Spatial variation in cockle growth (*Cerastoderma edule)* in the Dutch Wadden Sea

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Abstract

Sea-level rise is expected to affect agricultural land in low-lying coastal areas by salinization of the groundwater as the result of seawater intrusion. One of the potential solutions to the decreasing yield on salt affect agricultural land is the change in land-use from traditional agriculture to inland marine aquaculture, e.g. sustainable cultivation of marine shellfish. Exploration of presence and ambient growth rates of shellfish in surrounding coastal seas might aid in finding suitable locations for sustainable inland shellfish cultivation. At present, cockles (*Cerastoderma edule*) are a national export product of the Netherlands and are manually harvested in the Dutch Wadden Sea. However, the cultivation of cockles is being considered for low-lying polders in this area. To find suitable locations for these activities, we calculated the growth rates of cockles from annual SIBES (Synoptic Intertidal Benthic Sampling Program) field surveys that started in 2008, covering all tidal flats of the Wadden Sea. Data on shell length and age was used to fit Von Bertalanffy growth functions. To better understand the potential causes of the observed variation in growth, the relationship between cockle growth and environmental conditions was modelled by means of a generalized additive model. Cockle growth was related to sampling year, distance to gullies and median grain size. Model outcomes were used to map the growth conditions for cockles on the tidal flats of the Wadden Sea. Cockle growth is predicted to be high near tidal inlets (in particular those near the islands of Texel, Vlieland, Terschelling and Borkum) and low at the tidal divides. This map and its underlying information on growth conditions provides a baseline to identify and modify suitable inland locations for sustainable cockle cultivations along the coastlines of the Wadden Sea.

Introduction

Due to the increasing human population, food demand will increase while arable land decreases as the result of urbanization, salinization and desertification (Pitman and Läuchli, 2002; Fedoroff et al., 2010). Salinization is, in addition to drought, globally one of the most limiting environmental influences on agricultural crops mainly because of the crop damage due to the high salinity in the root zone (Lee and Song, 2006). This is an especially large problem in the low-lying areas, such as polders, close to the sea where the salinized agricultural land is expected to expand as the result of sea level rise (Pauw et al., 2012). There are numerous studies and successful stories on the use of salt tolerance crops and methods to actively decrease the groundwater salinity (Qadir et al., 2000; Pitman and Läuchli, 2002). However, not every method is successful in every situation, the actual solution to a decrease in agricultural yield on salt affected land should therefore be found on a local scale. Fedoroff et al. (2010) suggest that a change in land use from fresh-water agriculture to saline aquaculture might be part of the answer.

The Wadden Sea, the world’s largest area of interconnected tidal flats, is located along the coastline of Denmark, Germany and the Netherlands, and became a World Heritage in 2009 (Reise et al., 2010). A large part of the Dutch Wadden Sea is surrounded by low-lying reclaimed land with an increasing groundwater salinity (Reise, 2005; Pauw et al., 2012). This development has resulted in the exploration of the potential of saline agriculture and aquaculture in these areas, including the cultivation of cockles.

Cockles (*Cerastoderma edule*) serve as an important food source for various bird populations, and its biomass equals to 16% of the total zoobenthic biomass in the Dutch Wadden Sea (Beukema et al., 1993; Beukema and Dekker, 2006). Within this area, fishing of cockles is allowed but only manually. Dutch cockles are a national export product, primarily being shipped to Spain and Portugal (Ginkel, 2001). Cockles were initially harvested manually, but in the early 1960s the exploitation was scaled up by the introduction of mechanized suction-dredge cockle fishing technology. Cockle biomassa and production has, however, proven not to be sufficient to sustain both the commercial dredging as the bird population (Beukema et al., 1993; Beukema and Dekker, 2006). Following a strong public debate on the impacts of shellfish fishing on cockle stocks and shorebird populations, the mechanical dredging of natural stocks of cockles in the Dutch Wadden Sea was banned in 2005 (Swart and van Andel, 2008; Boere and Piersma, 2012; Pronker et al., 2013). With less than 20 fishing permits in the 1990s, manual cockle fisheries was considered to be a sustainable activity. However, according to van Leeuwe et al. (2008): this type of fishery still impacts the food supply for shorebirds and the recruitment of cockles in years of low cockle abundance (e.g. 2004).

The inland cultivation of cockles is thought to be possible in high numbers and in reliable succession of batches when the cockle is exposed to favourable environmental conditions (Pronker et al., 2013). This might not only be commercially attractive, but also aid in among others the protection of the bird population and therefore the natural values of the Wadden Sea. Thereby, a change in land use in several polders close to the Wadden Sea might be necessary due to the decrease in agricultural yield because of the high groundwater salinity levels (Pitman and Läuchli, 2002; Pauw et al., 2012). Within the Dutch part of this area, a shift from agriculture to inland cultivation of *Cerastoderma edule* (Cockle) in salt-affected polders is presently explored as a sustainable option to adapt to salinization (Waddenfonds, 2014).

To explore the possibilities of the sustainable cockle cultivation along the entire Dutch Wadden Sea, suitable inland locations must be identified. Areas are suitable for this cultivation if they contain favourable environmental conditions for cockle growth. In this paper we will calculate the cockle growth and its relationship with local environmental growth conditions. This correlation will then be used to predict the cockle growth on the tidal flats of the Dutch Wadden Sea and identify areas with favourable growth conditions. Growth was calculated by means of fitting the Von Bertalanffy growth function (VBGF) on field data of extensive tidal surveys that started in 2008. The results on the maximum asymptotic length and the growth constant are used to subsequently calculate the growth parameter ω (Bertalanffy 1938; Gallucci and Quinn 1979). The relationship between cockle growth and environmental conditions was modelled by means of a generalized additive model (GAM). This relationship was then used to extrapolate cockle growth on intertidal locations for which it cannot be calculated due to either an absence of cockles or non-compliance with the conditions for estimating growth. This map and its underlying information on environmental growth conditions can be used as a baseline to identify and modify suitable inland locations for sustainable cockle cultivations along the coastlines of the Wadden Sea.

Material and methods

Field data

Field data on cockles was derived from the Synoptic Intertidal Benthic Sampling (SIBES) program covering the entire intertidal zone of the Dutch Wadden Sea. The sample points are located at 500 meter intervals and complemented with random sampling points (Bijleveld et al., 2012; Compton et al., 2013b; Compton et al., 2013c). Sampling of macrozoobenthos was performed by foot during low tide or by inflatable boats during high tide from June to October. When sampling was done by foot, one sediment core with an area of 0.0177m^2 was taken and if by boat then two cores were taken with a combined area of 0.0177m^2. At both sampling strategies, the depth of the core was approximately 20 cm. The cores were sieved over a 1 mm mesh and all individual shellfish were counted and stored in freezers (-20 °C) until further analyses in the laboratory. Here, the bivalves were identified up to species level and their shell length was measured (along the anterior-posterior axis). Cockle age was determined by counting the growth rings on the shell (Kristensen, 1958; Kraan et al., 2007; Compton et al., 2013b).

The data on the median grain size was developed by Folmer et al. (submitted) and Grawe et al. (submitted) within the framework of the German Coastal Engineering Research Council AufMod project ("Aufbau integrierter Modellsysteme zur Analyse der langfristigen Morphodynamik in der Deutschen Bucht"). In these papers, the sediment data was compiled and harmonized from various sources and developed approximation and interpolation methods. The exposure time, distance to inlet and distance to gullies were calculated with the use of the bathymetry with scale of 200 × 200 m. This bathymetry was based on a data set that was made available by Rijkswaterstaat (resolution 50 m). Both the bathymetry as the calculated exposure time, distance to inlet and distance to gullies were constructed by Folmer et al. (submitted) and Grawe et al. (submitted). There are missing environmental variables, such as food availability and influences of river run-off, for which there is no data available. For this research, therefore, we divided the Wadden Sea into tidal basins according to Kraft et al. (2011) for comparative research (Figure 1 and Table 1). Tidal basin was used as a proxy in an attempt to capture most of the missing environmental variables that are not covered in the local environmental variables (Zimmerman, 1976; Dastgheib et al., 2008).

Cockle growth analysis

The growth of the cockle was described by the Gallucci and Quinn (1979) growth parameter and calculated with the use of the Von Bertalanffy growth function (VBGF) parameters. The VBGF can be mathematically expressed for shell length (L; mm) as:

$$(1)\quad L_t = \mathrm{L}_\infty(1 - e^{-K*(t-t_0)})$$

This VBGF describes the shell length of the Cockle (L_t; mm) as a function of the age of the Cockle (t; yr), growth constant (K; yr^{-1}), the maximum asymptotic shell length (L_∞; mm) and the time where the shell length is zero (t_0) (Appeldoorn, 1983). The growth parameter ω (mm yr^{-1}; Gallucci and Quin, 1979), is mathematically expressed as:

$$(2)\ \omega = K * L_\infty$$

Pauly (1979) described a negative correlation between $Ln(K)$ and $Ln(L_\infty)$ and suggested a measurement of growth of $W = Ln(\omega) = Ln(K * L_\infty)$. The Gallucci and Quin growth parameter (ω) is equivalent to the immediate growth at t_0 in mm yr^{-1} and unlike the individual parameters, indicates a fundamental difference in the growth instead of a mutual change in K and L_∞ (Gallucci and Quinn, 1979; Pauly, 1979; Appeldoorn, 1983).

After an initial data exploration where the outliers were removed (Zuur et al., 2010), the VBGF parameters were fitted from the shell length and the age of the cockle for every sampling year and sampling point. We fitted this VBGF per measuring year; this means that at least three different ages per sampling location per measuring year were needed. The fitting of the VBGF per cohort resulted in less successful fits and a decreased fit accuracy, this method was therefore not used. The fit was performed by the use of the nonlinear least squares Levenberg-Marquardt algorithm with the use of the Minpack.LM package (Elzhov et al., 2013) in R 3.1.2 (R Development Core Team, 2015). Subsequently the negative correlation of K and L_∞ was tested and the VBGF parameters were used to calculate the growth parameter W.

Model

We modelled the relationship between the growth parameter W and explanatory variables with the Generalized Additive Model (GAM) approach using the package mgcv (Wood, 2015) in R. For the GAM, all possible models were tested with a combination of sampling year and tidal basin as factors and the 6 other environmental influences, i.e. median grain size, salinity, exposure time, distance to tidal inlet, distance to gully and cockle density, as smoothers due to the unknown relationship (Table 2).

The year in which the samples were taken was used as a proxy for the annual differences in environmental conditions such as temperature and food availability. The sampling year was used in every input due to a known annual variability in growth, this variability was expected to be seen in the influence of this parameter in the model (Kristensen, 1958; Seed and Brown, 1978). The exposure time (Montaudouin, 1996; Compton et al., 2013a), density of the cockle (Jensen, 1992), distance to tidal inlet and more specifically distance to the gully (Cadée, 1980) were all expected to have a negative influence on the growth rate. On the other hand, the median grain size was expected to have a positive influence on the growth, i.e. coarse sediment favours cockle growth (Appeldoorn, 1983; Cardoso et al., 2006). For the salinity, however, both high and low salinities were expected to have a negative influence on the growth rate (Kristensen, 1958). The tidal basin was expected to have a variable influence on the growth parameter.

For the data exploration of the environmental variable we followed the procedure of Zuur (2012). During this exploration, the cockle density was log-transformed to create a normal distribution. The multicollinearity in the environmental variables was checked with the calculation of the VIF values, where a VIF value higher than 10 gives a strong indication of multicollinearity. The assumptions are not violated by this multicollinearity but it does affect the significance of the parameter estimates of the model because it increases the standard error of the parameter estimates (Lin, 2008). The models were also validated according to Zuur (2012); histograms and QQ-plots where created to check the normality, the homogeneity was assessed by verifying the consistency of the spread in a residuals vs. fitted values plot, the independence was verified by plotting the residuals versus each covariate and the Cook's distance values where used to check for influential observations.

To select the best model, we used the Akaike information criterion where the lowest AIC (AIC_{min}) is the best model (Akaike, 1973). However, because models with a ΔAIC ($\Delta AIC = AIC - AIC_{min}$) lower than two still have substantial support, we will use the model that has substantial support and the lowest complexity, i.e. number of factors and/or smoothers (Burnham and Anderson, 2004).

Growth map

The best model was used to construct a map of the growth parameter based on the environmental variables. The modelled growth parameters were plotted versus the calculated growth parameters to visualize the accuracy of the fit. Due to local disturbances that were not included in the model (e.g. predation, interspecific competition), a larger variation in the observed growth parameters is expected. The growth parameter will be extrapolated to areas where cockles are absent; the cockle density can therefore not be used for this extrapolation. The extrapolation was constructed for grid cells based on the values of the predictor variables for each cell. The extrapolated growth parameters were used to calculate the modelled range of the Gallucci and Quinn (1979) growth parameter (ω; mm yr^{-1}). This Gallucci and Quinn (1979) growth parameter was calculated as: $\omega = e^{W}$.

Results

Growth analysis

The VBGF was fitted on 322 samples and based on these fits; the parameters of the VBGF were calculated (Figure 2). Most of these samples are located at the eastern Wadden Sea, for only a few sampling locations it was possible to fit the VBGF for multiple years. The parameters of the VBGF, shown in figure 3, confirm the negative correlation between Ln(K) and $Ln(L_\infty)$ found by Pauly (1979). With these VBGF parameters, the growth parameter W is calculated. Neither the mapped growth parameter (Figure 4a) nor the amount of cockles present at the sampling locations in all years (Figure 4b), show a spatial pattern. In fact, neighbouring sampling points can differ substantially in growth or presence. The mapped growth parameter does show that there are more samples fitted on the eastern Wadden Sea.

Model

The highest VIF value of 2.81 showed that there was no significant multicollinearity present between the explanatory variables (Table 2). The residuals did not show any dependence and the model validation based on Zuur (2012) showed no evidence of strong violation of the model assumptions.

All explanatory variables were included as smoothers in all possible combinations in the input of the GAM (Appendix S1). The lowest AIC per complexity shows that a model containing four variables has the AIC_{min} and that models with three, five and six environmental variables have substantial support (Figure 5).

Model 52 containing the median grain size, distance to gully and the Ln(density) as environmental smoothers and the sampling year as factor has the best fit ($\Delta AIC = 0$). This fit explains 14.6% of the observed variance with p-values for both the median grain size and the distance to gullies higher than 0.1 and for the Ln(density) lower than 0.05. The model shows significant variations in the sampling years as can be seen in Table 3. Model 62 containing the distance to inlet, distance to gully and Ln(density) as environmental smoothers and sampling year as factor has an $\Delta AIC < 2$ (1.710). This model explains 14.7% of the observed variance and has p-values lower than 0.1 for distance to gully and Ln(density) but higher than 0.3 for distance to inlet (Table 3).

Model 16, containing the median grain size and the distance to gully as environmental smoothers and sampling year as factor, has both a ΔAIC lower than two (1.965) as the lowest complexity. This model explains 13.5% of the observed variance and has p-values higher than 0.1 for both median grain size as the distance to gully (Table 3). Figure 6c shows that both high (> 160μm) as low (< 140μm) median grain sizes have a positive influence on the growth parameter while figure 6b shows that the distance to the gully a negative influence has on the growth parameter. The sampling year shows that only the year 2009 has a negative influence while 2010 till 2014 have a large positive influence, the year 2010 has the most general influence on the growth parameter (Figure 6a).

Growth map

To construct the map of the growth parameter on the Dutch Wadden Sea (Figure 7), model 16 was used because it has a $\Delta AIC < 2$ (1.965) and has the lowest complexity. Thereby, model 16 contains two environmental parameters that could be extrapolated to intertidal areas where no cockles were present. For the construction of this map, the year that had the most general influence on the growth parameter (year 2010, figure 6a) is used.

Growth appeared to be especially fast close to the coast at the western tidal inlets (Marsdiep, Eijerlandse Gat and Vliestroom) and south of the island of Borkum. Growth was relatively slow at the tidal divides (Figure 7 and Appendix S2). The accuracy of the model is shown in figure 8 where a larger range can be seen in the observed growth parameters as was expected. Despite this difference in range, the slope of the regression line is close to 1. This indicates that a change in the calculated growth parameter probably coincide with an equal change in the modelled growth parameter. The range of the Gallucci and Quinn (1979) growth parameter ω ($mm\ yr^{-1}$) in the model was also calculated (Figure 9). This shows that this growth parameter varies from 18.88 till 85.84 $mm\ yr^{-1}$ with the highest abundance between 20 and 30 $mm\ yr^{-1}$.

Discussion

Growth

The growth parameter of cockles on the Dutch Wadden Sea is calculated from the maximum asymptotic length and the growth constant of the VBGF. These parameters were fitted on the on the population of cockles per year that are present on a location. The growth of a population might differ from the individual growth due to among other size dependent mortality (Andresen et al., 2013). An example is the size-selective predation: shore crabs favour relatively small cockles while most birds selectively consume the larger cockles from the population (Sanchez-Salazar et al., 1987). From the maximum asymptotic length and the growth constant we calculated the growth as Pauly (1979) suggested by taking the natural logarithm of the Gallucci and Quin growth parameter ω. This modification on ω was based on the negative correlation between Ln(K) and Ln(L_∞) as was also seen in our data.

The relationship of the cockle growth with the local environmental conditions was predicted by means of a Generalized Additive Model (GAM). It cannot be excluded that environmental conditions other than the used explanatory variables, influence the cockle growth. This might result in an overestimation of the influences of the used explanatory variables. For example: we did use multiple environmental variables, e.g. tidal basin, distance to gully and distance to inlet, as proxies for the water quality but the absolute data on water quality does not exist and is therefore not incorporated in the GAM. In addition, the growth parameter of the cockles is calculated on a year to year basis, in contrast to the averaged local environmental conditions. It is however known, that some environmental variables like the grain size can vary between years (Sha, 1989).This might result in an overestimated influence of the sampling year and an underestimated influence of the other environmental variables.

The relationship between the environmental conditions and the growth parameter was used to extrapolate the cockle growth on the intertidal flats of the entire Dutch Wadden Sea. Most of the samples where the growth parameter could be calculated are located at the eastern part of this area. The relationship between the environmental conditions and the growth parameter is therefore mainly based on this eastern Dutch Wadden Sea. The fit of the extrapolation might therefor be better in this area.

Growth and environmental conditions

Growth showed to be correlated, according to the best usable model, to the sampling year, mean grain size of the sediment and the distance to the gully. As expected, there was a high variability between years what might be caused by the differences in environmental conditions such as temperature and food availability (Smaal and Haas, 1997; Wijsman and Smaal, 2011; Philippart et al., 2014). Apart from 2009, all sampling years appear to show a slightly increasing positive correlation with the growth parameter until 2014. The data for the sampling year 2014 is not complete because not all samples of this year are processed yet. This gap in data might affect the influence of this sampling year on the growth parameter. The growth of the cockle is as expected positively influenced by coarser sediment. The coarser sediment not only allows drainage and exchange of the water. The heavier and thus coarser the sediment, the less it is resuspended in the water column and it therefore also has a positive influence on the filtration efficiency (Appeldoorn, 1983; Cardoso et al., 2006). It is however surprising that a positive influence increases when the median grain size gets smaller than 140µm. This positive influence might either be the result of an increase in stability due to the consolidation of fine sediment or the result of the tidal resuspension of not only the sediment but also microphytobenthos that is bound to these sediments (Roman and Tenore, 1978; Grabowski et al., 2011). This resuspension of the microphytobenthos results in an increase in food abundance for the cockle (de Jonge and van Beusekom, 1995). The negative influence of the distance to the gullies on the growth parameter was expected; this is due to the food availability. High densities of cockles can filter nearly all the suspended matter that is present, so with a larger distance to the gullies (the source of the suspended matter), more filter feeders had the chance to filter the water (Cadée, 1980; Kamermans, 1993).

Growth map

The extrapolation showed that a large range in growth, 18.88 till 85.85 mm yr^{-1}, is possible. Fast growth is predicted close to tidal inlets and the larger gullies. This distribution is caused by relatively large median grain size due to the high flow velocities that these locations encounter, and low distances to the gully (Ridderinkhof, 1988; Flemming and Ziegler, 1995). The tidal divides however have low flow velocities thus low median grain size and a high distance to the gully, this causes slow predicted growth. Close to the western tidal inlets (Marsdiep, Eijerlandse Gat and Vliestroom) and south of the island of Borkum, particularly rapid predicted growth can be seen. This fast growth is due to the presence of especially large grain size compared to the grain size of the sample locations that were used to create the model. The predicted growth on these areas is therefore an extrapolation based on just a few points.

The extrapolated growth parameter shows that a fast predicted growth does not always coincide with the presence of cockles. Some of the earlier mentioned fast predicted growth areas have an absence of cockles. This might indicate that the presence of the cockle cannot be solely predicted by good growth conditions but might also be explained by other influences like the settlement and survival of cockles, local dynamics and fishery (Montaudouin, 1997; Piersma et al., 2001). For example: locations with high flow velocities contain most of the fast predicted growth due to the large grain size that is present at these areas. But an increase in flow velocity results in a decrease in settling opportunity, an increase in the chance of secondary settlement and therefor it decreases the presence of cockles (Montaudouin, 1997; Montaudouin et al., 2003).

Implications

The relationships between the environmental conditions and the growth parameter are used as predictor variables in the model. These environmental variables can be either true influential variables or proxies for other factors that we did not incorporate in the model, such as the earlier mentioned food availability. The model derived effects of the predictor variables can show what is needed for optimal growth if the predictor variables are in fact the real influential environmental variables. These variables can then also be used as a guide for the design of a cockle cultivation area. The model can still be used to extrapolate the growth parameter spatially if the predictor variables are a proxy of actual influential environment variables. This extrapolation will then provide an indication of the local water quality for cockle growth. Further laboratory experiments must be done to identify the true influences of the environmental conditions.

Conclusion

Based on the model, the main influential variable on the growth of the cockle are: the variation between years, the median grain size and the distance to the gullies. However, these environmental variables can be either true influential variables or proxies for other environmental variables that we did not incorporate in the model. This difference needs to be known for the cultivation of the cockle, therefore further research must be done to identify the true environmental influences on cockle growth. The predicted growth map of the cockle on the Dutch Wadden Sea is the first step in identifying potential areas for cockle cultivation.

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References

Akaike, H., 1973. Information Theory And An Extension Of The Maximum Likelihood Principle By Hirotogu Akaike. Second Int. Symp. Inf. Theory 267–281. doi:10.1007/978-1-4612-1694-0_15

Andresen, H., Dorresteijn, I., van der Meer, J., 2013. Growth and size-dependent loss of newly settled bivalves in two distant regions of the Wadden Sea. Mar. Ecol. Prog. Ser. 472, 141–154. doi:10.3354/meps10011

Appeldoorn, R.S., 1983. Variation in the growth rate of Mya arenaria and its relationship to the environment as analyzed through principal components analysis and the W parameter of the von Bertalanffy equation. United States, Department of Commerce, National Oceanic and Atmosph. Fish. Bull. 81, 75–84.

Bertalanffy, L. Von, 1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 10, 181–213.

Beukema, J.J., Dekker, R., 2006. Annual cockle Cerastoderma edule production in the Wadden Sea usually fails to sustain both wintering birds and a commercial fishery. Mar. Ecol. Prog. Ser. 309, 189–204.

Beukema, J.J., Essink, K., Michaelis, H., Zwarts, L., 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: How predictable is this food source for birds? Netherlands J. sea Res. 31, 319–330.

Bijleveld, A.I., van Gils, J. a., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W., Piersma, T., 2012. Designing a benthic monitoring programme with multiple conflicting objectives. Methods Ecol. Evol. 3, 526–536.

Boere, G.C., Piersma, T., 2012. Flyway protection and the predicament of our migrant birds: A critical look at international conservation policies and the Dutch Wadden Sea. Ocean Coast. Manag. 68, 157–168.

Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol. Methods Res. 33, 261–304. doi:10.1177/0049124104268644

Cadée, G., 1980. Reappraisal of the production and import of organic carbon in the western Wadden Sea. Netherlands J. sea Res. 14, 225–226.

Cardoso, J.F.M.F., Witte, J.I., van der Veer, H.W., 2006. Intra- and interspecies comparison of energy flow in bivalve species in Dutch coastal waters by means of the Dynamic Energy Budget (DEB) theory. J. Sea Res. 56, 182–197. doi:10.1016/j.seares.2006.03.011

Compton, T.J., Bowden, D. a., Roland Pitcher, C., Hewitt, J.E., Ellis, N., 2013. Biophysical patterns in benthic assemblage composition across contrasting continental margins off New Zealand. J. Biogeogr. 40, 75–89.

Compton, T.J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H.W., Piersma, T., 2013a. Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. J. Sea Res. 82, 103–116.

Compton, T.J., van der Meer, J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Klunder, L., McSweeney, N., Brugge, M., van der Veer, H.W., Piersma, T., 2013b. Synoptic Intertidal Benthic Surveys across the Dutch Wadden Sea 2008 to 2011; NIOZ 2013-1.

Dastgheib, A., Roelvink, J.A., Wang, Z.B., 2008. Long-term process-based morphological modeling of the Marsdiep Tidal Basin. Mar. Geol. 256, 90–100.

de Jonge, V.N., van Beusekom, J.E.E., 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. Limnol. Oceanogr. 40, 776–778. doi:10.4319/lo.1995.40.4.0776

Elzhov, T. V, Mullen, K.M., Spiess, A., Bolker, B., Mullen, M.K.M., 2013. R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds.

Fedoroff, N. V., Battisti, D.S., Beachy, R.N., Cooper, P.J.M., Fischhoff, D.A., Hodges, C.N., Knauf, V.C., Lobell, D., Mazur, B.J., Molden, D., Reynolds, M.P., Ronald, P.C., Rosegrant, M.W., Sanchez, P.A., Vonshak, A., Zhu, J.-K., 2010. Radically Rethinking Agriculture for the 21st Century. Science 327, 833–834. doi:10.1126/science.1186834

Flemming, B., Ziegler, K., 1995. High-Resolution Grain Size Distribution Patterns and Textural Trends in the Backbarrier Environment of Spiekeroog Island (Southern North Sea). Senckenbergiana maritima 26, 1–24.

Gallucci, V.F., Quinn II, T.J., 1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108, 14–25.

Ginkel, R. van, 2001. The Netherlands, in: D. Symes and J. Phillipson (eds.), Inshore Fisheries Management. Kluwer Academic Publishers, Dordrecht, pp. 79–96.

Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: The importance of sediment properties. Earth-Science Rev. 105, 101–120. doi:10.1016/j.earscirev.2011.01.008

Jensen, K., 1992. Dynamics and growth of the cockle, Cerastoderma edule, on an intertidal mud-flat in the Danish Wadden Sea: effects of submersion time and density. Netherlands J. sea Res. 28, 335–345.

Kamermans, P., 1993. Food limitation in cockles (Cerastoderma edule (L.)): Influences of location on tidal flat and of nearby presence of mussel beds. Netherlands J. sea Res. 31, 71–81. doi:10.1016/0077-7579(93)90019-O

Kraan, C., Dekinga, A., Folmer, E.O., Veer, H.W. Van Der, 2007. Macrobenthic fauna on intertidal mudflats in the Dutch Wadden Sea : Species abundances , biomass and distributions in 2004 and 2006. NIOZ Rep. 2.

Kraft, D., Folmer, E., Meyerdirks, J., Stiehl, T., 2011. Data inventory of the tidal basins in the trilateral Wadden Sea, Programma naar een Rijke Waddenzee.

Kristensen, I., 1958. Differences in Density and Growth in a Cockle Population in the Dutch Wadden Sea. Arch. Néerlandaises Zool. 12, 351–453.

Lee, J.-Y., Song, S.-H., 2006. Evaluation of groundwater quality in coastal areas: implications for sustainable agriculture. Environ. Geol. 52, 1231–1242. doi:10.1007/s00254-006-0560-2

Lin, F.-J., 2008. Solving Multicollinearity in the Process of Fitting Regression Model Using the Nested Estimate Procedure. Qual. Quant. 42, 417–426.

Montaudouin, X. De, 1997. Potential of bivalves' secondary settlement differs with species: a comparison between cockle (Cerastoderma edule) and clam (Ruditapes philippinarum) juvenile resuspension. Mar. Biol. 128, 639–648.

Montaudouin, X. De, 1996. Factors involved in growth plasticity of cockles Cerastoderma edule (L.), identified by field survey and transplant experiments. J. Sea Res. 36, 251–265.

Montaudouin, X. De, Bachelet, G., Sauriau, P.G., 2003. Secondary settlement of cockles Cerastoderma edule as a function of current velocity and substratum: a flume study with benthic juveniles. Hydrobiologia 503, 103–116. doi:10.1023/B:HYDR.0000008493.83270.2d

Pauly, D., 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy´s growth formula. Berichte aus dem Inst. für Meereskd. Kiel.

Pauw, P., De Louw, P.G.B., Oude Essink, G.H.P., 2012. Groundwater salinisation in the Wadden Sea area of the Netherlands: Quantifying the effects of climate change, sea-level rise and anthropogenic interferences. Geol. en Mijnbouw/Netherlands J. Geosci. 91, 373–383. doi:10.1017/S0016774600000500

Philippart, C.J.M., van Bleijswijk, J.D.L., Kromkamp, J.C., Zuur, a. F., Herman, P.M.J., 2014. Reproductive phenology of coastal marine bivalves in a seasonal environment. J. Plankton Res. 36, 1512–1527.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R., Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. J. Appl. Ecol. 38, 976–990.

Pitman, M.G., Läuchli, A., 2002. Global Impact of Salinity and Agricultural Ecosystems, in: Läuchli A, Lüttge U, Eds. Salinity: Environment - Plants - Molecules. Kluwer, Dordrecht, pp. 3–20. doi:10.1007/0-306-48155-3_1

Pronker, A.E., Peene, F., Donner, S., Wijnhoven, S., Geijsen, P., Bossier, P., Nevejan, N.M., 2013. Hatchery cultivation of the common cockle (Cerastoderma edule L.): From conditioning to grow-out. Aquac. Res. 2005, 302–312. doi:10.1111/are.12178

Qadir, M., Ghafoor, A., Murtaza, G., 2000. Amelioration strategies for saline soils: a review. L. Degrad. Dev. 11, 501–521. doi:10.1002/ldr.458

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

Reise, K., 2005. Coast of change: habitat loss and transformations in the Wadden Sea. Helgol. Mar. Res. 59, 9–21. doi:10.1007/s10152-004-0202-6

Reise, K., Baptist, M., Burbridge, P., Dankers, N., Fischer, L., Flemming, B., Oost, A.P., Smit, C., 2010. The Wadden Sea – A Universally Outstanding Tidal Wetland. Wadden Sea Ecosyst. 29, 7–24.

Ridderinkhof, H., 1988. Tidal and residual flows in the Western Dutch Wadden Sea I: Numerical model results. Netherlands J. sea Res. 22, 1–21. doi:10.1016/0077-7579(88)90049-X

Roman, M.R., Tenore, K.R., 1978. Tidal resuspension in Buzzards Bay, Massachusetts:: I. Seasonal changes in the resuspension of organic carbon and chlorophyll a. Estuar. Coast. Mar. Sci. 6, 37–46. doi:10.1016/0302-3524(78)90041-5

Sanchez-Salazar, M.E., Griffiths, C.L., Seed, R., 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle, Cerastoderma edule. Estuar. Coast. Shelf Sci. 25, 245–260. doi:10.1016/0272-7714(87)90125-9

Seed, R., Brown, R.A., 1978. Growth as a strategy for survival in two marine bivalves, Cerastoderma edule and Modiolus modiolus. J. Anim. Ecol. 47, 283–292.

Sha, L.P., 1989. Sand transport patterns in the ebb-tidal delta off Texel Inlet, Wadden Sea, The Netherlands. Mar. Geol. 86, 137–154. doi:10.1016/0025-3227(89)90046-7

Smaal, A.C., Haas, H.A., 1997. Seston Dynamics and Food Availability on Mussel and Cockle Beds. Estuar. Coast. Shelf Sci. 45, 247–259.

Swart, J.A.A., van Andel, J., 2008. Rethinking the interface between ecology and society. The case of the cockle controversy in the Dutch Wadden Sea. J. Appl. Ecol. 45, 82–90.

van Leeuwe, M., Folmer, E.O., Dekinga, A., Kraan, C., Meijer, K., Piersma, T., 2008. Staat handkokkelvisserij op gespannen voet met behoud biodiversiteit in de Waddenzee? Levende Nat. 109, 15–19.

Waddenfonds, 2014. Project Kokkelteelt in polder Wassenaar [WWW Document]. URL http://www.waddenfonds.nl/Projecten_detail.2918+M53f748b6b09.0.html (accessed 12.29.15).

Wijsman, J.W.M., Smaal, A.C., 2011. Growth of cockles (Cerastoderma edule) in the Oosterschelde described by a Dynamic Energy Budget model. J. Sea Res. 66, 372–380.

Wood, S., 2015. Mixed GAM Computation Vehicle with GCV/AIC/REML Smoothness Estimation.

Zimmerman, J.T.F., 1976. Mixing and flushing of tidal embayments in the western Dutch Wadden Sea part I: Distribution of salinity and calculation of mixing time scales. Netherlands J. sea Res. 10, 149–191. doi:10.1016/0077-7579(76)90013-2

Zuur, A.F., 2012. A Beginner's Guide to Generalised Additive Mixed Models with R. Highland Statistics Ltd., Newburgh.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.

Tables

Table 1. The area, percentage of intertidal area and average depth of the tidal basins in the Dutch Wadden Sea (Kraft et al., 2011).

Tidal Basin	**Total Area (km^2)**	**Intertidal (%)**	**Average depth (m)**
Marsdiep	678.22	20 – 36 %	3.4 - 4.8
Eierlandse Gat	158,27	59 – 72 %	3.4 - 4.8
Vlie	690,00	36 – 59 %	4.8 – 6.2
Amelander Zeegat	332,92	36 – 59 %	3.4 - 4.8
Pinkegat	61,56	72 – 86 %	0.6 – 2.0
Zoutkamperlaag	160,11	59 – 72 %	2.0 – 3.4
Eielander Balg	36,83	72 – 86 %	0.6 – 2.0
Lauwers	141,97	59 – 72 %	2.0 – 3.4
Schild	35,86	72 – 86 %	0.6 – 2.0
Eems-Dollard	570,34	36 – 59 %	6.2 – 7.6

Table 2. VIF values indicating a multicollinearity between the explanatory environmental variables.

Environmental variables	**VIF**
Sampling year	1.24
Tidal basin	2.81
Median grain size	1.90
Salinity	2.20
Exposure time	1.49
Distance to inlet	1.50
Distance to gully	1.26
Ln(Density of the cockle)	1.15

Table 3. The results for the best three models. The significance (p-value) and degrees of freedom (df) are given for each environmental variable. The adjusted R^2, percent of deviance explained and AIC are given for each model

Model	**Environmental variables**	**p-value**	**Year**			**df**	**R^2 adj**	**Deviance explained**	**AIC**	**ΔAIC**
16	Median grain size	0.116	2.96	2008	0	3.240	0.105	13.5%	478.831	1.965
				2009	-0.104					
				2010	0.175					
	Distance to gully	0.139		2011	0.246	3.097				
				2012	0.261					
				2013	0.328					
				2014	0.290					
52	Median grain size	0.174	2.94	2008	0	2.94	0.11	14.6%	476.866	0
				2009	-0.099					
	Distance to gully	0.113		2010	0.174	3.37				
				2011	0.294					
	Density	0.048		2012	0.315	1.00				
				2013	0.358					
				2014	0.306					
62	Distance to inlet	0.340	2.95	2008	0	4.01	0.11	14.7%	478.576	1.710
				2009	-0.096					
	Distance to gully	0.052		2010	0.161	3.53				
				2011	0.280					
	Ln(Density)	0.025		2012	0.294	1.00				
				2013	0.335					
				2014	0.286					

Figures

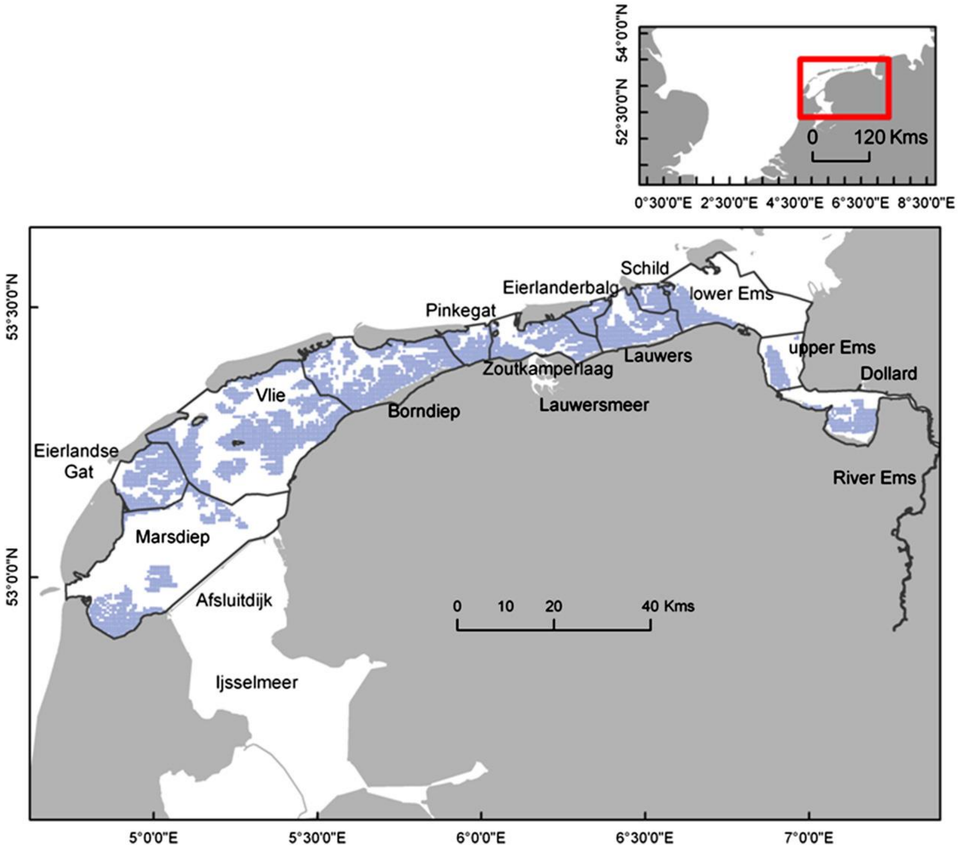


Figure 1. The locations of the sampling points of the SIBES monitoring programme across the Wadden Sea. The samples are taken during the summer period. The tidal basins are named and drawn in the map as the solid black lines. We use the classification of the tidal basins according to Kraft et al. (2011) where the three basins shown as lower, and upper Ems and Dollard are seen as one Tidal basin (Ems Dollard). The inset shows the Dutch Wadden Sea relative to The Netherlands (Compton, Holthuijsen, et al., 2013).

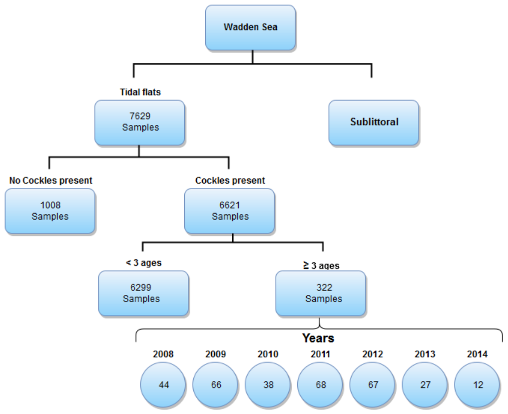


Figure 2. Number of samples that are in compliance with the conditions for the fit of the VBGF. Samples were only taken on tidal flats, and cockles needed to be present with at least three different ages per sampling location per year. The number of samples that are in compliance with the conditions per sampling year are also shown.

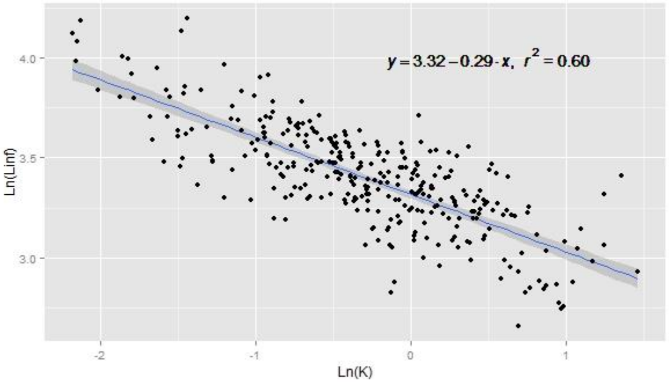


Figure 3. Correlation between the log VBGF parameters L_∞ and K with a regression line fit to all data. The regression line shows an R^2 of 0.60 and a p-value < 0.001.

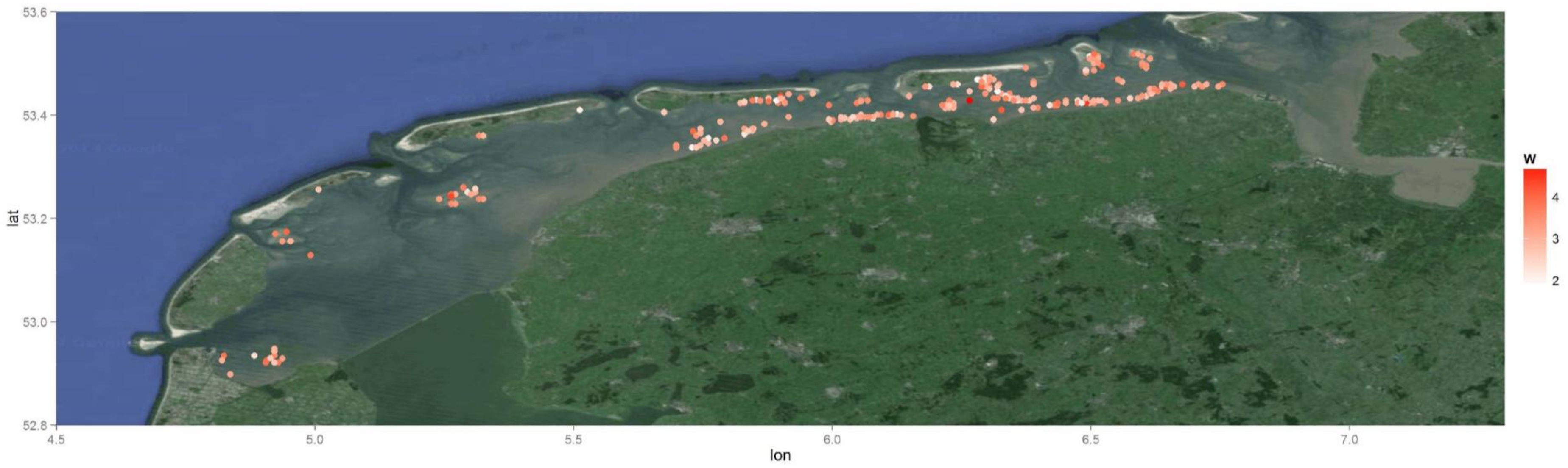


Figure 4a. The fitted growth parameter on the Dutch Wadden Sea. This growth parameter is equivalent to the immediate growth at t_0 in mm/yr and indicates a fundamental difference in the growth of the cockle. No spatial pattern can be seen despite the present variation.

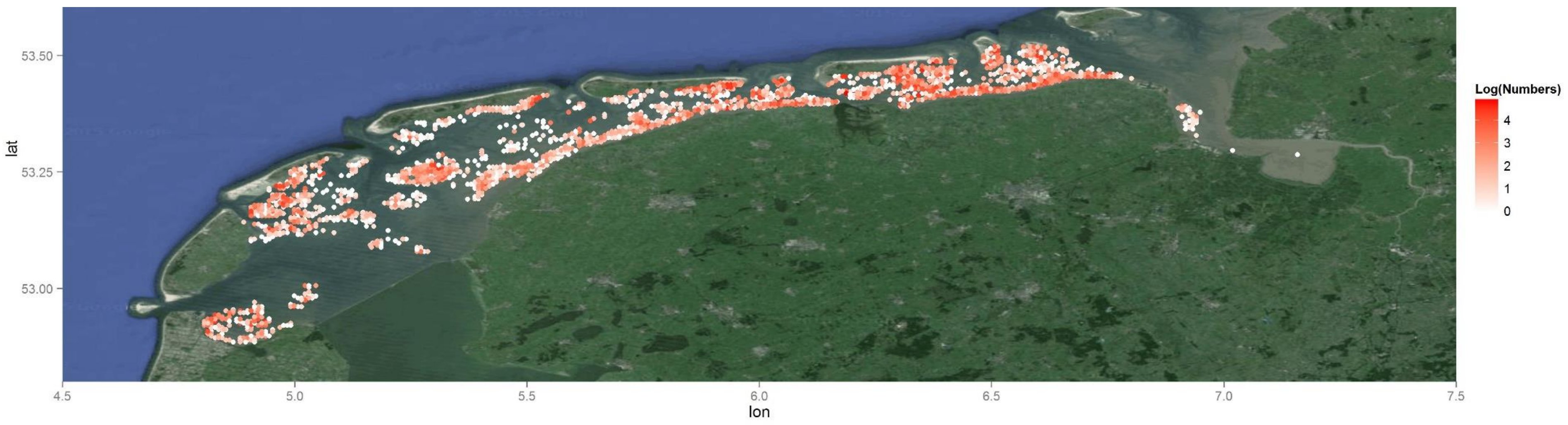


Figure 4b. The natural logarithm of the amount of cockles found at the SIBES sampling locations on the Dutch Wadden Sea in the years 2008 till 2014. It shows a large variation with apparent larger presence in the eastern Wadden Sea.

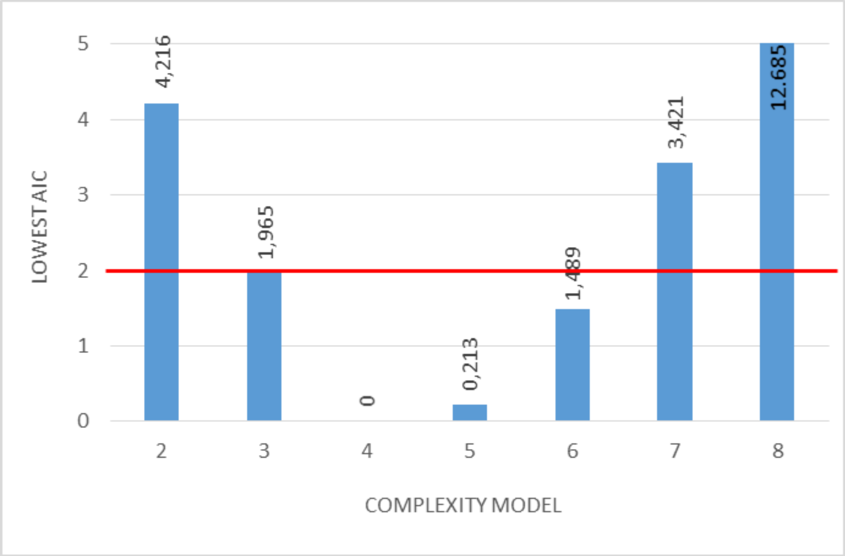


Figure 5. The lowest AIC per complexity shows that a model with 4 environmental variables has the lowest AIC. Models with three, five and six environmental variables have an AIC < 2 and have therefore substantial support, indicated by the red line.

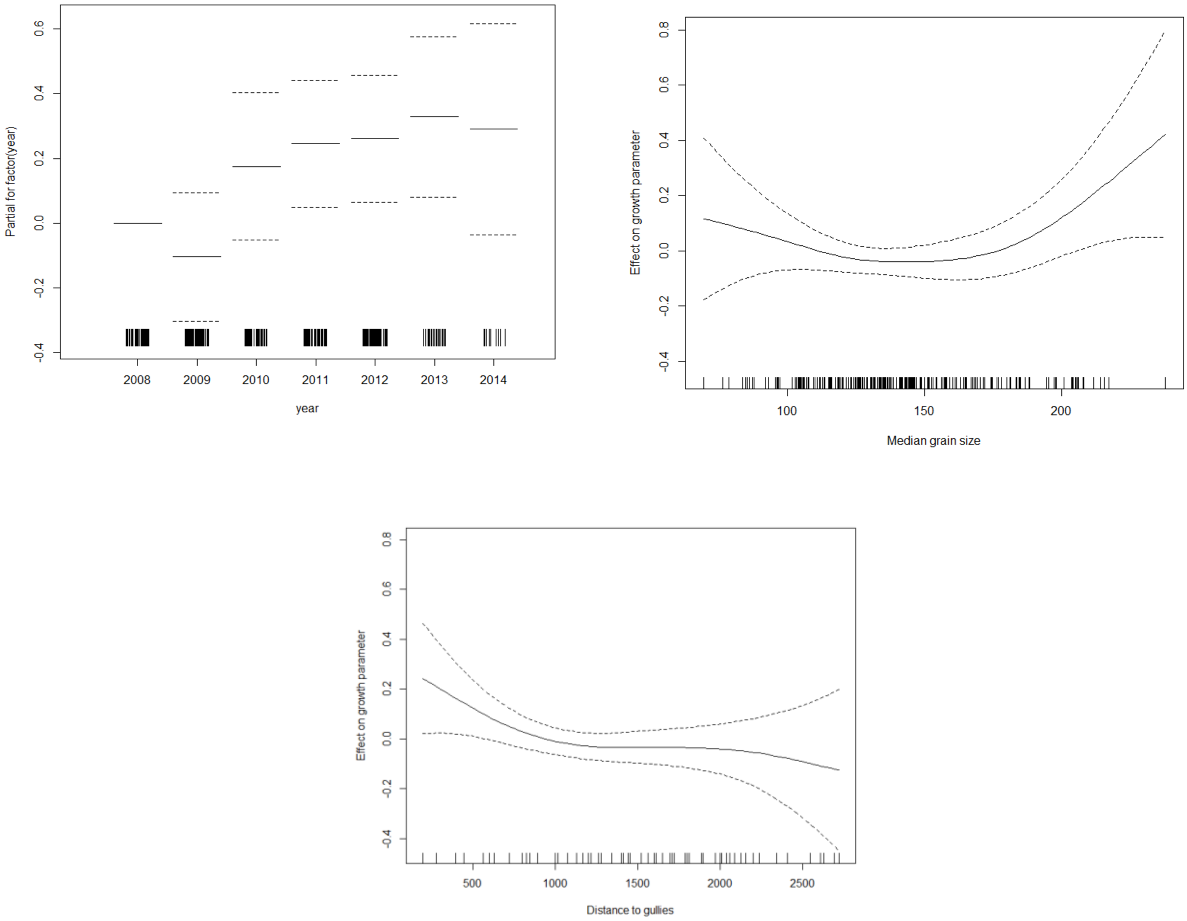


Figure 6. Generalized additive model (Model #16) derived effects of the (a) factor(year), (b) Distance to gullies and (c) Median grain size on the growth parameter. The y-axis is the normalized effect of the variable and the rugplot on the x-axis shows the number of observations. The dashed lines are the ± 2 standard error confidence belts.

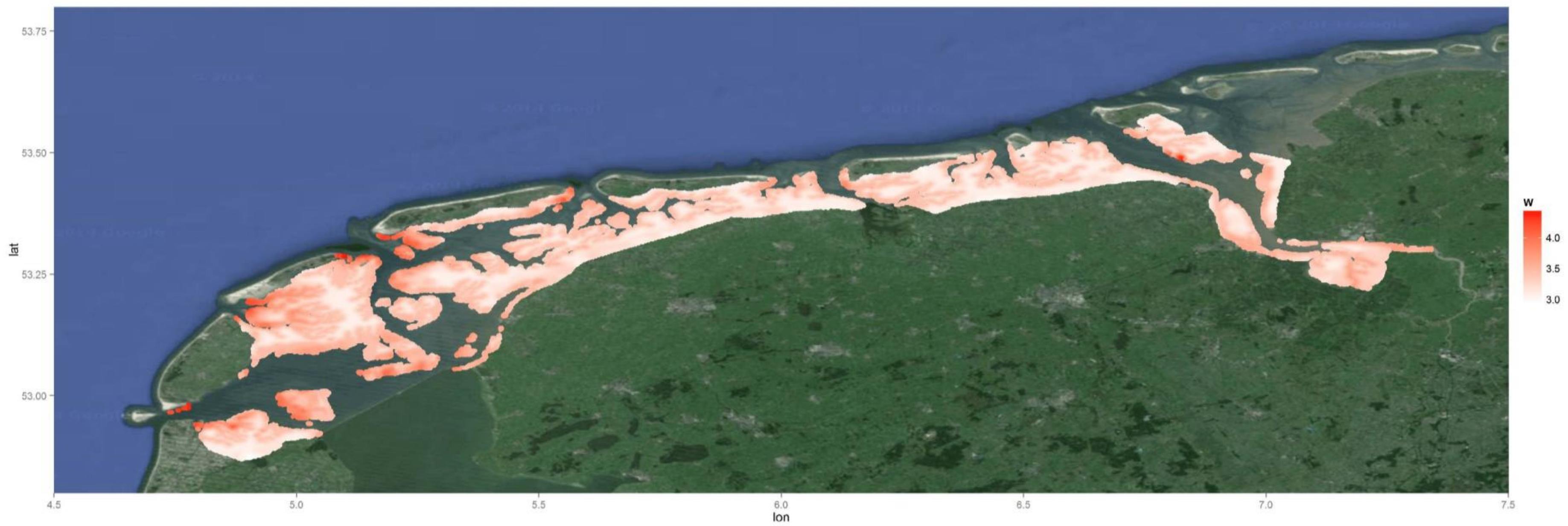


Figure 7. The growth parameter that is extrapolated over the Dutch Wadden Sea. The map is based on the best model that contains the sampling year, median grain size, distance to gully and the median density measured as explanatory variables. For this construction of the map, the year which has the most general influence on the growth parameter (year 2010) is used

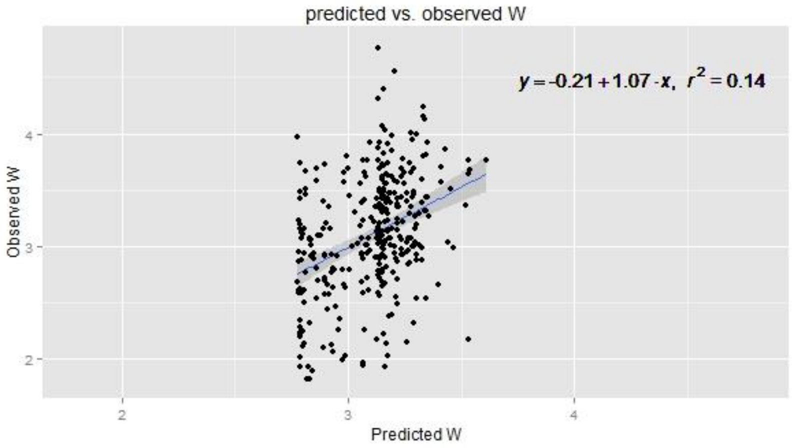


Figure 8. The modelled growth parameter compared against the calculated growth parameter with a regression line fit to all data. The regression line shows an R^2 of 0.14 and a p-value < 0.001.

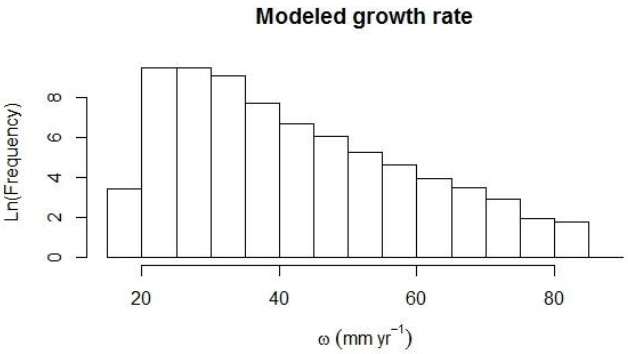


Figure 9. The frequency of the calculated Gallucci and Quin (1979) growth parameter calculated from the extrapolated growth parameter W.

Appendix

S1

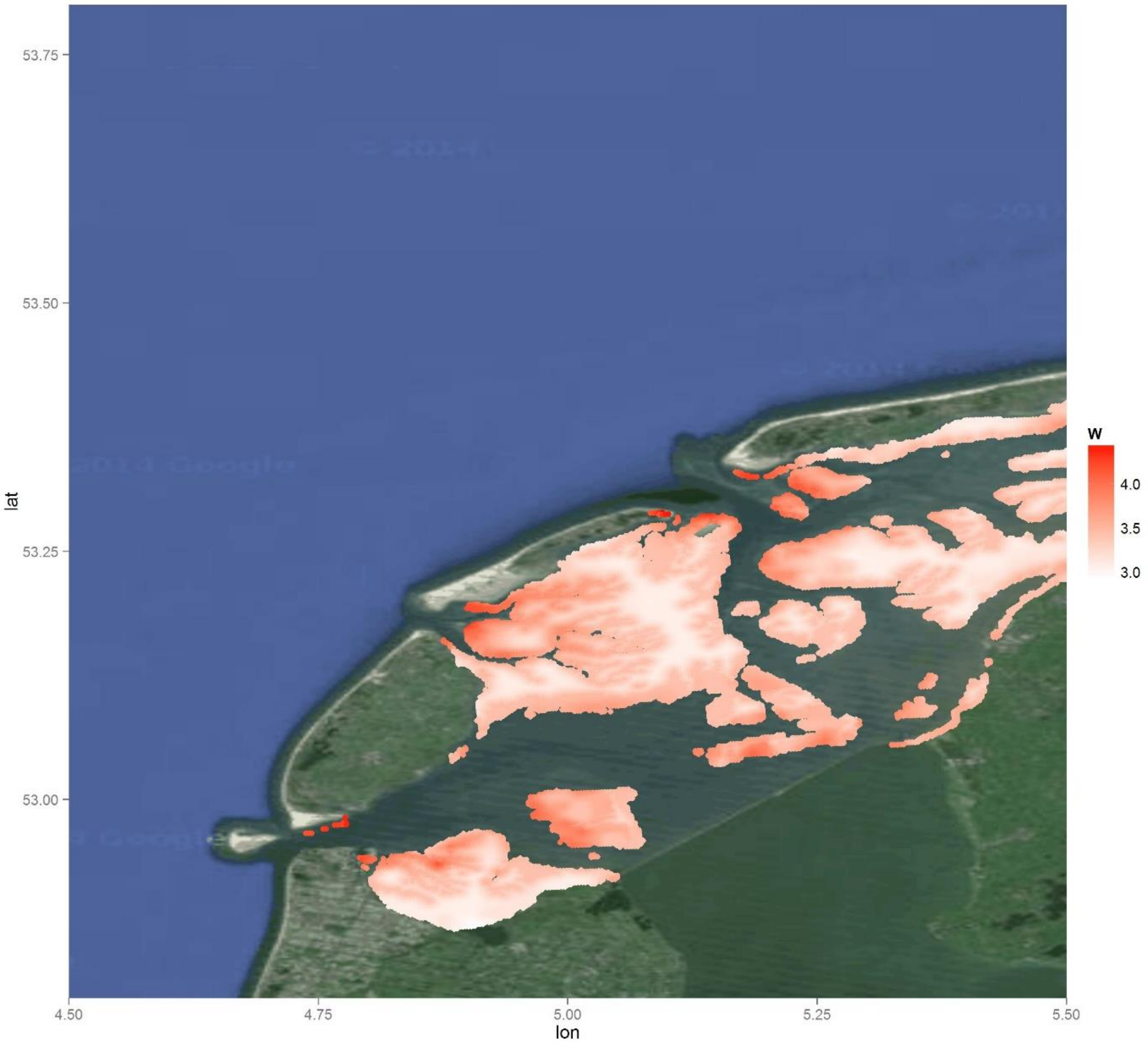
All possible combinations of explanatory variables were used as input of the GAM. The Akaike information criterion shows the best model where the highlighted bright yellow shows the AIC_{min} *and the dark yellow show all models with substantial support (AIC<2).*

Model number	**f(Sampling year)**	**f(Sub Area)**	**s(Median grain size)**	**s(Salinity)**	**s(Exposure time)**	**s(Distance to inlet)**	**s(Distance to gully)**	**s(Density of the Cockle)**	**AIC**	**ΔAIC**
1	X		X						488.446	11.580
2	X			X					486.473	9.607
3	X				X				481.964	5.098
4	X					X			481.082	4.216
5	X						X		484.791	7.925
6	X							X	487.000	10.134
7	X	X	X						490.827	13.961
8	X	X		X					491.584	14.718
9	X	X			X				490.031	13.165
10	X	X				X			489.094	12.228
11	X	X					X		489.418	12.552
12	X	X						X	488.368	11.502
13	X		X	X					482.845	5.979
14	X		X		X				482.418	5.552
15	X		X			X			481.697	4.831
16	X		X				X		478.831	1.965
17	X		X					X	479.791	2.925
18	X			X	X				487.544	10.678
19	X			X		X			488.329	11.463
20	X			X			X		482.978	6.112
21	X			X				X	484.115	7.249
22	X				X	X			485.793	8.927
23	X				X		X		483.929	7.063
24	X				X			X	485.528	8.662
25	X					X	X		481.995	5.129
26	X					X		X	483.680	6.814
27	X						X	X	478.919	2.053
28	X	X	X	X					492.792	15.926
29	X	X	X		X				490.955	14.089
30	X	X	X			X			490.591	13.725
31	X	X	X				X		490.551	13.685
32	X	X	X					X	489.468	12.602
33	X	X		X	X				491.668	14.802
34	X	X		X		X			490.989	14.123
35	X	X		X			X		491.306	14.440
36	X	X		X				X	490.132	13.266
37	X	X			X	X			488.09	11.224
38	X	X			X		X		490.598	13.732
39	X	X			X			X	487.217	10.351
40	X	X				X	X		489.33	12.464

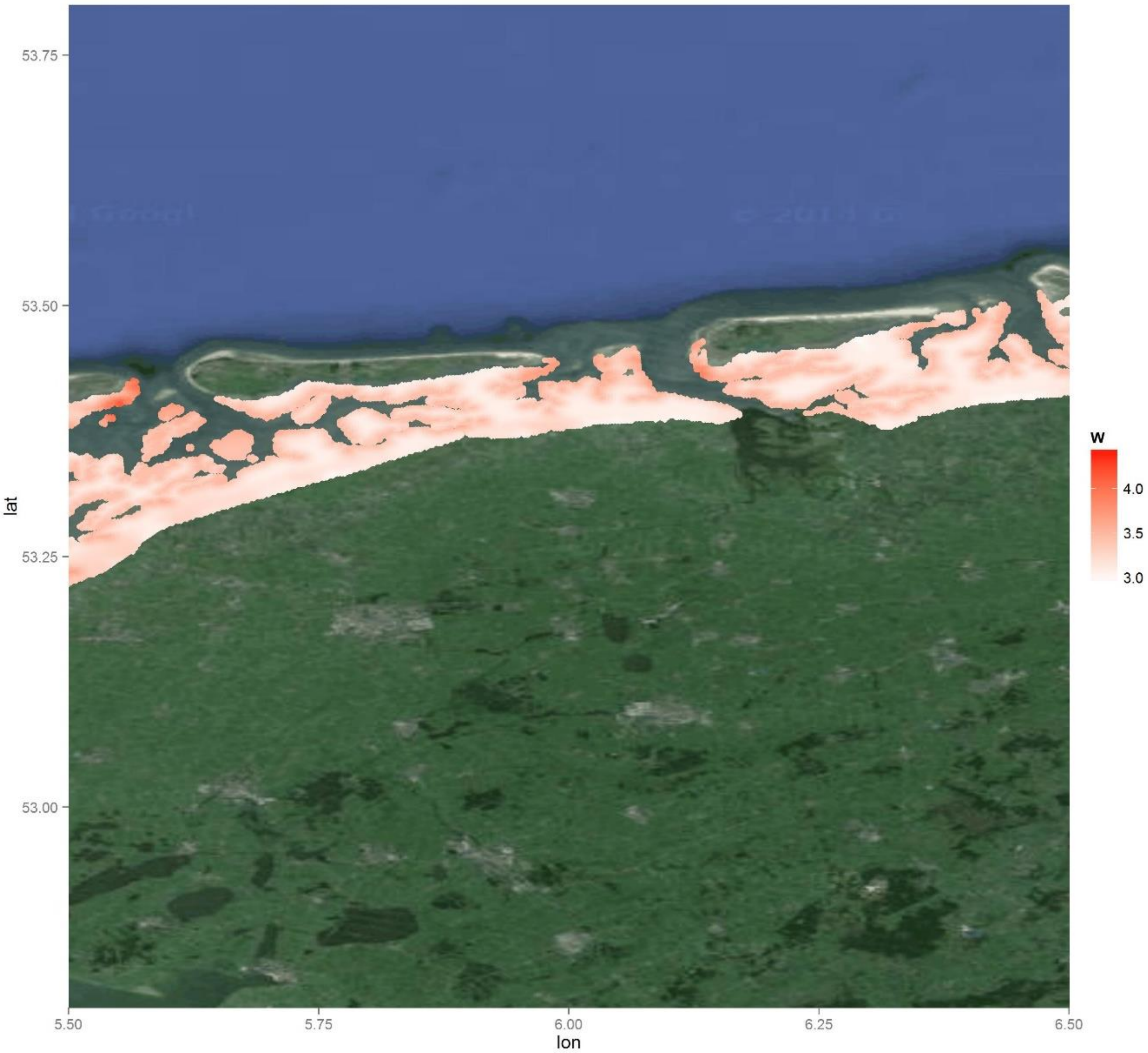
41	X	X				X		X	487.542	10.676
42	X	X					X	X	487.265	10.399
43	X		X	X	X				484.119	7.253
44	X		X	X		X			483.158	6.292
45	X		X	X			X		480.675	3.809
46	X		X	X				X	481.285	4.419
47	X		X		X	X			481.574	4.708
48	X		X		X		X		480.778	3.912
49	X		X		X			X	480.615	3.749
50	X		X			X	X		479.335	2.469
51	X		X			X		X	480.093	3.227
52	X		X				X	X	476.866	0
53	X			X	X	X			487.746	10.88
54	X			X	X		X		484.934	8.068
55	X			X	X			X	483.661	6.795
56	X			X		X	X		483.781	6.915
57	X			X		X		X	485.288	8.422
58	X			X			X	X	479.83	2.964
59	X				X	X	X		483.569	6.703
60	X				X	X		X	481.191	4.325
61	X				X		X	X	480.905	4.039
62	X					X	X	X	478.576	1.710
63	X	X	X	X	X				492.918	16.052
64	X	X	X	X		X			492.420	15.554
65	X	X	X	X			X		492.482	15.616
66	X	X	X	X				X	491.432	14.566
67	X	X	X		X	X			489.917	13.051
68	X	X	X		X		X		491.932	15.066
69	X	X	X		X			X	488.366	11.500
70	X	X	X			X	X		490.529	13.663
71	X	X	X			X		X	488.859	11.993
72	X	X	X				X	X	488.578	11.712
73	X	X		X	X	X			489.912	13.046
74	X	X		X	X		X		492.451	15.585
75	X	X		X	X			X	488.998	12.132
76	X	X		X		X	X		491.142	14.276
77	X	X		X		X		X	489.265	12.399
78	X	X		X			X	X	489.217	12.351
79	X	X			X	X	X		489.552	12.686
80	X	X			X	X		X	484.941	8.075
81	X	X			X		X	X	487.672	10.806
82	X	X				X	X	X	487.238	10.372
83	X		X	X	X	X			483.447	6.581
84	X		X	X	X		X		482.658	5.792
85	X		X	X	X			X	481.858	4.992
86	X		X	X		X	X		481.213	4.347
87	X		X	X		X		X	481.479	4.613
88	X		X	X			X	X	478.631	1.765
89	X		X		X	X	X		481.032	4.166
90	X		X		X	X		X	478.73	1.864
91	X		X		X		X	X	478.858	1.992
92	X		X			X	X	X	477.079	0.213
93	X			X	X	X	X		485.325	8.459

94	X			X	X	X		X	483.37	6.504
95	X			X	X		X	X	481.566	4.700
96	X			X		X	X	X	480.391	3.525
97	X				X	X	X	X	479.548	2.682
98	X	X	X	X	X	X			491.773	14.907
99	X	X	X	X	X		X		493.861	16.995
100	X	X	X	X	X			X	490.320	13.454
101	X	X	X	X		X	X		492.252	15.386
102	X	X	X	X		X		X	490.569	13.703
103	X	X	X	X			X	X	490.497	13.631
104	X	X	X		X	X	X		491.249	14.383
105	X	X	X		X	X		X	486.721	9.855
106	X	X	X		X		X	X	489.299	12.433
107	X	X	X			X	X	X	488.136	11.270
108	X	X		X	X	X	X		491.335	14.469
109	X	X		X	X	X		X	486.449	9.583
110	X	X		X	X		X	X	489.605	12.739
111	X	X		X		X	X	X	488.838	11.972
112	X	X			X	X	X	X	486.354	9.488
113	X		X	X	X	X	X		482.974	6.108
114	X		X	X	X	X		X	480.634	3.768
115	X		X	X	X		X	X	480.588	3.722
116	X		X	X		X	X	X	478.935	2.069
117	X		X		X	X	X	X	478.355	1.489
118	X			X	X	X	X	X	481.306	4.440
119	X	X	X	X	X	X	X		493.089	16.223
120	X	X	X	X	X	X		X	488.299	11.433
121	X	X	X	X	X		X	X	491.214	14.348
122	X	X	X	X		X	X	X	489.724	12.858
123	X	X	X		X	X	X	X	487.965	11.099
124	X	X		X	X	X	X	X	487.818	10.952
125	X		X	X	X	X	X	X	480.287	3.421
126	X	X	X	X	X	X	X	X	489.551	12.685

S2



The growth parameter that is extrapolated over the western part of the Dutch Wadden Sea. The map is based on the best model that contains the sampling year, median grain size, the distance to gully and the median density measured as explanatory variables. For this construction of the map, the year which has the most general influence on the growth parameter (year 2010) is used.



The growth parameter that is extrapolated over the middle part of the Dutch Wadden Sea. The map is based on the best model that contains the sampling year, median grain size, the distance to gully and the median density measured as explanatory variables. For this construction of the map, the year which has the most general influence on the growth parameter (year 2010) is used.

The growth parameter that is extrapolated over the eastern part of the Dutch Wadden Sea. The map is based on the best model that contains the sampling year, median grain size, the distance to gully and the median density measured as explanatory variables. For this construction of the map, the year which has the most general influence on the growth parameter (year 2010) is used.