



# Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 1. Causal analysis

Mayya Gogina, Michael Glockzin, Michael L. Zettler \*

Leibniz Institute for Baltic Sea Research, Seestrasse 15, D-18119 Rostock, Germany

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## ABSTRACT

In this study we relate patterns in the spatial distribution of macrofaunal communities to patterns in near-bottom environmental parameters, analysing the data observed in a limited area in the western Baltic Sea. The data used represents 208 stations, sampled during the years 2000 to 2007 simultaneously for benthic macrofauna, associated sediment and near-bottom environmental characteristics, in a depth range from 7.5 to 30 m. Only one degree of longitude wide, the study area is geographically bounded by the eastern part of the Mecklenburg Bight and the southwestern Darss Sill Area. Spatial distribution of benthic macrofauna is related to near-bottom environmental patterns by means of various statistical methods (e.g. rank correlation, hierarchical clustering, nMDS, BIO-ENV, CCA). Thus, key environmental descriptors were disclosed. Within the area of investigation, these were: water depth, regarded as a proxy for other environmental factors, and total organic content. Distinct benthic assemblages are defined and discriminated by particular species (*Hydrobia ulvae*–*Scoloplos armiger*, *Lagis koreni*–*Mysella bidentata* and *Capitella capitata*–*Halicryptus spinulosus*). Each assemblage is related to different spatial subarea and characterised by a certain variability of environmental factors. This study represents a basis for the predictive modeling of species distribution in the selected study area.

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## 1. Introduction

The relative roles of the environment, competition, predation and chance in determining the composition of communities have been largely debated in animal ecology (Austin, 1987). Some main factors usually named as responsible for benthos distribution are: food supply, water salinity, oxygen concentrations, current energy, temperature, turbidity, substrate composition, sedimentation rates and bathymetry (e.g. Wildish, 1977; Wilson, 1991; Bromley, 1996; Olenin, 1997; Laine, 2003; Coleman et al., 2007). It is important that a heuristic approach is taken for both validation and iterative development of ecological models across a range of spatial scales. An exploratory statistical description of the prevailing ecological structure of the observations made on site is always the indispensable first step (Bourget and Fortin, 1995); it should also be supported by an improving mechanistic understanding (Thrush et al., 2003).

The following study can be referred to a comparatively fine spatial scale. Depending on the scale, different processes determine the spatial structure; therefore, inferences derived for one spatial scale cannot be extrapolated to another scale (Legendre and Legendre, 1998). Our results comprise a detailed analysis of benthic community

composition regarding near-bottom habitat characteristics of the area stretching through the Kadettrinne incision from the eastern Mecklenburg Bight to the southwestern Darss Sill area. The aim of the present investigation was to analyse the causal relations between benthic macrofauna and selected environment variables: water depth, near-bottom salinity and oxygen concentrations, total organic content, median grain size, as well as sorting, skewness, and permeability. An appropriate technique for predictive modeling of species distribution regarding the available abiotic data was defined and applied in Gogina et al. (2009–this volume). Additionally, the modeling results for selected species were mapped. Hence, the present work describes a causal analysis – a basis and a necessary first step towards the design of models able to predict species distribution.

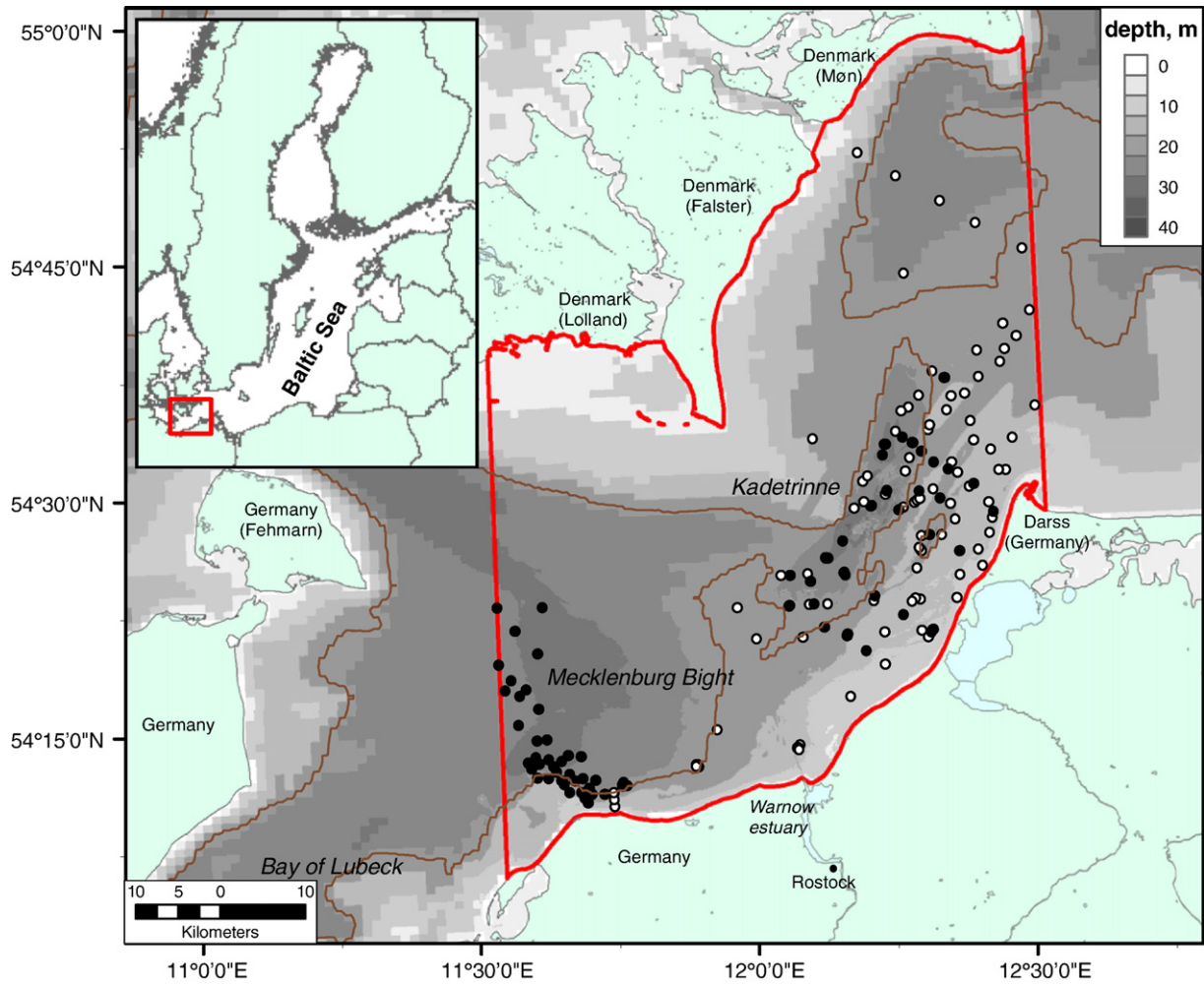
## 2. Materials and methods

### 2.1. Study area

Depending on the scale and region, salinity together with near-bottom oxygen concentration is often regarded among the major factors affecting the species richness and composition of macrozoobenthic communities (e.g. Olenin, 1997; Zettler et al., 2000; Laine, 2003). By defining the study area, we aimed to lessen the dominance of these two factors in the analysis to illuminate the impact of others. The study area is attached to the region of Mecklenburg Bight (Fig. 1) close to the very beginning of the Baltic salinity gradient and that is

\* Corresponding author. Present address: Department of Biological Oceanography, Baltic Sea Research Institute (IOW), Seestr. 15, D-18119 Rostock, Germany. Fax: +49 381 5197 440.

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



**Fig. 1.** Investigation area is bordered by the thick line, distribution of 208 sampling stations is presented; dots are stations covered with quantitative (abundance of benthic species) data; filled dots indicate 72 stations with a full set of data available for all eight abiotic variables. Thin line is the 18 m isobath which separates the two depth subareas of our region. Geographical data ESRI (1998); projection UTM on WGS84. The colour version of this figure is available online. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

why it is richer in macrofaunal species (with significant presence of both marine and brackish water species at the same time) than the inner, less saline, parts of the Baltic Sea.

The study area is assigned to the transition zone between the North Sea and the Baltic Sea. Barotropic and baroclinic gradients and local winds force currents that are controlled here by the bathymetry and stratification. Positive water balance caused by freshwater supply results in the outflow of brackish Baltic Sea water at the sea surface. Sea level differences forced by large scale winds drive the inflow of high saline Kattegat water into the transition zone. Density differences, mainly due to salinity, dominate the farther transport into the central parts of the Baltic. Local winds and thereby generated waves are important for vertical mixing in shallow waters. Particularly in summer, the thermal stratification stabilizes the water column and supports the salinity stratification, with halocline and thermocline occurring in the central part of the investigation area at around 12–16 m (Siegel et al., 2009). Generally, near-bottom salinity declines in the eastwards direction, dropping down in areas near the coastline due to the freshwater river runoff or the isolation from currents. Depending on the scale and region, salinity together with near-bottom oxygen concentration is often regarded among the major factors affecting the species richness and composition of macrozoobenthic communities. To lessen the dominance of those two factors and illuminate the effects of others

we restricted the area to reduce the variability of both factors in distinct depth-zones, whereas other factors are represented in wide ranges. Whereas the range of near-bottom salinity in the whole area is relatively high (99.5% of sampling points lie within a salinity range of 8.3–21.8 PSU), the variability in distinct depth-zones is lower (i.e. salinity varied from 9 to 16 PSU at approximately 75% of stations shallower than 18 m; and ranged from 15 to 22 PSU at the same percentage of stations below 18 m). The hypoxic events, connected with absence of oxygen-rich saline water inflows and formation of steady hydrographical stratification in the water column, run differently in various locations of the region and irregularly take place in the late summer–autumn period, e.g. in deepest parts of Mecklenburg Bight. However, they are not as frequent and their effect is not as dramatic (at least within the investigation time) and long-lasting as it is known for the deep basins of the Baltic Proper.

The study site ranges in the northwards direction approximately from 45 to 75 km and about 63 km in the eastwards direction. Within these boundaries the area amounts to about 4000 km<sup>2</sup>. With an average depth of 16 m (depth at sampling points ranges from 7.5 to 29.9 m) its water volume approximates 46 km<sup>3</sup> (data origin: this study). The sea floor is characterised mainly by postglacial sand and gravel deposits, with organic-rich silt-size sediments observed in the deepest parts of Mecklenburg Bight (Bobertz and Harff, 2004).

## 2.2. Macrobenthic sampling

Our data represents 208 stations, sampled over 8 years (2000–2007) simultaneously for benthic macrofauna, associated sediment and near-bottom environmental characteristics.

For 72 of the overall 208 stations a full set of abiotic variables considered is available. For macrofauna, 2 to 3 replicate samples per site were taken with a van Veen grab (0.1 m<sup>2</sup>, 10–15 cm penetration depth) and sieved on a 1.0-mm screen. Samples were preserved in 4% buffered formaldehyde–seawater solution. 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, 2008).

## 2.3. Hydrographic measurements

Hydrographic characteristics were measured simultaneously with macrozoobenthic sampling for most data points. At each station a water sample was taken by shipboard CTD (0.5 m above the sea floor). Oxygen content was determined by immediate potentiometric titration, near-bottom salinity was estimated by CTD as well and the depth at each station was measured and logged via shipboard sonar system. All abiotic variables considered are listed in Table 1.

## 2.4. Estimation of sediment characteristics

With regard to the sediment characteristics measurements (completed fully for 72 out of 208 stations), an additional grab sample was taken to extract the upper surface sediment layer ( $\leq 5$  cm) for the analyses. Grain size distribution was analysed using approximately 50 g of dried sediment, dry sieved on a RETSCH sieving machine (sieve set: 63  $\mu\text{m}$ , 75  $\mu\text{m}$ , 90  $\mu\text{m}$ , 106  $\mu\text{m}$ , 125  $\mu\text{m}$ , 150  $\mu\text{m}$ , 180  $\mu\text{m}$ , 212  $\mu\text{m}$ , 250  $\mu\text{m}$ , 400  $\mu\text{m}$ , 630  $\mu\text{m}$ , 2000  $\mu\text{m}$ ) and laser sizing (CILAS 1180 Laser Particle Analyser). Total organic content was measured as loss on ignition (3 h at 500 °C) of water-free material. Parameters describing cumulative grain size distribution as median grain size, sorting, and skewness were then calculated by using a skewed s-shape function, fitted to the cumulative grain size data with the least sum of squares method, applying a special fitting algorithm (the description is given in Bobertz and Harff, 2004). Permeability was estimated using the data of grain size distribution employing the relation derived by Krumbein and Monk (1942).

**Table 1**  
List of environmental parameters considered in the study.

Parameter	Units	N stations	Method
Water depth	m	208	Determined and logged with shipboard sonar
Near-bottom oxygen	ml/l	181	Sampling by shipboard CTD system 0.5 m above the sea bottom, oxygen content determined by immediate potentiometric titration
Near-bottom salinity	PSU	185	Salinity estimated by shipboard CTD system 0.5 m above the sea bottom
Median grain size	$\mu\text{m}$	110	Sieving, laser sizing
Total organic content	%	109	The total organic content was measured as loss on ignition (3 h at 500 °C) of water-free material
Sorting	phi	72	Derived from grain size distribution curve as described in Bobertz and Harff (2004)
Skewness	phi	72	Derived from grain size distribution curve as described in Bobertz and Harff (2004)
Permeability	darcy	72	Determined according to Krumbein and Monk (1942) using the data from median grain size analysis (see above)

Sampling, measurement and determination techniques and the number of stations with each parameter observed are given.

## 2.5. Statistical methods and data treatment

To focus the investigation on biotic/environmental interactions rather than on other aspects (e.g. energetic criteria vs. species development) only species abundance as a biotic variable was subjected to statistical analyses (Young and Young, 1998).

Since spatial distribution patterns of species are influenced by biological processes structured by physiography, they can be spatially autocorrelated—the location of sampling points in space influences the values of random variables (Legendre, 1993). We calculated the amount of spatial autocorrelation for 72 stations (abiotic data) and 208 sampling sites (species abundance data) via Morans's I index using ArcView 9.1 software (ESRI). To examine correlations between species abundance and corresponding environmental data, Spearman's rank correlation coefficients were evaluated. To analyse the structure of coherencies among environmental variables normal and partial Pearson correlation factors were also computed (SPSS Inc.). This disclosed a primary environmental descriptor. Its effect 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; Glockzin and Zettler, 2008).

For mapping purposes, methods of gradient analysis were complemented by numerical classification that allows to cut the continuum even if there are no distinctive boundaries (Leps and Smilauer, 2003). Ordination contributes to the detection of systematic patterns and can disclose transitional zones. Therefore, multivariate analysis was carried out by superimposing the results of group averaged hierarchical clustering based on Bray–Curtis similarities of 4th-root transformed abundance data for 208 stations on a non-metric multidimensional scaling (nMDS) surface. In this way, distinct benthic communities could be defined. Species responsible for classification were determined applying SIMPER exploratory analysis and visual re-examination of the modified data matrix whereupon benthic communities have been determined and described (PRIMER; Clarke and Warwick, 2001). Correlations between biological and environmental variables were examined via BIO-ENV procedure of PRIMER software (Clarke and Ainsworth, 1993) and canonical correspondence analysis (CCA) via CANOCO (ter Braak, 1986), applying the necessary data transformations (Legendre and Gallagher, 2001; Davis, 2002).

## 3. Results

### 3.1. Data reduction

A total of 240 species were identified at 217 sampling stations. For 9 of the sites no quantitative community assemblage data was available, reducing the number of analysed stations to 208. Polychaetes ranked first with 71 species, followed by the mollusca (56), crustacea (43), cnidaria (24), bryozoa (11), oligochaeta (9), nemertea (5), porifera (5), chordata (4), pycnogonida (3), echinodermata (2), kamptozoa (2), priapulida (2), arachnida (1), insecta (1), plathelminthes (1).

In order to employ various statistical methods, appropriate data sets were formed by applying the following steps: exclusion of all uncountable species, retention of strictly endobenthic species, removal of species with high patchiness that causes unreliable sampling (e.g. *Mytilus edulis*), and finally, extraction of all species with a frequency of less than 6% at all stations and species which account for less than 0.3% of total abundance over all stations (Legendre and Gallagher, 2001; Lozán and Kausch, 2004). Using those criteria together with a general knowledge of species' habitat preferences and habits, the most dominating species were extracted separately for each of the two depth subareas of our region. In the southwestern Baltic Sea at depths between 15 and 20 m, a transition zone with

substantial shift in community composition from shallow- to deep-water species occurs. There is no certain value defined as a boundary, but we had to decide the fixed limit value to work with the data, so the 18 m isobath was assumed to separate two depth subareas of our region in a proper way (Fig. 1). This formed a list of 29 species of interest, cited in Table 2.

Matrices of biotic data with abundance values of 29 species at 208 stations and a full set of all available 8 environmental variables for 72 stations were created.

Benthic sampling was carried out throughout the year, 38% of the stations were sampled during spring (March, April, May) and summer (June, August) periods, each, whereas 11% and 13% of samples were taken during autumn (September, October) and winter (January, February) periods, respectively. We were interested in general all-seasonal distribution patterns; therefore no seasonal harmonisation of data was carried out.

### 3.2. Spatial autocorrelation via Moran's I Index

For all abiotic variables defined at the 72 sampling stations (see Fig. 1) a positive autocorrelation is assumed and the hypothesis of a random distribution of stations should be rejected. The Index values range between 0.06 and 0.4, with Z values by far exceeding the confidence interval (2.78–14.8). The index values calculated for most of the 29 species sampled at the 72 stations range from  $-0.04$  to  $0.04$  with corresponding Z values between  $-1.14$  and  $2.15$ . Here, species abundance data appears to have a generally random pattern. Data point distribution of species *Cerastoderma glaucum*, *Gastrosaccus spinifer* and *Pygospio elegans* exhibit a slightly clustered pattern (index values 0.09 to 0.22) with Z scores slightly exceeding the confidence interval ( $p = 0.05$ ); for some taxonomic units, the Z score noticeably exceeds the confidence interval (e.g. for *Abra alba*, *Arctica islandica*, *Bylgides sarsi*, *Diastylis rathkei*, *Dipolydora quadrilobata*, *Halicryptus spinulosus*, *Mya arenaria* and *Polydora ciliata*). Moran's I

Index values calculated for the data set containing species abundance data sampled at 208 stations indicate nearly the same patterns for most species ( $-0.04$  to  $0.14$ ) with Z values by far exceeding the confidence interval ( $-3.01$  to  $12.77$ ). For this data set a positive autocorrelation is also assumed. However, the autocorrelation coefficients have possessed no values near  $\pm 1.0$ , that would indicate strong clustering or dispersion, for any variables of the datasets analysed. The obtained results rather indicate a slight tendency that has to be considered in further analyses and results interpretation.

### 3.3. Spearman's rank correlation

To gain an insight on how the underlying processes of biotic/abiotic interactions cause species distributions and benthic zoning, Spearman's rank correlation factors were calculated for 29 species along with 8 environmental variables (Fig. 2). Because of the formerly described positive autocorrelation, no significance levels but descriptions of weak or strong correlations are given here.

The strongest Spearman's rank correlations between species abundance and environmental variables were found for water depth and salinity. A particularly strong and positive correlation with depth was indicated for *B. sarsi*, *Trochochaeta multisetosa* and *A. alba*. Beside depth and salinity, total organic content ranged on third position regarding the number of strong correlations calculated. The highest positive correlations between species abundance and sedimentological parameters median grain size, skewness and permeability were found for *Macoma balthica*.

### 3.4. Multiple causality–correlation among environmental variables

Pearson's correlation coefficients are calculated considering all the available abiotic data for 208 stations (Fig. 1). Prior to the analysis, the data matrix was z-transformed to make the data dimensionless, thus avoiding problems with the different measuring units used. Calculated values indicate a complex and relatively strong mutual association between environmental parameters prevailing in this region of the Baltic Sea (Table 3).

After computing Pearson's correlation coefficients for the z-transformed abiotic matrix, path analysis was applied in accordance with the model analysis described in (Legendre and Legendre, 1998). Therefore, all possible three-variable combinations derived from the matrix of partial correlation coefficients were considered and tested (not presented here for brevity). Path analysis revealed water depth as a primary descriptor for all other environmental factors in our study area.

### 3.5. Cumulative distribution curve analysis

To analyse the effect of water depth as the primary descriptor on all other environmental factors and its consequential influence on the spatial distribution of benthic species and communities, cumulative frequency distributions of depth and species abundances were tested versus each other (Fig. 3). Cumulative histograms represent 9 depth classes in a range from 7.5 to 30 m with a bounding step of 2.5 m. As a measure of dependency, the congruency between cumulative distribution curves of species and an environmental variable was used. The sharp increase of deviation, for instance for *A. islandica* between depth classes 4 and 5 (15 to 20 m), indicates the range of maximum response of the species against depth. The depth-dependence hypotheses can only be rejected for bivalve *M. balthica* with the significance level assumed. Some other species, bivalves *Mysella bidentata*, *Astarte borealis*, *Corbula gibba* and polychaeta *Ampharete baltica*, can be considered as only slightly depth-dependant species. Settling preferences are often reflected by the position of the species curve against the depth curve: for those species favoring shallower waters, the cumulative abundance curve lies above the depth curve.

**Table 2**

List of 29 species under interest.

N	Group	Species	6-letter code	Dominating in
1	Bivalvia	<i>Abra alba</i>	Abralb	Deeper waters (>18 m)
2	Polychaeta	<i>Ampharete baltica</i>	Ampbal	Both depth regions
3	Bivalvia	<i>Arctica islandica</i>	Arcisl	Deeper waters (>18 m)
4	Bivalvia	<i>Astarte borealis</i>	Astbor	Deeper waters (>18 m)
5	Polychaeta	<i>Bylgides sarsi</i>	Bylsar	Both depth regions
6	Polychaeta	<i>Capitella capitata</i>	Capcap	Both depth regions
7	Bivalvia	<i>Cerastoderma glaucum</i>	Cergla	Shallow waters ( $\leq 18$ m)
8	Bivalvia	<i>Corbula gibba</i>	Corgib	Both depth regions
9	Cumacea	<i>Diastylis rathkei</i>	Diarat	Both depth regions
10	Polychaeta	<i>Dipolydora quadrilobata</i>	Dipqua	Both depth regions
11	Mysidacea	<i>Gastrosaccus spinifer</i>	Gasspi	Shallow waters ( $\leq 18$ m)
12	Priapulida	<i>Halicryptus spinulosus</i>	Halspi	Deeper waters (>18 m)
13	Polychaeta	<i>Hediste diversicolor</i>	Heddiv	Shallow waters ( $\leq 18$ m)
14	Oligochaeta	<i>Heterochaeta costata</i>	Hetcos	Shallow waters ( $\leq 18$ m)
15	Polychaeta	<i>Heteromastus filiformis</i>	Hetfil	Deeper waters (>18 m)
16	Gastropoda	<i>Hydrobia ulvae</i>	Hydulv	Both depth regions
17	Polychaeta	<i>Lagis koreni</i>	Lagkor	Both depth regions
18	Bivalvia	<i>Macoma balthica</i>	Macbal	Both depth regions
19	Bivalvia	<i>Mya arenaria</i>	Myaare	Shallow waters ( $\leq 18$ m)
20	Bivalvia	<i>Mysella bidentata</i>	Mysbid	Both depth regions
21	Bivalvia	<i>Parvicardium ovale</i>	Parova	Shallow waters ( $\leq 18$ m)
22	Polychaeta	<i>Polydora ciliata</i>	Polcil	Deeper waters (>18 m)
23	Polychaeta	<i>Pygospio elegans</i>	Pygele	Both depth regions
24	Polychaeta	<i>Scoloplos armiger</i>	Scoarm	Both depth regions
25	Polychaeta	<i>Spio goniocephala</i>	Spigon	Shallow waters ( $\leq 18$ m)
26	Polychaeta	<i>Terebellides stroemi</i>	Terstr	Deeper waters (>18 m)
27	Polychaeta	<i>Travisia forbesii</i>	Trafor	Shallow waters ( $\leq 18$ m)
28	Polychaeta	<i>Trochochaeta multisetosa</i>	Tromul	Deeper waters (>18 m)
29	Oligochaeta	<i>Tubificoides benedii</i>	Tubben	Both depth regions

Group, species name, abbreviation used in further analysis, and depth regions where species dominate are indicated.

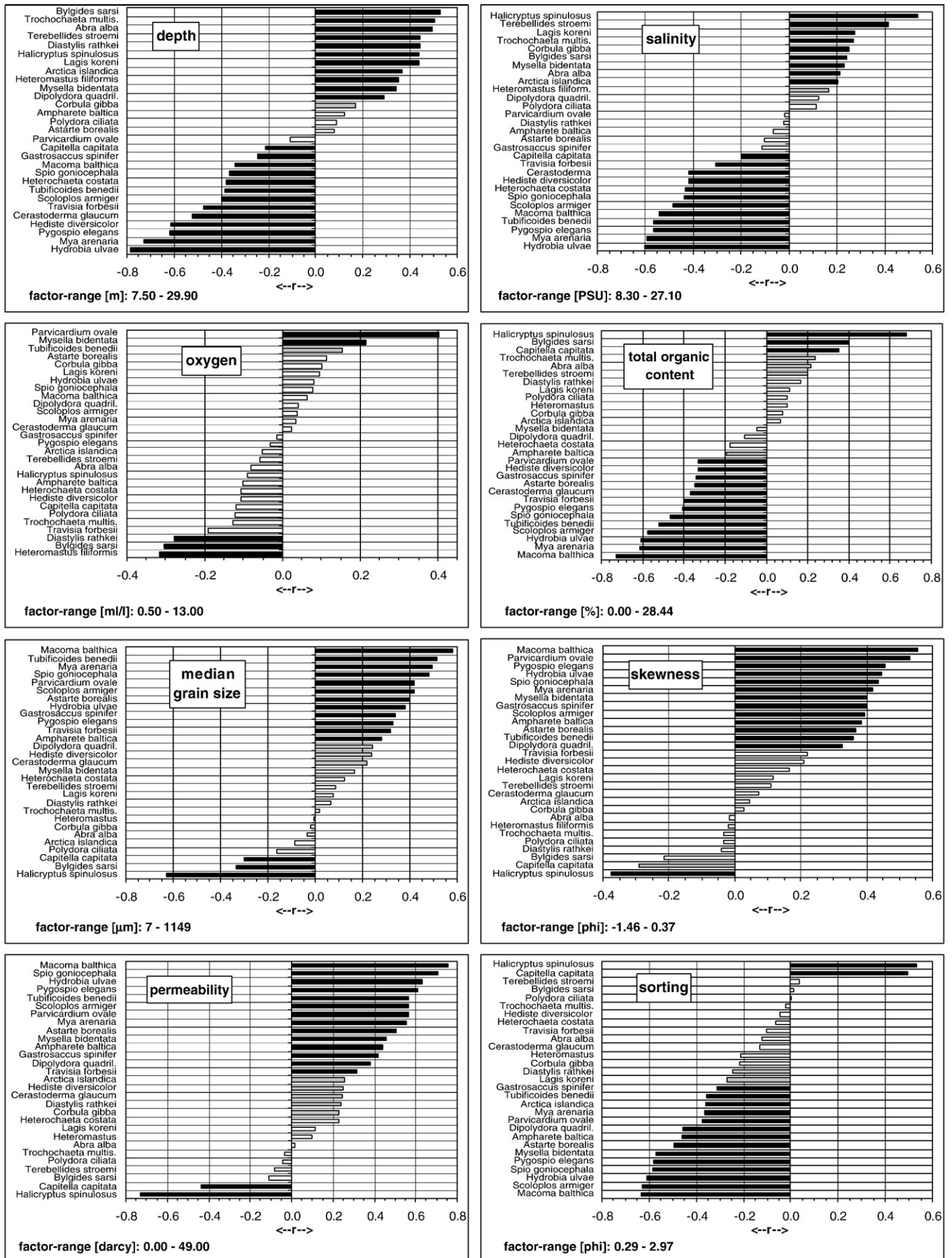


Fig. 2. Spearman's rank correlation factors calculated for 29 species along 8 environmental and sedimentological variables. Black and gray bars indicate significance levels of 0.01 and 0.05 (2-tailed), interpreted as strong and some correlation, correspondingly.

**Table 3**

Pearson correlation coefficients estimated for the full set of z-transformed environmental data sampled at 208 stations: sample size is indicated in brackets, coefficient values corresponding to  $p < 0.01$  are in bold font.

Environmental factors	Total organic content	Median grain size	Oxygen	Salinity	Depth	Sorting	Skewness	Permeability
Total organic content	1 (109)							
Median grain size	<b>-0.363</b> (109)	1 (110)						
Oxygen	-0.187 (109)	<b>0.262</b> (110)	1 (181)					
Salinity	<b>0.544</b> (109)	<b>-0.338</b> (110)	-0.082 (180)	1 (185)				
Depth	<b>0.670</b> (109)	<b>-0.354</b> (110)	-0.130 (181)	<b>0.597</b> (185)	1 (208)			
Sorting	<b>0.701</b> (72)	<b>-0.509</b> (72)	-0.269 (72)	<b>0.500</b> (72)	<b>0.608</b> (72)	1 (72)		
Skewness	-0.227 (72)	<b>0.439</b> (72)	.257 (72)	-0.226 (72)	<b>-0.319</b> (72)	<b>-0.460</b> (72)	1 (72)	
Permeability	<b>-0.549</b> (72)	<b>0.923</b> (72)	<b>0.305</b> (72)	<b>-0.574</b> (72)	<b>-0.747</b> (72)	<b>-0.521</b> (72)	<b>0.487</b> (72)	1 (72)
Factor unit	%	µm	ml/l	PSU	m	phi	phi	darcy
Factor range	0–28.44	7–1149	0.5–13	8.3–27.1	7.5–29.9	0.29–2.97	-1.46–0.37	0–49

The results described above fully correlate with the results of Spearman's rank correlation analysis.

### 3.6. Macrobenthic communities and their discriminating species

Before computing the similarity matrices, the data for the selected 29 species at 208 stations was 4th-root transformed to reduce the impact of the species with the highest abundances on the assessment of the community similarities (Clarke and Warwick, 2001). Hierarchical clustering analysis based on Bray–Curtis similarity and unweighted group average linking was then carried out to test the similarity among the species.

At the 35% similarity level, a division into three groups of sampling stations and one single site emerged. Results of hierarchical clustering analysis were supplemented by the nMDS ordination (Fig. 4, left). The inverse analysis with the grouping of species corresponding to a 15% similarity level is presented in Fig. 4, right.

The SIMPER tool of the PRIMER software (Clarke and Corley, 2006) combined with visual re-examination of the modified display of the original data matrix (Clarke and Warwick, 2001) is able to identify the species responsible for the defined clustering pattern. Thus, three main benthic macrofaunal communities were distinguished and allocated in the investigation area (Fig. 5).

Group a: *Hydrobia ulvae*–*Scoloplos armiger* community inhabited the area of the shallow sandy bottom along the coast. The water depth of the stations ranged from 7.5 to 18.9 m. Median grain size varied from 108 to 527 µm, sorting and skewness ranged from 0.57 to 1.12 and from -0.31 to 0.33 phi respectively, organic content was low (0 to 1.2% with mean value ( $\bar{x}$ ) of 0.4%). Hydrological conditions in the areas inhabited by this community were typical for shallow waters of the region: relatively low salinity (8.3 to 17.9 PSU), high oxygen content (3.0 to 12.9 ml/l, all values below 5 ml/l are dated by the August 2000). Other species numerically dominating in the community were the polychaete *P. elegans*, the bivalves *Macoma baltica* and *M. arenaria*, and the cumacean *D. rathkei*. The total number of species observed at the stations in the boundary of the community reached 111.

Group b: *Lagis koreni*–*M. bidentata* community occupied a deeper area, stretching from the south-west to the north-east (middle of the Kadetrinne and the Darss Sill), including the southern and northern parts of the Mecklenburg Bight. The shallowest stations were at 12 m, deepest—at 29.5 m. Sediments were characterised by median grain size of medium silt to fine sand, mainly moderately sorted, the average organic content was 2.5%, ranging from 0.2 to 17.4%. Environmental conditions were defined by higher salinity (9.9 to 27.1,  $\bar{x}$  = 16.3 PSU) and variable oxygen conditions (0.5 to 13.0,  $\bar{x}$  = 6.5 ml/l).

In terms of both occurrence and abundance, the cumacean *D. rathkei* and the bivalve *A. alba* were also characteristic for this community. In total, 137 taxa were recorded.

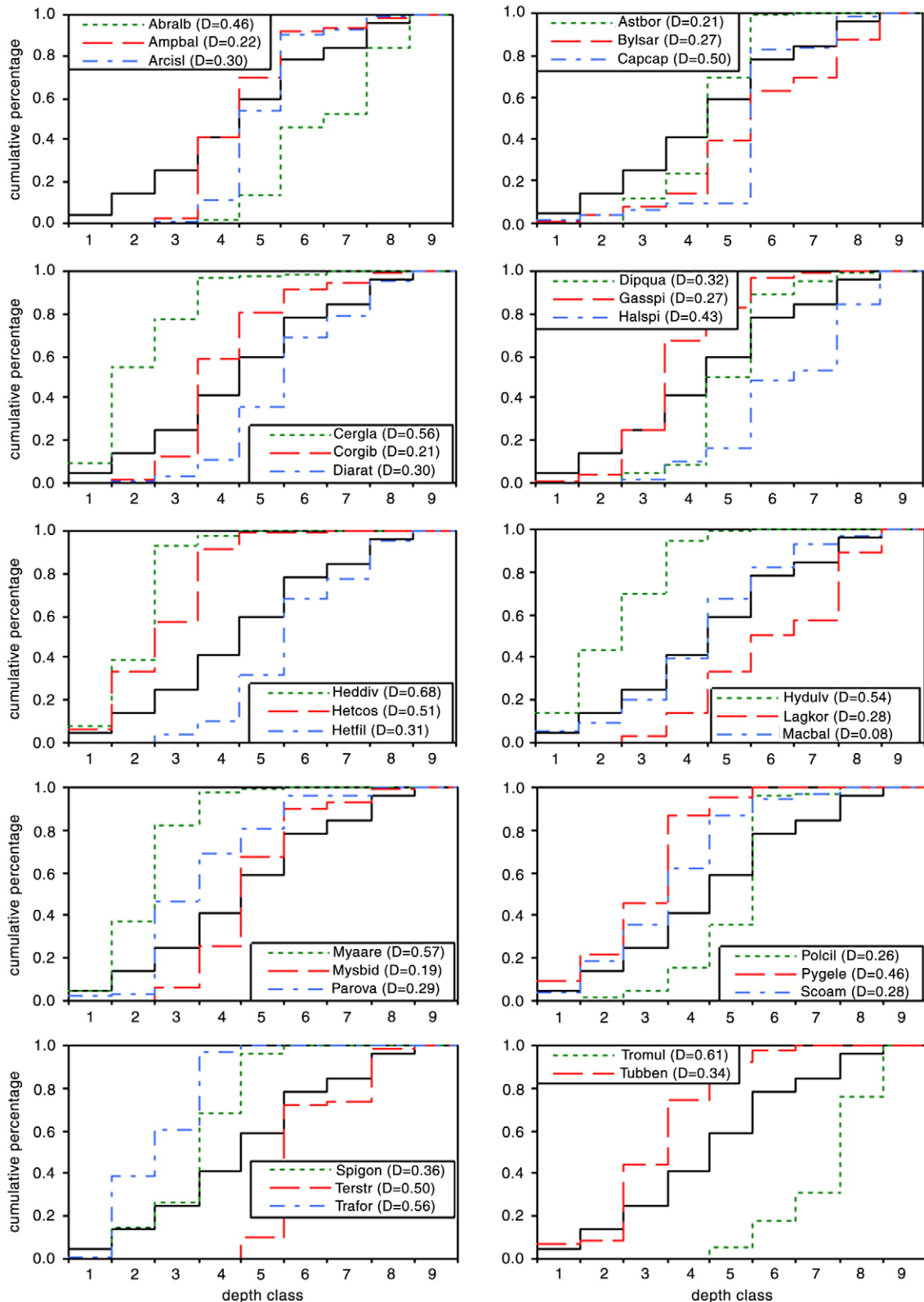
Group c: *Capitella capitata*–*H. spinulosus* community. This community inhabited the deepest area in the Mecklenburg Bight (20.9 to 29.9,  $\bar{x}$  = 24.7 m), characterised by high organic content (2.3–28.4,  $\bar{x}$  = 11.3%), and poorly sorted fine to coarse silt. All measurements at stations assigned to the community were performed in February–March 2006, the observed salinity ranged from 17.4 to 21.1 PSU, oxygen varied from 4.6 to 7.0 ml/l. This community was characterised by a low number of taxa (23). *P. ciliata* was an additional characteristic species here. In terms of occurrence, the polychaete *B. sarsi* dominated in the community (high frequency of this taxon was typical for the whole investigation area). Other species under interest found in the community were the bivalves *C. gibba*, *A. islandica*, the cumacean *D. rathkei* and the polychaete *L. koreni*.

### 3.7. Distribution of benthic communities along environmental factors

To relate macrobenthic assemblages to environmental factors on the multivariate level, hierarchical clustering, Bray–Curtis similarity together with unweighted group average linking was applied to the 4th-root transformed abundance data of 29 species for 72 sites with the full set of abiotic variables observed and complemented by the nMDS. At the 43% similarity level, three classes representing different community structure and corresponding to different sea areas or depth-zones emerged. They matched (with few exceptions) the groups defined from the whole dataset of 208 stations (see Section 3.6). We have not adduced here the dendrogram and nMDS plots for this dataset, but abbreviated the groups distinguished based on the 72-stations data matrix as groups A, B and C, overlapping with groups (communities) a, b and c, respectively (see Fig. 5). Table 4 provides the average and standard deviation values of species abundance and environmental factors in three groups.

### 3.8. Linking macrobenthic community structure to environmental factors—BIO-ENV

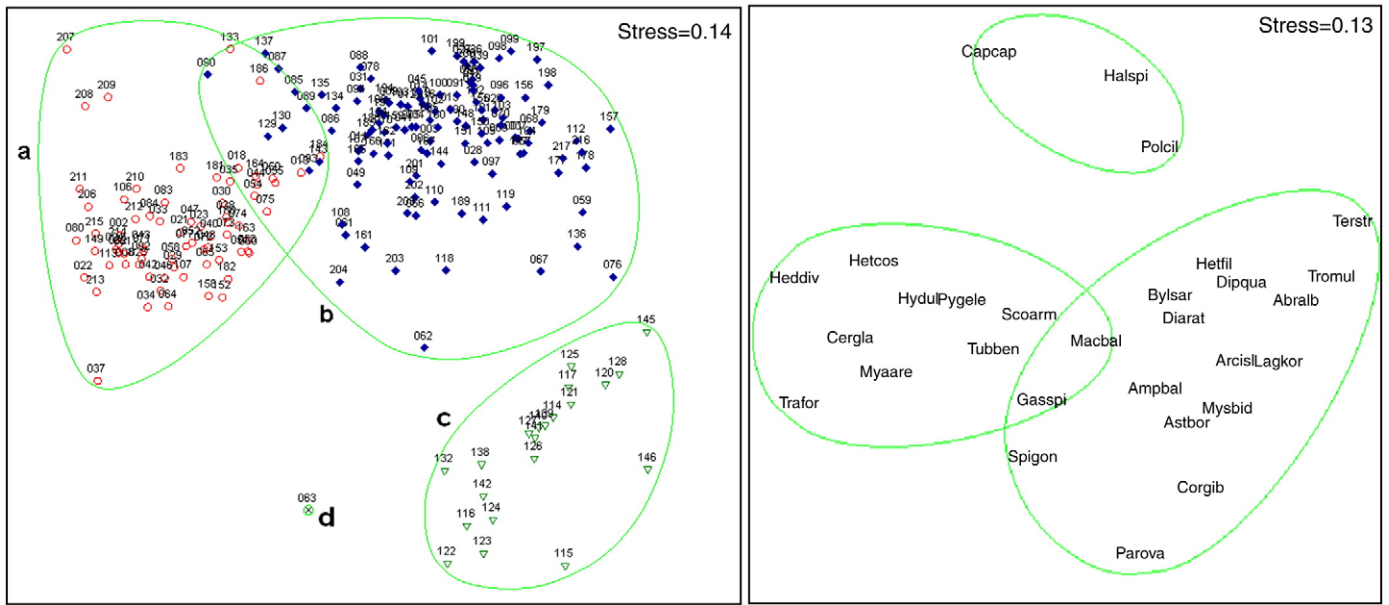
The BIO-ENV procedure was employed on a species assemblage similarity matrix adjusted for 72 sites (as in Section 3.7) and the resemblance matrices generated using three various transformations of primary environmental 72-by-8 matrix (overall z-transformed; total organic content, median grain size, sorting and permeability are log-transformed prior to the overall z-transformation; standardised residuals of 7 environmental factors detrended from depth by



**Fig. 3.** Cumulative histograms of depth versus species abundances. Taxon names are abbreviated as in Table 2. Values of two-tailed two-sample Kolmogorov–Smirnov statistic ( $D$ ) are given in brackets, for sample size  $n = 208$   $D_{critical} = 0.13$ . The repeated black continuous line represents water depth. If the calculated  $D$  is below  $D_{critical}$ , the dependence can be rejected under the correspondent significance level  $p = 0.05$  (Sachs, 1997), which is the case only for the bivalve *Macoma balthica* (result shown in bold). The color version of this figure is available online.

polynomial regression). The results are presented in Table 5. The Spearman correlation coefficient ( $r$ ) was chosen as a rank correlation measure. For the overall z-transformed environmental matrix, total

organic content revealed the best association with the observed species distribution, ( $r = 0.499$ ). It was followed by water depth ( $r = 0.431$ ). Those two factors were responsible for most of the



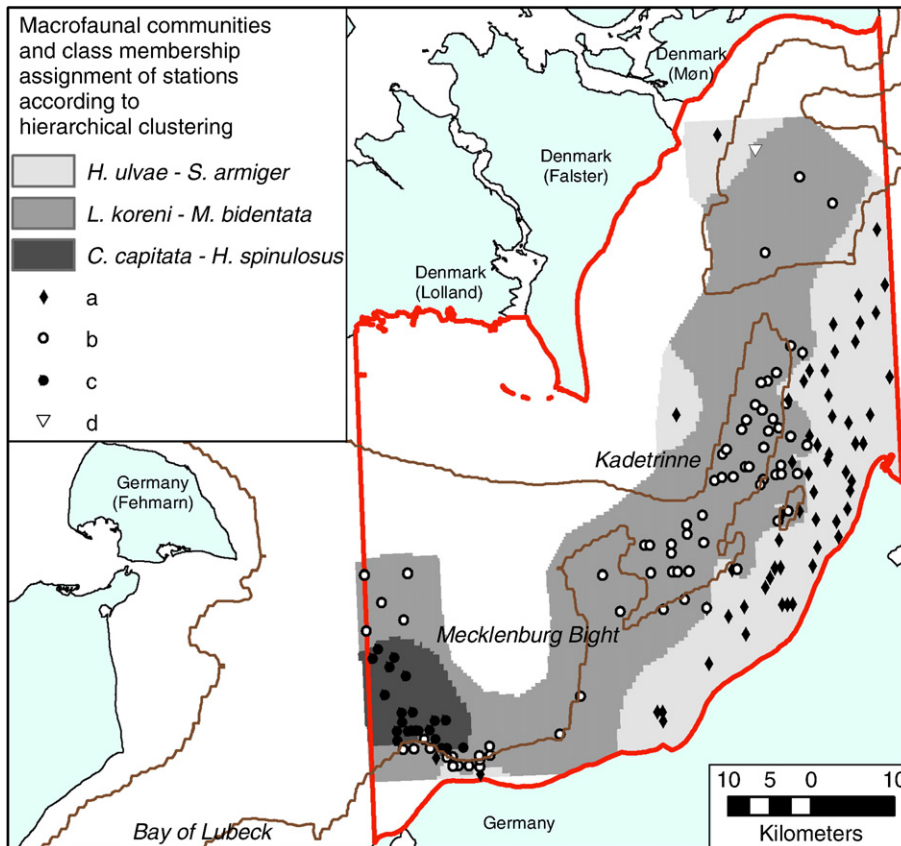
**Fig. 4.** Two-dimensional MDS-ordination of the 208 sampling sites regarding the Bray–Curtis dissimilarity based on 4th-root transformed abundance data for 29 selected species (left: normal analysis, grouping of sites correspond to 0.35 similarity level; right: independent inverse species analysis, grouping of species corresponds to 0.15 similarity level; dendrograms are not presented here for brevity). The color version of this figure is available online.

similarity between the biotic and abiotic matrices (total organic content alone accounted for over 80% of total similarity).

In the case of the prior log-transformation of selected abiotic variables, performed in order to reduce the heteroscedasticity of the descriptors, the highest overall correlation ( $r = 0.605$ ) is found for a

combination of 5 factors: median grain size, salinity, water depth, sorting and permeability.

For depth-detrended matrix of environmental descriptors, absolute correlations relating them to the community structure are very low for all possible combinations.



**Fig. 5.** Spatial distribution of macrobenthic coenoses. The zonation is based on the results of hierarchal clustering and nMDS analysis (class membership assignment of single stations is indicated as a, b, c and d according to Fig. 4, left). The colour version of this figure is available online.



**Table 4**

Average and standard deviation values of species abundance and environmental factors in three cluster groups based on the results of hierarchical clustering and non-metric MDS analysis for data set of 72 stations with all considered environmental data available.

Group	A	B	C
Number of sites	16	35	21
Polychaeta			
<i>Ampharete baltica</i>	15 ± 29	14 ± 27	
<i>Byligides sarsi</i>	16 ± 15	54 ± 44	22 ± 16
<i>Capitella capitata</i>	6 ± 10	1 ± 3	535 ± 1403
<i>Dipolydora quadrilobata</i>	7 ± 12	12 ± 20	
<i>Hediste diversicolor</i>	3 ± 9		
<i>Heteromastus filiformis</i>	2 ± 9	4 ± 8	
<i>Lagis koreni</i>	256 ± 482	521 ± 1029	1 ± 3
<i>Polydora ciliata</i>	11 ± 21	2 ± 5	44 ± 125
<i>Pygospio elegans</i>	559 ± 815	7 ± 15	
<i>Scoloplos armiger</i>	162 ± 161	48 ± 49	1 ± 5
<i>Spio goniocephala</i>	20 ± 27	5 ± 12	
<i>Terebellides stroemi</i>		29 ± 130	
<i>Travisia forbesii</i>	21 ± 53		
<i>Trochochaeta multisetosa</i>	1 ± 3	29 ± 88	
Oligochaeta			
<i>Heterochaeta costata</i>	12 ± 40	0 ± 2	
<i>Tubificoides benedii</i>	72 ± 77	8 ± 20	
Cumacea			
<i>Diastylis rathkei</i>	114 ± 192	1009 ± 1258	14 ± 14
Mysidacea			
<i>Gastrosaccus spinifer</i>	18 ± 23	2 ± 4	1 ± 4
Gastropoda			
<i>Hydrobia ulvae</i>	2080 ± 3162	100 ± 397	
Bivalvia			
<i>Abra alba</i>	1 ± 4	446 ± 528	
<i>Arctica islandica</i>	14 ± 18	142 ± 144	13 ± 19
<i>Astarte borealis</i>	29 ± 69	21 ± 32	
<i>Cerastoderma glaucum</i>	7 ± 17		
<i>Corbula gibba</i>	51 ± 83	51 ± 135	14 ± 18
<i>Macoma balthica</i>	186 ± 183	62 ± 100	0 ± 2
<i>Mya arenaria</i>	91 ± 101	1 ± 6	
<i>Mysella bidentata</i>	197 ± 283	362 ± 551	2 ± 5
<i>Parvicardium ovale</i>	31 ± 48	16 ± 63	
Priapulida			
<i>Halicryptus spinulosus</i>	1 ± 3	2 ± 5	33 ± 37
Sum of average abundance of 29 selected species	3984 ± 3675	2947 ± 1816	681 ± 1536
Total abundance	7611 ± 9158	3219 ± 1837	736 ± 1605
Environmental factors			
Depth (m)	14.3 ± 2.1	21.8 ± 3.8	24.7 ± 2.4
Salinity (PSU)	13.6 ± 2.2	15.8 ± 3.1	20.4 ± 0.8
Total organic content (%)	0.6 ± 0.4	3.5 ± 3.8	11.3 ± 5.8
Dissolved oxygen (ml/l)	6.9 ± 0.7	6.2 ± 1.2	6.1 ± 0.7
Median grain size (µm)	295.4 ± 131.5	128.2 ± 77.5	41.2 ± 73.5
Sorting (phi)	0.7 ± 0.2	1 ± 0.6	1.9 ± 0.4
Skewness (phi)	0 ± 0.2	-0.3 ± 0.4	-0.5 ± 0.4
Permeability (darcy)	26.9 ± 16.6	6.8 ± 6.4	0.8 ± 3.2

### 3.9. The species' response to the environment—CCA

To support the results of BIO-ENV findings, the canonical correspondence analysis (CCA) was performed using CANOCO software (ter Braak and Šmilauer, 2002) on macrobenthic species abundance data (29 species) and corresponding environmental factors sampled at 72 stations. Two separate analyses were performed: the first one with 4th-root transformed abundance data and an untransformed matrix of 8 environmental factors and the second one with 4th-root transformed abundance data and a matrix of standardised depth-detrended residuals of abiotic factors. The Monte-Carlo permutation tests accompanied both analyses to test the effects of each environmental variable on the explanation of total variance in species data. Ordination diagrams of canonical correspondence analyses are shown in Fig. 6.

In the case of undetrended environmental data, the first two CCA axes together account for approximately 79% of the relations between species and environmental data (Fig. 6, left). With the matrix of

**Table 5**

BIO-ENV procedure results.

K	Factor/-s	$r(\rho_{\text{normal}})$	Factor/-s	$r(\rho_{\text{log-transf\_normal}})$	Factor/-s	$r(\rho_{\text{depth-detrended}})$
1	1	0.499	8	0.575	1	0.127
1	5	0.431	2	0.514	8	0.119
2	1,5	0.543	5,8	0.595	1,8	0.152
3	4–6	0.575	4,5,8	0.600	1,6,8	0.169
4	1,4–6	0.597	2,4,5,8	0.601	1,2,6,8	0.164
5	1,2,4–6	0.596	2,4–6,8	0.605	1,2,4,6,8	0.154
6	1,2,4–7	0.590	2,4–8	0.605	1,2,4,6–8	0.120
7	1,2,4–8	0.569	1,2,4–8	0.599	1–4,6–8	0.094
8	1–8	0.540	1–8	0.571		

K indicated the number of abiotic factors considered at a time. The highest Spearman rank correlation coefficients ( $\rho$ ) evaluated between 4th-root transformed biotic similarity matrix (abundance data of 29 species, Bray–Curtis similarity) and three matrices of abiotic factor/-s (Euclidean distance) at 72 sampling sites are shown.

Abiotic matrix 1 ( $\rho_{\text{normal}}$ ): overall z-transformed; abiotic matrix 2 ( $\rho_{\text{log-transf\_normal}}$ ): prior log-transformation of total organic content, median grain size, sorting and permeability and the following overall z-transformation; abiotic matrix 3 ( $\rho_{\text{depth-detrended}}$ ): detrended from water depth component by means of polynomial regression of power 6 (calculated using the MATLAB as a tool), standardised regression residuals of 7 abiotic factors. The environmental factors associated to  $\rho$  are: 1 total organic content, 2 median grain size, 3 oxygen concentration, 4 salinity, 5 water depth, 6 sorting, 7 skewness, 8 permeability.

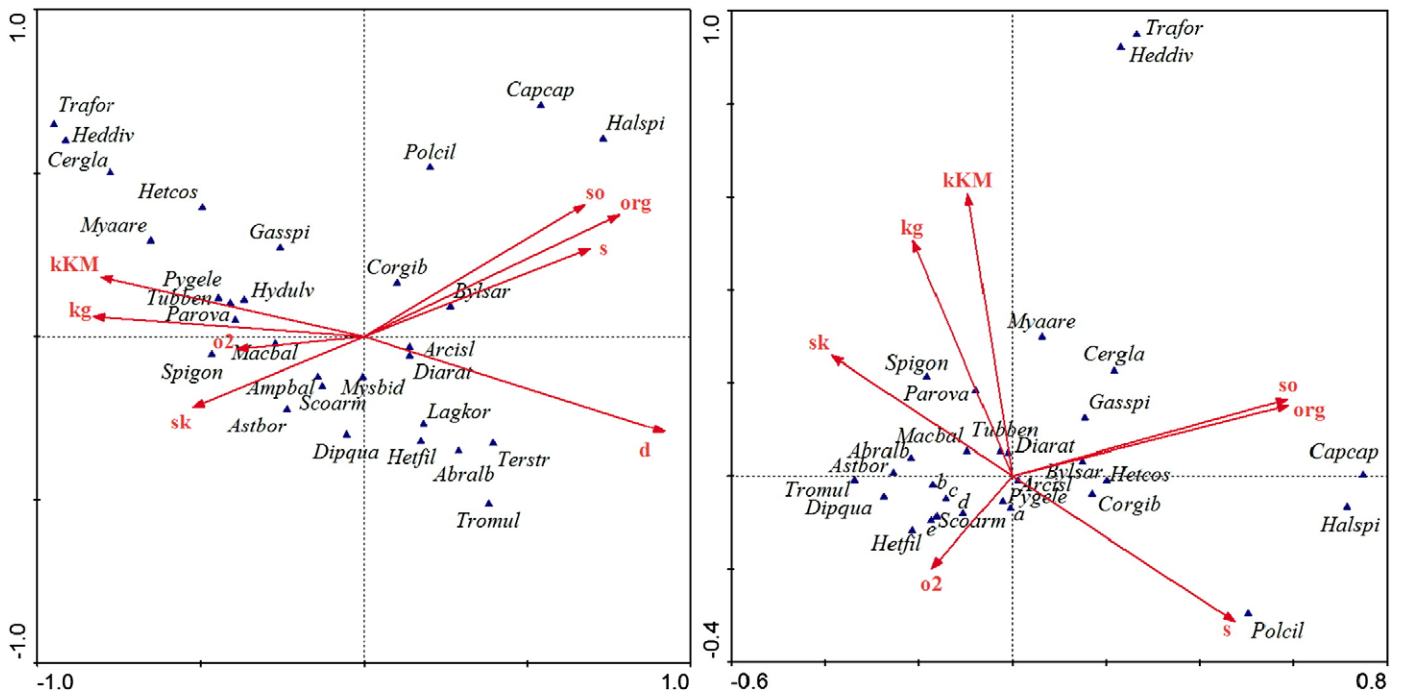
standardised residuals of abiotic factors detrended from depth, this percentage is reduced to 70% (Fig. 6, right). Water depth reveals the highest positive correlation with the first canonical axis in case of undetrended environmental data followed by total organic content, whereas median grain size and permeability indicate the strongest negative correlation (Fig. 6, left). Sorting shows the highest correspondence to the second canonical axis, with organic content being on the second position. Near-bottom oxygen concentration shows the least correspondence to both first and second axes.

In the results of the CCA accounting for the depth-detrended residuals of environmental variables (Fig. 6, right), the highest positive correlation with the first canonical axis is assigned to total organic content, followed by sorting and salinity, while median grain size, skewness and permeability indicate negative correlation. Permeability and median grain size show strong negative correlation with the second CCA axis.

Comparison of both ordination diagrams highlights the importance of the water depth.

## 4. Discussion

In general, the highest overall Baltic Sea diversity and number of macrobenthic species can be found in the southwestern region that is most strongly influenced by marine conditions (Zettler et al., 2008). The number of species declines to the north resulting in the low-diversity communities, for example, in the Gulf of Bothnia (Bonsdorff, 2006). The rank of dominance of polychaeta, mollusca, and crustacea in the study area observed during the time period of this study is identical to patterns of community structure in the southwest Mecklenburg Bight between 1980 and 1994, described by Prena et al. (1997). They characterise a general temporal variation in the number of species observed by a slight increase from spring to summer whereas a decline in abundances towards autumn was most evidently seen at stations deeper than 20 m, with slight or no decline occurring in the shallower and outer zones. This is in agreement with findings of Zettler et al. (2000). This assemblage was also characterised in earlier papers (e.g. Schulz, 1969; Gosselck and Georgi, 1984). These works documented the retreat of populations of *A. islandica* and *Astarte* species from the deep areas of the Bight affected by irregular hypoxic events, followed by the alternate replacement of the returning communities and populations of several species that are able to survive the temporal oxygen deficiency or even colonize a so-called “bottom deserts”. Oxygen-deficiency events, controlled by



**Fig. 6.** Ordination diagrams of canonical correspondence analyses (CCA) of macrobenthic species abundance data (29 species) and corresponding environmental factors sampled at 72 stations (see Fig. 1). Left: CCA calculated for 4th-root transformed abundance data and untransformed abiotic matrix of 8 environmental factors. Right: CCA calculated for 4th-root transformed abundance data and matrix of standardised residuals of abiotic factors detrended from depth. Species notation: a–*H. ulvae*, b–*T. stroemi*, c–*A. baltica*, d–*M. bidentata*, e–*L. koreni*, others as in Table 2. Environmental factors notation: d–water depth, s–near-bottom salinity, org–total organic content, o2–near-bottom oxygen concentration, kg–median grain size, so–sorting, sk–skewness, kKM–permeability. The colour version of this figure is available online.

bathymetry and hydrographical stratification, run differently in various locations of the region and usually take place in late summer–autumn, resulting in the retreat of species and low-diversity communities recorded during this season. However, those regions of poor bio-diversity or even deserted sea floor were always colonized within a relatively short time, leading to the general outcome: long-living species abandon the territory and are substituted by short life span polychaeta species (Zettler et al., 2000). This corresponds with the *C. capitata*–*H. spinulosus* community in our data, where *A. islandica* was absent or found in low abundances, and *A. borealis* was not observed at all. We deliberately avoided the analysis of temporal (seasonal or interannual) variability in our work. We had in the availability a relatively large dataset that covered both the distribution of macrobenthic species and simultaneously measured environmental variables. Analysing the data we aimed to identify ranges of abiotic parameters where certain species are in general likely to occur. Together with prior autecological knowledge this allows to recognize optimal, sub-optimal, or even pessimal conditions for them.

There is a potential of strong gradients to monopolize statistical analyses. Therefore, such gradients should be removed before unless it is the stated aim to explore the influence of these particular gradients (Legendre and Legendre, 1998; Bourget et al., 2003). We tried to reduce the effect of salinity gradient occurring in the Baltic Sea by restricting the study area and reducing the variability of salinity in distinct depth-zones. A smooth depth gradient could be allocated along the North–South axis of the area investigated. To examine the coherencies among environmental variables, Pearson's correlation coefficient was computed. However, correlation between parameters does not imply cause and effect. Path analysis may be used to assess the correspondence between the data and causal models, when causal ordering of the descriptors is stated by the prior information of ecological hypotheses (Legendre and Legendre, 1998). The complexity of abiotic interactions, reflected by the results of correlation analysis, does not allow the complete removal of either gradient without the loss of essential information. A solution was found in

depth-detrending of abiotic data for certain statistical analyses (see also Glockzin and Zettler, 2008).

Three distinct benthic communities were defined, each related to different spatial subareas, characterised by a certain variability in environmental parameters (see Fig. 5). Previous studies explain the division of benthic species or communities over depth classes by food availability and/or certain food quality due to various sedimentation and resulting accumulation rates of organic material (Elmgren, 1978; Pearson and Rosenberg, 1978; Olenin, 1997; Laine, 2003).

The observed biotic structure was linked to environmental variability by examining correlations between the two multivariate patterns applying the BIO-ENV procedure (Clarke and Ainsworth, 1993; Clarke and Warwick, 2001; Lu, 2005). CCA was done to describe the full community variation with respect to a particular complex set of measured environmental variables. The attendant evaluating numerical analyses (Monte-Carlo permutation tests) was important to provide a fairly accurate picture (ter Braak, 1986; Legendre and Gallagher, 2001; ter Braak and Šmilauer, 2002). The comparison of results of both analyses accounting for detrended and undetrended environmental data points out the predictors of benthic macrofauna composition. The influence of depth on all other factors becomes clear. Like altitude through its physical forcing on other environmental factors plays an essential role in plant ecology (Guisan et al., 1999), depth can be regarded as a master factor in marine benthology. A tribute to the importance of this factor for benthic distribution is paid by the analysis of estimated cumulative curves for depth classes versus species abundances (Fig. 3). According to BIO-ENV analysis calculated with the undetrended dataset using no prior log-transformation, the total organic content causes the best similarity between abiotic and biotic data. The same implies to the results of the analysis with depth-detrended abiotic dataset. This is also confirmed by the Monte-Carlo simulation of the CCA performed on the same data. At the same time, in BIO-ENV results for depth-detrended environmental descriptors absolute correlations relating them to the community structure are very low for all possible combinations. This can be

interpreted as an evidence of depth being the driving factor for community composition in the region. Considering the strong correlation between the total organic content and water depth, the first factor mentioned is likely to change drastically over relatively short distances. The same implies to both sorting and permeability. They differ in their rank in the results of BIO-ENV and CCA, but obviously remain dominating in explaining the benthic variance. The difference may be explained by the fact that BIO-ENV is based on similarity matrices, it might work best with sharp and short gradients (McGarigal et al., 2000) in contrast to CCA that most likely prefers distinct but uniformly continuous species response (Legendre and Legendre, 1998).

For *T. forbesii* and *H. diversicolor*, their habitat preferences seem to differ in correlation analysis and depth-detrended CCA. Such divergent results found for different statistical methods may account for the fact that our limited set of environmental variables did not fully reflect the complexity of natural species–environment relationships. This again does not only underline the importance of prior in-depth knowledge about species autecology for the interpretation of statistical results (Sachs, 1997), but furthermore illustrates the impossibility of deriving autecology from statistical results.

Our study defined dominating species and distinct benthic assemblages within the investigation area. It provides an insight on species that identify the strongest response to various factors and highlights environmental factors playing the major role for the distribution of benthic macrofauna. Hitherto, this is the most detailed study focused on benthic–abiotic interactions using a complex dataset of recent investigations performed for this region of the Baltic Sea. To that effect, it is an initial first step towards the design of models able to predict macrofaunal distribution regarding autecological species–environmental interactions (Glockzin and Zettler, 2008), that being the content of the second part of this work (Gogina et al., 2009–this volume).

It is obvious that only a fragment of the controlling factors network, responsible for macrozoobenthos distribution, could be covered with the available data. Additional factors, e.g. food web structure, complex predation interactions, currents, temperature, turbidity, chemical substrate composition etc., were not considered in this study. Additional variables incorporated would deliver a more insightful analysis (Guisan and Zimmermann, 2000). On different scales various factors take the leading stand in influencing species distribution. Biotic factors are expected to be the dominating ones more on the local scale, responsible for fluctuations of abundance within the community. On a large scale, e.g. Baltic-wide, salinity is likely to be the primary or even the only descriptor in species–environmental relationships (e.g. Laine, 2003; Bonsdorff, 2006). Moreover, the analysis of such short-term data is able to represent only the momentary state of benthic communities, whereas the temporal development of the southwestern Baltic Sea has shown both high variability in species abundance and shifts in species composition (e.g. Andersin et al., 1978; Perus and Bonsdorff, 2004; Zettler et al., 2008).

However, for the area examined, we gained new insights into the distribution and habitat selection of dominating benthic species and analysed the impact of different environmental factors on the distribution of benthic communities. Discriminating species are found responsible for distinct benthic assemblages, namely *H. ulvae*–*S. armiger*; *L. koreni*–*M. bidentata* and *C. capitata*–*H. spinulosus*. It was highlighted that depth, salinity and certain sediment characteristics, above all total organic content, seem to determine the suitability of habitats for various taxa. Our findings suggest the interpretation of water depth as a complex factor, which integrates the effects of several other parameters, such as annual temperature variation, nutrient supply etc. This factor also controls sedimentological parameters such as organic content, sorting or permeability in the study area. Numerous authors already assumed a depth dependency of environmental factors and thereby caused macrobenthic invertebrates spatial distribution (e.g. Wildish, 1977; Kube et al., 1996; O'Brien et al., 2003;

Perus and Bonsdorff, 2004; Kröncke et al., 2004; Bonsdorff, 2006; Zettler et al., 2006; Glockzin and Zettler, 2008). Our results show a significant response to change in water depth for 29 selected species and thus seem to approve the aforementioned hypothesis.

## 5. Conclusion and outlook

Predictions of the climate change models assume changes in the Baltic Sea ecosystem such as a drastic change in the food web structure, an increase of warm water species and growing benthic deserts on the sea floor (Philippart et al., 2007). Predictive modeling of species distribution can become an important tool in ecosystem/habitat management, supporting a sustainable development of the Baltic Sea ecosystem.

The analysis of causality performed in this study provides an essential basis and pre-work for the modeling of species distribution. In the second part of this work (Gogina et al., 2009–this volume), species response curves were estimated by means of logistic regression and used to model the spatial distribution of selected species utilising the Akaike's information criterion for multimodel inference (Ysebaert et al., 2002; Thrush et al., 2003; Burnham and Anderson, 2004; Guisan et al., 2006). On this basis, habitat suitability maps, representing the predicted probabilities of species occurrence, were created in GIS.

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