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Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 2. Modelling and prediction

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ABSTRACT

The detailed analysis of patterns of benthic community distribution related to selected environmental parameters provides a basis for predictive modelling of species distribution. Species-specific models predicting the probability of occurrence relative to environmental and sedimentological characteristics were developed in this study for 29 macrofaunal species common for our study area using a logistic regression modelling approach. This way, a good description of the occurrence of species along gradients of single environmental variables was obtained. Subsequently, we used a technique for a predictive modelling of species distributions in response to abiotic parameters based on single-factor logistic regression models, utilizing AIC and Akaike weights for multimodel inference. Thus, probabilities of occurrence for selected exemplary species (*Arctica islandica*, *Hediste diversicolor*, *Pygospio elegans*, *Tubificoides benedii* and *Scoloplos armiger*) were modelled and mapped. For all species the use of this newly available combination of methods provided fairly accurate results of a distribution prediction. Water depth that represents a type of integral parameter remained the key factor determining the species distribution among the parameters considered within the study scale. This is particularly relevant for species that find their optima habitat here, but also for those as *H. diversicolor* that occur only locally and in comparatively low densities. Total organic content, sorting and, for *S. armiger*, salinity also had noticeable effect in the determination of suitable habitats for benthic macrofauna. The employed technique proved to be appropriate for modelling of the benthic species habitat suitability, at least within comparable spatial scales and variability of environmental factors.

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1. Introduction

Climate change models assume a drastic change in the food web structure, a shift in species composition towards warm water species and growing benthic deserts on the sea floor as up-coming changes for the Baltic Sea ecosystem (Philippart et al., 2007). Predictive modelling of species distribution can be a valuable tool in management directed towards the sustainable development of the Baltic Sea. Studies on various scales are required to extend our knowledge of habitat change effects.

Response of macrofaunal assemblages to substrate composition, hydrographic parameters and their variation is declared by many different studies (e.g. Sanders, 1968; Rhoads, 1974; O'Brien et al., 2003; Laine, 2003; Perus and Bonsdorff, 2004; Ellis et al., 2006). Particular establishments regarding the dynamics and structure of biotic/environmental interactions are required to evaluate natural and anthropogenic influences and effects on the ecological systems (Pavlikakis and Tsihrintzis, 2000; Glockzin and Zettler, 2008a). An exploratory statistical description of the prevailing ecological structure based on observations is always the indispensible first step (Bourget and Fortin, 1995).

Recently, a number of studies have succeeded in the development of effective statistical models of benthic distribution. Ysebaert et al. (2002) successfully applied logistic regression to derive response surfaces of distributions for 20 common macrobenthic species found in the Schelde estuary in the Netherlands related to salinity, depth, current velocity, and sediment characteristics. Thrush et al. (2003) developed species-specific models for 13 benthic species of New Zealand estuaries that predicted probability of occurrence as well as maximum abundance relative to sediment mud content using logistic regression for distribution modelling and 'factor ceiling' method (Blackburn et al., 1992) for maximum density modelling. Ellis et al. (2006) modelled the distribution of 13 representative macrobenthic species in New Zealand estuarine gradients using logistic regression and classification system based on 'controlling factors' with sediment characteristics, elevation, tidal currents, and wind-wave disturbance employed as predictors. They faced complications to fully test the latter approach due to differences in scales of collected benthic data and of higher level physical variables. Meissner et al. (2008) developed habitat models for *Nephtys* species in the German Bight (North Sea) with median grain size, mud content, depth, and salinity as explanatory variables by application of

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multivariate adaptive regression spline techniques (MARS). Many researches indicated difficulties due to the complexity of identification of the underlying causal mechanisms controlling species distribution, further extended by the fact that animals modify their physical environment, and many physical parameters co-vary (Ellis et al., 2006).

The present study contributes to the development of statistical models that are able to predict the distribution of benthic macrofaunal species as a function of environmental variables. Models that forecast the behaviour of species distribution versus changes in environmental factors (sensu Legendre and Legendre, 1998) provide an insight into chronic habitat change (regarding these parameters), though they do not provide insight into the acute effects associated with disturbance events (Thrush et al., 2003; Ellis et al., 2006). Model estimations based on a data set consisting of the response variables (e.g. species occurrence or abundance) and on a set of predictor variables (e.g. environmental parameters) can be used to predict the spatial distribution of species in a habitat with known or defined environmental settings (Ysebaert et al., 2002; Ellis et al., 2006; Meissner et al., 2008). Statistical models are able to relate ecological features to environmental factors and, through validation and modification, are able to reveal details in the underlying mechanisms responsible for structure and organization of communities (Austin, 1987; Glockzin and Zettler, 2008a).

Our investigation is focused on a limited area in the south-western Baltic Sea. The pre-work of an exploratory statistical description of the prevailing ecological structure is an essential first step towards modelling, and it was completed for the area of interest beforehand (Gogina et al., 2010-this volume). The identified distinct benthic assemblages have proved to associate with certain spatial regions and specific limits of environmental parameters. The reduction of macrozoobenthic data to presence/absence is forced by the absence of temporal homogeneity and is used here to eliminate the influence of patchiness in spatial distribution that macrofauna exhibits (McArdle and Blackwell, 1989; Legendre et al., 1997; Thrush et al., 2003).

2. Materials and methods

2.1. Study area

The study area is located in the south-western Baltic Sea, between 11.55° to 12.55° E and 54.09° to 54.96° N (Fig. 1). It is bounded by the eastern part of the Mecklenburg Bight and the western region of the Kadetrinne, with its northern and southern limits defined by Danish and German land boundaries. Some geographical details about the area, which is characterised by a relatively high biodiversity of both saline and brackish water species, as well as the analysis of benthic community structure, can be found in Gogina et al., 2010-this volume.

2.2. Data used for model estimation

The study is based upon the data of benthic macrofauna and associated sediment and near-bottom environmental characteristics, sampled at 208 stations (Fig. 1a). For 72 of these stations a full set of the abiotic parameters considered is available. For modelling purposes the species abundance data was reduced to presence/absence.

The description of methods for benthic macrofauna sampling and abiotic factor determination, as well as the selection process for extraction of 29 representative macrobenthic species modelled here, can be found in Gogina et al., 2010-this volume.

2.3. Additional environmental data for predictive modelling

Additional data sets were required to compile the grids of each abiotic descriptor, needed for predictive estimates of species distribution (probability of occurrence) for the whole investigation area. The distribution surfaces obtained for each of the environmental variables considered are presented in Fig. 1.

For the bathymetry a high-resolution digital elevation model (DEM) was created using measured data provided by the Federal Maritime and Hydrographic Agency (BSH) and a regional grid data set from Seifert et al. (2001), covering the Belt Sea region. For more details see the description of DEM design in Meyer et al. (2008). Grid data sets for near-bottom oxygen content and salinity were based on the modelled hydrographical data, averaged for years 1960–2005 with the resolution of 3 nautical miles (Neumann and Schernewski, 2008), covering the whole western Baltic sea area. Grids for sediment parameters like median grain size, sorting, skewness and permeability are derived from the internal database of the Leibniz Institute for Baltic Sea Research Warnemuende (IOW; Bobertz and Harff, 2004), integrating the data of about five decades of marine investigations. The average distance between adjacent sample sites is less than 1 nautical mile. From the IOW database external data on total organic content was also available, however, only for a limited area. Hence, this data was agglomerated together with the observed data used for model estimation to increase the area covered and the density of data points. Nevertheless, only a part of the investigation area could be covered with the compiled grid of this parameter (Fig. 1d). Parameters were interpolated using ordinary kriging with spherical fitted models of semivariograms into a grid with the resolution of about 0.005 decimal degrees (approximately 0.5 km with respect to longitude).

Ysebaert et al. (2002) favoured the usage of modelled estimates of environmental variables over the data measured directly and simultaneously with benthic sampling. The argumentation included the available high spatial resolution and a sort of smoothing caused by simulation, e.g. elimination of outfits. However, taking into account the complexity of the functioning of ecosystems, the uncertainty of simulations may increase the complexity of the interpretation of derived empirical relationships. Utilization of simulated data for the model estimation is forced merely by the necessity and absence of alternatives. The preliminary explicit exploratory analysis of environmental framework should exclusively be based on direct in situ measurements. Therefore, to enable the investigation of autecological relationships we rely our model calibration on directly observed data to the highest extent possible, applying minimum transformations to lessen the reduction of information contained in the data (Gogina et al., 2010-this volume). Yet, the prediction is based partly on modelled data of sufficient resolution available for the study area, thus, allowing the validation of modelling success.

2.4. Statistical analysis and data treatment

2.4.1. Univariate logistic regression

Logistic regression of biotic data reduced to presence/absence was employed to model the probability of occurrence of 29 discriminating species, using the considered environmental factors (water depth, salinity, oxygen concentrations, total organic content, median grain size, sorting, skewness and permeability of sediments) as explanatory variables. These factors are generally assumed to have direct or indirect impact on distribution of macrobenthic species. The logit function in a logistic regression is the special case of a link in a generalised linear model, known as canonical for the binomial distribution. Application of logistic regression methods in modelling species distribution is not new. This method was widely used in plant ecology (e.g. Guisan et al. 1999) and also in aquatic ecology, but to a lesser extent. Thrush et al. (2003) concentrated their investigation on a single environmental factor—sediment mud content, Ysebaert et al. (2002) performed a comprehensive study, using salinity, depth, flow parameters, median grain size and mud content as predictors. The present study represents one of the first applications of this technique to benthic habitats of the Baltic Sea.

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