



## Distribution of *Magelona* species (Polychaeta: Magelonidae) in the German Bight (North Sea): a modeling approach

KARIN MEIßNER<sup>1,3</sup> & ALEXANDER DARR<sup>2</sup>

<sup>1</sup>Forschungsinstitut Senckenberg, Deutsches Zentrum für Marine Biodiversitätsforschung, Biozentrum Grindel, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany, E-mail: kmeissner@senckenberg.de

<sup>2</sup>Institute for Applied Ecology Ltd., Alte Dorfstraße 11, 18184 Neu Broderstorf, Germany, E-mail: darr@ifaoe.de

<sup>3</sup>Corresponding author.

### Abstract

The aim of the present study was the development of species-habitat models for four *Magelona* species (Polychaeta: Magelonidae) found in the German Bight in the SE North Sea. Analyses were based on field data and data obtained from reexamination of material deposited in museum collections. In addition, data on environmental variables were retrieved from the sediment map by Figge (1981) and from long-term monitoring data sets. The statistical modeling technique applied was multivariate adaptive regression splines (MARS). Predictive accuracy measures were calculated for each model. The candidate model with highest discriminatory power was selected for predictive mapping.

Models with excellent predictive performance were developed for *Magelona johnstoni*, *M. filiformis* and *M. alleni* based on the analyzed set of environmental predictors. In each of the developed habitat models the most important predictor was a sediment parameter, either median grain size diameter (*M. johnstoni*) or mud content (*M. alleni*, *M. filiformis*). Salinity and water depth were also of importance. Model predictions were aimed to allow evaluation of habitat suitability for the investigated species in the German Bight. According to our results suitable habitats for *M. johnstoni* are numerous and a wide distribution of this species could be expected. Habitat suitability for *M. filiformis* in the German Bight was suggested to be high in areas with mud contents below 10 % at water depths between 25 and 35 m. The *M. alleni* habitat model indicated the presence of suitable habitats where sands with elevated mud contents are present and where water depths exceed 30 m.

**Key words:** benthos ecology, ecological modeling, habitat model, *Magelona alleni*, *Magelona filiformis*, *Magelona johnstoni*, *Magelona mirabilis*, MARS, mapping, multivariate adaptive regression splines, species distribution

### Introduction

The environmental factors that influence species occurrence have always been a major focus for ecologists (e.g., Kirkegard 1969; Wolff 1971; Rachor 1982; Miron & Desrosiers 1990). A modern approach to this question is ecological modeling. Essentially, a model is a hypothesis about the behavior of a system. In ecology, a model may serve as a quantitative description of species response to environmental conditions, or the quantitative formulation of the species-habitat relationship.

Ecological modeling opens up completely new opportunities in ecological research. For example, a species-response model developed from a data set consisting of the response variable (species occurrence) and a set of predictor variables (e.g., environmental parameters) can be used to

predict the spatial distribution of a species in a habitat with known (or defined) environmental settings (= predictive modeling) (e.g., Ysebaert et al. 2002; Leathwick et al. 2005; Wintle et al. 2005; Elith et al. 2006; Moisen et al. 2006). In contrast to a map that simply shows species records, predictive modeling allows the analysis of species occurrence to be extended to areas lacking species records but of known environmental settings. A slightly different purpose is behind an approach often followed in studies related to environmental management, conservation biology or climate change (e.g., Lehmann 1998; Olden & Jackson 2002; Jowett & Richardson 2003; Thrush et al. 2003; Pearson et al. 2004). It is related to the subject of how species response is changed if one of the predictor variables included in a habitat model established for a certain study area is altered. Against this background ecological modeling can be regarded an important tool providing new input into the discussion on the impact of habitat change (including climate change) on species and faunal assemblages.

The significant increase in application of modeling techniques in species ecology over the last few years can certainly be attributed to the facilitated access to modeling due to the availability of appropriate software packages, a huge increase in data availability and, maybe most importantly, the progress in the theoretical background of modeling. Meanwhile, extensive literature exists on the strength and frailty of different modeling techniques and related statistics (Lehmann 1998; Brosse & Lek 2000; Pearce & Ferrier 2000; Guisan et al. 2002; Thuiller 2003; Reineking & Schröder 2003; Muñoz & Felicísimo 2004; Schröder & Reineking 2004; Elith et al. 2006; Guisan et al. 2006; Leathwick et al. 2006; Moisen et al. 2006). Also, there seem to be only a few constraints left in regard to the type of data used for modeling (Zaniewski et al. 2002, Wintle et al. 2005, Rondinini et al. 2006).

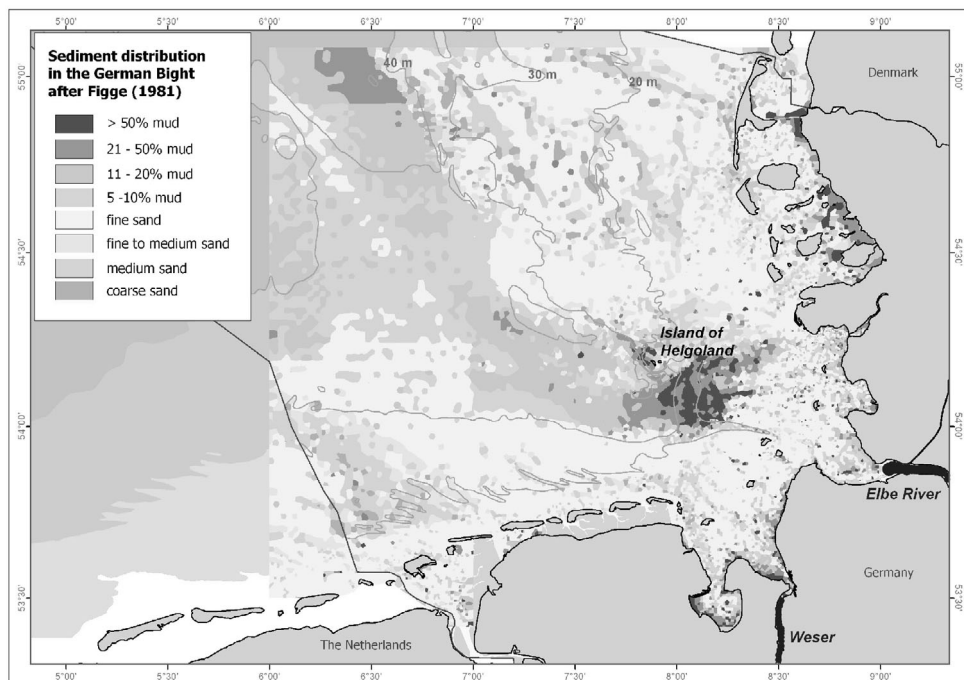
The aim of the present study was to develop distribution models for *Magelona* species (Polychaeta: Magelonidae) found in the German Bight in the SE North Sea. Although the magelonids are readily recognized and comprise only a single genus in the area, problems in regard to species identification for material from the North Sea have occurred in the past. These problems were resolved by the partial revision of European Magelonidae by Fiege et al. (2000). The identification of the different *Magelona* occurring in the area can now be undertaken on the basis of reliable diagnostic characters. Most importantly, the authors described *Magelona johnstoni* Fiege, Licher and Mackie, 2000 and separated this species from *Magelona mirabilis* (Johnston, 1865). Previously, the two species were collectively referred to as *M. mirabilis* by many authors, leading to the conclusion that the species was widely distributed in the German Bight. Records from recent ecological studies present another picture of the distribution of the different *Magelona* species. Together with data obtained from re-examination of material deposited in museum collections, such records provided the basis for the present study, which represents one of the first attempts to develop species-habitat models for polychaete species in the southern North Sea (compare Willems et al. 2008; Meißner et al. 2008). These models were then used to make predictions on distribution along with both a geographic and ecological discrimination of the various species.

## Materials and methods

**Area of investigation.** The area of investigation was the German Bight, the southeastern part of the North Sea, east of 6°E and south of 55°10'N. The nearshore areas with water depths <10 m are not considered in this study.

The German Bight is relatively shallow with water depths less than 45 m (except in the Helgoland Trench where depths may exceed 45 m). A characteristic topographic feature is the Elbe

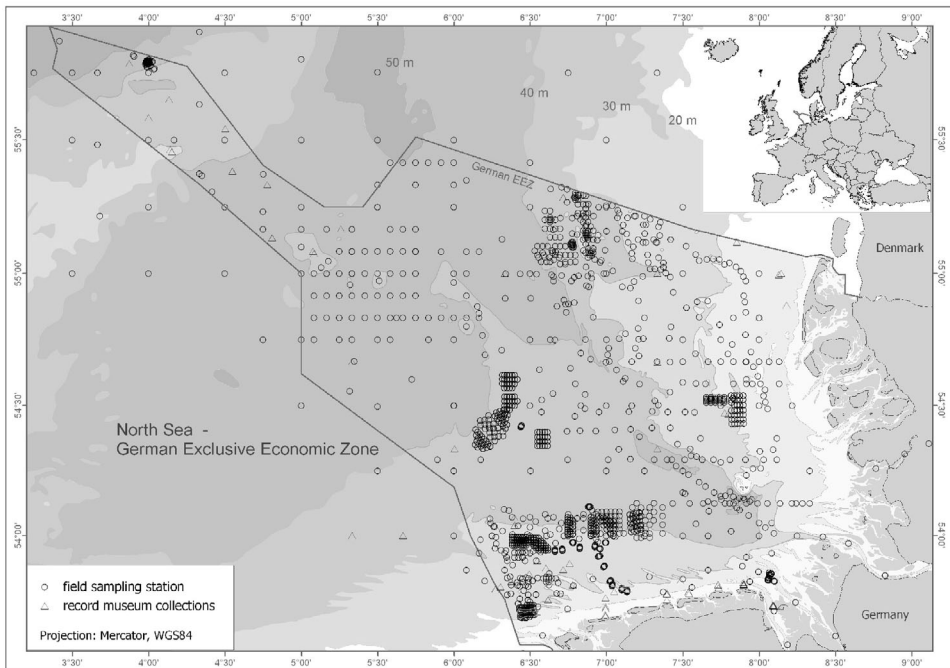
river valley, which was carved into the ground during glacial periods when the sea level was lower. The German Bight is a transition area between the relatively warm and saline water of the English Channel and colder and less saline waters of the central North Sea (Corten & van de Kamp 1996). Salinity beyond estuaries varies between 30–34 psu (OSPAR Commission 2000). Temperature follows a seasonal cycle with monthly means between 4 and 14 °C (OSPAR Commission 2000). The shallow parts of the southern North Sea usually remain well mixed throughout the year owing to strong tidal action. Sediments parallel to the coasts are dominated by fine to coarse sands; occasionally gravel or stony areas can be found. The mud content increases with water depth, particularly along the old Elbe River valley. Rocky substrates occur only locally close to the Island of Helgoland. The distribution of sediment types is illustrated in the map by Figge (1981) (Fig. 1).



**FIGURE 1.** Sediment distribution in the study area after Figge (1981).

**Data.** Species data were obtained by infauna sampling in the southeastern North Sea between 2000 and 2006 (Fig. 2). Sampling was undertaken with a Van Veen grab of 0.1 m<sup>2</sup>. Samples were sieved with 1-mm-mesh screens. Sorting of samples was done by means of a stereo microscope at 10 to 40 fold magnification. Additional species data were gathered by reexamination of material deposited in the collection of the Senckenberg Museum in Frankfurt, Germany (Fig. 2). The identification of *Magelona* species was based on the taxonomy proposed by Fiege et al. (2000).

Environmental variables used for model development were data from sediment analyses of samples taken during infauna sampling, data retrieved from the sediment map for the German Bight (Figge, 1981; Fig. 1) and from long-term monitoring data sets provided by the Alfred Wegener Institute (AWI), Bremerhaven and the BSH (German Federal Maritime and Hydrographic Agency).



**FIGURE 2.** Localities of infauna sampling stations and records of *Magelona* spp. from museum collections.

For compilation of the final data set a Geographic Information System (GIS) (software ArcView 8.0, ESRI, USA) was used. The study area was overlaid by a grid with cell sizes of 1x1 nautical miles. Information on environmental parameters was assigned to the grid cells by spatial join. Using this data, 9415 grid cells with information on sediment parameters (mud content, grain size), water depth and salinity were created. Original categorical data provided by the Figge sediment map were transformed into numeric data (see Table 1). This transformation was done by defining approximations for each of Figge's sediment classes based on the means of sediment parameters (mud content = fraction <63  $\mu\text{m}$  and grain size median  $d_{50}$ ) from the sediment samples taken during infauna sampling. Grid cells with unequal proportions of two different sediment classes as well as cells assignable to more than two classes or assignable to non-proximate sediment classes were excluded from the analysis. In case of equal proportions of different but proximate sediment classes the mean was calculated. Species data were linked to environmental data based on the geographic position. For 1503 grid cells information on species occurrence was available. Before starting with model development, data were examined and species-habitat relationships analyzed by application of appropriate methods of uni- and multivariate statistics (e.g., data mining, analysis of data distribution, correlation analyses, regression analyses).

**Modeling technique.** For model development species counts were converted into presence/absence data (species absent=0; species recorded=1). The statistical modeling technique used for development of habitat models was multivariate adaptive regression splines (MARS; software package MARS<sup>TM</sup> by Salford Systems, 2001). MARS was introduced by Friedman (1991) and has proven very successful for the development of species-habitat models (e.g., Guisan et al. 2002; Moisen & Frescino 2002; Muñoz & Felicísimo 2004; Leathwick et al. 2005; Elith et al. 2006;

Leathwick et al. 2006; Meißner et al. 2008). With MARS, complex regression models are built by fitting piecewise linear regressions. The overall non-linear response between a species and some set of predictors is approximated through the use of parsimonious regression slopes at distinct intervals that are located at optimized breakpoints of the predictor variable space (Salford Systems 2001). To reduce the potential of multicollinearity between predictor variables the function “penalty on added variables” is implemented in the software package (Salford Systems 2001). It favors reusing variables already in the model over adding new variables. The degree of interaction between variables can be specified. Interactions are treated locally for each interval rather than globally. A two-stage model selection method is followed: an overfit model is deliberately built first, and in a second step terms are eliminated in order of least contribution to the overall model performance until an optimal model is found. The optimal model is selected via cross-validation. A detailed introduction to the theoretical background of this modeling technique was provided by several authors and can also be found in the manual for MARS software (Salford Systems 2001; Moisen & Frescino 2002; Muñoz & Felicísimo 2004; Leathwick et al. 2006).

**TABLE 1.** Data transformation from Figge map for establishment of eight sediment classes (main categories). Additional intermediate classes were established for grid cells with almost equal parts of two sediment classes (not listed here).

<b>Sediment class (Figge 1981)</b>	<b>Grain size median (mm)</b>	<b>Mud content (%)</b>
>50% mud	0.05	60.0
21–50% mud	0.07	35.0
11–20% mud	0.09	15.0
5–10% mud	0.11	7.5
fine sand	0.13	3.0
fine to medium sand	0.20	0
medium sand	0.40	0
coarse sand	1.30	0

For MARS analyses, either no interactions, or, alternatively, two-way interactions were specified. Models were fitted individually for each species. Setting for cross-validation was 100-fold, setting for penalty on added variables was “no”, or, alternatively “moderate.” The model’s ability to discriminate between presence and absence sites was assessed using the area under the receiver operating curve (AUC) estimated by the bootstrapping method. For bootstrapping the statistics software R (R version 2.4.1 2006, R Development core team) with implemented package “gam” along with code 0.632plus provided by Elith & Leathwick (2005) was used. Alternatively, calculation of AUC values was done using a software tool “ROC/AUC calculation” provided by B. Schröder, University of Potsdam (<http://brandenburg.geocology.uni-potsdam.de/users/schroeder/download.html>). The tool also calculates confidence intervals for AUC values as well as other evaluation measures for predictive accuracy. The latter include the proportion of correct model predictions for presence (sensitivity) and absence (specificity) of the species in relation to the observed data and overall correct classification rate (CCR). The interpretation of AUC values was based on suggestions by Hosmer & Lemeshow (2000). According to that, evaluation of the model’s discrimination ability is as follows:  $AUC > 0.9$  outstanding,  $0.8 < AUC < 0.9$  excellent,  $0.7 < AUC < 0.8$  acceptable,  $AUC = 0.5$  and less no discrimination. The candidate model with highest discriminatory power (highest AUC value) was selected for mapping.

Mapping was done by calculating prediction values (index of relative occurrence in %) for each of the 9415 grid cells and exporting of the resulting data sheet to ArcView for display in a GIS. Projection in maps presented here is Mercator, WGS 84 (generated with ArcView 8.0, ESRI, USA). Metadata (modeling results) are available from the authors upon request.

## Results

Four species of *Magelona* were found in infauna samples from the German Bight: *Magelona mirabilis* (Johnston, 1865), *M. alleni* Wilson, 1958, *M. filiformis* Wilson, 1959 and *M. johnstoni* Fiege, Licher & Mackie, 2000 (Fig. 3). *M. johnstoni* was the most common species exhibiting a presence of 55 % (830 positive records) in our data set. The presence of *M. alleni* and *M. filiformis* was similar at slightly above 30 % (468 and 464 positive records, respectively).

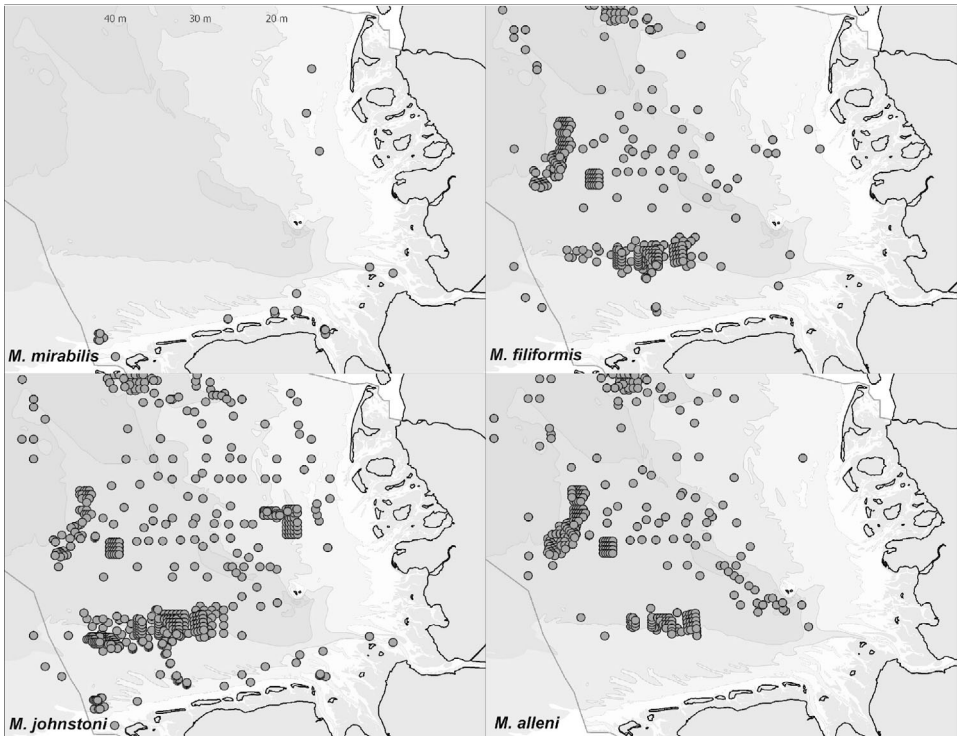


FIGURE 3. Records of *Magelona* species in the study area.

For *M. mirabilis* only few data were extant. Its presence in our data set was less than 2 % and thus insufficient for the development of a species-habitat model. However, the few data available revealed a distributional pattern different from that of the other species. *M. mirabilis* was found in relatively shallow waters at a closer distance to the coast (Fig. 4). These coastal waters are influenced by estuarine waters coming in from the river mouths so that salinities are slightly lower than in the offshore German Bight. Sediments were both fine and medium sands with very low mud content.

Models with excellent predictive performance ( $0.8 < \text{AUC} < 0.9$ ) were found for *M. johnstoni*, *M. filiformis*, and *M. alleni* (Table 2). AUC values differed significantly from that derived from prediction by chance ( $p < 0.001$ ). Predictive accuracy (evaluated by correct classification rate, sensitivity and specificity) of the habitat model was best for *M. johnstoni* and *M. alleni* whereas it was reduced in case of *M. filiformis* (Table 2). All final models contain the following four environmental predictors: mud content (“mud”), median particle diameter d50 (“grain”), salinity (“psu”), and water depth (“depth”). Clear differences were found for each species with respect to importance of each predictor in the model as well as model complexity (Tables 2–5).

*M. johnstoni* populates a wide range of habitats in the German Bight (Fig. 5). In the habitat model with the best predictive fit, the most important environmental predictor is grain size (100 %) closely followed by salinity (83.6 %) (Table 2). Of lesser importance are mud content (31.3 %) and water depth (10.3 %). The habitat model includes 10 terms (Table 3), all of which are significant ( $p < 0.5$ ). Based on the developed model, habitat suitability for *M. johnstoni* in the German Bight is high and a wide distribution of this species can be expected (Fig. 7). Occurrence is most likely in fine sands (grain size median  $< 200 \mu\text{m}$ ) with low to moderate mud content from the subtidal to about 35 m water depth (Figs. 6–7).

**TABLE 2.** Comparison of modeling results concerning predictive discrimination and predictive accuracy of developed models for three *Magelona* species. AUC = area under the receiver operating curve, CI = confidence interval; CCR = correct classification rate, sens. = sensitivity (true positive rate), spec. = specificity (true negative rate); CCR, sens. and spec. are given for threshold value  $P_{\text{kappa}}$  (*M. johnstoni* 0.65, *M. filiformis* 0.48, *M. alleni* 0.60).

Species	AUC (95% CI)		CCR (%)	sens. (%)	spec. (%)	Relative predictor importance (%)			
						grain	psu	mud	depth
<i>M. johnstoni</i>	0.884	(0.867–0.900)	82.5	76.3	90.2	100.0	83.6	31.3	10.3
<i>M. filiformis</i>	0.845	(0.826–0.863)	75.1	82.3	71.8	7.8	85.0	100.0	44.7
<i>M. alleni</i>	0.887	(0.871–0.902)	82.4	78.9	84.0	16.4	83.3	100.0	97.9

**TABLE 3.** Final habitat model for *Magelona johnstoni* using MARS.

***Magelona johnstoni***

AUC = 0.884

Piecewise Linear GCV = 0.132, effective parameters = 5.923

F-STATISTIC = 131.964, P-VALUE = 0.999201E-15

BF1 = max(0, grain - 0.120);

BF2 = max(0, 0.120 - grain);

BF3 = max(0, psu - 33.000);

BF4 = max(0, 33.000 - psu);

BF5 = max(0, grain - 0.250);

BF6 = max(0, 0.250 - grain);

BF8 = max(0, 33.000 - psu) \* BF6;

BF10 = max(0, 0.500 - grain) \* BF4;

BF11 = max(0, mud - 7.500) \* BF3;

BF12 = max(0, 7.500 - mud) \* BF3;

BF13 = max(0, depth - 20.000) \* BF4;

$Y = 1.010 - 6.555 * \text{BF1} - 9.244 * \text{BF2} - 0.669 * \text{BF3} - 0.085 * \text{BF4} + 6.580 * \text{BF5} - 3.174 * \text{BF8} + 1.099 * \text{BF10} + 0.010 * \text{BF11} + 0.075 * \text{BF12} - 0.029 * \text{BF13}$

**TABLE 4.** Final habitat model for *Magelona filiformis* using MARS.

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***Magelona filiformis***

AUC = 0.845

Piecewise Linear GCV = 0.144, effective parameters = 0.727

F-STATISTIC = 51.098, P-VALUE = 0.999201E-15

BF1 = max(0, mud - 4.0);

BF2 = max(0, 4.0 - mud );

BF3 = max(0, psu - 33.0);

BF4 = max(0, 33.0 - psu );

BF5 = max(0, psu - 33.0) \* BF2;

BF6 = max(0, 33.0 - psu ) \* BF2;

BF7 = max(0, depth - 30.0);

BF8 = max(0, 30.0 - depth );

BF9 = max(0, psu - 29.0) \* BF8;

BF10 = max(0, mud - 0.555318E-07) \* BF4;

BF11 = max(0, depth - 5.0) \* BF1;

BF12 = max(0, psu - 29.0) \* BF1;

BF13 = max(0, psu - 32.0);

BF14 = max(0, 32.0 - psu );

BF15 = max(0, grain - 0.05) \* BF14;

Y = 0.656 - 0.072 \* BF1 - 0.144 \* BF2 - 0.338 \* BF3 - 0.369 \* BF4 + 0.080 \* BF5 + 0.091 \* BF6 - 0.030 \* BF7 + 0.014 \* BF8 - 0.008 \* BF9 + 0.024 \* BF10 + 0.484704E-03 \* BF11 + 0.009 \* BF12 + 0.090 \* BF13 - 0.218 \* BF15

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**TABLE 5.** Final habitat model for *Magelona alleni* using MARS.

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***Magelona alleni***

AUC = 0.887

Piecewise Linear GCV = 0.128, effective parameters = 23.454

F-STATISTIC = 121.172, P-VALUE = 0.999201E-15

BF2 = max(0, 7.500 - mud );

BF4 = max(0, 30.000 - depth );

BF6 = max(0, 30.000 - depth ) \* BF2;

BF7 = max(0, psu - 33.000);

BF8 = max(0, 33.000 - psu );

BF9 = max(0, depth - 30.000) \* BF7;

BF10 = max(0, 30.000 - depth ) \* BF7;

BF11 = max(0, depth - 5.000) \* BF8;

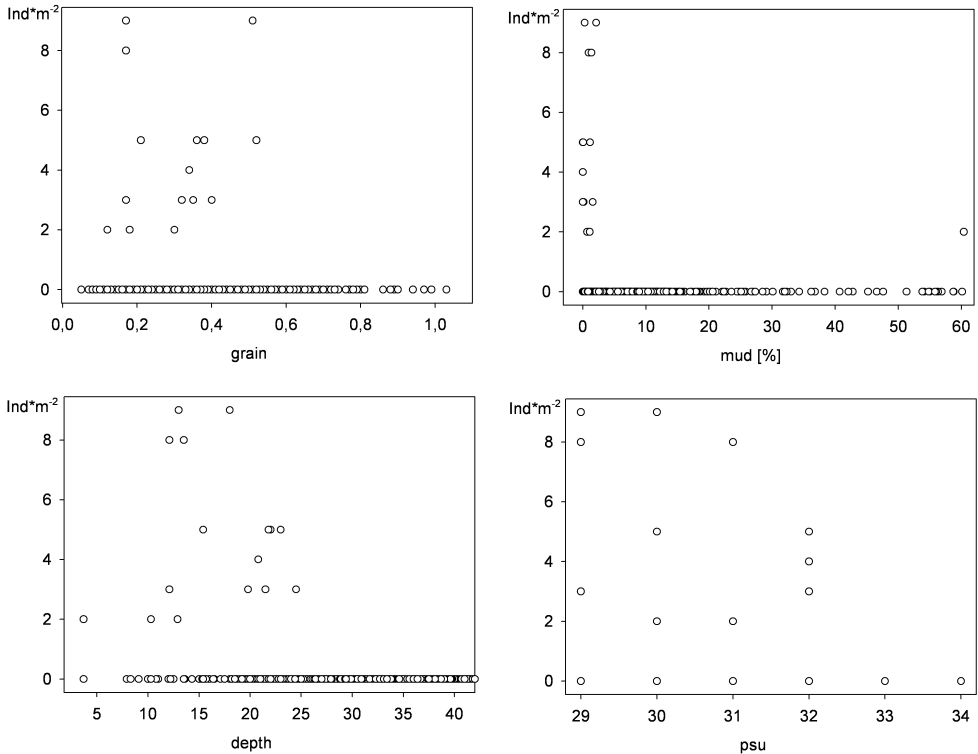
BF13 = max(0, 0.100 - grain ) \* BF7;

Y = 0.576 - 0.058 \* BF2 - 0.031 \* BF4 + 0.003 \* BF6 + 0.159 \* BF7 + 0.065 \* BF8 - 0.041 \* BF9 - 0.019 \* BF10 - 0.008 \* BF11 - 13.799 \* BF13

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*Magelona mirabilis*



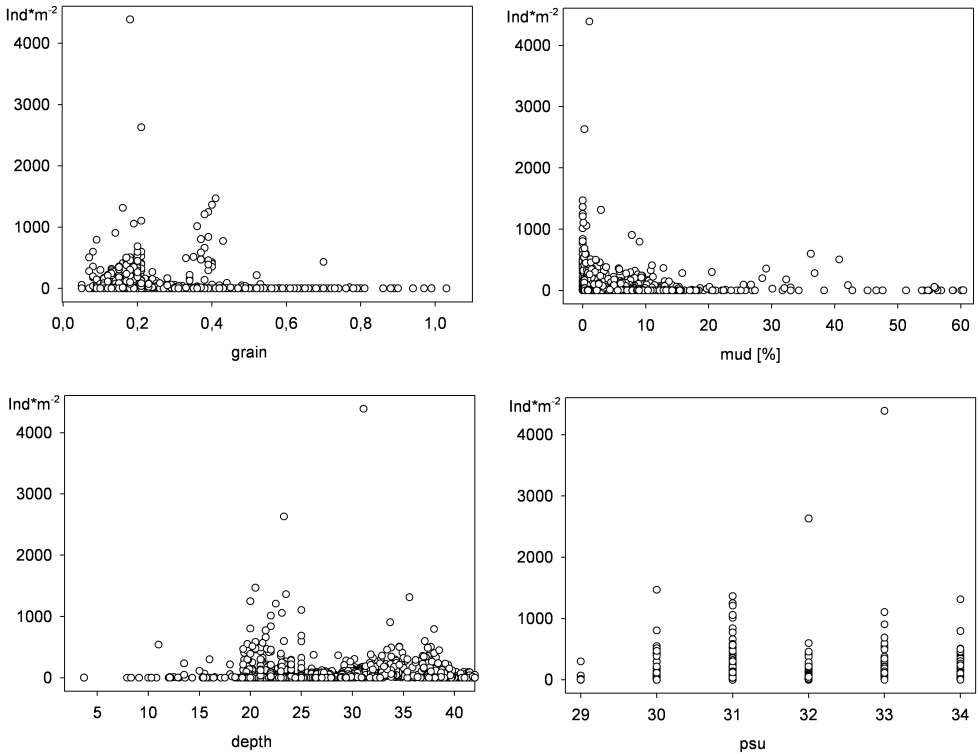
**FIGURE 4.** Species data for *M. mirabilis* included in the data set used in the present study; grain = median particle size diameter ( $d_{50}$ ) in mm, mud = mud content in %, depth = water depth in m, psu = salinity in practical salinity units.

In comparison to *M. johnstoni*, the habitat requirements of *M. filiformis* appear to be more specific (Fig. 8). Based on the habitat model for *M. filiformis*, the predictor with the highest importance for the occurrence of this species is mud content (100 %) (Table 2). Salinity is of similar importance (85.0 %). Importance of water depth is moderate (44 %) whereas grain size plays a minor role (7.8 % importance in the habitat model). The habitat model includes 14 terms, all being significant (Table 4). According to the model, habitat suitability for *M. filiformis* in the German Bight is high in areas with mud content below 10 % and at water depths between 25 and 35 m (Fig. 9). The prediction map depicts that such areas are found mainly in the vicinity of the former Elbe River valley (Fig. 10). Other localities with habitat characteristics suitable for the settlement of *M. filiformis* are expected in the northern part of the German Bight. Although median grain size diameter is not of major importance in the model, it should be emphasized that this species was found only in fine sand according to our sampling data (Fig. 8).

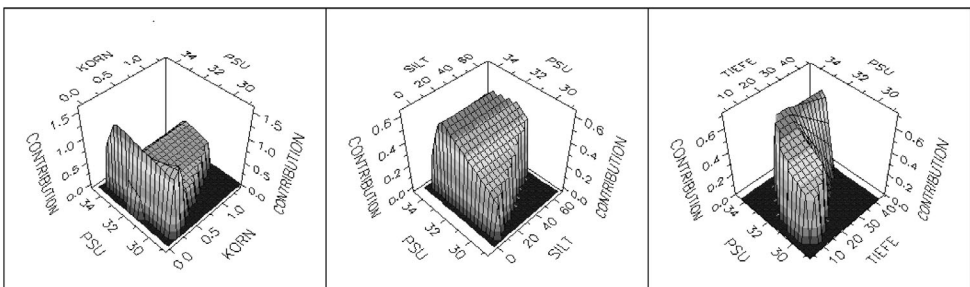
Species records for *M. allenii* suggest a kind of indifference towards mud content (Fig. 11). However, mud content together with water depth is the predictor of highest importance in the developed habitat model (Table 2). Salinity is also of high importance whereas grain size is of low importance only. The habitat model includes 9 terms, all being significant (Table 5). The most likely

occurrence of *M. alleni* is expected in sediments with elevated mud content in water depths >30 m (Fig. 12). Such habitats are found in the German Bight in the former Elbe River valley and adjacent areas (Fig. 13). In shallower waters and sands with very low mud content encountering *M. alleni* is unlikely in the investigation area.

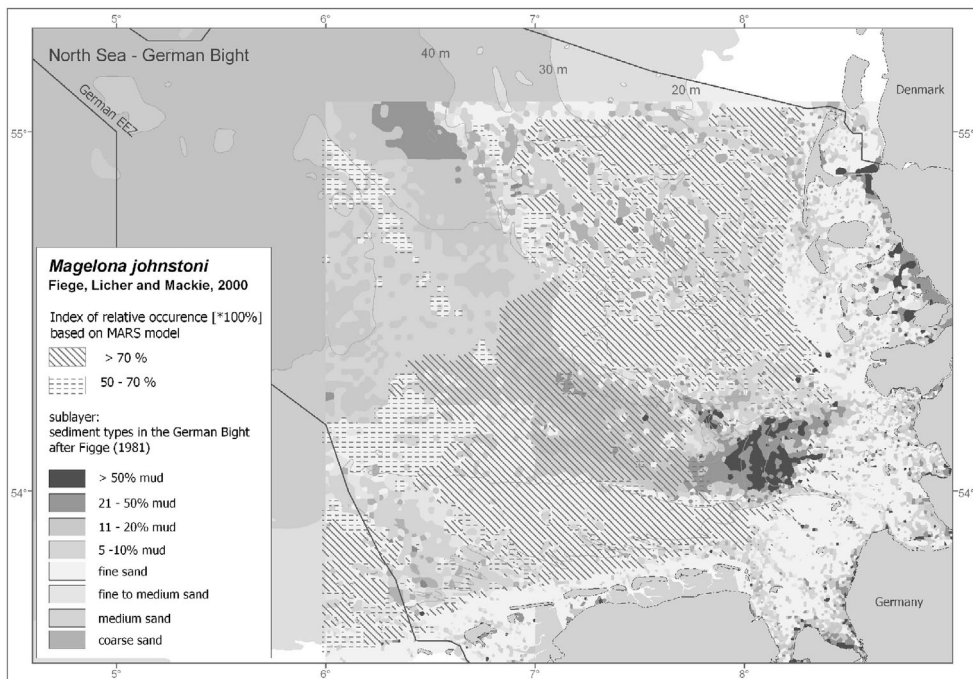
*Magelona johnstoni*



**FIGURE 5.** Species data for *M. johnstoni* included in the data set used in the present study; grain = median particle size diameter ( $d_{50}$ ) in mm, mud = mud content in %, depth = water depth in m, psu = salinity in practical salinity units.



**FIGURE 6.** Contour plots illustrating the relationship between a pair of predictor variables and the target variable (species response), KORN = grain size median  $d_{50}$ , TIEFE = water depth; from *M. johnstoni* habitat model.



**FIGURE 7.** Prediction map for *M. johnstoni* based on MARS model with best predictive fit; area of prediction restricted to grid cells with available information on predictor variables included in the species habitat model.

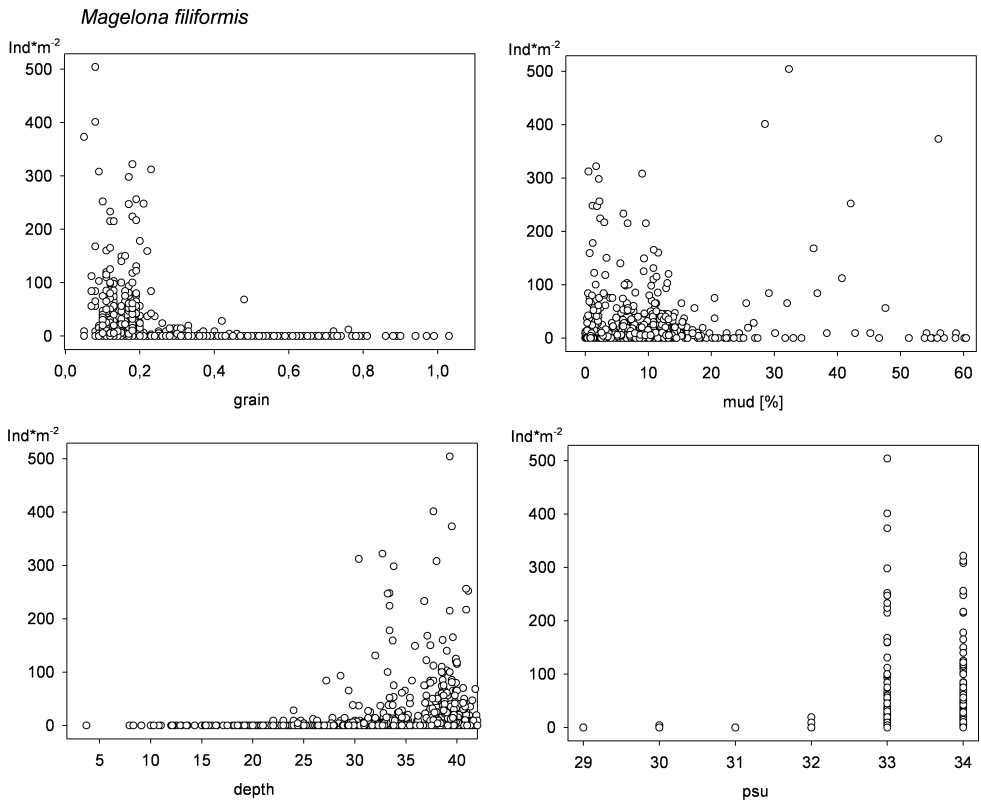
## Discussion

Almost all known magelonids, and certainly those species occurring in the German Bight, live in burrows (Fiege et al. 2000). The integrity of the burrow wall is established and maintained by mucous secretions (Jones 1968). The paired papillated tentacular palps, which are not withdrawn into the tube, are used to collect food particles such as diatoms or detritus (Jones 1968). The feeding mode is classified as surface deposit feeding (Fauchald & Jumars 1979). Planktonic larvae are able to seize active and relatively large food organisms (Wilson 1982). Settlement of *Magelona* larvae was observed at about the 20–30-setiger stage, varying with respect to the species (Wilson 1982).

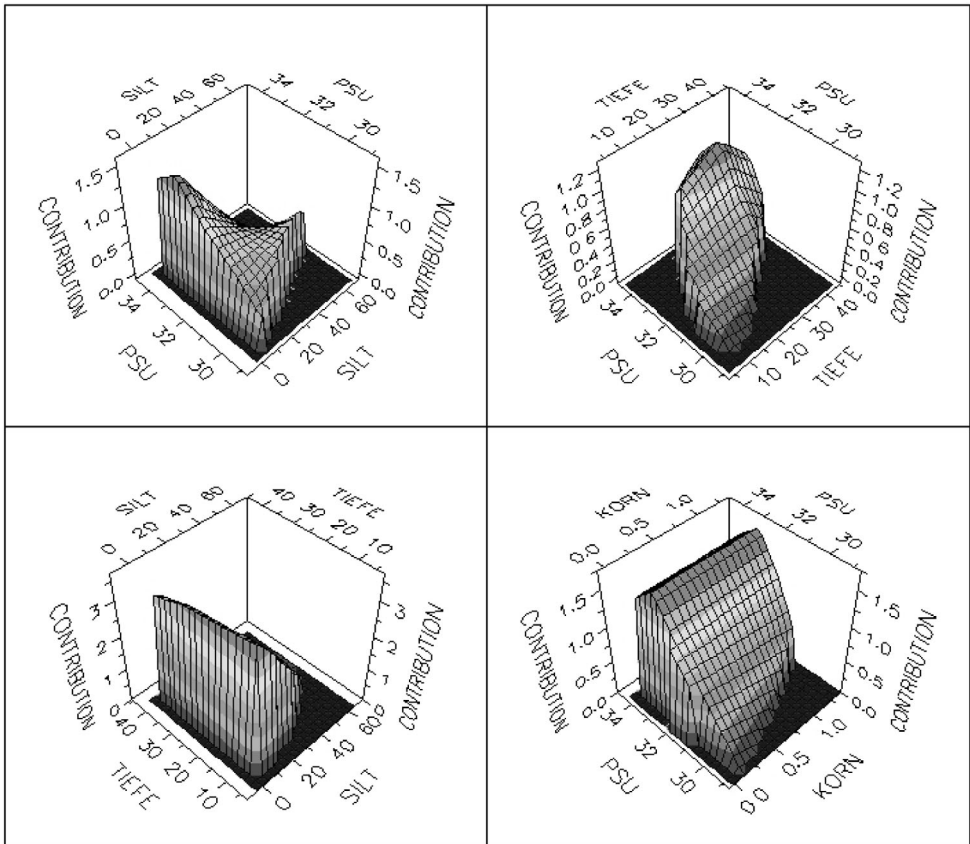
The biology of *Magelona* suggests the influence of several factors on the occurrence of the species. Such factors might be oceanographic parameters like current regime, temperature, salinity, or origin of water masses as well as substrate parameters. The set of predictors used for our analyses included only a few variables: median grain size diameter and mud content are important descriptors of sediment characteristics; water depth and salinity integrate oceanographic features. Despite the limited number of available predictors it was possible to develop models with high predictive performance for three out of the four species. The occurrence of *M. mirabilis* in our samples was insufficient for the development of a habitat model. In each of the habitat models, the most important predictor was a sediment parameter, either median grain size diameter (*M. johnstoni*) or mud content (*M. alleni*, *M. filiformis*). The determination of the occurrence of infaunal organisms by sediment

characteristics is not surprising. For many species a preference of certain sediment types has been observed. In the models, predictors other than sediment parameters are included. Salinity in particular, but also water depth (especially for *M. allenii*) is of importance in the developed species-habitat models. It has to be stressed that the conclusion from these results is not straightforward. For example, sediment characteristics are correlated with other local (e.g., oceanographic) conditions, e.g., strong currents will usually coincide with coarse sands and low mud content. In the German Bight, substrates with high mud content are mostly found in deeper waters. One also has to bear in mind that a parameter like water depth does not refer to water depth in the explicit sense only. With changing water depth many abiotic and biotic parameters change as well (e.g., turbulence, light exposure, availability of food, larval input, composition of the faunal assemblage).

Model predictions are aimed at allowing evaluation of habitat suitability for the investigated species in the German Bight. For assessment of the ecological realism of the results, it seems appropriate to check their accordance with available information on *Magelona* species.



**FIGURE 8.** Species data for *M. filiformis* included in the data set used in the present study; grain = median particle size diameter ( $d_{50}$ ) in mm, mud = mud content in %, depth = water depth in m, psu = salinity in practical salinity units.



**FIGURE 9.** Contour plots illustrating the relationship between a pair of predictor variables and the target variable (species response), KORN = grain size median d50, TIEFE = water depth; from *M. filiformis* habitat model.

### ***Magelona johnstoni***

For *M. johnstoni* information is sparse since it was only recently described. Fiege et al. (2000) give the habitat description as sandy sediments, intertidal (mid to lower shore) to 88 m. Material from Senckenberg Museum collection examined in the scope of this study came from locations within the German Bight between 2–46 m depth. Sediment type was described as sandy (fine, medium, and coarse). For the Belgian part of the North Sea a clear preference of finer sediments (150–300 µm median grain size) was observed for *M. johnstoni* (Degraer et al. 2006). The same authors also found the species at lower densities in even finer sands and coarser sediments but it was excluded from coarse-grained sediments with median grain sizes >500 µm. In regard to mud content the highest relative occurrence was recorded at 10–20 % although a wider range of this factor was tolerated (Degraer et al. 2006). Degraer et al. (2006) state the species to be restricted to the near-coastal zone (obviously water depths close to 10 m) within the Belgian EEZ. Precise information on the occurrence of *M. johnstoni* in the Outer Bristol Channel is provided by Mackie et al. (2006). In that study, the species was frequently found in both well and very well sorted fine sands (100–~200 µm

grain size mean) with mud content <10 % and in water depths up to about 35 m (tidally corrected). *M. johnstoni* was only rarely found in coarser sediments and deeper waters (Mackie et al. 2006).

In general, the described habitat preferences of *M. johnstoni* from the various locations are in good agreement. The species is found in a range of sediment types although a clear preference for fine sands with low mud contents could be postulated. Its high presence in waters not much deeper than 30 m also seems evident. Against that background, predictions on the likelihood of occurrence by the developed habitat model for the German Bight are sound (Fig. 7). *M. johnstoni* can be expected to be the most common *Magelona* species in the German Bight.

### *Magelona filiformis*

Our data and the resulting model for *M. filiformis* indicated a high degree of specificity in regard to habitat requirements, which also agrees well with the findings of other authors. Hartmann-Schröder (1996) states that *M. filiformis* is more likely to occur in pure to muddy sands than in mud. She also reports the depth range to be from the lower intertidal to the upper subtidal zone. Records published by Böggemann (1997) were exclusively from fine sands in water depths deeper than 30 m. In the Belgian part of the North Sea, *M. filiformis* was found locally only in fine sands with a median grain size between 125 and 250  $\mu\text{m}$  (Degraer et al. 2006). In the Outer Bristol Channel (UK) the species displayed a clear preference for fine sands between about 100–200  $\mu\text{m}$  median grain size, with the highest densities occurring at median grain sizes of 100–150  $\mu\text{m}$  (Mackie et al. 2006). These sediments were well sorted (sorting coefficient <0.5), had low mud contents (mostly <5 %, max 10 %) and were mostly in water depths less than 30 m (Mackie et al. 2006). The strongest correlation was between the density of occurrence and water depth as well as between density of occurrence and median grain size (-0.62 and -0.57 spearman rank correlation coefficient, respectively).

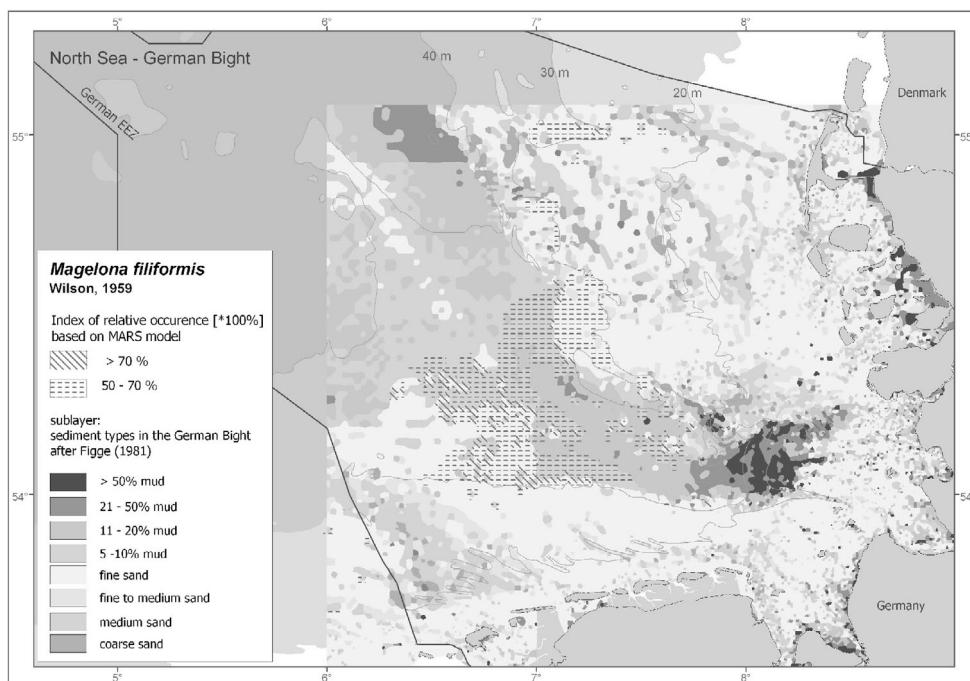
From that point of view it is not surprising that, according to our best model, areas with suitable habitat quality in the German Bight are far more restricted for *M. filiformis* than for *M. johnstoni*. Among the models, predictive accuracy, in particular, specificity (correct prediction of absence), was lowest for the *M. filiformis* habitat model (Table 2). Predictive accuracy of the habitat model depends on the threshold value  $P$  (Fielding & Bell 1997; Bonn & Schröder 2001). Here we chose  $P_{\text{kappa}}$ , the threshold value for maximum kappa (as advised by Boris Schröder, University of Potsdam, personal communication) (Table 2). However, the overall classification rate did not vary much when considering different threshold values (e.g.,  $P_{\text{fair}}$  = minimum difference between sensitivity and specificity, or  $P=0.5$ ). The comparably low predictive accuracy of the model indicates a slight weakness in accurately predicting the presence or absence of the species for a certain grid cell. But the AUC value was high and indicates high discriminatory power of the model. Based on that, evaluation of habitat suitability can be regarded reliable (Fig. 10).

### *Magelona alleni*

The *M. alleni* habitat model indicated the presence of suitable habitats in parts of the German Bight where sands with elevated mud content are present and water depths exceed 30 m. In fact, the region covered by the former Elbe River valley and in particular its deepest parts at the greatest distance from the coast seem to meet habitat requirements of the species best.

Hartmann-Schröder (1996) reported *M. alleni* occurring subtidally in sandy and muddy sediments, but also cites records from mixed substrates. Böggemann (1997), identifying material from the German North Sea, found *M. alleni* at stations with fine sand and muddy fine sand in water depths >40 m. Kirkegaard (1969) reported the species from locations near the Dogger Bank with clayey sand. On the Scottish coast the species was present in sandy mud and mud between 14–46 m water depth (McIntyre 1960). Occurrence of *M. alleni* in the Outer Bristol Channel appears to

deviate from the pattern known from other regions (compare data provided by Mackie et al. 2006). Here the presence of the species was positively correlated with the percentage of gravel in the sample, whereas the correlation with the percentage of sand was negative (0.51 and -0.60 spearman rank correlation coefficient, respectively). Mud content ranged between 0% and 36 %. There was no correlation between density of *M. allenii* and mud content of the sediment. Since comprehensive data were gathered in the course of the Outer Bristol Channel project, an inspection of video sequences showing bottom conditions at selected stations was possible. In some of the sequences pebbles or gravel loosely covering sandy sediment could be detected. The uppermost sediment layer was distributed into the water due to disturbance of the camera system during recording, indicating the presence of fine sediment fractions at that locality. It can therefore be concluded that mixed sediments (including fine grained fractions) were present at the stations. That is also indicated by the poor sorting coefficients of the coarse sediments in the area (Mackie et al. 2006). The preference of *M. allenii* for gravelly substrates in the area might be attributed to factors other than the percentage of gravel itself. Our data set for the German Bight did not include any record of *M. allenii* from coarser sediments.



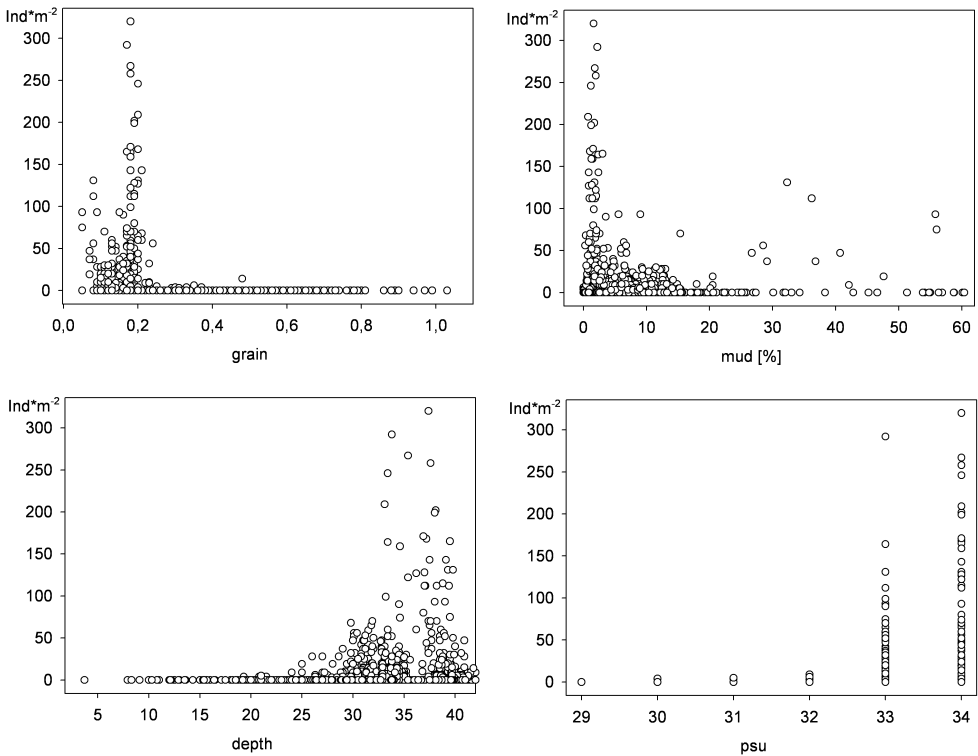
**FIGURE 10.** Prediction map for *M. filiformis* based on MARS model with best predictive fit; area of prediction restricted to grid cells with available information on predictor variables included in the species habitat model.

### *Magelona mirabilis*

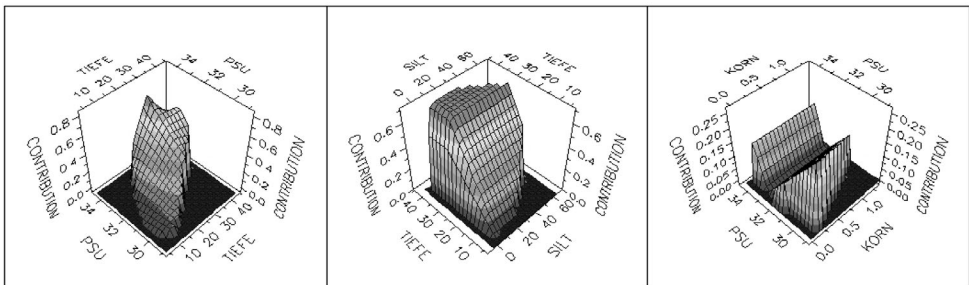
As already stated in the results section, the presence of *M. mirabilis* in our data set was very low and hence did not allow the development of a species habitat model. Despite the low number of records, a more frequent occurrence in near-coastal areas and regions influenced by estuarine waters could be suggested for the German Bight. Taxonomic problems surrounding *M. mirabilis* also contribute to

this deficiency of information. Accounts of *M. mirabilis* from before 2000 (description of *M. johnstoni* by Fiege et al. 2000) cannot be trusted since they might refer to *M. johnstoni*.

*Magelona alleni*



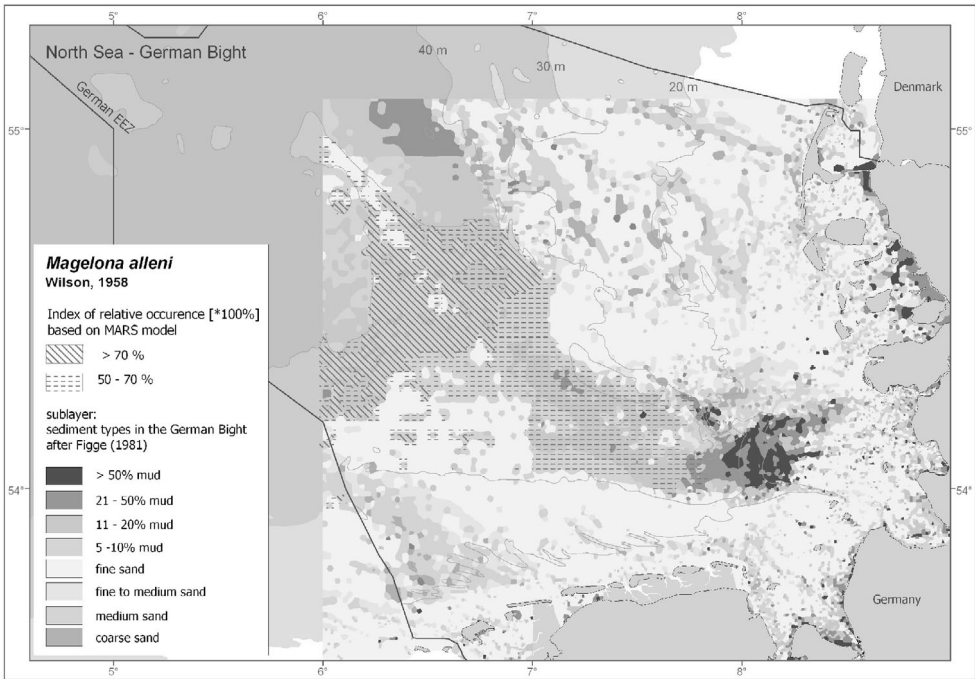
**FIGURE 11.** Species data for *M. alleni* included in the data set used in the present study; grain = median particle size diameter ( $d_{50}$ ) in mm, mud = mud content in %, depth = water depth in m, psu = salinity in practical salinity units.



**FIGURE 12.** Contour plots illustrating the relationship between a pair of predictor variables and the target variable (species response), KORN = grain size median  $d_{50}$ , TIEFE = water depth; from *M. alleni* habitat model.



The Outer Bristol Channel study by Mackie et al. (2006) provides reliable information on *M. mirabilis*. The highest densities were found at stations where sand content of the substrate was high and mud content rather low. There also seemed to be a trend of a decline in density with increasing water depth (-0.51 spearman rank correlation coefficient). However, in general the species was the least specific among the *Magelona* species in the Outer Bristol Channel region in regard to measured environmental parameters. There might be other factors involved in the determination of the occurrence of that species.

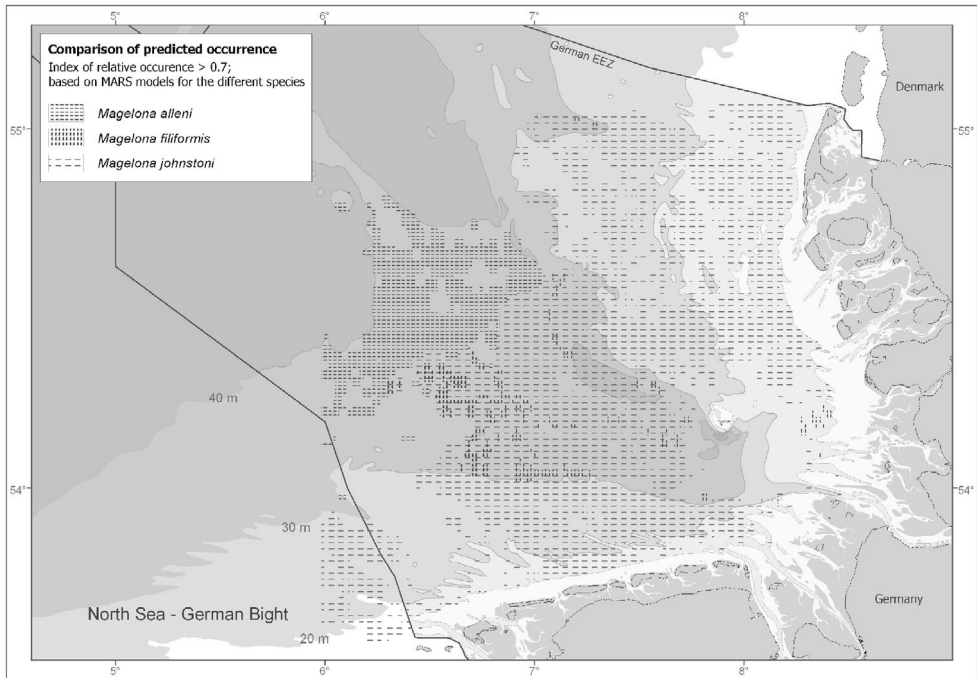


**FIGURE 13.** Prediction map for *M. alleni* based on MARS model with best predictive fit; area of prediction restricted to grid cells with available information on predictor variables included in the species habitat model.

### Concluding remarks

Species habitat models for three out of four *Magelona* species occurring in the German Bight (North Sea) are presented in the study. It was found that sediment parameters (either grain size median in respect to *M. johnstoni* or mud content in respect to *M. alleni* and *M. filiformis*) are the most important determinants for the occurrence of these species in the German Bight. Comparative mapping of modeling results allowed their geographic and ecological discrimination (Fig. 14).

An extension of the model over the full distribution range of the species would be desirable. In other regions additional parameters might be of importance. Also, the importance of environmental predictors already included in the model might change. The necessary requirements for such approaches are multifaceted studies for data collection as well as powerful and readily available databases for data aggregation so that they can be used for modeling and beyond.



**FIGURE 14.** Geographic differentiation of highest probability of occurrence of *Magelona* species in the German Bight (coastal areas with water depths <10 m and regions outside the area covered by the Figge map, compare Fig. 1, are not considered in the prediction map).

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