



Lower Saxony Wadden Sea mussel habitat suitability maps

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Vorwort

Das Vorkommen von Muschelbänken wird auf den Wattflächen des Nationalparks „Niedersächsisches Wattenmeer“ jährlich über die Auswertung von Luftbildern ermittelt. Aus dem sublitoralen, ständig von Wasser bedeckten Bereich haben wir jedoch keine ausreichenden Kenntnisse: hier sind bislang die von den Muschelfischern aufgefundenen und zur Gewinnung von „Saatmuscheln“ beim Staatlichen Fischereiamt in Bremerhaven beantragten Flächen, auf denen sich Jungmuscheln angesiedelt haben, die verlässlichsten Angaben, die regelmäßig vorliegen.

Mit diesen Daten zum beobachteten Vorkommen der Muschelbänke und Miesmuscheln rechnet die vorliegende Studie ein Modell anhand von Umweltparametern der aufgefundenen Flächen, um gewisse Vorhersagen treffen zu können, welche Areale des niedersächsischen Wattenmeeres grundsätzlich für die Ansiedlung von Muschelbänken geeignet erscheinen. Für das Sublitoral finden sich damit möglicherweise wertvolle Anhaltspunkte für die weitere Suche nach Muschelbänken in diesem nur schwer zu erfassenden Lebensraum. Und insgesamt kann eine solche Karte zum „Muschelbankpotenzial“ hilfreich sein, wenn es um Fragen des Managements geht oder um eine Bewertung des Ist-Zustandes dieses wichtigen Habitats im Nationalpark „Niedersächsisches Wattenmeer“.

Nationalparkverwaltung Niedersächsisches Wattenmeer

Zusammenfassung

Die räumliche Verteilung von eulitoralen Muschelbänken und von Fischereiflächen (d.h. für die Saatmuschelfischerei beantragten und genehmigten Miesmuschel-Brutfallflächen bzw. Jungbänken im Sub- und im Eulitoral) im niedersächsischen Wattenmeer wurde analysiert. Dies ist der gesamte Datensatz, der aus den Jahren 1999 bis 2016 für das niedersächsische Wattenmeer zum Vorkommen der Miesmuschel im Eulitoral und im Sublitoral vorliegt. Als Ergebnis wurden Lebensraumeignungskarten (Potenzialkarten) erstellt, wobei in beiden Fällen null-inflationäre negative Binomialmodelle (ZINB) verwendet wurden. Dieser Modelltyp ist besonders geeignet, das Problem einer hohen Anzahl von Nullwerten im Datensatz zu bewältigen.

Für das Vorkommen von Muschelbänken auf den Wattflächen sind die Auftauchzeit, die mittlere Korngröße, die Orbitalgeschwindigkeit des Wassers, die Sedimentsortierung und die Flutstromwerte die wichtigsten Variablen. Für sublitorale Fischereiflächen scheinen die Tiefe, Scherspannung bei ablaufendem Wasser, Einwirkung von Wellenschlag, Sedimentsortierung und Orbitalgeschwindigkeiten des Wassers entscheidende Faktoren zu sein.

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Summary

Mussel bed presence on tidal flats and fishery plots sites in the Wadden Sea area of Lower Saxony (Germany) have been analysed. As a result, habitat suitability maps have been constructed, in both cases applying zero-inflated negative binomial models (ZINB). This type is especially designed to cope with the problem of a high abundance of zero values in the data set.

For mussel beds on tidal flats, emersion time, median grain size, orbital velocities, sediment sorting and flood current values are the most significant variables. For subtidal fishing plots, depth, ebb shear stress, wave breaking energy dissipation, sediment sorting and orbital velocities appeared to be determining factors.

1 Introduction

1.1 Project description

The project description is short, and as follows: “Erstellung einer Muschelpotentialkarte für das Niedersächsische Wattenmeer”, thus: construction of a mussel habitat suitability map for the Lower Saxony Wadden Sea area.

It includes both the littoral and sublittoral area.

1.2 Structure of the report

After a short introduction into the research area (section 2), the available data are described, and briefly the ZINB-analysis method is explained (section 3). Some data had to be derived first from already available data; the conversion method is mentioned as well.

Next (section 4), the data analysis is divided into two parts: first the raw data are characterised, and second the habitat suitability results are presented. In the final section (5) habitat maps are summarised.

1.3 Acknowledgments

For this analysis, the products of the EasyGSH-DB project have been crucial. The EasyGSH-DB products and metadata have been obtained from the EasyGSH-DB Portal www.easygsh-db.org (BUNDESANSTALT FÜR WASSERBAU 2019). Also, the author thanks J. Cremer (Texel) for some necessary QGIS-assistance.

2 Introduction

The Lower Saxony Wadden Sea (Figure 1) covers an area of about 2,600 km², about 55% of it consisting of tidal flats. The Wadden Sea (including the Dutch and Danish part) is generally recognized as a natural area of primary importance. It is designated as a protection area under the Ramsar Convention, is included as part of the European Union's Natura-2000 network area and has the status of a UNESCO World Heritage Site.

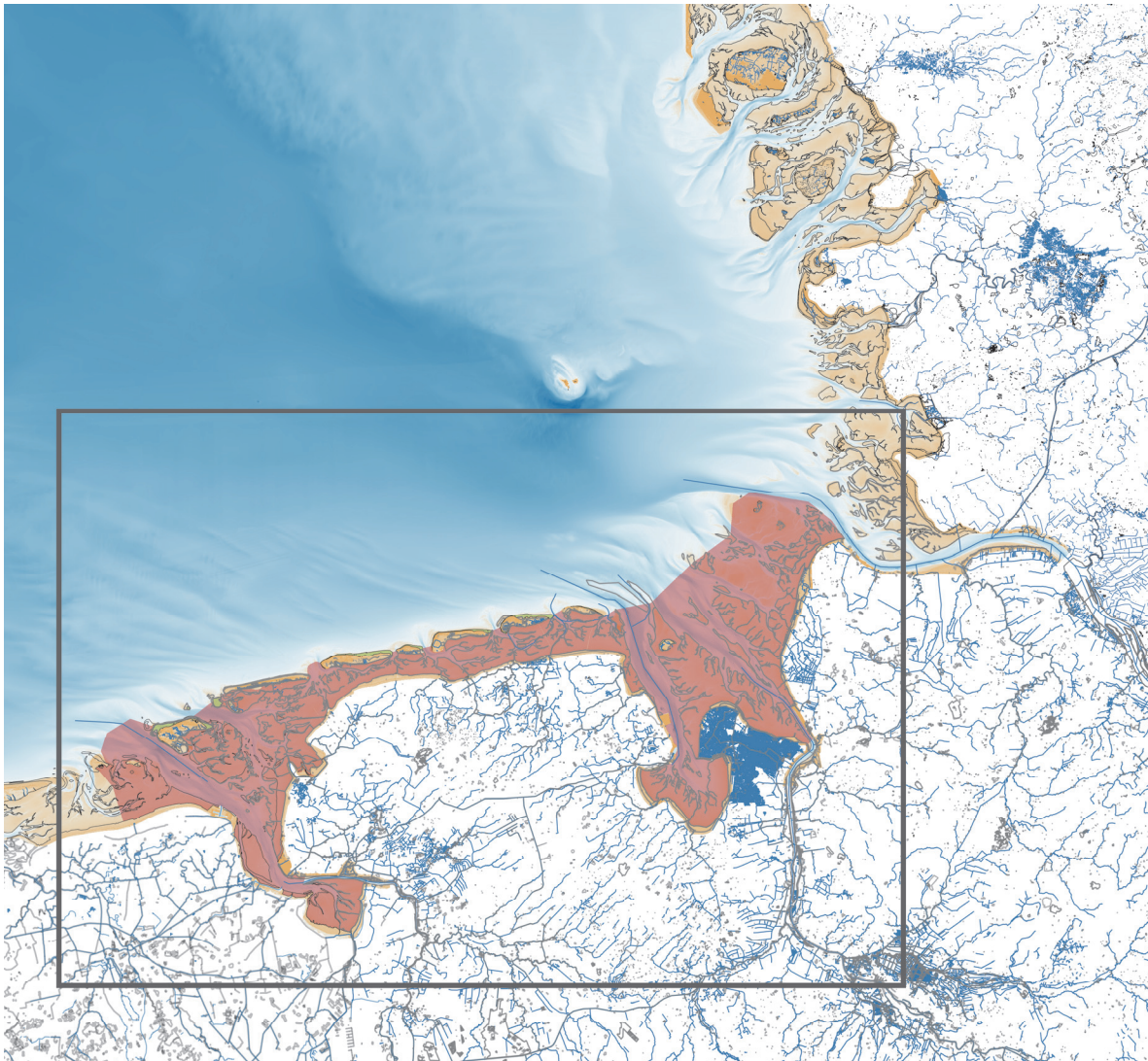


Figure 1 Depth map of the southern German Bight. Research area reddish coloured. Maps for Netherlands and Germany from Open Street Map (2020).

The Wadden Sea is one of the most important areas in Europe for several bird species (Blew et al, 2017) because of high benthic biomass densities (Drent et al, 2017) that form a crucial food source.

Intertidal mussel beds are an important class of characteristic structures, combining high biomass densities with a high species richness and high biochemical activity. They are considered as important food sources for e.g. Oystercatchers (*Haematopus ostralegus*) (Van de Kam et al, 1999, Blew & Südbeck, 2005), Turnstones (*Arenaria interpres*) and Curlews (*Numenius arquata*), the latter two mainly feeding on associated fauna (Smit et al, 2011).

After previous inventories in the Dutch Wadden Sea (Dijkema et al, 1989; Dijkema, 1991), a first mussel bed habitat map -for tidal mussel bed appearances only- has been constructed by Brinkman et al (2002). This map was upgraded in 2014 (Smaal et al, 2014).

By autumn 2019, the Nationalparkverwaltung Niedersächsisches Wattenmeer (NLPV) ordered a similar analysis for the tidal and subtidal mussel appearances in the Lower Saxony Wadden Sea area.

3 Material and methods

3.1 Data needed

A habitat suitability analysis is nothing else than comparing presence of mussel beds or appearances with several environmental characteristics. The latter must be discriminating -in some way- between areas where mussels (in this case) are present and those area where they aren't. And, these data must be sufficiently available; very scarce data usually will obstruct such an analysis.

Here, the results from the EasyGSH-DB-project have been crucial (<https://mdi-de.baw.de/easygsh/index.html#home>); it made a lot of abiotic data available for and the tidal and the subtidal areas. Downloads are from www.easygsh-db.org; see Bundesanstalt für Wasserbau et al (2019). For all supplementary metadata and other information, the reader is referred to these EasyGSH-DB websites. Data for orbital velocities and wave breaking energy were obtained separately from EasyGSH-DB partner SmileConsult GmbH (thanks to P. Milbradt).

These data are summarized below. Littoral biotic data were available from the Nationalpark-site (http://mdi.niedersachsen.de/HeronKaDI/JAVA_SCRIPT/37_Portal/); these concern mussel bed appearance on tidal flats; data on fishery licence areas (fishery plots) in the subtidal areas were obtained separately from the NLPV. These data from the fishing plots are currently the only available source of information about mussel settlements in the sublittoral area. They do not provide any information about the area that is actually fished. Areas named fishing plots have passed the necessary licensing procedure, but actual fishing was repeatedly prevented by the influences of the natural environment. Also, the approved area is seldom fully used.

3.2 The area

The Lower Saxony Wadden Sea area (Figure 1) is divided into 50*50 m cells, and for each cell the number of years with a mussel bed or fishery plot present was stored, together with the available abiotic data. Thus, about one million records were filled with data, of which 55% as tidal area, and 45% as subtidal area. These data are not independent from each other, having implications for the analysis results interpretation.

For summary purposes, the whole area was divided into twelve tidal areas, see Figure 2.

3.3 Biotic data

Data on the occurrence of mussel beds (littoral) have been collected for the years 1999 - 2016, except for the years 2012, 2014 and 2015; in total there are 15 data records. The data are marked per year but used together as the number of years with a mussel bed present. Thus, the data concern integers between 0 and 15, as maximum. See Figure 3 and appendix A1 for an overview.

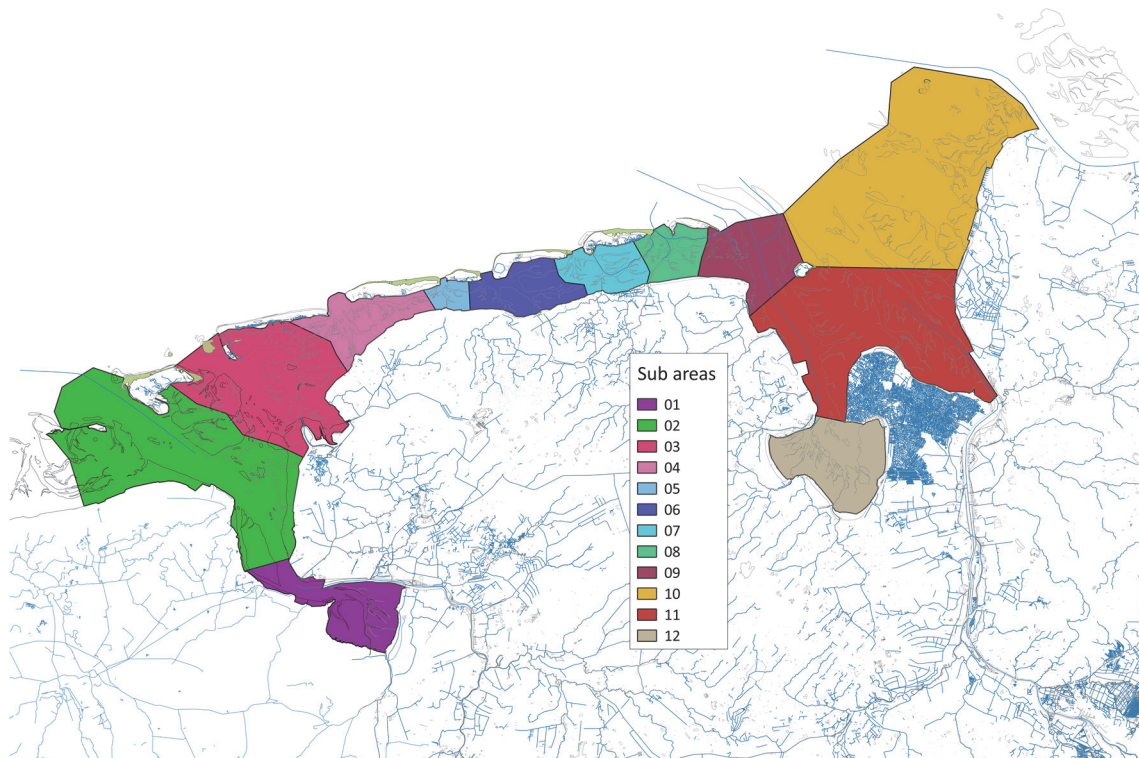


Figure 2 Sub areas distinguished in the Lower Saxony Wadden Sea.

Subtidal fishery licensed plots data are available for eight years. Cell record data represent the number of years a plot is present, thus data concern integers between 0 and 8, as a maximum.

3.4 Abiotic data

3.4.1 Elaboration

Several types of abiotic data for the whole Wadden Sea were available, albeit at different levels of accuracy and reliability. As stated before, all data used here come from the EasyGSH-DB project, covering the whole German bight (so, even larger than Figure 1 shows), including some Dutch areas. All data were restricted to the Wadden Sea itself, thus reducing the size of the data set. Some data were available on a 10*10 m grid basis, some of a 100*100 m grid basis. In the first case, a very simple approach was followed: just use only the centre value (one value out of 25). In the second case, a simple kriging-routine was applied (library(sp) and (gstat), see R (2020)).

The EasyGSH-DB project provides a lot of data for several years. It was decided to use one year, not an average of all years, or the most recent data set. Also, for different variables, sometime datasets for different years have been taken. One reason is that in a couple of cases, not all data sets were available for one year. A second one is that it might be a good idea to use data sets from different years since it gives an idea of the variation existing between years. Not that this variation is not large; values for one variable in different years do correlate very well.

3.4.2 Depth

Data were taken for 2010. The data set contains depth values as m depth relative to "Normalhöhennull ("standard elevation zero") or NHN. It is the same standard as the Dutch NAP ("Normaal Amsterdams Peil") or Amsterdam Ordnance Datum. Since negative data (deep is negative in the original set) are not allowed for the analysis, all data have been made positive: first multiplied by (-1) and then 2.5 m added. In that case also the highest levels of interest still have positive values (Figure 4).

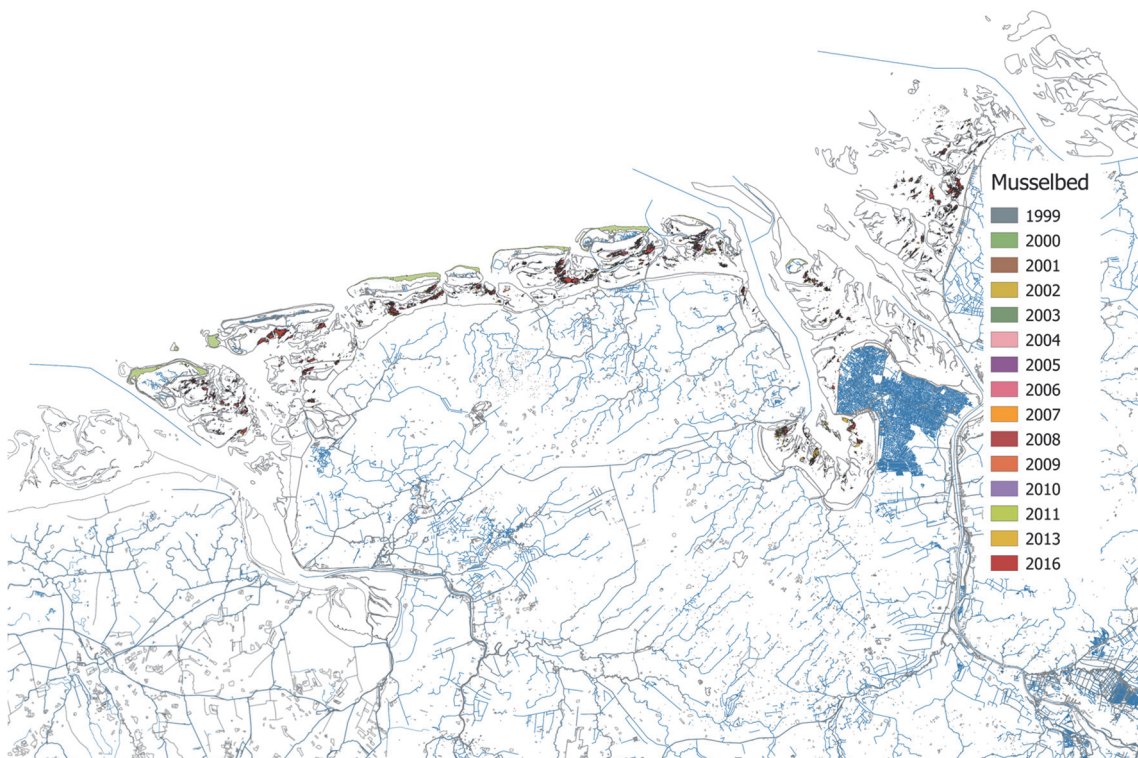


Figure 3 Mussel beds on tidal flats in the Lower Saxony area. See also appendix A1

3.4.3 Emersion

Emersion was available in the EasyGSH-DB data set, but not at the desired resolution. Therefore, available tidal ranges were used, and thus, *average* emersion times (as fraction of the time) were computed for each cell (with its *cell level*) following

$$emersperiod = 1 - \frac{(\pi/2 - \text{asin}(\frac{cell\ level - standard\ waterlevel}{Amplitude}))}{\pi} \quad (1)$$

Standard water level is the average water level relative to NHN and is about 5 cm + NHN. This value of 5 cm is derived from continuous level data monitoring by the Dutch Rijkswaterstaat near the Borkum island (Rijkswaterstaat, 2020). Amplitude data also originate from EasyGSH-DB.

This computed emersion time thus is an approximation because it does not account for neap and spring tides (Figure 4).

3.4.4 Flow velocities and bed shear stress

For bed shear stress and current velocities 50 and 95% quantile data are available. The 50%-quantile value reflects the median value, and the 95%-quantile the value close to the maximum values. But both are closely related, and for the habitat analysis itself it does not really matter whether the median of the maximum values are taken. For bed shear stress, the 2010 95% values are used, for current data the 2010 50% quantile maximum flood current values. Current velocities are in m s^{-1} and shear stress data in N m^{-2} (Figure 4).

3.4.5 Salinity

Salinity data (unit PSU, practical salinity unit, roughly (but not exactly) the content (g l^{-1}) of dissolved ions, were taken for 2013 (Figure 4). The 95% quantile data (of mean values) give the values that are not exceeded in 95% of all cases.

3.4.6 Porosity

One of the sediment properties is porosity: the volume fraction of water in the sediment, varying from about 0.3 for very sandy sediments to about 0.7 for silty areas. EasyGSH-DB data are for 2006 (Figure 4).

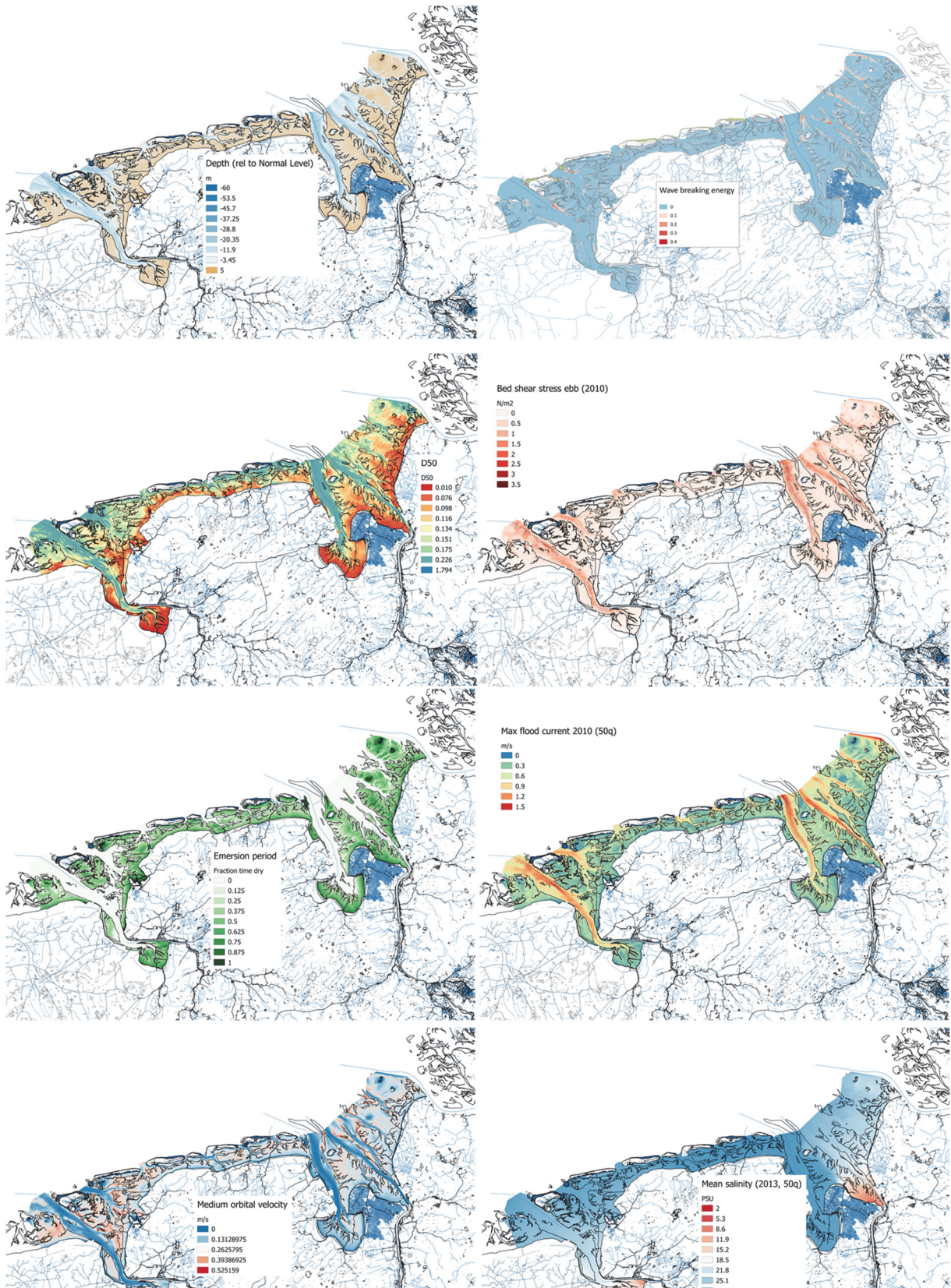


Figure 4 Abiotic data available for the Lower Saxony area. From upper left> right > lower left> right: depth, medium wave breaking energy, D50, Ebb bed shear stress, Emersion period, max flood current, medium orbital velocity & mean salinity. For more explanation see text. All data originate from the EasyGSH-DB project

3.4.7 Skewness, D50 and sorting

All three characteristics are based on the Krumbein ϕ -scale: $\phi = -^2 \log D / D_0$, with D the particle diameter in mm, and D0 a reference diameter (usually 1 mm, just to make it dimensionless). The distribution of all ϕ -values characterises the sediment. For example, ϕ_{16} denotes the ϕ -value for percentile of the grain size distribution. The grain size data are as D50, being the median diameter of the grain size distribution in the sample, in mm.

Sorting (-) of a sediment is a measure for the spread in grain sizes; the larger the value, the larger the range of grain sizes in a cell. Defined as:

$$Sorting = \frac{\phi_{16} + \phi_{84}}{4} + \frac{\phi_{95} - \phi_5}{6.6} \quad (2)$$

Sorting ranges are summarized in Table 1.

Table 1 Classification of sorting

Sorting (based on ϕ -units)	Characteristic (taken from Wikipedia)
Sorting < 0.35	Very well sorted
0.35 < Sorting < 0.50	Well sorted
0.50 < Sorting < 1.00	Moderately sorted
1.00 < Sorting < 2.00	Poorly sorted
2.00 < Sorting < 4.00	Very poorly sorted
4.00 < Sorting	Extremely poorly sorted

Skewness (“Schiefe” in German”) is a measure for how non-normally the grain size distribution is, and is defined by

$$Skewness = \frac{\phi_{16} + \phi_{84} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})} + \frac{\phi_5 + \phi_{95} - 2\phi_{50}}{2(\phi_{95} - \phi_5)} \quad (3)$$

See Figure 4 for an overview (D50 and sorting only). Skewness: Figure 5.

Values range from about -1 to +1. A value of 0 denotes a completely symmetric grain size distribution, values from 0 to 1 say that the smaller particle fraction is dominating, while values from -1 to 0 denote a dominance of coarse particles.



Figure 5 Skewness in the Lower Saxony Wadden Sea area

3.4.8 Orbital velocity and wave breaking

Not available from the EasyGSH-DB portal, but separately obtained from Smile Consult GmbH, Hannover (see EasyGSH-DB website partners), with thanks to prof. Peter Milbradt.

Orbital velocity, as averaged values, is in $m s^{-1}$, and represents the intensity of wind induced action on sediment beds. Wave breaking (in $W m^{-2}$) especially affects shores in the system, data concern long-term averages. For both, see (Figure 4).

3.4.9 Summary of abiotic data

In Table 2, an overview is presented which abiotic data were used, and from which years.

Table 2 Overview of used abiotic data. All data have been recomputed to a 50 50 m grid*

Variable	Unit	Year	Original resolu.	Comment
Depth	m	2010	10	Centre value used out of 25 cells
Emersion	fraction of time		(50)	Computed from depth and tidal range
Flow velocity	$m s^{-1}$	2010	100	
Bed shear stress	$N m^{-2}$	2010	100	
Salinity	PSU	2013	100	
Porosity	-	2006	100	
Orbital velocity	$m s^{-1}$	Mean	100	Not a specific year given
Wave breaking energy	$W m^{-2}$	Mean	100	Not a specific year given
D50	μm	2006	100	
Sorting	-	2006	100	
Skewness	-	2006	100	
Tidal range	m	2010	100	Average amplitude used for computing emersion period

3.5 Statistical method

3.5.1 General and data exploration

For the statistical analysis the R-environment (Version 3.5.3, R Development Core Team, 2020) was used. Packages used are {lattice} (Sarkar & Deepayan (2008)), {pscl} (Zeileis et al, 2008), {gstat} (Pebesma, 2004). Only a univariate analyses technique was applied; other possible techniques have not been considered (e.g. multivariate methods such as (boosted) trees (Ysebaert, 2000; De'ath, 2007; Compton et al, 2012)).

A few aspects must be considered and investigated before the univariate analysis can be done.

One is to start with checking the correlation between the abiotic variables mentioned in section 2: if two variables are very well correlated, then it is not wise to use both at the same time: they represent the same system characteristics.

Secondly, the univariate analysis produces a habitat suitability model, plus the results that reflect the reliability of the result. However, these reliability values (p-values) suppose independence of all variables. This is not the case here: the nature of the data set is that neighbour 50*50 m grid cells usually are only slightly different from each other. Thus, the spatial variance must be checked (Zuur et al, 2009).

Third, because of the previous step: if only a small part of the grid cell data is used one must also be certain that the set still represents the whole data set. Thus, does the set remain its characteristic distribution after data reduction?

3.5.2 Is it necessary to get rid of the spatial correlation?

If a spatial correlation exists, the number of independent measurements (response variable and independent variables) seems to be (much) higher than it really is, and therefore, results seem to be much more significant than they really are. At the other hand, the relationships found may not or only slightly be affected by a small or even a large spatial correlation; the resulting model may almost be the same. This aspect is checked during the computations.

Thus, removing spatial correlation is necessary when the significance of independent variables is to be discussed, but probably is *not* an equally necessary condition for finding a habitat model that fits the data best.

3.5.3 Habitat analysis method

Originally, more than one statistical method was to be applied analysing the data set. But, based on previous analysis, it was decided to stick to a Zero Inflated Negative Binomial approach. Thus, other possibilities like a GLM (Generalised Linear Models), NB (Negative Binomial models) or GAM (Generalized Additive Models) have not been considered here. The main reason is that ZINB's are best suited to deal with the present data set characteristic: a relatively small part of the cell does have mussel beds or fishing plots, and most of the cells have not. In other words: there is a very large number of zero's in the model (over 95% of the data: only 0.3% of the subtidal cells have had a fishing plot, and 0.6% of the tidal flat is mussel bed). A part of the zero observations is a result of the way the surveys have been performed:

- (1) Presence of a mussel bed is more or less a fact. Some mussel beds may have been missed.
- (2) On the other hand, in areas where there have not been mussel beds at all, these sites may still be suitable. So, a zero may indicate an absence because of unsuitable conditions, or an absence because of coincidence.

Thus, (see e.g. Zuur et al (2009) for a more complete explanation), the probability of having a zero $\Pr(Y_j=0)$ is

$$\Pr(Y_j=0) = \Pr(\text{false zero}) + (1 - \Pr(\text{false zero})) * \Pr(\text{count distribution gives a zero}) \quad (4)$$

The ZINB two-component mixture model consists of (a) a zero-inflation model that describes the probability of finding false and true zeros (the negative binomial part), and (b) of a count model that describes the distribution of the counts (including the chance having a true zero), having a Poisson distribution. This part is handled through a GLM-model (see Zuur et al 2009, 2012).

The count model thus predicts the number of years (out of the total number of years) that a grid cell contains a mussel bed.

The zero-inflation model accounts for the cases where the observations have been poor (the mussels were present in at least one year, but have not been observed), plus the number of years where the mussels have not been present although they should have: the habitat is OK, but the mussels are simply absent.

The count model used is a negative binomial regression model (with a log link). For the zero-inflation model, a binomial model with a logit-link (eq. 6, below) is applied, which is logical since eq(8) contains $\Pr(\text{zero})$ and $(1-\Pr(\text{zero}))$, and corresponds more or less to the description above for the quasi-binomial model.

The presence-absence data, transformed to frequency data ($0 \leq \text{frequency} \leq 1$), give the relative number of years a mussel bed was present in each grid cell. The predicted response variable \hat{Y}_j (the predicted fraction of years a mussel bed is present in a grid cell j given the conditions x_{ji} , $i=1..N$) depends on the independent variables X_i .

Thus, if x_i are the independent variables ($i=1..N$: flow velocity, salinity, etc) then the predictor \hat{Y}_j for the presence of a mussel bed in cell j is

$$\hat{Y}_j = \frac{\exp(a + \sum_{i=1}^N b_i \cdot x_{ji} + \sum_{i=1}^N c_i \cdot x_{ji}^2)}{1 + \exp(a + \sum_{i=1}^N b_i \cdot x_{ji} + \sum_{i=1}^N c_i \cdot x_{ji}^2)} \quad (0 \leq \hat{Y}_j \leq 1) \quad (5)$$

with a , b_i and c_i as model parameters. In eq. 4, squared terms are used. Eq. 4 allows for bell-shaped dependencies, implying that conditions are optimally suitable at certain values for x_{ji} and not or less suitable at larger or smaller values. The use of squared terms is not typically necessary for a bell-shaped response but increases flexibility.

The fit routines consider the squared (x_{ji}^2) terms in equation (4) as separate variables, being strongly correlated with the linear terms (x_{ji}). In R, this can be eliminated by using the *poly*-function (package {stats} (R Development Core team), see e.g. Chambers and Hastie (1992), and (eq.4) changes to

$$\hat{Y}_j = \frac{\exp(a + \sum_{i=1}^N b_i \cdot \text{poly}(x_{ji}, \text{degree}=2))}{1 + \exp(a + \sum_{i=1}^N b_i \cdot \text{poly}(x_{ji}, \text{degree}=2))} \quad (0 \leq \hat{Y}_j \leq 1) \quad (6)$$

The quasi-binomial model has a mean-variance structure of the form

$$\text{Var}(Y_l) = \phi Y_l (1 - Y_l) \quad (7)$$

with ϕ as the dispersion parameter, which is typically fixed at 1 in the binomial case. If overdispersion occurs, $\phi > 1$, implying a variance (much) larger than expected (therefore, the model is called quasi-binomial).

In R, the model reads

$$\text{Model} = \text{zeroinfl}(Y \sim \sum_{i=1}^N \text{poly}(X_i, 2) \mid \sum_{i=1}^N \text{poly}(X_i, 2), \text{dist} = \text{"negbin"}, \text{link} = \text{"logit"}) \quad (8)$$

This implies that basically the same variables are used to construct the count model and to construct the zero-inflated model. Which variables finally appear to be relevant may differ for both parts.

3.5.4 Eliminating non-relevant predictors

Statistical routines produce characteristics or indices that can be used to decide whether one model is better than another. The preferred model has the best fit and the lowest number of parameters used; the problem only is how to decide for a certain fit and number of parameters. An often-used characteristic for GLM-model selection (Zuur et al, 2009) is the Akaike-index (AIC, Akaike, 1974; Sakamoto et al, 1986).

The ZINB-routines produce such an AIC (Zuur et al, 2009), which now includes the log-likelihood $\ln(L)$ of the estimate

$$AIC = 2 * npar - 2 \ln (L) \quad (9)$$

Next, the computed significance (p-values) for each variable is a useful characteristic. To decide with variables are the best to remove from the model, those two explaining variables that appear to be least-significant (have highest p-values) are selected at each computation.

Next, the analysis is performed two times again, each without one of these selected explaining variables. The worst performing variable, based on the ('adapted') AIC-value, is then removed from the list.

For the ZINB-models this parameter selection is performed for the count and the zero-inflated model separately. Then, the variable to be eliminated is selected; this is or a variable for the count model or one for the zero-inflated model.

Next, the whole procedure is repeated until no further improvement is computed. For the ZINB-model it might well be that finally the count model is based upon other variables than the zero-inflated model is.

There is one 'however': the AIC-values almost completely depend on the L values (the deviances), and the number of parameters has almost none effect simply because $\ln(L)$ is much larger than the number of parameters $npar$. So, this method is useful to find out which parameters are most reliable, but the model best describing the habitat suitability is the full model (using all variables), simply because the explained deviance (deviance (without a model)- deviance (with the model)) is largest.

3.6 Applied software

The software used has been written in R (R Core team, 2020), especially the `zeroinfl`-routine (Zeileis et al, 2008) from the `pscl`-package (Jackman, 2020). All maps were produced using QGIS (QGIS, 2020), and for further data and word processing Microsoft Office 365 was used (Microsoft, 2020). Geographical maps used are from Open Street Map (2020).

4 Results (1): data exploration

4.1 Observations

4.1.1 Littoral mussel beds and sublittoral fishing plots

An overview of mussel bed appearance (the number of years that a mussel bed was present in a grid cell) is shown in Figure 6; the same for fishing plot presence in Figure 7. It concerns a 5% selection from the data. These figures give a first idea of the abiotic environment of mussel beds and fishing plots.

4.1.2 Pairplots

The next part concerns pairplots: plots of independent data (the abiotic variables) and dependent data (here: the mussel bed appearance or the fishing plots) versus each other in one figure (Figure 8 and Figure 9). These figures represent possible correlation between the independent variables. Thus, if, in such a case, both variables are included in the same model, both represent roughly the same system characteristic. Most striking, this is the case for Emersion time and Depth. This is logical also: the emersion period was derived from depth (and tidal amplitudes). A second close relationship exists between D50 (median of the grain size distribution) and porosity. A high porosity usually is found in silty areas, thus areas with low grainsizes. Other variables are less related; even flood current velocity and ebb shear stress do not show a close correlation. Thus: only depth and emersion, and D50 and porosity should not be used together in one model.

This does not automatically mean that the other variables are important. Some may show to have very low discriminating power (mussel beds or fishing plots appear over the whole range of values), or, what sometimes also may happen: values of the variable are very similar for the whole except for some marginal sites with very different values.

Other pairplots are gathered in a separate ppt-file.

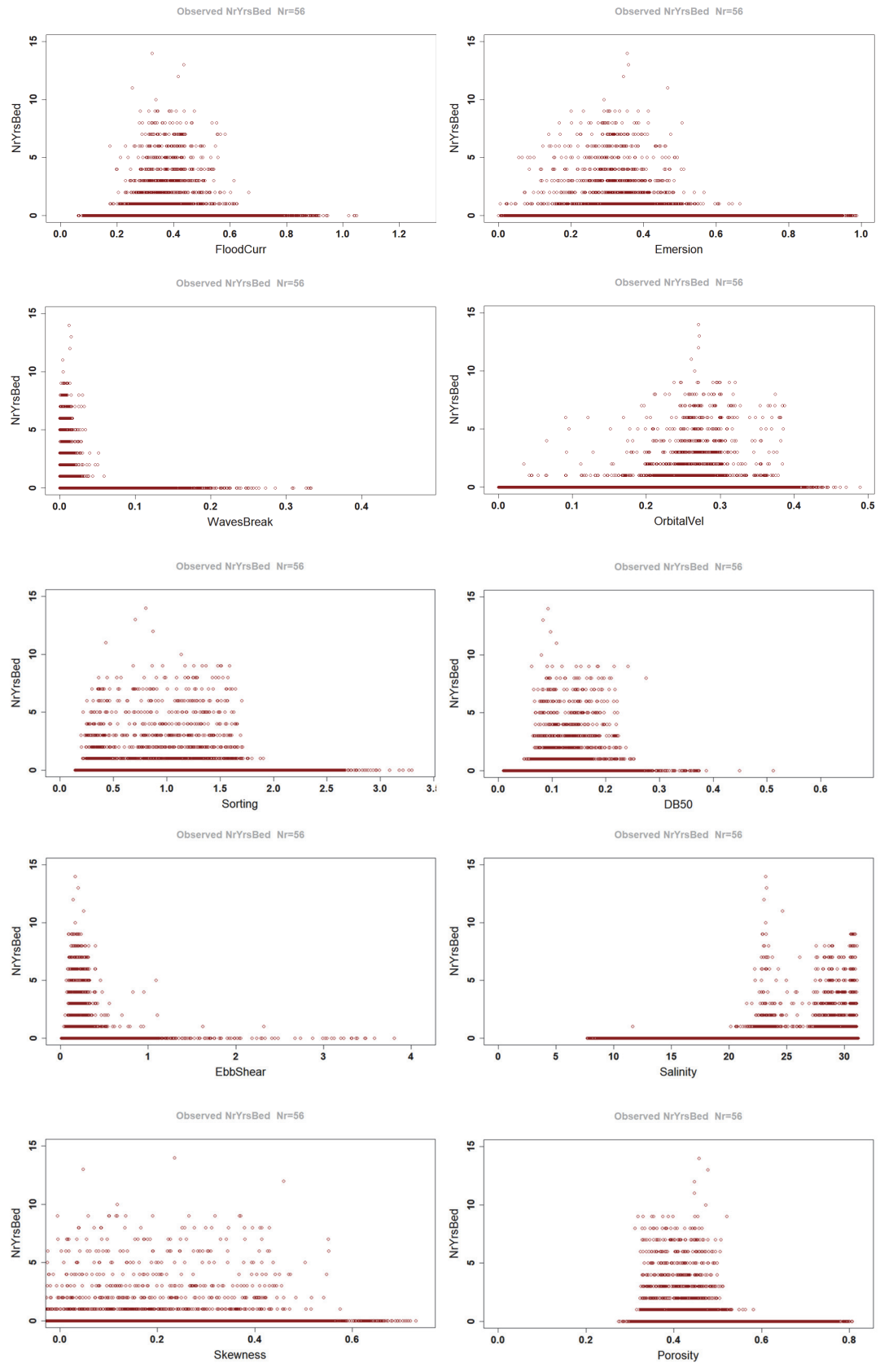


Figure 6 Cells with number of years of mussel bed appearance vs abiotic characteristic of the cell. For units see text. Note that D50 is called DB50, here.

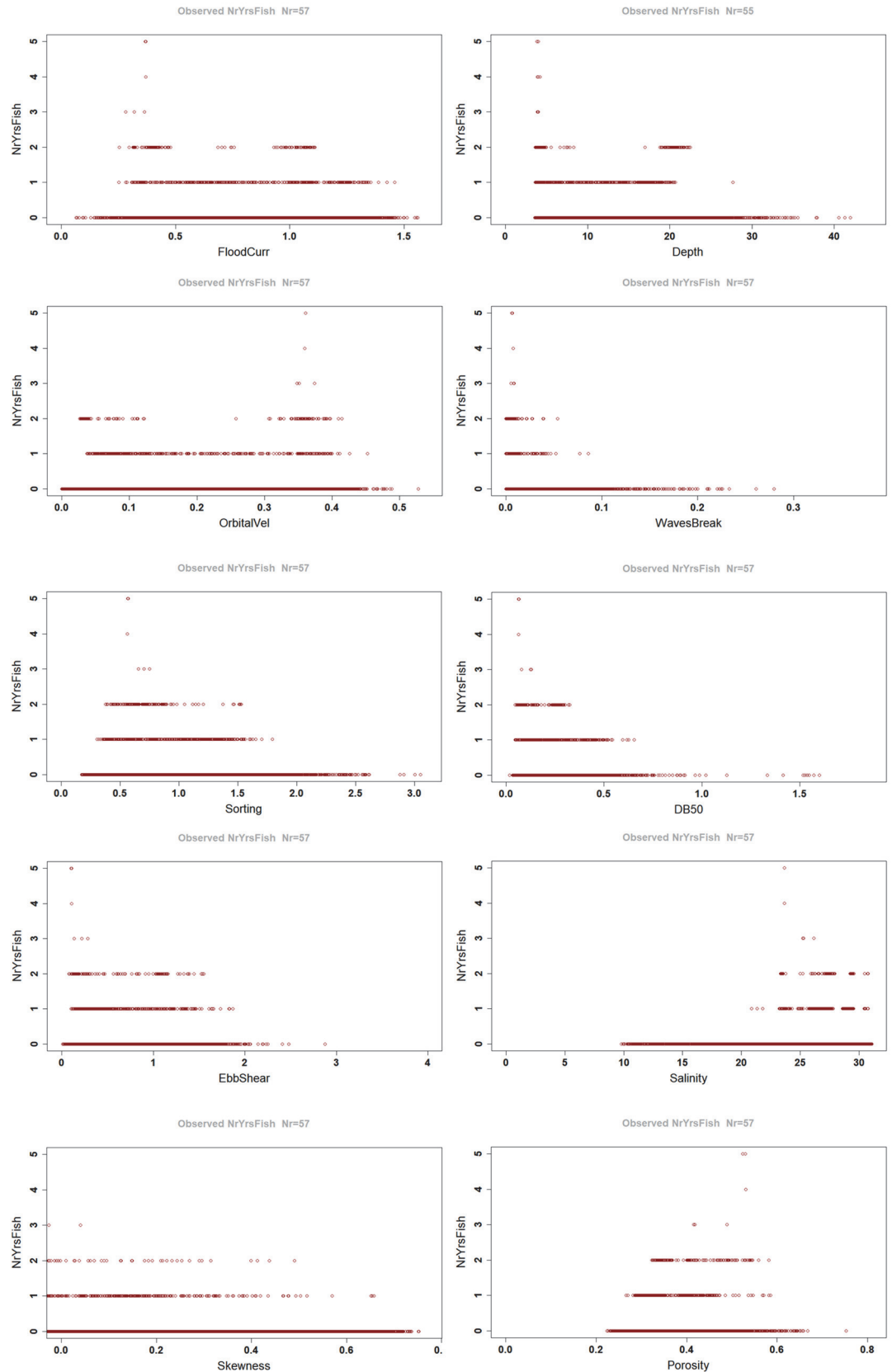


Figure 7 Cells with number of years of fishing plot presence vs abiotic characteristic of the cell. For units see text. Note that D50 is called DB50, here.

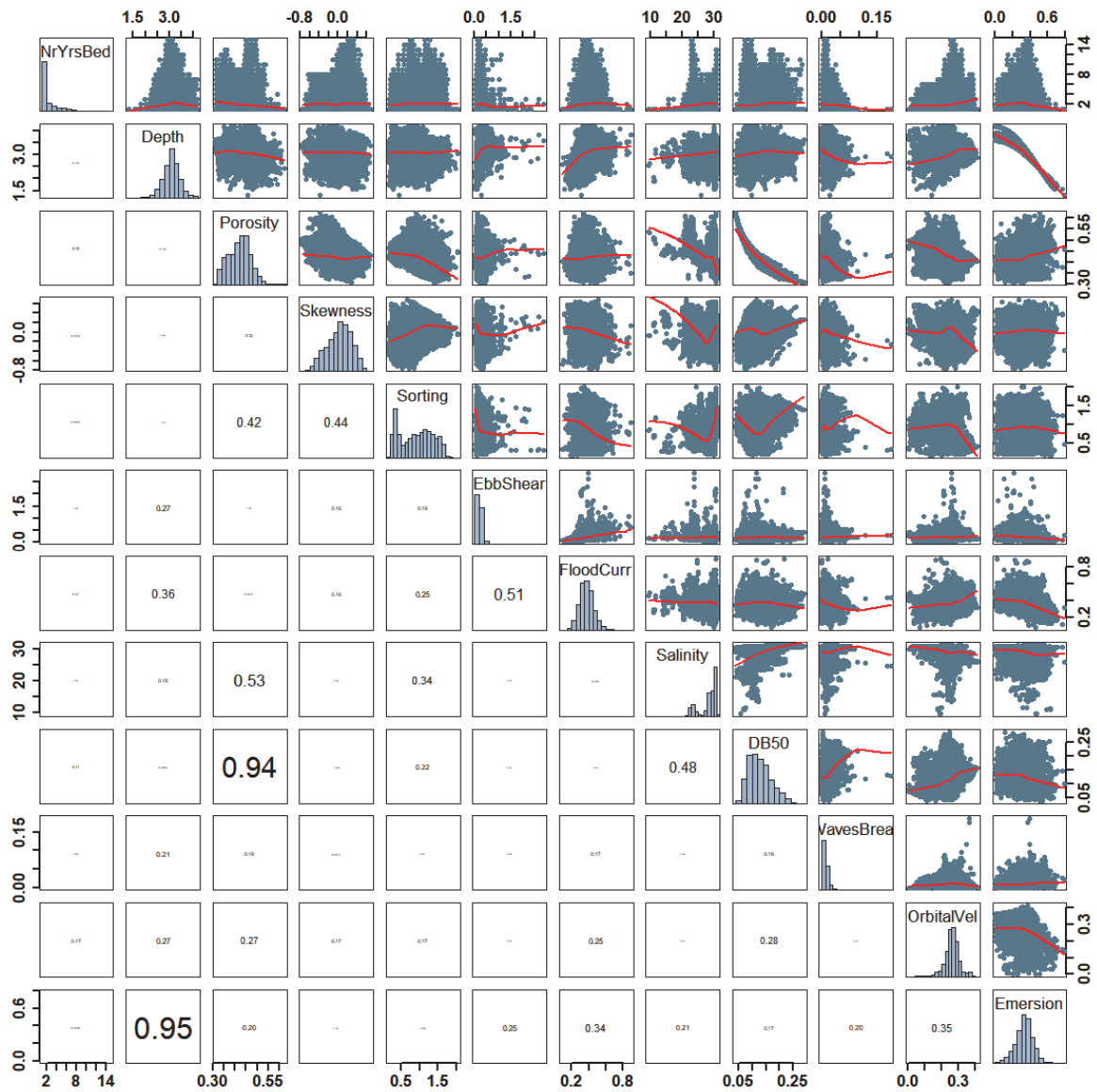


Figure 8 Littoral situation: pairplot for all variables plus the response variable (mussel bed), only those cells with mussel beds present. Mussel bed present = number of years present out of the maximum of 15. Note that D50 is called DB50, here.

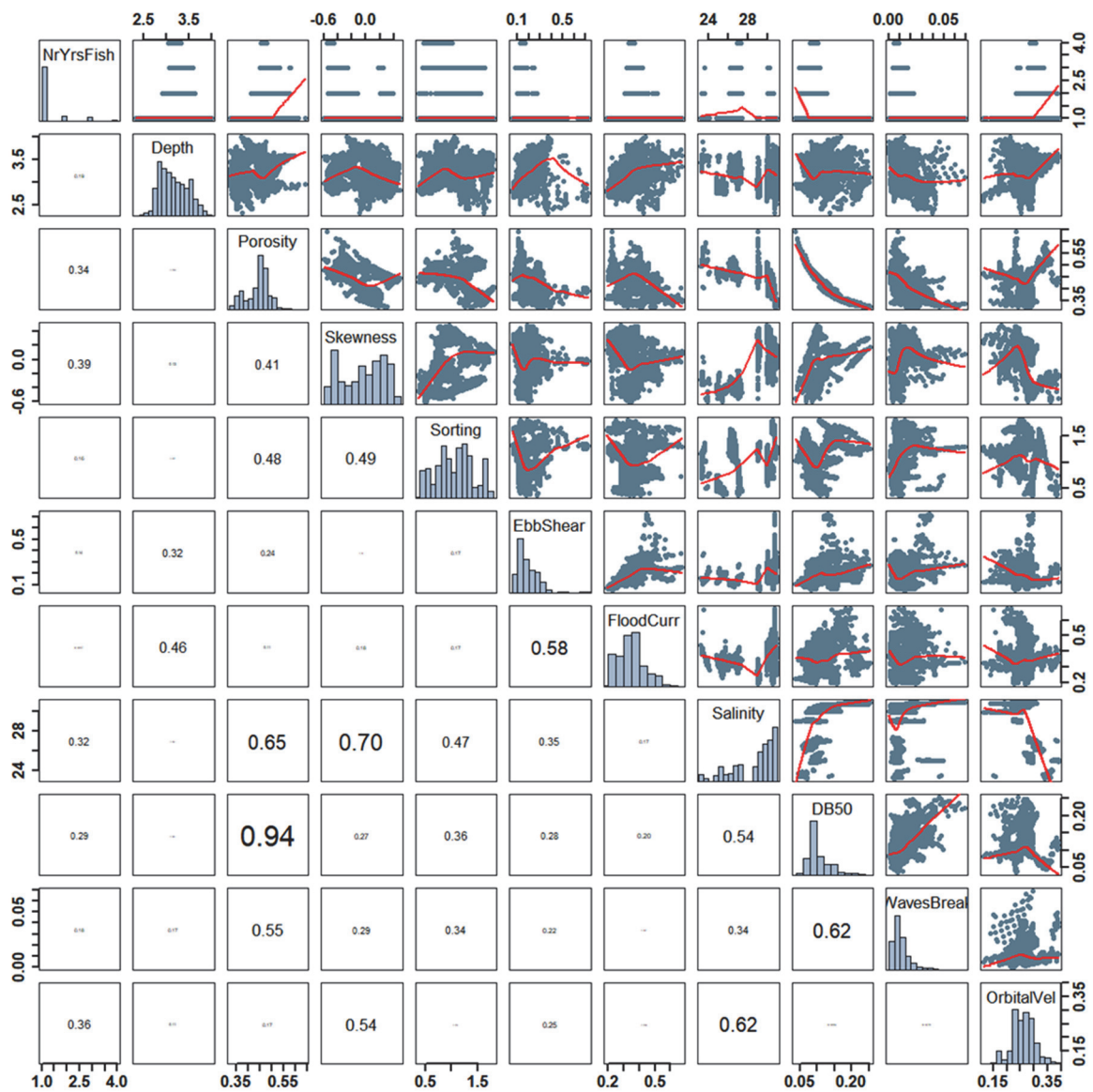


Figure 9 Sublittoral situation: pairplot for all variables plus the response variable (fishing plots), only those cells with fishing plots present. Fishing plots present = number of years present out of the maximum of 8.

Residues for FloodCurr compared to average Langeoog

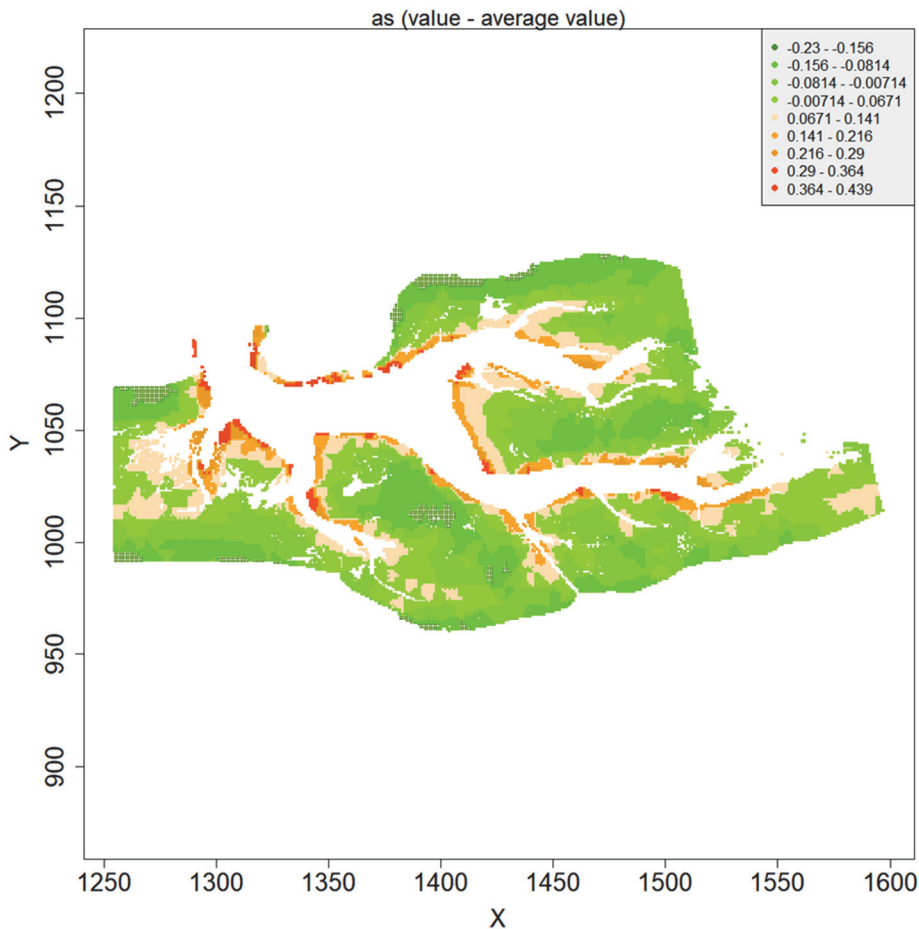


Figure 10 Bubble graph for the Langeoog area (nr in 6 in Figure 2). Colours show the differences from the average value (flood currents, in this case).

4.1.3 Bubble graphs

Bubble graphs represent a way to illustrate differences within an area; these graphs were made for each sub-area (Figure 2) and all abiotic variables. One illustration is presented in Figure 10; more graphs are in the separate ppt-file.

4.1.4 Spatial variograms of residuals

From bubble graphs (as Figure 10) and the data overview maps (Figure 4 and Figure 5) it is clear that from the abiotic data set many data are very correlated, simply because of being characteristics of neighbour grid cells (this consideration is also valid for the mussel beds and fishing plots). So, the question is at what distance cell characteristics can be considered as independent from each other.

Therefore, spatial variograms (see Zuur et al, 2009) have been produced of all residuals: residue = cell value – average value of all cells. As soon as the semi-variogram line reaches a plateau, cell values tend to be uncorrelated. In the present situation, where neighbour cells resemble a lot, it is

obvious that independence of data is far from reality. As an example, emersion data are presented in Figure 11, showing that independence is reached at a distance of about 100 cells, or, since a cell is 50*50 m, 5 km. Other data give similar results, albeit that the number of cells required for (some) independence differ. This implies that for a basic data set only a very small part of the data can be used if full independence is a strict condition: may be only 1 out of $100^2 = 0.0001$ of all data should be used when performing the suitability analysis.

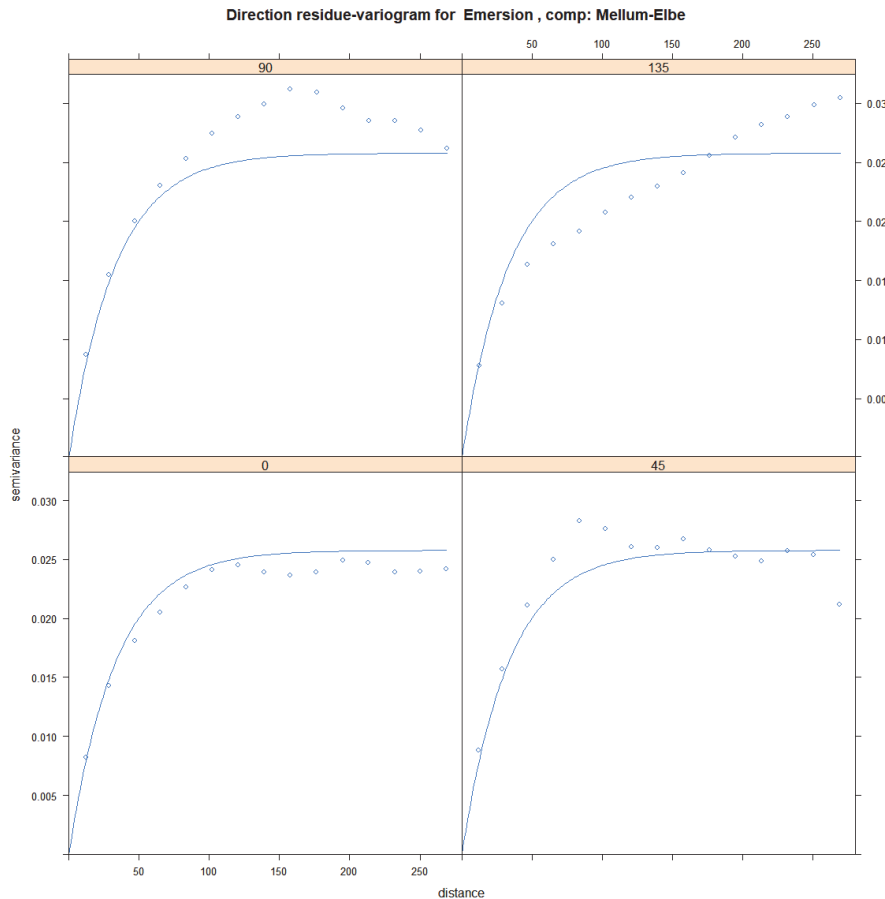


Figure 11 Spatial residual variogram for emersion values in the Mellum-Elbe compartment (nr 10 in Figure 2). Data on top give the angles of direction.

4.1.5 Does a selection from the data set still represent all data?

That brings up the next question: how well the original data set is represented in case only a small part of the data is used. This is tested with a t-test. For the random selections, a fraction α of all the data was chosen, and for the relevant variables the mean value was computed as a characteristic value. Then a t-test was computed

$$t = \frac{(m_a - \mu_b)}{\sqrt{\frac{\sigma_a^2}{n_a} + \frac{\sigma_b^2}{n_b}}} \quad (10)$$

to check whether the results were significantly different from the complete dataset or not. The distribution characteristics of the variables have been considered; non-normal distributions have been transformed to normal.

In (eq. 10), m_a is the real mean of all data and μ_b the sample mean, σ_a and σ_b is the standard deviation and n_a and n_b the number of all the data (a) and of the sample (b). The tests have been performed for several values of α . In the cases that these tests reveal that a specific sample size is not sufficiently representing the complete data set it may be decided not to use it, or to reproduce the random sampling a number of times and still come to a representative result. Also, as illustration, histograms of the resting data sets were produced. In Figure 12, an example for flood

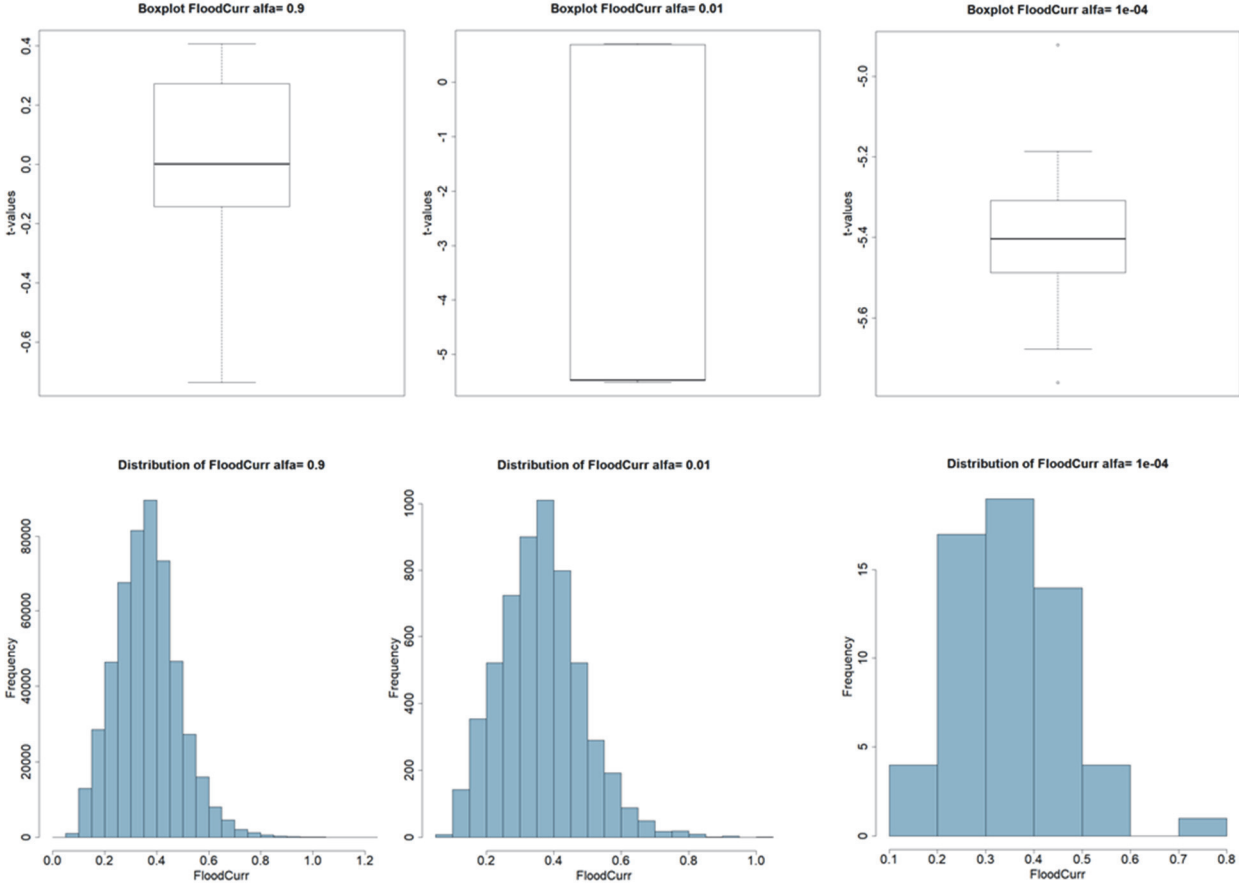


Figure 12 t-plots and histograms for variable flood current, for four different sample sizes. From left > right: 0.9, 0.01 and 0.0001 of all data. Histograms illustrate that at sample size (α)=0.01, the original data set is still represented quite well, although the spread of data (boxplot) did increase. At α =0.0001, there is little left of the original set.

current values is presented. This result is similar for all variables. Thus, the condition (from section 4.1.4) that only a small part of the data should be used, does not hold: although the data independence is assured, the data set itself it badly represented.

5 Results (2): habitat maps

5.1 Type of maps and classification

The habitat analyses produce two types of maps: the chance of finding a mussel bed or fishing plot in each 50*50 m cell of the area, and a classification of the area suitability. The first is expressed in a real chance (0..1), and as the number of years a mussel bed (out of the maximum of 15) or a fishing plot (out of the maximum of 8) may be expected.

A classification is used to indicate the most promising areas. This has been done before for the Dutch Wadden Sea (Brinkman et al, 2002), and Smaal et al (2014): the 1% areas with highest computed probabilities are gathered in class 1, the 30% areas with the lowest probabilities in class 12. Percentages refer to the number of grid cells. Since there are roughly 500.000 grid cells, the 1% 'best' areas contain about 5000 grid cells, the 30% areas in the lowest class represent about 150.000 grid cells. The class ranges are mentioned in Table 3.

Table 3 Model results as habitat suitability classes. The models produce a probability \hat{Y} for mussel bed appearance ($0 \leq \hat{Y} \leq 1$). The 1% grid cells with highest values are class 1, the next 1% class 2, etc.

Class	%-range	Class	%-range
1	0-1	7	20-25
2	1-2	8	25-30
3	2-5	9	30-40
4	5-10	10	40-50
5	10-15	11	50-70
6	15-20	12	70-100

5.2 The maps

Next, both maps, for mussel bed suitability and for fishing plot suitability, are presented. Both were produced using all (non-correlated) variables.

5.2.1 Mussel beds on the tidal flats

In Figure 13 an overall habitat suitability map (based on the classification from Table 3) is presented, with and without mussel bed appearance, showing that high scoring area indeed often have mussel beds present, but also that mussel beds appear in lower scoring areas. This especially is the case for the Mellum-Elbe-area (nr 10 in Figure 2).

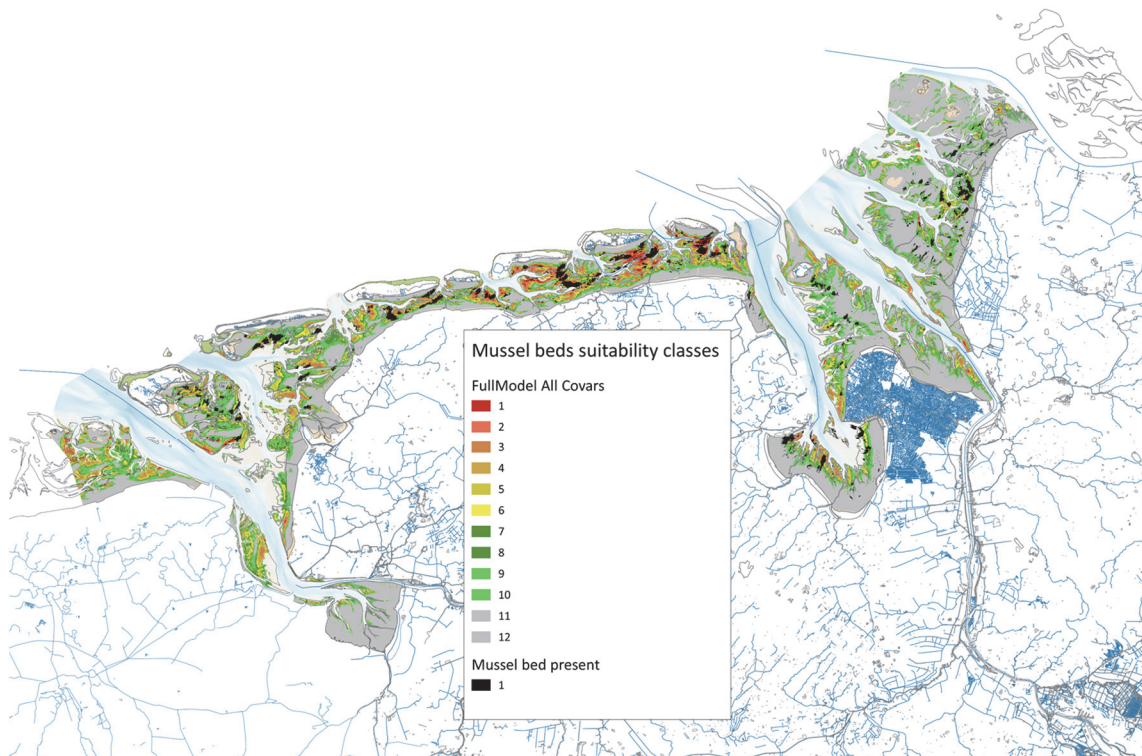
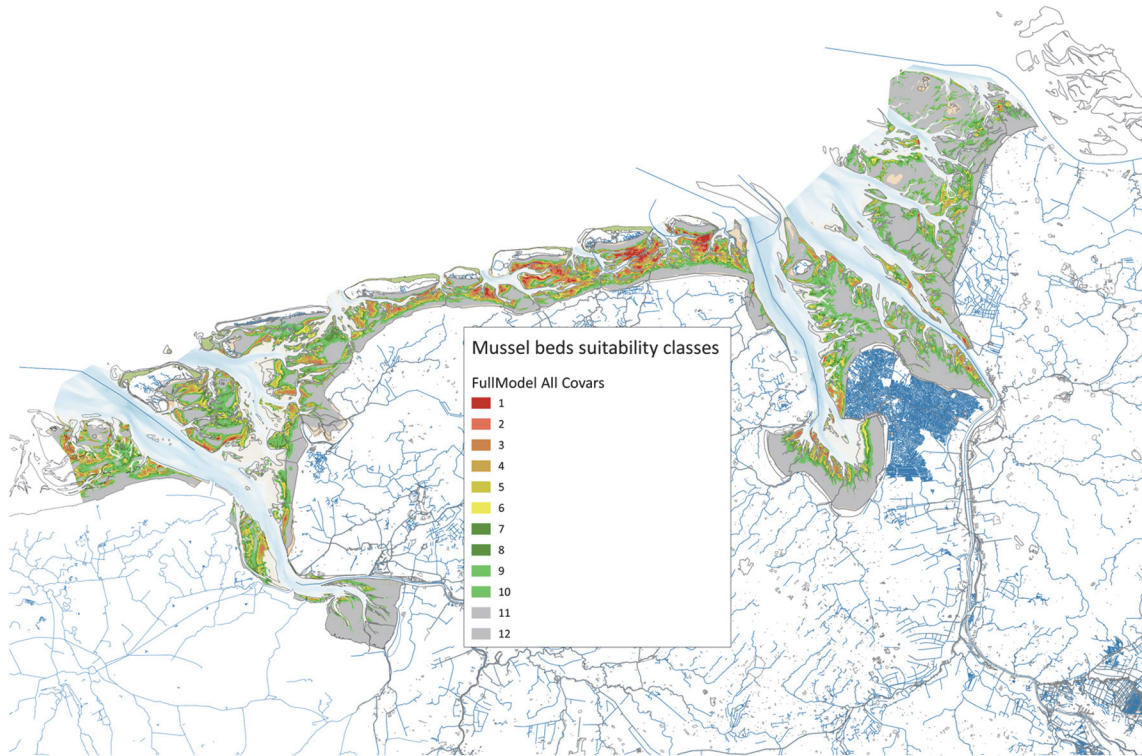


Figure 13 Mussel bed habitat suitability, classification after Table 3. Upper: classes alone, lower: mussel bed presence (once or more during the 15 years data) included. See appendix A1 for more detailed maps.

When looking at the chances of appearance instead of classes, it becomes clear why: the class 1- areas do have the highest chance for mussel bed appearance, but classes 5 and 6, for example, still

have considerable chances. This is illustrated in Figure 14 (as the number of years -out of 15- that a cell can be expected to have a mussel bed).

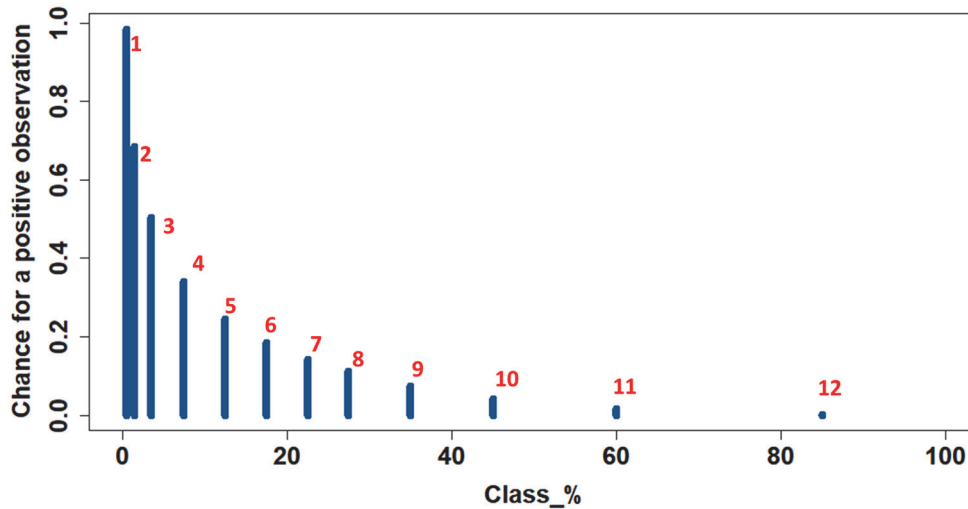


Figure 14 Number of years of finding a mussel bed in a cell (out of 15), vs the class range (percentage of all cells), see Table 3. Class numbers mentioned as well (in red).

Cells in class 1 have the highest chance (of course), but cells that fall in class 5 still can be expected to have a mussel bed in 0.3 years (out of the 15 years). And, from the previous analyses in the Dutch Wadden Sea (Smaal et al, 2014) it already was clear that, despite chances are highest in classes 1, mussel beds still may appear in area classes 8 or 9.

5.2.2 Fishing plots

The number of data available for fishing plots was a lot smaller than for littoral mussel beds and this had consequences for the model results. The iteration, for finding the best parameter set, had more trouble with convergence, it crashed more often, and differences between results from models using different variable sets also differed more than model results for the tidal mussel beds.

Results for the analysis using all relevant variables are presented in Figure 15. Analogue to the littoral mussel bed situation, also here some of the fishing plots seem to occur in areas with a lower classification score (not shown in the plot). What the classes mean in terms of years of fishing plots to be expected (out of the 8 years of observations) is presented in Figure 16.

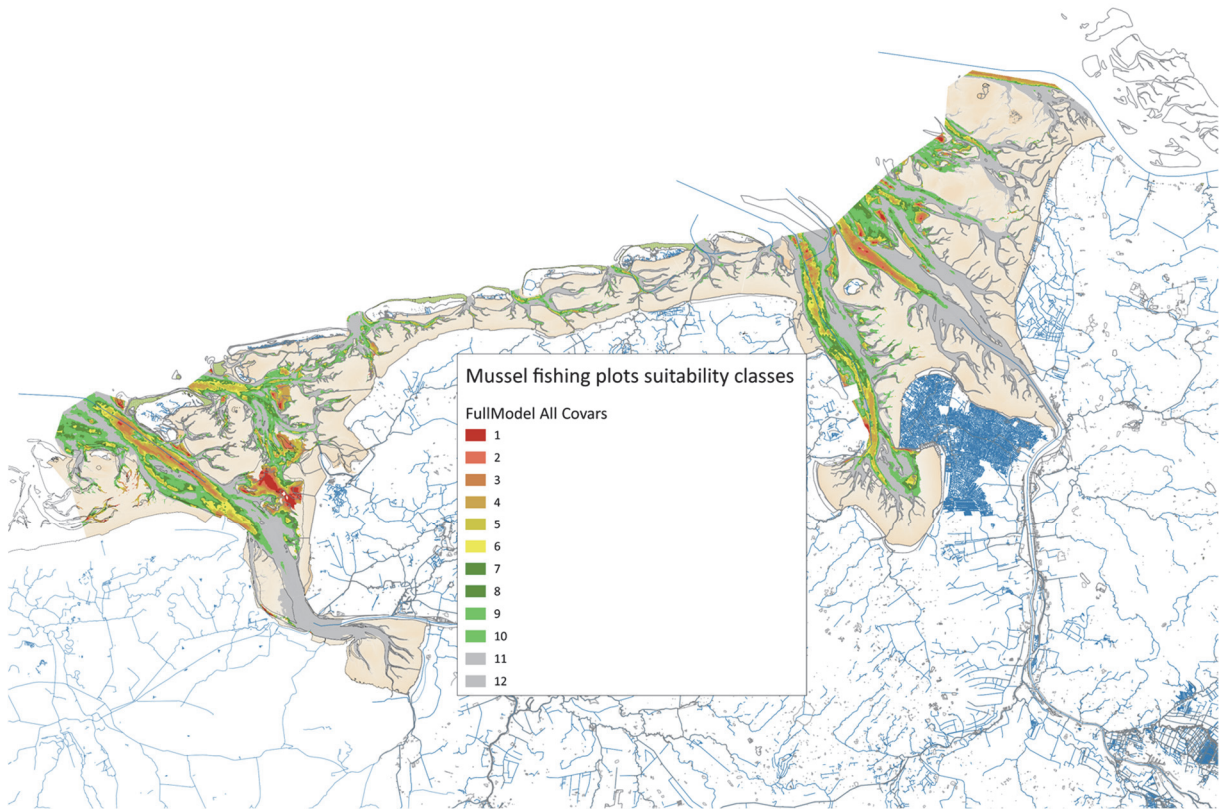


Figure 15 Fishing plot habitat suitability, classification after Table 1.

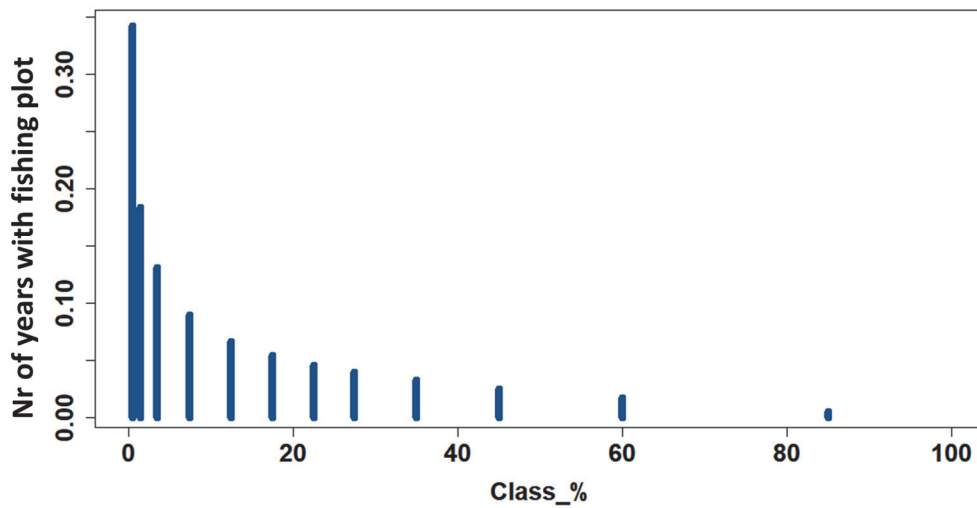


Figure 16 Number of years of finding a fishing plot in a cell (out of 8), vs the class range (percentage of all cells, see Table 3. See for class numbers also Figure 14.

5.3 Individual response curves

Finally, individual response curves are presented, giving a better idea of where most suitable mussel bed or fishing plot areas may be found. These have been derived from the models, and present chances of finding a bed or plot at averaged values of all variables, except the one the response is computed for. All other variables were varied a bit, stochastically; that is the reason why the response lines are not completely smooth.

5.3.1 Tidal areas

In Figure 18, individual response curves are presented for five variables. These curves have been taken from the model analysis with just these five variables. Median D50-values for best mussel bed expectations are about 0.2, emersion period about 0.25 (fraction of the time dry), orbital velocity 0.2 m s⁻¹ (so: low effects of waves, but very sheltered areas are less preferred), sorting

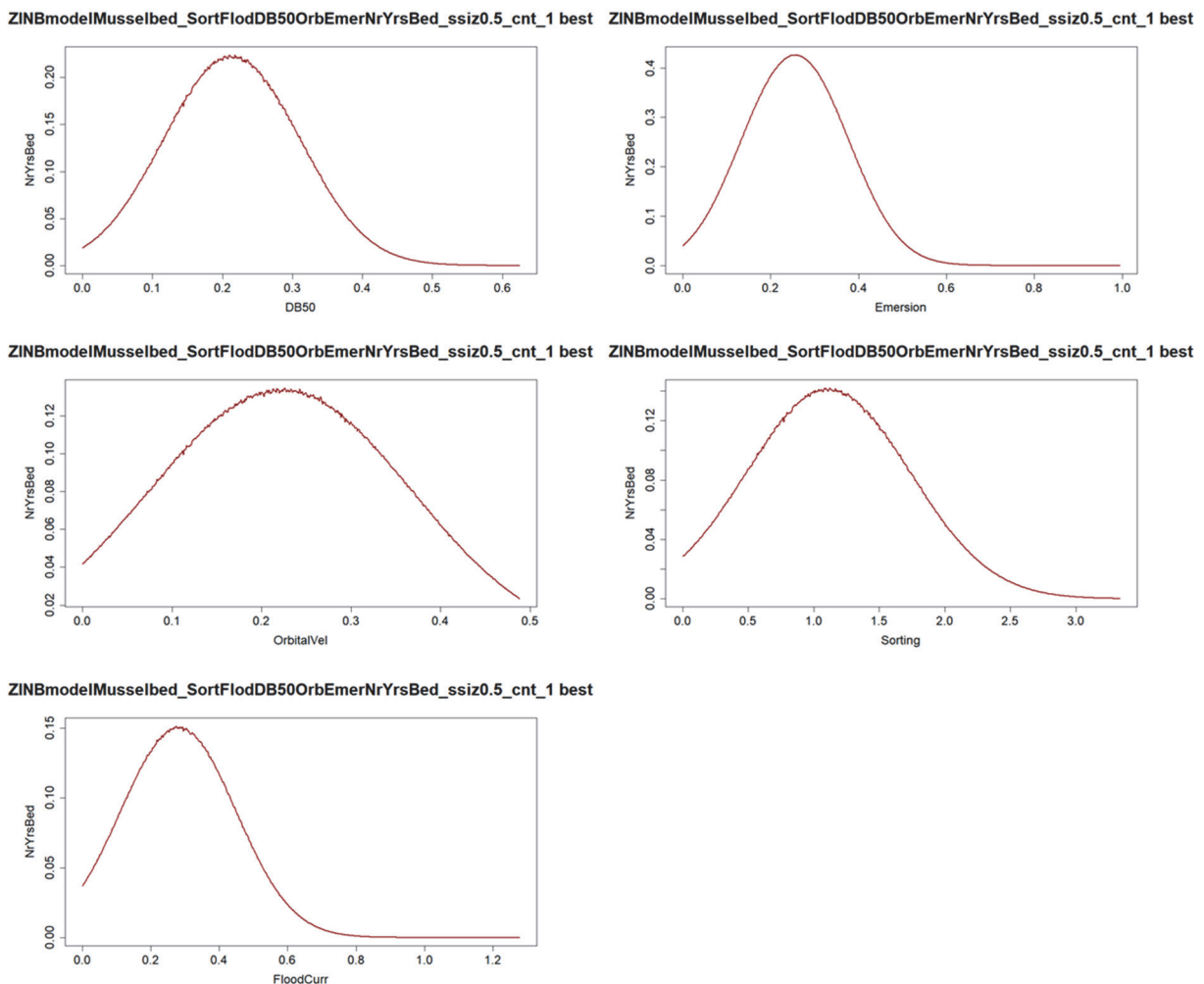


Figure 17 Individual response curves for five variables. Relationship between variable value and chance of finding a mussel bed. Comes from the model analysis with sorting, flood current velocity, D50 (called DB50 here), orbital velocity and emersion period as independent variables.

about 1.0, and about 0.3 ms⁻¹ flood current velocity. The latter must be considered as a condition where food is transported towards and over the mussel beds, without disturbing structures.

5.3.2 Subtidal areas

In Figure 18, individual response curves are presented for five variables. Three of these have proven to form important factors for the analysis. Fishing plots occur there where effects of breaking waves are low, salinity is high with an optimum around 28 PSU, and a median grain size D50 of 0.5. Depth and Porosity were important according to the numerical model summary, but here it can be seen that at large depths and at high porosity values the response curves run into very unrealistic values. Thus, both may be considered as less determining for where the best fishing plot areas are.

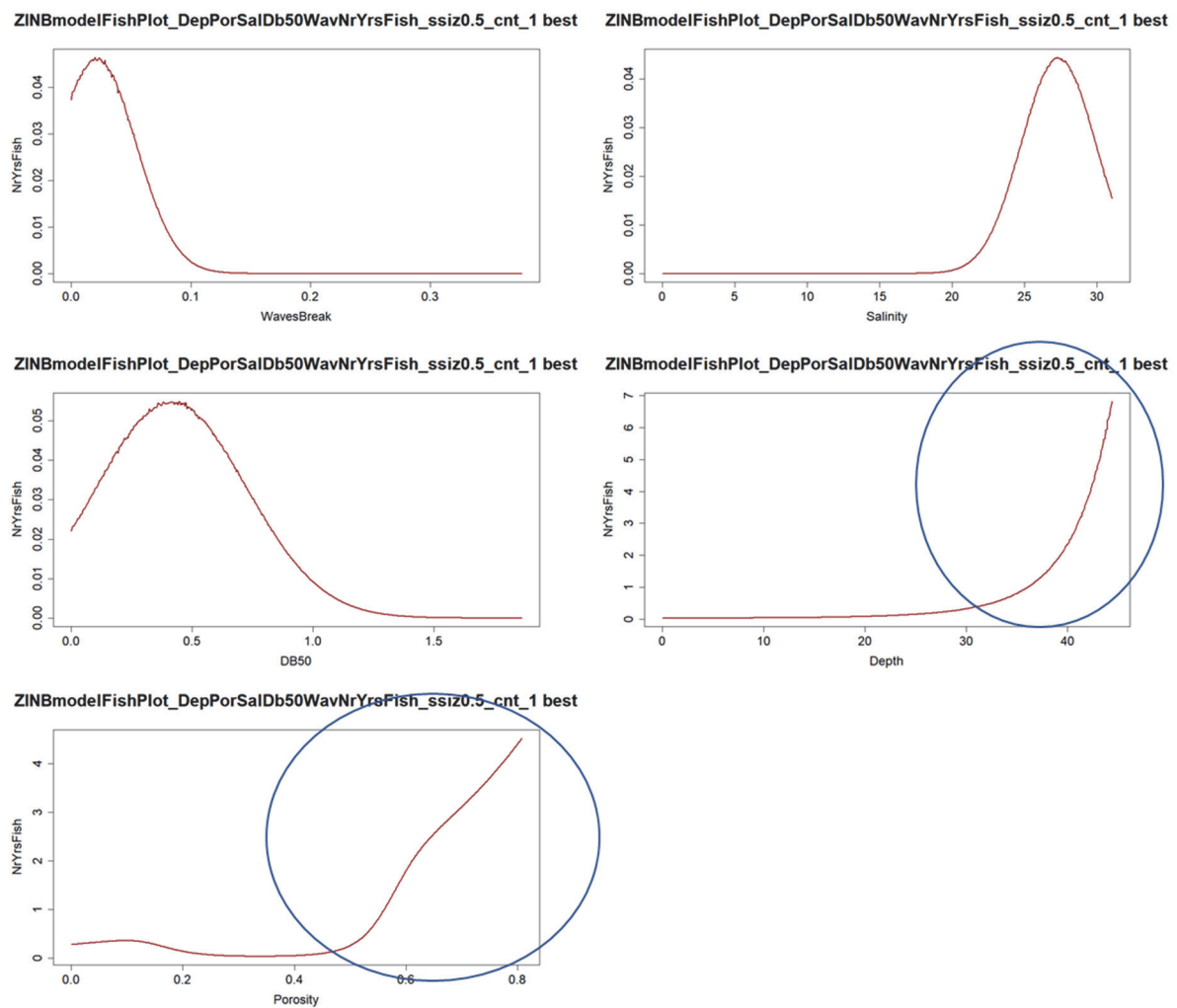


Figure 18 Individual response curves for five variables. Relationship between variable value and change of finding a fishing plot. Circles are around both ranges where the values are completely unrealistic, and thus, reliability for both variables is low.

5.4 Observed and expected number of mussel beds and fishing plots in each tidal area

5.4.1 Mussel beds

Comparing observed and predicted number of mussel beds and fishing plots in each of the twelve tidal areas distinguished (Figure 2) shows that total mussel bed area is somewhat underestimated, but that locally much larger differences occur. This is a characteristic that was also observed in the Dutch Wadden Sea, and probably is related to the analysis method. Since data are Poisson-distributed, a log-transformation takes places, eliminating the effect of some high values. When averaging mussel bed presence, this effect is not present.

Table 4 Observed (all years together) and computed area (ha) of mussel beds in the Lower Saxony tidal area.

Nr	TidalArea_Nam	Size(ha)	AreaBed	AreaPred
1	Dollart	8361	0.0	12.0
2	Ems_Bor	20588	23.6	136.9
3	Bork_Juis	17657	172.2	78.1
4	Jui_NordN	6717	55.2	54.6
5	Baltrum	1973	29.6	12.9
6	LangeO	6524	80.4	74.4
7	Spieker	5412	107.3	70.9
8	Wanger	4929	102.9	52.1
9	Mel_Wst	5080	42.6	32.1
10	Mel_Wes	34942	193.2	77.1
11	Mel_Elb	24500	50.2	80.8
12	Jade	10347	85.1	43.3
	Lower Saxony (total)	147029	942.3	725.2

Note that all areas (observed and predicted) have been computed as the number of years observed (cq predicted) /15 (the total number of years) * 0.25 (the area of a single grid cell, ha). Thus, it is the whole period-average occupation by a mussel bed.

5.4.2 Fishing plots

Like the mussel beds in the previous section, the expected fishing plot area is lower than the observed one. And, for most areas considerable deviations can be observed between predicted values and observed ones.

Table 5 Observed and computed area (ha) of fishing plots in the Lower Saxony tidal area.

Nr	TidalArea Name	Size(ha)	AreaBed	AreaPred
1	Dollart	4832	0.0	2.0
2	Ems_Bor	29684	185.2	113.8
3	Bork_Juis	12684	180.4	39.3
4	Jui_NordN	3142	0.0	8.5
5	Baltrum	317	0.0	0.5
6	LangeO	2437	22.8	5.2
7	Spieker	1754	23.5	3.2
8	Wanger	1527	0.4	1.7
9	Mel_Wst	7197	1.9	19.2
10	Mel_Wes	28296	35.0	69.8
11	Mel_Elb	20076	6.1	31.6
12	Jade	5308	0.0	12.2
99	Lower Saxony (total)	117253	455.4	306.9

Note that all areas (observed and predicted) have been computed as the number of years observed (cq predicted) /8 (the total number of years) * 0.25 (the area of a single grid cell, ha). Thus, it is the whole period-average occupation by a fishing plot. Note that "Fishing plot" means "areas requested for fishing" and does not mean that these areas have actually been fished, see chap. 3.1 *Data needed*).

6 Discussion and conclusion

Mussel bed appearance and fishing plot presence in the Lower Saxony Wadden Sea area were analysed, producing habitat suitability maps for both the tidal flats and the subtidal areas. These show the spots that are most (and least) suitable for mussel beds to appear, and fishing plots to choose.

These analyses were based on available abiotic variables, and the result can never be better than the quality of the underlying data. These have been provided in great detail, but still, part of the data is from models (with their own uncertainties) and in case derived from samples, the sample density is much lower than the 50*50 grid cell size used in the analysis.

Next to all the available data, some data are missing. Most important are the food resources mussel need for their own growth (the magnitude of primary production or phytoplankton presence), and other conditions in the water column, such as turbidity. The higher the content of silt in the water column, the more energy it takes for mussels to select the food particles needed, and thus, the more negative the conditions for growth are.

But one must deal with the data available.

The ZINB-approach is most suitable for the available data set, because of the large amount of zero values in the dataset. Usually, a few percent of the area is covered with mussel beds; over 98% of all data are zero's.

The results for the tidal areas indicate that mussels need a certain water flow, probably one that is enough to provide food for and distribute this food over the mussel beds. Best habitats are in sheltered areas, with low orbital velocities (thus: low exposure to wind), but not too sheltered. This may be because most sheltered areas also are areas close to the shore. And then emersion plays an important role. Optimum values are found at about 25 % emersion time; value that are a bit lower than found in the Dutch Wadden Sea (there about 35- 40% emersion time seemed to be the optimum). This value is closely connected to predation and to food collection: high on the tidal flats time for filtering water is short, and thus, growth is low. In the subtidal area and close to the low water line, food availability is much better, but predation by shrimps, crabs and starfish also is (see e.g. Saier 2001^{a,b}, 2002). And, next to low food conditions, high on the tidal flat predation by gulls and oystercatchers results in a high mortality. Wave breaking can be considered as a negative condition, which sounds logical since mussels -and especially freshly fallen seed mussels- need to avoid being washed away. Finally, the median grain size (expressed as D50): a preferred value is about 0.2, implying that the median grain size is 200 μm .

Some additional questions

At the end of the project, some additional questions arose on a couple of aspects mentioned in the report. These questions are summarized and answered below.

- 1) Wouldn't it have been a good idea to split the analysis into two parts: 1999-2005, and 2006-2016, because of the appearance of oyster by about 2005.

Answer: Yes, it would have been a good idea, but it must be a question for a follow-up. It would require doing all analyses again, including production of all maps.

- 2) The mussel bed habitat map shows good possibilities for the areas south of Spiekeroog and Langeoog, although no mussel beds did appear there. What could be the reason?

Answer: one cannot answer that. Definitely, some independent variables are NOT in the analysis. Turbidity, but also larvae drift, shrimps, name it. And sometimes it is bad luck. In the Netherlands we could see that it may take over ten years before certain areas are colonized (again). Although mussel larvae are available, this can easily be observed nowadays since mussel collector nets present there get mussel spat seed almost every year, while settlement at the sediment sometimes is completely absent.

One should also realize that a habitat map reflects the best fit, regarding the data used. And, it may serve as a guide which areas might be worth protecting for e.g. conservation reasons.

In case there are unexpected results, like this Spiekeroog and Langeoog-case, it usually means that one may do research after the reasons. Or, in other words: a habitat map is not the endpoint of a study, but moreover the starting point for further investigations.

- 3) Is it possible to estimate the uncertainty of the results because of the autocorrelation of variables?

Answer: No. The point is that it possibly only affects the p-values for the model and for judging how relevant the independent variables are. But, not for the model itself. So, the model is as good as it can be.

- 4) Why it is that class 1 is not fully occupied by mussel beds?

Answer: That is a usual question. But as Figure 14 shows, the average change for class 1 having a mussel bed is not more than 1/15. Also: class 1 is 1% of the total area. And the (tidal +subtidal area) occupation with mussel beds is about $940/147000 = .6\%$. Thus, if even all mussel beds would be in class 1, even then not the whole class 1 area would have been filled. Of course, the model would be nearly perfect, AND the mussel beds should behave perfectly. But where mussel beds appear is partly determined by chance: stochastic processes like drifting larvae clouds. Where they settle mostly is undetermined. Where they survive, that is what is predicted by the analysis. And where you see them (during the inventories) are those places where the mussel spat was not eaten by crabs, gulls, or whatsoever.

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A1 Some extra charts

After some questions asked by the Nationalparkverwaltung Niedersächsisches Wattenmeer, some extra charts have been produced. As an alternative for the map in Figure 3, a map with the number of years a mussel bed has been present, is shown in Figure 19.

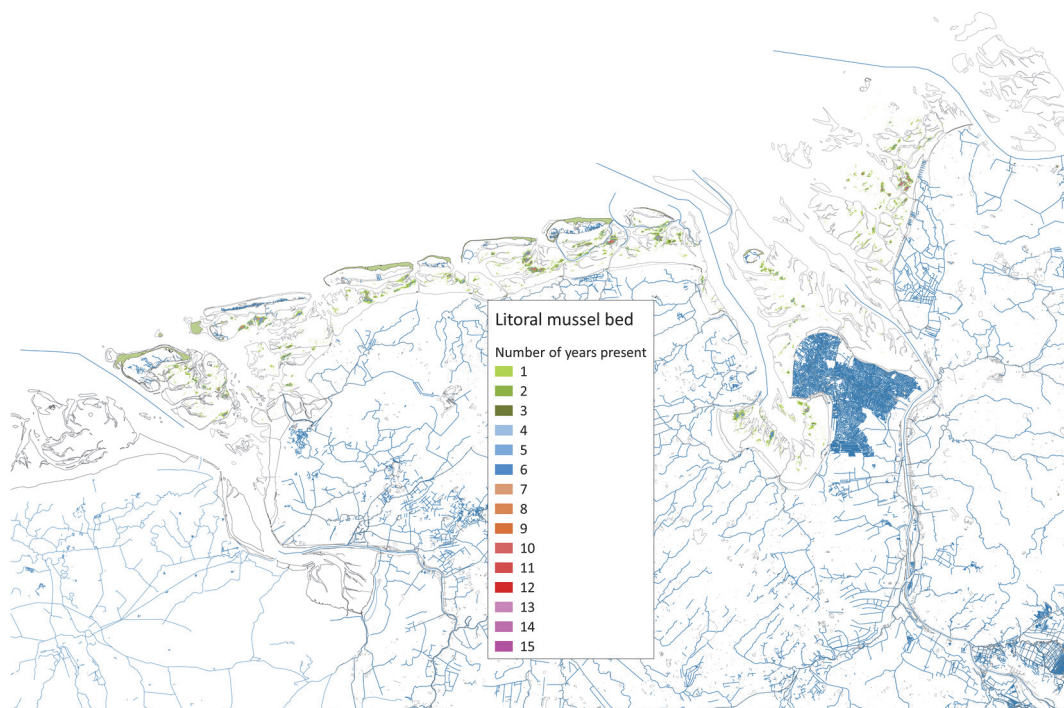


Figure 19 Number of years mussel beds a mussel bed was present at each cell.

And, the number of years a mussel bed was present has its real maximum at 10 years. Next, the maps have been split into three separate parts. All combined: habitat map without and with observations.

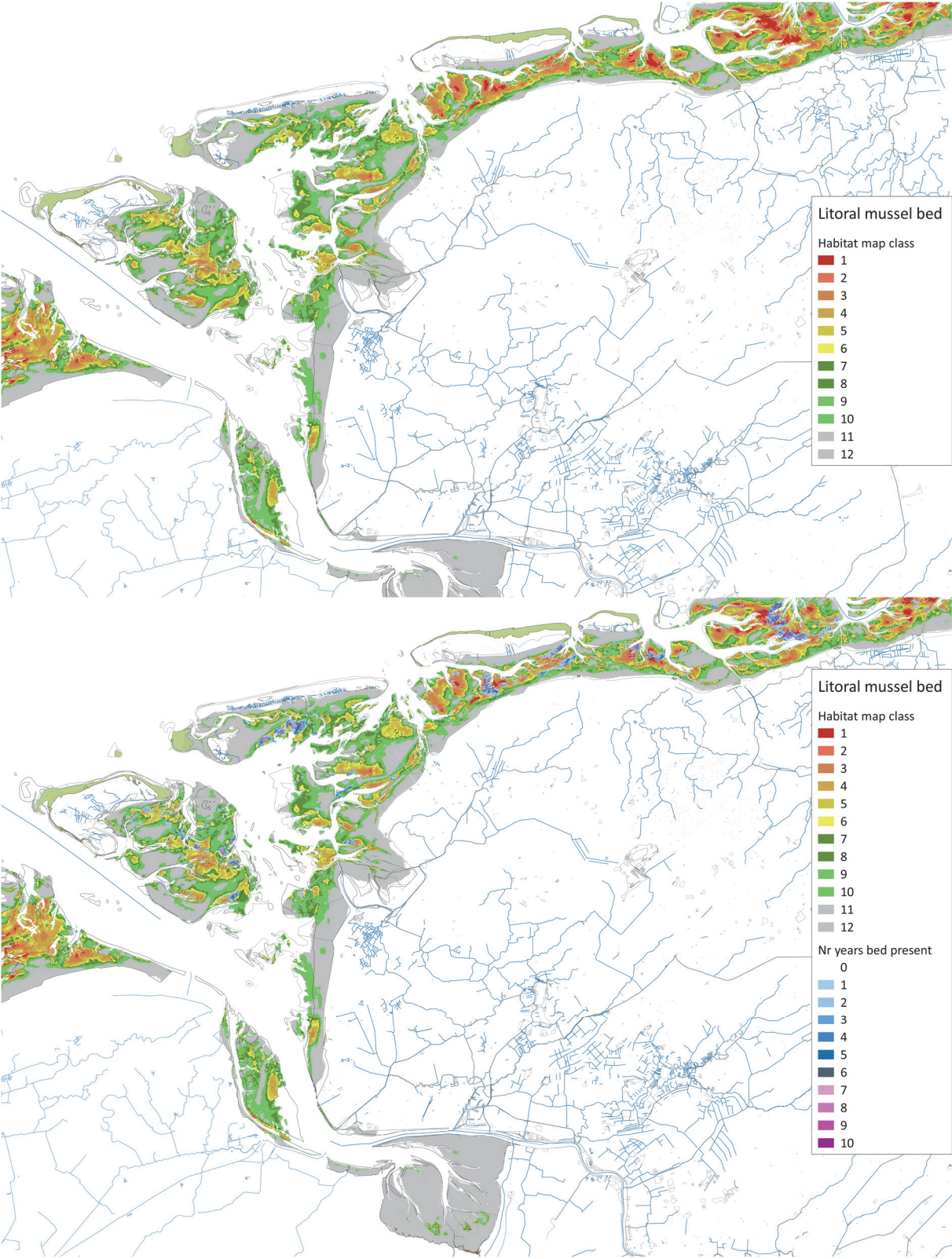


Figure 20 Upper: mussel bed habitat map, lower: ditto, now with observations included. Classes according to Table 3

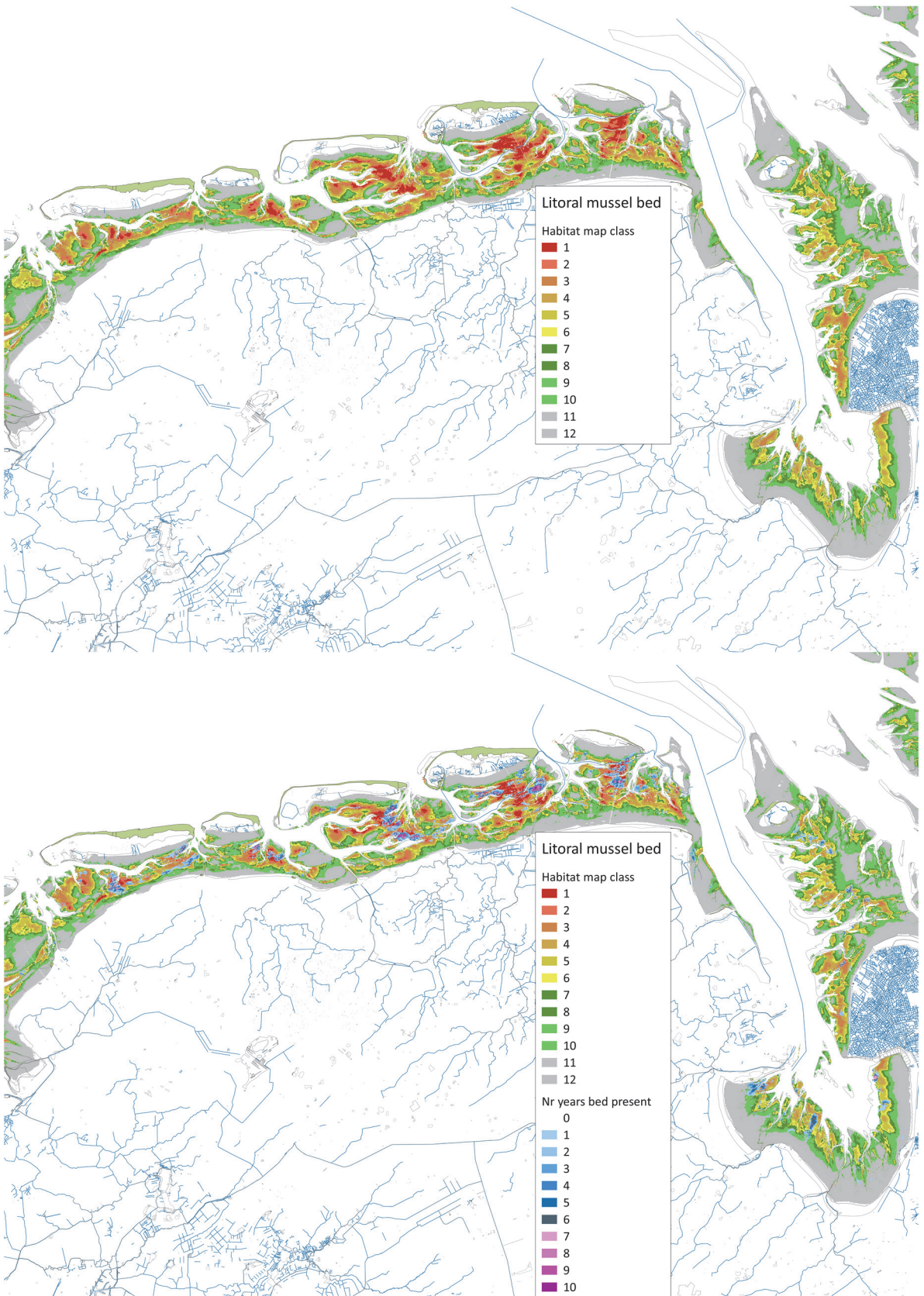


Figure 21 Upper: mussel bed habitat map, lower: ditto, now with observations included. Classes according to Table 3

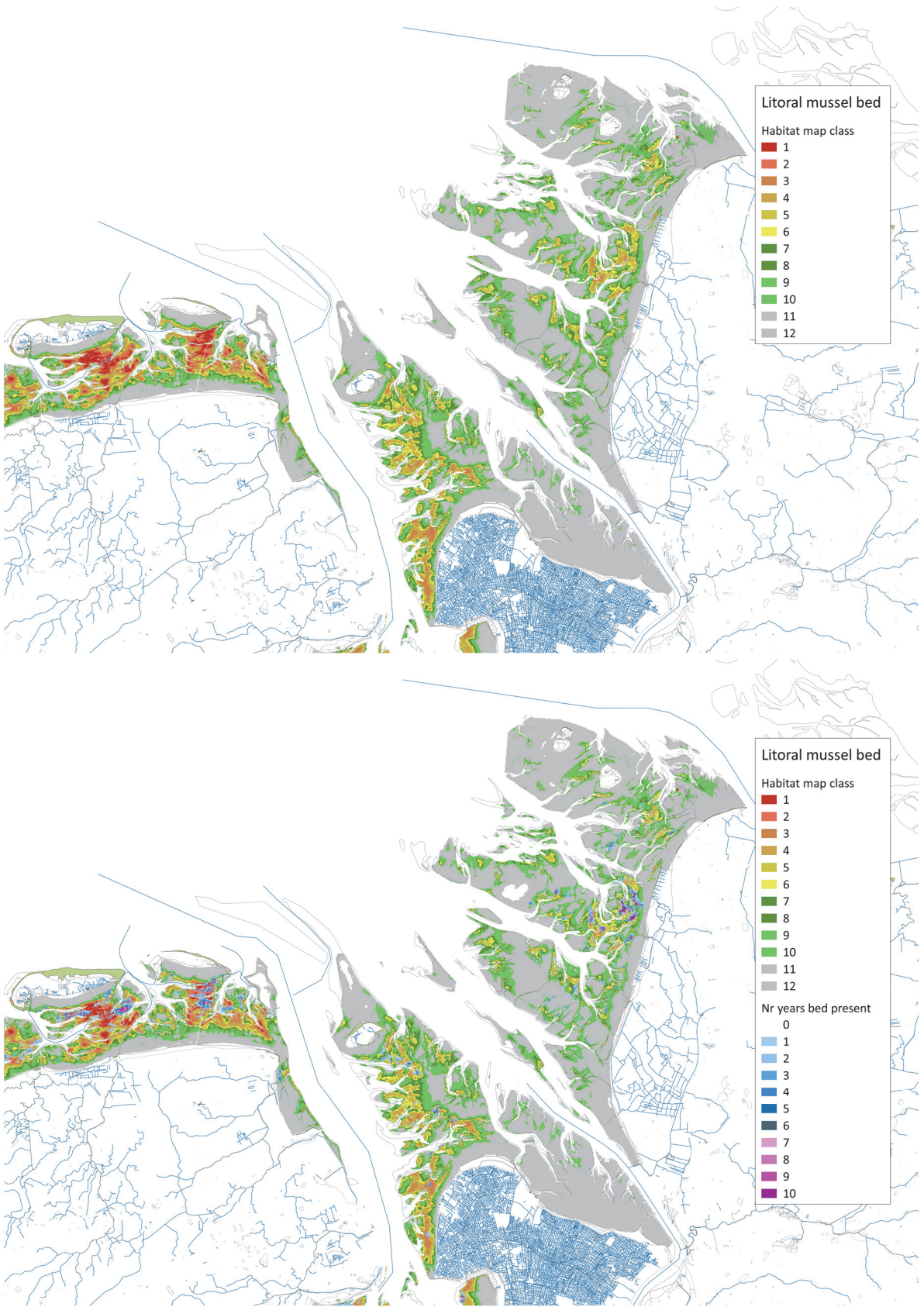


Figure 22 Upper: mussel bed habitat map, lower: ditto, now with observations included. Classes according to Table 3

The number of years a fishing plot was present has its maximum at 5 years. Next, the maps have been split into three separate parts from west to east.

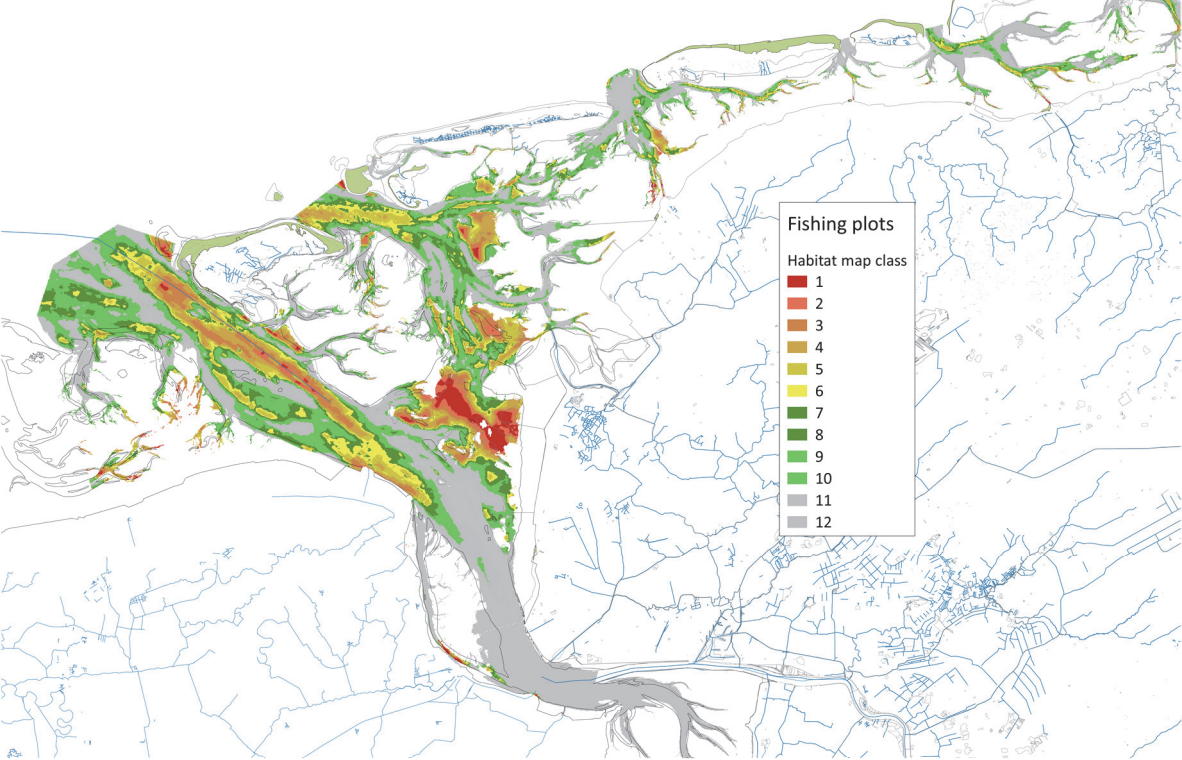


Figure 24 Upper: fishing plot habitat map (Ems estuary to the island of Baltrum). Classes according to Table 3

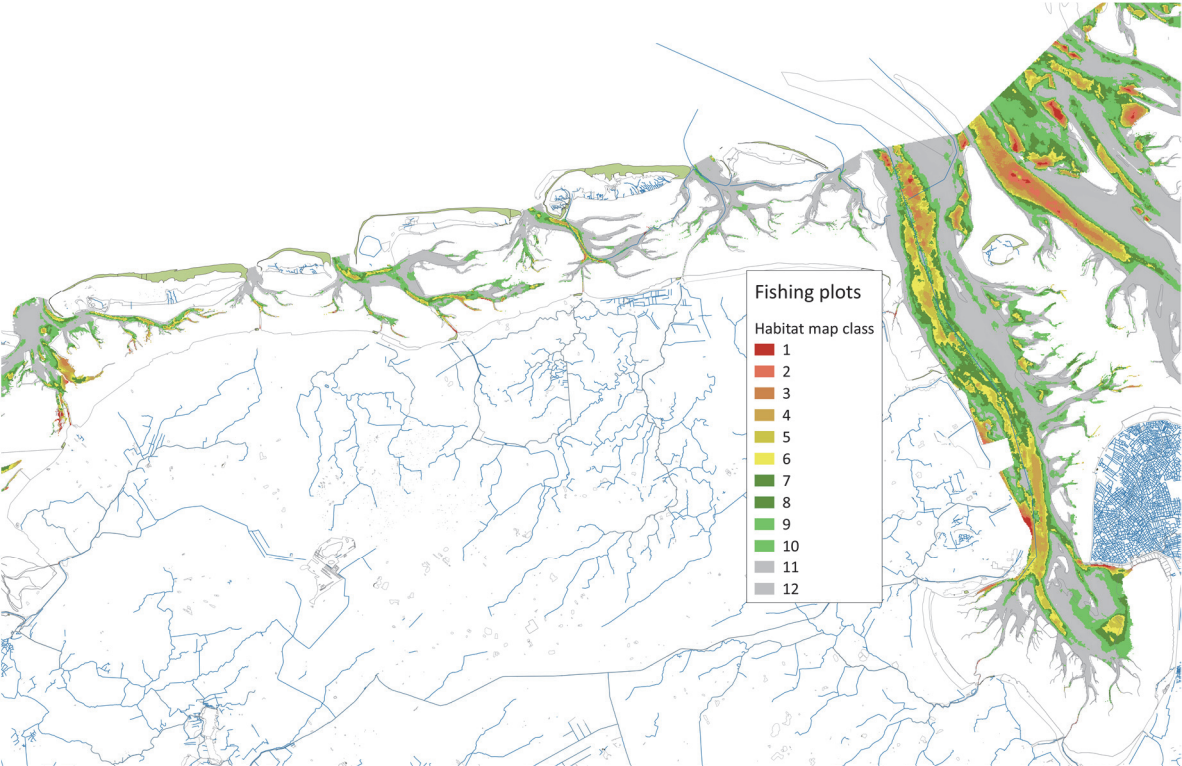


Figure 23 Upper: fishing plot habitat map (island of Norderney to Jade estuary). Classes according to Table 3

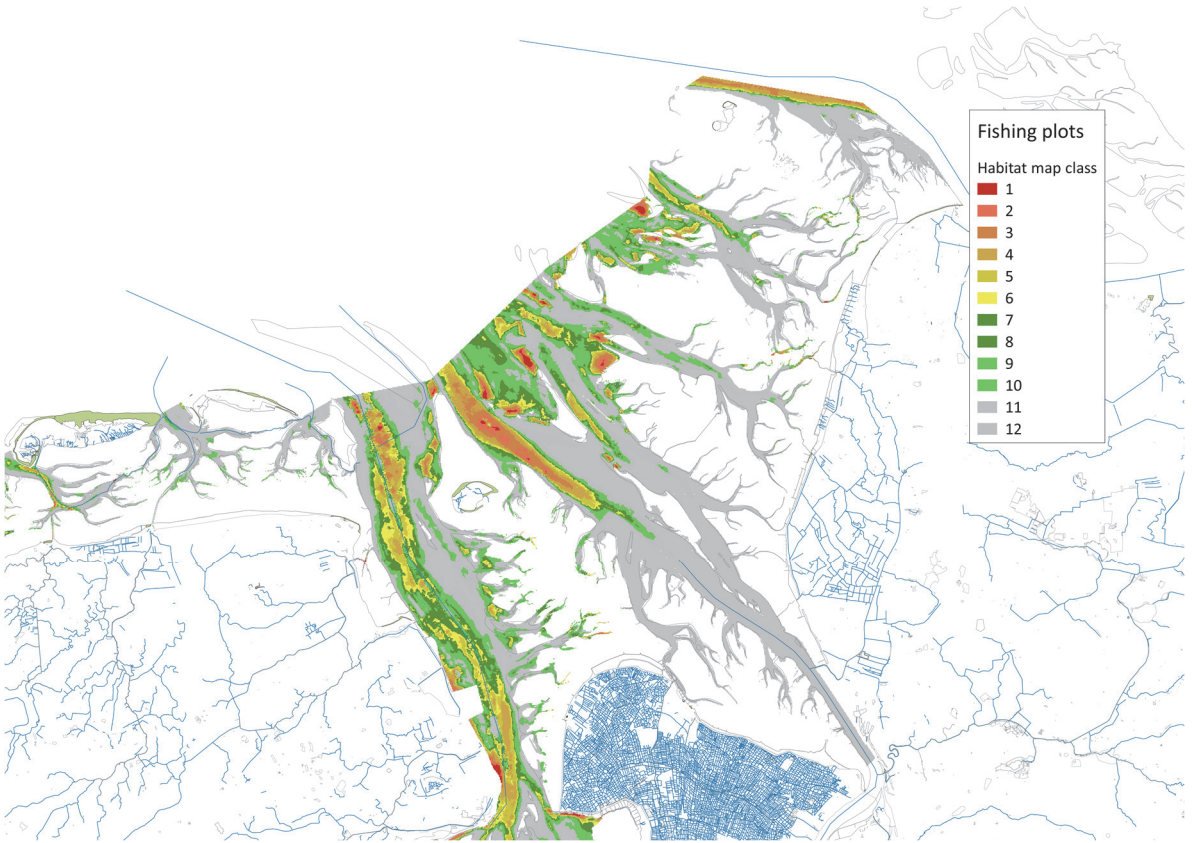


Figure 25 Upper: fishing plot habitat map (Jade to Elbe estuary). Classes according to Table 3.

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Bilder Umschlag:

Titelseite – Unterwasseraufnahme von Miesmuscheln (Foto: Winny Adolph/NLPV Nds. Wattenmeer);
Rückseite – Trockengefallene Jungmuschelbank bei der Insel Minsener Oog (Foto: Winny Adolph/
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