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Authors: J.W.M. Wijsman

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Author(s):   J.W.M. Wijsman

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Contents

Summary

In this study, the food conditions for mussels are estimated at different locations within the Oosterschelde. In 2014, 2015 and 2016, mussels with a uniform size were placed in baskets at the borders of commercial culture plots distributed over the Oosterschelde. Each month, a subsample was taken from each basket to measure growth (shell length and individual weight) of the mussels. The results show a variation in growth performance, both in shell length as in flesh weight, between the different locations. A model approach was used to translate the spatial differences in growth to spatial differences in food conditions.

A Dynamic Energy Budget (DEB) model was fitted to the data in order to trace-back the food conditions. During this fitting, the food correction factor (ψ) was optimized. ψ can be interpreted as an indication of the food conditions (algae concentration, quality, current velocity) at that specific location in comparison to the average food conditions in the whole Oosterschelde.

The results show that there is a spatial, but also year-to-year variation in food conditions within the Oosterschelde. Locations with the best food conditions were Neeltje Jans N in 2015 and Hammen 9, Dortsman and Krabbenkreek in 2016. Growth of the mussels in the baskets in 2014 was lower than in 2015 and 2016. This is probably caused by the larger size of the mussels that were used in 2014 and the fact that the growth of mussels reduces with size.

In contravention to the expectations, there was no clear pattern in growth conditions from the western part of the Oosterschelde to the eastern and northern part. For example, the growth of the mussels at the two locations in the northern part of the Oosterschelde (Krabbenkreek and Viane) where ralatively good compared to the other locations. In practice, however, mussel farmers use the culture plots in the northern part mainly for storage of seed and halfgrown mussels. Possibly the mussels in the baskets perform better in this area than on the bottom culture plots.

The DEB model is a good tool to trace-back the food conditions from the measured growth data. The parameters for blue mussel, that is used for the DEB model should be updated. The parameters are presently based on historical data, whereas new data are available.

Samenvatting

Als onderdeel van het project PROFMOS (Productie Factoren Mosselcultuur Oosterschelde), is in 2014, 2015 en 2016 het groeipotentieel voor mosselen in de Oosterschelde onderzocht. Hiertoe zijn er mosselen van gelijke grootte in mandjes geplaatst op of op de grens van kweekpercelen. Iedere maand is er een subsample uit de mandjes genomen en de mosselen zijn opgemeten (schelplengte, versgewicht, vleesgewicht en vleespercentage). In dit onderzoek zijn deze gegevens gebruikt om op basis van de geobserveerde groei in de mandjes, de voedselcondities van betreffende locatie in dat jaar te herleiden. Hiervoor is een Dynamic Energy Budget (DEB) model gebruikt. De uitvoer van het model (schelplengte en vleesgewicht) is gefit aan de gemeten waarden, waarbij een parameter ψ (voedsel correctie factor) is gevarieerd. De ψ waarde van het model met de beste fit is daarmee een maat voor de voedselsituatie (hoeveelheid en kwaliteit) die de mosselen in het mandje hebben ondervonden.

De resultaten van deze analyse laten zien dat er een behoorlijke ruimtelijke variatie is in voedselcondities binnen de Oosterschelde, maar ook dat deze van jaar tot jaar verschilt. Locaties met goede voedselomstandigheden voor de mosselen waren Neeltje Jans N in 2015 en Hammen 9, Dortsman en Krabbenkreek in 2016. In 2014 was de groei van de mosselen in de mandjes minder dan in 2015 en 2016, maar dat kan deels worden verklaard doordat er in 2014 grotere mosselen zijn uitgezet, die sowieso niet meer veel konden groeien.

In tegenstelling tot de verwachtingen was er geen duidelijk patroon zichtbaar in groeicondities gaande van de stormvloedkering in het westelijk deel van de Oosterschelde naar de noordelijke tak in het noordoosten. Zo was bijvoorbeeld de groei van de mosselen op de twee locaties in de noordelijke tak (Krabbenkreek en Viane) relatief goed vergleken met de overige locaties. Vanuit de praktijk is bekend dat de bodempercelen in de noordelijke tak voornamelijk worden gebruikt voor opslag van zaad en halfwas mosselen. Mogelijk doen de mosselen in de mandjes (die iets boven de bodem staan) het in dit gebied beter dan de mosselen op de kweekpercelen.

Uit deze studie blijkt dat de trace-back methode met behulp van het DEB model een eenvoudige tool is om de voedselcondities te herleiden uit de metingen. De specifieke DEB parameters voor de mossel dienen echter wel te worden herberekend omdat deze op dit moment nog zijn gebaseerd op verouderde gegevens. Hiervoor zijn op dit moment betere, en meer up-to-date gegevens beschikbaar.

1 Introduction

1.1 Background

The Oosterschelde is the centre of the Dutch Mussel culture, which is mainly based on bottom culture. The seed resources are fished from natural beds in the Wadden Sea or collected by seed mussel collectors (SMC) in the Oosterschelde and the Wadden Sea and seeded on subtidal culture plots in the Oosterschelde and the Wadden Sea. After a period of 2-3 years, the mussels are harvested and sold at the auction in Yerseke. In order to reduce the impact of the seed fishery to the natural values of the Wadden Sea, the mussel farmers and NGO's agreed to implement a gradual transition from seed from fishery to the more expensive seed from SMC's. Due to the higher costs of SMC seed, there is a need to optimise the culture process by reducing the losses and increasing the growth.

This research is part of the Centre of Expertise project PROFMOS (Productie Factoren Mosselcultuur Oosterschelde). The main goal of the PROFMOS project is to get more insight in the factors that influence the productivity of culture plots in the Oosterschelde and to provide the mussel farmers with practical tools to improve the productivity in a sustainable, goal oriented way.

This study focusses on the optimization of the growth in the Oosterschelde. Growth of mussels in the Oosterschelde is influenced by environmental conditions such as food (availability and quality) and temperature. The temperature fluctuations are quite comparable throughout the Oosterschelde, but the food conditions vary largely. In total about 3 5000 ha of culture plots are present in the Oosterschelde, of which 2 250 ha is used by mussel farmers (Capelle, 2017). The culture plots are organised in clusters spread over the Oosterschelde and are often located on the edges of the intertidal flats. It is known that the quality of the culture plots vary. In general the best plots are assumed to be located in the western part of the Oosterschelde near the storm surge barrier. The culture plots in the northern part of the Oosterschelde are mainly used for storage of seed and half grown mussels, while the growth is assumed to be low.

1.2 Goal

The main goal of the present project is study the spatial variation in growth and food conditions within the Oosterschelde by fitting a Dynamic Energy Budget model for mussels to measured data.

1.3 Approach

As part of the PROFMOS project an extensive monitoring was initiated in the Oosterschelde. Mussels of equal size (shell length) and origin were placed in baskets on culture plots at different locations within the Oosterschelde. The baskets were sampled monthly during the growing season and growth was measured by the increase in shell length and biomass.

A dynamic energy budget (DEB) model will be fitted to the field observations to reconstruct the growth of the mussels. In the DEB model, food and temperature are the main environmental conditions that determined the growth of the mussels. Since the temperature fluctuations are known the food conditions can be traced-back with the model based on the growth measurements (e.g. Lavaud, 2014).

2 Field observations

2.1 Monitoring locations

In 2014, 2015 and 2016, growth of mussels was measured at 15 locations on the culture plots distributed over the Oosterschelde (Figure 1). At the start of the experiment in each year, mussels with the same size were placed in baskets on the bottom on, or at the border of a culture plot. During the growing season, monthly subsamples were taken from the baskets and the mussels were measured for different parameters (shell length, fresh weight, flesh weight, ash-free dry weight).

Figure 1: Monitoring locations (coloured dots) and distribution of the mussel culture plots in the Oosterschelde.

Not every location was monitored in all of the years (Table 1). In total 9 locations were monitored in 2014. In 2015 and in 2016 13 locations were monitored. Monitoring location Engels vaarwater N is replaced by Engels vaarwater Z in 2015. In 2014 only one location at Neeltje Jans (Neeltje Jans M) was monitored. From 2015 on this location was replaced by two locations (Neeltje Jans Z and Neeltje Jans N), located at the Roompotgeul and Roggenplaatgeul respectively. Location Viane was included in the monitoring programme in 2015 and location Wissenkerke was included in 2016. Location Zandkreek was not monitored in 2016.

Location	Culture plot	2014	2015	2016
Dortsman	OSWD 80/81	8	7	4
Engels vaarwater N	OSWD 182B	6	-	-
Engels vaarwater Z	OSWD 185	-	7	6
Hammen 9	Hammen 9	-	7	5
Kattendijke	OSWD 200	8	7	6
Krabbenkreek	Mastgat 22	9	7	5
Neeltje Jans M	Hammen 180B	8	-	-
Neeltje Jans N	Hammen 174/175	-	7	6
Neeltje Jans Z	Hammen 184/185	-	6	6
Roggenplaat N	Hammen 68B	7	6	5
Roggenplaat Z	Hammen 102	8	7	4
Stelletje	OSWD 10/11	8	6	4
Viane	Mastgat 6/7	-	7	5
Wissenkerke	Zandkreek 3	-	-	4
Zandkreek	Zandkreek 57/59	9	6	-

Table 1: Number of sampling moments at the various locations in the different years. The second column gives the names of the culture plots where the baskets were placed.

2.2 Monitoring results length

In Figure 2 to Figure 4 the development of shell length for the different locations is plotted. As can be seen from this figure, in 2014, the mussels were larger (45.0 mm) at the start of the experiment compared to 2015 and 2016 (33.7 and 32.0 mm, respectively). In 2014 there is no large difference in shell length growth between the different locations. Mussels at location Zandkreek grew slower than the mussels at the other locations. Also the growth at locations Dortsman and Stelletje was lower than the growth at the locations Neeltje Jans M, Roggenplaat Z, Roggenplaat N and Krabbenkreek. Although negative growth is not possible, it can happen that the average shell length decreases, as can be seen for example at location Engels vaarwater N from 3rd June to 1st July. This is caused by a subsample of relative small mussels at July 1st.
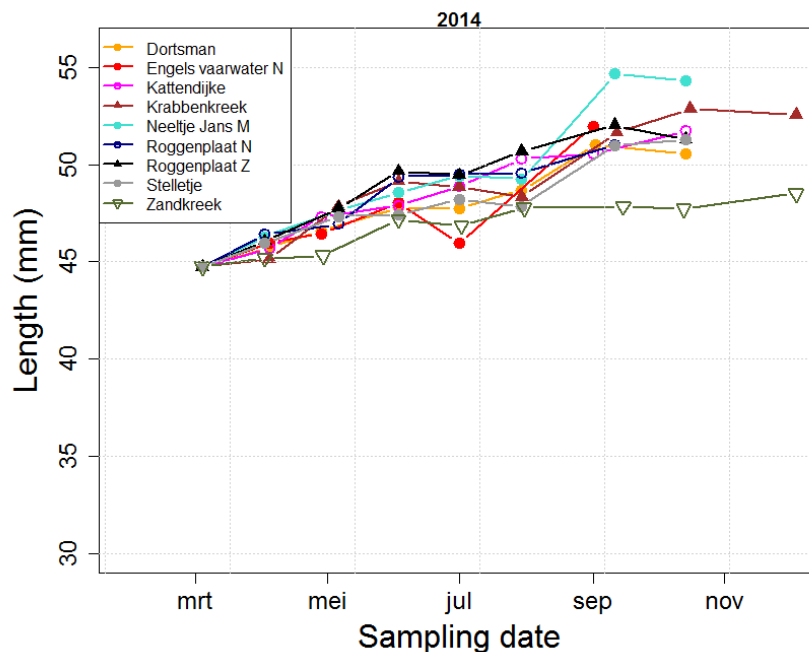

Figure 2: Development of shell length (mm) of the mussels at the various locations in 2014. The colours correspond to the colour of the markers in Figure 1.

In 2015 the differences are more pronounced (Figure 3). This is partly due to the smaller size of the mussels at the start of the experiment. As can be seen from this figure, the mussels at location Zandkreek were smaller (30.3 mm) at the start of the experiment compared to the other locations (33.7 mm), so growth at this location cannot be compared directly with the other locations. At location Hammen 9, the mussels were replaced with new mussels at 22nd July. From this figure it can be seen that the mussels at locations Neeltje Jans N, Neeltje Jans Z, Roggenplaat N, Dortsman grow faster than at locations Rogenplaat Z, Krabbenkreek, Stelletje and Viane. Also the growth at Hammen 9 is good, however, the mussels at this location have been replaced with new, smaller mussels in July, so it is difficult to compare the growth with the other locations (first week of October).
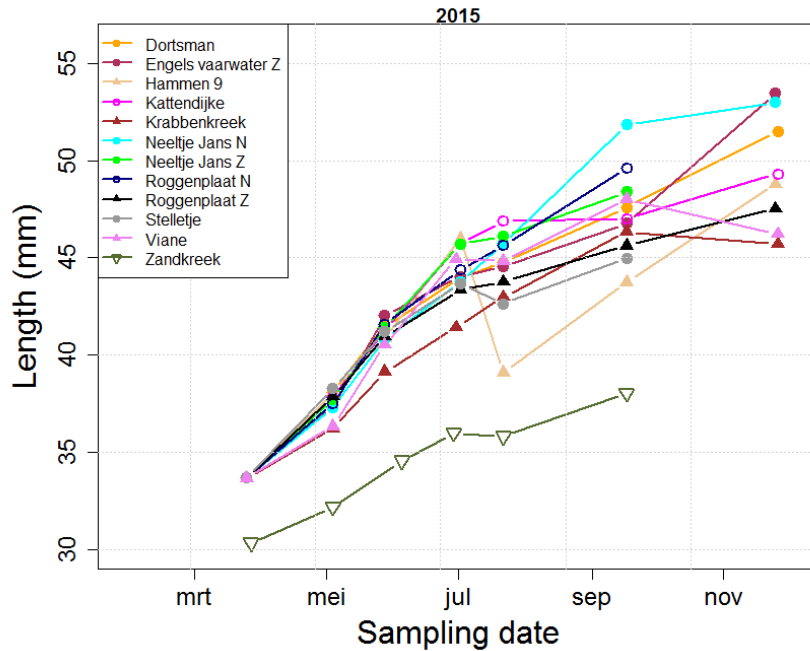

Figure 3:   Development of shell length (mm) of the mussels at the various locations in 2015. The colours correspond to the colour of the markers in Figure 1.

In 2016 there is a more distinct difference between the various locations (Figure 4). Locations with good growth are Hammen 9, Dortsman, Stelletje and Krabbenkreek. Growth is less at Neeltje Jans Z and Kattendijke and intermediate at locations Engels vaarwater Z, Viane and Neeltje Jans N. Unfortunately, in 2016 many baskets with mussels were lost in the cause of the year. Therefore, only four locations could be sampled until the end of the experiment.
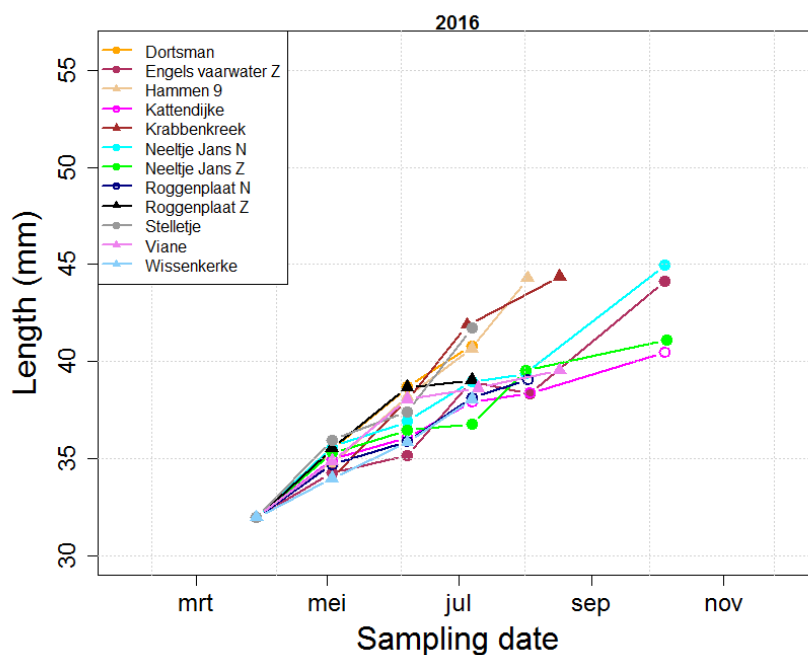
Figure 4:   Development of shell length (mm) of the mussels at the various locations in 2016. The colours correspond to the colour of the markers in Figure 1.

2.3   Monitoring results flesh weight and meat content

In Figure 5 and Figure 6 the development of flesh weight (g) and meat content (%) is presented. The meat content at the start of the experiment is not measured. Figure 5 shows that the best growth in terms of flesh weight was at locations Neeltje Jans M and Krabbenkreek, in the northern part of the Oosterschelde. At those locations also the growth in shell length was the best. Growth at locations Roggenplaat Z, Dortsman and Stelletje was relatively good. Relatively poor growth in flesh weight was observed at locations Zandkreek and Kattendijke. The development in meat content (Figure 6) shows a very diffuse pattern.

The development in flesh weight in 2015 (Figure 7) shows comparable patterns than the length development. Mussels at the locations Neeltje Jans N, Neeltje Jans Z, Roggenplaat N, Viane, and Engels vaarwater Z have the highest flesh weight at the end of the year. Mussels at the locations Kattendijke, Krabbenkreek, Roggenplaat Z and Stelletje have lowest flesh weights at the end of the year. Note that the mussels at location Zandkreek were smaller at the start of the experiment and the mussels at location Hammen 9 have been replaced in the summer. From Figure 8 it can be seen that the meat content increases quickly in the beginning of the summer, and decreases in October and November. The same pattern can also be found in 2016 (Figure 10). However, in that year the decrease in meat content seems to start earlier, in July, August.

Figure 5: *Development of flesh weight (g) of the mussels at the various locations in 2014. The colours correspond to the colour of the markers in Figure 1.*

Figure 6: *Development of meat content (%) of the mussels at the various locations in 2014. The colours correspond to the colour of the markers in Figure 1.*

Figure 7: *Development of flesh weight (g) of the mussels at the various locations in 2015. The colours correspond to the colour of the markers in Figure 1.*

Figure 8: *Development of meat content (%) of the mussels at the various locations in 2015. The colours correspond to the colour of the markers in Figure 1.*
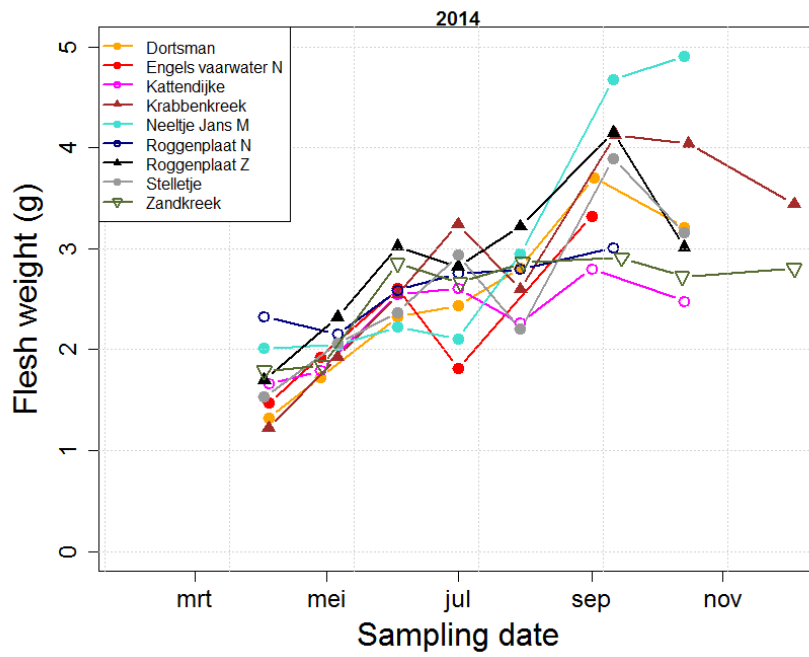
Figure 9: Development of flesh weight (g) of the mussels at the various locations in 2016. The colours correspond to the colour of the markers in Figure 1.
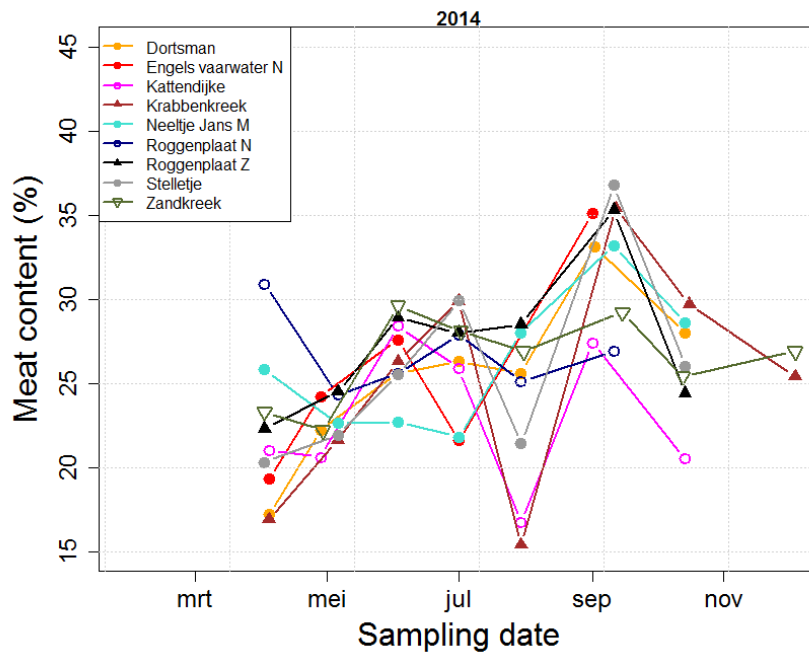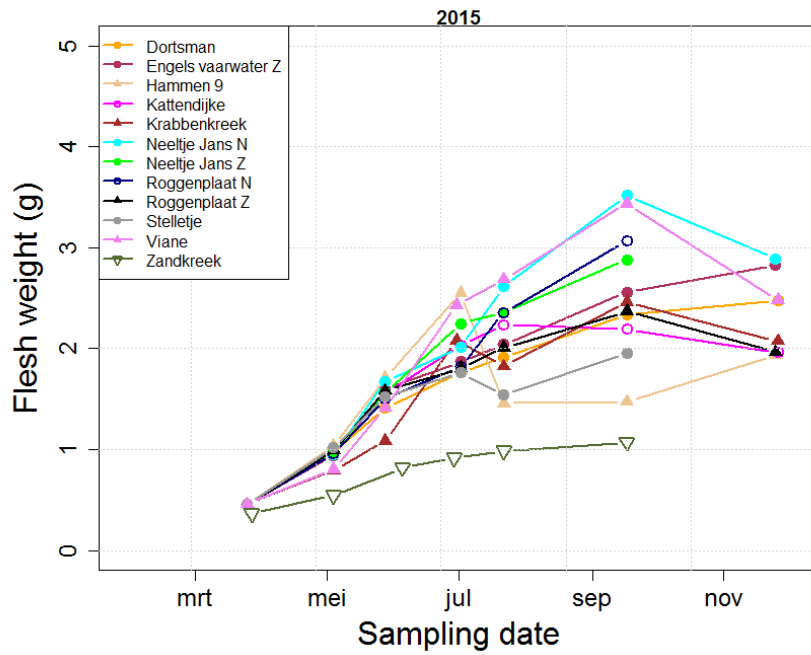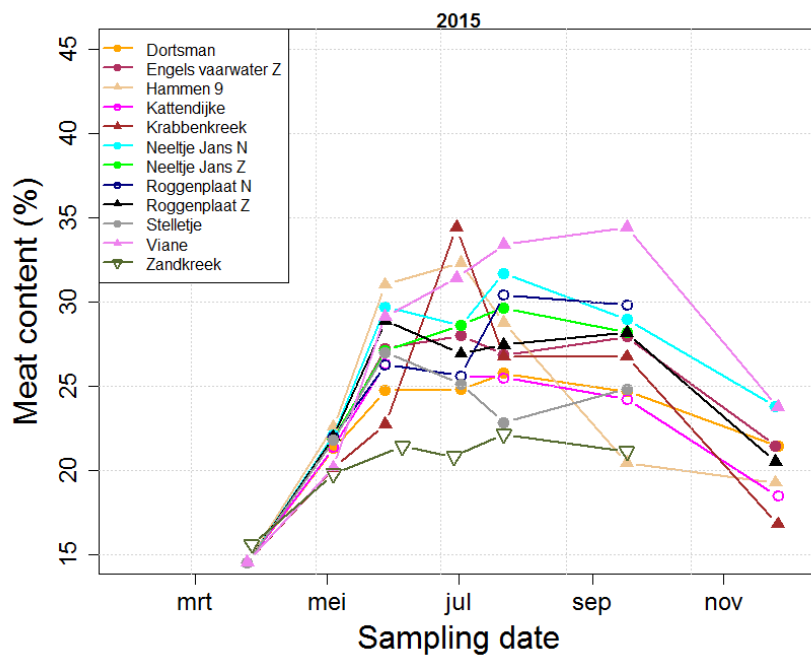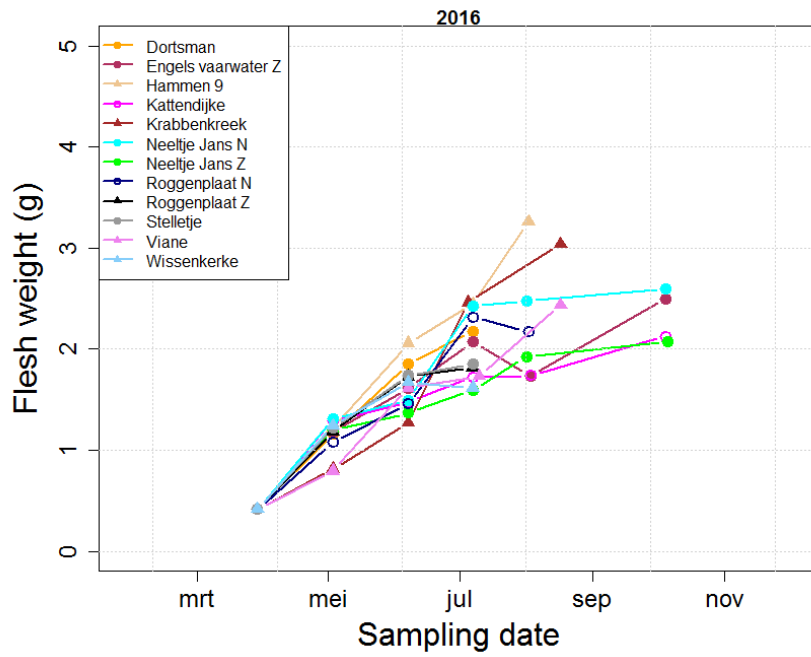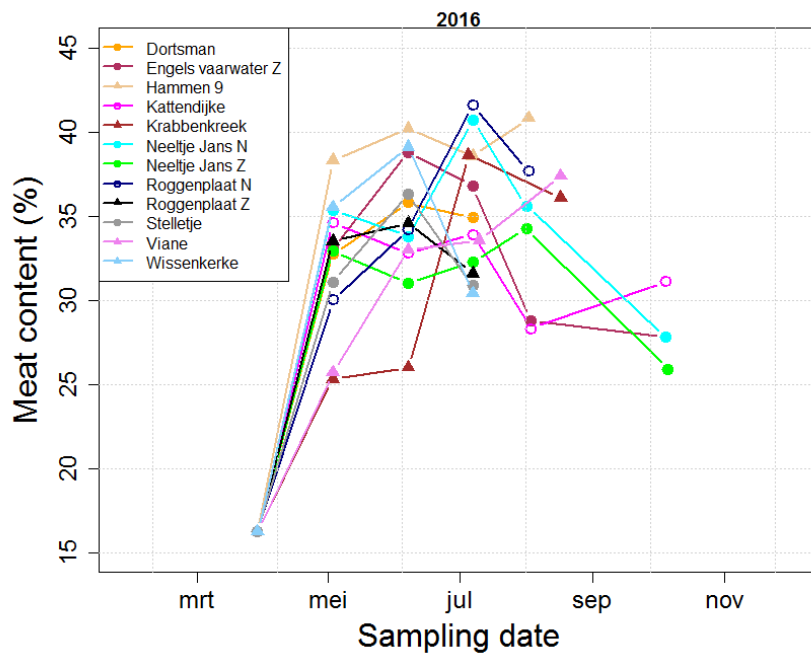

Figure 10: Development of meat content (%) of the mussels at the various locations in 2016. The colours correspond to the colour of the markers in Figure 1.

3 Model approach to trace-back food conditions

3.1 Conceptual scheme

The conceptual scheme for the method that is used to trace-back the food conditions based on the growth measurement is presented in Figure 11. Environmental conditions (water temperature and Chla) are forced to the model (black lines left panels). The output of the model is compared to the observations (dots in right panel). By means of a Monte-Carlo simulation, where the food concentration is multiplied by a factor (ψ), the parameter ψ is optimised. If this parameter is low, the food conditions for that specific dataset are poor and when the ψ-value is high, the food conditions are good.
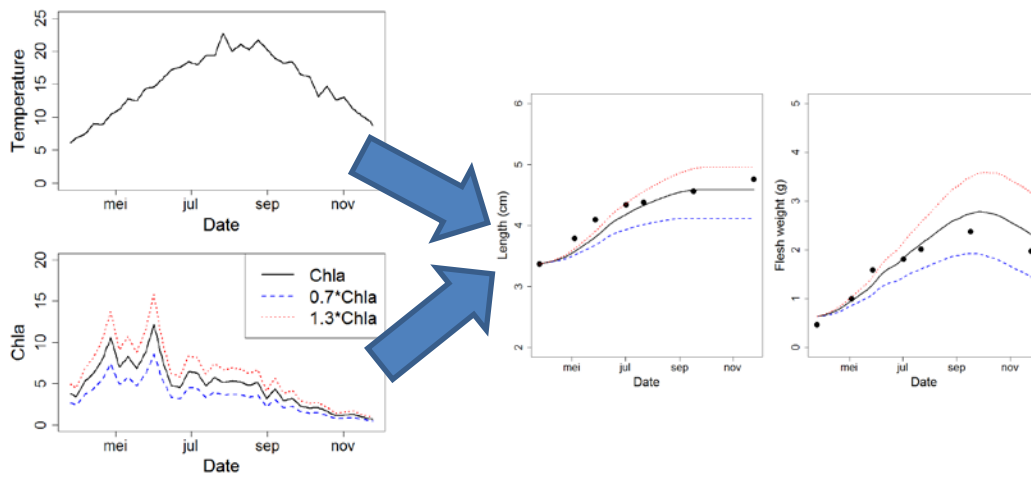
Figure 11: Schematic overview of the trace-back method using the DEB model.

3.2 DEB model for mussels

The growth and development of mussels are modelled using a Dynamic Energy Budget model (Appendix 1)(Kooijman, 2010). 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 three state variables: structural body volume (V, cm³), reserves (E, J) and reproduction buffer (R, J). The reserves are often quantified as energy density. The input of the DEB model is food and water temperature (Figure 12). Food is converted into food uptake rate by a Monod function, where the uptake rate increases with the food density to an asymptotic value (maximum uptake rate).

$$f = \frac{X}{X_k + X}$$

In this function f is the functional response (value between 0 and 1), X is the food concentration (µg Chla l⁻¹) and X_k is the half rate constant (µg Chla l⁻¹). This half rate constant is the concentration of Chla at which the uptake rate is 50% of the maximum uptake rate.

The output of the DEB model are the three state variables (V, E and R). These variables are converted into variables that are measured in the field (shell length, fresh weight, flesh weight, dry weight and ash-free dry weight).

3.3 Data temperature and Chla

Data on water temperature and Chla concentrations are derived from the database of Rijkswaterstaat. The data that are used in this study are described in (Wijsman and Smaal, 2011), and presented in Figure 12. The data were derived from different locations in the Oosterschelde over the years 1993 - 2007. From the raw data, the weekly averaged values were calculated in order to get an "average" seasonal curve for both water temperature and Chla-concentration in the Oosterschelde (line in Figure 12).

The "average" temperatures in the Oosterschelde show a sinusoidal function with highest water temperatures in August and lowest temperatures in January and February. As shown in Wijsman and Smaal (2011), there is not much spatial difference in water temperatures within the Oosterschelde. This is not the case for Chla concentrations, where the concentrations in the eastern part are relatively low compared to the rest of the Oosterschelde. The Chlorophyll-a concentrations in the Oosterschelde show a clear peak in Spring (April, May). However, in the northern part of the Oosterschelde, the high Chlorophyll-a concentrations are found during the whole summer period (May–August) (Wijsman and Smaal, 2011).
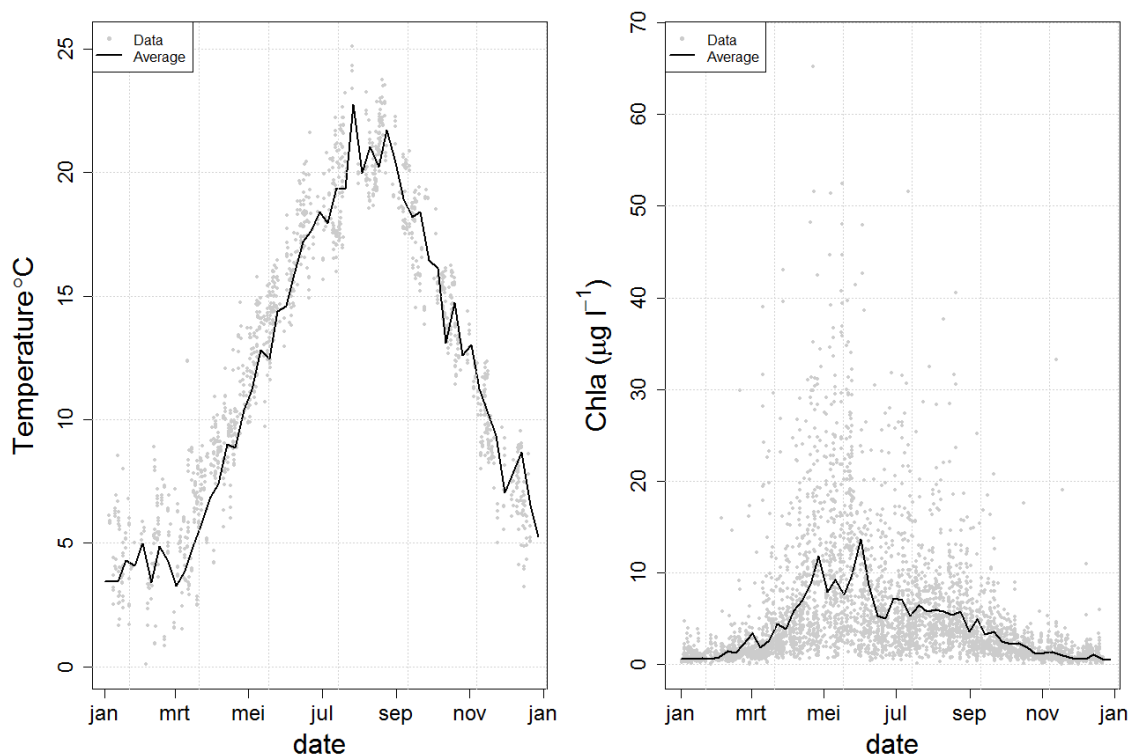
Figure 12: Temperature and chlorophyll-a measurements (dots) and weekly averaged data (line) in the Oosterschelde over the period 1993 – 2007. Same data was also used in (Wijsman and Smaal, 2011).

3.4 Optimization

In this study, we assume that the differences in growth that is observed at the various locations (Figure 2 to Figure 10) are caused by differences in food availability. Because the mussels are in low densities in the cages, just above the sea floor, intra-specific competition for food is expected to be absent. For example, the growth rate of the mussels at Hammen 9 in 2016 is much higher compared to the mussels at Kattendijke in the same year. These differences could be caused by the better food conditions for the mussels at Hammen 9. The DEB model was fitted to the observations by varying the food correction factor (ψ) to the functional response:

$$f = \frac{\psi \cdot X}{X_k + \psi \cdot X}$$

The weekly averaged values for Chla concentration (Figure 12) are multiplied by the food correction factor (ψ). If ψ is high, the food availability is relatively good at that location. If ψ is low, the food conditions are relatively poor. In this way, ψ is a measure for the relative food conditions (concentration and quality) at a certain location.

The DEB model was fitted to the field observations (shell length and flesh weight) by varying ψ. The goodness of fit is expressed by the COST functions.

$$\text{COST}_L = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{(\text{Mod}_{L,i} - \text{Obs}_{L,i})^2}{(average\ \text{Obs}_L)^2}\right)$$
$$\text{COST}_W = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{(\text{Mod}_{W,i} - \text{Obs}_{W,i})^2}{(average\ \text{Obs}_W)^2}\right)$$

Where n is the number of observations, $\text{Obs}_{L,i}$ and $\text{Obs}_{W,i}$ are the shell length and flesh weight, respectively for the ith observation and $\text{Mod}_{W,i}$ and $\text{Mod}_{L,i}$ are the modelled shell length and flesh weight, respectively. The total COST is the weighted average of COST_L and COST_W. The lower the COST values the better the model fit to the data. For each year, the food correction factor was determined by minimising the total COST, where ψ was allowed to vary between 0.1 and 2.

In Figure 13, the COST factors for Roggenplaat Z in 2015 are plotted as a function of the food correction factor. As can be seen from this figure, the minimum values for COST_L and COST_W are at different values of ψ. The best fit for the length data is as a slightly higher value for ψ (0.98) than the best fit for the weight data (ψ = 0.71). As a consequence the minimum value of the total COST is somewhere in between (ψ = 0.89). The total COST at a food correction factor (ψ) of 0.89 is 0.150.

Figure 13:   Goodness of fit (COST) as a function of the food correction factor (ψ) for the location Roggenplaat Z in 2015. The best fit is where the COST is minimum. In this case, the minimum COST is 0.150 at a food correction factor of 0.89.

In Figure 14, the modelled shell length (cm) and flesh weight (g) for the location Roggenplaat Z in 2015 is plotted together with the field observations. The model was run with the optimum food correction factor for this location (0.89, see Figure 13). As can be seen from this figure the shell length is slightly underestimated by the model, while the weight is slightly overestimated. This is also

reflected in in the differences in optimum food correction factors (ψ) depending on weather the calibration is performed on length or weight data (Figure 13).

As can be seen from this figure, the patterns in length and flesh weight are well represented by the model. The increase in shell length at the start (May, June) is underestimated by the model. Also the shell length at the end of the year (25 November) is underestimated. At the end of the year, the flesh weight is a bit overestimated. The decrease in flesh weight at the end of the year (October, November), however, is well described by the model.

The model was fitted to the data at all stations for all years. The models with the best fit (optimal values for ψ) are presented in Figure 20 to Figure 30, in appendix 3. Location Hammen 9 was not modelled in 2015, because the mussels were replaced by new mussels in the summer. In Table 2, the optimal food correction factor (ψ) for each location in each year is presented. As shown before, this food correction factor can be seen as a measure for food conditions. The COST value is also given in this table. The lower this value, the better the model fit.
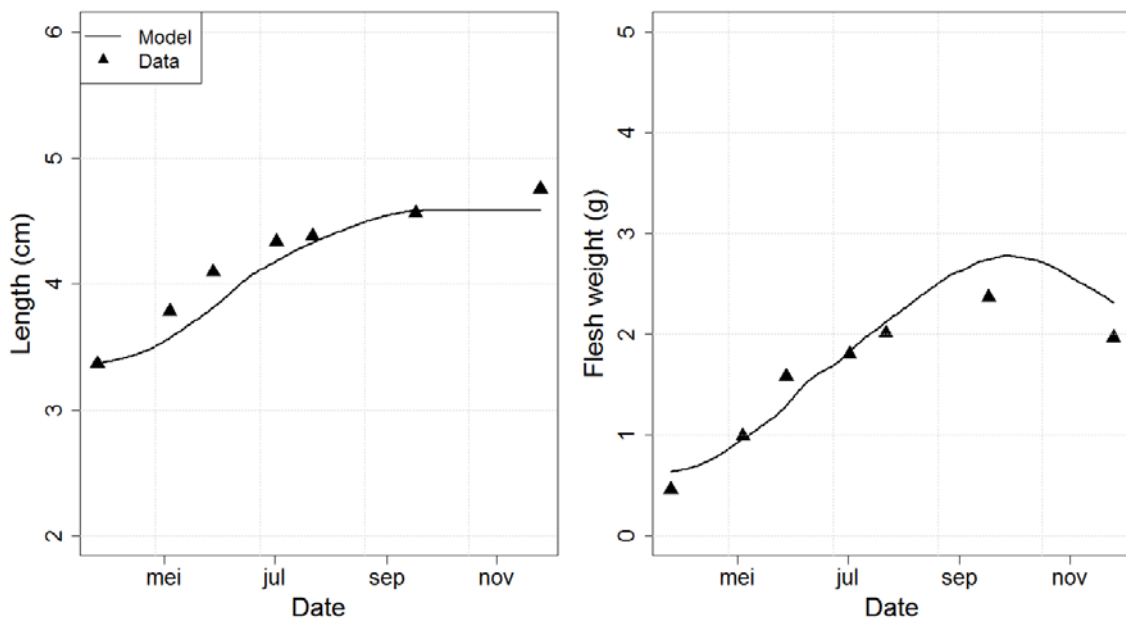
Figure 14:   Optimal model results (shell length and flesh weight) for the location Roggenplaat Z in 2015. The model was run with ψ = 0.94. The markers indicate the measured data.

Locations with good growth are Neeltje Jans N in 2015, and Dortsman, Hammen 9 and Krabbenkreek in 2016. Poor growth is observed at locations Zandkreek in 2014 and locations Kattendijke and Neeltje Jans Z in 2016. In general the locations monitored in 2014 show all relatively poor growth. This could be caused by the larger mussels that have been used in this year (45.0 mm compared to 33.7 and 32.0 mm in 2015 and 2016, respectively). Larger mussels have lower growth rates.

Table 2:   Food correction factors (ψ) and COST (measure for goodness of fit) for the different locations at the various years.

	2014		2015		2016	
	ψ	COST	ψ	COST	ψ	COST
Dortsman	0.75	0.063	0.99	0.257	1.13	0.340
Engels vaarwater N	0.73	0.313	-	-	-	-
Engels vaarwater Z	-	-	1.04	0.280	0.79	0.246
Hammen 9	-	-	-	-	1.22	0.374
Kattendijke	0.74	0.158	0.96	0.303	0.69	0.139
Krabbenkreek	0.87	0.144	0.86	0.057	1.19	0.216
Neeltje Jans N	-		1.20	0.107	0.90	0.322
Neeltje Jans M	0.95	0.302	-	-	-	-
Neeltje Jans Z	-	-	1.08	0.181	0.70	0.118
Roggenplaat N	0.77	0.204	1.09	0.132	0.84	0.504
Roggenplaat Z	0.84	0.135	0.89	0.150	0.93	0.470
Stelletje	0.75	0.125	0.81	0.310	1.04	0.360
Viane	-	-	1.06	0.136	0.84	0.311
Wissenkerke	-	-	-	-	0.76	0.528
Zandkreek	0.66	0.051	0.52	0.031	-	-

In Figure 15 to Figure 17, the values of the food correction factors for the various locations are plotted on a map. The larger dots represent locations with high values for ψ which is reflected in good growth of the mussels (both in length and weight). As can be seen from these figures, the pattern varies from year to year. Locations where the food conditions were good in 2015 (Roggenplaat N, Neeltje Jans N and Z, Viane and Engels Vaarwater Z) seemed to have reduced food conditions in 2016. On the other hand locations with poor food conditions in 2015 like Stelletje and Krabbenkreek seemed to have better food conditions in 2016.

Figure 15:   Spatial map of food correction factors (ψ) for all stations in 2014. The size of the marker is proportional to the value of ψ.
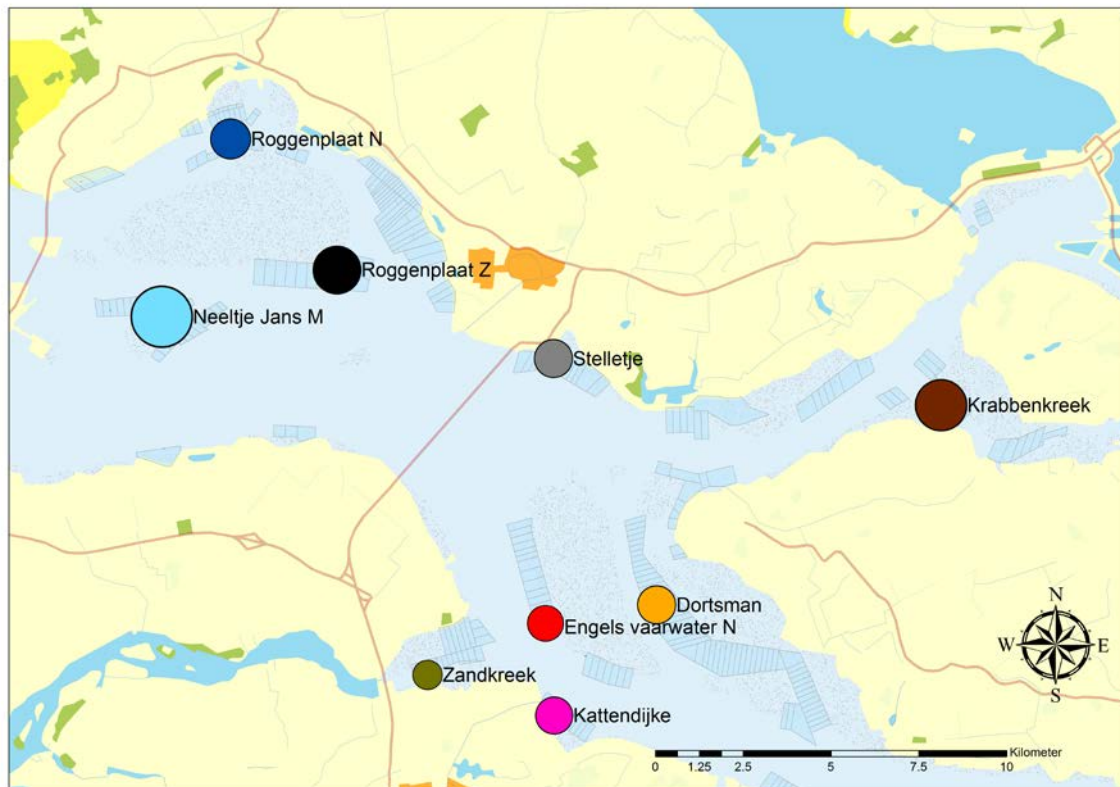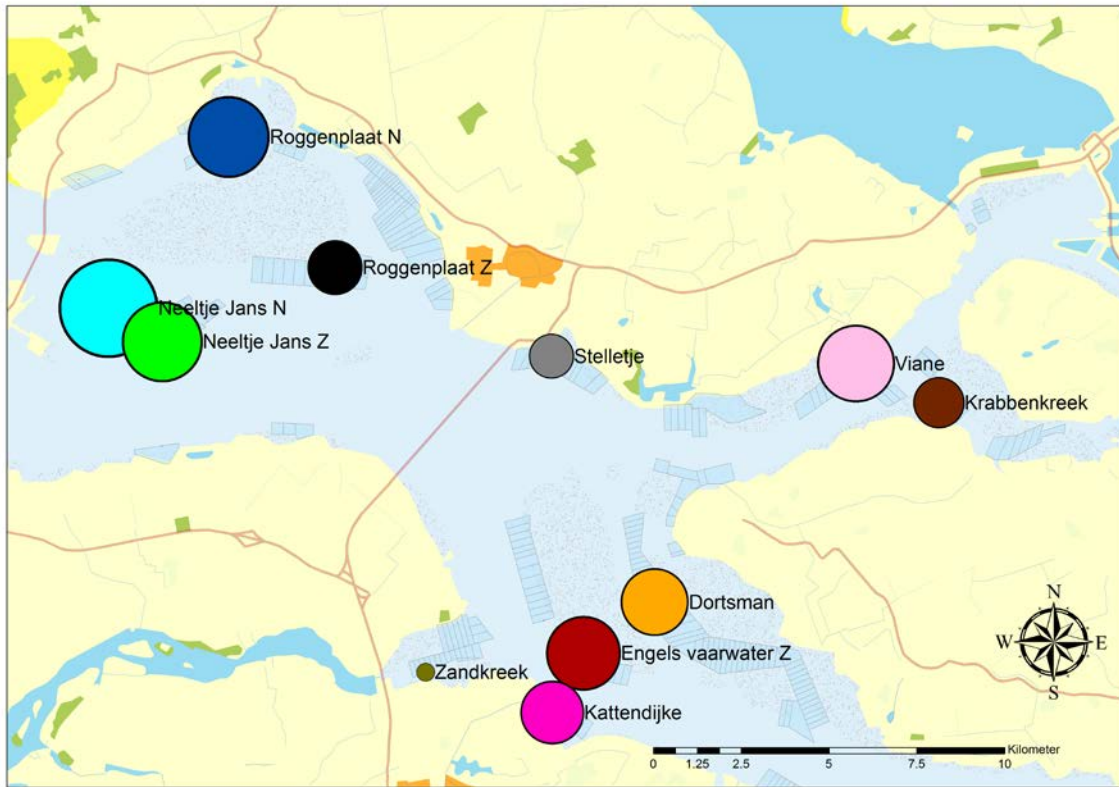
Figure 16:   Spatial map of food correction factors (ψ) for all stations in 2015. The size of the marker is proportional to the value of ψ.
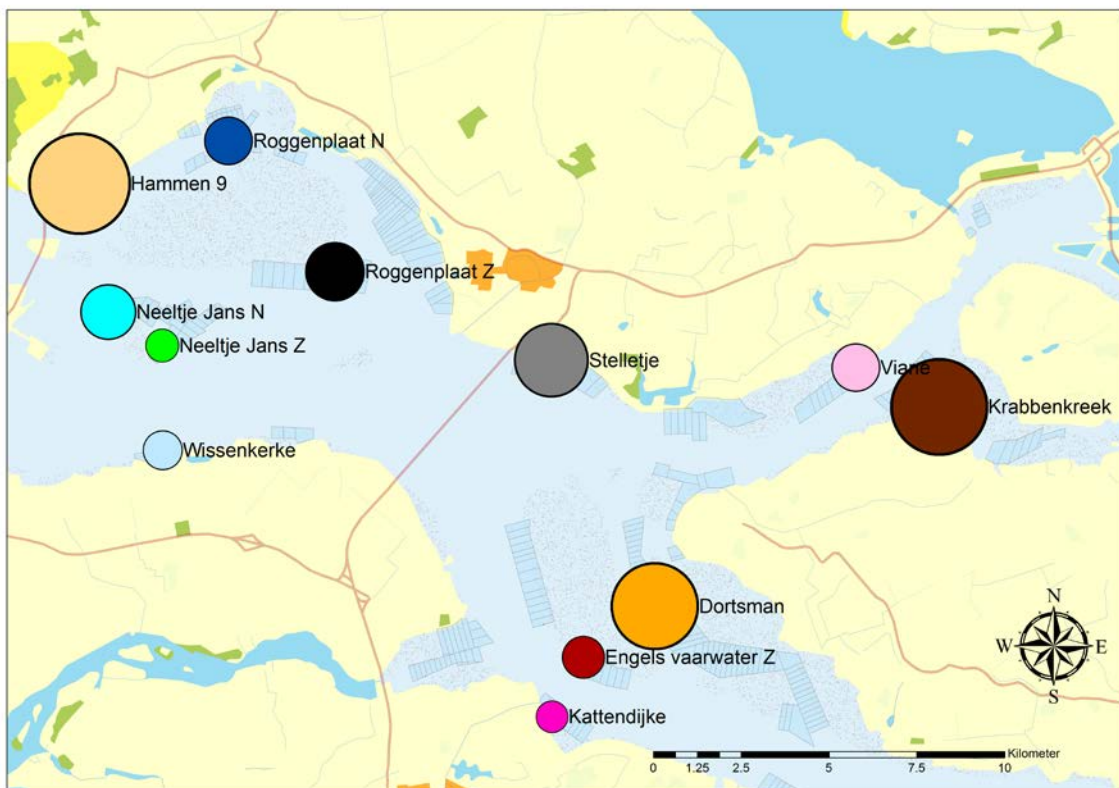

Figure 17:   Spatial map of food correction factors (ψ) for all stations in 2016. The size of the marker is proportional to the value of ψ.

4 Conclusions and Discussion

The DEB model is a useful tool to back-trace the food conditions from the measured growth data of mussels in the Oosterschelde. The model was fitted to the observed shell length and flesh weight by adjusting the food correction factor (ψ). This food correction factor is a relative measure for the average food conditions (over the whole year) at a specific location in a specific year compared to the relative food conditions measured at all locations in all years. Locations with good growth (high value for ψ) are Neeltje Jans N in 2015, and Dortsman, Hammen 9 and Krabbenkreek in 2016. Poor growth (low value for ψ) is observed at locations Zandkreek in 2014 and locations Kattendijke and Neeltje Jans Z in 2016. In general, the results suggest that the growth conditions were less in 2014 compared to 2015 and 2016. In general, it is suggested by mussel farmers that growth conditions are the best in the western part of the Oosterschelde, near the storm-surge barrier. However, in our data we could not see a clear pattern in growth conditions from the western part of the Oostershelde to the eastern and northern part. The growth of the mussels at the two locations in the northern part of the Oosterschelde (Krabbenkreek and Viane) where ralatively good compared to the other locations. Mussel farmers, however, use the culture plots in the northern part mainly for storage of seed and halfgrown mussels. Possibly the mussels in the baskets perform better in this area than on the bottom culture plots. Growth measurements of mussels at the culture plots, as well as auction data could possibly give more insight in these differences.

The results of the growth measurements of the mussels in the baskets can, however, not be translated directly to the quality of the culture plots where they were placed. This is because there are also other parameters next to food availability that determine the quality of a culture plot (e.g. substrate, predators). However, the growth of the mussels in the baskets can be used as an indicator for the relative food availability at a specific locations. Since the origin of the mussels in the baskets at the different locations are the same, the differences in growth can be assumed to be caused by differences in food conditions.

In 2014, there was not a clear difference in growth at the monitored locations. This is probably caused by the fact that in that year larger mussels (45.0 mm) were used than in 2015 and 2016 (33.7 and 32.0 mm, respectively). Smaller mussels grow faster than large mussels, and therefore differences in growth rate are easier to detect in small mussels. Moreover, the flesh weight of the larger mussels is more variable due to gonad development and reproduction. Therefore, it is advised to use small mussels (30 – 35 mm) for the monitoring of growth in the baskets.

The food correction factor (ψ), as applied in this study, does not vary during the year. This means that the seasonality in Chla concentration is identical at each location. From field observations we know that, especially in the Northern part of the Oosterschelde, the seasonality in Chla concentration differs from the rest of the Oosterschelde (Wijsman and Smaal, 2011). In order to correct for these differences in seasonality, separate Chla patterns can be used for the different compartments (west, middle, east and north). Alternatively, also another approach can be used. Lavaud (2014) presents a method to derive the functional response (f), by fitting the growth DEB equation to daily shell growth rate (L_w') and the increase in growth rate (L_w''). This method was based on daily growth measurements (derived by shell-readings). It is not clear if the monthly measurement that are used in this study are sufficient for this method. In the study of Lavaud (2014), the measurement were based on daily recordings

5   Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2008 certified quality management system (certificate number: 187378-2015-AQ-NLD-RvA). This certificate is valid until 15 September 2018. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V.

Furthermore, the chemical laboratory at IJmuiden has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2017 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation. The chemical laboratory at IJmuiden has thus demonstrated its ability to provide valid results according a technically competent manner and to work according to the ISO 17025 standard. The scope (L097) of de accredited analytical methods can be found at the website of the Council for Accreditation (www.rva.nl).

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

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

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

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

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Justification

Report C049/17
Project Number: 4313100011

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

Approved: Dr. Jacob Capelle
Researcher shellfish culture

Signature:

Date: June 20, 2017

Approved: Dr. Tammo Bult
Director Wageningen Marine Research

Signature:

Date: June 20, 2017

Annex 1   Dynamic Energy Budget model

General structure

A Dynamic Energy Budget (DEB) model (Kooijman, 1986; Kooijman, 2000) describes growth, energy dynamics and reproduction as a function of environmental conditions such as temperature and food. The DEB theory is a generic theory that can be applied to different species and life stages by using species specific parameters (Kooijman, 2001). An individual organism is described by three state variables: structural body volume (V, cm^3), reserves (E, Joule) and reproduction buffer (R, Joule) (Figure 18). The reserves are often quantified as energy density ($[E] = \frac{E}{V}$, J cm^{-3}). Filterfeeding bivalves like the blue mussel (*Mytilus edulis*) filter food from the water column with their gills. A fraction of the filtered food is assimilated, the rest is released as faeces and pseudo-feaces. The assimilated energy is incorporated into a reserve pool (E) from which it is used for maintenance, growth, development and reproduction. A fixed fraction (κ) of the mobilization energy flux from reserves is utilized for growth and somatic maintenance, but maintenance is given first priority under energy limitation. The remaining energy flux from the reserve pool ($1 - \kappa$) is spent on maturation and reproduction in juveniles and adults, respectively, including maintenance of these components.
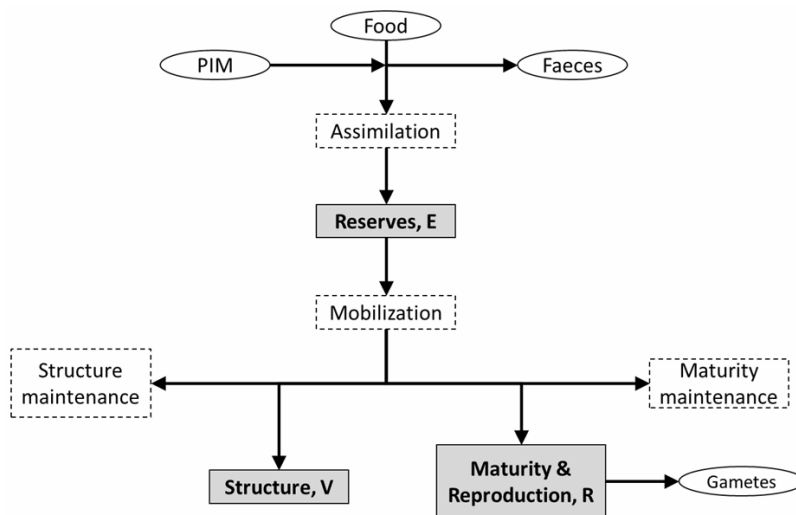

Figure 18:   Schematic presentation of the DEB model

Temperature

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

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

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

Shape coefficient

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

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

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

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

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

$$L = \delta_M \cdot L_w$$

Functional response

The relation between food uptake and food density is described by a scaled hyperbolic functional response f (Figure 19). At increased concentration of inorganic particles, a part of the filtered material is excreted as pseudo-faeces (Wijsman e.a., 2012). The functional response is defined by:

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

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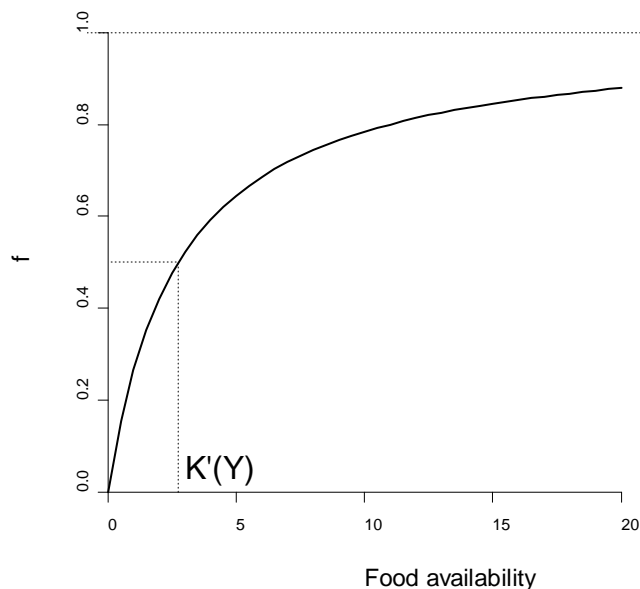

Figure 19: *Functional response relation. At finite food availability, the relative food uptake is maximum (f=1). When the food ability is K'(Y), the food uptake rate is half the maximum uptake rate (f=0.5).*

Assimilation

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

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

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

$$\dot{p}_A = \{\dot{p}_{Am}\} \cdot f \cdot V^{\frac{2}{3}} \cdot \dot{k}(T)$$

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

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

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

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

Growth and somatic maintenance

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

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

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

The energy flow required for maintenance is
$$\dot{p}_M = [\dot{p}_M] \cdot V$$

The dynamics of the structural volume can be derived according to the κ-rule by:
$$\frac{dV}{dt} = GR = \frac{\kappa \cdot \dot{p}_C - [\dot{p}_M] \cdot V}{[E_G]}$$

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

Maturity and reproduction

DEB describes the maturation and reproduction though different development stages of the organism. During the juvenile stage, energy is used to develop reproductive organs which increases the level of maturation of the organism. When the organism reaches a certain maturity level, the reproductive

organs are fully developed and the organism reaches the adult stage. From that moment on, it allocates the reproductive flux to gamete (eggs and sperm) production. Maturity also requires maintenance which is proportional to the maturity level. A fixed proportion (1- κ) of the utilized energy ($\dot{p}_C$) goes to maturity maintenance, development (juveniles) and reproduction (adults). The energy allocation to reproduction equals:

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

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

Spawning

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

Acceleration

The model allows for metabolic acceleration. It is assumed that species change their shape during early juvenile period, leading up to a metamorphosis after which they reach adult shape. This change in shape alters the surface to volume ratio. During the acceleration phase , the parameter $\{\dot{p}_{Am}\}$ and $\dot{v}$ increase with the length (Zimmer e.a., 2014).

Annex 2   DEB parameters

Primary DEB parameters

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

A DEB model consists of primary and compound parameters. The primary parameters are most intimately connected to a single underlying process, while compound parameters typically depend on several underlying processes. The compound parameters can be derived from the primary parameters using the formulations of the DEB theory. The primary DEB parameters can be split into the core parameters and auxiliary parameters (Lika e.a., 2011). Core DEB parameters directly control the state variables (except the defecation efficiency) and are linked to the concepts of the standard DEB model. The core DEB parameters are described in Table 3. Auxiliary parameters primarily converts various measurements and quantify the effect of temperature on the rates. The auxiliary parameters are listed in Table 4.

Core DEB parameters

Table 3:   Core DEB parameters

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Auxiliary parameters

Table 4: Auxiliary DEB parameters, temperature and scaling parameters

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

Shape coefficient

The shape coefficient (δ_M,-) converts the physical length (L_w) to the volumetric structural length (L).

$$L = \delta_M \cdot L_w$$

Structural volume (V) can be calculated from the structural length (L) using the shape factor by:

$$V = L^3$$

Consequently the structural volume can be calculated from the physical length (L_w) by

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

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

Specific densities

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

Chemical potentials

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

Chemical indices

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

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

Molecular weights

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

Reference temperature

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

Arrhenius temperature

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

Temperature tolerance range

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

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

DEB parameters used in this study

Table 5:   DEB parameters used in this study

Parameter	Value	Unit	Description
δ_M	0.231	-	Shape coefficient
$\{j_{Xm}\}$	249.5	J cm^{-2} d^{-1}	Maximum surface-specific ingestion rate
$[\dot{p}_M]$	24.0	J cm^{-3} d^{-1}	Volume-specific somatic maintenance
$[E_m]$	2190	J cml^{-3}	Maximum storage density
$[E_G]$	1900	J cm^{-3}	Specific cost for structure
κ	0.45	-	Allocation fraction to soma
κ_R	0.45	-	Reproduction efficiency
L_b	0.02	cm	Length at birth
L_p	1.2	cm	Length at puberty
μ_E	17500	J g^{-1}	Energy content of reserves
X_k	8.0	µg Chla l^{-1}	Half saturation constant Functional response
T_{ref}	293	K	Reference temperature
T_A	5800	K	Arrhenius temperature
T_L	275	K	Lower boundary temperature tolerance range
T_H	296	K	Upper boundary temperature tolerance range
T_{AL}	45430	K	Parameter that controls the rate around lower border of temperature tolerance
T_{AH}	31376	K	Parameter that controls the rate around upper border of temperature tolerance

Annex 3 Model results

In this Annex the results of the model with the best fit are presented for the different locations and in the three years.
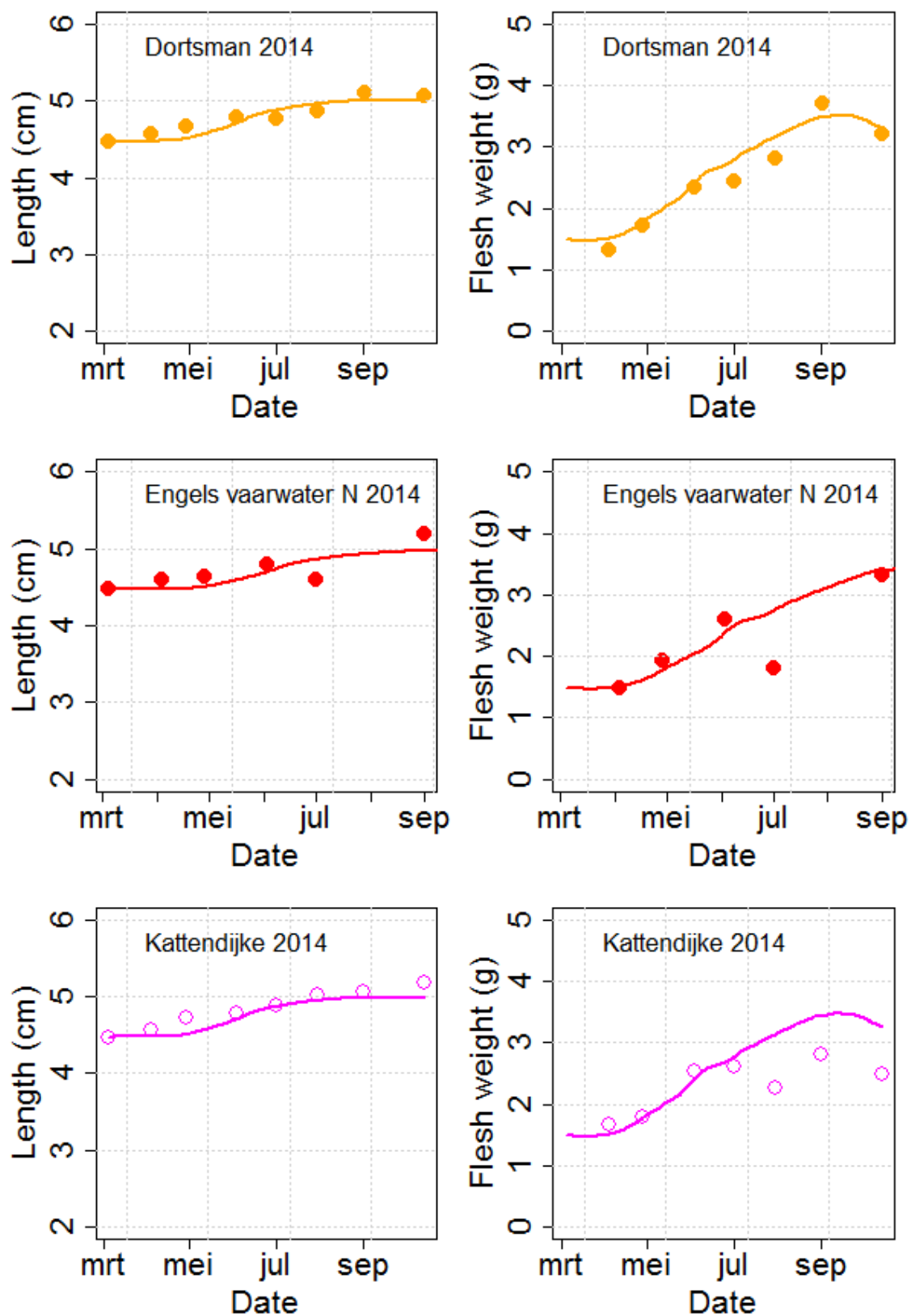
Figure 20: *Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Dortsman, Engels Vaarwater N and Kattendijke in 2014.*
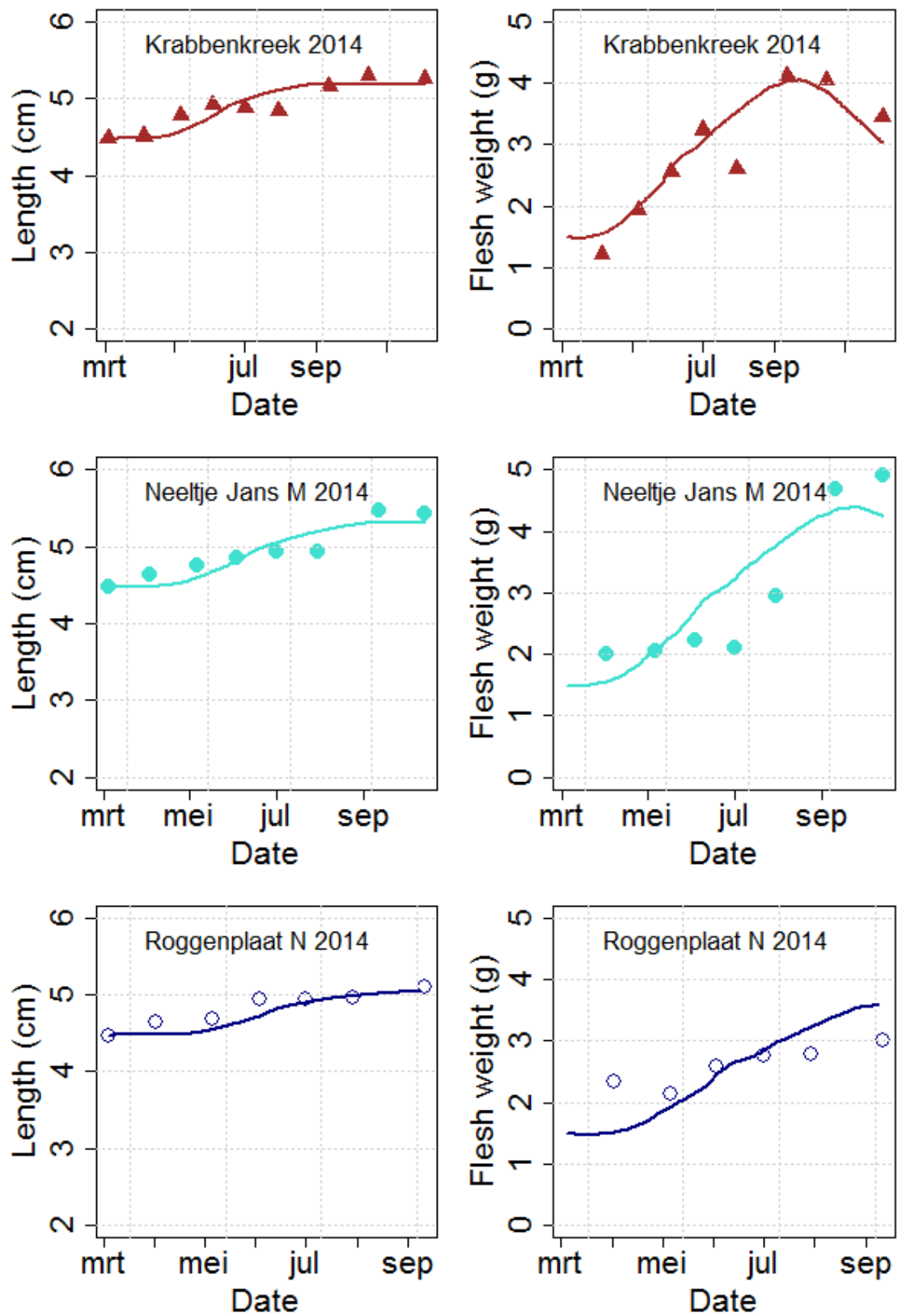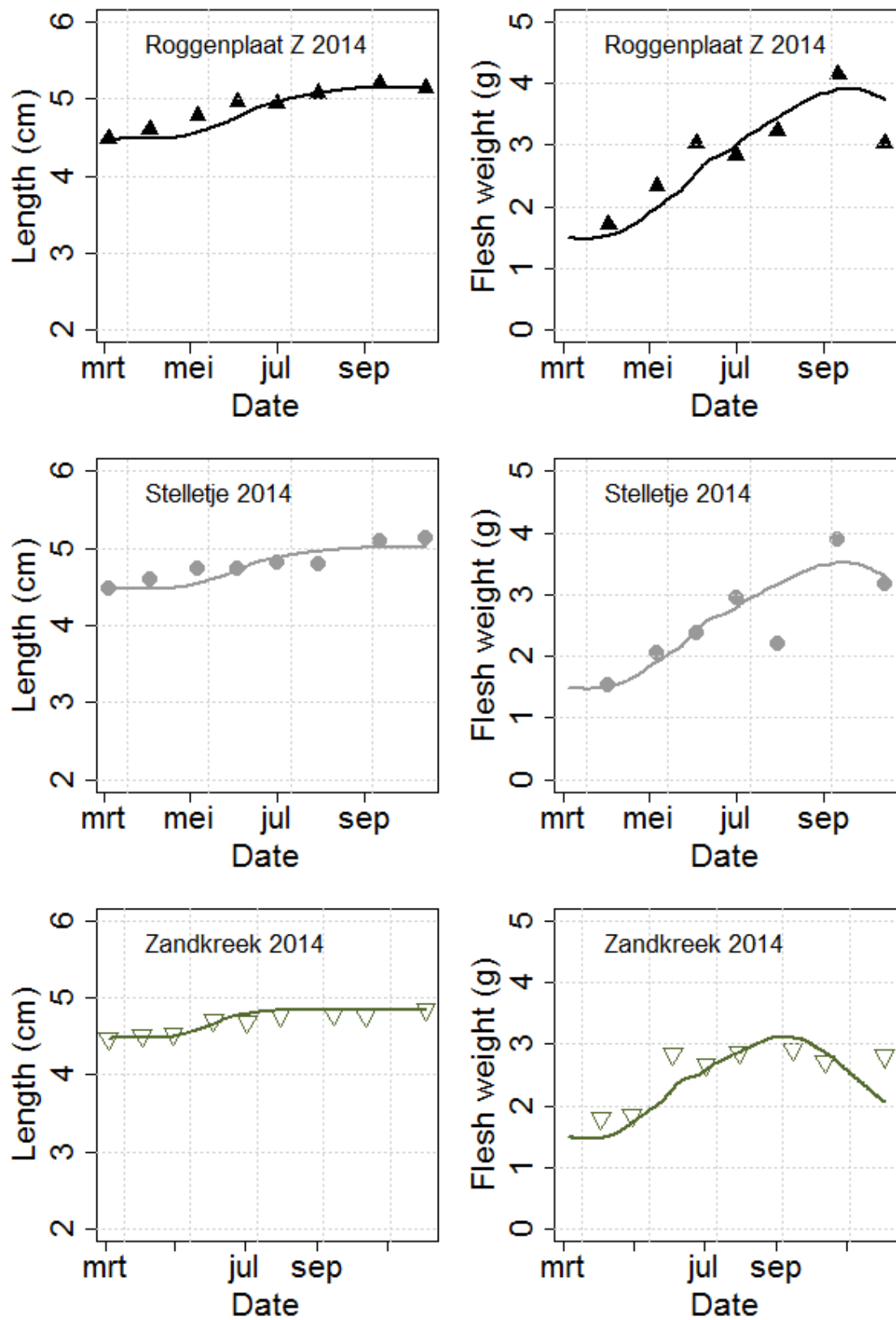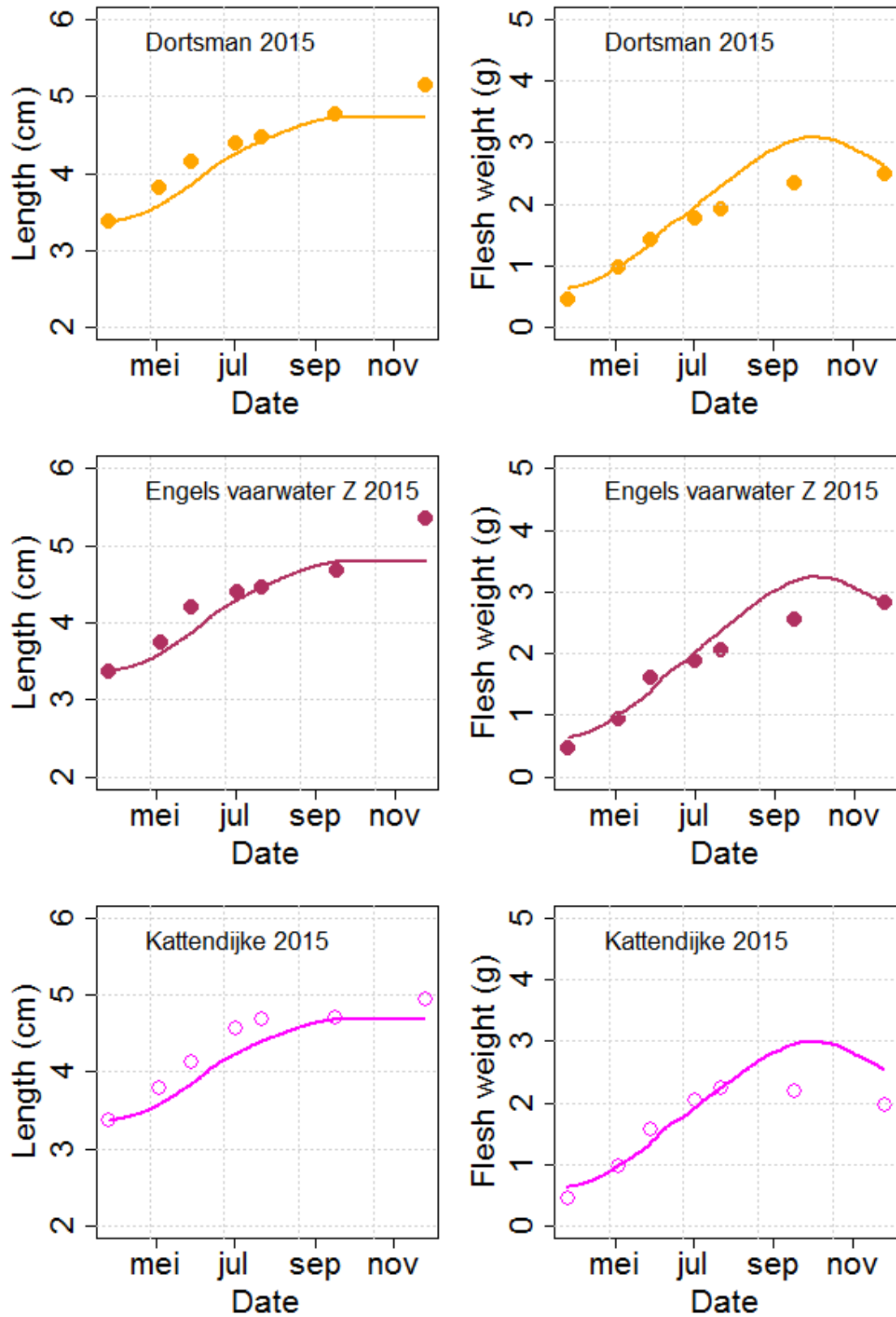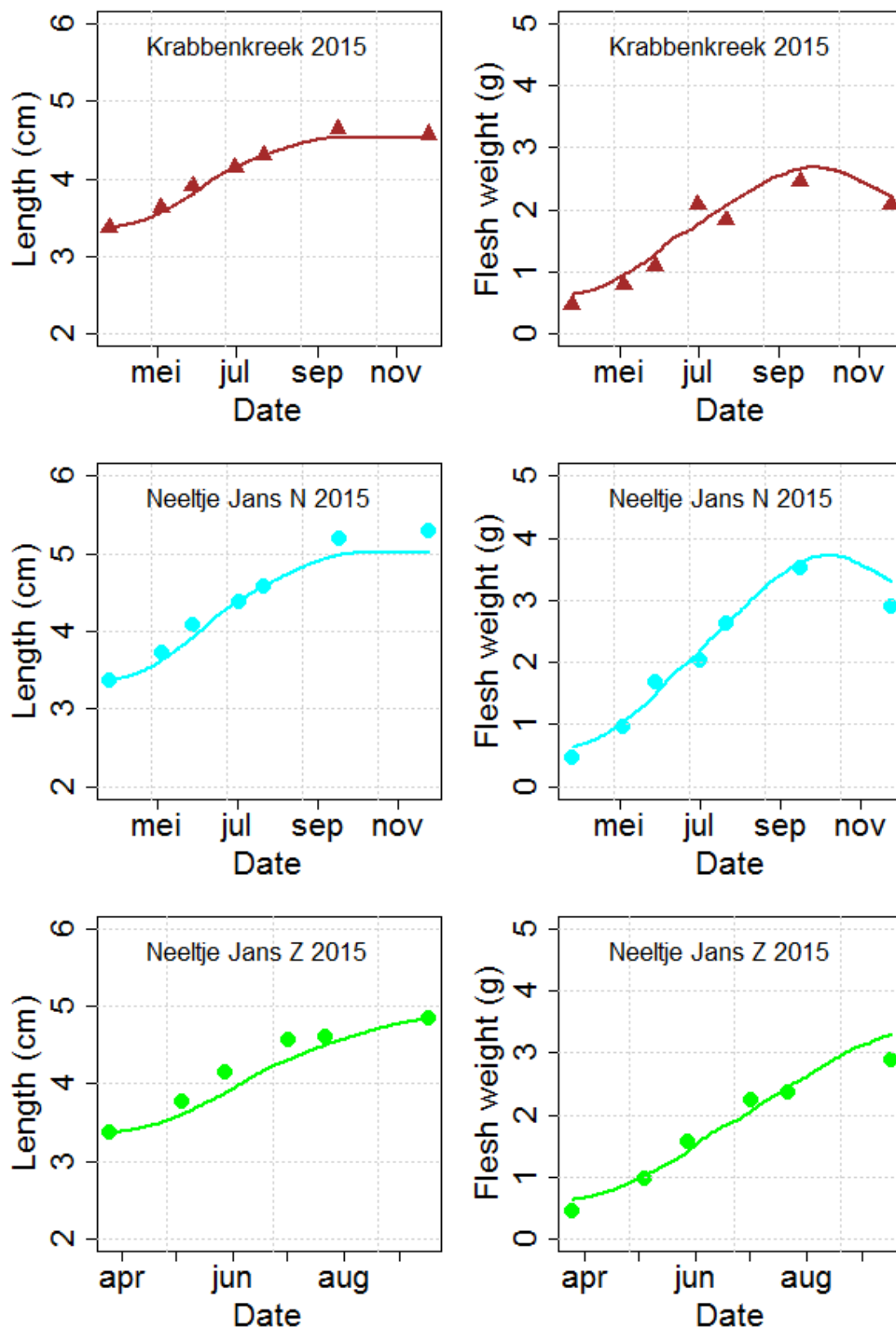
Figure 21:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Krabbenkreek, Neeltje Jans M and Roggenplaat N in 2014.
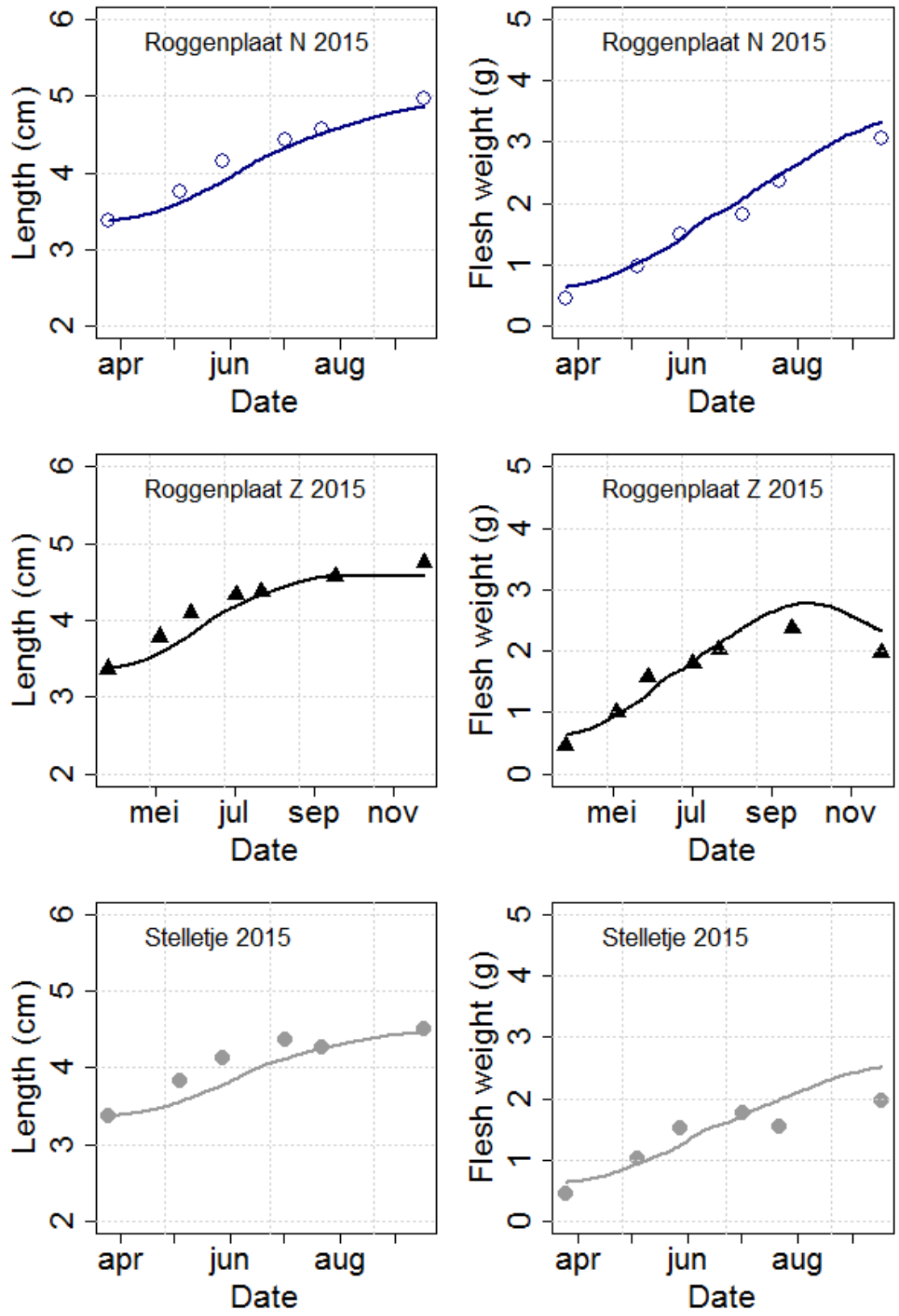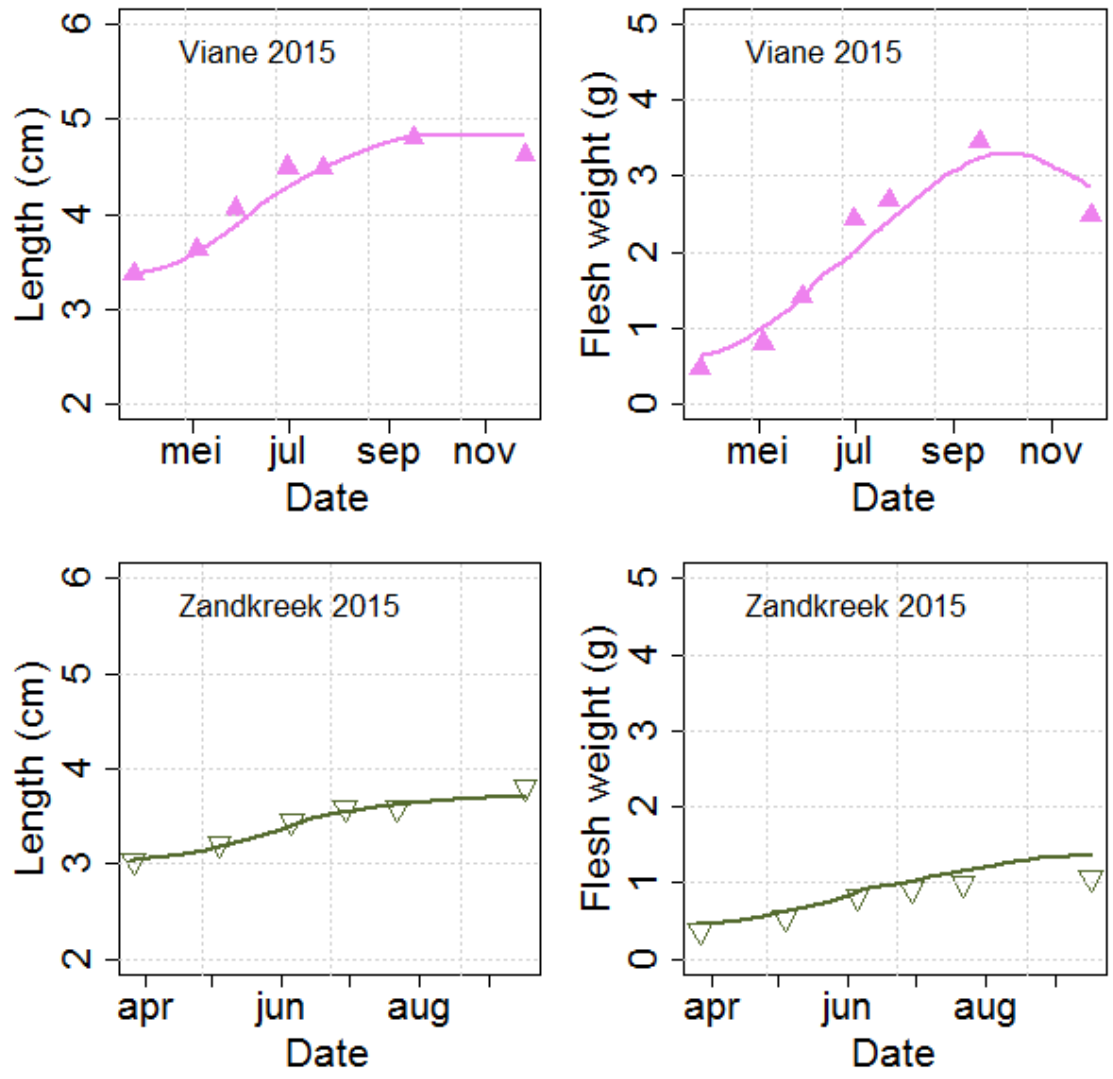
Figure 22: Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Roggenplaat Z, Stelletje and Zandkreek in 2014.
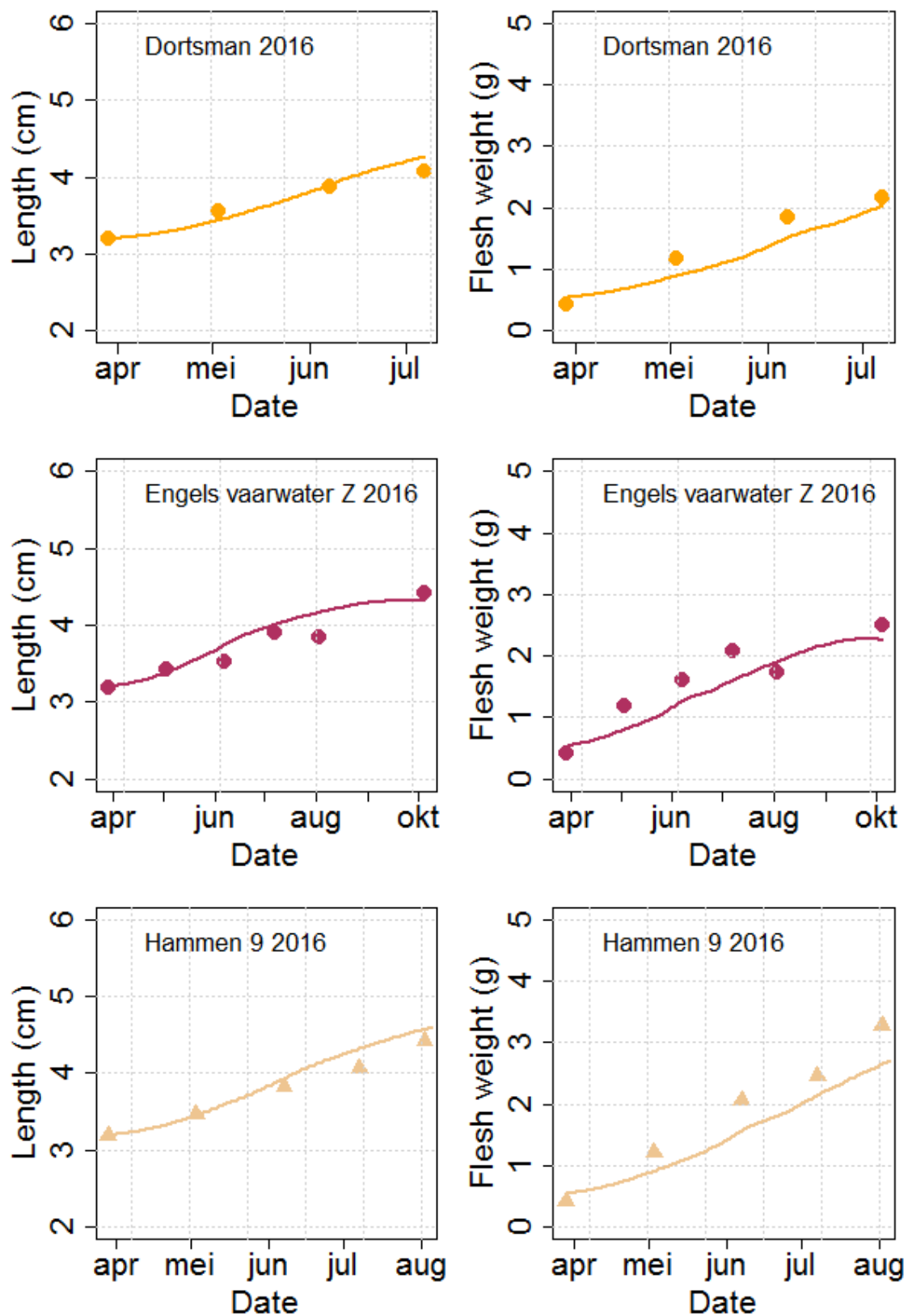
Figure 23:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Dortsman, Engels Vaarwater Z and Kattendijke in 2015.
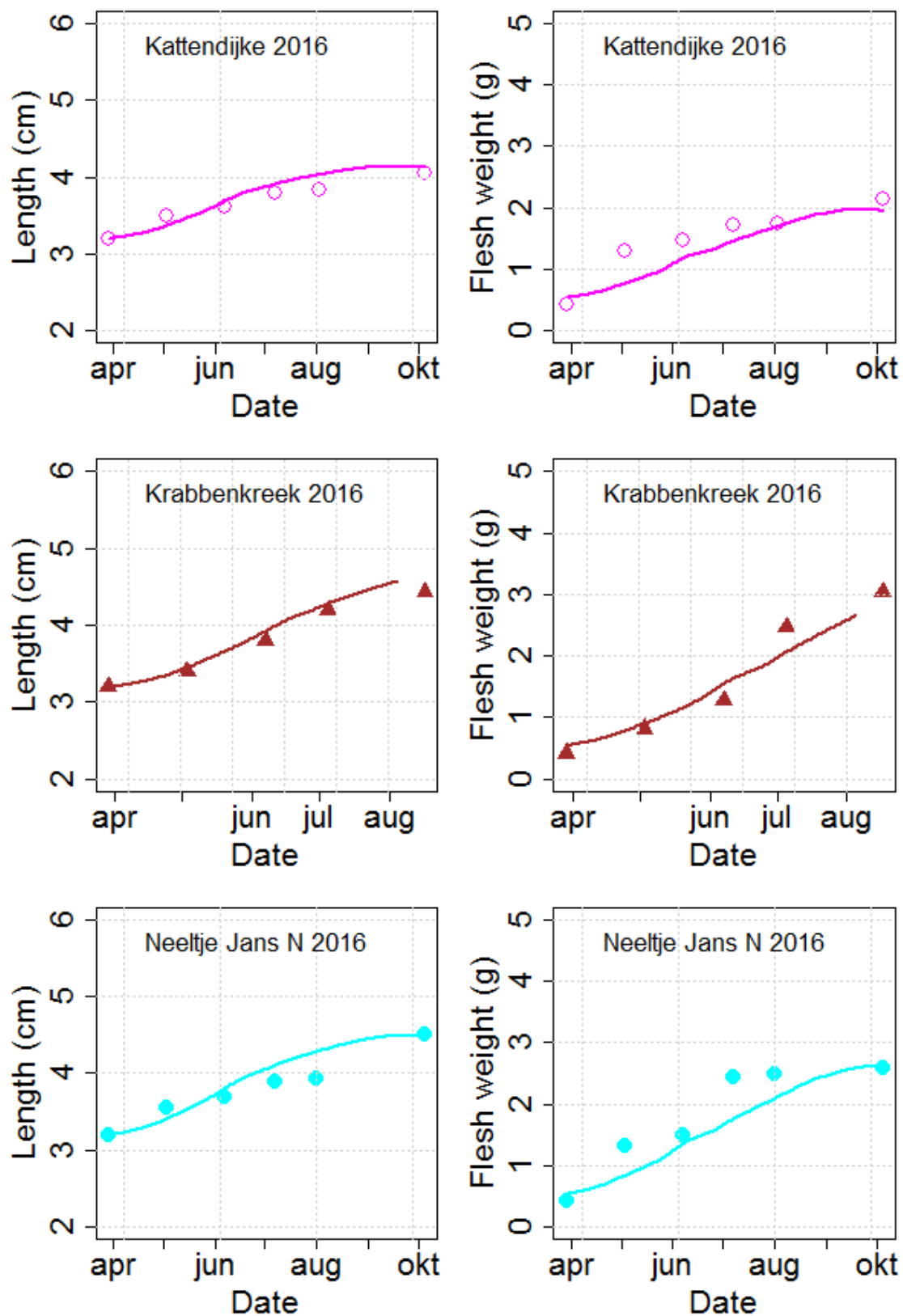
Figure 24:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Krabbenkreek, Neeltje Jans N and Neeltje Jans Z in 2015.

Figure 25: *Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Roggenplaat N, Roggenplaat Z and Stelletje in 2015.*

Figure 26:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Viane and Zandkreek in 2015.

Figure 27:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Dortsman, Engels Vaarwater Z and Hammen 9 in 2016.

Figure 28:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Kattendijke, Krabbenkreek and Neeltje Jans N in 2016.
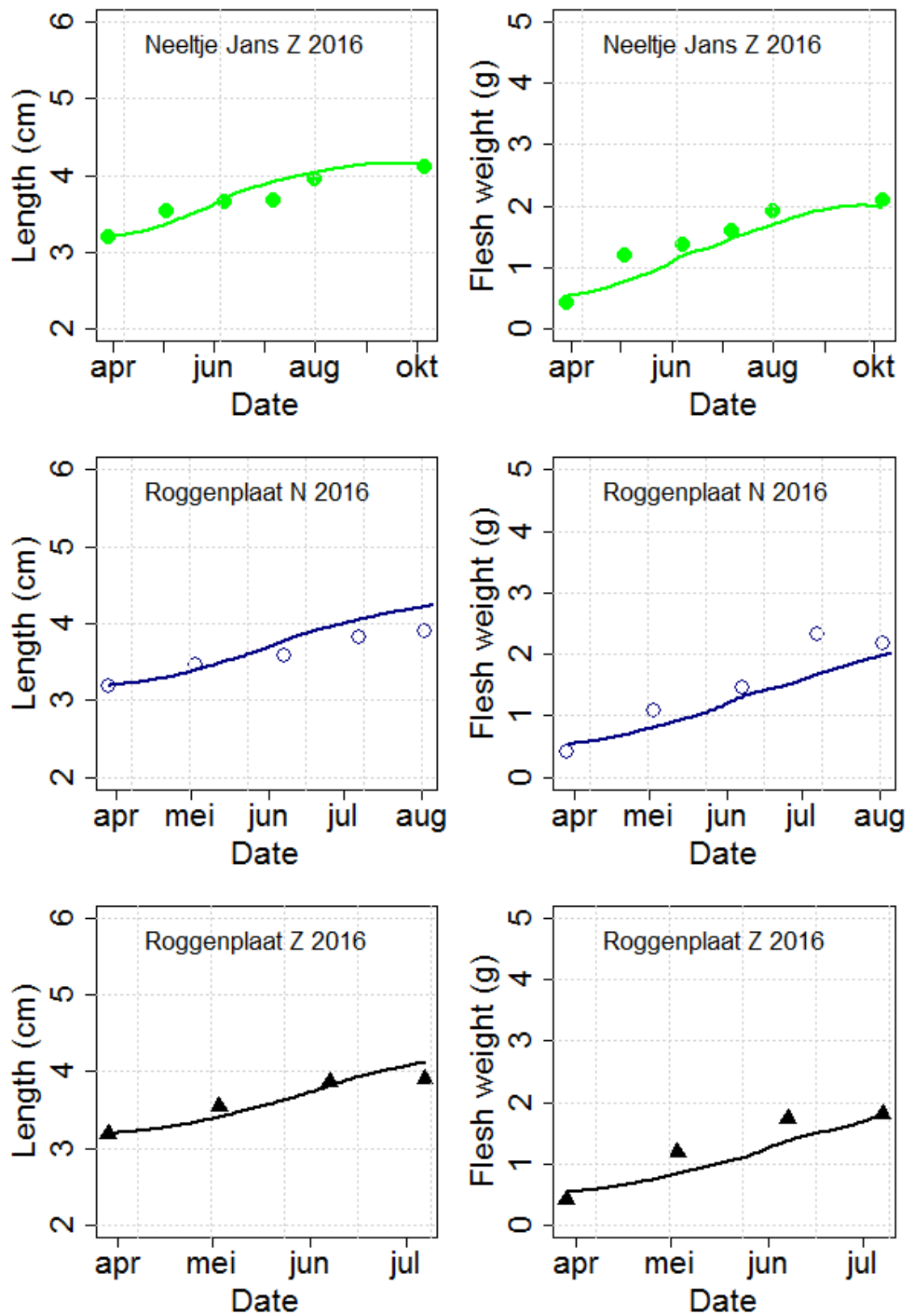
Figure 29:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Neeltje Jans Z, Roggenplaat N and Roggenplaat Z in 2016.
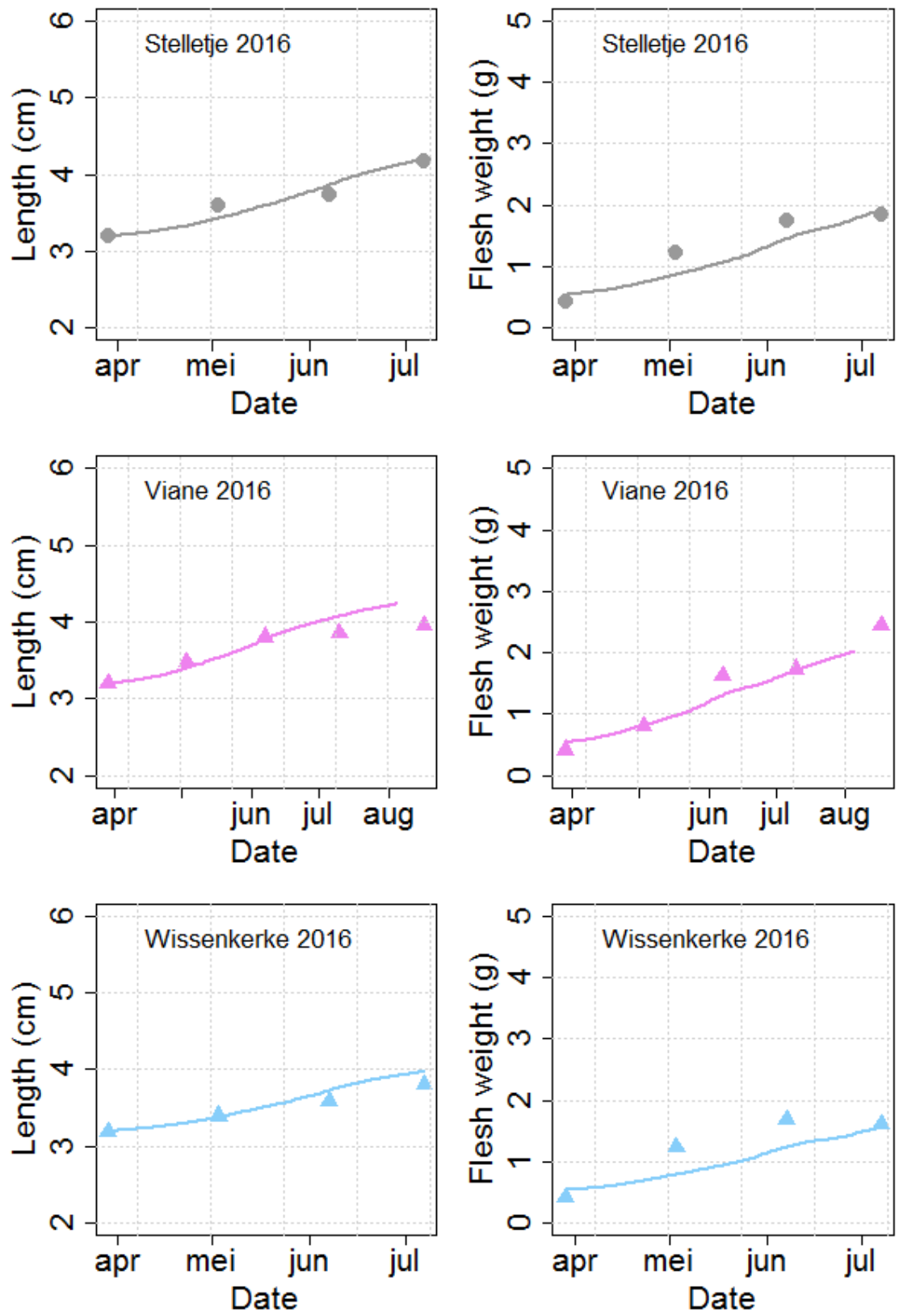
Figure 30:   Model results (lines) and observed values for shell length (left panel) and flesh weight (right panel) at locations Stelletje, Viane and Wissenkerke in 2016.

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