Chapter 5

Habitat suitability as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea

PUBLISHED AS:

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Van Lancker, V. and Vincx, M., 2008. Habitat suitability as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. Continental Shelf Research 28(3), 369-379.

5 Habitat suitability as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea

Abstract

Being ecologically important and well-known, the spatial distribution pattern of the macrobenthos is often used to support an ecologically sustainable marine management. Though in many cases the macrobenthic spatial distribution is relatively well-known, this information is merely restricted to point observations at the sampling stations: although being increasingly demanded, full coverage spatial distribution maps are generally lacking. This study therefore aimed at demonstrating the usefulness of habitat suitability modelling as a full coverage mapping tool with high relevance for marine management through (1) the construction of a habitat suitability model for the soft sediment macrobenthic communities in the Belgian part of the North Sea (BPNS) and (2) predicting the full coverage spatial distribution of macrobenthic communities within the BPNS. The BPNS was selected as a case study area because of the high data availability on both macrobenthos and environmental characteristics. Discriminant function analysis (DFA) objectively selected median grain size and sediment mud content and omitted bathymetry, slope and distance to the coast to represent the most important environmental variables determining the macrobenthic community distribution. The consequent crossvalidated, empirical habitat suitability model, using both median grain size and mud content, showed an a posteriori average correctly classified instances (CCI) of 79% (community-dependent CCI ranging from 72% to 86%) and a Cohen's kappa of 0.71, pointing towards a very good agreement between model predictions and observations. The application of the habitat suitability model on the full coverage maps of median grain size and sediment mud content, taken from literature, allowed to reliably assess the distribution of the macrobenthic communities within 96.3% of the 53,297 BPNS grid cells with a resolution of 250 m. Next to its applicability to the BPNS, the model is further anticipated to potentially perform well in the full Southern Bight of the North Sea: testing is advised here. Since the habitat suitability is considered far more stable through time compared to the permanently fluctuating macrobenthic communities, information on the habitat suitability of an area is considered highly important for a scientifically sound marine management.

Keywords: Benthos; aquatic communities; habitat selection; mathematical modelling; habitat suitability; discriminant function analysis

5.1 Introduction

Due to its ecological importance and obvious presence within the marine ecosystem, the macrobenthos is one of the most intensively investigated marine ecosystem components. Data on the spatial distribution of macrobenthic species and species assemblages are available for many areas worldwide (e.g. North Sea: Rees et al. 2002). Being ecologically important and well-known, the spatial distribution patterns of the macrobenthos is often used to support an ecologically sustainable marine management (e.g. Borja et al. 2000).

Though in many cases the macrobenthic spatial distribution is relatively well-known, this information is merely restricted to point observations at the sampling stations: although being increasingly demanded, full coverage spatial distribution maps are generally lacking (Young 2007). In general, two strategies could be followed to attain full coverage distribution maps: (1) spatial interpolation based on sampling point information (e.g. Dutch part of the North Sea: Holtmann et al. 1996) or (2) the development of habitat suitability models that predict the presence of macrobenthos based on the suitability of the physical habitat. Though being attractive, spatial interpolation is perilous since often community structure might change over very short distances. Another drawback of spatial interpolation is that the resulting map is highly dependent on the density of the samples. Degraer et al. (2002) demonstrated that – for instance in the geomorphologically highly diverse Belgian coastal zone – even a dense grid of sampling stations (120 sampling stations in 5x5 km area) did not allow to spatially extrapolate the macrobenthic community distribution patterns. Spatial interpolation further has the disadvantage that a rather static map is produced: whenever new data become available, the whole interpolation exercise has to be repeated. Predictive habitat suitability modelling, on the other hand, allows to objectively produce distribution maps at a level of detail limited only by the availability and resolution of environmental data. Being generally less costly to gather, compared to the collection of the labour-intensive biological information, environmental data is detailedly available in many areas. In such areas, small-scale patchiness within the macrobenthos will be detected as such. Once the predictive model is developed, this strategy further allows to easily update the spatial distribution whenever more detailed abiotic habitat data become available. If full coverage maps of the environmental variables (e.g. physical habitat) are available, it is even possible to create a full coverage map of the macrobenthos' spatial distribution.

This study aims at demonstrating the usefulness of habitat suitability modelling as a mapping tool with high relevance for marine management. This exercise will be performed using data from the well-investigated Belgian Part of the North Sea (BPNS) and dealt with in two steps: (1) the construction of a habitat suitability model for the macrobenthic communities in the BPNS (i.e. modelling) and (2) an extension of the knowledge of the spatial distribution of macrobenthic communities on the BPNS to the level of full coverage community distribution maps.

5.2 Material and methods

5.2.1 The Belgian part of the North Sea: current knowledge

The BPNS has a surface area of only 3600 km², but comprises a wide variety of soft sediment habitats (Verfaillie et al. 2006). Due to the presence of several series of sandbanks, the area is characterized by a highly variable and complex topography. Consequently, sediment types are highly variable throughout the area. Since the spatial distribution of the macrobenthos is largely dependent on the physical environment, a high macrobenthic diversity can be expected (Degraer et al. 1999a).
Because of the limited spatial extent of the BPNS in combination with the large interest in marine research, detailed knowledge on the macrobenthos' spatial distribution became available through several Flemish and Belgian research projects. Based on a combination of these datasets, Degraer et al. (2003) and Van Hoey et al. (2004) summarized the soft sediment macrobenthic community structure. They discerned between four subtidal communities: (1) the *Macoma balthica* community, (2) the *Abra alba – Mysella bidentata* community (or *A. alba* community; Van Hoey et al. 2005), (3) the *Nephtys cirrosa* community and (4) the *Ophelia limacina – Glycera lapidum* community (further abbreviated as *O. limacina* community). Next to these communities, several transitional species assemblages, connecting the four communities, were defined.
Because of its high macrobenthic diversity, in combination with a detailed knowledge of the macrobenthic community structure, the BPNS represents an ideal case study area for the development of a predictive model to attain a (full coverage) spatial distribution map of the macrobenthos.

5.2.2 Research strategy

Two major steps can be distinguished within the research strategy: (1) habitat suitability modelling and (2) full coverage mapping of the macrobenthic habitat suitability (Figure 5.1). The first step comprised to model the link between the biological point data and the accompanying physical data, aiming at creating a solid mathematical habitat suitability model. In the second step the habitat suitability model was applied to the full coverage maps of the ecologically most relevant physical variables in order to attain a full coverage habitat suitability map.

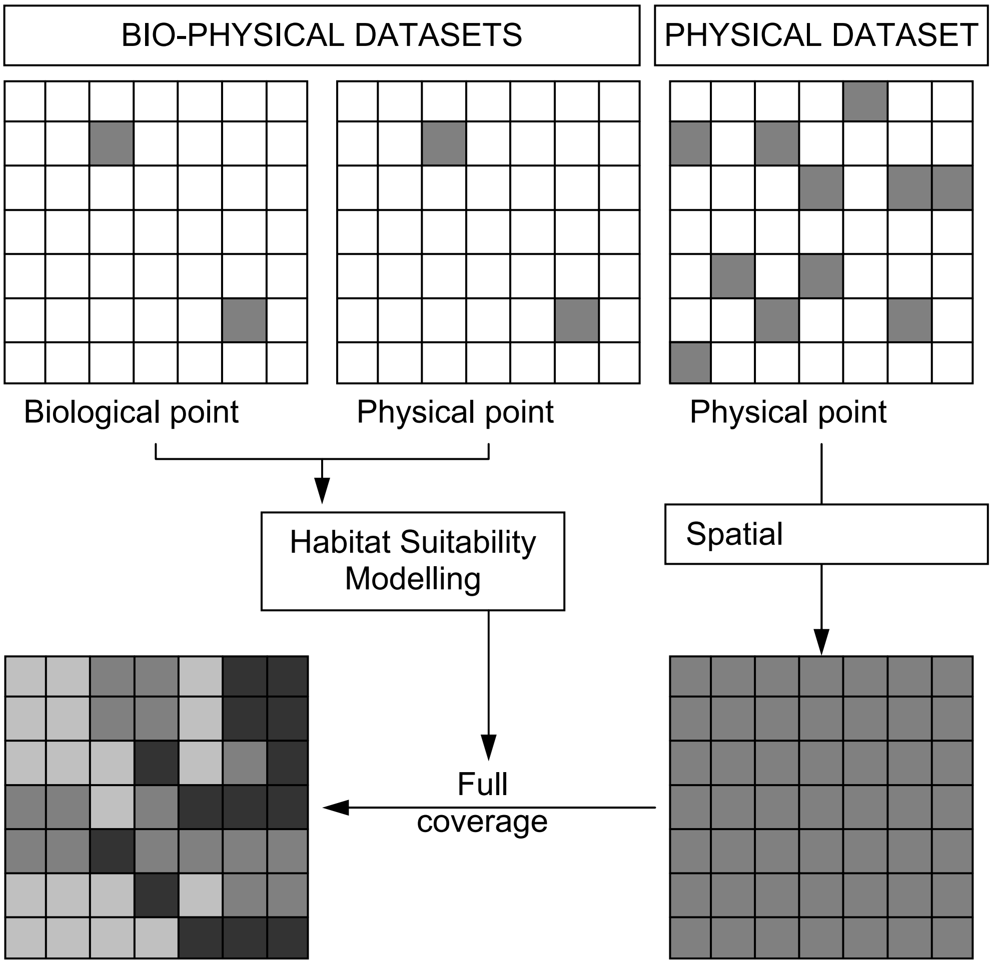

Figure 5.1: Schematic presentation of the research strategy, starting from bio-physical and physical point data to a full coverage macrobenthic habitat suitability map.

5.2.3 Data availability

Biological data

Within the framework of several projects 1197 macrobenthos samples were collected at the BPNS between 1994 and 2004. The samples were all collected with a Van Veen grab (sampling surface area: 0.1 m²) and sieved over a 1 mm mesh-sized sieve. All organisms were identified to species level, whenever possible, and species-specific densities (ind./m²) were determined.

Before analysis, a thorough data quality control was performed. Non-representatively sampled species were excluded from the dataset. A first set of non-representatively sampled species consisted of non-macrobenthic species, such as hyperbenthic mysids, fish and pelagic larvae, which cannot representatively be sampled with a Van Veen grab. A second set consisted of rare species, here defined as any species with a frequency of occurrence of less than 2% and encountered with a maximum of three individuals per sample. Because datasets, derived from different research projects, were combined, the dataset was further checked for inconsistent species identifications. In case of inconsistent species identifications (e.g. *Bathyporeia* spp., *Capitella* spp. and *Ensis* spp.), the species were lumped to the taxonomically highest common denominator. To avoid temporal autocorrelation, temporal series were excluded from the analysis. Given (1) a distance of at least 350 m between any pairs of sampling stations and (2) the high spatial heterogeneity in macrobenthos (Degraer et al. 2002), spatial autocorrelation was considered negligible in our data set. After data quality control the final dataset comprised 773 samples and 123 species.

Environmental data

Habitat suitability model input data

To maximise the applicability of the habitat suitability model, only frequently measured and/or widely available environmental variables were offered in the modelling exercise. A first set of environmental data was composed of variables measured *in situ*, i.e. median grain size, sediment mud content and depth. Slope was calculated on the basis of detailed bathymetric maps. Finally, distance to the coast, calculated from the geographic position of the sampling points, was included in the list of potentially explanatory variables.

Full coverage maps

The bathymetric map of the BPNS is based on single beam echosounder data from the Maritime Services and Coast Agency, Flemish Hydrography and completed with data from the Hydrographic Office of the Netherlands and the United Kingdom. This dataset was interpolated using a simple inverse distance algorithm to a digital terrain model with a resolution of 80 m. The slope map is the first derivative of the bathymetric map. It is expressed in degrees and has a resolution of 80 m. Full coverage median grain size and mud content maps with a resolution of 250 m were derived from the 'sedisurf@' database (UGent-RCMG), containing more than 6000 data points, spread throughout the BPNS and collected since 1976. At first, the database was cleaned using a 'zonation approach' and extreme or unrealistic data points were removed. To create full coverage median grain size maps, Kriging with an external drift was used, taking into account bathymetry as a secondary variable to assist in the interpolation (for more detailed information: Verfaillie et al. 2006). The map of the mud content was created, using Ordinary Kriging with directional variograms for the anisotropy of the data (for more detailed information: Van Lancker et al. 2007).

5.2.4 **Habitat suitability modelling**

Modelling strategy

Since the relevance for marine management is a major aim of this paper, the outcome of the modelling and mapping exercise should be easy to communicate to politicians, policy-makers and managers (Olsson and Andersson 2007). Hence, although we acknowledge macrobenthos to be structured along gradients, for sake of an easy communication an abstraction of this complexity was set (Turney 1995): instead of modelling the detailed macrobenthic gradients, we deliberately focused our model on the prediction of the chance of occurrence of each of the four macrobenthic communities, given a set of environmental factors. As such, the macrobenthos was modelled and mapped at the community level (i.e. clearly delineated entities), a level of detail allowing an easy communication and interpretation of the final outcome within a management perspective. To assure the incorporation of only well-delimited macrobenthic communities into the model (i.e. distinct sample groups from the multivariate analyses), transitional species assemblages were hence excluded from the predictive modelling exercise. To allow an easy communication of the model outcome, continuous variables are often converted into discrete variables (Turney 1995). The biological variation for certain endpoints may be too large to make reasonable predictions, therefore the modeller may decide to convert the data into two or more categories (Worth and Cronin 2003).

Biological data exploration: Community analysis

The community structure was investigated by several multivariate techniques: Group-averaged cluster analysis based on Bray-Curtis similarity (Clifford and Stephenson 1975), Detrended Correspondence Analyses (DCA) (Hill and Gauch 1980) and Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979; Gauch and Whittaker 1981), based on the final dataset with 773 samples and 123 taxa. For cluster analysis and DCA the data were fourth-root transformed prior to analysis. TWINSPAN was run using both the species density data as well as the presence/absence data.

The outcome of each multivariate analysis was compared to extract consistent groups of samples. Samples that were placed in different sample groups by the different multivariate analyses were considered as inconsistently grouped and were excluded from further analysis. This strategy assured that atypical observations (i.e. inconsistently grouped samples) did not bias any further analysis.

To designate the newly defined multivariate sample groups to the macrobenthic communities identified in previous research in the BPNS (Van Hoey et al., 2004) (i.e. *A. alba*, *N. cirrosa* and *O. limacina* communities), the relative distribution (%) of the samples over the macrobenthic communities was calculated per sample group. Because samples, belonging to the *M. balthica* community, were not present in the database, used by Van Hoey et al. (2004), sample group designation to the latter community was based on Degraer et al. (2003). Each sample group was designated to the community or transitional species assemblage (TSA) with the highest relative distribution value. For a detailed description (biology and environment) of all communities and TSAs one is referred to Degraer et al. (2003) (*M. balthica* community) and Van Hoey et al. (2004) (*A. alba*, *N. cirrosa* and *O. limacina* communities).

Discriminant Function Analysis

Discriminant function analysis (DFA) was used (1) to objectively select abiotic habitat variables that allow to discriminate between the four macrobenthic communities and (2) to develop a habitat suitability model. Finally, the habitat suitability model was applied to the full coverage environmental maps, generating full coverage distribution maps for the macrobenthic communities.

The forward procedure was used to detect the best set of abiotic habitat variables. The Wilk's Lambda statistics was applied to test the significance of the discriminant functions. The standardized coefficients for the discriminant functions allow to determine the contribution of each abiotic habitat variable to the separation of the macrobenthic communities: the larger the standardized coefficient, the greater is the contribution of the respective variable to the discrimination between groups. DFA assumes low multicollinearity of the independents and the same within-group variance covariance matrix for all groups. Variables are redundant when the pooled within-groups absolute correlation is equal or higher then 0.75, when this is the case one of the correlated variables is excluded from the analysis. The homogeneity of the variance covariance matrix was assessed by the log determinants.

To test the predictive performance of this approach on test data, not used to construct the model, a three-fold crossvalidation was applied. First, the data was split up in three parts. Care has been taken to assure that the proportion of each community in the three parts resembled the proportion in the whole data set (Witten and Frank 2000). Then two parts of the data set were used as a training set to develop a DFA habitat suitability model. This model was then applied to the third part of the data set. The predictions for the third part, not used to develop the model, were compared with the actual observations. This procedure was iteratively repeated, each part of the data set being used to train or test the model. If the performance of the three models is good and consistent we can conclude that the modelling approach is appropriate: a final model could then be constructed using all data points.

Two model performance indices were calculated: the % Correctly Classified Instances (CCI) and the Cohen's kappa. The formulae and a discussion on these model performance indices is given by Fielding and Bell (1997). Cohen's kappa is compensated for the prevalence of the entity to predict. It takes into account the chance that a sample would be attributed to a community by chance. No weighting was used in the calculation of the Cohen's kappa.

5.2.5 Habitat suitability mapping

The habitat suitability model was used to calculate the classification probabilities (i.e. community-specific habitat suitability) of each grid cell within the full coverage maps of each of the selected explanatory environmental variables (see Data availability: Full coverage maps). This habitat suitability measure was based on the grid cell's Mahalanobis distance from the different community centroids. The Mahalanobis distance (measure of distance between two points in the space defined by two or more correlated variables) is the distance between each sample and the macrobenthic community centroid in the multivariate space defined by the variables in the model. In general, the further away a grid cell is from a community centroid, the less likely it is that the habitat of the grid cell is suitable for that community. As such, a habitat suitability map (0 to 100%) for each macrobenthic community was derived. However, not all grid cells allowed a reliable habitat suitability estimate: grid cells with a Mahalanobis distance of three times the standard deviation from any macrobenthic community centroid (as calculated from the Mahalanobis distances from the model input data) were considered outliers and excluded from the map. Hence, we ascertained that no predictions were made beyond the range of the data set, used to develop the model. Using the model beyond this range could potentially lead to artefacts.

5.3 Results

5.3.1 Community analysis

Based on DCA, Cluster Analysis and TWINSPAN, 690 samples were consistently assigned to eight sample groups: 83 samples (11%) were inconsistently grouped and were excluded from further analysis. All groups consisted of 23 (sample group B) to 228 samples (sample group F), except for sample group H, which consisted of no more than five samples. Group H was therefore excluded from further analyses.

An uneven relative distribution of the samples of each sample group over the formerly defined macrobenthic communities and transitional species assemblages in the BPNS was found (Table 5.1). Because the major part of the group C samples (83%) corresponded with the *A. alba* community, defined by Van Hoey et al. (2004), group C was here defined as the *A. alba* community. Likely, groups A (max. 58%), E (max. 47%) and G (100%) were defined as the *M. balthica*, *N. cirrosa* and the *O. limacina* community, respectively. The major part of groups D and F samples (96% and 69%, respectively) were part of TSAs, each representing a link between two "parent communities". Sample group B could not be assigned to any community or TSA.

Table 5.1: Relative distribution (%) of the samples of each multivariately defined sample group over the formerly defined macrobenthic communities (¹ Van Hoey et al. 2004; ² Degraer et al. 2003). TSA 1, transitional species assemblage (TSA) between *A. alba* and *N. cirrosa* communities; TSA 2, TSA between *N. cirrosa* and *O. limacina* communities; TSA 3, TSA between *N. cirrosa* and intertidal communities.

	Multivariately defined sample groups						
Formerly defined communities	A	B	C	D	E	F	G
Abra alba community (1)			**83**				
← TSA 1 → (1)			14	**96**	21	2	
Nephtys cirrosa community (1)					**47**	2	
← TSA 2 → (1)			2	4	25	**69**	
← TSA 3 → (1)					7	3	
Ophelia limacina community (1)			1			24	**100**
Macoma balthica community (2)	**58**	4	1	5			

5.3.2 Community habitat preferences

Clear differences in habitat preferences were found for all macrobenthic communities and for all environmental variables taken into account in this study (Figure 5.2). From the *M. balthica* community to the *O. limacina* community a preference for increasing median grain size was detected. Although less consistent, a similar positive relationship was found for depth, distance to the coast and slope. An opposite trend was detected considering sediment the mud content.

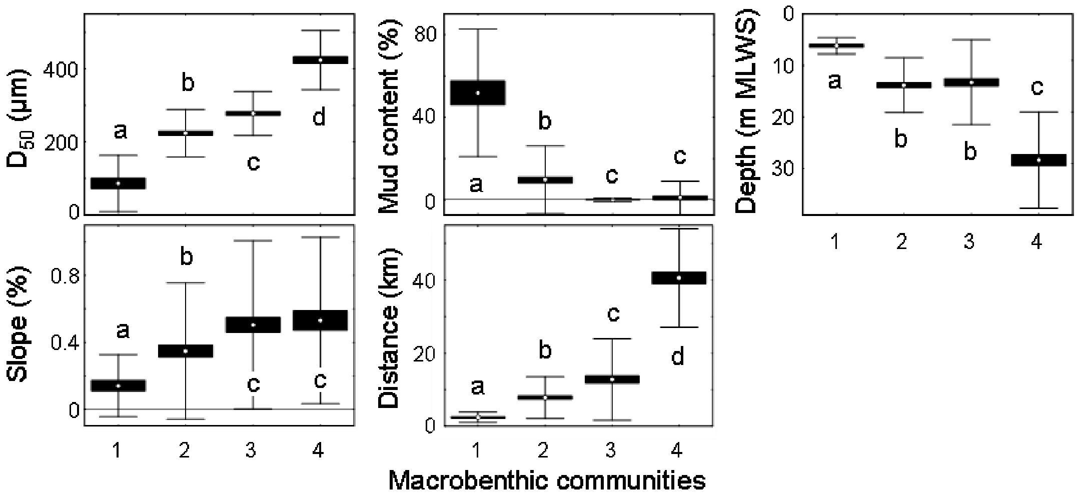

Figure 5.2: Habitat preferences of all macrobenthic communities: 1, *Macoma balthica* community; 2, *Abra alba* community; 3, *Nephtys cirrosa* community; 4, *Ophelia limacina* community. Mean, box: standard error, whiskers: standard deviation. Different letters (a, b, c, d) point to significant differences (post hoc LSD test: $p < 0.05$).

5.3.3 Community habitat suitability modelling

At first several combinations of environmental variables were used to develop preliminar habitat suitability models, in order to search for the optimal combination of predicting environmental variables. Prior to the analysis, the mud content, depth, distance to the coast and the slope were log transformed to obtain a homogeneous variance covariance matrix.

The slope was never selected in the preliminary models by the discriminant function analysis and was thus automatically rejected from further modelling exercises. The correlation matrix showed that the log-transformed depth and distance to the coast were correlated ($r = 0.75$). Because the standardized discriminant function coefficient of the depth (-0.167) was smaller in comparison to the distance to the coast (0.329), it was decided to exclude depth from the modeling exercise. As a result only three environmental variables were used in the preliminar models: median grain size, sediment mud content and distance to the coast. Only the first two discriminant functions (DF) were significant (DF1 Wilk's $\lambda = 0.180$, $\chi^2 = 609.5$, df = 9, $p < 0.001$ and DF2 Wilk's $\lambda = 0.593$, $\chi^2 = 185.8$, df = 4, $p < 0.001$) and explained 77.0% and 22.8% of the variance. Since the median grain size and the mud content were the most important explanatory variables for these functions (highest standardized discriminant function coefficients) only these variables were included in the final model.

Cross-validation

The performance of the habitat suitability model was tested by means of a threefold cross-validation procedure (Table 5.2). The agreement between model predictions and observations was very good and consistent between the three cross-validation model runs (e.g. Cohen's kappa: 0.70 – 0.73). This demonstrated that the modelling approach is suitable and a final model could be developed using all available samples.

Table 5.2: Model performance for a threefold cross-validation.
The data were stratified in such a way that the prevalence of a community in each fold, is proportional to the prevalence in the complete data set. CCI, % Correctly Classified Instances.

	Model run		
	1	2	3
CCI (all samples)	80.2	78.3	82.3
CCI (validation)	79.8	80.7	79.0
Cohen's kappa	0.71	0.73	0.70

Final model

Two DFs were proposed. The first DF, explaining 76.6 % of the variance, was mainly determined by the median grain size (Wilk's $\lambda = 0.37$, $p < 0.01$, standardized coefficient = -0.62 versus 0.55 for mud content). Mud content was slightly more relevant then the median grain size within the second DF (Wilk's $\lambda = 0.36$, $p < 0.01$, standardized coefficient = -1.00 versus -0.95 for median grain size), accounting for 23.4 % of the variance.
Four classification functions (i.e. one per macrobenthic community) were derived (Table 5.3).

Table 5.3: Community specific weights of all variables taken into the classification functions.
Cases are classified to the community rendering the highest score, by applying $S_i = w_{i(\text{Median grain size})}$*(Median grain size) + $w_{i(\text{Mud content})}$*($\log_{10}$(Mud content+1)) + Constant, with i = community i.

	Macoma balthica community	*Abra alba* community	*Nephtys cirrosa* community	*Ophelia limacina* community
Median grain size	0.063	0.082	0.079	0.121
Log_{10}(Mud content + 1)	17.685	13.421	7.541	11.457
Constant	-17.637	-15.716	-12.541	-27.323

The performance of the final model constructed with all samples, was assessed for the whole data set. Overall, 79% of the samples were assigned to the correct community. Uncorrectly classified samples were generally assigned to a neighbouring community (*M. balthica* community ↔ *A. alba* community ↔ *N. cirrosa* community ↔ *O. limacina* community) (Table 5.4). The CCI per community was between a minimum of 72% (*A. alba* community) and a maximum of 86% (*O. limacina* community), but was not related to the prevalence of each community in the original data set. The latter observation, combined with a Cohen's kappa of 0.71, indicated a very good agreement between observed and modelled macrobenthic communities (Monserud and Leemans 1992).

Table 5.4: *A posteriori* accuracy and sample classification, rows: observed classifications and columns: predicted classifications. CCI, % Correctly Classified Instances.

	Community prevalence	CCI	*M. balthica* community	*A. alba* community	*N. cirrosa* community	*O. limacina* community
M. balthica community	7.8%	82%	23	3	2	0
A. alba community	36.9%	72%	10	97	24	4
N. cirrosa community	35.3%	83%	0	5	107	17
O. limacina community	20.0%	86%	1	0	9	62
Total		79%	34	105	142	83

5.3.4 Habitat suitability maps

The habitat suitability could reliably be assessed for 53297 grid cells (resolution: 250 m; i.e. 96.3% of the BPNS): the prediction for the remaining 3.7% was considered beyond the range of the model development data (i.e. Mahalanobis distance > 3 SD from any macrobenthic community centroid, see Materials and Methods), which consequently does not allow a reliable prediction.

The habitat suitability for the four macrobenthic communities is clearly zoned throughout the BPNS (Figure 5.3). At first, a clear onshore-offshore gradient in habitat suitability can be discerned. The offshore benthic habitats are suited mainly for the *O. limacina* community (maximum modelled suitability: 99.9%), while the *A. alba* community is expected to dominate the onshore area (maximum modelled suitability: 88.8%). The habitat of the *N. cirrosa* community is taking an intermediate position (maximum modelled suitability: 92.1%). A second longshore gradient can further be found in the onshore zone. In the western part of the onshore zone a clear dominance of the habitat of the *A. alba* community is found, whereas this community is expected to co-dominate the eastern part, together with the *M. balthica* community (maximum modelled suitability: 98.9%).

5.4 Discussion

5.4.1 Habitat suitability model

From a conceptual viewpoint three different types of models exist: (1) theoretically based analytical models (cf. simplified reality), (2) process-based mechanistic models (cf. cause-effect relationships) and (3) empirical models (Levins 1966). The main purpose of the latter type being to accurately condense empirical facts, its mathematical formulation is not expected to describe realistic "cause-effect" between model input variables and predicted responses, nor to inform about underlying ecological functions and mechanisms. Because our aim was to model and predict as precisely as possible the habitat suitability our model should thus be regarded as empirical (Guisan and Zimmermann 2000).

Considering the statistical approach we selected DFA. DFA is considered a valid modelling technique, since in our case the selected response variable is a categorical entity (i.e. macrobenthic community), (Guisan and Zimmermann 2000). Such approach has already been widely applied for habitat suitability modelling of e.g. marine benthic communities (Shin 1982; Vanaverbeke et al. 2002; Caeiro et al. 2005), seagrasses (Fourqurean et al. 2003), alpine marmots (Borgo 2003), nesting griffon vultures (Xirouchakis and Mylonas 2005), freshwater benthic diatoms (Pan et al. 1999), freshwater fish (Nate et al. 2003) and black terns (Naugle et al. *2*000).

Out of a suit of five environmental variables (bathymetry, slope, median grain size, sediment mud content and distance to the coast), the forward selection procedure of the discriminant function analysis indicated median grain size and mud content to be the most important environmental variables determining the distribution of the macrobenthos. The structuring importance of both variables has already been indicated by many other studies (e.g. Wu and Shin 1997; Van Hoey et al. 2004, Willems et al. 2008). Assigning all variability in macrobenthic distribution patterns to solely the latter variables would however be an oversimplification of reality. Many other environmental variables might also contribute, as demonstrated by many other studies (e.g. hydrodynamics: Caeiro et al. 2005; turbidity: Akoumianaki and Nicolaidou 2007; primary productivity: Smith et al. 2006; organic matter: Verneaux et al. 2004). Next to the potential direct influence of median grain size and mud content on the macrobenthic distribution (e.g. burrowing capacity, de la Huz et al. 2002), both variables can however also be considered as a proxy for at least some of these other potentially structuring variables, more difficult to measure (e.g. hydrodynamics and food supply to the bottom, Herman et al. 1999). Considering median grain size and mud content as indirect gradients (*sensu* Austin et al. 1984), our model should be regarded as an empirical model (Guisan and Zimmerman 2000), and caution is thus needed when applying the model outside of the geographical range of the original model construction data. The main advantage of the selection of median grain size and mud content however is the fact that both variables were measured systematically and available at full coverage not only within our case study area, but also in many other marine areas.

Because the modelling approach generated a high and consistent predictive performance, it was considered sound to develop a final model with all data. The Cohen's kappa for the three folds of the crossvalidation was 0.70 to 0.73, which indicates a very good agreement between model and observations (Monserud and Leemans 1992). A high kappa indicates that the model is also making correct predictions for the rarer communities (e.g. *Macoma balthica* community).

The final predictive model constructed with all data showed an average CCI of 79% when applied to all samples. For each community separate, the CCI varied between 72 and 86%. The *a posteriori* (i.e. no independency of construction and test data) Cohen's kappa for the final model of 0.71 was found to be very similar to the *a priori* kappa of the models developed during the crossvalidation process (maximum Cohen's kappa: 0.70 – 0.73), indicating the good estimate of Cohen's kappa. The final model agreement should be considered very good, following Monserud and Leemans 1992).

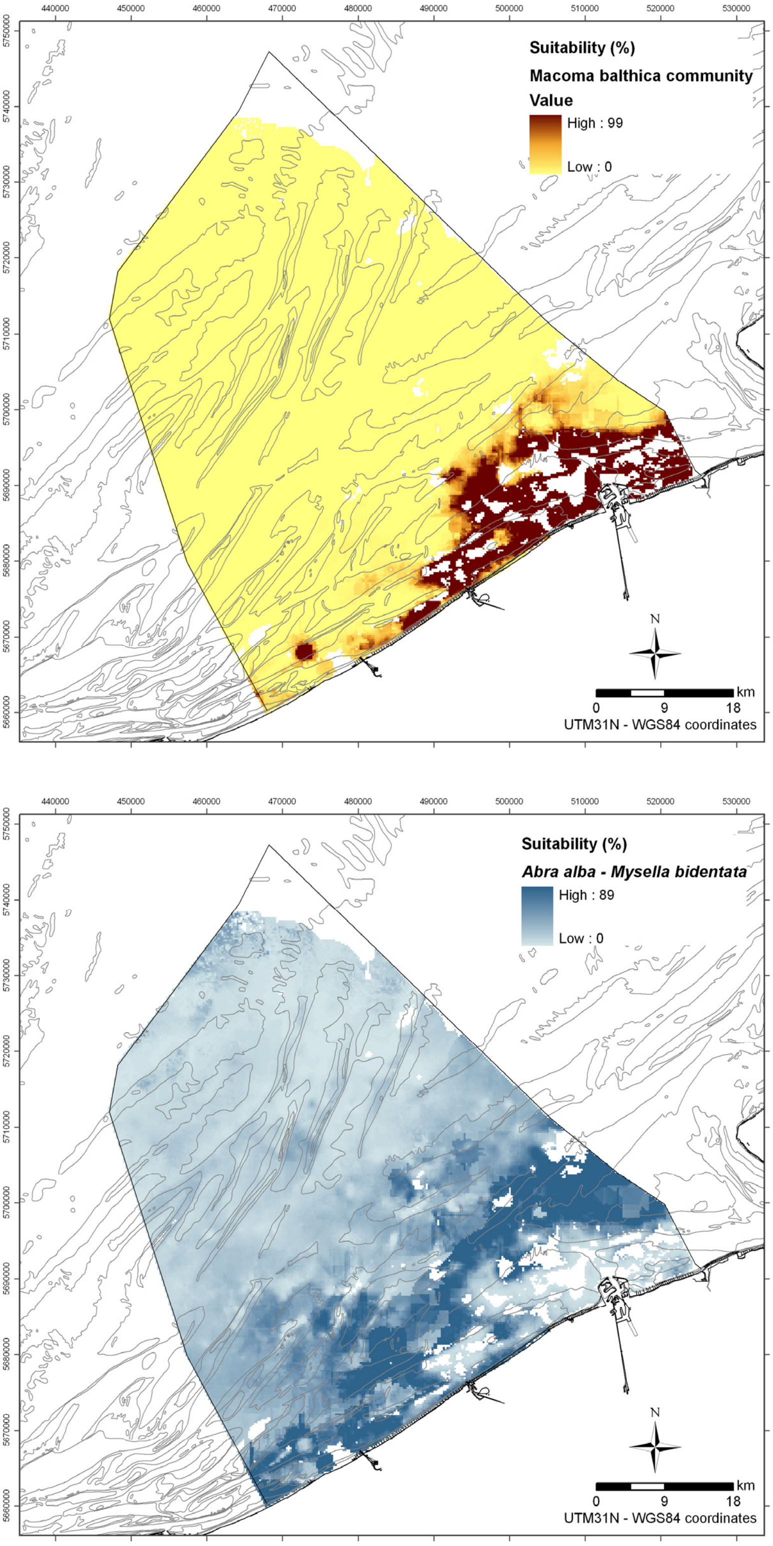
Suitability (%)
Macoma balthica community
Value
High : 99
Low : 0
N
km
0
9
18
UTM31N - WGS84 coordinates
Suitability (%)
Abra alba - Mysella bidentata
High : 89
Low : 0
N
km
0
9
18
UTM31N - WGS84 coordinates
440000
450000
460000
470000
480000
490000
500000
510000
520000
530000
5750000
5740000
5730000
5720000
5710000
5700000
5690000
5680000
5670000
5660000

Figure 5.3a

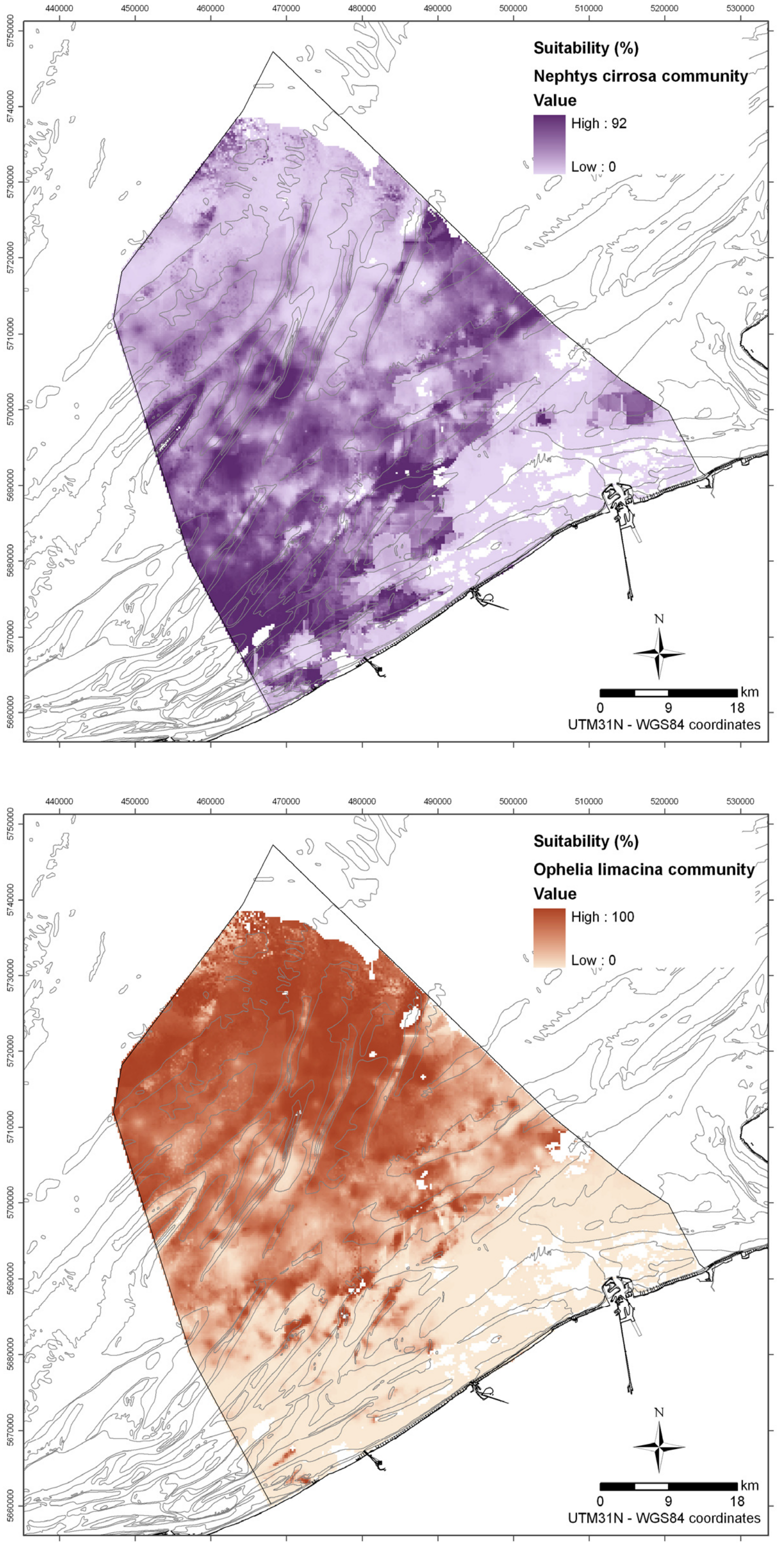

Figure 5.3b: Predicted habitat suitability maps for the *Macoma balthica* community, the *Abra alba* community, the *Nephtys cirrosa* community and the *Ophelia limacina* community in the Belgian part of the North Sea. White; no environmental data or prediction beyond the range of the model development data set.

5.4.2 Habitat suitability mapping

As demonstrated in this study the habitat suitability model can be used to predict the full coverage spatial distribution of the macrobenthic communities. Such detailed knowledge should be considered as highly relevant for marine management: a well-equilibrated marine spatial planning is particularly dependent on the data availability. However, the use of a model to increase the volume of data availability also includes some risk, of which two aspects are discussed below.

The habitat suitability model was developed based on a large data base (364 sampling stations were assigned to one of the four macrobenthic communities), but solely derived from the BPNS. Whereas the high number of sampling stations (as well as their spatial spread) included in the modelling exercise points towards a high reliability of model application within the BPNS, outside of the BPNS the model should only be used with great care. Two main types of problems may possibly be encountered. (1) Sediment types (and hence, most probably also macrobenthic communities) may be differing from the ones in the BPNS, leading to the use of the model beyond the range of the model development data set. Such error can be avoided if a threshold for maximum Mahalanobis distance from the communities centroid is set. In our mapping exercise this maximum Mahalanobis distance was set at three times the standard deviation from any macrobenthic community centroid (see Materials and Methods). (2) Although the sediment types encountered fall well within the range of sediments included in the model, the sediments host a different macrobenthic community, not present in the BPNS. Such errors are likely to occur when applying the model in other biogeographic regions, constituting a different macrobenthic species pool and/or where, next to sediment composition, other environmental variables are important in structuring the communities. It is therefore of utmost importance only to apply the model within the biogeographic region of origin. The BPNS being part of the biogeographic region of the Southern Bight of the North Sea (southern limit: 51°00'N, northern limit: 53°30'N), our model could thus be used (with care) within this region. This hypothesis is strengthened by the fact that, based on a thorough analysis of the present-day community structure in the North Sea, the macrobenthic communities from the BPNS are similar in the Southern Bight (Rachor et al. 2007). Next to its applicability to the BPNS, the model might thus be expected to perform properly in the full Southern Bight of the North Sea. Further testing is advised.

One should however always be aware that the reliability of the generated maps is depending on many aspects, of which data availability is considered extremely important. Data availability is impacting the reliability during all three stages of the habitat suitability mapping: (1) discriminating between the communities, (2) constructing the model, and (3) mapping the habitat suitability. When discriminating between the communities it is particularly important to make use of a fair amount of biological data: only when the communities can be discriminated reliably, one can go to the next step in habitat suitability modelling at the level of communities. Although there is no unambiguous method to assess this type of reliability, analytical tools such as ANOSIM (Clarke 1993) may be useful. To construct the model it is necessary to make use of enough data, linking the biological characteristics to the environmental variables: in general, the more data are available the higher the model performance. This model performance can be checked by various indicators, of which CCI and Cohen's kappa were used in this paper. Finally, the availability of environmental data becomes particularly crucial when selecting the resolution of the habitat suitability map. During this stage it is important to take care of a good balance between detail (e.g. spatial heterogeneity) and reliability. Alternatively, one could also decide not to aim at full coverage habitat suitability maps: if no spatial interpolation of environmental data is done, this last aspect of reliability can be called off.

5.4.3 Relevance for marine management

Although the spatial distribution of the macrobenthic community habitat suitability allows an easy communication with managers and policy-makers, it is important to detailedly define and comprehend its content. In this study the habitat suitability is defined as the probability to encounter a macrobenthic community in a specific habitat. Predicting the spatial distribution of a macrobenthic community however does not mean that we are able to detailedly predict its species composition at a specific site and moment. Because of short- to long-term temporal variability within temperate macrobenthic communities, the community structure should be regarded dynamic rather than static (e.g. Beukema et al. 1993; Meire et al. 1994; Turner et al. 1995; Essink et al. 1998; Herman et al. 1999). Yet, each (stable) community is expected to maintain a distinctly specific species composition and abundance respective to other communities (Turner et al. 1995), as demonstrated for the BPNS by Degraer et al. (1999b). In other words, if a habitat is found suitable for a macrobenthic community, its composing species have the possibility of colonizing the habitat, but may as well be absent because of anthropogenic impacts, such as fisheries, or natural temporal variability. Habitat suitability thus predicts the specific ecological potentials of a habitat rather than the realized ecological structure (Degraer et al 1999b).

The use of habitat suitability maps within marine management is therefore twofold: (1) a warning signal for potential anthropogenic impact and (2) a baseline map for marine spatial planning. A significant mismatch between the actual community structure and the habitat suitability map might trigger further investigation on its causes and might, as such, highlight anthropogenic impacts or eventually an ineffective marine management. Habitat suitability maps should thus be considered complementary to, rather than a substitution of, direct observations of the macrobenthic community structure. Secondly, distinguishing between areas with higher and lower macrobenthic potentials, habitat suitability maps might serve as a baseline map for marine spatial planning: taking into account the precautionary principle, high potential areas can now be avoided when spatially planning new marine activities, such as wind farms. Because, in absence of major anthropogenic impacts, the habitat suitability and thus ecological potential are far more stable through time compared to the permanently fluctuating macrobenthic communities, information on the ecological potentials of an area is of utmost importance for a scientifically-sound marine spatial planning, including MPA selection.

5.5 Conclusions

I. Median grain size and sediment mud content were selected above bathymetry, slope and distance to the coast to represent the most important environmental variables determining the macrobenthic community distribution.
II. The empirical habitat suitability model allowed to accurately predict the macrobenthic community distribution based solely information on median grain size and sediment mud content.
III. The habitat suitability could be reliably assessed for 53297 grid cells (resolution: 250 x 250 m; i.e. 96.3% of the BPNS).
IV. Next to its applicability to the BPNS, the model is anticipated to perform well in the full Southern Bight of the North Sea. Its applicability outside the Southern Bight of the North Sea should be considered at least questionable. Further testing is advised.
V. Since the habitat suitability is considered far more stable through time compared to the permanently fluctuating macrobenthic communities, information on the habitat suitability of an area is considered highly important for a scientifically-sound marine management.

5.6 Acknowledgements

The second and third author acknowledge a grant from the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen). The research was conducted under the Belgian Science Policy projects *BWZee* (contract n° EV/02/37A and EV/88/37B), *HABITAT* (contract n° MN/02/89), *MAREBASSE* (contract n° EV/02/18A), and *GAUFRE* (contract n° MA/02/009 and MA/02/007), and the Agency of Maritime and Coastal Services – Coastal Division project *HABITAT* (dossier n° 99380 and 200.455). This publication contributes to the EU INTERREG III B *MESH* project (http://www.searchmesh.net), the EU Network of Excellence *MarBEF* (contract n° GOCE-CT-2003-505446; http://www.marbef.org), the Gent University *BBSea* project (contract n° GOA 01G00705; http://biology.ugent.be/bbsea), and the ICES *Study Group on the North Sea Benthos Project 2000* (http://www.ices.dk/iceswork/wgdetail.asp?wg=SGNSBP).