DEB_{Ensis} vs. data

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Summary

Along the Dutch coast (North sea) large quantities of sand are mined in certain locations to supply sand for coastal defence at other locations in order to retain the existing coastline. Without these nourishments of sand the coast would erode and eventually this erosion would lead to an increased risk of flooding. This project provides the unique opportunity to use measured environmental data to predict growth of *Ensis directus* using the DEB_{Ensis} model and compare it to measured biotic data on *Ensis*. Here we report on the findings of the comparison of field data and model estimates and suggest improvements, both in field measurements, experiments and (adjustments to DEB) modelling.
We state that the fit of the DEB_{Ensis} model is adequate and use of DEB_{Ensis} for predictive purposes on the effect of environmental changes in silt, temperature and chlorophyll are justified with this study, even though growth may be overestimated and effects of sand mining on growth and condition underestimated. Considering the overestimation of growth, to improve the fit efforts should go in determining the quantitative effects of winter- and daily feeding activity and intraspecific competition on growth.

1. Introduction

Along the Dutch coast (North Sea) large quantities of sand are mined in certain locations to supply sand for coastal defence at other locations in order to retain the existing coastline. Without these nourishments of sand the coast would erode and eventually this erosion would lead to an increased risk of flooding.

During sand mining silt is released in the water column. This silt increases light-attenuation in the water column, leading to reduced primary production in areas where light becomes limiting (see for instance figure 1). Since heterotrophic organisms rely on primary production, a reduction therein can affect growth and reproduction in for instance shellfish. To quantity these effects monitoring, experiments and the-development of a shell fish DEB growth model was initiated. For this study, *Ensis directus* was taken as a model organism, because of its high dominance in biomass in the Dutch coastal zone (>75% of total benthic biomass in 2010, Goudswaard et al., 2010). The dynamic energy budget model for *Ensis* (DEB_{Ensis} in short) made by Cardoso et al. (2011) was adjusted on basis of data collected by, Kamermans et al. (2011), Wijsman et al (2011) and Kamermans and Dedert (2012). Incorporation of these new results made it possible to account for the effect of silt on the uptake of algae. The improved model was used to predict growth of *Ensis* on several locations in the North sea on the basis of modelled environmental data and these calculations were used to assess the effect of sand mining on the growth of *Ensis* (Schellekens 2012). In the meanwhile, Witbaard et al. (2012) followed the growth of *Ensis directus* in relation to measured environmental data over a two year period off the coast of Egmond aan zee (NL).

Therefore, this project provides the unique opportunity to use measured environmental data (instead of calculated) to predict growth of *Ensis* using the DEB_{Ensis} model and compare it to measured growth data on *Ensis* from the same site. The client (Stichting La Mer) wants to validate the quantification of effects done by Schellekens (2012) with this project and at the same time identify the most effective steps forward to be taken in the study of effects of sand-mining on shellfish. Here, we report on the findings of the comparison of field data and model estimates and suggest improvements, both in field measurements, experiments and (adjustments to DEB) modelling.

2. Assignment

The objective of this project is to qualify and validate the DEB_{Ensis} model in comparison with independently collected field data of *Ensis* collected off the coast of Egmond aan zee (NL). How precise can the model predict growth of *Ensis* in size, weight, gonads and development of condition over time on basis of field data of temperature, chlorophyll and silt concentration (feb-2011 until aug-2012). What model parameters need to be and can be adjusted or researched to increase the model-fit?

3. Materials and Methods

Lander Deployments

At about one kilometre off the coast of Egmond a lander platform was placed at a depth of 11 meter (table 1). Equipment mounted on the lander monitored the main hydrographical parameters. Around the lander four sampling stations were located where additional sampling of bottom parameters and *Ensis directus* took place. These stations were given abbreviated names to describe their location in relation to the central lander station.

Table 1: Positions of and around the central lander position at where boxcore samples are taken to follow the seasonal development of sediment grain size and to follow the wax and wane of the local *Ensis* population.

station	gr min dec min N	gr min dec min E	gr dec gr N	gr dec gr E
LNE (Lander North East)	52° 38.28'	4° 36.356'	52.6380°	4.605933°
LSE (Lander South East)	52° 38.216'	4° 36.380'	52.6369°	4.606333°
LSW (Lander South West)	52° 38.22'	4° 36.22'	52.6370°	4.603667°
LNW (Lander North West)	52° 38.281'	4° 36.22'	52.6380°	4.603667°
Lander	52° 38.249'	4° 36.294'	52.63748°	4.6049°

Environmental Data

The lander platform consists of a triangular aluminium frame (Height Width: 2 x 2 m) with a series ballast weights (total 500 kg) fixed onto the lower support that stands on the seafloor. In this way the centre of gravity is lowered as much as possible preventing the platform from falling over during storms. On top of the platform is a pop-up system with a 50 m rope connected to 40 kg floatation. The pop-up is triggered from the surface by 2 acoustic releasers (http://www.ixsea.com/). Later in the project the setup was slightly changed so that in case of excessive fouling the lander could be retrieved by means of the line and buoy which floated on the surface. This speeded up lander exchange times considerably.

The lander platform was equipped with a series of sensors measuring the following physical parameters: current, temperature, salinity, turbidity and fluorescence. Current speed and direction (3D) were measured every 10 min at 140 cm above the bottom with a NORTEK Aquadopp Doppler current meter. This instrument also yielded a record of the acoustic backscatter. Temperature and Salinity were measured every 10 min with a pumped version of the Seabird SM37 CTD system (http://www.seabird.com/). The CTD sensors are protected from effects of fouling by the presence of a TBT impregnated plastic ring inside the dead volume of the pump.
In addition to the NORTEK aquadopp current meter a NORTEK Vektor current meter (http://www.nortek-as.com/) was mounted at the lander at a height of 30 cm from the sediment surface. Every 10 minutes this instrument made high frequency burst measurements during 2 minutes with a frequency of 1 MHz. Sensor "glasses" from both the Vektor and aquadopp current meters were protected against fouling by applying a light veneer of udder ointment.
Turbidity and fluorescence were measured optically at four heights above the bottom, i.e. 30, 80, 140 and 200 cm, using ALEC Compact-CLW's (http://ocean.jfe-advantech.co.jp) with wipers to keep fouling under control. The measurement at the lowest height (30cm) was done with the infinity version of the instrument as it can deal with a higher turbidity. The wiped versions appeared all to be crucial for obtaining optical records in coastal environments with heavy fouling. All Alec sensors have been calibrated in the lab over a range of local SPM and chlorophyll concentrations. In this report we refer to the material being measured as turbidity as SPM or silt. The fluorescent part of it, that is simultaneously measured is referred to as Chlorophyll. Turbidity and Chlorophyll were being measured every 10 minutes in burst mode, containing 10 samples which have been averaged and were being regarded as the 10 minute average.

The platform was launched on 22/Feb/2011 with the RV Terschelling (RWS). The position of the platform was marked by two cardinal buoys protecting it from trawling activity. In Appendix A table 1A an overview of the deployment and retrieval dates is given.

In spring and autumn the platform is retrieved for maintenance and data collection every 5th or 6th week. During the summer the platform was retrieved every third week to prevent problems and minimize the effects of fouling by barnacles and other epifaunal organisms. For most of these 1 day maintenance cruises the RWS ship Terschelling has been used. This with the exception of two occasions, when RV Pelagia was used for these operations (24th June & 27th September 2011) (See table 1A Appendix A). During such a service date sea bed sampling around the lander took place. In addition to these occasions in 2011 and 2012, there were additional sampling campaigns within other projects (BWN, RWS and MEDUSA) in 2010 and in 2009. Data on densities and size of *Ensis* during these occasions have been incorporated in the model validation.

Biometric Data

During each service operation two boxcore samples at each of the four corner locations around the (central) lander platform position were taken (see table 1; LSE,LSW,LNE,LNW). A subcore for sediment grain size analyses was preserved. These samples have been split into two layers of 5 cm height and kept frozen until freeze dried. The remainder of the boxcore was sieved over a 1 mm screen and the live *Ensis* were collected and stored for size measurements and ash-free dry weight (AFDW) determination. In this way, a time series of the growth and population development of the local *Ensis* stock is obtained on basis of population averages.
In addition to these samples, additional boxcores were taken to collect 50 *Ensis* individuals for determination of the seasonal change in gonado-somatic index and change in glycogen and energy reserve content. On board, all samples were refrigerated.

Lab procedures

Population development and average growth.

Directly after being caught, all living animals were measured routinely with digital callipers. Three measurements were made, length, width and thickness. After these measurements all animals were stored at 4-6°C on board of the ship. Ash-free dry weight (AFDW) was determined in the lab two days after landing of the ship to enable calculation of the condition index. For this, the soft tissue was removed, dried at 60°C until constant weight and then incinerated at 540°C during 4 hours. The weight difference of dry weight and ash weight is the ash-free dry weight. This type of analyses has been done for samples taken by all different projects in the period 2009-2012.

Condition Index.

The ash free dry weight (AFDW) divided by the volume of an individual (calculated as length*width*girth = length*(length/77)*(length/141.1), with length expressed in cm, measured in mm) determined the condition index (CI) of an individual. The factors 77 and 141.1 have been determined on basis of all measured shells >5000) and represent the relationship between length, width and thickness/girth (see Appendix B for regressions and model fits). This overall relationship was used because collected shells were sometimes damaged.

Weights-Gonado somatic index.

In the lab, a selection of 50 individuals of different size classes from the entire size range was made after landing of the ship. Of these animals the shell size (length, width and thickness) was measured as well as their wet weights. These animals were stored at -80°C until the end-phase of the project when all animals were further analysed at the same time. In the end-phase of the project, gonads were separated from the somatic tissue and after drying both fractions were incinerated to obtain the ash-free dry

weights of these tissues. These weights were used to calculate the contribution of the gonadal mass in the total weight of the animals. Based on these determinations and the collection of data over the seasons, the change in gonadal mass over the season could be determined. This dataset is collected only for 2011 and 2012.

Model

The DEB_{Ensis} model was previously developed by Cardoso et al. (2011), Kamermans et al. (2011) and Wijsman et al (2011) on the basis of univariate data on growth, respiration and size at maturation and birth. Later the model (in effect it's functional response) was adjusted by Schellekens (2012) to account for the effect of silt on the uptake of chlorophyll and growth experimentally measured by Kamermans and Dedert (2012). For further details of the model set-up we refer to the above references. For parameter settings used as default in this study see Appendix A table 2A.

Model classification

Lika et al. (2011) developed a way to assess the completeness of real data in a ranking. In their definition the completeness of available data can be ranked with marks from low to high at the following levels; each level including previous levels (table 2). In red we have indicated the data we did not have prior to this study, whereas all black text in table 2 indicates all data we did have.
Following the classification in table 2 we can state that the most obvious gaps in knowledge concerned reproduction. Quantity of reproductive output, as well as both timing of reproduction over a year and growth cycle, and the timing of recruitment following reproduction were unknown. Each of the last two processes is covered in the DEB model by a parameter (Appendix A, table 2~~A~~, 'minimum temperature to spawn' and 'day of birth', respectively), which we will vary to assess its effects on the fit to field data. What table 2 points out implicitly is that these processes are also influenced by food levels, in our case chlorophyll concentrations. To account for this dependence we will also vary chlorophyll concentration.

Table 2: ranking of DEB models on the basis of the availability of data. The colour in this table indicates the availability of data of the DEB_{Ensis} model; red data is not available.

0	Maximum length and body weight; weight as function of length
1	Age, length and weight at birth and puberty for one food level; mean life span (due to ageing)
2	Growth (curve) at one food level: length and weight as functions of age at constant (or abundant) food level
3	Reproduction and feeding as functions of age, length and/or weight at one food level
4	Growth (curve) at several (N1) food levels; age, length and weight at birth and puberty at several food levels
5	Reproduction and feeding as functions of age, length and/or weight at several (N1) food levels
6	Respiration as function of length or weight and life span at several (N1) food levels
7	Elemental composition at one food level, survival due to ageing as function of age
8	Elemental composition at several (N1) food levels, including composition of food
9	Elemental balances for C, H, O and N at several body sizes and several food levels
10	Energy balance at several body sizes and several food levels (including heat)

Comparison

On the basis of the environmental data collected on site (temperature, chlorophyll, silt) the DEB_{Ensis} model is run to predict growth of *Ensis* individuals over time. The environmental data has only been measured in the period 2-2011 to 7-2012, whereas the DEB_{Ensis} model needs environmental data from the moment of recruitment to calculate the growth of a cohort. To fulfil this need of the model, we assumed that the environmental data measured was not different in the period prior to 2011, and we copied the environmental data of a full year (2-2011 to 2-2012) to get a time series of environmental data from 2-2005 to 2-2012. See figure 1 for an abstract of this compiled time-series.

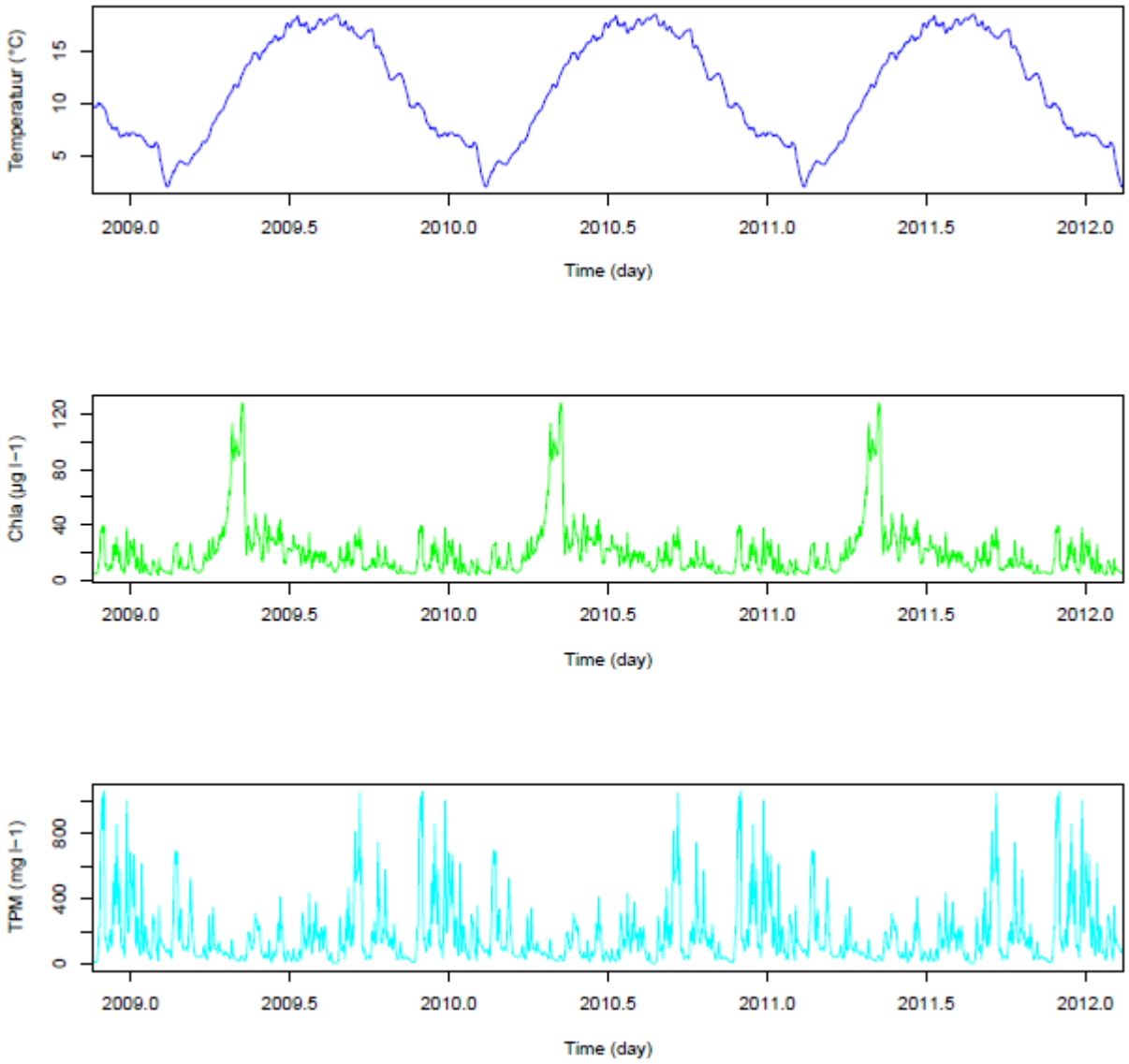


Figure 1: Compiled time-series of temperature, chlorophyll and silt (TPM) based on environmental data acquisition performed by the lander in the period 2-2011 to 7-2012 and copied for the period prior to 2-2011.

Both the dynamics and concentration of chlorophyll in the period prior to 2011 will have been different in the field from what we assumed. Assuming another dynamic pattern of chlorophyll concentration prior to 2011 is cumbersome if a stable concentration is not assumed (which does not seem relevant). The absolute concentration of chlorophyll prior to 2011 can easily be changed, however, without changing the dynamics. Figure 2 shows that for a small change in timing of growth (days-week) and growth rate (a difference of 0.5cm/year) large changes in chlorophyll concentrations are necessary (50-70%). Normally, chlorophyll concentrations between years will not vary this much. This leads to the conclusion that variation in chlorophyll concentrations prior to 2011 will not significantly affect the outcomes of this study.

The prediction of growth from the model is compared with the biometric field data of growth. Several growth variables were used in the comparison, namely length, weight (in as-free dry weight, AFDW hereafter), condition index and gonad development. Length and total weight and gonad weight have been measured by Witbaard et al. (2012) and are an output of the DEB model as well. Condition index is a composite variable of AFDW and length which "corrects" the AFDW for differences in shell size. It expresses the weight (volume) of soft tissue to the volume of the shell, i.e. the extent to which the shell is filled. Witbaard et al. (2012) showed that for *Ensis directus* the condition index is strongly correlated with glycogen-content (explained variance 76%), the latter being a measure for the energy reserves in

shellfish. Glycogen is not an output of the DEB model, however, but is one of many energy reserve components considered as total reserve *R*. The strong correlation between condition index and glycogen (Witbaard et al., in review) shows, however, that the condition index is also a good predictor of the energy stored in the animal. Condition index will therefore be used as predictor of energy stored of the individual *Ensis*.
Several initial conditions for and parameters of the model were varied to assess the effect of these parameters and the initial conditions on the goodness of fit of the model outcomes. After each adjustment of a model parameter a new model-run leads to an output of growth in length, AFDW, condition index and gonad development over time. Outputs of the various model runs (of growth in length, weight, condition index and gonads in time) were tested against each other for Goodness Of Fit of the biometric field data. Model runs with the least sum of squared residuals (indicated by GOF, Wijsman & Smaal 2011) were used as best-fit. Also the timing of the onset of growth and the onset of a decrease in weight (of gonads) over time was used to test the fit of the model to the data.

Most of the sampled individuals in the biometric field data were assessed to be of the cohort of 2009 (Witbaard et al. 2012). Although most of the population consists of one cohort (2009), other cohorts may have influenced the population averages and therefore may have influenced both the timing of a growth episode and the rate of growth in the population averages. To distinguish the cohort of 2009 in the dataset, a cohort analysis was done using the method described by Bhattacharya (1967). Essentially, this method identifies a median of a peak in a frequency-length plot, identifying it as the median of the cohort, and determines the normal distribution around the median. The median and its normal distribution were then followed over time. All data points outside this normal distribution of lengths over time were omitted. An alternative method to identify the individuals of a cohort is to perform a Monte-Carlo simulation varying forcing factors like chlorophyll concentration to get a range of possible growth curves that can describe the growth measured in the field. This method has certain advantages, namely that it can indicate the range of value at which certain (interacting) parameters and forcing factors have possibly influenced the growth of individual in the field. The method also has disadvantages, namely that it is time-consuming to perform. Instead, we chose here to use the more simple, but just as effective method of Bhattacharya (1967), to identify the cohort 2009. Furthermore we varied a number of parameters (time of recruitment, minimum temperature to spawn, Appendix A table 2A) and forcing functions (chlorophyll) that affect processes we have not yet researched experimentally (see table 2). What is the effect of a change in these parameters and forcing factors on the fit of the model to the field data?

4. Results

Effects of chlorophyll

Given the concentration of chlorophyll calculated from the fluorescence measured by the ALEC JFE sensors at the lander at the site, the DEB_{Ensis} model overestimates average growth(rate) of *Ensis* (fig. 2). Chlorophyll concentrations 30%-35% of the concentrations measured in the field led to the best fit of the data (fig 2). Although the measured chlorophyll concentration led to an overestimation of average growth, the model does describe maximum growth rather well.

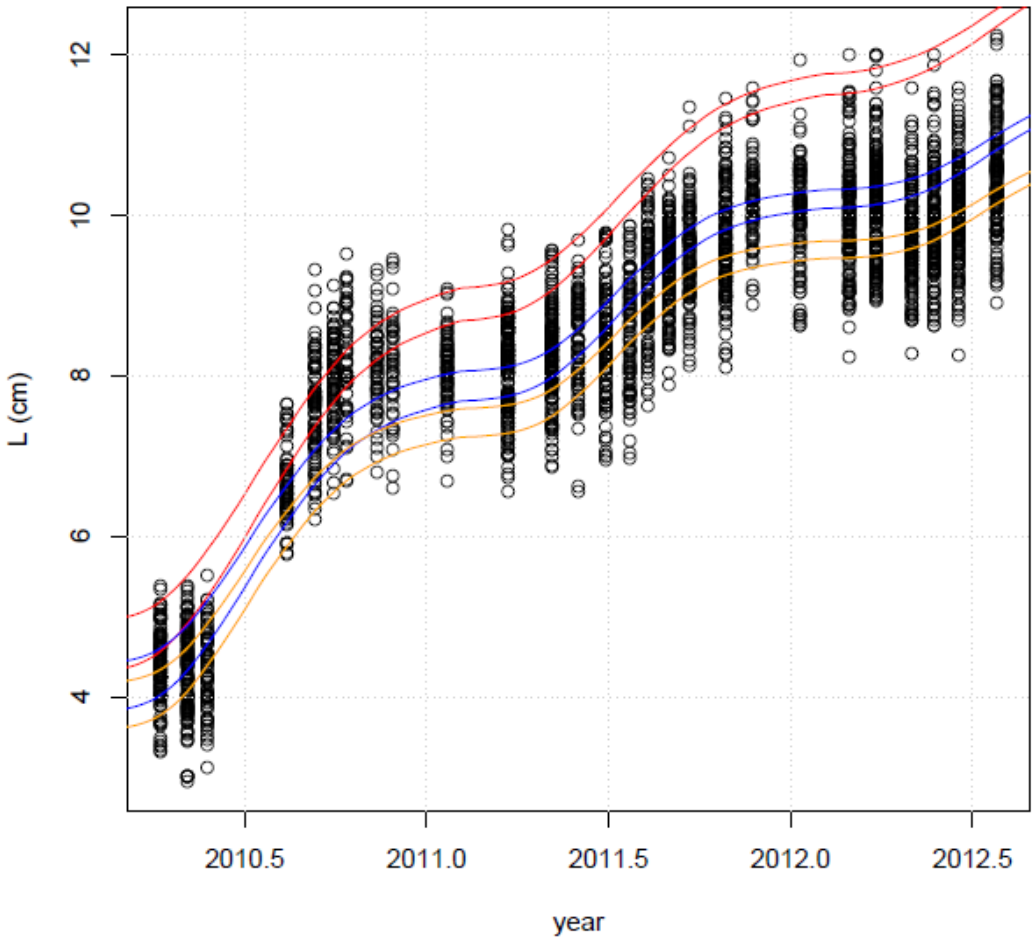


Figure 2: Development of shell length of *Ensis*. Black dots: measured length. Lines: modeled length. Red lines: model outcome on basis of measured chl-a concentration assuming two occurrences of recruitment (top line: 1st of May and lower line: 1st of June). Blue lines: idem except for 40% of measured chl-a concentration. Yellow lines: idem except for 30% of measured chl-a concentration.

Moment of settlement

Witbaard (personal communication) reported that growth of *Ensis* follows a sequence of growth in gonads and AFDW first, until spawning takes place, after which growth in shell length occurs. This observation called for an inspection of the calculated onset of growth and of decrease in gonads, AFDW and length. Although moment of recruitment can improve the fit (beginning of May gives the best goodness of fit (GOF), fig. 2, yellow top line), the model predicts an earlier onset of growth in length at all parameter combinations, especially at sizes under 6cm. This is visible in the lower panel of figure 3 by the increase in (weighted) residuals of the data, indicating an overestimation of length. The lack of fit in the start of the measuring period can be ascribed to two factors: 1) the environmental data used to model length (or any other DEB variable) in that period are copied values of the period 2-2011 to 2-2012 (see Materials and Methods, comparison) . 2) Because only a limited amount of samples were taken in that period (Witbaard et al., 2012), the samples might not be representative of the population at that time.

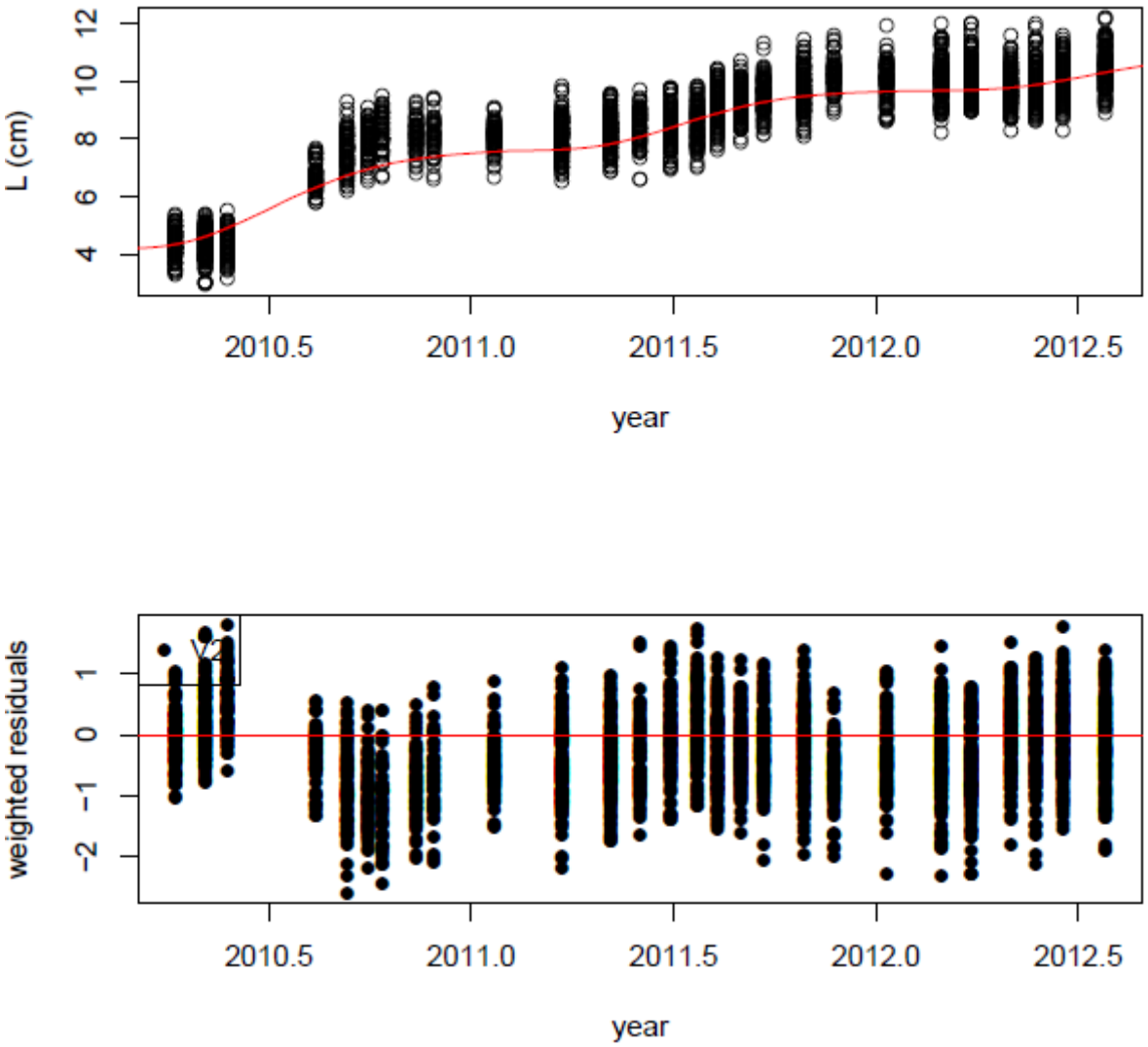


Figure 3: Development of shell length of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel). Black dots: measured length. Red lines: modeled shell length at chlorophyll= 30%.

Dynamics in the AFDW of gonads can be described by the onset of change in AFDW and the rate at which this happens. The rate of change in AFDW of gonads in the DEB model is determined by growth and release of gonads, which the model is assumed to happen simultaneously. The rate of change in the field data of AFDW of gonads is rather smooth, both when increasing and decreasing in weight (fig. 4). The smoothness of change in the field data indeed suggests that gonad release and growth happens simultaneously like the model assumes. The minimum temperature to spawn determines the onset of decrease and increase in AFDW of gonads (fig. 3). The best GOF in gonad weight was at a temperature of 13.3°C (GOF=$7.817 \circ 10^{-10}$), while the best timing was obtained at a temperature of 13.5°C (GOF=$7.857 \circ 10^{-10}$). We have no experimental data to determine the minimum temperature to spawn. From Witbaard et al. (2012), however, we do see that the onset of spawning indeed corresponds to a temperature of 12-14°C along with an increase in chlorophyll (Appendix D).

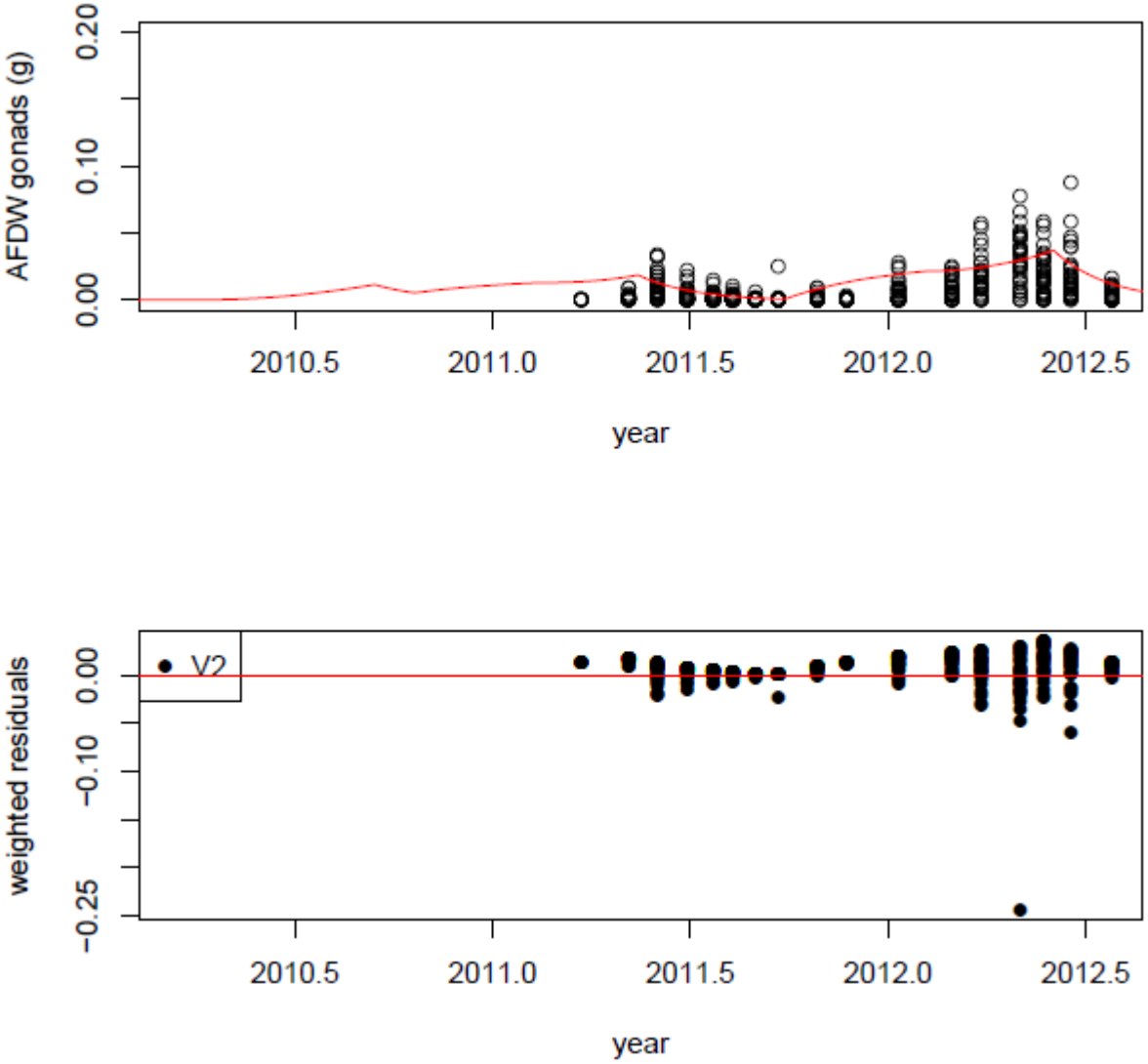


Figure 4: Development of gonad mass (in AFDW) of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel). Black dots: measured gonad mass. Red lines: modeled gonad mass at chlorophyll= 30%.

Condition index (CI)

At every model parameter-setting the condition index (CI) of *Ensis* was overestimated by the DEB_{Ensis} model during autumn and winter due to the lack of decrease in CI in those periods predicted by the model (fig. 5). In general, CI will be a hard variable to fit for the model, because it is a compound variable of AFDW/Volume of which Volume in the model is determined by shell length. So the CI is composed of several components with each their uncertainty and also natural deviations. As we can see from the wavy pattern in the bottom panel figure 3, the onset of growth starts earlier in the model than in the field data. This difference between model and data is multiplied in the comparison for CI (fig. 5). On the other hand, the lack of decrease in the model's prediction of CI can be ascribed to the lack of decrease in AFDW in the same periods (fig. 6, lower panel). In Appendix C we show that the assumption of a winter-pause for feeding enables a better fit of the model to AFDW and CI.

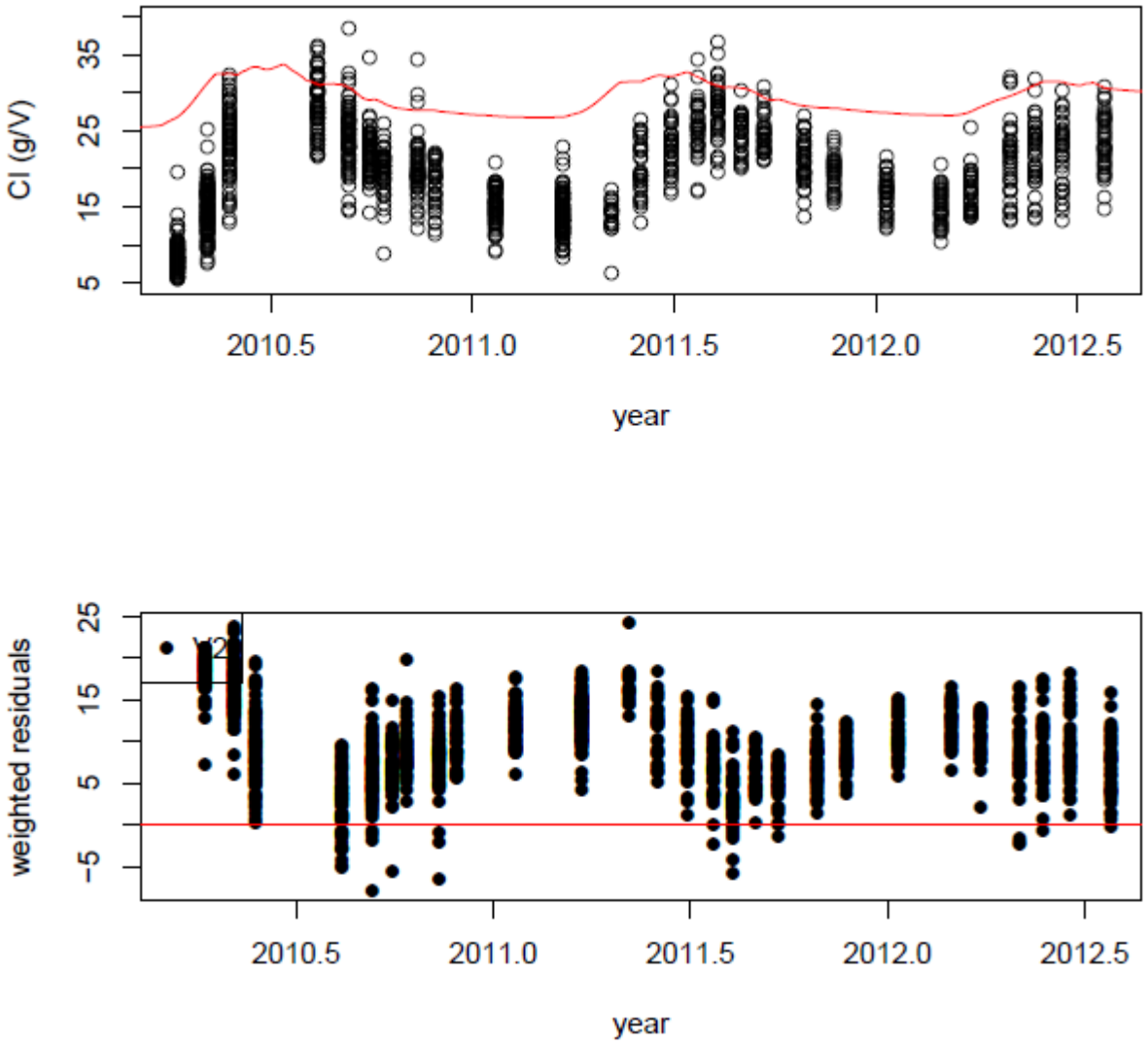


Figure 5: Development of Condition index of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel). Black dots: measured Condition index. Red lines: modeled Condition index at chlorophyll= 30%.

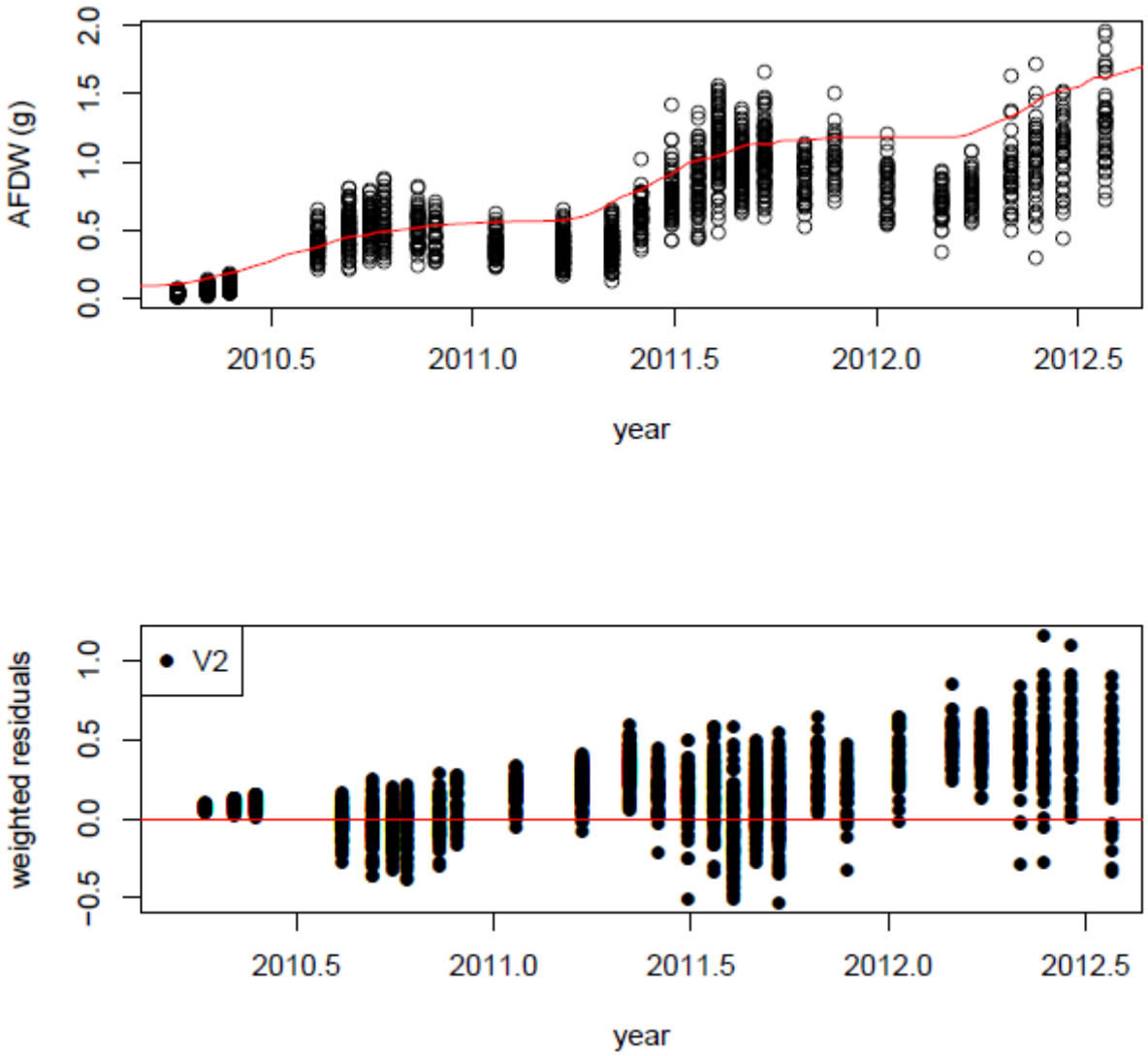


Figure 6: Development of total AFDW of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel). Black dots: measured AFDW. Red lines: modeled AFDW at chlorophyll= 30%.

5. Discussion

This project provided the unique opportunity to use measured environmental data (instead of calculated) to predict growth of *Ensis* using the DEB_{Ensis} model and compare it to measured biotic data on *Ensis* collected from the same site over a two year period similar to the comparison which has been made for cockles (Wijsman & Smaal, 2011). Yet, most studies that compared data with DEB model predictions used experimental laboratory data (Nisbet et al., 2004), which leads to a more predictable efficiency of food-use and growth, and can exclude the effect of competition for food. Although one cannot directly compare the fits of different models on data of different species in different circumstances, one could state that the fit of the DEB_{Ensis} model presented here is better when compared to the fit of DEB models applied to other species. Therefore the use of DEB_{Ensis} for predictive purposes on the effect of environmental changes in silt, temperature and chlorophyll seems justified within the study on the effects of sand-mining.

All residual plots in figures 3 to 6 (except maybe that in figure 4) show a non-random pattern around the model estimates. Between the 31st of December and the 1st of June the model overestimates AFDW (both total and gonadal) and underestimates length. The combination of length and AFDW in the Condition Index strengthens the wavy pattern in the residuals of figure 5. The wavy patterns suggest that the

model is not (fully) considering some structuring influences which evidently exist for the field population and causes body mass to vary over seasons. One of these influences may be the timing of the onset of growth, which is not quite correct in the model (in the case of length (fig. 3, lower panel), the wavy pattern is not particularly strong). A second, stronger influence that the model does not consider is the influence of winter on body condition (the cohort keeps on growing or remains constant in AFDW), while the biometric field data show a decline in AFDW over winter. This causes the model to overestimate AFDW in winter-spring until development in biometric AFDW surpasses modelled increases. This pattern was also evident in the estimation of growth of cockles by a DEB model (Wijsman & Smaal 2011), and as such thus indicates a lack in the model's generic set-up because it insufficiently accounts for mass losses in the food poor season.

The unadjusted form of the model (fig 2) does fit maximum growth rather well and thus suggest that the model describes potential shell growth quite well. The fact that the model needs adjustments to give a good estimate of average growth might indicate that other factors not taken into account in the model can modify growth rates. For instance Freudendahl et al. (2010) showed that *Ensis* under threat of predation by birds buried themselves more often and for longer periods, leading to a decrease in condition. Other factors might be small spatially scaled differences in topography, sediment composition and food supply (Yager et al., 1993)

Another factor that is not accounted for in the DEB model is intraspecific competition. Intraspecific competition might lead to competition for food and reduce the average uptake of chlorophyll when chlorophyll locally becomes limiting for *Ensis*. Daan & Mulder (2005) have shown that density-dependent growth and therewith intraspecific competition for food can be responsible for reduced growth of *Ensis* at high densities. Similar observations have been published by Palmer (2004) and Dekker and Beukema (2012). Neither of these authors, however, quantified the effect of density-dependence on growth. Therefore, we cannot adjust the model accordingly or give a quantification of the effect.

The DEB_{Ensis} model assumes individuals to be active whole year round, while a decrease in temperature may decrease physiological rates such as ingestion of algae. The biometric data suggest that feeding-activity is reduced below certain temperatures, while maintenance and respiration (metabolic rates) reduce reserves and AFDW (as suggested by Honkoop, 1998). Whether reserves in harsh winters are positively or negatively affected compared to milder winters depends on the balance between temperature-dependent metabolic and feeding rates. Honkoop (1998) also indicated that low winter temperatures affect reproductive effort positively in some shellfish species. In that case, lower temperature during harsh winters cause metabolic rates to lower more than feeding rates, leading to a less severe decrease in reserve mass than in milder winters. This might explain why after a severe winter the gonadal output is larger as the animals can reallocate more reserves into gonads. On the other hand, the larger reallocation to gonads after harsh winters may reduce reserve mass in relation to the reserve left after milder winters.
We know very little about the day-to-day feeding-activity of shellfish, let alone the effect of winter on the feeding-activity of *Ensis*. The analyses of the valve gape monitor results show that valve gape varies over a day and is affected by SPM concentrations (Witbaard and Kamermans, 2010). Whereas the DEB model does assume an effect of SPM on feeding rate of chlorophyll, and assumes an average feeding activity over a day, it does not account for seasonal variation in feeding activity. Up to now no seasonal analyses have been made of the valve gape monitor results, but this could enlighten seasonal patterns in feeding activity.

Another reason for the overestimation of average shell growth in the model might be related to the fact that the model uses chlorophyll concentrations in stead of particle concentrations. Filtration response in bivalves is to a large extend determined by the number of food items in combination with their quality. Describing the food conditions in terms of chlorophyll concentration only accounts for the qualitative aspect but neglects the quantitative aspect, i.e. phytoplankton cells and species can have wide ranging

chlorophyll concentrations and as such the chlorophyll measurement does not give insight into this relationship between particles and quality characteristics.
Not all food items are measured by fluorescence; dead algae, detritus and other sources of carbon can also be consumed. Partly degraded food particles will, however, provide less nutrition than live algae. Food preferences of *Ensis* might also lead to a selection of certain algae species over others. *Ensis* might even be unable to consume a part of the algal community, or nutritional value of algae species might differ. Unbalanced combination of algae might therefore lead to suboptimal growth. This is supported by growth experiments which showed that *Ensis* might need a variety of species to maintain growth (Kamermans et al. 2011). The DEB_{Ensis} model's reaction to chlorophyll and silt (Xk and Yk, table 2A) is fitted on data of Kamermans and Dedert (2012), who used a mix of two species of algae (*Pavlova* sp. and *Chaetoceros muelleri*). Whereas the single species did not result in prolonged growth (Kamermans et al. 2011), the mix of two species did lead to prolonged growth (Kamermans and Dedert, 2012). This indicates the sensitivity of a species to the composition of its food on growth; another mix of algae species might result in a reduced assimilation efficiency, but may also increase it relative to the efficiency assumed in the DEB_{Ensis} model.
The DEB_{Ensis} model assumes a continuous effect of silt and algae on the uptake of algae (see Schellekens, 2012), a sudden halt of filtration-activity over a certain threshold is not considered. Witbaard and Kamermans (2010) studied the effect of silt on the shell-opening of *Ensis* in a series of laboratory experiments and observed that filtration rate dramatically decreased at SPM concentrations above 200 mg/l. Because it was unclear from these short term experiments whether *Ensis* is able to recover feeding activity under prolonged exposure to such high silt concentrations, Kamermans and Dedert (2012) performed long –term growth experiments using high (16.5 µg/l) and low (5 µg/l) chlorophyll concentrations and five silt concentrations up to 300 mg/l. Kamermans and Dedert (2012) showed that *Ensis* grew well over 10 weeks even with a constant silt concentration of 300mg/l as long as the chlorophyll concentration was high. Furthermore, they showed that the decline in clearance rates that did occur (and was significantly different at 300 mg/l from that at lower silt concentrations) was linear over silt concentration and no threshold was crossed.

A parameter that influenced the timing of gonadal decrease and increase was the minimum temperature to spawn. This temperature has never been experimentally determined. Therefore the model parameter adjustment to the data in this report provide a hypothesis. The minimum temperature to spawn for *Ensis* should, according to the data and the model-fit lie between 13.3 and 14°C.
The environmental data of Witbaard et al. (2012) indicates at least that the temperature at which spawning takes place is indeed between 12-14 °C (see Appendix D). The environmental data of Witbaard et al. (2012) also indicate other possible influences on the start of spawning. Because these data cannot identify the mechanisms that start spawning, however, experiments designed to test the influence of temperature specifically should be performed to investigate the hypothesis that temperature triggers spawning at 13.3-14°C.

6. Conclusions

This study evaluated the DEB_{Ensis} model on predicting the average growth of *Ensis* in the field using a few (a)biotic variables (temperature, silt and chlorophyll concentration). The study showed that on average the growth of *Ensis* can be predicted, but some non-linear and/or seasonal heterogeneity of explained residuals remains. These supposed non-linear and/or seasonal effects that influence growth of *Ensis* are not taken into account in the DEB_{Ensis} model and may cause an underestimation of the effect of sand-mining on the growth of *Ensis*. To incorporate these into the model , a mechanistic understanding and a quantitative description of these influences is needed. The non-linear and/or seasonal effects likely control the biology and ecology of *Ensis*. These aspects are discussed below.

Feeding activity-levels and behaviour

The DEB model is capable of predicting the average length, AFDW and gonad development over time as long as the level of chlorophyll used in the model is adjusted to 30% of the measured values. Then still, the model does not account for the decrease in AFDW and CI in winter observed in the field data unless a winter rest in metabolism of *Ensis* is assumed (see Appendix C). In unadjusted form the DEB model therefore overestimates average growth and does not foresee a decrease in AFDW and CI over winter. Analyses of the feeding activity (Witbaard et al, 2012) from day to day and along the year can possibly show whether *Ensis* intrinsic factors cause the observed condition decrease, or whether this is caused by food availability and quality. Another aspect that could influence the decrease in AFDW and CI in the autumn - spring period could be related to increased need of reburying in this period of the year when wind induced wave action causes movement and mobilisation of sediments. This increased burying activity could lead to extra energy consumption which in the food deprived season might lead to a loss of reserves.

Physiology

Table 2 shows the current state-of-knowledge on the physiology of *Ensis*. It also identifies the areas of information that lack in our knowledge prior to this study. Reproduction was the first knowledge-gaps in line to be studied. Reproduction is a notoriously difficult variable to study, Witbaard et al. (2012) have already given us the development of gonadal mass over time with a varying food-level. In this report we have fitted the development of gonads calculated by the DEB_{Ensis} model to the biometric data of Witbaard et al. (2012) adjusting the minimum temperature to spawn. The range of minimum temperatures to spawn that best fits the biometric field data corresponds quite nicely to that found in the environmental data (Appendix D). Because the environmental data are not from an experimental set-up, however, we cannot from that data identify one variable as the driving factor that determined spawning. Also, Appendix D shows that a phytoplankton-bloom also correlates with the start of spawning, indicating other influences may play a role. An experiment to identify whether and at what temperature spawning is initiated is relatively simple, but has never been performed. We suggest this experiment should be performed to justify the use of values used in the DEB_{Ensis} model in this report.

Field aspects: algae, food selection

Figure 2 indicates a problem for the DEB model to use the chlorophyll levels as measured by the lander and we have discussed the possible causes of this problem and showed that a level 30-35% of the measured level results in a better fit of average shell size, AFDW, CI and gonad mass. One line of research should be to experimentally identify daily activity-levels of *Ensis*; what proportion of the day do they filter and what is the dependency of this activity to temperature and environmental conditions such as spatial position, predators or water-quality? Some of these questions can be answered reanalysing data from Witbaard et al. (2012). Furthermore, it is seen as important to know to what extent *Ensis* selectively feeds on various algal species and silt/algae compositions and to quantify the effect on tissue growth.

Population dynamics

Yet another line of research to identify the reason why only 30-35% of chlorophyll concentration is used should deal with the quantitative effect of intraspecific competition on growth of *Ensis*. Where the effect has been long identified (Daan & Mulder, 2005) the relation between density and growth retardation or feed-uptake is still unclear.

All these lines of experimental research require considerable effort (which could start by reanalysing data already acquired by Witbaard and Kamermans, 2010).
One line of research, namely the study of feeding activity-levels is expected to result in a considerable increase in knowledge that could benefit the DEB model (see Appendix C) and benefit the quantitative prediction of the effect of sand-mining on *Ensis* (table 3). We therefore strongly advise the client to invest in this line of research.

Table 3: proposed future research, the knowledge it will affect, relative cost and priority.

Proposed research	**Effect on**	**costs**	**priority**
Minimum temperature to spawn	Onset of release of gonads	low	low
Feeding activity	Decrease in AFDW	low	high
behaviour	Decrease in AFDW	high	middle
Intraspecific competition effect on growth	Proportional use of chlorophyll	high	high
Algal species selectivity	Proportional use of chlorophyll	high	middle

Most development of knowledge on the effects of sand-mining on shellfish is needed in the form of experiments, following the list in table 3. As this study shows, it is useful, however, to use the insights from modelling to design efficient experiments on subjects we need to know to proceed in our knowledge. On the one hand, results from experiments can fine-tune a model and its parameters, while on the other hand model analysis may lead to insights that cannot be gained with a simple experiment. In turn, these insights may create hypotheses that should be tested with experiments of a more complicated sort. In this report, we hypothesized on the causes for a lack of maximum growth of *Ensis*. Experiments proposed in table 3 test these hypotheses. The next step in modelling the effect of sand-mining on shellfish, is to account for population dynamics. Following the results of the proposed experiments, simple ‘conceptual’ population models that incorporate the effects of food, silt, population density and mortality on individual growth can enable a more complete insight in how sand-mining influences shellfish populations.

7. Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 57846-2009-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

References

Cardoso, Nieuwland, Wijsman, Witbaard, Van der Veer, 2011, Validation of a method for age determination in the razor clam *Ensis directus*, with a review on available data on growth, reproduction and physiology. NIOZ-rapport 2011-9.

Daan, Mulder (2006) The macrobenthic fauna in the Dutch sector of the North Sea in 2005 and a comparison with previous data. NIOZ-Rapport 2006-3.

Dekker, Beukema (2012). Long-term dynamics and productivity of a successful invader: The first three decades of the bivalve *Ensis directus* in the western Wadden Sea. Journal of Sea Research, Volume 71, p. 31-40.

Freudendahl, Nielsen, Jensen, Jensen (2010). *Ensis americanus* in the Wadden Sea: field experiment on impact of bird predation and tidal level on survival and growth Helgoland Marine Research Volume 64, Issue 2, pp 93-100.

Honkoop, 1998. Bivalve reproduction in the Wadden Sea. Effects of winter conditions on reproductive effort and recruitment. PhD thesis. Rijksuniversiteit Groningen. 135pp.

Kamermans, Brummelhuis, Wijsman, 2011, First pioneering laboratory experiments on filtration, respiration and growth of the razor clam (*Ensis directus*, Conrad). IMARES rapport C115/11.

Kamermans and Dedert, 2012, Effect of variations in concentration of algae and silt on filtration and growth of the razor clam (*Ensis directus*, Conrad). IMARES rapport C017/12.

Lika, Kearney, Kooijman, 2011b, The “covariation method” for estimating the parameters of the standard Dynamic Energy Budget model II: Properties and preliminary patterns. J. Sea Research, volume 66.

Lika, Kearney, Freitas, Van der Veer, Van der Meer, Wijsman, Pecquerie, Kooijman, 2011a, The “covariation method” for estimating the parameters of the standard Dynamic Energy Budget model II: Philosophy and approach. J. Sea Research, volume 66.

Nisbet, McCauley, Gurney, Murdoch and Wood, 2004, Formulating and testing a partially specified Dynamic Energy Budget model. Ecology 85(11): 3132–3139.

Palmer, D. W. (2004). "Growth of the razor clam *Ensis directus*, an alien speices in the Wash on the east coast of England." J.Mar Biol. Ass. UK 84: 1075-1076.Rozemeijer, 2012. Monitoring and Evaluation Pragram sand extraction of Rijkswaterstaat, LaMer and sand extraction Sand Engine (The Netherlands): a compact outline and first results. IMARES rapport C072/12.

Schellekens, 2012, Groei en conditie van zwaardschede (*Ensis directus*, Conrad) voor, tijdens en na geplande zandwinning in 2013-2017. IMARES Rapport C089/12.

Wijsman, 2011, Dynamic Energy Budget (DEB) parameters for *Ensis directus*. IMARES rapport C116/11.

Wijsman and Smaal, 2011, Growth of cockles (*Cerastoderma edule*) in the Oosterschelde described by a Dynamic Energy Budget model. J. Sea research, Volume 66, Issue 4

Witbaard, Duineveld, Bergman, 2012, Progress report on the study into the dynamics and growth of *Ensis directus* in the near coastal zone of Egmond, in relation to environmental conditions in 2011. NIOZ-rapport 2011-project 2735.

Witbaard and Kamermans, 2010. De bruikbaarheid van de klepstandmonitor op *Ensis directus* ten behoeve van de monitoring van aan zandwinning gerelateerde effecten. NIOZ rapport 2009-10.

Yager, Nowell and Jumars (1993). Enhanced deposition to pits: a local food source for benthos. Journal of marine research 51: 209-236.

Justification

Rapport C155/12
Project Number: 4303104201

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

Approval:	Pauline Kamermans senior researcher
Signature:	
Date:	12-12-12

Approval:	Birgit Dauwe Head of Department Delta
Signature:	
Date:	12-12-12

Appendix A. tables

Table 1A: Overview of deployment dates and ships used in 2011.

Year	Visit nr	Week period	Start date	End date	Nr. of Days
2011	1	wk08_14	25/02/2011 18:00	07/04/2011 09:40	41
2011	2	wk14_18	07/04/2011 18:00	03/05/2011 09:00	22
2011	3	wk18_22	03/05/2011 18:00	31/05/2011 10:20	28
2011	4	wk22_25	31/05/2011 18:00	24/06/2011 08:15	24
2011	5	wk25_28	24/06/2011 18:00	12/07/2011 10:25	18
2011	6	wk28_31	12/07/2011 18:00	02/08/2011 11:00	21
2011	7	wk31_34	02/08/2011 18:00	23/08/2011 13:40	21
2011	8	wk34_39	23/08/2011 18:00	27/09/2011 14:50	35
2011	9	wk39_43	28/09/2011 23:00	25/10/2011 10:50	26
2011	10	wk43_02	25/10/2011 18:00	11/01/2011 15:00	43
2012	11	wk02_09	11/01/2012 18:00	29/02/2012 10:00	49
2012	12	wk09_13	29/02/2012 18:00	27/03/2012 10:00	27
2012	13	wk13_18	27/03/2012 18:00	02/05/2012 10:00	36
2012	14	wk18_21	02/05/2012 18:00	24/05/2012 10:00	22
2012	15	wk21_25	24/05/2012 18:00	18/06/2012 10:00	25
2012	16	wk25_30	18/06/2012 18:00	26/07/2012 10:00	38

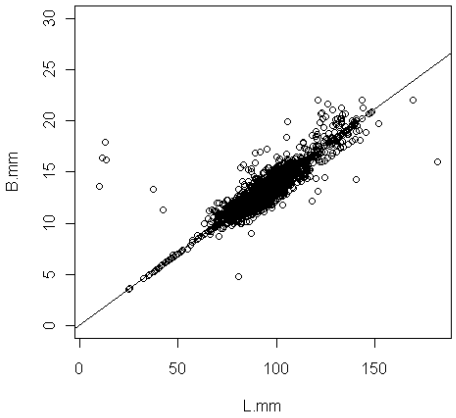
Table 2A: parameters of DEB_{Ensis} model.

Parameter	waarde	eenheid	omschrijving
shape	0.1786	-	Shape factor delta_m
JXm_L2	200	J cm^{-2} d^{-1}	Maximum surface-specific ingestion rate
Pm_L3	45.7	J cm^{-3} d^{-1}	Volume-specific maintenance costs
Em_L3	4005.26	J cm^{-3}	Maximum storage density
Eg_L3	3415	J cm^{-3}	Volume-specific costs of growth
Ev_L3	1350	J cm^{-3}	Volume-specific energy-content of structural tissues
Kappa	0.9731	-	Fraction of catabolic energy used for Maint+Growth
Kappa_R	0.95	-	Fraction of reproductive power that goes to reproductive reserves
Lb	0.01729	cm	Length at embryo -> juvenile transition
Lp	4.369	cm	Length at juvenile -> adult transition
SpecMass	1	g cm^{-3}	Specific mass of body structure
Mu_E	17500	J g^{-1}	Energy content of reserves (in ash-free dry mass)
Ta	6000	K	Arrhenius temperature
Tl	278	K	Lower boundary of tolerance range
Th	306	K	Upper boundary of tolerance range
Tal	51154	K	Arrhenius temperature for rate of decrease at lower boundary
Tah	47126	K	Arrhenius temperature for rate of decrease at upper boundary
Day of birth	varied	-	Day of birth
MinSPtemp	varied	°C	Minimum temperature for spawning
GSI_upper	0.025	-	Upper GSI boundary to trigger spawning
GSI_lower	0.0005	-	Lower GSI boundary to stop spawning
DoSpawn	0	-	At start of simulation there is no spawning
rSpawn	0.02	d^{-1}	Rate of gonad release Fraction of gonads per day
Xk	0.74	ug Chla_l^{-1}	Half saturation constant Functional response
Yk	68	mg PIM_l^{-1}	Half saturation constant TIM
AE	0.8	-	Assimilation efficiency (1-fraction loss due to digestion)
AFDW_WW	0.093	-	Conversion factor WW to AFDW (g AFDW / g WW)

Appendix B. regressions over Length

LENGTH ~ WIDTH

Width (B)=0.14109*Length (L)



Residuals:

Min	1Q	Median	3Q	Max
-9.650	-0.560	-0.047	0.270	124.750

Coefficients:

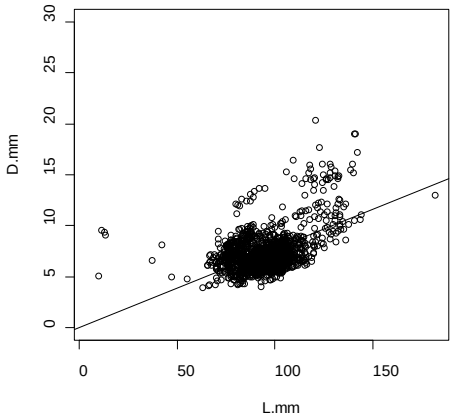
	Estimate	Std. Error	t value	Pr(>|t|)	
L.mm	0.1410919	0.0009396	150.2	<2e-16	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 3.987 on 2011 degrees of freedom
(2771 observations deleted due to missingness)
Multiple R-squared: 0.9181, Adjusted R-squared: 0.9181
F-statistic: 2.255e+04 on 1 and 2011 DF, p-value: < 2.2e-16

LENGTH ~ GIRTH.

Girth (D) =0.077 *Length (L)



Residuals:

Min	1Q	Median	3Q	Max
-3.196	-1.224	-0.478	0.662	82.339

Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)	
L.mm	0.0773799	0.0009491	81.53	<2e-16	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 3.577 on 1526 degrees of freedom
(3256 observations deleted due to missingness)
Multiple R-squared: 0.8133, Adjusted R-squared: 0.8132
F-statistic: 6647 on 1 and 1526 DF, p-value: < 2.2e-16

Appendix C. winter activity

To explain the 'wavy' pattern in the residuals of AFDW and CI in figures 4 and 5, we explored the explanatory value of a winter rest period induced by temperature. In this exercise we have altered the environmental data set such that at temperatures below 7°C the individual only experiences 1.5 µg Chlorophyll per litre. Effectively, this reduces the chlorophyll concentration from the 20th of December to 1st of April measured between 3.2-28.7 µg/L to concentrations constant at 1.5 µg/L.
Although this is a very simple measure the wavy pattern of figures 4 and 5 is reduced in figures 1C and 2C compared to figures 4 and 5, respectively (see table 1C for GOF). The fit for Length is somewhat poorer that in figure 2. However, if we assume 35% chlorophyll instead of 30%, the overall fit is better, while the fit on Length is comparable to the model without winter rest (see table 1C).

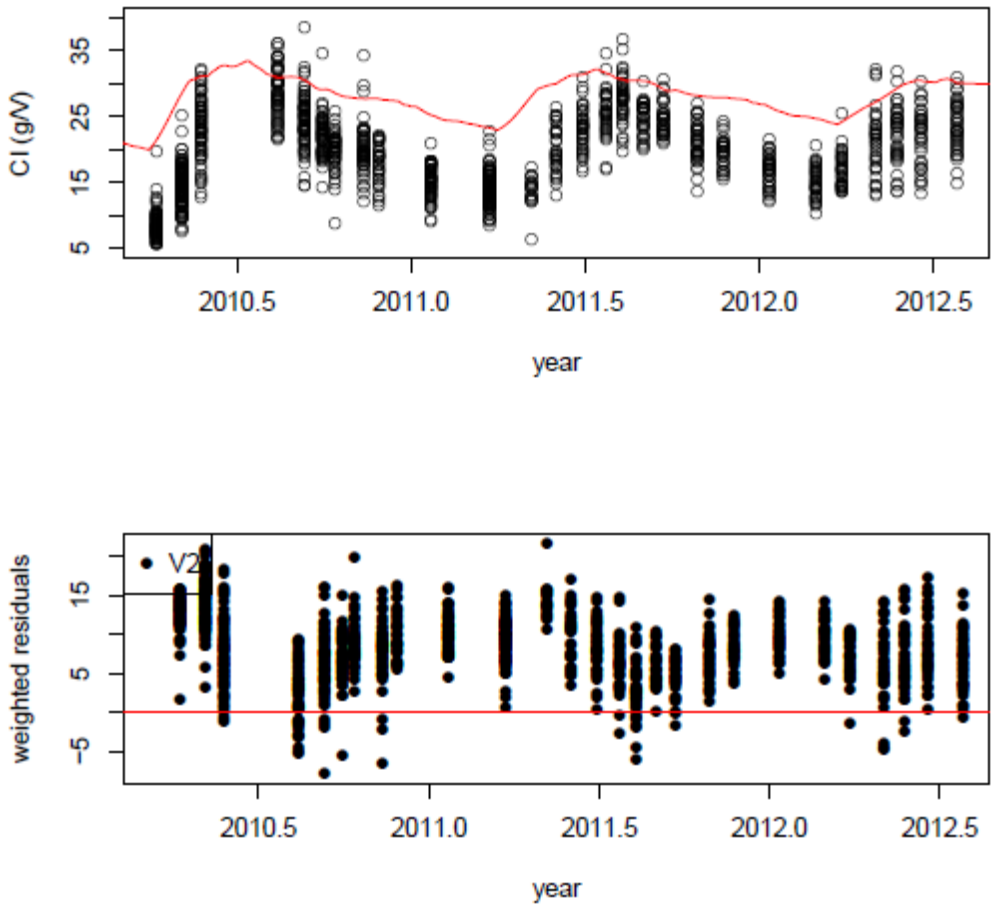


Figure 1C: Development of Condition index of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel) assuming a winter rest period below 7°C. Black dots: measured Condition index. Red lines: calculated Condition index at chlorophyll= 30%.

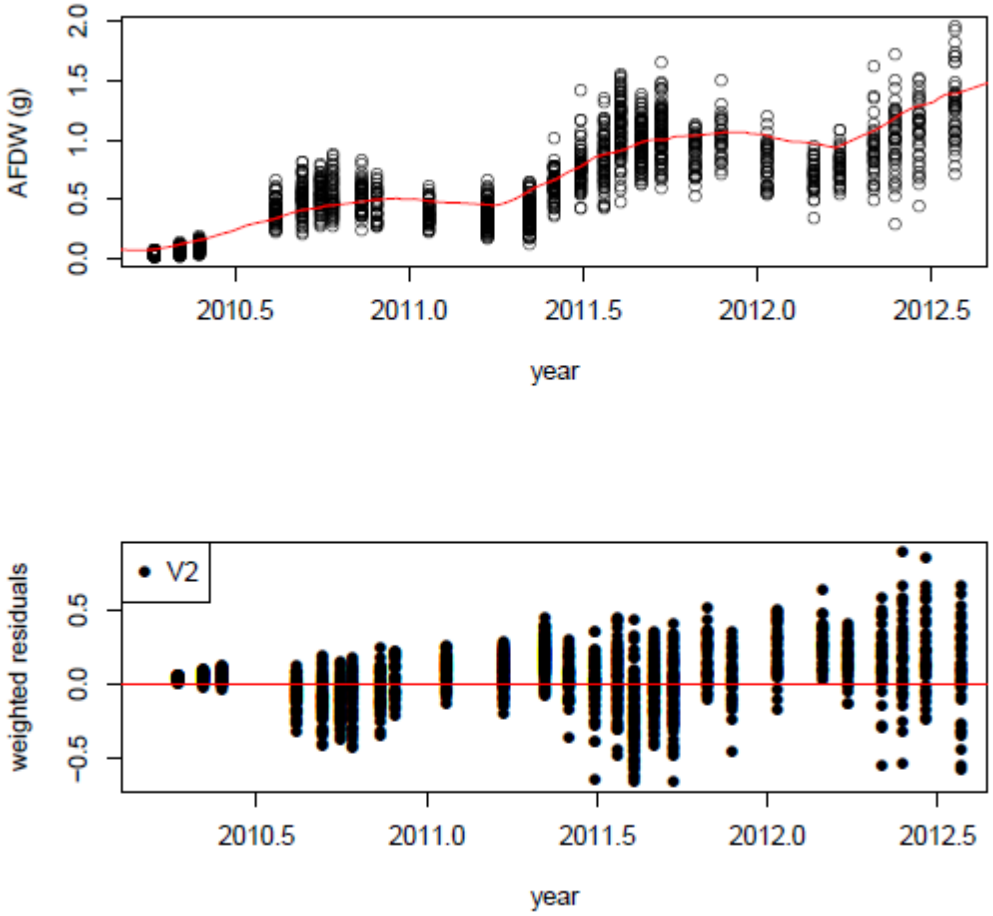


Figure 2C: Development of total AFDW of *Ensis* (upper panel) and residuals of data compared to model fit (lower panel) assuming a winter rest period below 7°C. Black dots: measured AFDW. Red lines: calculated AFDW at chlorophyll= 30%.

Table 1C: Goodness Of Fit measure (residuals squared summed) of 4 variables in two models, one accounting for a reduced activity below 7°C.

	Without rest (30% Chla)	Winter rest (30% Chla)	Winter rest (35% Chla)
CI	$6.59*10^{-5}$	$4.65*10^{-5}$	$5.35*10^{-5}$
AFDW	$2.16*10^{-8}$	$1.12*10^{-8}$	$1.80*10^{-8}$
gonads	$3.67*10^{-8}$	$7.46*10^{-10}$	$7.79*10^{-10}$
Length	$4.81*10^{-8}$	$7.18*10^{-8}$	$4.85*10^{-8}$

Appendix D. minimum temperature to spawn

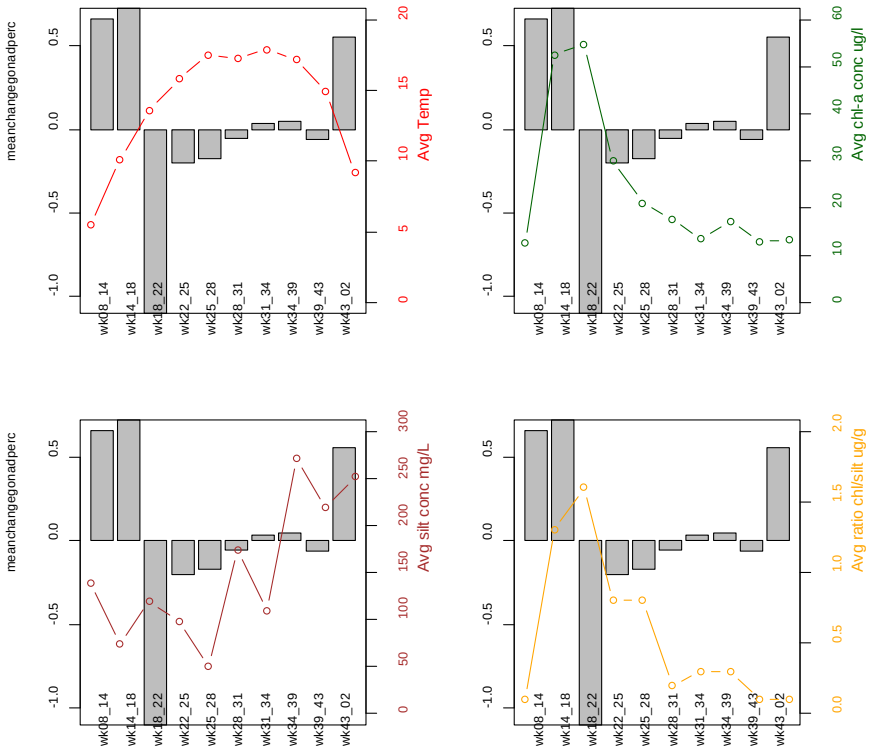


Figure 1D: Change in gonadal mass correlated with the changes in environmental variables: Average temperature (top left), Average chlorophyll concentration (top right), Average silt concentration (bottom left), Average ratio Chl/silt (bottom right).