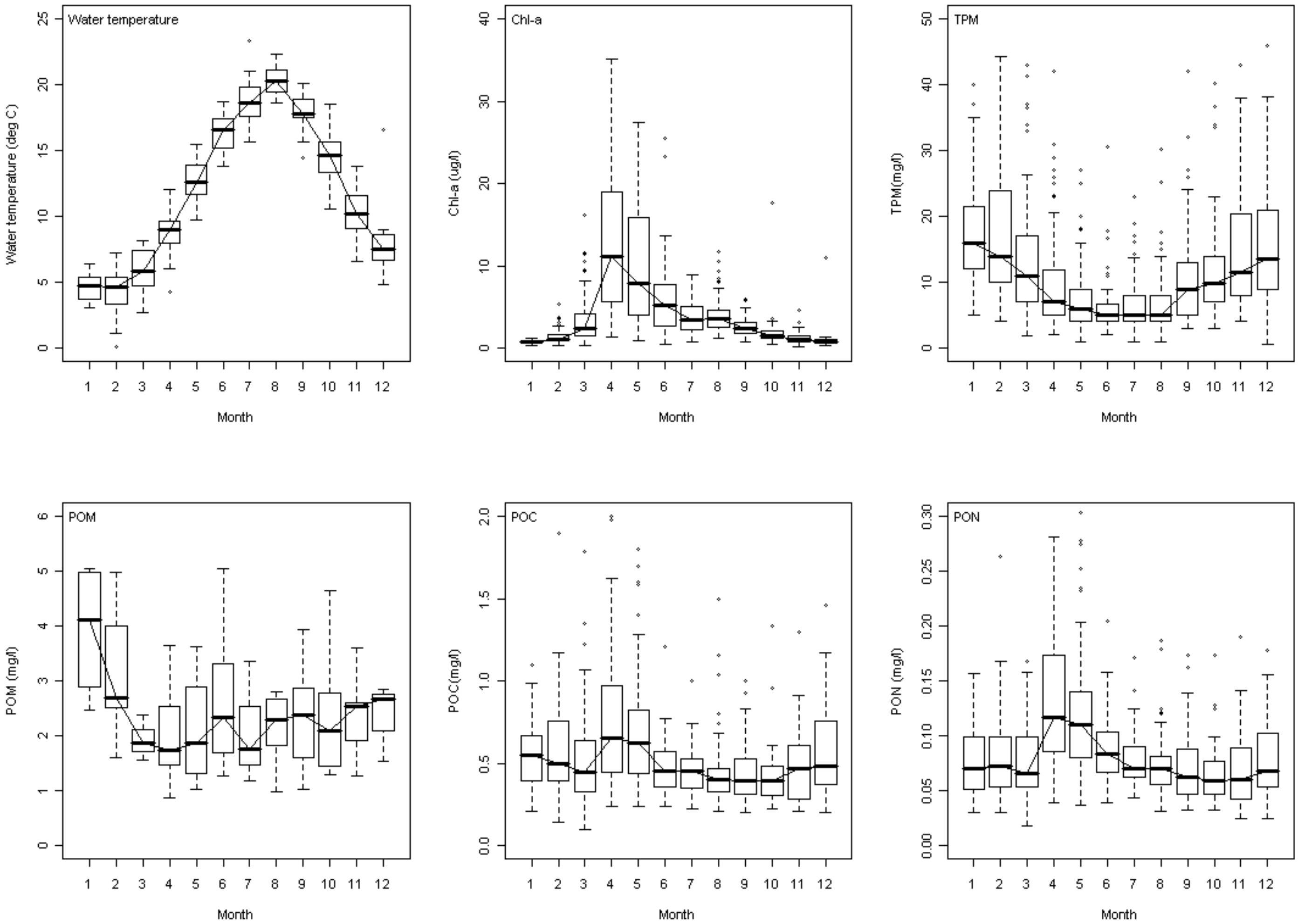


Figure 20 *Overview environmental conditions in the Western part of the Oosterschelde (1993 – 2007).*

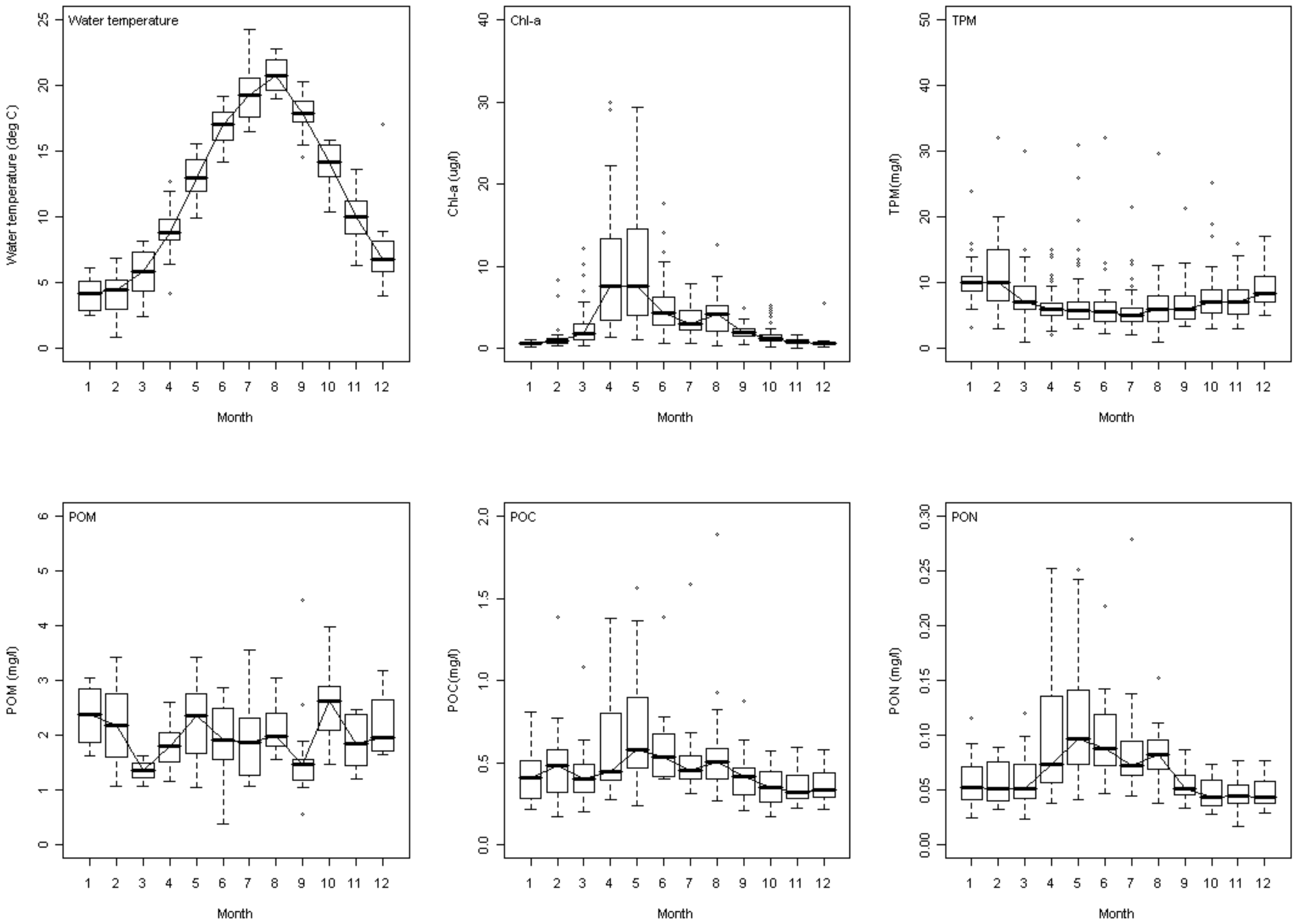


Figure 21 *Overview environmental conditions in the Central part of the Oosterschelde (1993 – 2007).*

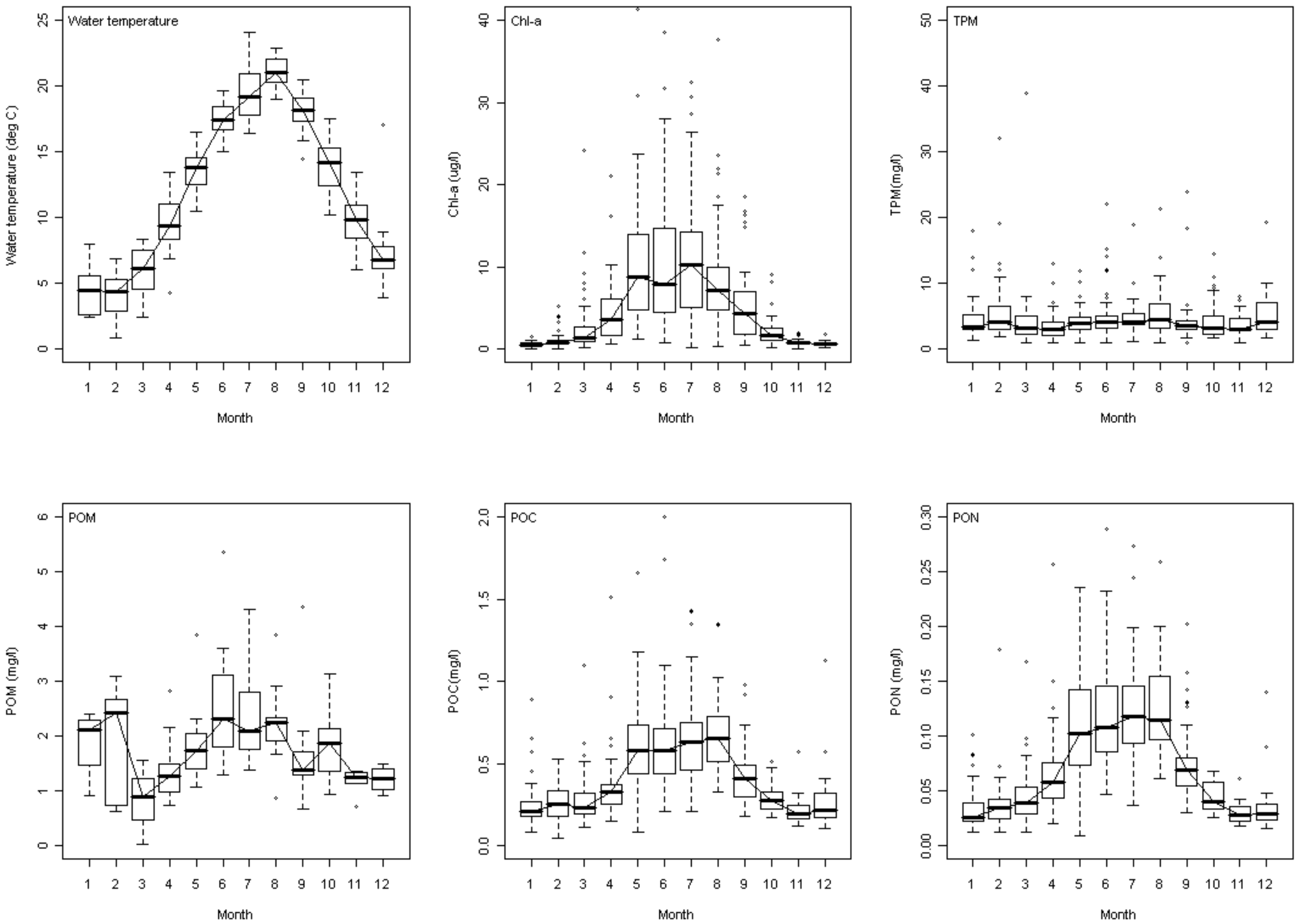


Figure 22 *Overview environmental conditions in the Northern part of the Oosterschelde (1993 – 2007).*

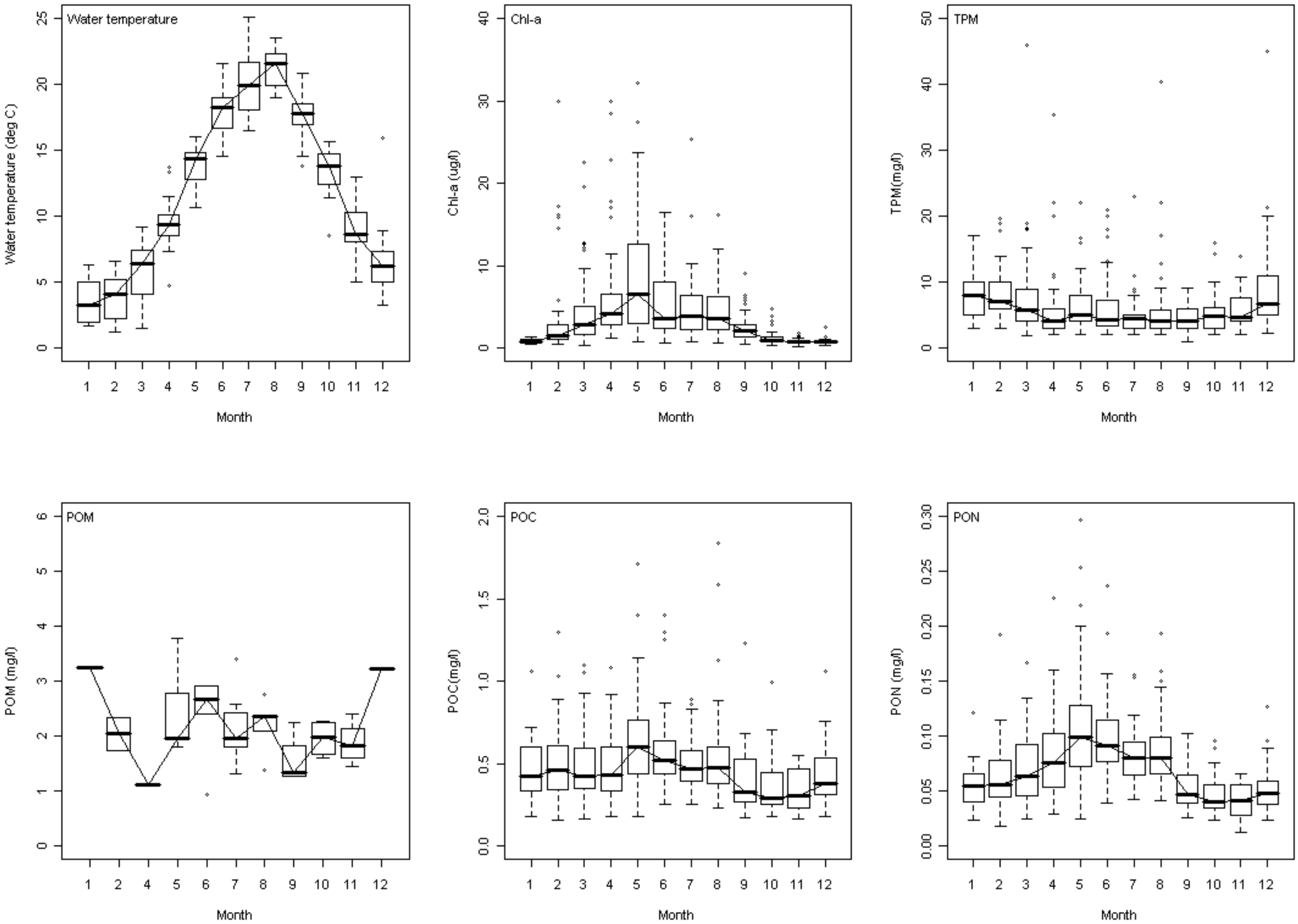


Figure 23 *Overview environmental conditions in the Eastern part of the Oosterschelde (1993 – 2007).*

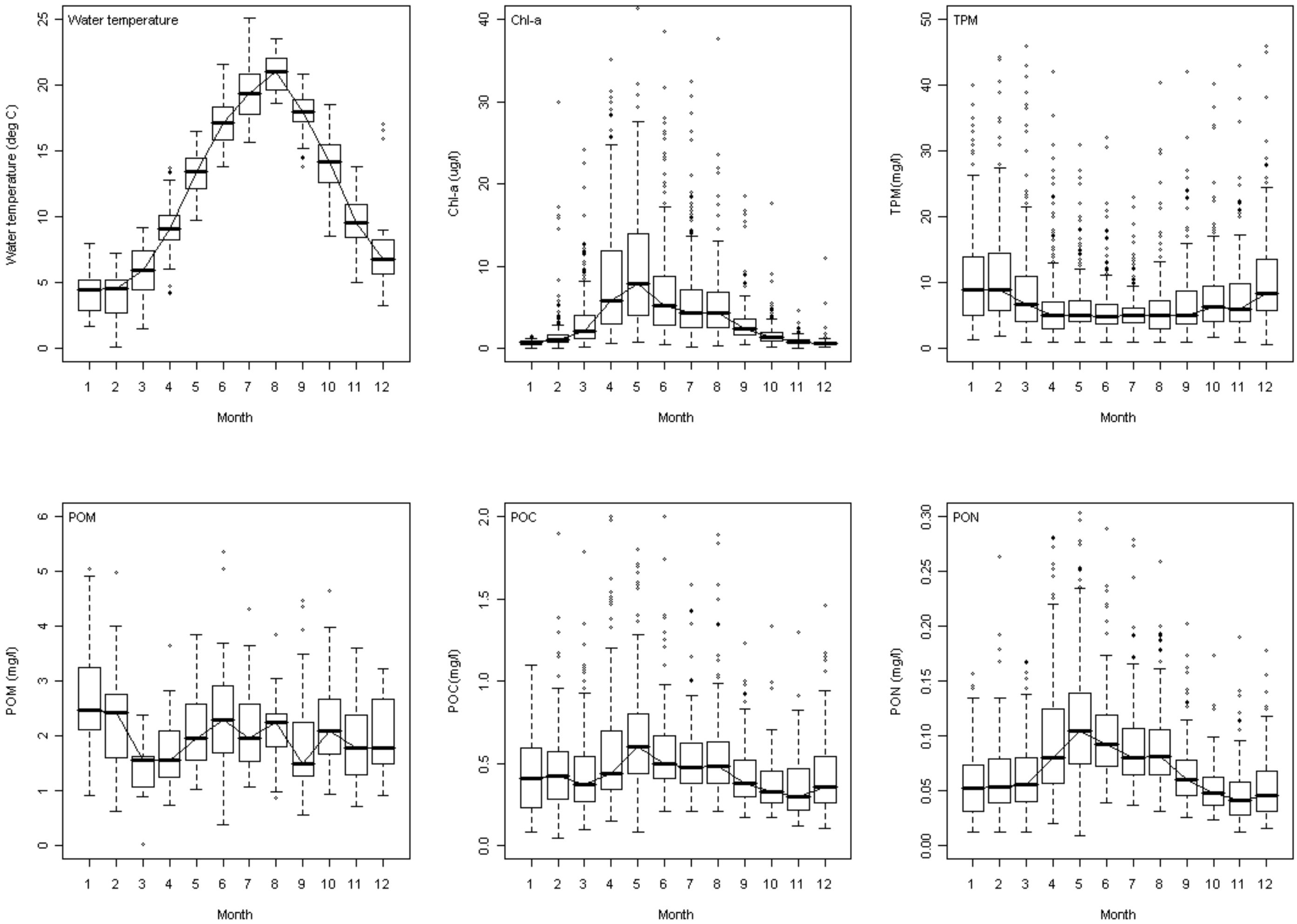


Figure 24 *Overview environmental conditions in the whole of the Oosterschelde (1993 – 2007).*

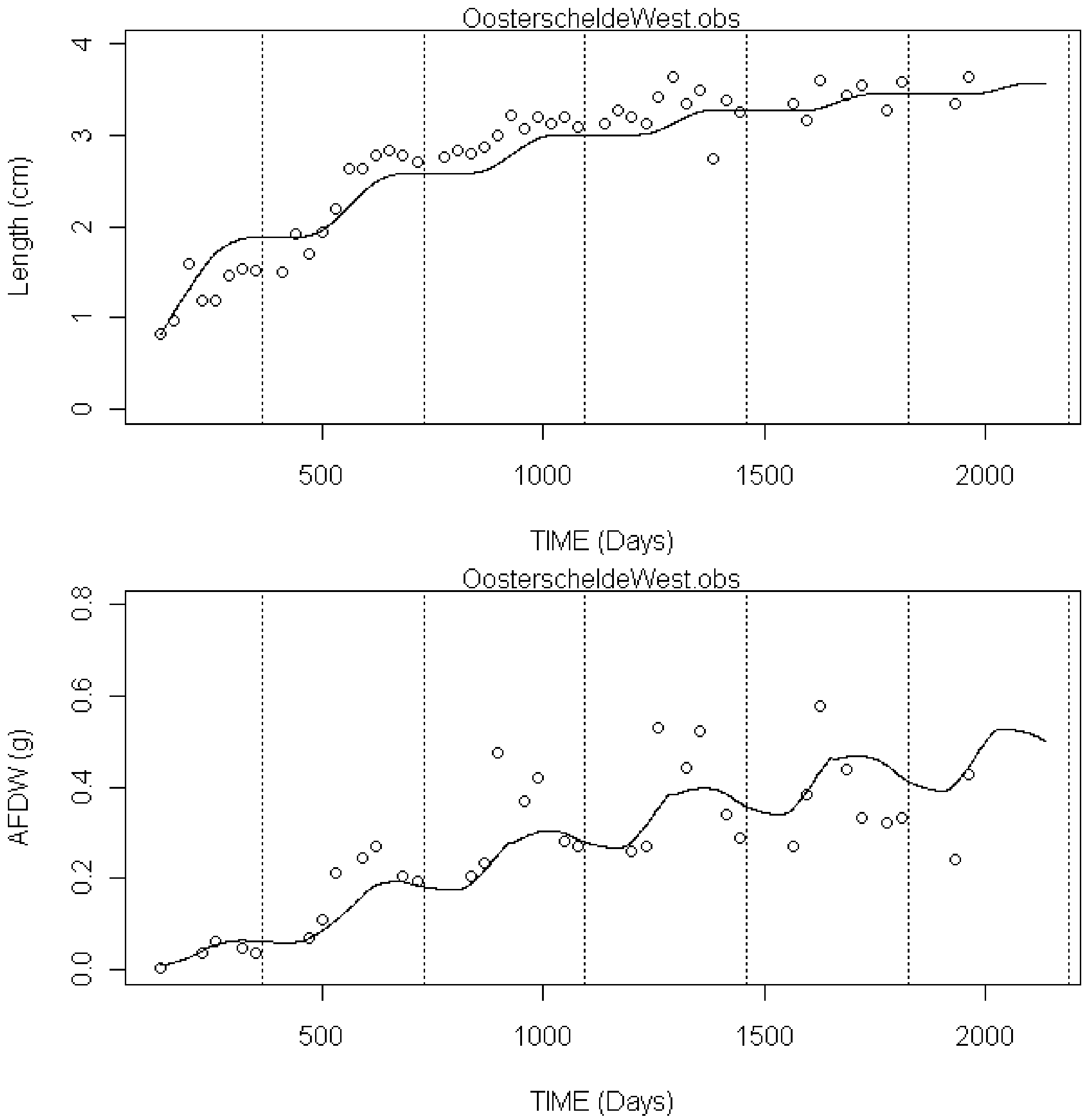
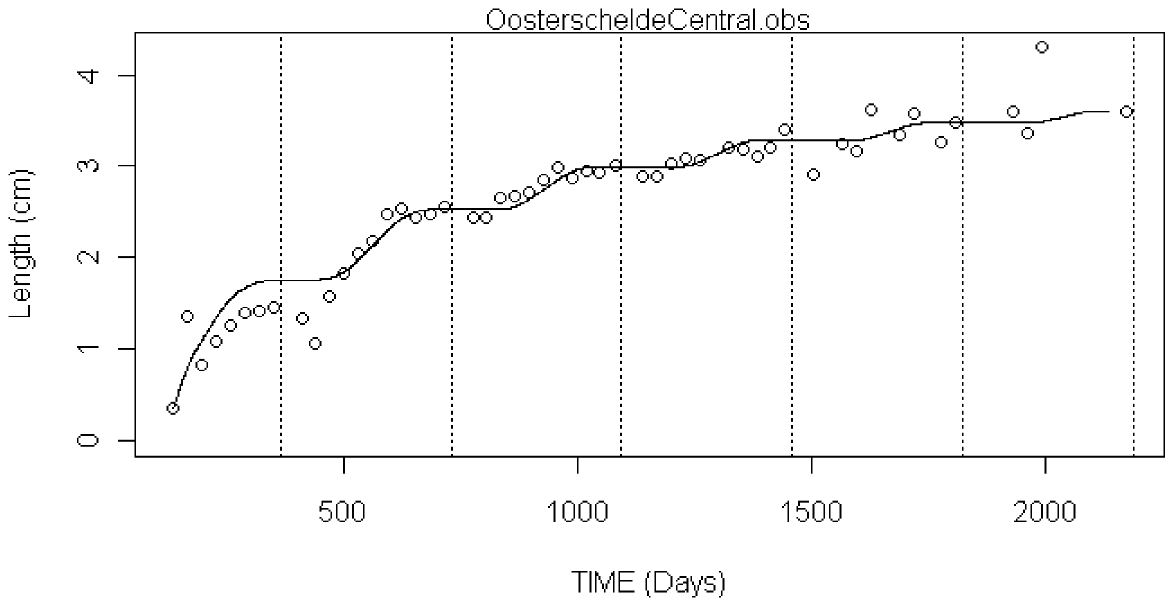


Figure 25 *Evaluation of the output of the DEB model with the observed data (dots) for length (upper figure) and ash free dry weight (lower figure) for the Western part of the Oosterschelde.*



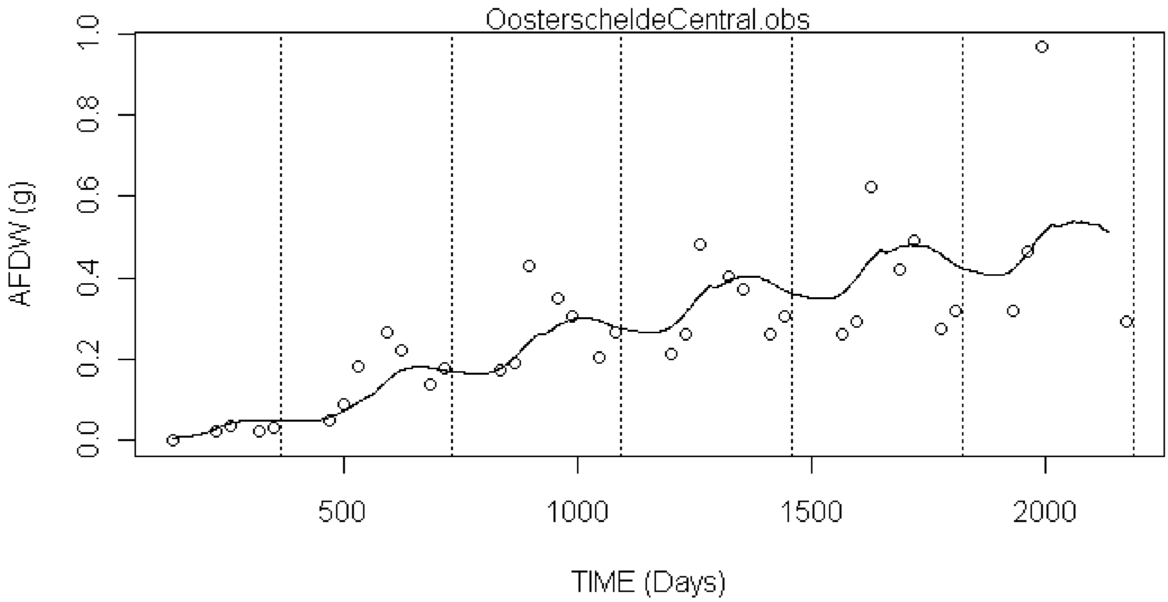


Figure 26 *Evaluation of the output of the DEB model with the observed data (dots) for length (upper figure) and ash free dry weight (lower figure) for the Central part of the Oosterschelde.*

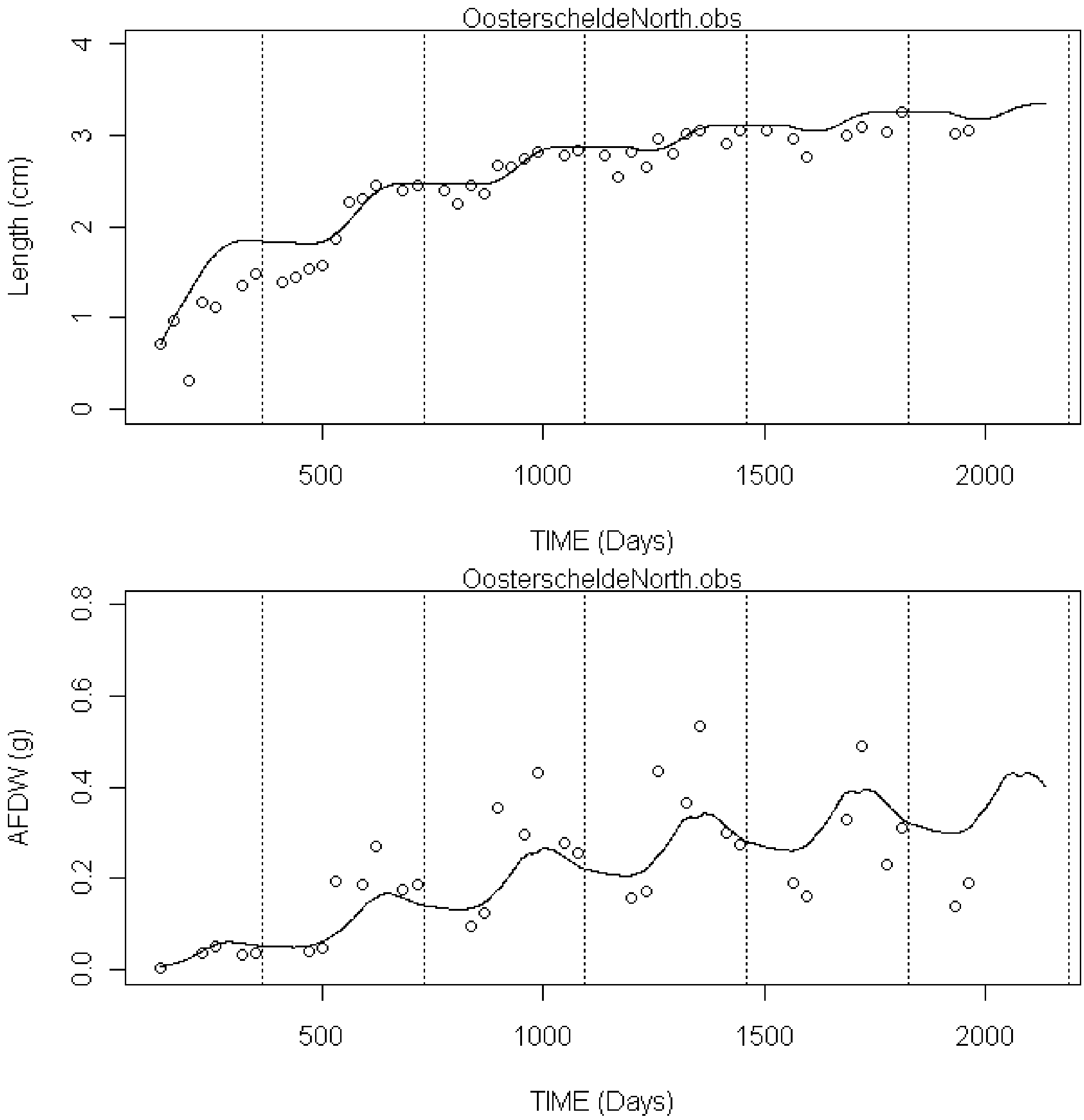


Figure 27: *Evaluation of the output of the DEB model with the observed data (dots) for length (upper figure) and ash free dry weight (lower figure) for the Northern part of the Oosterschelde.*

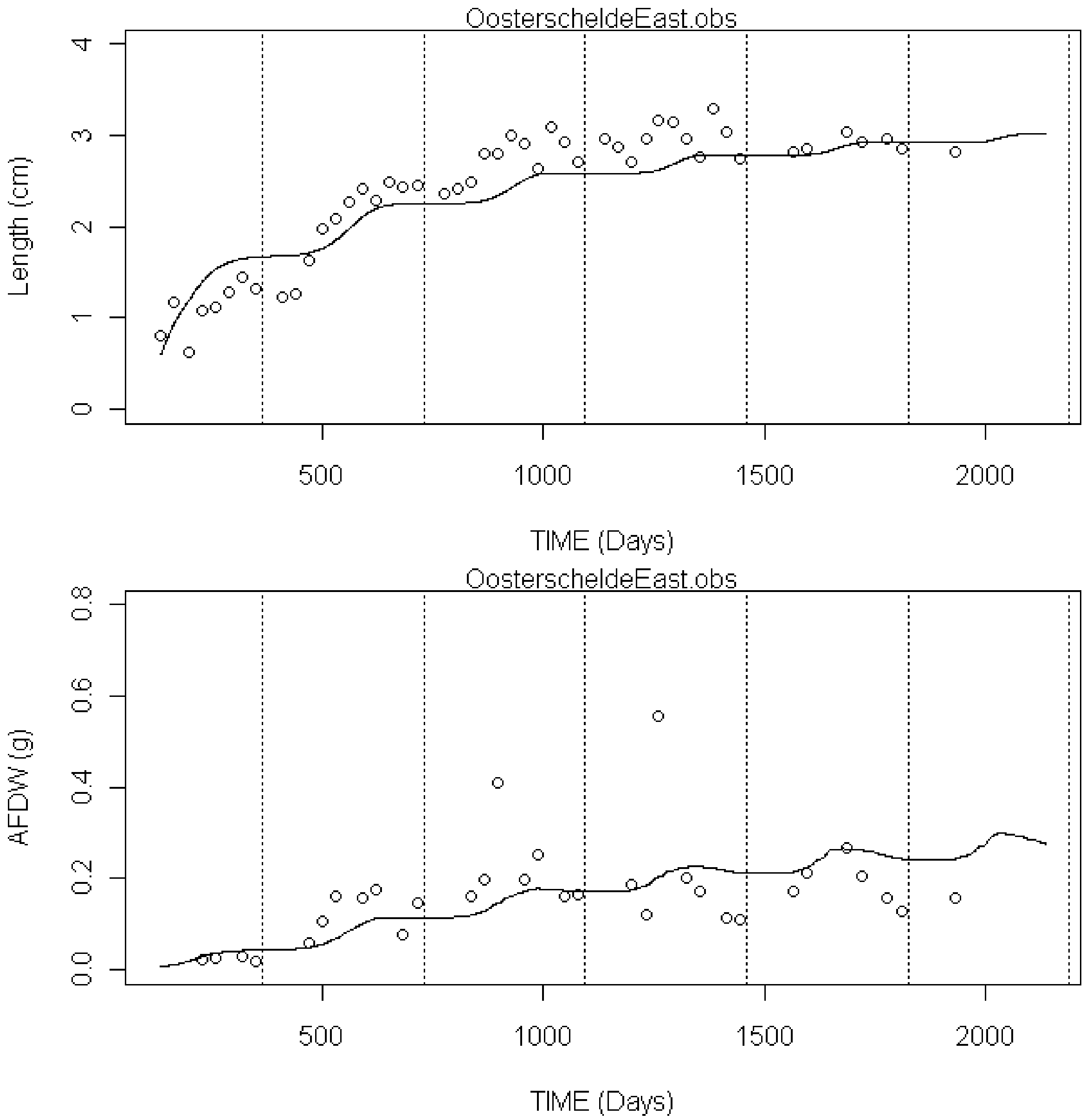


Figure 28 *Evaluation of the output of the DEB model with the observed data (dots) for length (upper figure) and ash free dry weight (lower figure) for the Eastern part of the Oosterschelde.*

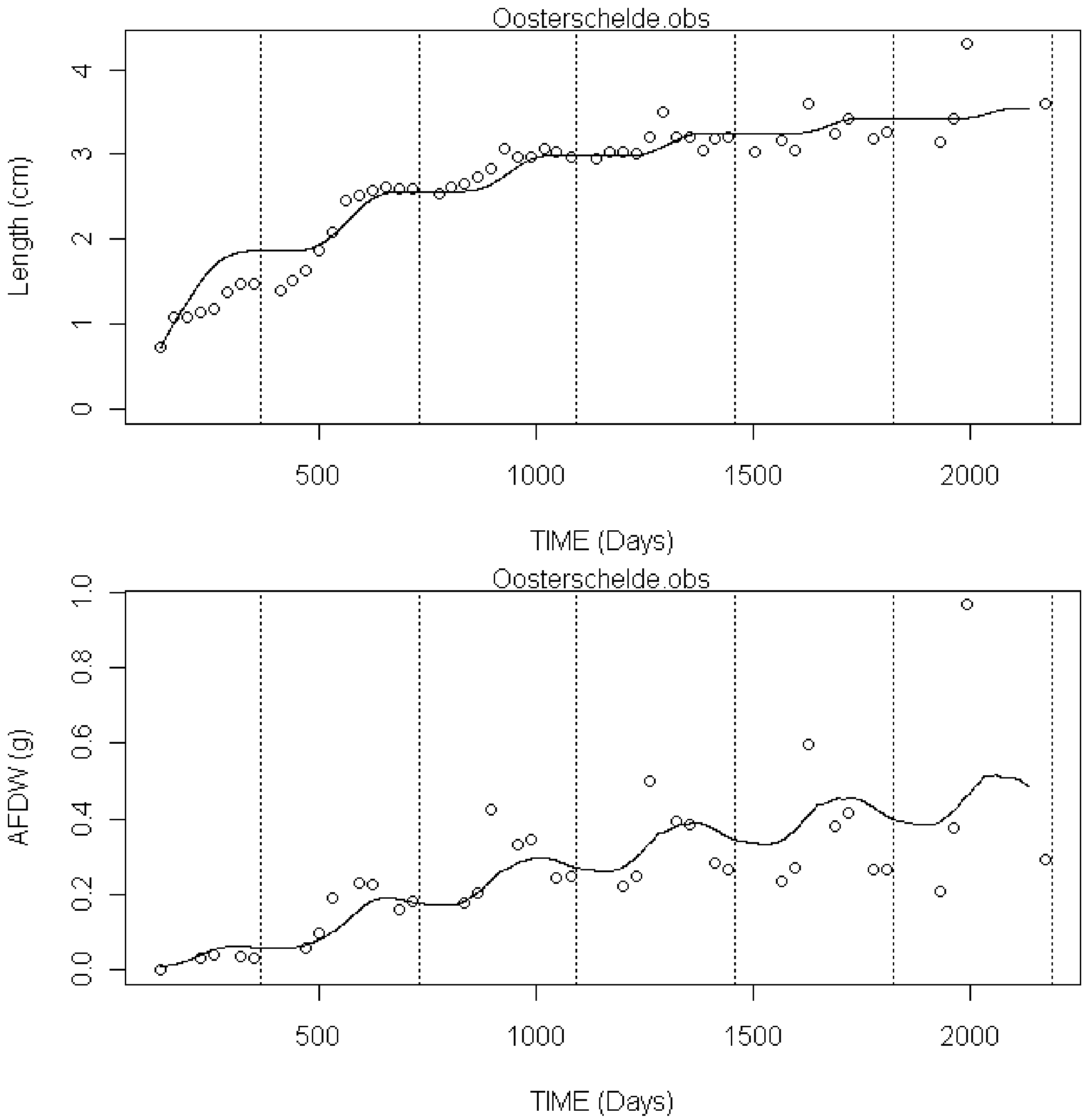


Figure 29 *Evaluation of the output of the DEB model with the observed data (dots) for length (upper figure) and ash free dry weight (lower figure) for the whole Oosterschelde.*

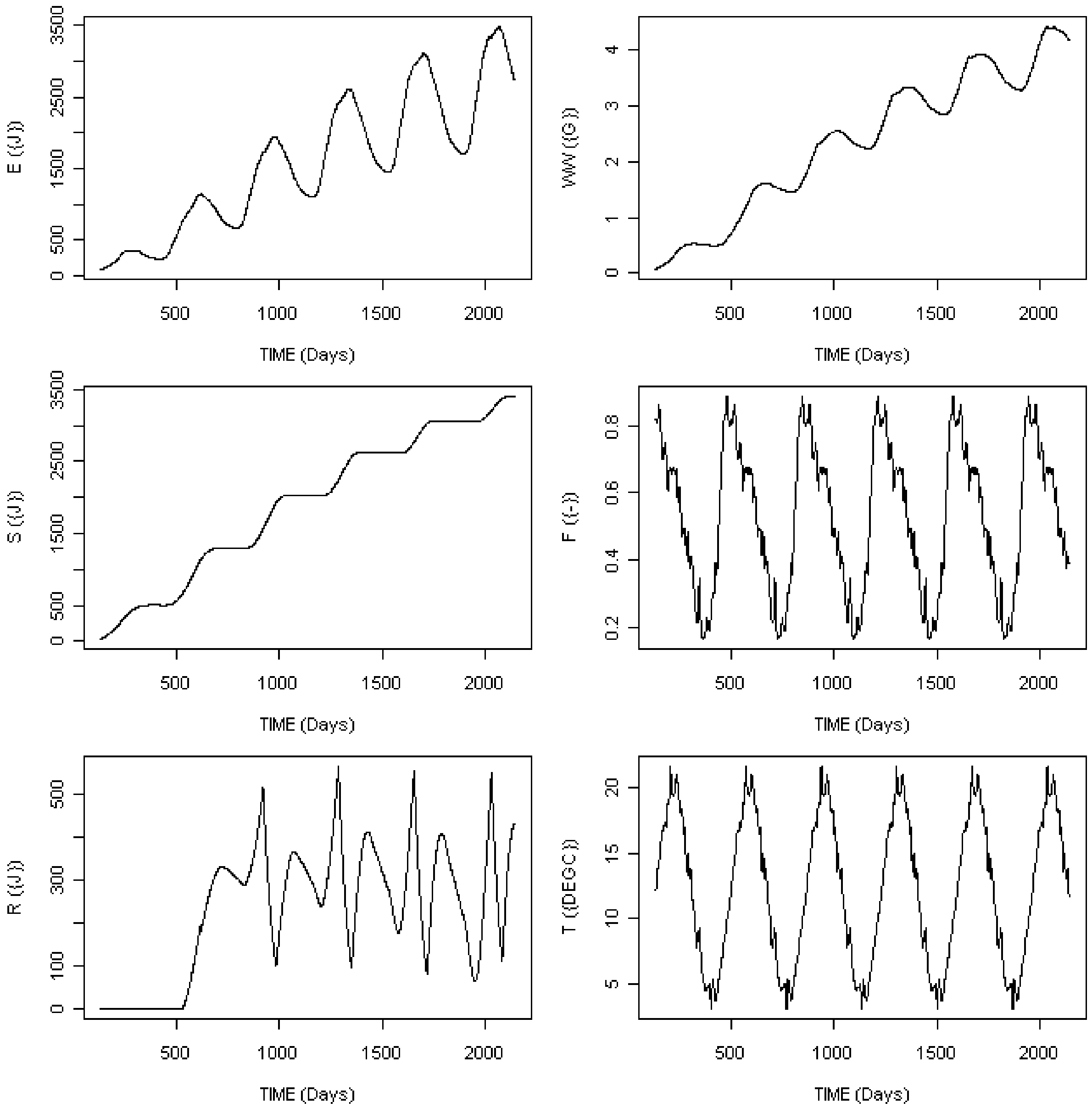


Figure 30 *Evaluation of the output of the DEB model for the Western part of the Oosterschelde. Variables plotted are (E) Energy in reserves, (S) Energy in structural body mass, (R) Energy in reproductive organs, (WW) Total wet weight, (F) scaled functional response and (T) water temperature.*

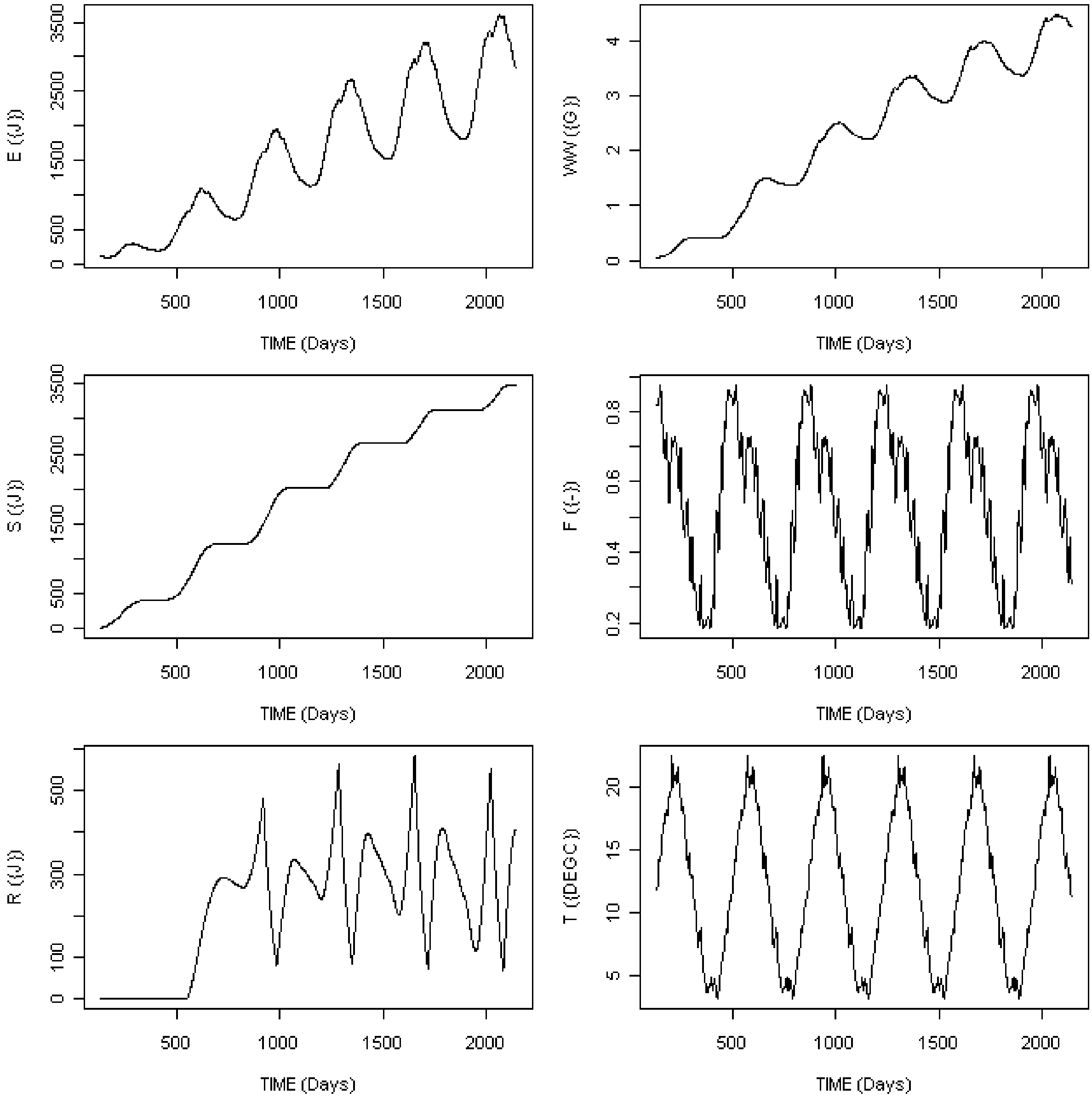


Figure 31 *Evaluation of the output of the DEB model for the Central part of the Oosterschelde. Variables plotted are (E) Energy in reserves, (S) Energy in structural body mass, (R) Energy in reproductive organs, (WW) Total wet weight, (F) scaled functional response and (T) water temperature.*

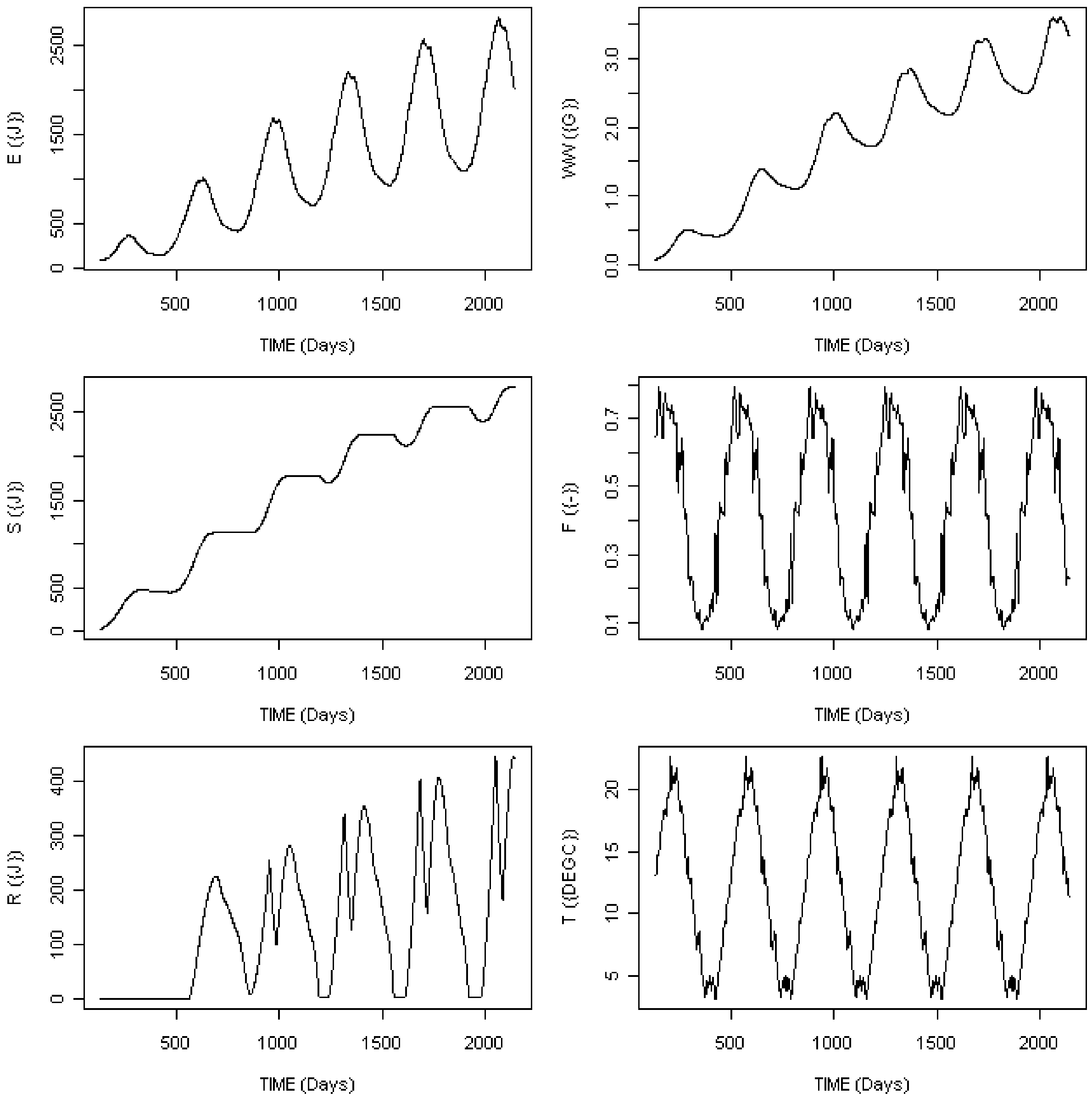


Figure 32 *Evaluation of the output of the DEB model for the Northern part of the Oosterschelde. Variables plotted are (E) Energy in reserves, (S) Energy in structural body mass, (R) Energy in reproductive organs, (WW) Total wet weight, (F) scaled functional response and (T) water temperature.*

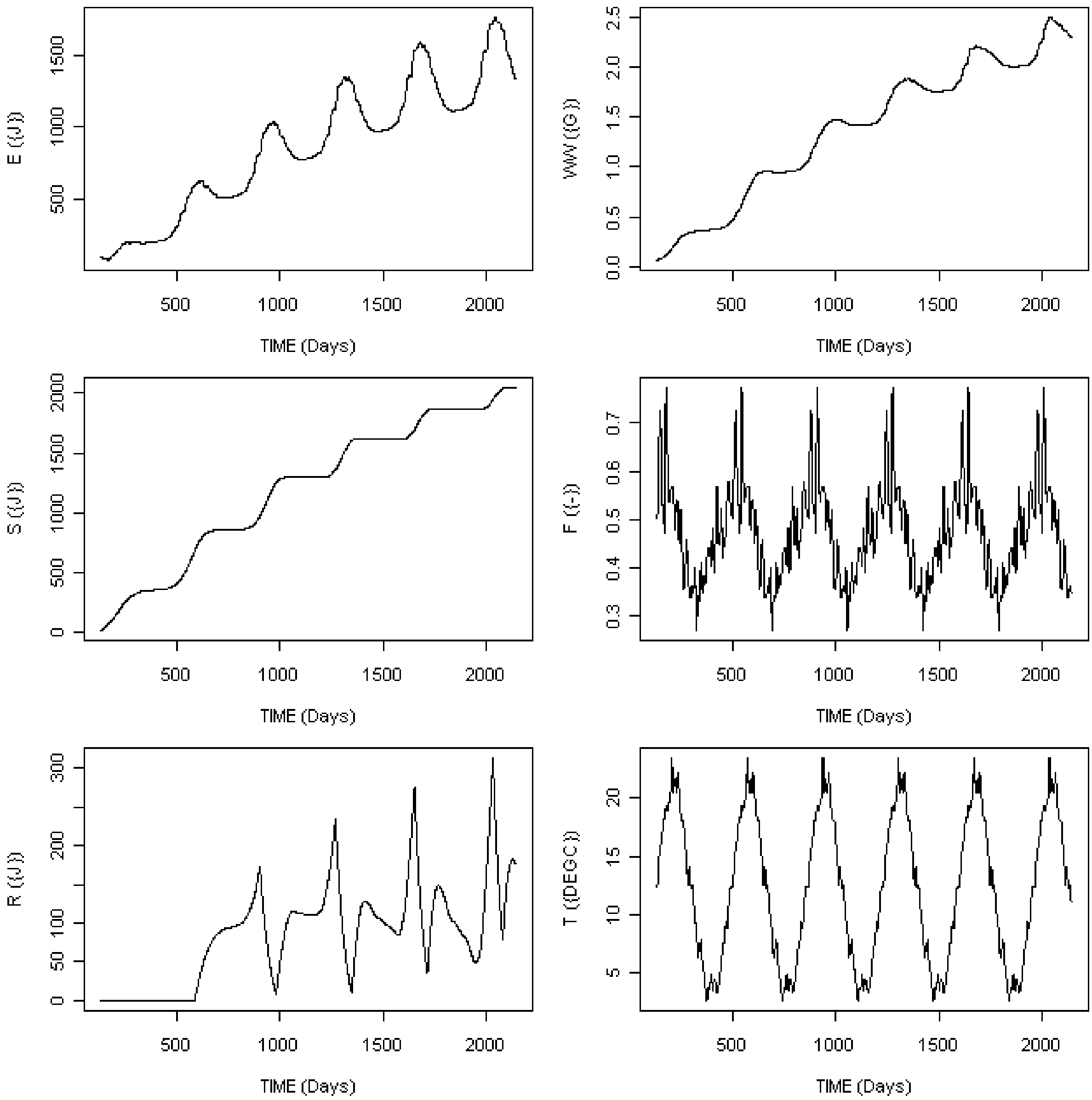


Figure 33 *Evaluation of the output of the DEB model for the Eastern part of the Oosterschelde. Variables plotted are (E) Energy in reserves, (S) Energy in structural body mass, (R) Energy in reproductive organs, (WW) Total wet weight, (F) scaled functional response and (T) water temperature.*

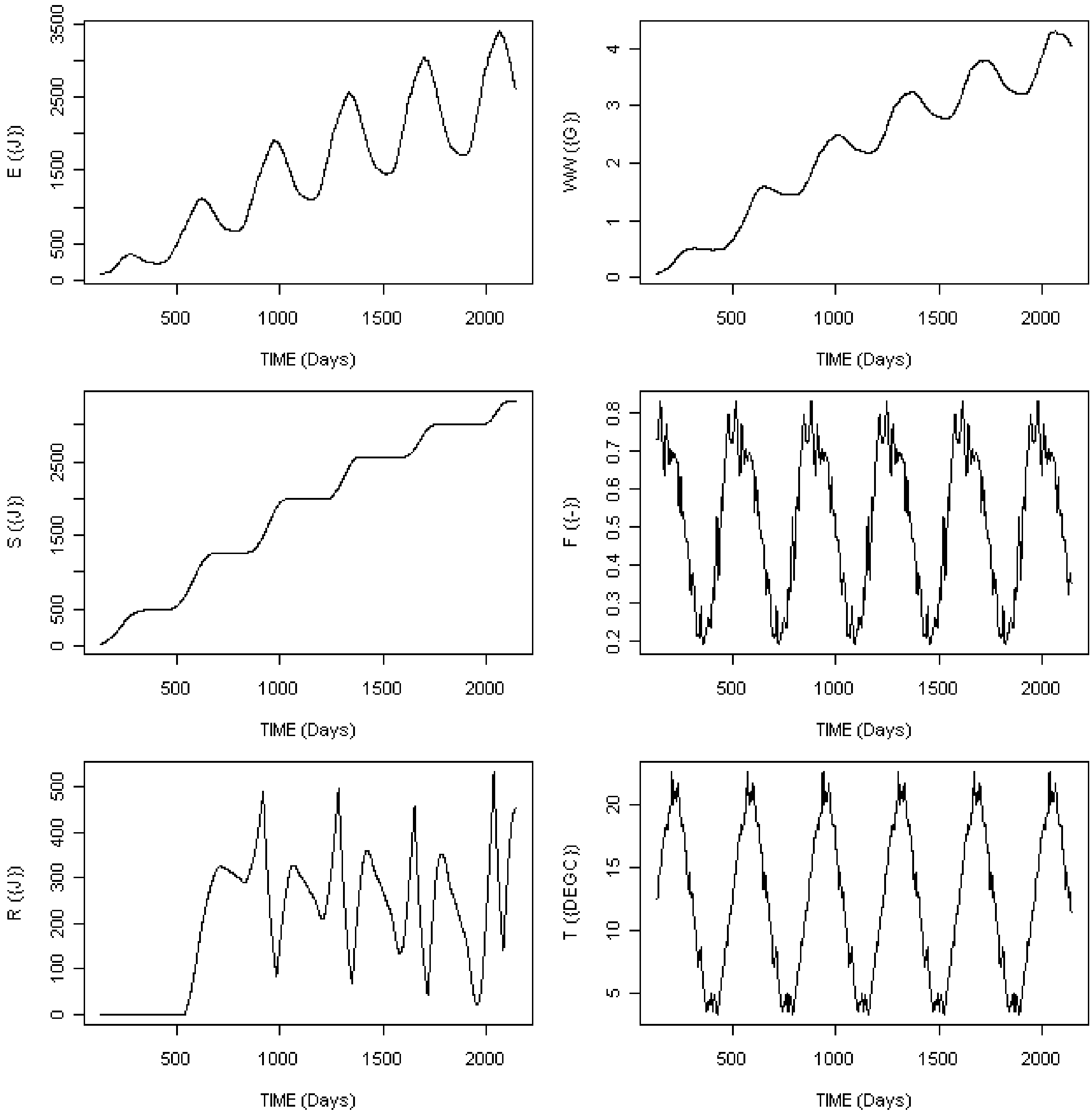


Figure 34 *Evaluation of the output of the DEB model for the whole Oosterschelde. Variables plotted are (E) Energy in reserves, (S) Energy in structural body mass, (R) Energy in reproductive organs, (WW) Total wet weight, (F) scaled functional response and (T) water temperature.*