ORIGINAL ARTICLE

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An analysis of mussel bed habitats in the Dutch Wadden Sea

Abstract A habitat suitability analysis for littoral mussel beds in the Dutch Wadden Sea was carried out. The analysis was based on the presence of mussel beds in the years 1960–1970, and a number of environmental characteristics: wave action, flow velocity, median grain size, emersion times and distance to a gully border. The habitat model describes mussel bed appearance quantitatively. It predicts the distribution of mussel beds quite well, as well as the distribution of spatfall in the years 1994 and 1996. From the analysis we found that wave action (maximum orbital velocity) was the main structuring factor. A low orbital velocity was preferred. Neither very low, nor maximum flow velocities were favourable for mussel beds. Very coarse sands or silty environments were not preferred. Sites close to the low water line showed lower mussel bed appearance; when emersion time was above 50%, hardly any mussel beds could be found. The habitat suitability analysis and the construction of a habitat suitability map was performed in the framework of the discussions on a further or reduced exploitation of the tidal flats in the Dutch Wadden Sea by cockle and mussel fishery activities.

Keywords Mussel beds · Tidal flats · Wave action · Sediment composition · Habitat suitability map

Introduction

The Dutch Wadden Sea (Fig. 1) covers an area about 2,500 km², half of it being tidal flats. The Wadden Sea (including the German and Danish part) is generally recognised as a natural area of primary importance. It is

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designated a protection area under the Ramsar Convention, and by the Dutch government it is included as part of the European Union's Habitat Directive as well as of the European Bird Directive.

In the Netherlands, the use of the Wadden Sea area is restricted; the most important activities concern tourism, military exercises, transport, mining and fisheries. The latter mainly concern cockle and mussel fishery. Cockle fishery is an intertidal activity, mussel fishery mainly a sub-tidal one.

The Wadden Sea area is characterised by a high biomass density (Beukema 1989; van de Kam et al. 1999): large amounts of benthic shellfish, worms and crustacea are a high-quality food source for migrating birds (Beukema et al. 1993). The area is thus one of the most
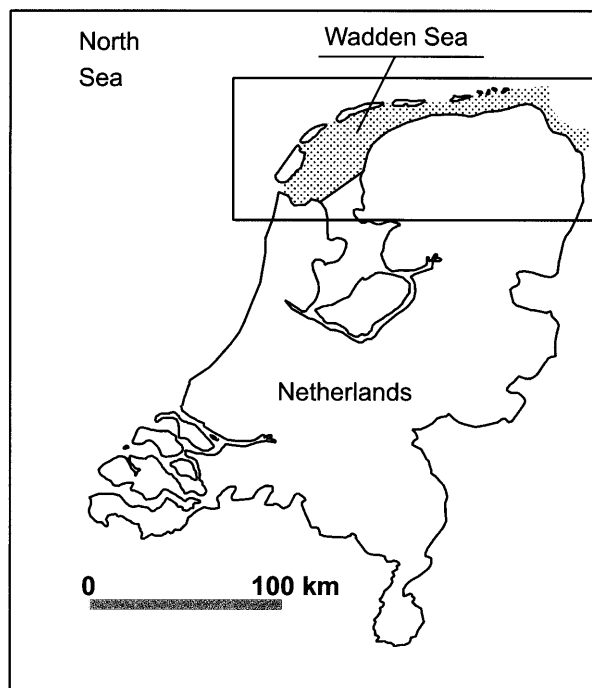

Fig. 1 Location of the study area in the Netherlands

important areas in Europe for a number of bird species. Among the habitats, intertidal mussel beds form an important class of characteristic structures, combining high biomass densities with a high species richness and high biochemical activity.

Dijkema (Dijkema et al. 1989; Dijkema 1991) performed an intertidal mussel bed inventory, based on aerial photographs from 1969 and 1976, combined with actual ground observations in 1978; he arrived at a total area of about 4,100 ha of mussel beds. At the end of the 80's, the last of these habitats were removed. The decline was a result of both natural causes and of fisheries.

The current national policy (LNV 1999) is to re-establish a mussel bed area of about 4,000 ha. One measure to enable this is to close part of the Wadden Sea tidal flats for fishery activities. Nowadays, about 25% of the intertidal area is closed for any economic activity; in the rest of the area fishery is strictly regulated according to a number of rules. A certain amount of shellfish is reserved as food for migrating birds; fishery is not allowed if the food stock is lower than this threshold level. Also, it has been decided to stop intertidal mussel bed fishery but in some exceptional cases, to forbid cockle fishery there where mussel spatfall is observed and to additionally close those areas for fishery that are most suitable for new mussel bed establishment. The last decision presently concerns about 6% of the Dutch Wadden Sea intertidal area, in addition to the 25% which is already closed.

In order to find out which areas are most suitable for the natural establishment of mussel beds, a habitat suitability analysis has been carried out. We hoped to find relationships between the occurrence of mussel beds in the past and a number of physical characteristics and, through this, to be able to predict which parts of the area could be considered as most suitable for the natural establishment of mussel beds.

Mechanisms relevant for mussel bed establishment

The blue mussel (*Mytilus edulis*) has very opportunistic reproduction mechanisms. Per animal, more than a million eggs can be produced, of which ultimately only a very few will survive. Larvae are pelagic, and are distributed through the system by wind and tidally driven currents (Pulfrich 1995; de Vooys 1999). When the larvae are large enough (about 0.2 mm) they search for a substratum to attach to. The chance of finding a suitable substratum depends on the amount of the substratum in the system; but it does not mean that all the suitable substrata will be used. The geographical location of settlement seems to be unpredictable. Pulfrich (1995) and Ruth (1994) found settlement in one tidal area and not in another, and sometimes settlement occurred on one side of a gully and not on the other, although suitable substratum was available there. After settlement, the action radius is small (order of decimeters, Maas-Geesteranus 1942). Only release and renewed pelagic transport allows a young shellfish to be transported to other areas (de Blok and Geelen 1958; Dare 1976). Finally, only a small proportion of the larvae will find some substratum, which in the Wadden Sea consists of adult mussels, cockles (*Cerateroderma edule*), shell beds, hydropolyps, tubes of *Lanice*, macroalgae, or even bare sand or silt (Verwey 1952; de Blok and Geelen 1958; Dare 1976; Pulfrich 1995). After all, stochastic mechanisms play a major role. Hard substratum is very suitable, but not readily available in the Wadden Sea.

After settlement, the shells produce very tight byssus threads, which they use to keep attached to a substratum and to each other.

A number of loss processes will affect the survival of mussels after settlement, and this will affect the distribution of beds. Physical factors (currents, waves) will affect losses, but will be less when the attachment to a substratum or to other mussels is well developed (McGrorty et al. 1990; Seed and Suchanek 1992). Currents can influence supply of food (low flow velocities) and therefore affect growth possibilities; or they may cause removal of mussels or burial after sand deposition (high flow velocities) (Seed and Suchanek 1992). Waves have a similar effect; an important difference is that waves may be more effective during storm periods and the effects are more perceptible in the more shallow regions of the area (RIKZ 1998). Sediment composition is expected to be of importance as well (van der Meer 1991); mussels usually avoid the more silty areas (McGrorty et al. 1993).

Since mussels feed by filtering particles from the overlying water, emersion is a disadvantage as far as food collection is concerned. Although mussels can appear where submersion time is short (not more than several hours), growth of these animals is low. Most mussels appear below the line of 50% submersion time (McGrorty et al. 1993).

Biological factors such as predation by birds, especially oystercatchers (*Hematopus ostralegus*) (Zwarts 1996; Hilgerloh et al. 1997) or gulls, will affect abundance on higher elevated tidal flats. Eider ducks (*Somateria mollissima*) are the most important sub-tidal or near-sub-tidal predators on mussels (Nehls 1995; Nehls et al. 1997).

Crabs, in particular (*Carcinus maenas* eating small sized mussels, and the larger *Cancer pagurus*, capable of consuming full-sized mussels), can reduce mussel density substantially (Dankers and Zuidema 1995). Sometimes the starfish (*Asterias rubens*) can also fulfil a structuring function (Seed 1992; Saier 2001). Such predation pressure acts especially in near sub-tidal areas, since natural enemies such as gulls may predate on shore crabs and starfish under emerged conditions.

We have outlined those physical and biological mechanisms that may have a structuring effect on mussel bed establishment and losses (after spatfall). The biological mechanisms that are mentioned are related to emersion time: crabs, starfish and eider ducks are (mainly) sub-tidal predators, and oystercatchers and gulls are intertidal

Fig. 2 Overview of mussel beds in the Dutch Wadden Sea: inventories in 1969 plus 1976 are described by Dijkema et al. (1989). Inventories from 1995 to 1998 were done by RIVO-DLO. All results have been pooled
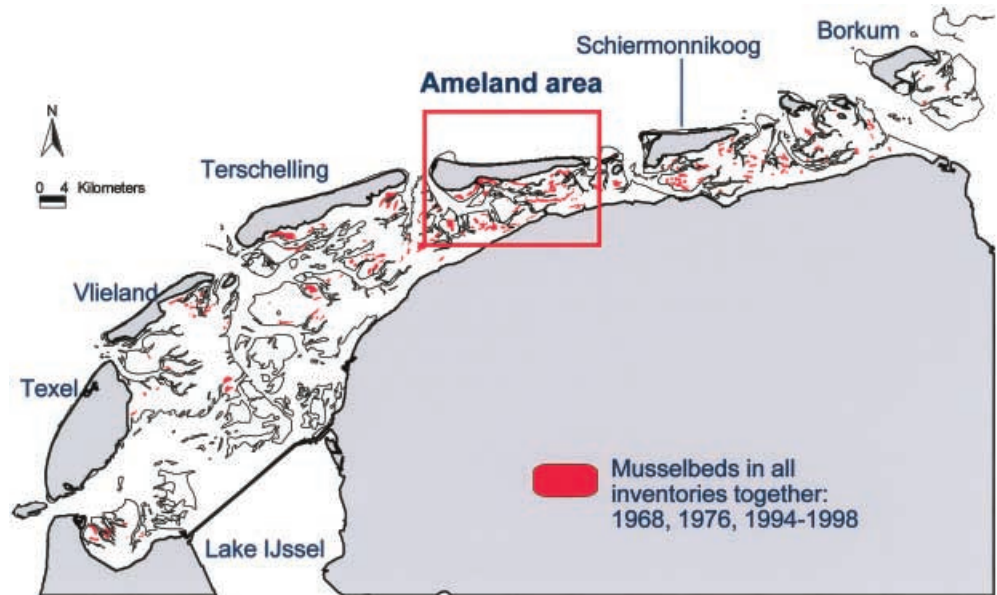
predators, since they need emersion to reach the prey. Therefore, the physical factor, emersion time, may be considered as a substitute variable for these biological phenomena. Emersion time, together with wave action, flow velocity and sediment characteristics have to be related to the mussel bed distribution in our analysis.

Data

Biotic data

Regarding mussel bed appearance, we had four data sets at our disposal.

The first two data sets concern mussel beds in the period before 1990. Around 1990, almost all the mussel beds disappeared from the area.

Dijkema data

The first, and largest data set is the one compiled by Dijkema (Dijkema et al. 1989; Dijkema 1991). He performed an analysis based on aerial photography, done in 1969 and 1976 by KLM Aerocarto, and on the ground visual surveys in 1978. He arrived at a total area of about 4,100 ha of mussel beds. In Brinkman et al. (2001), a short check supported this figure. An overview is presented in Fig. 2. In this period, in the western part of the Dutch Wadden Sea fishing on littoral mussel beds took place. Thus, there was some human influence on the data set.

RIN data

A second data set originates from the 1980s, when the former RIN (Research Institute for Nature Management)

did research on mussel bed characteristics and mussel growth. Only sites, not sizes of beds, are known. This second data set is more or less a follow-up of the first one, since mussel beds did not disappear in the meantime. Geographic location is supposed to be more or less the centre of the beds, although this was not very precise.

The next two data sets cover a newly developed situation. After the removal of the last littoral mussel beds at the end of the 1980s, only a very few hectares were left. In 1994, there was a very good spatfall (sub-tidal mussel beds had been present also in the intermediate period). About 1,500 ha of mussel seed was found in 1994. From 1995 until 1998, the area decreased substantially; in 1998 only about 100 ha of the original 1,500 ha were left. In 1996, a good spatfall was also observed: about 600 ha of mussel seed beds were found. The remains of these as stable beds have not been incorporated into the present analysis.

RIVO data

From 1994 to 2000, the National Institute for Fishery Research (RIVO) did inventories on the occurrence of mussel beds. For site determination a global positioning system (GPS) was used. The data are named RIVO-1 (seed beds from 1994 plus 1996, observations from spring 1995 and 1997, respectively) and RIVO-1998 (3-year-old beds, observations in 1998).

IBN data

From 1993 to 2000, the former Institute for Forestry and Nature Research (follow up of RIN, predecessor of Alterra) measured sizes and sites of mussel beds. Sites

Fig. 3 Emersion times for
the tidal flat area south of the
Ameland island
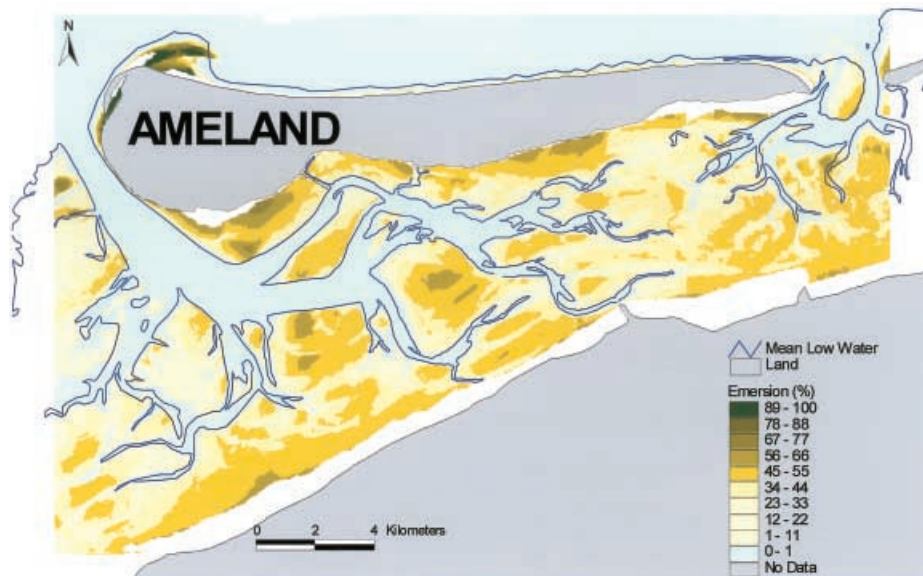
were registered using a differential global positioning system (DGPS).

The question of what has been considered as a mussel bed and what not is strictly coupled to what the investigators have reported. Brinkman et al. (2001) showed that there probably was not a major discrepancy between the four inventories.

We did not use information that might be available in fishermen's logbooks.

Biotic data were available as GIS polygons (geographic location, area and shape were known). The RIN data set only contained information on geographical location, not mussel bed size.

Abiotic data

Most of the abiotic data were supplied by the National Institute for Coastal Zone Management (RIKZ). The abiotic data we used were limited, simply by the fact that there were no more available. At the same time, we hoped and assumed that the key factors were covered by these available data. Abiotic data were all available as grid cell information.

Level and emersion time

From the level, and the tidal curves, emersion time (percentage of the tidal period) was computed. Level measurements are performed by the Dutch authorities about every 5 years. In some areas of importance (e.g. ship fairways) level soundings have been done often and on many sites close to each other. In other areas, sounding sites were less dense. The data have been interpolated, which sometimes gives local errors. Emersion time was thus available on a 20×20 m grid scale. In Fig. 3 an example for the Ameland area is given.

Mean particle size

In the period 1989–1997, the RIKZ had over 7,000 sediment samples taken, covering the whole Dutch Wadden Sea (RIKZ 1998), using a Van Veen sediment sampler, which is a type of grab-sampler. The upper 10 cm was mixed, and from this, a wet sample was analysed with a Malvern 2600L laser particle sizer (GeoSea Consulting, UK). The samples were not treated in advance, that is, neither carbonates nor organic matter was removed by the addition of acid or peroxide. This results in an underestimation of the proportion of finer particles. Sampling density was 1 sample km^{-2}, up to 2 km^{-2} in those areas where a higher variability was expected. The data have been interpolated to a 25×25 m grid size data set, using three points within a search distance of 1,000 m. The data have not been mapped in the field, which means that they do not necessarily match the natural boundaries of the sediment types. For the analyses, only the median grain size for all particles larger than 16 μm is used (M16, μm). It turned out to be important to make the correct choice: for our investigation, M16 values are much more discriminating than, for example, silt content. Silt content for most of the samples was low (less than 1%) and thus the variations of mussel bed appearance are found in those regions with a low variation in silt content. On the other hand, in those regions with a low variability (relatively) in mussel bed appearance, silt content variations are high. Thus, they do not match. M16 variations do match and that is the reason we applied M16 and not silt. For other analyses, silt content might be a better independent variable to use (van der Meer 1991; Zwarts 1996).

Physical characteristics:
flow velocities and wave action (orbital velocities)

From RIKZ, we had orbital velocity data and maximum flow velocity data at our disposal. The data were both based on dynamic model computations for one particular situation. For tides on 13–15 February 1989, a NW storm and increased level, flow velocities were computed (500×500 m grid size) using the WADPLUS model. The maximum change in tidal level near Harlingen amounted to 2.80 m for the flood tide, and 3.30 m for the ebb tide. The maximum values obtained during this simulation have been used for the analysis (Wintermans et al. 1996).

Wave action is presented as the root-mean-square value of the maximum near-bottom orbital velocities (m s^{-1}) under storm conditions, computed with the HISWA model. Circumstances were the same as for the flow velocity computation: NW storm, 15 m s^{-1} wind velocity, which is about 7 Beaufort. Note that a 7 Beaufort average over 48 h implies 10 min average maximum wind speeds that approximately represent Beaufort 10.

The main shortcoming of these figures is that they are characteristic for the considered situation only; other wind directions or level set-ups would result in other values. But, up until now, there have been no other data available.

What we expected was that a high orbital velocity would be unfavourable for mussel bed appearance; as would high flow velocities. Flushing of sediment (and settled mussels) and suspension of sand and silt, negatively affecting filtration possibilities, would be the main causes. For low flow velocities or orbital velocities, we did not have such expectations in advance, except that very low maximum flow velocities would imply that there is hardly any refreshment of water, and thus, feeding conditions might turn out to be poor.

Distance to a gully

It was suggested that the distance of the site to a gully might possibly affect feeding conditions for mussels. A gully serves as a transport route for food and, thus, a large distance would cause less favourable feeding conditions for mussels. There might be a relationship between this variable and emersion time, as emersion times are low close to a gully. For each 50×50 m grid cell, the average distance to a gully (the 0% emersion time boundary polygon) was computed with the ArcView GIS-system (ESRI; PCArcInfo, New York). Sites with 0% emersion times were left out of all computations.

Materials and methods

Compilation of information

First we compiled the available GIS information to a uniform grid cell structure. The abiotic data were available in different grid cell sizes (from 20×20 m up to 500×500 m), and the mussel bed data were available as polygons or simply site coordinates. A 50×50 grid structure was designed, and for each new cell it was checked whether it contained a mussel bed or not, and what the average (area weighted) value for each of the five abiotic variables (emersion time ET, orbital velocity OV, flow velocity VW, median grain size M16, distance to a gully DG) was.

For the whole Dutch Wadden Sea, about 550,000 grid cells (for those grid cells that had a positive emersion time) contained relevant information; this concerns almost 1,400 km^2 of tidal area. We finally chose a clustering of information: for all the five abiotic variables, eleven ranges (ten plus a rest class) were distinguished. We counted how many grid cells belonged to each range, and whether it was a mussel bed cell or not, and then computed for each range their quotient. This relative appearance (RA) of mussel beds in each of the eleven ranges of each of the five abiotic variables (*j*) reads:

$$RA_j = \frac{\text{number of cells with a mussel bed}}{\text{total numbers of cells in that range}} \quad (1)$$

Whether the information from Eq. 1 can be used or not, depends on the mutual independence of the abiotic variables. Therefore, we classified all the grid cell characteristics and tested their independence by visual analysis of the contour plots (according to Fig. 5: independent variables should show horizontal and vertical main axes).

Analysis

Through the clustering mentioned above, we arrived at a data set with independent (X_i) and dependent variables (*Y*) that show a certain relationship:

$$Y = f(X_1, X_2, \ldots X_N)$$
$$(Nlt; = 5, \text{the number of abiotic variables}) \quad (2)$$

First we had to choose the type of relationships to be tested, and secondly, we had to choose an estimation method to find the model parameters.

First inspection of the data set showed that for the five sub-models $f(X_1, \ldots X_N)$ a non-linear function was to be expected. This expectation limited the number of relationships that could be considered.

A second point of interest is the way the model parameters are estimated. Linear models (that is, linear in the parameters) can easily be processed. For non-linear models, the parameter estimation procedure becomes complex. One of the possibilities is to transform the equation into a linear one. Since the error structure is transformed as well, this is a technique that is only allowed (and necessary) if the transformed errors are of the same order for the whole range. If this is not the case, such transformation should not be done. In the present situation, a transformation is not appropriate. In a number of cases, the computational draw-backs of non-linear parameter estimation can be avoided by using a general linear modelling technique (GLM) (McCullagh and Nelder 1989; Dobson 1990), being part of the Genstat statistical package [Oude Voshaar 1994; Genstat version 5.41 (NAG 1997)]. GLM allows the use of (a limited number of) non-linear relationships where the evaluation of the success (how well do the computed RA values fit the observed ones) is done on the original (non-transformed) observations, and offers a fast response. Usually, fully non-linear iterations are time-consuming.

The observed mussel bed appearances or densities RA_i (for each cluster *i*) have to be compared with expected densities $\hat{RA}_i$ (the predictor for *Y* in Eq. 2). The coupling between the non-linear model and the observations is called the link-function. As a result of the shapes of the measured RA curves, we restricted ourselves to normal distribution equations (like Eq. 4). In GLM terminology, the argument of the exponential function is the model, the link

function describes the relationship between the model and the expectation. In our case, this link function is logarithmic in the case of a Poisson or a normal distribution of $\hat{RA}_i$:

$$\ln\left(\hat{RA}\right) = \text{MODEL} \tag{3}$$

A (sub-)model reads, when such a density distribution has to be described:

$$\hat{RA} = \exp\left(a + bX + cX^2 + dX^4\right) \tag{4}$$

The parameters a, b, c and d may be zero. The term X^4 is introduced to make a pronounced relationship with X possible. Where $d=0$, we kept $c=0$, and vice versa. When two models are compared, the residual deviance rd is of importance:

$$\text{rd} = -2\ln\left(\frac{\{P\,(\text{realised results with the model})\}}{\{P\,(\text{realised results with saturated model})\}}\right) \tag{5}$$

A saturated model shows a perfect fit. This deviance is often called the log likelihood ratio, and can always be applied to show how good the fit is, irrespective the link function.

Where the response is normally distributed, the deviance equals the residual sum-of-squares. For other distributions, the deviance has the role of the residual sum-of-squares.

If the model fit is good, this residual deviance is more or less χ^2-distributed. This is applied to test the quality of the model.

The approach in Eq. 4 concerns only one independent variable X; it can be expanded to more than one. We tested that necessity, and concluded that we could do with single variable sub-models (like Eq. 4).

To arrive at the complete model, the estimator $\hat{RA}$ can be formulated as the product of separate functions. If relationships with all the five abiotic characteristics are used, the final $\hat{RA}$ reads:

$$\hat{RA} = \hat{RA}_{ET} * \hat{RA}_{M16} * \hat{RA}_{OV} * \hat{RA}_{VW} * \hat{RA}_{DG} \tag{6}$$

where subscripts ET = emersion time (% of tide), M16 = median grain size for all particles larger than 16 μm (μm), OV = orbital velocity (m s^{-1}), VW = flow velocity (m s^{-1}), and DG = distance to gully (m).

The final model (the multiplication of two or more sub-models according to Eq. 6) is scaled in such a way that the total mussel bed area (the sum of all densities × areas) is the same as the observed total area.

Testing the results

Above, we explained how sub-models were to be found that described the relationship between mussel bed occurrence and one abiotic characteristic, or more of these simultaneously. Finally, following Eq. 6, a mussel bed habitat suitability for all 50×50 m grid cells in the Wadden Sea is computed.

In order to test the quality of the thus derived model, we ranked all the 550,000 cells from highly suitable (according to the model) to slightly suitable. Then, we took the best 1% together, then the next 1%, the next 3%, 5%, and so on, and thus, with increasing ranges up to 100% of the area, we created about 12 classes of suitability. We also counted those cells that had mussel beds, and with that we knew the relative appearance of mussel beds in each of the suitability classes. It may be expected that the "best" class contains the highest density of mussel beds, although it is *not* to be expected that *all* the mussel beds appear in class number 1.

Usually, the quality of a model can be computed by

$$R^2 = 1 - \frac{\text{KS}_m}{\text{KS}_g} \tag{7}$$

where KS_m is the estimator for the rest variance when using the model, and KS_g the sum-of-squares when no model at all is used. The sum-of-squares reads:

$$\text{KS} = \sum_{j=1}^{12}\left(\hat{RA}_j - RA_g\right)^2 \tag{8}$$

where $\hat{RA}_j$ is the expected mussel bed density in each class and RA_g the observed density. For KS_m (Eq. 7) RA values are the RA values computed with Eq. 6. For KS_g, RA values are the average densities, thus the same value for all the classes. Usually, degrees of freedom are to be incorporated in a computation of a model quality. Here, the 12 classes are constructed from 550,000 data points and using a model with about ten parameters. Since the degree of independence of data is not known, degrees of freedom are not known either; and therefore, we refrained from a discussion on the significance of the results.

Another problem with this qualification is that one compares model results with observations that are grouped according to classes that were constructed as a result of the same model. The method can be applied, but one has to realise what it does.

It is also possible to check whether the objectives of the project are met: to distinguish highly suitable and least suitable mussel bed areas. The larger the difference is between predicted (model) RA values for the best and the less suitable areas, the better the discrimination of the model is. Therefore, we computed in which part of the Wadden Sea area (as percentage of the total tidal flat area) 50% of the mussel beds could be found, according to the model. This is called the C_{50} value. The lower this C_{50} value, the better the model discriminates between suitable and less suitable areas.

From here onwards, we omit the estimator symbol ^.

Results

Choices of data sets

As argued above, we had four biotic data sets at our disposal. All the four data sets have been subject of the analysis, but not all analyses are fully explained here. For this paper, we used the Dijkema data set to calibrate the model, and the RIVO data set to do the validation. The 1980 RIN data set turned out to be not very different from the Dijkema data set; the IBN data set was much like the RIVO data set.

Abiotic characteristics of the Dutch Wadden Sea, clustered into 11 classes, are shown in Fig. 4.

Correlation between abiotic variables

The choice of abiotic characteristics as independent variables is only allowed when they do not show a statistical relationship. Otherwise, if they do, the same information may be used more than once in the descriptive Eq. 6. For all combinations of the five characteristics, we plotted contour diagrams (Fig. 5 shows some relevant ones). It turned out that most of the variables were more or less independent. Only the distance to the gully border and mean emersion times are clearly correlated. This latter conclusion implies that as soon as both characteristics are used in Eq. 6, one puts in the same information more than once, although it will be less than twice (emersion and distance are not 1:1 related).

Fig. 4 Characteristics of the tidal flats in the Dutch Wadden Sea
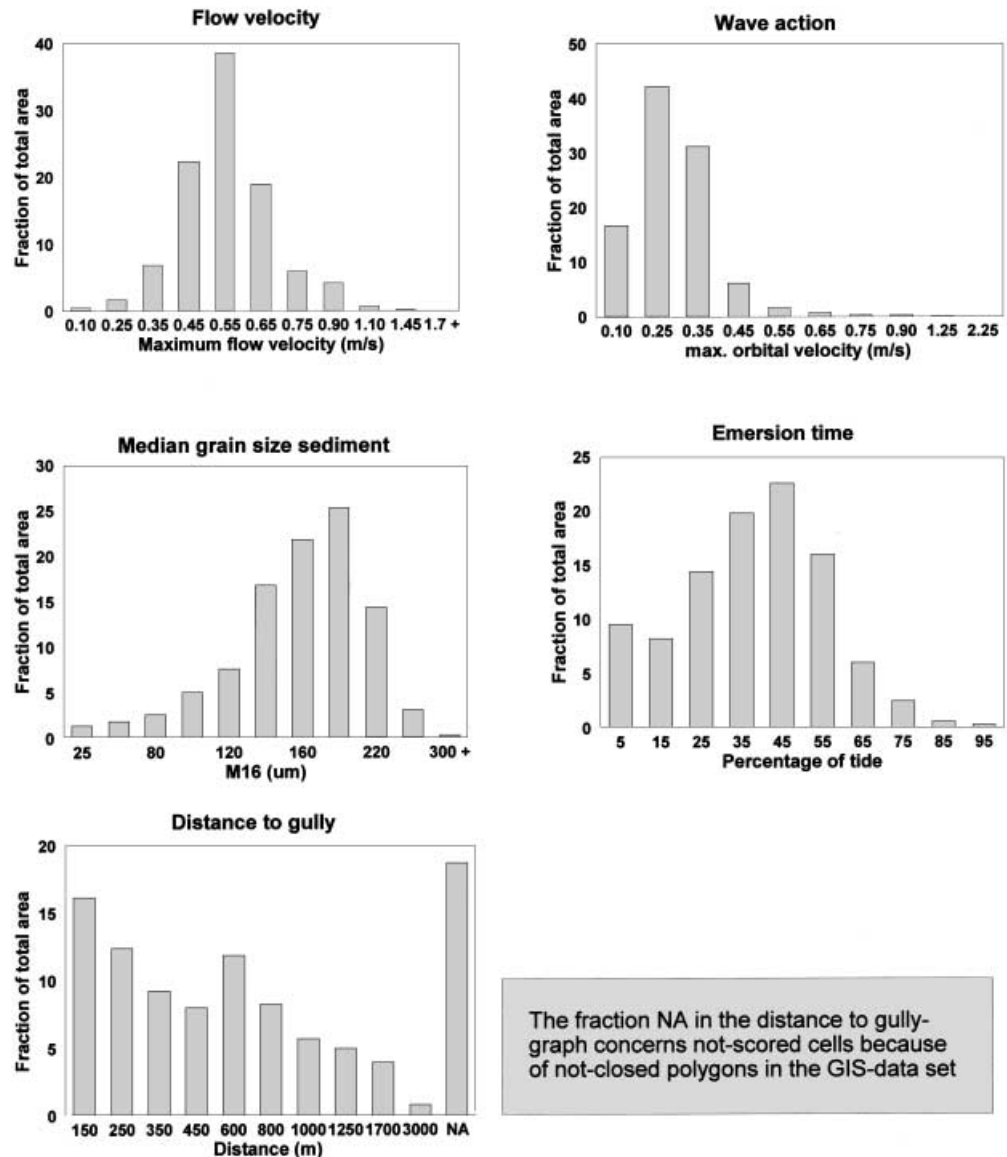
Relative appearance of mussel beds for all five abiotic variables

Relative mussel bed appearances (RA values) combined with all the five abiotic variables are shown in Fig. 6. Mussel beds seem to prefer low maximum values for orbital velocities, but not very low flow velocities (maximum values below 0.3 m s^{-1} apparently are not preferred). Maximum flow velocities above about 1.5 m s^{-1} seem to be unfavourable. Note that this is a situation with fast flowing water. M16 values of about 170 μm are preferred, silty areas or areas with coarse sand are not. Emersion times above 50% of the tide are not suitable, but also areas with low emersion times seem to be less suitable. This lower part of the curve sometimes is very pronounced (the RIVO data set, not shown here) or present but less marked, as it is here in the Dijkema data set. Distance to the gully shows a similar relationship, there

are very few mussel beds more than 1.5–2 km away from a gully.

Relationship between mussel bed appearance and abiotic characteristics

Model results for four combinations RA-abiotics (distance to gully is left out here) are shown in Fig. 7. Parameters and qualifications for the sub-models are listed in Table 1, in Table 2 the reliability of the parameters is quantified, and in Table 3 the sub-model quality is quantified.

Construction of the final model

In order to arrive at the final model, we started with models based on one variable only (e.g. wave action
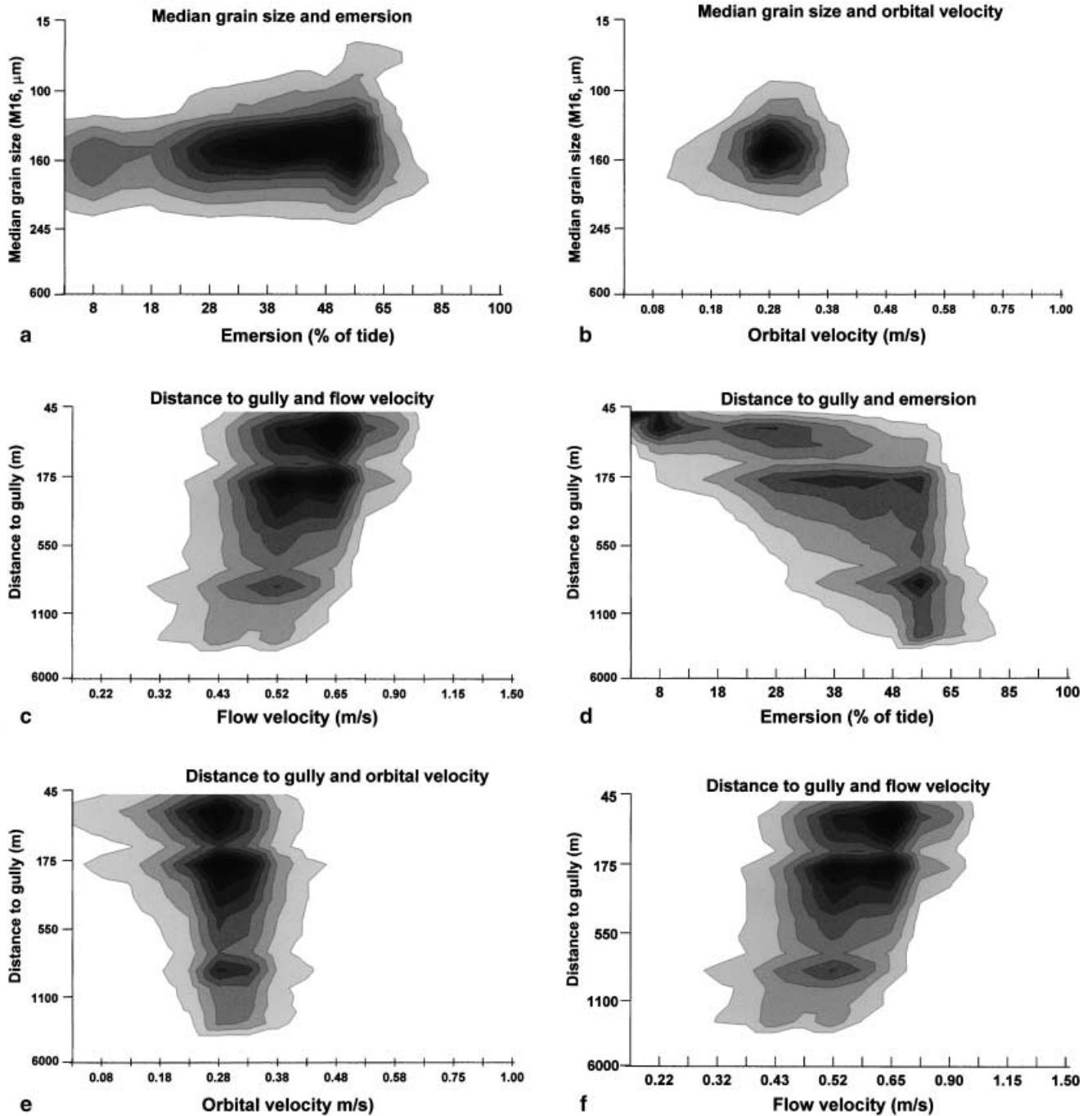
Fig. 5 Contour plots for six combinations of abiotic variables (**A** median grain size and emersion, **B** median grain size and orbital velocity, **C** distance to gully and flow velocity, **D** distance to gully and emersion, **E** distance to gully and orbital velocity and **F** distance to gully and flow velocity) to check the correlation between these variables. See text for explanation

Table 1 Summary: parameters for the five regression models Eq. 4) for each abiotic variable

Parameter values for analysis of Dijkema data					Corrected[a] a''
Abiotic	a	b	c	d	
VW Maximum flow velocity (m/s)	−6.29e+00	9.77e+00	−8.51e+00		−2.804
ET Emersion time (%)	−4.05e+00	2.70e−02		−1.50e−07	−0.719
OV Maximum orbital velocity (m/s)	−2.77e+00	−3.18e+00			0.000
M16 Median grain size (μm)	−7.39e+00	4.83e−02	−1.45e−04		−4.028
DG Distance to gully (m)	−3.63e+00	1.97e−03	−2.81e−06		−0.346

[a] Corrected a'' means that with this value the maximum RA value for the sub-model becomes 1.0

Fig. 6 Relative appearances of mussel beds (ha ha^{-1}) related to the five abiotic variables (at mean low water level)
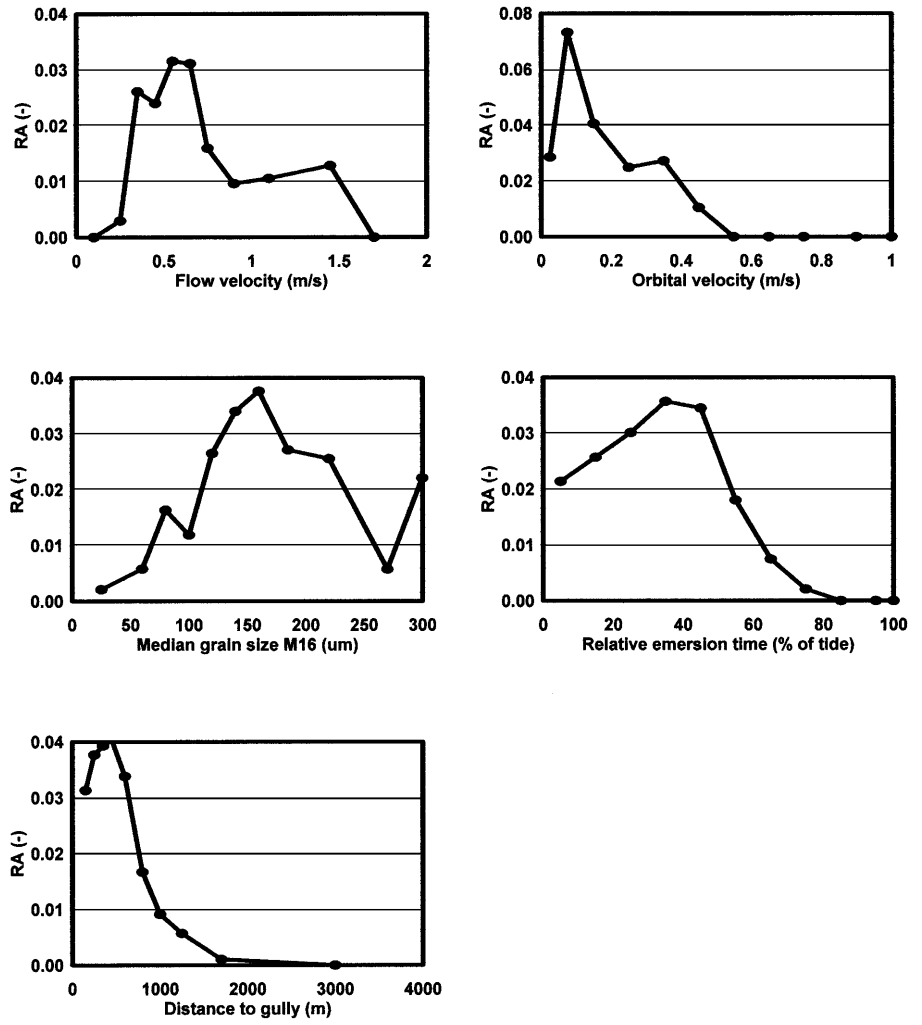

Fig. 7 Results of model analysis: relative appearance of mussel beds (RA values), related to four of the five abiotic variables. *Dashed line* model, *solid line* data
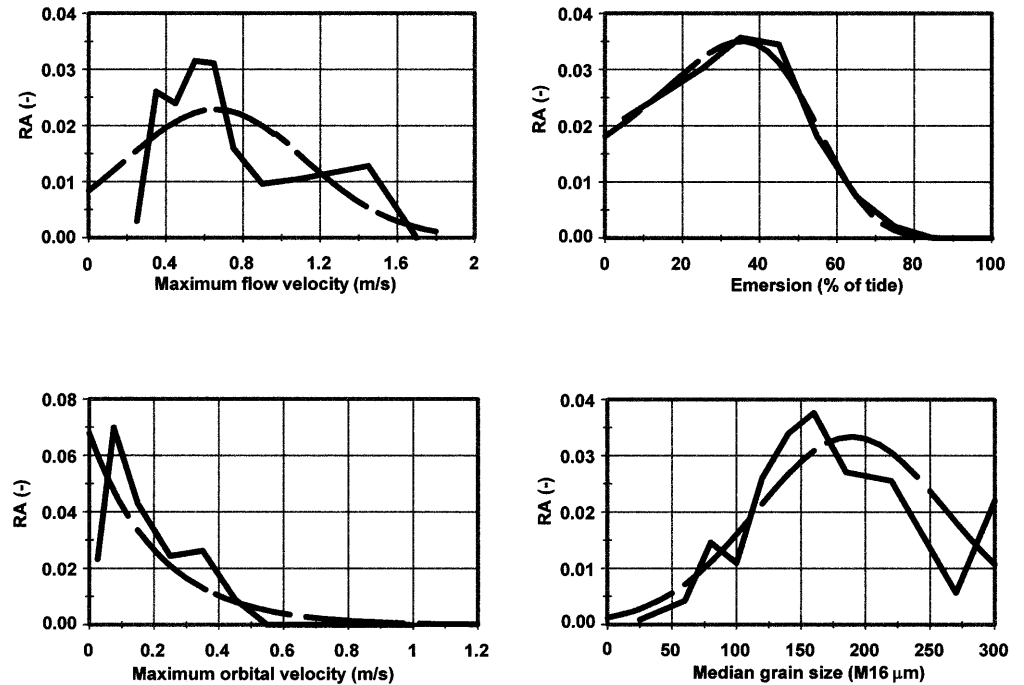
Table 2 Model results: all parameters *a*, *b*, *c* and *d* (ET alone) for the five sub-models. Estimated value, standard error, *T* value and a Student's *t*-test value, with 11 data points and three (or two, in case of OV) parameters

			Value	Stand error	*T*	*t*
Flow velocity water	VW					
Constant		*a*	–6.290E+00	1.020E+00	–6.160E+00	<.001
VW		*b*	9.770E+00	3.520E+00	2.770E+00	2.400E-02
VW^2		*c*	–8.510E+00	3.010E+00	–2.830E+00	2.200E-02
Emersion time	ET					
Constant		*a*	–4.048E+00	7.860E-02	–5.146E+01	<.001
ETb		*b*	2.696E-02	2.890E-03	9.330E+00	<.001
ET^4		*d*	–1.500E-07	1.200E-08	–1.262E+01	<.001
Waves	OV					
Constant		*a*	–2.773E+00	2.480E-01	–1.117E+01	<.001
OV		*b*	–3.182E+00	9.270E-01	–3.430E+00	7.000E-03
Median grain size	M16					
Constant		*a*	–7.392E+00	9.140E-01	–8.090E+00	<.001
M16		*b*	4.830E-02	1.110E-02	4.360E+00	2.000E-03
M16^2		*c*	–1.448E-04	3.320E-05	–4.360E+00	2.000E-03
Distance to gully	DG					
Constant		*a*	–3.626E+00	1.340E-01	–2.709E+01	<.001
DG		*b*	1.970E-03	5.820E-04	3.380E+00	1.000E-02
DG^2		*c*	–2.805E-06	5.280E-07	–5.310E+00	<.001

Table 3 Quality of the sub-models. Poisson-distribution, link-function: logarithm. Observations weighted according to the number of grid cells in each of the 11 classes. In the two-parameter models tested here (only for OV and DG), the quadratic term (X^2) is omitted. For the other three abiotic factors, a two-parameter model was not appropriate, given the bell-shape of the distribution. Finally, the three-parameter models have been applied for flow velocity *VW*, emersion time *ET*, median grain size *M16* and distance to gully *DG*, and the two-parameter model (having a better *F* value) for the orbital velocity *OV* sub-model

	Three-parameter model					Two-parameter model				
	df	Deviance	Mean dev	Ratio	*F*	*df*	Deviance	Mean dev.	Ratio	*F*
VW										
Regression	2	1.44E-03	7.22E-04	6.0	<0.001					
Residual	8	9.65E-04	1.21E-04							
Total	10	2.41E-03	2.41E-04							
ET										
Regression	2	4.24E-03	2.12E-03	146.9	<.001					
Residual	8	1.16E-04	1.44E-05							
Total	10	4.36E-03	4.36E-04							
OV										
Regression	2	3.34E-03	1.67E-03	6.6	0.021	1	3.10E-03	3.10E-03	12.2	0.007
Residual	8	2.04E-03	2.55E-04			9	2.28E-03	2.53E-04		
Total	10	5.39E-03	5.39E-04			10	5.39E-03	5.39E-04		
M16										
Regression	2	3.04E-03	1.52E-03	14.7	0.002					
Residual	8	8.26E-04	1.03E-04							
Total	10	3.86E-03	3.86E-04							
DG										
Regression	2	1.54E-02	7.71E-03	209.2	<.001	1	1.38E-02	1.38E-02	64.2	<.001
Residual	8	2.95E-04	3.69E-05			9	1.93E-03	2.15E-04		
Total	10	1.57E-02	1.57E-03			10	1.57E-02	1.57E-03		

Table 4 Fit of the habitat model. R^2 values according to Eq. 7

Data set	R^2 (based on RA values)	R^2 (based on absolute areas)
Dijkema	0.95	0.98
RIVO-1 (1994+1996)	0.89	0.99
RIVO-1998	0.29	0.56
RIN-1980–1990	0.65	0.69
GPS-1994–1998	0.35	0.73

(OV) alone). We tested the results as described above. Next, we constructed models with combinations of two or more abiotic factors. In total, we tested about 60 models.

It turned out that the maximum orbital velocity was the most discriminating variable, followed by emersion time (ET), distance to gully (DG) and median grain size (M16). Maximum flow velocity (VW) was least discriminating. This means that a model with OV alone is better than one of the others alone, and that a combination of OV with ET or M16 is better than OV alone, and so on. With the distance to the gully or emersion time as the abiotic factor, the model already shows a good fit, but the discriminating power is much lower than it is for orbital velocity as the abiotic variable. In Fig. 8, some of these models are shown. In Fig. 8, the Dutch Wadden Sea area is clustered, following the ranking procedure explained above (the high RA value areas on the right hand side, and the low RA predictions on the left hand side). Observed RA values are included; the model should follow the observations as closely as possible, *and* the model should be discriminating (have a low C_{50} value). Finally, the complete model (all five abiotic factors included) turned out to produce to most accurate description of mussel bed appearance. This means that the use of both distance to the gully and emersion time gives a better result than when one of these is omitted.

The total analysis comprised about 240 model tests, each of the about 60 models is tested against each of the four biotic data sets. And thus, we arrived at the final version of the habitat suitability description model.

The final habitat map

The final habitat suitability model is presented in Fig. 9 as a mussel bed habitat suitability map. The model is a combination of all five sub-models, and the applied parameters are listed in Table 1. In Fig. 10, we plotted for the Ameland area mussel beds and mussel bed sites in the habitat suitability map, showing that the overall picture matches quite nicely. How well the model fits the observations is shown in Fig. 11A. With a R^2 value of 0.95 (Table 4), the fit is quite good. The discriminating power of the model is not as high: $C_{50}=26.5$. This means that according to this classification, half of the beds are expected in the best 26.5% of the total Wadden Sea area.

The model predicts the chances of mussel bed appearance. Thus, when one stands somewhere on a tidal flat
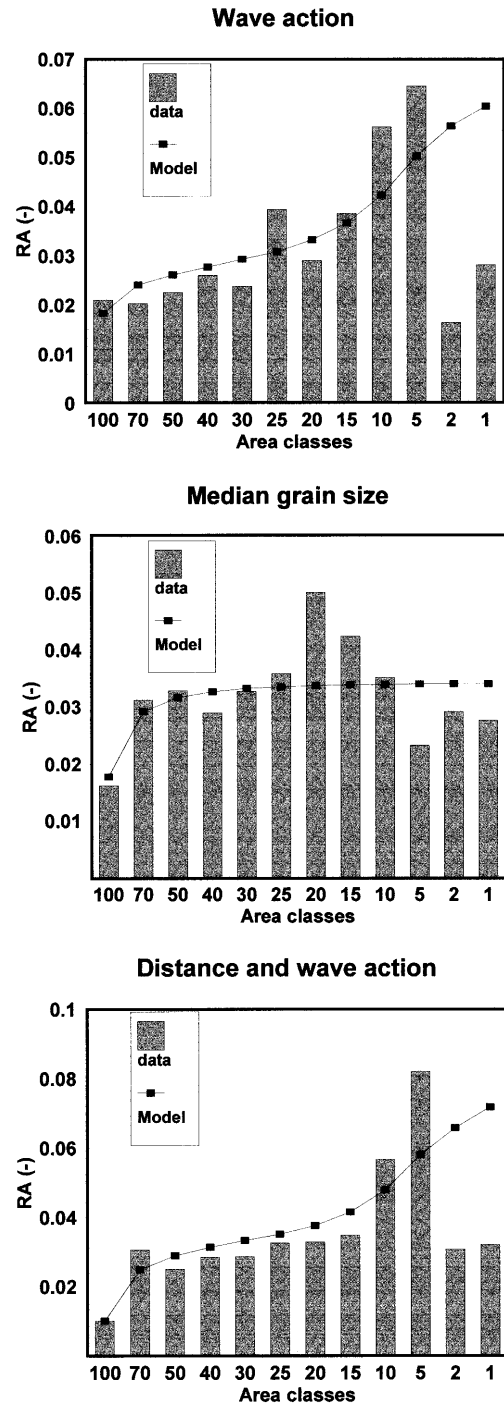

Fig. 8 Some steps in the development of the final model. *Top* prediction of habitat suitability based on wave action as abiotic factor alone and the presence of mussel beds in the distinguished suitability classes. *Middle* M16 as abiotic factor alone. *Bottom* distance to gully and wave action together as abiotic factors. The data were Dijkema data. In total about 60 of these single models and combinations of models have been tested

with its known abiotic characteristics, the model tells you what chance you have of being on top of a mussel bed. In fact, this chance is low. The highest chance is no more than about 9%; in the least suitable areas we computed a chance of about 0.7%. The difference between

Fig. 9 Final result, based on the best developed model, based on Dijkema data. The code for this model is KDD1A2. Habitat suitability map for the Dutch Wadden Sea, with areas ranked according to their suitability, and clustered as explained in the text
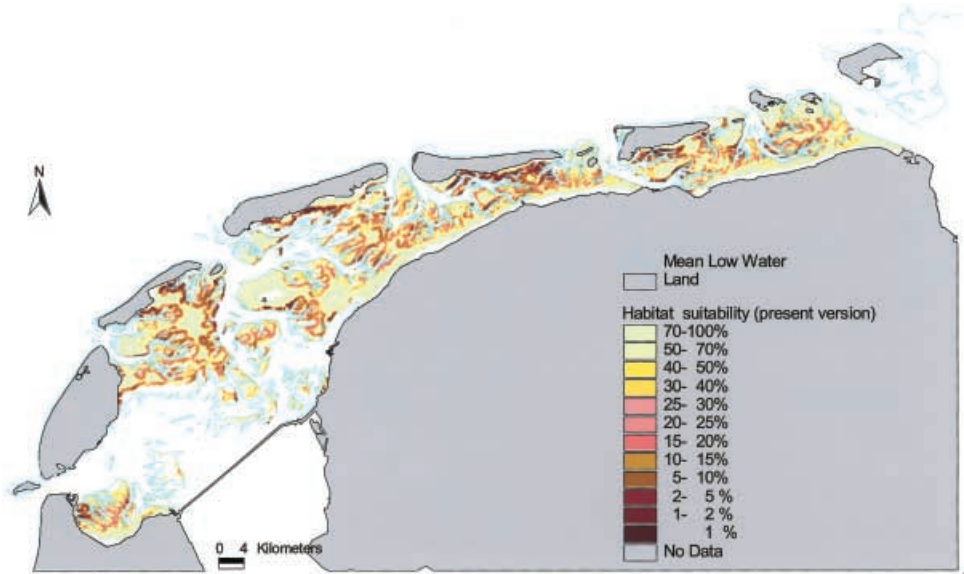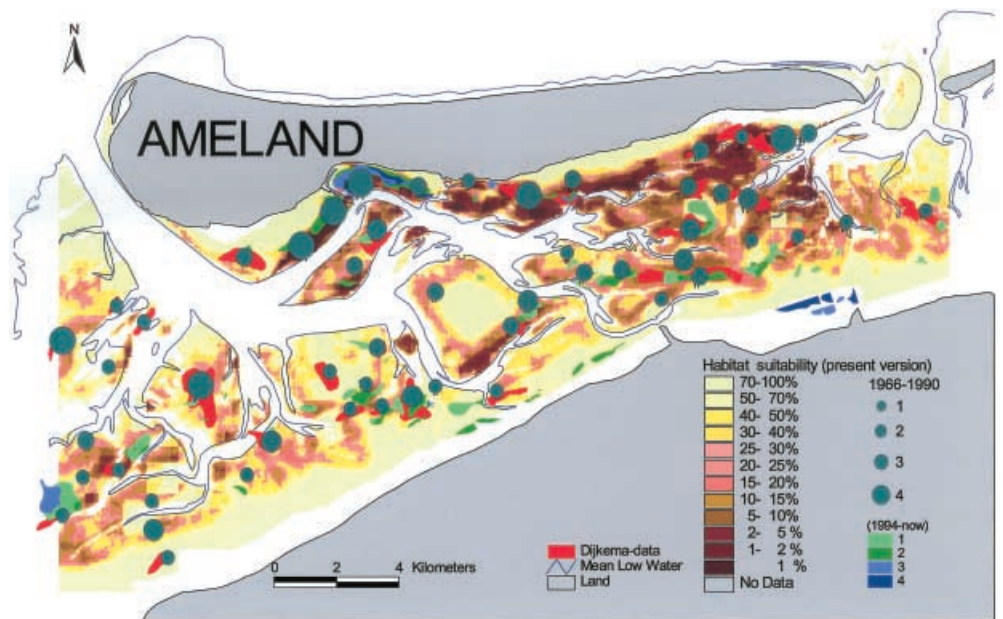

Fig. 10 Final result showing the Ameland area, habitat suitability (as in Fig. 9), including sites of mussel beds

the most suitable areas and the average is a factor of 2–2.5.

Validation with other data

As shown above, the final habitat model is capable of describing the mussel bed environment quite well. To test its validity, model predictions are compared with observations for the other three data sets available. The 1980 (RIN) data and the model prediction show a good similarity (Fig. 11E), which could be expected since the mussel beds in those years were more or less a continuation of those from the Dijkema set. After the total disappearance of mussel beds from the Dutch Wadden Sea around 1990, a new mussel bed area had to develop. Any

physical coupling with 1970 and 1980 beds was absent. Both the IBN (Fig. 11F), and the RIVO data sets (Fig. 11B) showed a poor resemblance to each other, although the observations are concentrated in those areas that are qualified by the model as most suitable. However, densities differed greatly; the model predicts a broader appearance where the observations show a pronounced presence in the best 5% area of the Dutch Wadden Sea. R^2 values (Table 4) are low. Finally, we compared model predictions with 1994+1996 seed bed appearance (Fig. 11C, D); together about 2,000 ha of young mussel beds. It was this spatfall that formed the basis for the 1998 beds we used in the previous comparison (Fig. 11B). Here, it turned out that the model, based on data from 1960–1980, was perfectly capable of predicting the distribution of mussel spatfall in 1994+1996.
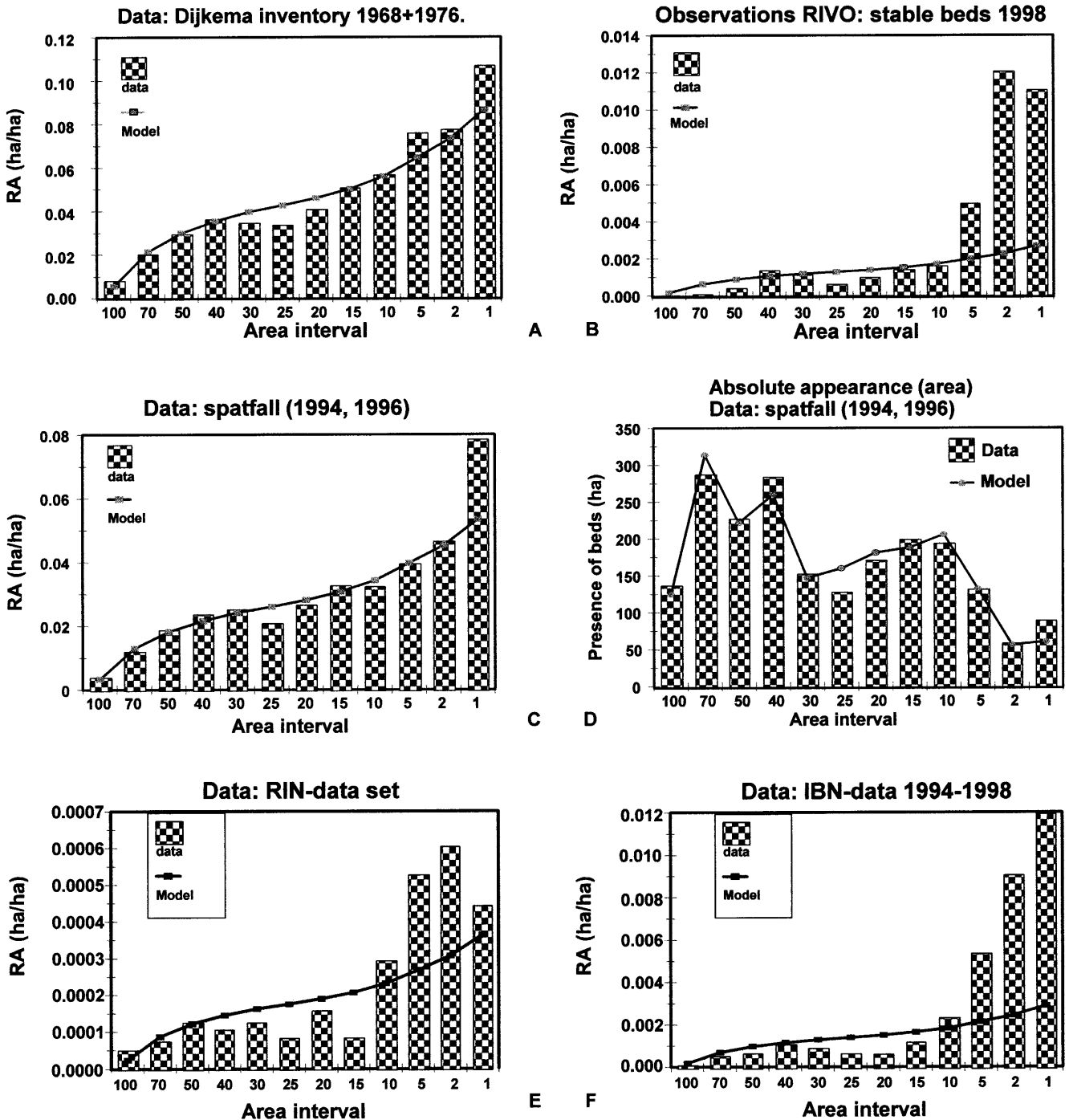
Fig. 11A–F Model test: the tidal flats are ranked according to their suitability, and clustered as explained in the text. **A** Predicted RA values (*line*) by the final model and the observations (Dijkema data). **B** Observations: RIVO stable beds (1998 data). **C** Observations: distribution of 1994 and 1996 seed beds. **D** as **C** but now absolute areas (ha) have been plotted. **E** Observations: RIN data for the years 1980–1990 **F** most stable beds from IBN-observations in the years 1994–1998

Dutch Wadden Sea area, the predicted mussel seed bed area fits the observed one. In the most suitable areas, the RA values are most illustrative for the difference between model and observations; because of the larger interval sizes, total bed areas are most illustrative for the model fit in the least suitable areas.

Computed and observed RA values in Fig. 11C show an almost perfect fit; in Fig. 11D real areas (ha) are shown, with a similar agreement. Figure 11D emphasises that also for the class 70–100%, which covers 30% of the

Characteristics of the most and least suitable areas

We analysed what the abiotic factors meant for the structuring of the mussel bed appearance. We computed the
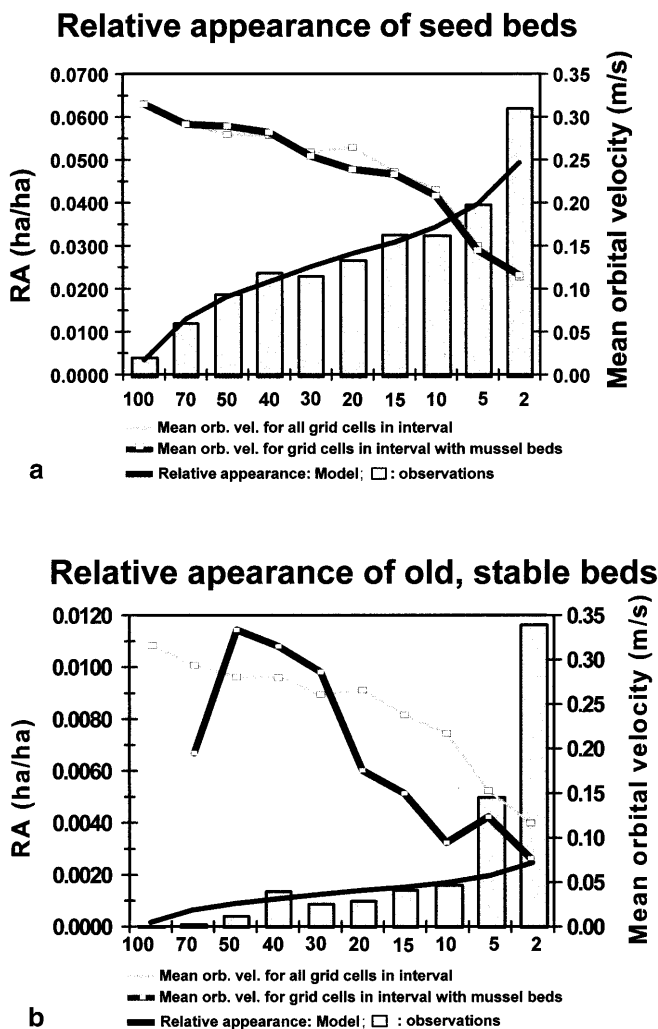
Relative appearance of seed beds

a

Relative apearance of old, stable beds

b

Fig. 12 A As Fig. 11C, with average (maximum orbital velocity) for all the cells in a cluster, and with average (maximum orbital velocity) for those cells in a cluster that contain a mussel seed bed (data 1994+1996 spatfall). **B** As **A**, but now for the 1998 stable mussel beds

average value of maximum orbital velocities for each of the 12 separate Wadden Sea suitability classes. This was also done for those grid cells in each class that contained mussel beds. Since the 1994–1998 observations by the RIVO distinguished seed beds and old mussel beds, both observations have been plotted: in Fig. 12A seed beds and in Fig. 12B old beds are used as observations. The shape of the predicted RA values is (practically) the same for both situations. Because RA values are scaled such that the total bed area matches the observed total, the absolute RA values are different for both graphs.

For the seed beds, the mean maximum orbital velocities are almost the same for the cells with and without mussel beds. The orbital velocities are the lower the better the area is suited for mussel beds. A comparison with the situation for the old beds (Fig. 12B) shows that there is an "improvement" of conditions from seed beds to old beds: the remaining old beds undergo even less wave action than the former seed beds.

This exercise was also performed with the other four abiotic factors; the differences in RA values in each area interval from seed beds to old beds can be plotted against the average value of each abiotic factor (Fig. 13). These differences cannot be considered as complete losses, since the seed bed data set contains 1994 plus 1996 spatfall, and old beds are remains of the 1994 spatfall only. The shapes of the lines in Fig. 13 are more or less the reverse of the model shapes in Fig. 7. However, here they have another meaning. Figure 7 shows a situation: the chance of finding a mussel bed somewhere, based on the abiotic characteristics. Figure 13 shows the difference between seed beds and older, more stable beds. And thus, it informs us about a process: the chance of a young mussel bed staying somewhere and becoming a more stable, old bed. The reversal of the lines in Fig. 13 shows us a first guess of the stability of the beds related to the abiotic characteristics.

Combining both types of information, it seems that those areas that are preferred best by spatfall also offer better survival conditions than other areas.

Discussion

The study was done with a relatively low density of sampling points. Depth, and thus emersion time was known in the most detail, but physical factors were available as model results on a 500×500 grid cell basis, and for median grain size we had only 7,000 points (of which about 50% were sub-tidal and thus not relevant to the study). Of 550,000 cells, only about 14,000 contained a mussel bed, that is 2–3% of all cells. And yet, it was possible to derive a sound relationship between mussel bed appearance and abiotic characteristics, and to derive stability information from the data set.

The relationships with abiotic factors revealed quantitative information. The relationship with emersion time is in good agreement with McGrorty et al. (1993): not only do higher elevated tidal flats have almost no mussel beds, but also areas with low emersion times are shown to be less favourable for mussel beds. We did not study the causes of such a characteristic. A suggested predation by crabs and starfish might be a possible cause; Seed (1992) and Saier (2001) mentioned that predation by starfish may affect mussel densities and sometimes starfish may even act as a key predator determining mussel bed structure or disappearance in sub-tidal areas; this was also mentioned by van de Kam et al. (1999). Van der Meer's study (van der Meer 1991) also revealed similar relationships of benthic animals with their environment, but lacked quantitative results.

The relationship of mussel bed appearance with sediment characteristics are also in accordance with McGrorty et al. (1993), and with van der Meer (1991). In very coarse sand, mussels hardly ever appear, nor in very silty areas. However, the larger part of the Dutch Wadden Sea has suitable median grain size conditions.

Fig. 13 Differences between
the 1994+1996 seed beds and
the 1998 stable beds. For all the
five abiotic variables, the dif-
ference (in percentage of the
area) is shown. These graphs
are partly the reverse of the
graphs in Fig. 6, and thus show
that mussel seed beds in the
most suitable areas also have
the best chances of surviving
over several years

WHERE ARE THE DIFFERENCES ?

1994+1996 : 2000 HA SEED BED
1998 : 110 HA OLD BED
TOTAL DIFFERENCE 95 %
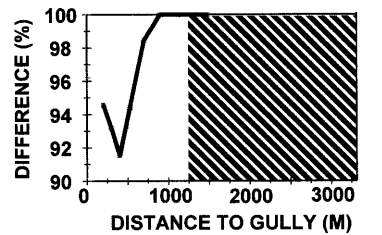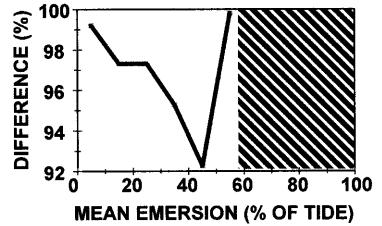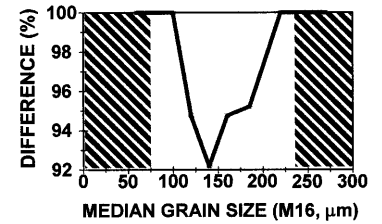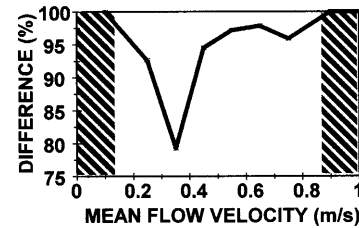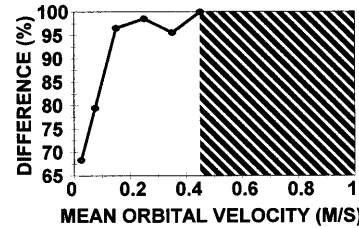
The relationship with distance to the gully was also used by Ballhausen and Holzapfel (1997) for the East-Friesian Wadden Sea tidal flats, and they found a maximum density of beds between 100 and 300 m distance from a gully for spatfall in cases where there were no mussel beds present already; and between 200 and 500 m in cases where there were mussel beds present. This is in good agreement with our maximum at 500 m distance.

We are well aware that in the use of both emersion time and distance to gully as variables for our model, we applied some of the same information twice. But, in practice it merely means an emphasis of the variable site.

Quantitative relationships between mussel bed appearance and wave action or maximum flow velocity has not been available until now, mainly as a result of lacking model computations. Obviously, highly exposed areas with high orbital velocities and/or high maximum flow velocities offer poor conditions for seed beds. Because losses afterwards are also larger in such areas, conditions are even worse for more stable mussel beds. The best conditions are found in those areas where orbital velocities are low. Low flow velocities obviously are not preferred. Reduced food supply or too favourable sedimentation conditions for (fine) sediments hindering filtration activities both seem plausible causes, although the real reason is not clear.

We computed a suitability map that covers most of the mussel bed sites quite well. However, this does not mean that the results can be transferred to other areas without additional studies. The basis of the analysis has been the abiotic data available, and these were local data. They have to do with the local situation, i.e.

the combination of sediment types and wave action, flow velocity, and thus, the character of the Wadden Sea. It will be an interesting exercise to test how well the relationships predict mussel bed occurrence in other areas.

We started our project in 1999 (Brinkman and van Stralen 1999) with an analysis based on the RIVO 1998 data (RIVO-4) for stable mussel beds. The model constructed then showed a very good agreement with the observations (R^2=0.86), and showed a low C_{50} value of about 4.3. That means that in that analysis half of the beds were found in the best 4.3% of the area. However, this was an exceptional situation, in our opinion. The beds in 1998 were a result of the 1994 spatfall, and a heavy NW storm in 1995 (3 March). Exactly this situation was present in our wave data, and therefore, the model turned out to be a very good fit. In other cases, and these were present in the Dijkema data set, the model was less suitable. On the other hand, the present model, that is based on the Dijkema data, produced a good model fit when regarding the Dijkema data, and not when we considered the RIVO 1998 data for stable beds.

It is for this reason that we were pleasantly surprised by the good fit the Dijkema model showed with the 1994+1996 spatfall.

Thus, the sites where the mussel beds were located in 1969 and 1976 were almost identical (regarding their abiotic characteristics) to those that served as substratum for the spatfall in 1994 and 1996. The stable beds that were left in 1998 were mainly structured after the 1995 spring NW storms, and probably after the 1995–1996 icy winter. The mussel beds in the 1960s and 1970s described by Dijkema (Dijkema et al. 1989; Dijkema 1991)

are a result of more than one spatfall [also confirmed by results from van Stralen (2001)], and several events like storms and freezing winters. And therefore, the discriminating power of our present model, which is based on one NW storm as main physical event, cannot be expected to be very good. We hope that the model can be improved by including results from physical model computations for storms from other directions.

Our idea is that the formation of mussel beds may be a process of many opportunities (see the 1994+1996 spatfall) and also of many losses (see the differences between this spatfall and the area of 1998 stable beds). The reproductive power of mussels is large: they produce over a million eggs per animal, but such opportunistic reproduction behaviour is always coupled with a situation where there is a large chance of losses. Sometimes we may be lucky, and a large part of the seed beds survives a winter period, and sometimes most of the spatfall gets lost. It might be a matter of years before a large area of mussel beds, like the one that was present in the beginning of the 1970s, is present again in the Dutch Wadden Sea. But sometimes, such a re-establishment may take place in just one season; it will very much depend on the negative effects of physical events which part of the seed beds will survive. A north-western storm will affect different areas than a south-western one. In particular, Fig. 13 supports this view.

Future analysis, with new information on mussel bed distribution, on wave action and on developments of seed beds to more stable older beds may inform us better about the stability of beds in the distinguished suitability areas.

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