

Spatial macrozoobenthic distribution patterns in relation to major environmental factors- A case study from the Pomeranian Bay (southern Baltic Sea)

M. Glockzin, M.L. Zettler*

Department of Biology, Leibniz Institute of Baltic Sea Research (IOW), Seestr. 15, D-18119 Warnemuende, Germany

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Abstract

The aim of this study was to identify potential environmental “key factors” causing spatial distributions of macrozoobenthic communities to improve our understanding concerning benthic biotic/abiotic interactions and ecosystem functioning. To this end benthic and environmental data, collected over a period of 4 years (2003–2006) at 191 sampling stations in the Pomeranian Bay (southwest Baltic Sea), were analysed. This represents the most comprehensive study performed in this respect in the Baltic Sea up to date and also the necessary first step towards a model able to predict macrofaunal distributions regarding autecological species-environment interactions. Based on species abundances, distinctive macrobenthic community patterns were identified and evaluated via univariate correlation methods, multivariate numerical classification and ordination techniques (e.g. PCA, CCA). These patterns were caused by clear responses of several benthic species to certain prevailing environmental conditions. The observed distribution of selected species followed a strong gradient of depth and was explained best by the sediment parameters total organic carbon (TOC), median grain size and sorting. By using different statistical methods these abiotic/biotic interactions were modelled allowing to extend our knowledge concerning ecosystem functioning, and provide a tool to assess natural and anthropogenic forced changes in species distribution.

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1. Introduction

Different studies have suggested that substrate composition, hydrographic parameters and their variations seem to determine macrofaunal assemblages and abundances (e.g. Rumohr et al., 1996; Ellis et al., 2006; Fortin

et al., 2005; O’Brien et al., 2003). A link between benthic infauna distribution and environmental factors has been assumed but has so far not been established particularly for the southwest Baltic Sea. However, to examine and understand the structure and dynamics of biotic/environmental interactions is of great importance to improve our knowledge regarding biological and ecological processes not only in the Baltic; it is mandatory to evaluate natural and anthropogenic influences and effects on ecological systems (Pavlikakis and Tsihrintzis, 2000). Statistical

* Corresponding author. Fax: +49 381 5197440.

E-mail address: michael.zettler@io-warnemuende.de (M.L. Zettler).

models provide a useful tool to relate ecological features to environmental factors and, through validation and modification, they can reveal the underlying mechanisms responsible for the structure and organisation of communities (Austin, 1987). However, an exploratory statistical description of the prevailing ecological structure based on observations always is the indispensable first step (Bourget and Fortin, 1995). The comparison of benthic communities normally comprise the analysis of species data obtained from a variety of depths and geographical locations. That in turn yields the possibility of a limited exploration of variables, distorted by strong gradients (Bourget et al., 1994) or biased by autocorrelation (Legendre, 1993). Previous benthic studies in the Pomeranian Bay and in other regions in a more global perspective simply have neglected this. The present study for the first time takes into account both biotic/environmental interactions and the possibility of spatial side effects on statistical analyses in the Pomeranian Bay.

Due to the variability of species in terms of habitat selection, reciprocal effects between species' distribution and environmental factors are manifested in patterns, visible in their abundances or assemblages (Kolasa and Strayer, 1988; Keitt et al., 2002). Understanding these patterns requires a two-stage procedure. At first, the patterns in the distribution of the organisms are described and secondly, the parameters causing this distribution are determined. Alternatively, patterns in environmental variables can be determined first and then the reactions of organisms to these patterns are described (Legendre and Legendre, 1998). However, in both cases, in-depth knowledge is needed regarding the autecology of the species for the interpretation of the relationships revealed (Sachs, 1997).

The area investigated in this study, the Pomeranian Bay, is situated in the southwestern part of the Baltic Sea. Due to its hydrology and morphology, distinct gradients in environmental variables are present, resulting in a well-defined division of benthic communities (Kube et al., 1996; Warzocha, 1995). This offers a good basis to study biotic/abiotic interactions and to identify the main environmental factors controlling species distributions. The objectives of the present study were to (i) relate macrozoobenthic data to selected abiotic factors, (ii) test the applicability of univariate and multivariate statistical approaches in order to evaluate spatial distribution patterns of species caused by their variability and response toward habitat selection and (iii) undertake a first step towards creating a model to assess species response to natural and anthropogenic effects on a temporal-spatial scale along environmental gradients such as in the Baltic Sea.

2. Materials and methods

2.1. Study area

This study was performed in the Pomeranian Bay, a relatively shallow brackish water coastal area in the southwestern Baltic Sea. It is situated north of the Oder River and borders to Germany and Poland. Regarding the data available, we chose the German part of the Pomeranian Bay as the actual area of investigation (Fig. 1). It stretches over 90 km from the Isle of Rügen in the west up to the international border of Poland in the east. To the south, it borders on the Isle of Usedom (Germany). As northern barrier, the 25 m depth line was used because it represents a relative "continuous" barrier to the open sea. Likewise, the Greifswalder Bodden Sill functioned as a seawards barrier to the southwest. Within these boundaries, the area of the German part of the Pomeranian Bay amounts to 3,500 km². With an average depth of about 13 m, its water volume equals approximately 46 km³ (dataorigin: this study). The submarine morphology of the Bay is predominantly shaped by gutters and basins of glacial origin (Neumann and Bublit, 1968). A large seasonal and therefore pulse-like freshwater discharge of about 17 km³ yr⁻¹ from the Oder River in the south and a steady inflow of saltwater from the north results in an almost steady spatial gradient of salinity along the north-south axis of the Bay (Mohrholz, 1998). But the inflow not only brings freshwater into the Bay- it is also a steady source of nutrients and particular organic matter and carbon (FPOM, POC). This allochthonous material is mixed with the autochthonous material of the Pomeranian Bay (Christiansen et al., 2002). Due to the shallowness of the Bay and prevailing wind-driven currents, the water column is vertically well mixed up to depths of approximately 30 m during the year (Kuhrt et al., 2006). Therefore hardly any spatio-temporal stable vertical layers of oxygen emerge in the Bay. Bottom near salinity, in narrow bounds, shows a clearly recognizable pattern, particularly along the deeper bathymetry (Lass et al., 2001). The wind driven currents also carry and distribute the nutrients throughout the Pomeranian Bay (Pastuszak et al., 2005). The main accumulation areas of the Oder River loads are the Arkona Basin and the Bornholm Basin (Christiansen et al., 2002). But they also accumulate strongly at the slopes and in much smaller amounts in ripples on the northwesterly plateau of the Oder Bank, an ancient sanddune of glacioaeolian origin (Bobertz and Harff, 2004, own video data). Extensive areas of the central Bay are covered with fine and medium grain sand which

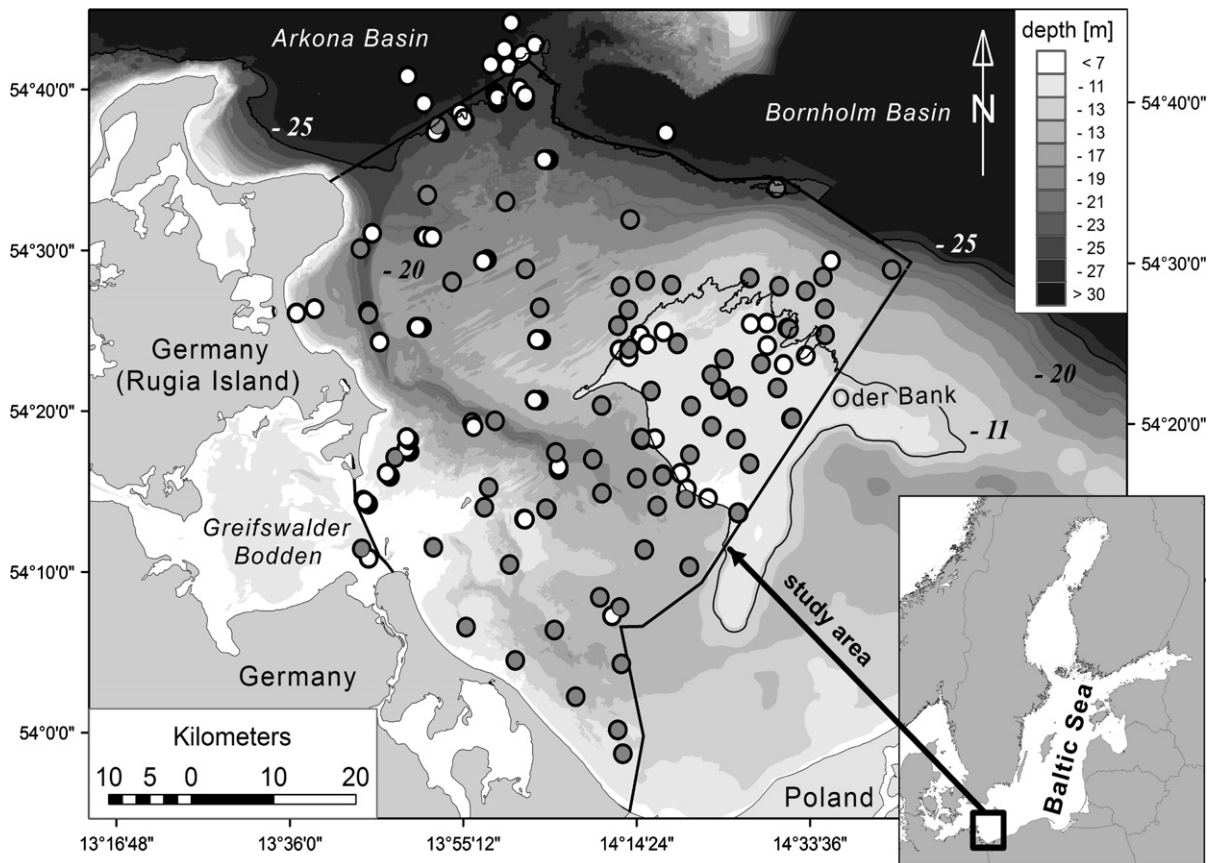


Fig. 1. Study area and distribution of the 191 sampling stations, filled circles indicate stations with a full set of data available for all seven abiotic variables. Sampled stations per year: 2003 (53 stations), 2004 (78 stations), 2005 (30 Stations), 2006 (30 Stations).

originates mostly from aeolian and coastal erosion and glacioluvial dislocation. To our knowledge, no drastic event (e.g. hypoxia etc.) occurred in the timeframe of this study. General characteristics of the Pomeranian Bay such as bottom water salinity, species richness, diversity indices and the species composition and its abundance was the purpose of previous studies (Zettler and Gosselck, 2006; Zettler et al., 2007).

2.2. Sampling

This study is based upon quantitative macrozoobenthic abundance data collected at 191 stations in the German part of the Pomeranian Bay over a period of 4 years (2003–2006) (Fig. 1). The sampling each year was carried out between April and October. The respective stations, except already defined monitoring stations, were randomly distributed over the whole investigation area. Two to three replicate samples were taken at each station with a van Veen grab (0.1 m², 70 kg, 10–15 cm penetration depths). The contents of the grab

were sieved through a 1.0 mm sieve and the residue preserved in 4% buffered formaldehyde-seawater solution. In addition to macrobenthic sampling, a water sample was taken by a shipboard CTD system (SBE 9, Seabird Electronics) 0.5 m above seafloor. Oxygen content was determined by immediate potentiometric titration in the ship laboratory. Near-bottom conductivity was estimated by CTD as well. Depth at each station was determined and logged with a shipboard sonar system (Behm-Echograph XL). An additional sample was taken to extract an upper surface sediment layer (≤ 5 cm) for analyses of median grain size (mgs, completed for 85 out of 191 stations) and determination of total organic carbon (TOC, completed for 115 out of 191 stations). In the laboratory, the formalin was washed out of the samples prior to sorting. The organisms were sorted, identified to the lowest possible taxon and counted. Sampling and preparation were conducted in accordance with institutional, national and international guidelines concerning the use of animals in research (HELCOM, 1988).

2.3. Sediment parameters

Organic content (TOC) was measured as loss on ignition (3 h at 500 °C) after drying for 24 h at 60° (HELCOM, 1988). For grain size analysis, approximately 50 g of dried sediment was dry sieved using a RETSCH sieving machine (sieve set: 63 µm, 75 µm, 90 µm, 106 µm, 125 µm, 150 µm, 180 µm, 212 µm, 250 µm, 400 µm, 630 µm, 2000 µm). Median grain size was calculated according to McManus (1988). Sorting was calculated according to Folk and Ward (1957) and permeability determined according to Krumbein and Monk (1942) using the data for median grain size of 85 out of 191 stations. After all, a complete set of all seven environmental parameters was available for 78 out of 191 Stations (Fig. 1).

2.4. Statistical analyses

To focus the investigation on biotic/environmental interactions rather than on other aspects (e.g. energetic criteria vs. species development etc.) only species abundance was subjected to statistical analyses (Young and Young, 1998). Furthermore, interannual and inter-seasonal effects on species abundances were neglected to filter out short-term effects and factors. Blanking out short-term fluctuations of species abundance we were able to get a broader view on long term environmental-autecological interactions and species habitat selection. For each sample the abundance of species was counted separately. Afterwards these replicate abundances were averaged to a total per square meter at each station (HELCOM, 1988; no pooling). Because different statistical analysis methods were employed in this study, some of the overall number of 80 recent species had to be excluded prior to statistical analysis (Legendre and Gallagher, 2001). This was done successively by means of different criteria, thus forming the appropriate data sets for the various statistical methods. Firstly, all indeterminate (e.g. *Oligochaeta* indet.) and uncountable species (e.g. Hydrozoa) were excluded. Only endobenthic species were regarded in the analysis, hence all inappropriate species were removed. The blue mussel *Mytilus edulis* was excluded due to its high patchiness and therefore unreliable sampling with a van Veen grab (own investigation). Then, according to Lozán and Kausch (2004), all species with a frequency of less than 6% at all stations and finally, regarding Field et al. (1982), all remaining species which account for less than 3% of total abundance over all stations were excluded from the data set, leaving a data matrix of 17 species and 191 stations. Due to the prevailing

environmental conditions in the Pomeranian Bay, e.g. its shallowness and wind driven currents, no distinctive gradient for near bottom oxygen content does emerge here, so this environmental parameter was excluded from further analysis and a matrix of 6 environmental variables and 78 stations was created.

Since spatial distribution patterns of species are often to a great extent influenced by spatially structured environmental or biological processes, they can be spatially autocorrelated – the location of sampling points in space influences the values of random variables (Legendre, 1993). The spatial autocorrelation between sampling sites for the 78 stations of abiotic parameter data and for the 191 sampling sites of species abundance data was calculated using the Moran's I Index function (Legendre and Legendre, 1998) implemented in ArcView 9.2. To examine correlations between environmental variables and species exploratory, a Spearman's rank correlation was computed between the abundance data of 17 species and the corresponding environmental data. Coherencies among 6 environmental variables were examined via normal and partial correlation (Pearson correlation coefficients) and path analysis applied to the z-transformed abiotic matrix, following the model analysis described in Legendre and Legendre (1998). Spearman rank correlation coefficients and partial correlation coefficients were calculated using SPSS software (SPSS Inc.). This way, a primary environmental descriptor could be isolated. Its effect on other environmental descriptors and, as a consequence, on species distribution was analysed by means of testing cumulative frequency distributions of the primary predictor versus species abundances using the Kolmogorov-Smirnov test of significance (Perry and Smith, 1994; Simpson and Walsh, 2004; Sachs, 1997; Sturges, 1926). Furthermore, a map of the detailed bathymetric structure is given (Fig. 1), thus describing the main physical control factor (represented by the primary descriptor) for most of the environmental conditions prevailing in the Pomeranian Bay. For statistical determination of benthic colonization zones, a covariance-based principal component analysis (PCA) was performed. Prior to this, the abundance data of the species matrix were subjected to fourth root ($\sqrt[4]{}$) transformation and then tested on statistical normal distribution with a Kolmogorov-Smirnov test and box plots, again using SPSS software. Only for 12 species out of 17 a statistical normal distribution was proven. PCA was applied to the already $\sqrt[4]{}$ -transformed abundance data matrix of this 12 species found at 191 sampling sites, in order to group the stations within the region studied by their similar variance in site patterns. According to McGarigal et al. (2000) a scree-plot (a plot of all

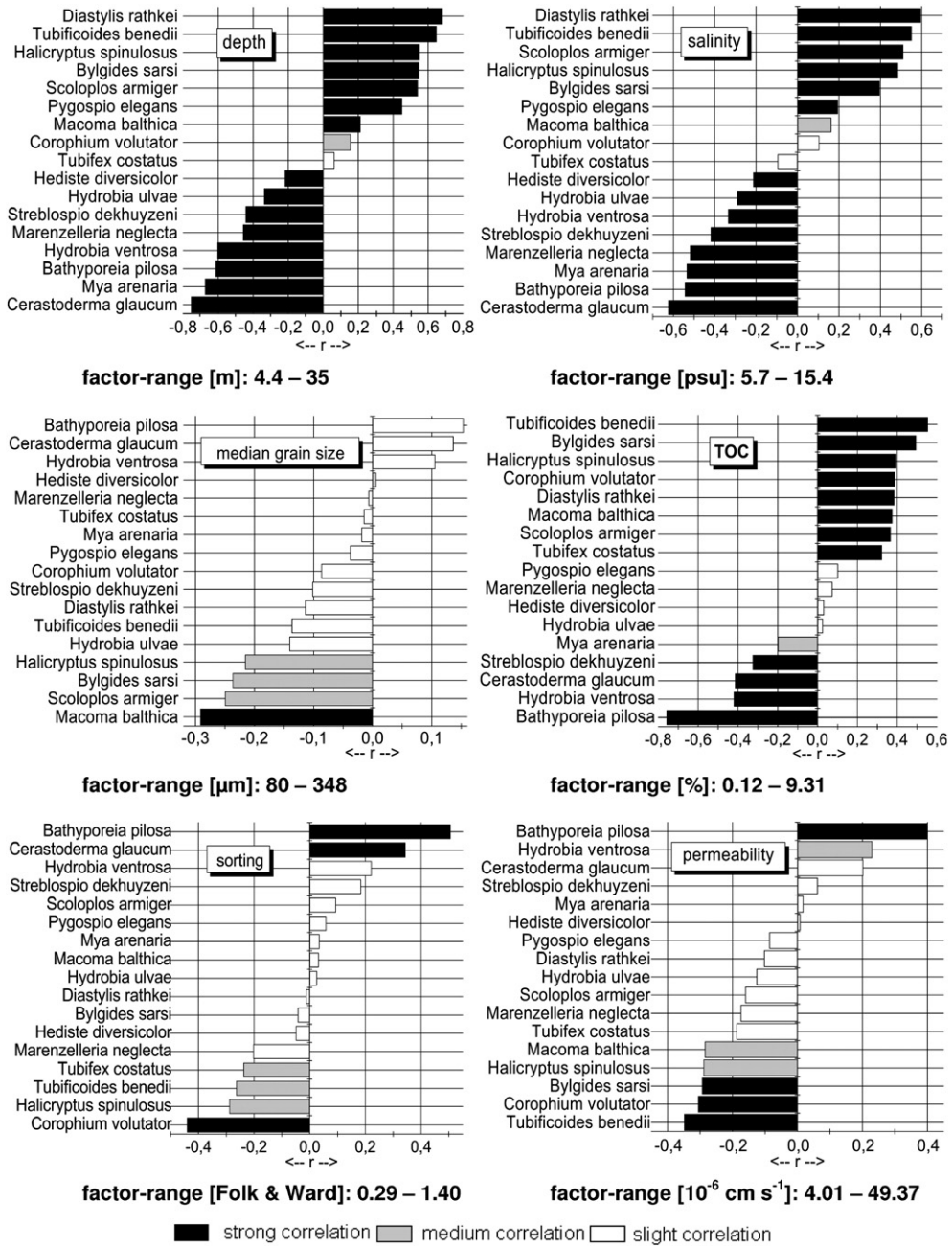


Fig. 2. Spearman's rank correlations for species abundances and water depth, salinity, median grain size, organic content (TOC), sorting and permeability. Because of possible autocorrelation, the significance levels should be taken as first indication.

eigenvalues in their decreasing order) was drawn and, as a result, the first and second axes of principal components were retained and projected separately on two maps of the Pomeranian Bay, using Kriging interpolation and GIS software (Legendre and Legendre, 1998). In this way, areas with similar species composition of the Pomeranian

Bay were derived. PCA was calculated with Matlab software (The MathWorks, Inc.), the principal components were subjected to kriging interpolation with SURFER (Golden Software, Inc.) and the zonation was projected with ArcView (ESRI). For the statistical evaluation of correlations between biological and

environmental parameters which may cause the observed benthic zonation, all stations with a complete set of abundance data and corresponding environmental data were chosen from the data set used for PCA. This left data matrices of 78 sampling sites with $\sqrt{\sqrt{\cdot}}$ -transformed abundance data of 12 species and corresponding z-transformed environmental data. Additionally, the environmental data matrix was detrended from the primary descriptor by means of polynomial regression (SIGMAPLOT Software package) and the standardised residuals preserved, thus forming a second abiotic matrix of 5 detrended environmental variables and 78 stations. Then the matching of biotic to environmental patterns (BIO-ENV procedure, PRIMER-E Ltd.) and canonical correspondence analysis (CCA) were calculated, successively using both environmental matrices. For the calculation of similarity matrices in the BIO-ENV procedure Bray-Curtis similarity was used for species data and simple Euclidian distance for the corresponding sets of environmental data (Clarke and Warwick, 1998). The gradient length in standard deviation (SD) units was estimated per detrended correspondence analysis (DCA with detrending by segments, CANOCO, ter Braak, 1988, 1989) to test the applicability of CCA and a posterior numerical analysis involving techniques based on a unimodal species response model (ter Braak and Smilauer, 1998). Gradient length did slightly exceeded 3 SD and CCA was carried out with a subsequent Monte-Carlo permutation test, using 999 unrestricted permutations under full model with

automatic forward selection of 6 environmental parameters (CANOCO, ter Braak, 1988, 1989).

3. Results

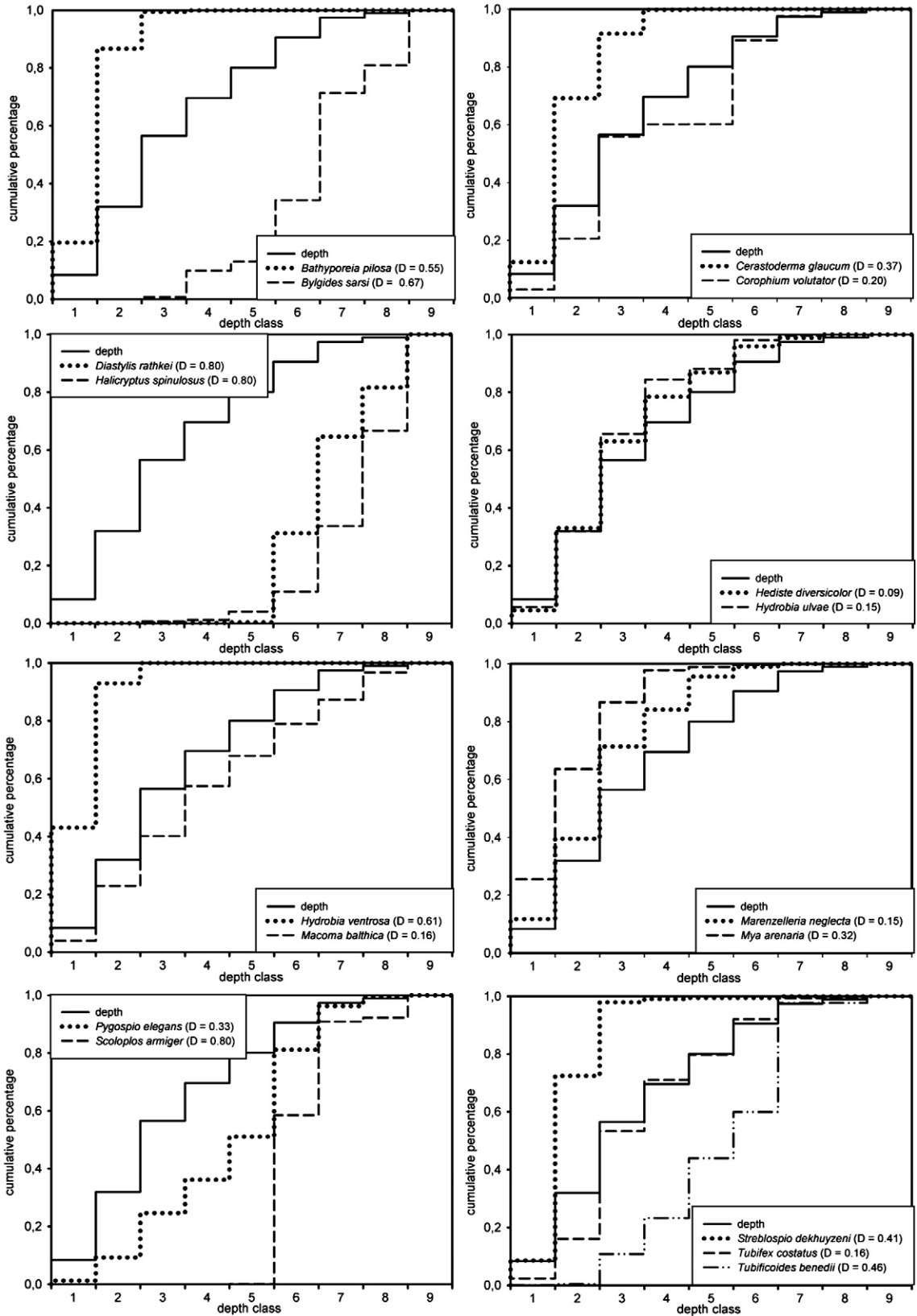
3.1. Moran's I Index

The Moran's I tool implemented in ArcView measures spatial autocorrelation (feature similarity) based on both feature locations and feature values simultaneously. It calculates a Moran's I Index value evaluating whether the pattern expressed is clustered ($\approx +1.0$), dispersed (≈ -1.0), or random (≈ 0). Additionally a Z score (as a measure of standard deviation) evaluating the significance of the index value is given. For all abiotic parameters found at the 78 sampling stations with a full set of environmental variables (Fig. 1) no autocorrelation could be detected. They appear rather randomly distributed with Index values between -0.13 and 0.20 and corresponding Z scores ranging from -0.46 to 0.86. The index values calculated for the species sampled at the very 78 stations range from -0.20 to 0.50 with corresponding Z values between -0.76 and 2.14. Here, the data point distributions of the species *Hydrobia ulvae* and *Hydrobia ventrosa* show a slightly clustered pattern with Z scores slightly exceeding the confidence interval ($p=0.05$). Moran's I Index values were also calculated for the data set containing species abundance data sampled at 191 stations. Though the stations sampled were randomly

Table 1

Pearson correlation coefficients calculated for the full set of z-transformed environmental variables sampled at 78 stations, coefficients corresponding to $p < 0.01$ and $p < 0.001$ significance levels are printed in bold and n-values are given in brackets ($p = \text{two-tailed}$)

Environmental factor	Depth	salinity	Median grain Size	Organic content	sorting	permeability
water depth	1 (191)					
Salinity	0.616 (78) $P < 0.001$	1 (78)				
Median grain size	-0.342 (78) $P = 0.002$	-0.341 (78) $p = 0.002$	1 (78)			
TOC	0.332 (78) $P = 0.003$	0.477 (78) $p < 0.001$	-0.414 (78) $p < 0.001$	1 (78)		
Sorting	-0.166 (78) $p = 0.145$	-0.172 (78) $p = 0.133$	-0.099 (78) $p = 0.391$	-0.734 (78) $p < 0.001$	1 (78)	
Permeability	-0.347 (78) $P = 0.002$	-0.276 (78) $p = 0.015$	0.932 (78) $p < 0.001$	-0.424 (78) $p < 0.001$	0.112 (78) $p = 0.329$	1 (78)
Factor – unit	[m]	[psu]	[μm]	[%]	[Folk and Ward]	[$10^{-6} \text{ cm s}^{-1}$]
Factor – range	4.4–35	5.7–15.4	80–348	0.12–9.31	0.29–1.40	4.01–49.4



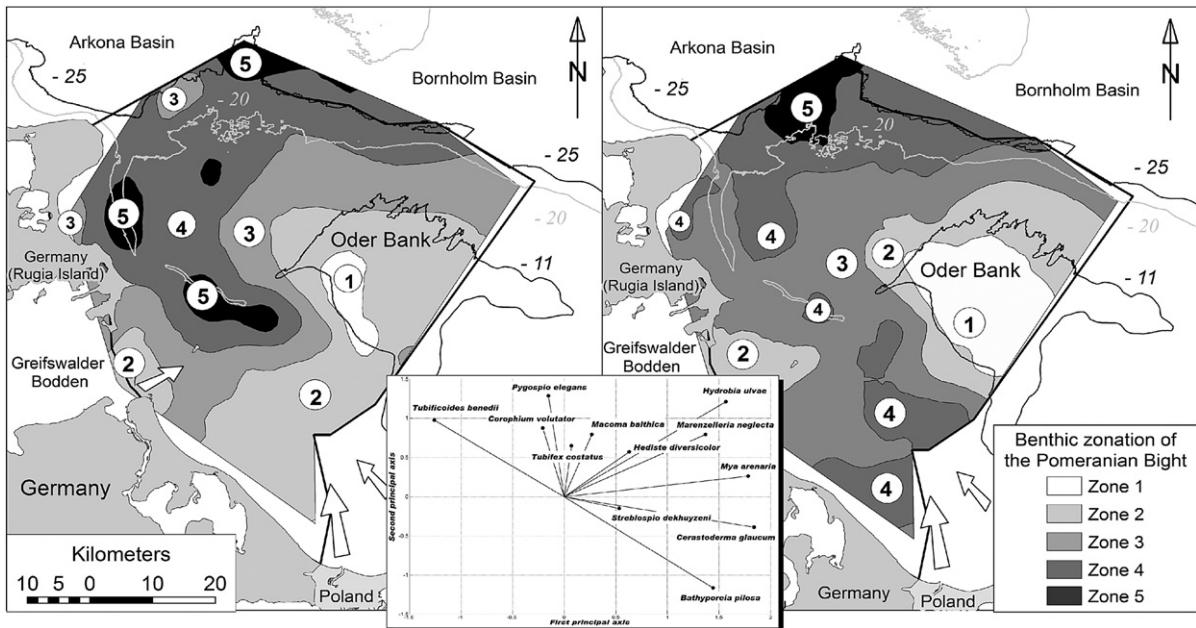


Fig. 4. Benthic zonation of the Pomeranian Bay obtained by Kriging of principal components of a PCA with abundances of 12 species at 191 sampling sites (lower middle, small Figure). Left side: Kriging of 1st principal components, Right side: Kriging of 2nd principal components. Arrows indicate main discharge outflow from Oder River. Areas were classified by using the method of natural breaks (implemented in ArcGis) on the interpolated principal components.

distributed over the entire sampling period the Moran's I Index values indicate more clustered patterns for most species (0.03–0.62) with Z values by far exceeding the confidence interval (0.8–14.9). For this data set autocorrelation is assumed. These results had to be taken into consideration in further analyses and result interpretation.

3.2. Spearman's rank correlation

Spearman's rank correlation factors were calculated for 17 species and 6 environmental variables (Fig. 2). The analysis may be biased by autocorrelation (Legendre, 1993) because all available data points of environmental data (not the full set available for 78 stations, Fig. 1) was used and has therefore a more exploratory character; however, the rank correlation factors between species and environmental parameters give a good insight on how the underlying processes of biotic/abiotic interactions cause species distributions and the benthic zoning in the Pomeranian Bay. The most significant Spearman's rank correlations between species abundance and environmental factors were found

for water depth and salinity. All species examined with Spearman's rank correlation were strongly correlated with water depth, except the oligochaete *Tubifex costatus*. The highest positive correlation factors were calculated for a cumacean and an oligochaete: *Diastylis rathkei* and *Tubificoides benedii*. As for negative correlation factors, the bivalves *Cerastoderma glaucum* and *Mya arenaria* showed the highest negative dependency from water depth. More or less the same applies for salinity. *D. rathkei* and *T. benedii* again reach highest positive correlation factors. No Spearman rank correlation with salinity can be proven for *Corophium volutator* and *T. costatus*. Highest negative correlation factors with salinity were found for *C. glaucum* and *Bathyporeia pilosa*. Remarkably, a strong negative dependency between median grain size and species abundance could only be found for *Macoma balthica*. Three other species (*Bylgides sarsi*, *Scoloplos armiger* and *Halicryptus spinulosus*) revealed less dependencies. Beside depth and salinity, TOC ranged on third position regarding the number of significant correlations calculated. Again nearly the same correlations and species

Fig. 3. Cumulative frequency distribution of depth (solid line) plotted versus species abundance. Kolmogorov-Smirnov coefficient D calculated after (Sachs, 1997) and given for each species, Calculated $D_{critical} = 0,14$ ($p = 0,05$, $n = 191$) for each species curve, For ($D > D_{critical}$) the two distribution curves are not identical. Depth classification calculated after Sturges (1926), Class-nr.(depth [m]): 1 (4.5–8), 2 (8 – 11.5), 3 (11.5 – 15), 4 (15 – 18.5), 5 (18.5 – 22), 6 (22 – 25.5), 7 (25.5 – 29), 8 (29 – 32.5), 9 (32.5– 36).

appeared as already found for water depth and salinity. *T. benedii* and *B. sarsi* show the best positive correlations with the organic content of sediment. On the negative side of the ordinate, species with strong and negative correlation factors for sediments poor in TOC do emerge. *B. pilosa* appeared to have the strongest negative correlation with TOC found for all species. Among the species which correlate best and positively with the sorting of sediment are *B. pilosa* and *C. glaucum*. Strongly and significantly negatively correlated with this factor are *C. volutator*, *H. spinulosus*, *T. benedii* and *T. costatus*. Those species which were positively influenced by permeability are the amphipod *B. pilosa* and the gastropod *H. ventrosa*. Strong but negative is the correlation between species abundance and permeability for the oligochaete *T. benedii*, the amphipod *C. volutator* and the polychaete *B. sarsi*. To a lesser degree in terms of significance, *H. spinulosus* and *M. balthica* can be found nearby on the same side of the axis.

3.3. Pearson correlation

To avoid the influence of autocorrelation, Pearson correlation coefficients were calculated for the z-transformed data matrix containing the full set of environmental parameters found at 78 stations (Fig. 1.). The results show more or less strong and complex correlations between environmental variables prevailing in the Pomeranian Bay (Table 1). Water depth correlates significantly ($p < 0.001$) positively and highest with salinity and sedimentary organic content ($p < 0.01$). Permeability, on the other hand, shows significantly ($p < 0.01$) negative correlations with depth. The same applies to median grain size ($p < 0.01$) which is also significantly ($p < 0.01$) negatively correlated with salinity. Salinity correlates significantly ($p < 0.001$) positively with the organic content of sediments which in turn shows significantly ($p < 0.001$) negative correlations with all other sediment characters like median grain size, sorting and permeability. Permeability eventually correlates significantly ($p < 0.001$) positively with median grain size.

3.4. Partial correlation and path analysis

In order to evaluate existing coherencies among environmental parameters, and to assess the primary descriptor predicting all other environmental variables in the Pomeranian Bay, a partial correlation analysis (path analysis) was conducted according to the methods described in Legendre and Legendre (1998). Therefore all possible and meaningful three-variable combinations were built from a matrix of partial correlation coefficients calculated for 6 environmental parameters sampled at 78

stations (Fig. 1) and tested (over 50 single matrices, not presented). Depth was found as the primary descriptor for salinity, organic content and, to a small degree, for median grain size. Median grain size again directly controls sorting and permeability. The organic content affects the median grain size, sorting and permeability (interstice-blocking). Sorting again affects permeability.

3.5. Cumulative distribution curve analysis

The effect of depth as the primary descriptor on all environmental descriptors and, as a consequence, on species distribution was analysed by means of testing cumulative frequency distributions of the primary predictor versus species abundance (Fig. 3). Congruency between the cumulative distribution curve of a species and an environmental descriptor is deemed to be a measure of dependency among them (Jongman et al., 1987). For all species with a calculated Kolmogorov-Smirnoff coefficient $D \leq D_{\text{critical}}$ ($D_{\text{critical}} = 0.14$) such a dependency can be rejected with $p = 0.005$ (Sachs, 1997). This applies to *Hediste diversicolor* ($D = 0.09$) only, a species colonising the Pomeranian Bay apparently homogeneously and completely independent from depth. Some others, like *Hydrobia ulvae* ($D = 0.15$), *Macoma balthica* ($D = 0.16$), *Marenzelleria neglecta* ($D = 0.15$), *Tubifex costatus* ($D = 0.16$), rank as only slightly depth-dependent species. Often, the depth class showing the highest difference among the cumulative distribution curves can be regarded as an indicative value in terms of a favoured depth range for species settling here. In general, the position of the species curve in relation to the depth curve gives information about the preferred depth range. Lies the species curve above the curve for depth the species settles in more shallow waters. This is obvious for *Bathyporeia pilosa*, *Cerastoderma glaucum*, *Hydrobia ventrosa* and *Streblospio dekhuyzeni*. Others, like *Bylgides sarsi*, *Diastylis rathkei*, *Halicryptus spinulosus* and *Tubificoides benedii* prefer the deeper areas of the Bay. For *Scoloplos armiger*, water depths shallower 20 m seem to be a real settling barrier in the Pomeranian Bay.

3.6. Principal component analysis (PCA)

The usage of only one fraction of all available principal axes for analysis will reduce interfering background noise contained in the data. Like in our study, points (sampling stations) with same variances represent equal abundance characteristics. Kriging of these points allows defining areas with distinct benthic communities. The corresponding correlation biplot is also given (Fig. 4). The first and

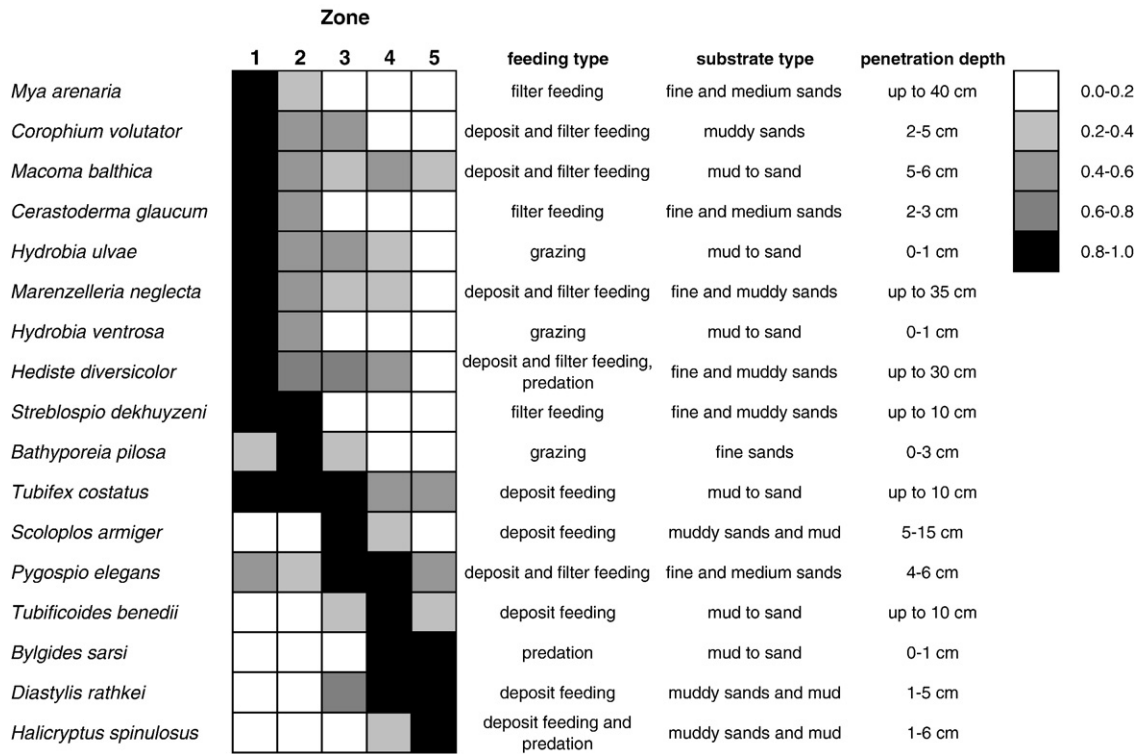


Fig. 5. Display of the shift in benthic assemblage of 17 species over all zones (Fig. 4, left side). Mean abundance of single species was calculated as a percentage of total abundance per zone and normalized to 1. The feeding type, preferred substrate type and the penetration depth of each species is given.

second principal components together account for 61% of the total variance (first principal axis: 39%, second principal axis: 22%). The position of the species in the correlation biplot clearly indicates the prevailing correlations between them. In this respect, *B. pilosa* and *T. benedii* seem to represent some kind of “ecological antagonists” whereas all other species can be regarded as

“intermediate stages” between these two extremes. Projection of the interpolated variances for the 1st principal components on a map of the Pomeranian Bay revealed five areas which clearly differ in their benthic species composition (Fig. 4, left). Additionally, the 2nd principal components were also subjected to kriging and projected separately (Fig. 4, right). Variances of species

Table 2

Minimum/maximum values of environmental parameters and average abundance of the most common species at benthic sample stations in the 5 zones shown in Fig. 4 (left)

Parameters	Zones				
	1	2	3	4	5
water depth [m]	8–15	4–16	7–26	11–27	15–32
Salinity [psu]	7.2–7.9	5.7–8.0	6.2–13.8	7.2–11.4	7.5–12.4
Median grain size [µm]	178–191	110–201	80–335	107–348	107–270
Permeability [10^{-6} cm s ⁻¹]	13.5–16.8	9.6–10.0	10.7–31.9	11.5–49.4	4.01–11.7
Sorting [Folk and Ward]	0.4–0.5	0.3–0.7	0.3–1.0	0.3–1.4	0.4–0.6
TOC [%]	0.2–0.3 <i>H. ulvae</i> (6717 ind. m ⁻²)	0.1–3.1 <i>H. ulvae</i> (3620 ind. m ⁻²)	0.1–1.5 <i>H. ulvae</i> (2710 ind. m ⁻²)	0.2–9.3 <i>P. elegans</i> (1637 ind. m ⁻²)	0.2–9.3 <i>P. elegans</i> (635 ind. m ⁻²)
Most abundant species per zone (average abundance)	<i>M. arenaria</i> (4168 ind. m ⁻²)	<i>M. arenaria</i> (1171 ind. m ⁻²)	<i>P. elegans</i> (1251 ind. m ⁻²)	<i>H. ulvae</i> (1085 ind. m ⁻²)	<i>M. balthica</i> (237 ind. m ⁻²)
	<i>C. glaucum</i> (1158 ind. m ⁻²)	<i>M. neglecta</i> (645 ind. m ⁻²)	<i>M. neglecta</i> (367 ind. m ⁻²)	<i>M. balthica</i> (395 ind. m ⁻²)	<i>T. benedii</i> (64 ind. m ⁻²)
	<i>M. neglecta</i> (1136 ind. m ⁻²)	<i>B. pilosa</i> (544 ind. m ⁻²)	<i>M. arenaria</i> (298 ind. m ⁻²)	<i>T. benedii</i> (389 ind. m ⁻²)	<i>T. costatus</i> (57 ind. m ⁻²)

Table 3

Highest Spearman rank correlation coefficients (ρ_{normal} ; $\rho_{\text{depth-detrended}}$) from BIO-ENV procedure based on Spearman rank correlation calculated separately between a $\sqrt{\cdot}$ -transformed species-based similarity matrix (12 species, Bray–Curtis similarity) and two matrices of k tested environmental factors/-combinations sampled at 78 sampling stations

K	factor /-combinations	ρ_{normal}	factor /-combinations	$\rho_{\text{depth-detrended}}$
1	a	0.465	d	0.447
2	a, c	0.552	c, d	0.462
3	a, c, d	0.573	b–d	0.489
4	a–d	0.576	b, d–f	0.485
5	a–d, f	0.579	b–f	0.476
6	a–f	0.569	-	-

Factor matrix 1 (ρ_{normal}): 6 factors, z-transformed, simple euclidean distance, Factor matrix 2 ($\rho_{\text{depth-detrended}}$): standardised residuals of 5 environmental factors detrended from depth by polynomial regression, simple euclidian distance. The environmental factors (a: water depth; b: near-bottom salinity; c: median grain size; d: organic content; e: sorting; f: permeability) associated to Spearman’s correlation coefficients (ρ_{normal} ; $\rho_{\text{depth-detrended}}$) are given.

associated with the first principal axis are responsible for the zonation (Fig. 4, left) whereas, due to the orthogonally rotated and maximised variances along main axes in a PCA, species variances along the second principle axis give another picture (Fig. 4, right). First axis principal components seem to divide the Bay in a North-West direction, second principal components apparently do it along the South-West axis. Though the calculation rests solely upon species abundance, it clearly indicates different environmental conditions such as the bottom morphology of the Pomeranian Bay (Figs. 1 and 4). The assemblage of selected species over all 5 zones indicated by the interpolation of the 1st principal components (Fig. 4, left) is graphically displayed and the autecology of species roughly described (Fig. 5). A steady shift in

benthic species from an assemblage characterized by molluscs and polychaetes to a more polychaete/oligochaete dominated community over the different zones can clearly be seen. The different environmental conditions prevailing in each zone are described in terms of minimum and maximum values for all abiotic parameters regarded in Table 2. Here, the most common species per area are named and their average abundance is given.

3.7. Link between biotic and environmental patterns (BIO-ENV procedure)

The correlation factors calculated via BIO-ENV are given in Table 3. In the BIO-ENV analysis of the z-transformed matrix of 6 environmental parameters, the

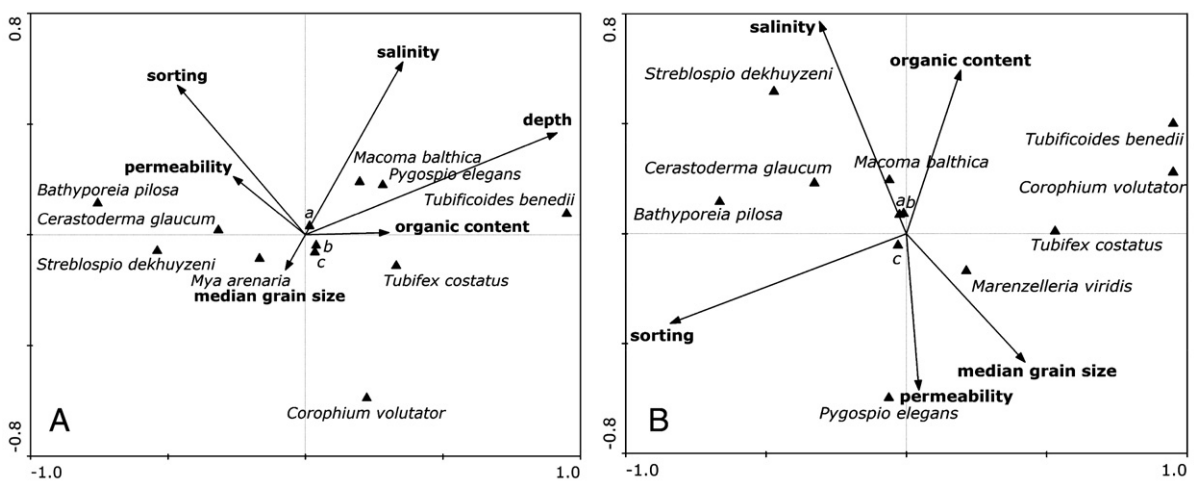


Fig. 6. Results for two separately calculated canonical correspondence analyses (CCA) of macrobenthic species abundance data (12 Species) and corresponding environmental factors sampled at 78 stations. Figure A (left side): CCA calculated for $\sqrt{\cdot}$ -transformed abundance data and z-transformed abiotic matrix of 6 environmental factors. Species situated close to the center of the biplot are a) *H. ulvae*, b) *M. arenaria*, c) *H. diversicolor*. B (right side): CCA calculated for $\sqrt{\cdot}$ -transformed abundance data and matrix of standardised residuals of 5 abiotic factors detrended from depth. Species situated close to the center of the biplot are a) *H. diversicolor*, b) *H. ulvae*, c) *M. neglecta*.

single abiotic factor which is associated best with the observed species distribution in the Pomeranian Bay was the water depth. However, its correlation factor was outranked by nearly all other variables calculated for factor combinations. With a Spearman's rank coefficient of about 0.465, depth alone seems to be responsible for almost 80% of the total similarity between biotic and abiotic matrices. Adding more factors, the correlation of 0.465 increases only about 0.114 up to 0.579 for a 5-factor combination of water depth, salinity, median grain size, organic content and sorting. For the

environmental matrix undetrended from water depth, this factor combination seems to describe best the benthic community structure which occurs in the Pomeranian Bay. Noticeably, the variable water depth can be found among almost every tested factor combination, almost always accompanied by salinity. As for the Spearman rank correlation between the biotic and the detrended abiotic matrix, an entirely different picture emerges. Here, the organic content accounts for over 90% of the calculated similarity. By adding other factors to the matrix, only a slight increase in similarity

Table 4

Results for two separately calculated canonical correspondence analyses (CCA) including the results of Monte-Carlo permutation test of macrobenthic species abundance data (12 Species) and corresponding environmental factors sampled at 78 stations

A: CCA–z-transformed abiotic matrix

	Axis 1	Axis 2	Axis 3		
Eigenvalue	0.129	0.024	0.018		
Species-environment correlations	0.826	0.528	0.572		
Cumulative percentage variance					
Of species data	24.80	29.4	32.8		
Of species-environment relation	70.9	83.9	93.6		
Environmental variable	Inter-set correlations with			Marginal effects	Conditional effects
	Axis 1	Axis 2	Axis 3		
Depth	0.755	0.195	-0.015	11% (p<0.001)	11% (p<0.001)
Sorting	-0.385	0.285	-0.217	4% (p<0.001)	3% (14%) (p<0.001)
Salinity	0.292	0.330	0.389	3% (p<0.001)	2% (16%) (p<0.001)
Organic content	0.250	0.004	0.275	2% (p<0.001)	1% (17%) (p<0.001)
Median grain size	-0.061	-0.067	-0.147	2% (p<0.001)	1% (18%) (p<0.001)
Permeability	-0.217	0.111	-0.206	1% (p<0.001)	0% (18%) (p<0.001)

B: CCA - matrix of residuals detrended from depth

	Axis 1	Axis 2	Axis 3		
Eigenvalue	0.129	0.024	0.018		
Species-environment correlations	0.826	0.528	0.572		
Cumulative percentage variance					
Of species data	24.80	29.4	32.8		
Of species-environment relation	70.9	83.9	93.6		
Environmental variable	Inter-set correlations with			Marginal effects	Conditional effects
	Axis 1	Axis 2	Axis 3		
Sorting	-0.364	-0.188	-0.109	3% (p<0.001)	3% (p<0.001)
Salinity	-0.134	0.445	0.047	2% (p<0.001)	1% (4%) (p<0.001)
Organic content	0.084	0.343	0.093	2% (p<0.001)	2% (6%) (p<0.001)
Median grain size	0.183	-0.269	0.266	1% (p<0.001)	1% (7%) (p<0.001)
Permeability	0.019	-0.328	0.283	1% (p<0.001)	0% (7%) (p<0.001)

Inter-set correlations between the first 3 canonical axes and environmental variables are presented. Marginal effects describe percentage variance explained (percentage of the total variance in the species data explained) by using each environmental variable as the sole predictor. Conditional (unique) effects describe variance explained by each environmental variable with the variable(s) already selected treated as covariable(s) based on forward selection. Environmental variables are listed by the order of their inclusion in the forward-selection model. Subtable A: CCA calculated for $\sqrt{\sqrt{}}$ -transformed abundance data and z-transformed abiotic matrix of 6 environmental factors. Subtable B: CCA calculated for $\sqrt{\sqrt{}}$ -transformed abundance data and matrix of standardised residuals of 5 abiotic factors detrended from depth.

can be observed. The factor combination which is linked best with the biotic matrix consists of salinity, median grain size and the organic content of the sediment.

3.8. Canonical correspondance analysis with Monte Carlo permutation

In addition to the BIO-ENV procedure, a CCA was calculated for matrices of 78 sampling sites (Fig. 1) with $\sqrt{\sqrt{\cdot}}$ -transformed abundance data of 12 species and corresponding z-transformed environmental data (Fig. 6, A) and, separately, with an environmental data matrix of standardised residuals of 5 environmental variables and 78 stations (Fig. 6, B). The Biplot (Fig. 6, A) and the output from the Monte-Carlo permutation test (Table 4) clearly depict the dependencies among environmental factors. In this environment the species are arranged according to their ecological optima. The first and second CCA axes together account for ca. 84% of the relations between species and environmental conditions, highest correlated along the first CCA axis. Water depth shows the highest correspondence to the first CCA axis followed by salinity and organic content whereas all other factors are negatively correlated. With the second CCA axis only median grain size shows a negative correlation, all other environmental factors are positively correlated. Depth and sorting together account for 16% of the overall variance among the environmental variables. In this setting, *B. pilosa* shows a high affinity to well sorted and permeable sediments. This applies to *S. dekhuyzeni* and *C. glaucum* as well but to a lesser degree. *C. volutator* and *T. benedii* prefer higher amounts of organic carbon in the sediment than *S. dekhuyzeni* and *C. glaucum*. *B. pilosa* seems to avoid these sediments completely. With respect to water depth, *T. benedii* occurs in deeper areas of the Pomeranian Bay whereas *T. costatus*, *C. volutator*, *P. elegans* and *C. glaucum* can be found in intermediate depths. *B. pilosa* and *S. dekhuyzeni* on the other hand prefer shallow waters. Species arranged towards the center of the plot, e.g. *C. glaucum* and *P. elegans*, either are unrelated to the environmental axes or find their optimum here. Other species such as *H. ulvae*, *M. neglecta* and *H. diversicolor* are situated in the center of the plot and represented by lower case letters (a, b, c). Vice versa, species arranged more towards the border of the plot, e.g. *B. pilosa*, *C. volutator* and *T. benedii*, can be regarded as “specialists” with reference to certain environmental parameters.

The biplot of the CCA calculated for species abundance data and environmental factors detrended from depth (Fig. 6, B) shows a similar configuration of

species along the ecological vectors. But there are differences. First, the space of environmental vectors seems more spread and is able to give a more detailed picture of the abiotic background on species-environment interactions. The first two axes are responsible for the exact amount of species environment relations as it was calculated for the first CCA biplot. Here, the first CCA axis is positively correlated with median grain size. Sediment sorting and salinity correlate negatively with the first axis. Permeability and organic content show only weak correlations. All environmental factors are correlated stronger with the second than with the first CCA axis. And in this ecological space, the species seem to behave in a slightly different way. *M. neglecta* has moved to the center of the biplot whereas *M. arenaria* has moved slightly outwards. *S. dekhuyzeni* formerly associated with low organic content and low salinity, now seems to prefer higher amounts of both factors. The species *P. elegans* is associated with high values of organic content and salinity in CCA biplot A, in CCA biplot B this species prefers high permeable and good sorted sediments of low organic content. However, both CCA biplots show an environment strictly divided into deep (lower permeability, bad sorting, high organic content, increased salinity) and shallow (good sorted, finer grained and more permeable substrate with low organic content), areas of the Pomeranian Bay.

4. Discussion

4.1. Models

The present study was the first attempt towards a benthic – abiotic interaction model using a complex data set of recent investigations in the Pomeranian Bay. Such model allows to predict better on how and to what extent natural or anthropogenic influences affect benthic community assemblages not only in the Pomeranian Bay but other areas of the Baltic Sea. However, an exploratory statistical description of the prevailing ecological structure of the observations made on site always is the indispensable first step (Bourget and Fortin, 1995). The extraction of patterns of benthic community distributions using large-scale studies is characterized by a large number of data points randomly sampled over long distances and in irregular spatial intervals. A task not easily solved by using only one statistical method. We therefore considered the following hierarchical approach as an appropriate method of resolution: i) detection of induced spatial dependencies, ii) examination of the environmental framework, iii) statistical description of patterns in environmental and

species data matrices, iv) combination of abiotic and biotic matrices in order to isolate abiotic factors responsible for species assemblages and distributions.

4.2. Induced spatial dependences

The results of the statistical analyses using spatially and temporally distributed data may be severely biased either by spatio-temporal autocorrelation (Legendre, 1993; Diniz-Filho et al., 2003) or forcing of strong gradients (Bourget et al., 1994). To avoid this, the data used in our analysis were tested on autocorrelation beforehand and the results obtained were taken into account in further analysis. Strong gradients can monopolise much of a statistical analysis (Bourget et al., 2003) and should be removed before analysis unless it is the stated aim to explore the influence of this particular gradient (Legendre and Legendre, 1998). In our case we discovered a strong gradient of depth along the North-South axis of the Bay. Correlation analysis revealed a complex framework of abiotic interactions and simply removing one part possibly would make it impossible to see the whole picture. Here, we have chosen a compromise and detrended the abiotic matrix but did use the untreated data set as well as initial data applied in statistical analysis. To our knowledge, this is the first study which takes spatial autocorrelation and trend into account for this kind of analysis in the Baltic Sea.

4.3. Environmental framework

As calculated by correlation analysis, a complex framework of inter-environmental relationships shapes the ecological background of the Pomeranian Bay. To utilize this knowledge for further interpretation, taking a closer look on the prevailing environmental conditions in the study area is indispensable. Due to prevailing wind and wave conditions, saline water inflows from deeper areas of the Bay and fresh water from the coastal river runoff no homogeneous salinity zonation could develop. The deeper areas of the southern Baltic as Sassnitzrinne, Arkona and Bornholm Basin are the main accumulation areas for fine particles with input of high organic material from the Pomeranian Bay (Kuhrts et al., 2006). This explains the apparent correlation between salinity and organic content, i.e. with increasing water depths and equally rising salinity, the content of organic carbon in the sediment also increases. With increasing amounts of fine particles at the sea bottom, permeability of the sediment in turn decreases rapidly because of the blocking of the interstice (Forster et al., 2003). Due to the glaci-fluvial and glacio-aeolian genesis of the Bay,

median grain size and sorting are merely modified by the hydrography, but not created.

4.4. Pattern analysis

In order to identify environmental factors responsible for benthic species distribution from our complex set of ecological data, we first analysed the patterns contained in the data set of species abundance. To detect differences in community structure and to estimate the degree of variations in environmental conditions, application of ordering techniques is the best alternative because they are more reliable than numerical classification methods, e.g. clustering techniques (Clarke and Warwick, 1998; Legendre and Gallagher, 2001). This proved to be true, since a valid (evaluated with an ANOSIM) and sufficiently detailed zonation could not be obtained by clustering of species abundance data (not presented). The projection of the first principal components, calculated by a PCA of selected species abundance data, allows a division of the Pomeranian Bay into 5 different zones with specific benthic community compositions with their boundaries running almost exactly along the bathymetric morphology of the Bay's seafloor. Thus, the computed zonation divides the benthic realm of the Pomeranian Bay into shallow and deep water communities, inhabiting areas of similar sediment composition (Oder Bank and Greifswalder Bodden Sill) on both sides of the Bay and areas of high and low water depths and likewise organic enrichment (Arkona Basin and Oder River mouth) in the North and South. The distribution of the species in the PCA biplot provides a clear picture of interspecific correlations. In this reduced space, *Tubificoides benedii* (see Fig. 7, right picture) opposes *B. pilosa* (see Fig. 7, left picture), its autecological counterpart. Both species can be regarded as representatives of two extreme environmental conditions, with the ecological preferences of all other species examined distributed in between – a picture clearly illustrated not only by the abundance plots but also by the results of the CCA analysis. The PCA biplot of the 2nd principal components shows a mere “orthogonal” impact of environmental factors along the North-South and East-West axis. From South to North the main river runoff discharges into the Bay with a high organic input, whereas in the eastern and western parts remains of ancient sandunes dominate the seafloor, formed by glacial and post-glacial processes. As a consequence, species preferring such conditions, i.e. high organic content (e.g. *T. benedii*) or good sorted fine sand with low organic content (e.g. *B. pilosa*), settle here. The distribution of the species regarded in this

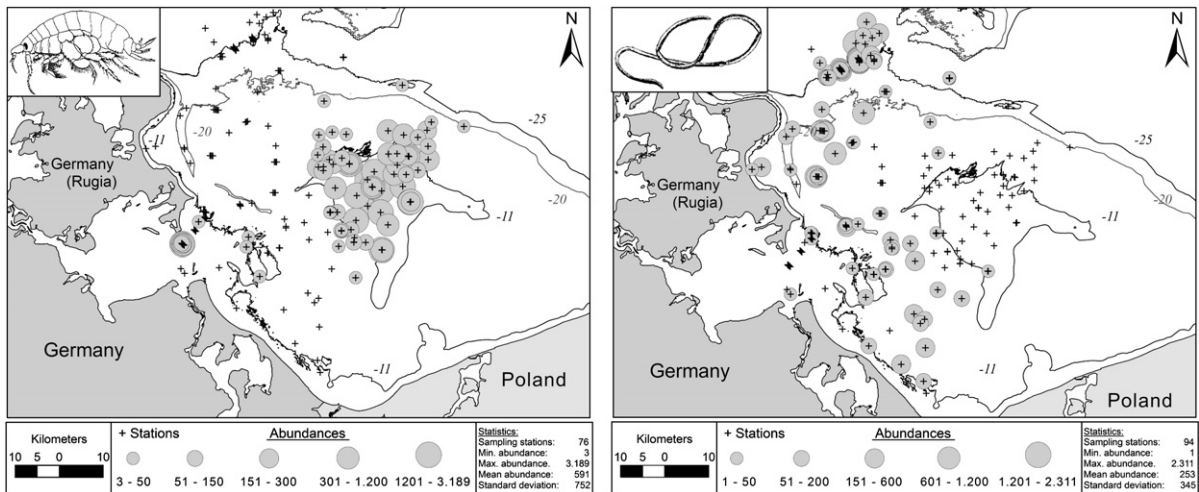


Fig. 7. Abundance plots of *Bathyporeia pilosa* (left) and *Tubificoides benedii* (right) for the time period 2003 to 2006.

study according to their presence in the different zones (see Fig. 5) shows mostly filter feeders in the shallow areas of the Bay. With increasing water depth, the species assemblage shifts from filter feeders and grazers toward communities dominated by deposit feeders and predators. According to Pearson and Rosenberg (1978), Rumohr et al. (1996) and O'Brien et al. (2003) such a benthic compartmentation over depth classes may be caused by food quality or at least food availability due to high sedimentation and resulting accumulation rates of organic material. Such accumulation of organic material occurs throughout the year in the Pomeranian Bay. It causes shifts in macrobenthic community assemblages and thus is not necessarily a result of eutrophication (Pearson and Rosenberg, 1978; Zettler et al., 2006). It seems more likely that such community shifts are typical for estuarine ecosystems, favoured by physical abrasion, accumulation or biological decomposition of the above mentioned organic enrichments. Together with other major environmental parameters, this most likely causes the periodically occurring “bouncing” of benthic zonation borders (Pazdro et al., 2001; O'Brien et al., 2003). As Bonsdorff (2006) pointed out, an anthropogenic input can cause significant changes in benthic communities but a shift from an oligotrophic towards an eutrophic state may also reflect a long-term successional status of the ecosystem.

4.5. Biotic – abiotic interactions

Canonical correlations and variance analysis mirror ecological preferences of the species colonising the available habitat. Combined with evaluating numerical analysis (e.g. Monte-Carlo permutation tests, ter Braak

and Smilauer, 1998) they provide a fairly accurate picture of biotic – abiotic interactions. By performing analysis with both the untreated and detrended data set of environmental factors we were able to detect the predictors of benthic assemblage and to compare both results to gain a better estimate of the trend. Especially for the BIO-ENV and CCA analyses differences between results for detrended and undetrended abiotic data and between the two techniques themselves were obvious. BIO-ENV is a technique based on the calculation of similarity matrices, which some authors (McGarigal et al., 2000 and others) reasoned can be misleading in case of strong gradients over long distances (e.g. salinity), forcing a slow and steady change in species composition. As in BIO-ENV, with the strong gradient of water depth the results are obvious. But without the trend, the best similarity between biotic and abiotic environment was caused by the organic content. With the strong correlation between organic content and water depth, this factor is likely to change drastically over relatively short distances, especially in the deeper areas of the Bay where organic material accumulates (Christiansen et al., 2002). The same applies to salinity, with highest values in the deeper parts of the Bay but in constantly lower amounts in shallow areas (Lass et al., 2001). Canonical correspondence analysis (CCA) is best applicable if the species response to a factor is unimodal (Legendre and Legendre, 1998). In the Monte Carlo simulation of CCA, calculated with exactly the same data sets used in BIO-ENV, the variable sorting was responsible for most of the variance. Not surprisingly, in path analysis salinity and organic content were the factors directly and solely influenced by water depth. The factor sorting

seems to be merely modified by median grain size which in turn is distributed more evenly throughout the Bay (Bobertz and Harff, 2004). This indicates that BIO-ENV seems to be better working with short and sharp gradients in contradistinction to CCA which most likely prefers distinct but uniformly continuous species response. Unimodal species response has been in accordance with the continua concept (Pearson and Rosenberg, 1978; Gray, 1984) where community structure changes continuously along environmental gradients, each species having its optimum at a different point of the gradient. Regarding this response, the CCA of detrended abiotic data depicts the autecologic behaviour of species more detailed than the CCA with untreated ecological parameters. Here, the length of factor axes, representing their influence, is almost equal. By comparison of the CCA biplots, the influence of depth on all other factors becomes clear. An example gives the comparison of the results for two species: *B. pilosa* and *T. benedii* are far apart in the spatial and autecological sense (Fig. 7). These two species are situated furthest apart in both CCA biplots (Fig. 6., A, B). *B. pilosa*, a coast-dwelling, sandlicking amphipod which grazes diatoms off the surface of sand grains (Nicolaisen and Kannevorff, 1969; Sundbäck and Persson, 1981) inhabits the shallow areas of the German Part of the Bay, the Oder Bank and the Greifswalder Bodden Sill, all sea-bottom elevations of post-glacial origin (see Fig. 7, left picture). They consist of well sorted fine sand, deposited and sorted here by postglacial aeolian processes. Wind and wave energy induce currents strong enough to vent these fine grained sediments and to keep them organic-poor through abrasion. In sharp contrast, the euryoec and euryhaline deposit feeder *T. benedii* is most abundant in sediments rich in nutrients and organic carbon which form a trail along the North-South axis of the Pomeranian Bay, formed by the deposition of sedimented fine material, discharged by the Oder River in great amounts (ca. 39 kt year⁻¹ total nitrogen, ca. 3.1 kt year⁻¹ total phosphorus, Pastuszak et al., 2005). For this opportunistic oligochaete, mass reproductions in areas with high accumulation rates of organic carbon in sediments are known (Diaz, 1984). Such sediments are distributed from the Oder River mouth up to the northwest and along the submerged ancient riverbed of the Oder, the Sassnitzrinne, all the way to the Arkona Basin. The preference of *T. benedii* for impermeable silty sediments seems to originate from his apparent tolerance of hydrogen sulphide occurrence and oxygen deficiency (Giere et al., 1999). The environmental preferences of *B. pilosa* and *T. benedii* are very special and this is clearly illustrated by the CCA results for the undetrended factor matrix. However, there are inconsistencies in the

autecological needs illustrated for *B. pilosa* by the CCA analysis of the detrended abiotic data. In this biplot, *B. pilosa* seems fairly uninfluenced by organic content which is regarded as an “switch-off” parameter even in small quantities for this species. Moreover, the association with high permeable sediments stated by the CCA – biplot of untreated abiotic parameters seems to have vanished. Regarding the functioning of CCA analysis, this could be caused by the simple “yes or no” response of *B. pilosa* to this environmental parameters. This makes the importance of specialised knowledge clear concerning species autoecology for the interpretation causal coherencies when using statistical results (Sachs, 1997).

4.6. Factor identification

As already discussed for BIO-ENV and CCA, the benthic colonization of the species regarded in this analysis is associated with depth, since the main physical forcings influencing species distribution are mainly driven by this primary descriptor. The depth-dependency of benthic species distribution is also manifested in the results concerning the estimated cumulative curves for depth versus selected species abundances (Fig. 3). The indicative value for the depth-mode of certain species can be estimated simply by looking for the highest difference between abundance and depth curve. Notably, most species inhabiting shallow parts of the Bay have their mode in depth class 2 (8–11.5 m). That is simply attributed to the marked elevation of the Oder Bank and the Greifswalder Bodden Sill, rising in some places from about 15 m water depth up to 7 m depth within a few meters. This represents an insurmountable barrier for many species, even more as the environmental conditions change drastically along the slope within short distance. If considering the fact that wind and wave driven currents periodically sweep the surface of the Bank (Bobertz and Harff, 2004), it is clear that mainly endobenthic species adapted to this conditions like *B. pilosa*, *Streblospio dekhuyzeni*, *Hydrobia ventrosa* and *Marenzelleria neglecta* find their optimum here.

5. Conclusions

As already pointed out, environmental parameters describing sediment characteristics such as organic content, sorting or permeability seem to be controlled primarily by water depth. Since this factors were found to cause highest similarity and variance between biotic and abiotic parameter, water depth could even be described as

a “masterfactor”. It is likely, through its impact on all other factors, to be mainly responsible for the zonation of the benthic species studied. Such depth-dependency of environmental factors and benthic zonations is not new, it has already been observed in other marine habitats as well (e.g. Kube et al., 1996; Bonsdorff et al., 2003; Bonsdorff, 2006; O’Brien et al., 2003; Perus and Bonsdorff, 2004; Kröncke et al., 2004; Warzocha, 1995; Wildish, 1977; Zettler et al., 2006). Often salinity is regarded as the one and only primary descriptor in brackish estuarine ecosystems. Our study disputes this assumption even though we have tested this so far only for the Pomeranian Bay. Considering that all 12 species used in the ordination techniques are regarded as euryhaline and that the salinity doesn’t vary strongly in center of the Pomeranian Bay, the apparent influence of salinity as the main predictor on the benthic assemblage becomes insignificant. By using other species and examining the species-environmental relationships over a greater distance along a latitudinal gradient, the salinity-induced stress on species distribution would be dominant and our results might differ (Bonsdorff, 2006).

Based on the application of a set of well established methods our study clearly demonstrates the need to analyse species’ relationships in gradient systems such as the Baltic Sea where their patterns of distribution are strongly and directly coupled to abiotic processes. Though the represented community structure may represent only a momentary state of the benthic colonization in the Pomeranian Bay, it can be used to assess biotic-environmental processes (Laine, 2003). By using different statistical methods these abiotic/biotic interactions were modelled allowing to extend our knowledge concerning ecosystem functioning, and provide a tool to assess natural and anthropogenic forced changes in species distribution. In a next step, species response curves, calculated on the basis of this study using an appropriate model (e.g. GAM or GLM model presented in CANOCO, ter Braak, 1988, 1989; Guisan et al., 2006) shall enable us to create a two-dimensional ecological model of the Pomeranian Bay in a GIS based approach, thus predicting species assemblages of 12 species by two-dimensional morphological, geological or hydrological data sets.

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