

Spatial variability in structural and functional aspects of macrofauna communities and their environmental parameters in the Jade Bay (Wadden Sea Lower Saxony, southern North Sea)

Ulrike Schückel · Melanie Beck · Ingrid Kröncke

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Abstract Spatial distribution and functional structure of intertidal benthic macrofauna in relation to environmental variables in the Jade Bay (southern North Sea) were studied and compared with other intertidal areas of the Wadden Sea. A total of 128 stations covering the whole Jade Bay were sampled in summer 2009. A total of 114 taxa were found. Highest species numbers occurred in the subtidal areas, whereas highest mean abundances were found in the upper intertidal areas. Based on species abundance data, six significantly distinct macrofauna communities in the Jade Bay were identified and evaluated with multivariate statistics, univariate correlations and canonical correspondence analysis. Differences in these community patterns were caused by the response of the dominant species (*Hydrobia ulvae*, *Tubificoides benedii*, *Pygospio elegans*, *Caulleriella killariensis*, *Scoloplos armiger*, *Urothoe poseidonis*, *Microprotopus maculatus*) to prevailing environmental conditions along the gradient from the lower and exposed sandy intertidal areas via intermediate mixed sediments to the upper mudflat areas. Distribution patterns in relation to tidal zonation were best explained by variability in submergence time, Chlorophyll *a* (chl *a*) content and sediment composition (mud content), which are proxies for

hydrodynamic conditions and food availability. Species inventory and species richness were comparable with other intertidal areas of the Wadden Sea, but the Jade Bay differs from these areas regarding dominant species. Differences in sediment composition and morphological characteristics (macrotidal versus mesotidal Wadden Sea areas) are discussed for comparison of regional differences.

Keywords Tidal flat systems · Submergence time · Food availability · Environmental gradients · Functional diversity · Spatial distribution · Wadden Sea

Introduction

Tidal flat ecosystems are dynamic and complex habitats. They represent highly productive areas for macrobenthic organisms (Heip et al. 1995), thus being used as important feeding and nursery grounds by fishes and shore birds (Kuipers 1977; Widdows et al. 2004). Macrofauna species inhabiting tidal flats are highly adapted to this dynamic environment characterized by tidal fluctuations, changing water currents, wave action, altering periods of submersion and exposure to air from low to high intertidal levels (Newell 1970; Hummel et al. 1994). The hydrodynamic force itself influences sediment characteristics (grain size, organic carbon and chl *a* contents), topography (intertidal height) and salinity (Snelgrove and Butman 1994; Ysebaert et al. 2003; Widdows et al. 2004; Gray and Elliott 2009). It is well known that the prevailing environmental conditions affect the distribution of tidal flat macrofauna species, resulting in a specific zonation pattern of the living communities (Linke 1939; Michaelis 1987; Beukema 1988; Hertweck 1994; Reise et al. 1994; Ysebaert et al. 2003; van Colen et al. 2009; Puls et al. 2011). In addition, several

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U. Schückel (✉) · I. Kröncke
Senckenberg am Meer, Marine Research Department,
Südstrand 40, 26382 Wilhelmshaven, Germany
e-mail: Ulrike.Schueckel@senckenberg.de

M. Beck
Institute for Chemistry and Biology of the Marine Environment
(ICBM), Carl von Ossietzky University of Oldenburg,
Carl-von-Ossietzky-Str. 9-11, 26129 Oldenburg, Germany

macrofauna species themselves, such as *Arenicola marina* or *Hydrobia ulvae* (e. g. Flach 1992; Orvain et al. 2006), act as bioturbators, which increase sediment erosion, turbidity, nutrient and carbon processing (Herman et al. 1999). In contrast, bio-stabilisers such as seagrass beds, mussel beds and microphytobenthos mats can modify the habitat by reducing turbidity, increasing light penetration and enhancing sedimentation processes (Kröncke 1996; Bergfeld 1999; Widdows and Brinsley 2002; Bos et al. 2007; van Katwijk et al. 2010).

The tidal flat systems in the European Wadden Sea along the coastal region of the North Sea between Den Helder (Netherlands) and Skallingen (Denmark) are classified according to their tidal range to define the geomorphological, hydrological and sedimentological environment (Diekmann et al. 1987). Depending on the tidal range, tidal flats are distinguished as macrotidal (>3.5 m), mesotidal (1–3.50 m) and microtidal (<1 m) (Hayes 1979; Flemming 2011). Mesotidal flats are bordered by barrier islands, whereas macrotidal flats are open to sea where barrier islands are no longer present (Diekmann et al. 1987). With a mean tidal range of 3.8 m (Götschenberg and Kahlfeld 2008), the Jade Bay belongs to a macrotidal flat system, but differs from other macrotidal areas due to its land-locked bay character. In contrast to other sandier mesotidal flats (e.g. Balgzand and Königshafen), the Jade Bay is characterized by a large mudflat belt with a unique, muddier sediment composition.

The spatial, temporal and seasonal variability of macrofauna species of European intertidal flat systems have been intensively studied (e.g. Beukema 1974, 1988; Jensen 1992; Essink et al. 1998; van der Graaf et al. 2009). Especially in the German intertidal Wadden Sea the classification in mud, mixed sediments or sandflats/*Arenicola*-sandflats, and mussel or seagrass beds for macrofauna studies is still common (e.g. Linke 1939; Michaelis 1987; Hertweck 1994; Reise et al. 1994; Steuwer 2002). In the present study, we have used a quantitative statistical approach to identify macrofauna community patterns, which was also applied for different subtidal areas in the East Frisian Wadden Sea (Reiss and Kröncke 2001; Nehmer and Kröncke 2003) and the Pomeranian Bay (southern Baltic Sea) (Glockzin and Zettler 2008) as well as for intertidal areas of the Belgian and Dutch Wadden Sea (van Colen et al. 2009)

The objectives in the present study were (1) to describe the present spatial distribution and functional structure of the macrofauna communities in the Jade Bay by applying a statistical approach, (2) to investigate their relations to environmental factors by using univariate and multivariate statistical approaches in order to explain the spatial distribution patterns of species and structuring forces for

zonation and (3) to compare the Jade Bay with intertidal macrofauna communities of other Wadden Sea areas.

Materials and methods

Study area

The Jade Bay (53°28'42"N, 8°12'5") is a shallow semi-diurnal tidal bay located in the central part of the German North Sea coast (Fig. 1). The shape of the Jade Bay is a result of several storm floods in the Middle Ages (Behre 2004). The Jade Bay is connected with the North Sea through the outer Jade, which enters the Jade Bay through a narrow bottle-neck east of Wilhelmshaven and branches into several channels (Ahne, Vareler Fahrwasser and Stenkentief), draining into a system of tidal inlets and gullies far into the backswamp area to the south. Each tide, a total volume of around 400 million cubic meter flows in and out of the Jade Bay. Freshwater discharge has only little influence on the salinity in the Jade, which varies between 2.9 and 3.2 ‰ (Götschenberg and Kahlfeld 2008). Mean ebb and flood current velocities were 46 and 53 cm/s (Götschenberg and Kahlfeld 2008).

During high tide, the water surface area is 158 km², whereas at low tide it decreases to 44 km² (H. Westphal unpublished data). Furthermore, the study area contains intertidal *Mytilus edulis* mussel beds, which covered an area of 2.07 km² in 2009 (G. Millat unpublished data), as well as *Zostera noltii* seagrass beds, which were mostly found in the eastern and south-western areas and contained 10.9 km² in 2008 (Adolph 2010).

Sampling and laboratory analysis

Macrofauna sampling design

In the intertidal zone, stations were located according to the historical investigations by Linke (1939) in the 1930s and Michaelis (1987) in the 1970s. The study area was divided into different transects (Fig. 1) covering the whole Jade Bay. A total of 128 stations were sampled from April to July 2009 during low tide. Based on maps given by Linke (1939) and Michaelis (1987) the station coordinates were matched as closely as possible. Sampling positions were located by using a hand-held GPS receiver (GPS 72, GARMIN, WGS 84). At each station, 5 replicates were taken with a 10-cm-diameter cylindrical corer (79 cm² total surface) to a depth of 30 cm. A total of 642 samples were taken. Samples were sieved over 0.5 mm mesh size and fixed in 4 ‰ buffered formaldehyde-seawater solution. In the laboratory, samples were stained with Bengal rose,

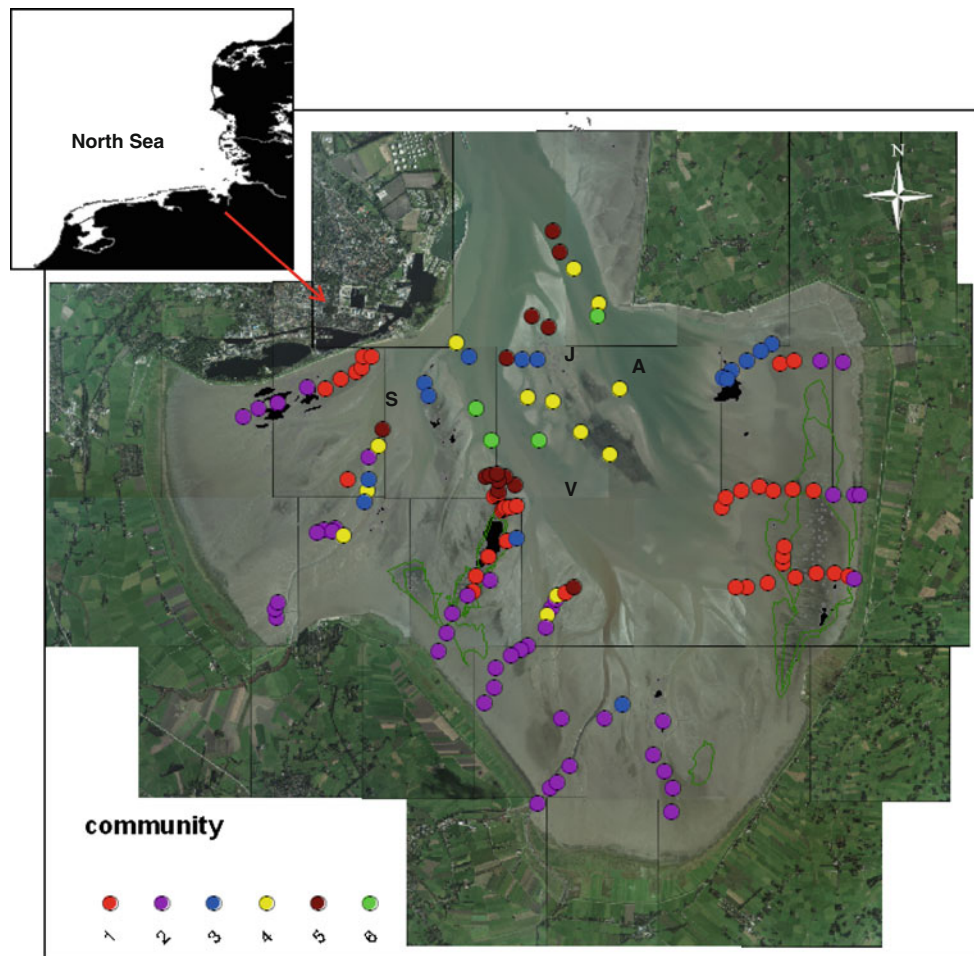


Fig. 1 Location of the Jade Bay. Sampling stations are marked according to their community (cluster): (1) red = *Hydrobia ulvae* partially covered with seagrass beds, (2) purple = mudflats, (3) blue = mixed sediments 1, (4) yellow = mixed sediments 2, (5)

brown = sandflats, (6) green = subtidal. A = Ahne, S = Stenkentief, V = Vareler Fahrwasser, J = Jappensand, *Mytilus edulis* beds = black, areas covered with *Zostera noltii* seagrass beds = green encircled (color figure online)

and all macrofauna was sorted and identified to the lowest possible taxonomic level and then counted.

Environmental variables

One surface sediment sample (<2 cm depth) was taken in parallel for analysing sediment characteristics (mud content <63 μm , median grain size), total organic carbon and chlorophyll *a* contents. Grain size distribution was analysed on fresh, ultrasonically suspended samples by means of Fritsch Analysette 22 laser granulometer. Sediment types were classified according to Kramer et al. (1994) based on differences in median grain size. The total organic carbon content (TOC) was determined according to Babu et al. (1999). The difference between total carbon and inorganic carbon was measured with a CS 500 IR analyser (Eltra, Neuss, Germany) and a CO_2 coulometer (UIC, Joliet, USA), respectively. Chl *a* was analysed by high-performance liquid chromatography (HPLC) by the extraction from 5 g of

homogenized sediment with 3 ml Dichlormethan-methanol (9 + 1). Chl *a* contents were calculated in mg/m^2 according to Brotas et al. (2007). Mean submergence time (given in hours per day) for each station was estimated using the finite-volume model FV COM (Lettmann et al. 2010).

Statistical analyses

Prior to data analysis, species abundance data were standardized to individuals per m^2 ; species number is given per sample (79 cm^2). Species such as Balanidae, which are typical for hard substrate, were excluded from the analysis. Each species was classified into functional feeding groups (surface deposit feeders, subsurface deposit feeders, suspension feeders, omnivores, predators, interface feeders and sand lickers based on available literature (Fauchald and Jumars 1979; Ysebaert et al. 2003; van Colen et al. 2009).

Data were first tested for normal distribution (D'Agostino and Pearson omnibus normality test). Multivariate

techniques on fourth root transformed abundance data were used to analyse the community structure. Group average cluster analysis based on Bray-Curtis similarity followed by a similarity profile test (SIMPROF; Clarke and Gorley 2006) and multidimensional scaling (MDS) were calculated. ANOSIM randomization test (Clarke and Green 1988) was used to test significant spatial differences in community structure.

Discriminating species, which significantly ($p < 0.05$) separated the different communities, were identified using the similarity percentage routine (SIMPER). Grouped clusters were characterized by their mean abundance, species richness, Shannon-Wiener diversity index, evenness index, characteristic species, feeding type composition in terms of abundance and environmental characteristics. Statistical analysis were performed by using GraphPad Prism 5, the multivariate analysis were performed using The Plymouth Routines in multivariate ecological research (PRIMER) package, version 6 (Clarke and Gorley 2006).

Multivariate canonical correspondence analysis (CCA) by using CANOCO 4 software (Microcomputer Power) was performed to detect the variation in the species data set and the relationship between species composition and measured environmental variables. Forward selection was used to determine and rank the importance of environmental variables, which in turn would be used for determining the species composition (Ter Braak and Verdonshot 1995). Monte Carlo permutation test was performed for statistical validity.

Relationships between species abundance and the environmental variables were also examined by using univariate (Spearman rank) correlations.

Results

General characterization of the macrofauna in the Jade Bay

A total of 114 taxa (45 polychaetes, 34 crustaceans, 20 molluscs, 6 oligochaetes and 9 others) were found during the study period. Number of taxa in a single sample (79 cm²) varied between 0 and 32 taxa, with a mean of 12 taxa. Total abundance varied between 0 and 480,380 ind./m², with a mean of $56,203 \pm 3,291$ ind./m². Gastropods (87 %) were the most abundant taxonomic group, followed by oligochaetes (6 %), polychaetes (6 %) and crustaceans (2 %).

The Jade Bay was generally dominated by *Hydrobia ulvae* (69 %), *Tubificoides benedii* (12 %), *Caulerliella killariensis* (5 %), *Pygospio elegans* (3 %) and *Scoloplos armiger* (3 %), contributing 92 % of the total macrofauna abundance. Excluding *H. ulvae*, species such as *T. benedii*

(29 %), *P. elegans* (15 %), *Retusa obtusa* (13 %), *C. killariensis* (11 %), *Cerastoderma edule* (6 %), *S. armiger* (5 %) and *Macoma balthica* (4 %) were most abundant and made up 83 % of the total macrofauna abundance. Trophic structure in terms of mean abundance was dominated by surface deposit feeders (89 %) followed by subsurface deposit feeders (7 %).

Community structure of the macrofauna

Six communities (Fig. 1) were significantly separated based on SIMPROF ($p < 0.05$) and multivariate data analysis (cluster analysis and MDS ordination) with fourth root transformed abundance data. The global R of ANOSIM analysis was 0.84 ($p < 0.001$) and supported the significant separation between the clusters. The biotic and abiotic characteristics of the six communities are summarized in Table 1, allocated in the different areas and habitats of the Jade Bay.

Figures 2, 3 and 4 show the grain size distribution and the spatial variability among the most dominant species (ind./m²) in the Jade Bay. The sediment composition (Fig. 2a) was predominated by muddy and very fine sand sediments arranged belt-shaped in the Jade Bay. Fine sands and medium sands found in the lower intertidal area mostly in the central part of the study area were of minor importance.

The *Hydrobia ulvae* community (Community 1) included 39 stations (mean similarity of 66 %) located in the eastern and western intertidal flats. The mostly very fine sand environment was characterized by moderate submergence time (8.5 h) and mud, chl *a* and TOC contents. This community was characterized by a species-rich benthic fauna, highest mean abundance but lowest Shannon-Wiener diversity and evenness. The dominant species was *H. ulvae* (99 %), which was widespread in high densities in the Jade Bay (Fig. 4f). A clustered pattern with maximum abundance of more than 370,000 ind./m² was found in close proximity to *Zostera noltii* seagrass beds in the eastern and south-western parts. Due to its dominance, the community structure was characterized by surface deposit feeders. By exclusion of *H. ulvae*, species such as *C. edule* (Fig. 3a), *M. balthica* (Fig. 3b), *Retusa obtusa* (Fig. 4e), *P. elegans* (Fig. 2e), *Nephtys hombergii* (Fig. 2c) and *T. benedii* dominated the community structure. This was the only community with high abundances of bivalves. *Scrobicularia plana* (Fig. 3c), commonly known for muddy sediments, occurred only at 29 stations, which were restricted to the southern and south-western upper intertidal areas.

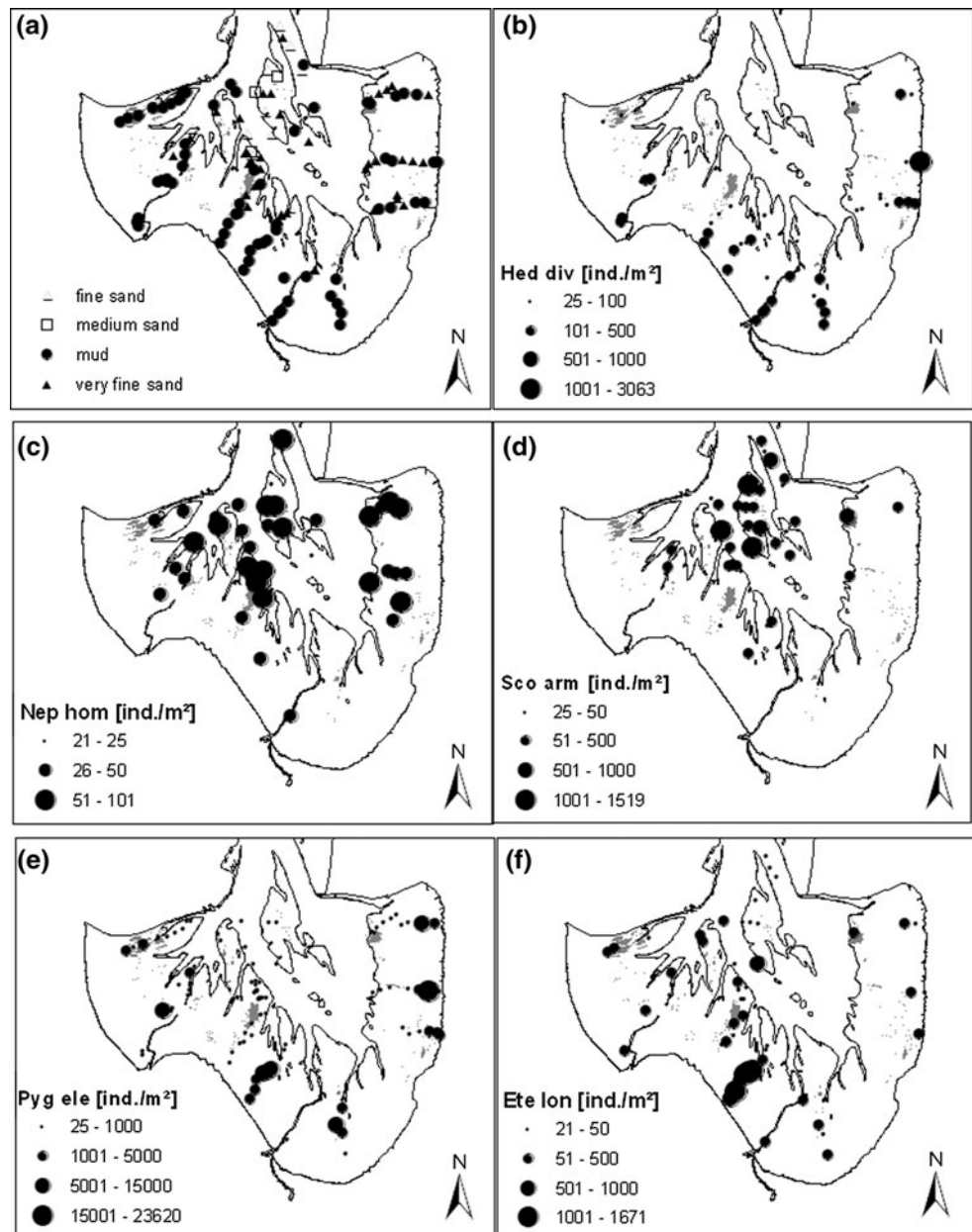
Forty-three stations (mean similarity of 32 %) belonged to the upper intertidal mudflats (Community 2) arranged belt-shaped with lowest median grain size and submergence time (6 h), but with highest mud, TOC and chl

Table 1 Summary of the six communities, their habitat types and environmental variables

	Community 1 <i>Hydrobia ulvae</i> partially covered with seagrass beds (n = 39)	Community 2 Mudflats (n = 43)	Community 3 Mixed sediments 1 (n = 15)	Community 4 Mixed sediments 2 (n = 13)	Community 5 Sandflats (n = 14)	Community 6 Subtidal (n = 4)
Environment						
Median grain size (µm)	66 (6)	30 (4)	59 (9)	76 (13)	166 (16)	153 (18)
Mud content (%)	49 (4)	76 (3)	55 (5)	46 (7)	9 (2)	18 (2)
TOC (%)	0.7 (0.1)	0.97 (0.1)	0.7 (0.1)	0.5 (0.2)	0.11 (0.01)	0.6 (0.3)
Chl <i>a</i> (mg/m ²)	9 (0.4)	54 (3.2)	3 (0.2)	7 (0.9)	0.6 (0.1)	0.4 (0.03)
Submergence time (h)	8.53	6.07	10.72	14.51	10.49	24
Macrobenthos						
S (total/79 cm ²)	37	33	26	14	26	47
S (mean/79 cm ²)	10 (0.7)	16 (0.6)	11 (0.69)	6 (0.68)	10 (0.81)	23 (8)
Mean abundance (ind./m ²)	145,165 (13614)	30,492 (3665)	3,791 (853)	940 (143)	4,977 (2375)	3,991 (2547)
H'	0.12 (0.03)	1.38 (0.06)	1.5 (0.13)	1.21 (0.13)	1.4 (0.16)	2.3 (0.19)
Evenness J'	0.05 (0.01)	0.5 (0.02)	0.62 (0.05)	0.67 (0.05)	0.62 (0.08)	0.81 (0.06)
Characteristic species (mean abundance ind./m ²)	Hyd ulv <i>Cer edu</i> <i>Ret obt</i> <i>Pygo ele</i> <i>Mac bal</i> <i>Tub ben</i> <i>Nep hom</i>	142,809 <i>Tub ben</i> <i>Hyd ulv</i> <i>Pygo ele</i> <i>Cor spp.</i> <i>Ner spp.</i> <i>Ret obt</i> <i>Cor vol</i> <i>Het fil</i>	9,241 <i>Cau kil</i> <i>Pyg ele</i> <i>Hyd ulv</i> <i>Tub ben</i> <i>Sco arm</i> <i>Nep hom</i> <i>Amp acu</i>	1,165 <i>Sco arm</i> <i>Hyd ulv</i> <i>Cau kil</i> <i>Ret obt</i> <i>Ret spp.</i> <i>Nep spp.</i>	3,968 <i>Hyd ulv</i> <i>Sco arm</i> <i>Uro pos</i> <i>Bat sar</i> <i>Nep spp.</i> <i>Nep hom</i> <i>Cum goo</i> <i>Bat pilosa</i> <i>Ete lon</i> <i>Phy muc</i>	728 <i>Mic mac</i> <i>Lan con</i> <i>Pyg ele</i> <i>Ari min</i> <i>Ret obt</i> <i>Nym brev</i> <i>Ete lon</i>
Trophic structure						
Surface deposit feeders	99	43	46	28	81	4
Subsurface deposit feeders	1	40	9	34	5	30
Interface feeders		5	36	22	1	40
Sand-lickers		0	0	0	11	0
Predators		10	7	14	2	20

The most dominant species characterizing the different communities are given in bold. Mean values are given for median grain size (µm), mud (%), TOC (%), Chl *a* (mg/m²) contents and submergence time (h), total number (S total) and mean number of species (S mean) per 79 cm², mean abundance (ind./m²), Shannon-Wiener diversity index (H'), evenness (J'), characteristic species (ind./m²) and feeding type structure (%). Standard errors are given in parentheses. For abbreviation of the macrofauna species names see Appendix Table 5

Fig. 2 Distribution patterns of grain size composition and dominant polychaete species (mean ind./m²) in the Jade Bay. **a** sediment composition, **b** *Hediste diversicolor*, **c** *Nephtys hombergii*, **d** *Scoloplos armiger*, **e** *Pygospio elegans*, **f** *Eteone longa*



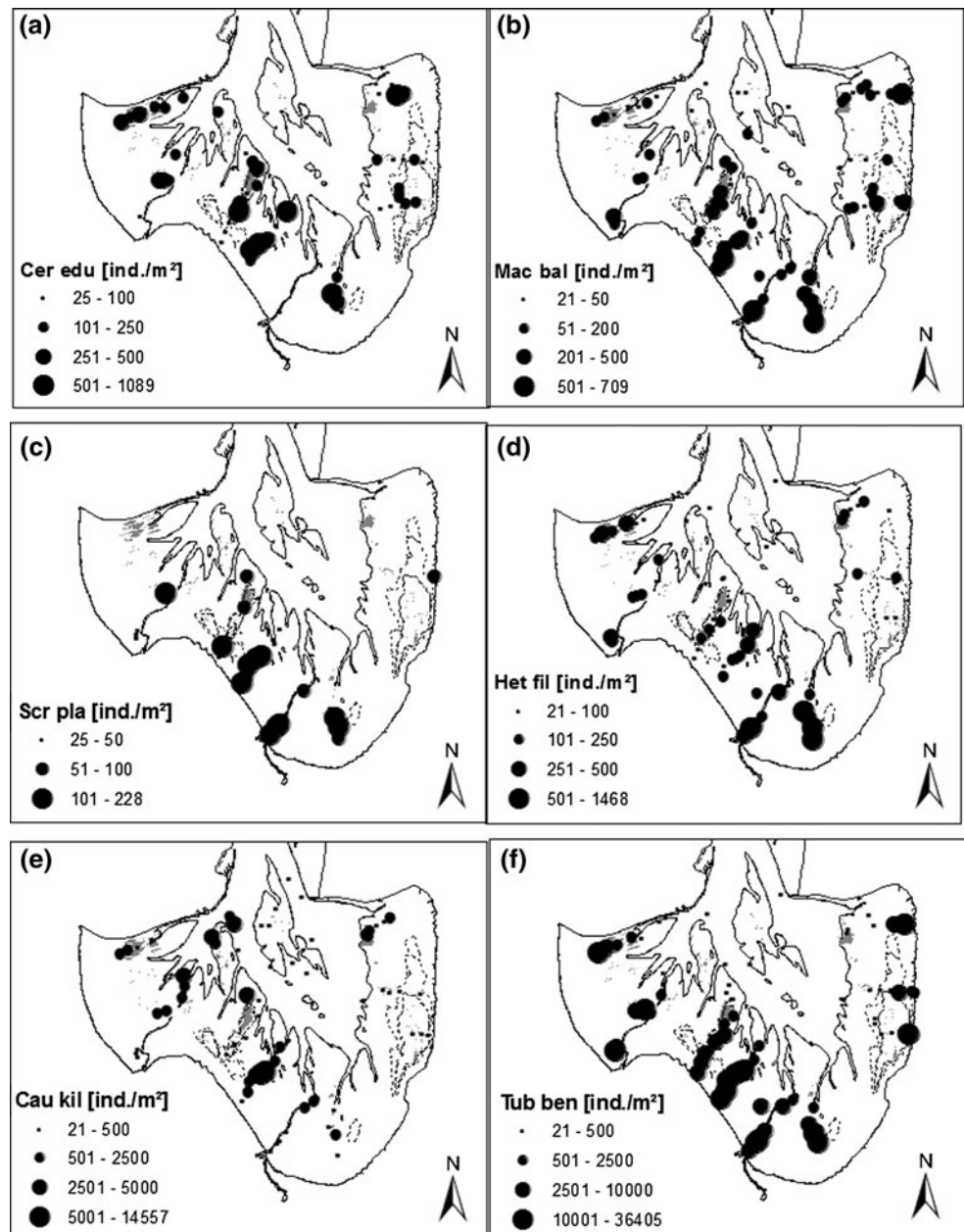
a contents. The community revealed the second highest mean abundance and moderate values of Shannon-Wiener diversity and evenness, respectively. The community was numerically dominated by the subsurface deposit feeding *T. benedii* (Fig. 3f), which reached abundances of more than 40,000 ind./m², and again *H. ulvae*. Higher abundances were also found for *P. elegans*, *Corophium volutator* (Fig. 4b), *R. obtusa*, *Heteromastus filiformis* (Fig. 3d) and Juveniles of *Nereis* spp.. In general, the omnivorous feeding ragworm *Hediste diversicolor* (Fig. 2b) occurred widespread in this muddier upper intertidal area. The dissimilarity between Community 2 and Communities 1, 3-6 was mainly caused by the two dominant species *T. benedii* and *P. elegans*. Classified as subsurface and surface deposit

feeders, both species presented also the dominant feeding modes of this community.

Communities 3 and 4 both were referred to as mixed sediments. Community 3 included 15 stations (mean similarity of 33 %), which were widely distributed over the lower intertidal flats of the Jade Bay area predominantly found along the margins of the tidal gullies and tidal channels. Six stations in the eastern Jade Bay were located near *Mytilus* beds. Community 4 was summarized by 13 stations (mean similarity of 23 %) located in the southern part of the Jappensand (central Jade Bay) and along the tidal inlets in the western part of the Jade Bay. The environmental characteristics of both communities were rather similar according to moderate mud, chl *a* and TOC

Fig. 3 Distribution patterns of dominant bivalve, polychaete and oligochaete species (mean ind./m²) in the Jade Bay.

a *Cerastoderma edule*,
b *Macoma balthica*,
c *Scrobicularia plana*,
d *Heteromastus filiformis*,
e *Caulleriella killariensis*,
f *Tubificoides benedii*



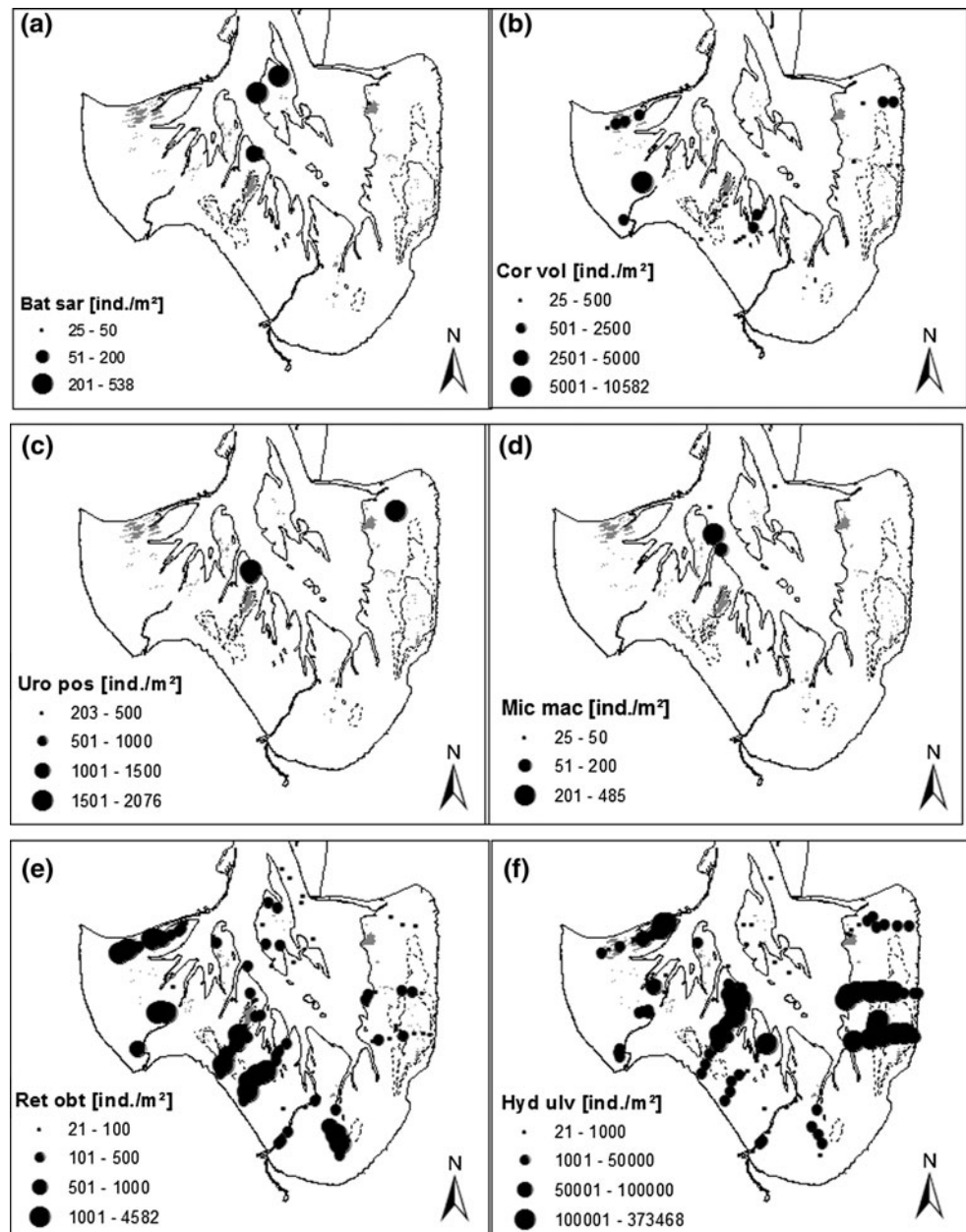
contents, but differed in median grain size. Submergence time varied between 10.7 and 14.5 h, respectively. In Community 3, species richness and mean abundance were low, but Shannon-Wiener diversity and evenness high. The community structure was numerically dominated by interface feeding polychaetes, such as *C. killariensis* (Fig. 3e) and *P. elegans*, as well as *H. ulvae*. These three dominant species, which contributed with 85 % to the total macrofauna abundance, were also responsible for the distinction with the five other communities. Surface deposit and interface feeders dominated the community structure in terms of feeding modes. Community 4 was characterized by the lowest species richness and the lowest mean abundance in contrast to the five others. Trophic structure in

terms of abundance was dominated by subsurface deposit-, surface deposit- and interface feeders, and predators caused by the characteristic species *S. armiger*, *H. ulvae*, *C. killariensis* and *R. obtusa*. *S. armiger* (Fig. 2d) represented the most and widespread polychaete of the lower intertidal area, reaching a maximum abundance of 1,519 ind./m².

The sandflat community (Community 5) included 14 stations (mean similarity of 15 %) characterized by the lowest mud, chl *a* and TOC contents in the Jade Bay, but highest median grain size. Submergence time was 10.4 h, respectively. Stations were found in the lower intertidal central part of the Jade Bay (Jappensand) and on sandflats along the adjacent channels Stenkentief and Vareler Fahrwasser, which consisted of very fine to medium sands.

Fig. 4 Distribution patterns of dominant amphipod and gastropod species (mean ind./m²) in the Jade Bay.

a *Bathyporeia sarsi*,
b *Corophium volutator*,
c *Urothoe poseidonis*,
d *Microprotopus maculatus*,
e *Retusa obtusa*, **f** *Hydrobia ulvae*



A total of 26 species were found. Mean abundance, Shannon-Wiener diversity and evenness revealed moderate values. Characteristic species were *H. ulvae* and *S. armiger*, several sand-licking amphipods (*U. poseidonis*, *Bathyporeia sarsi*; Fig. 4a, c) and juveniles of the polychaete *Nephtys* spp.. The two amphipod species occurred exclusively in Community 5, and were attributed to the differences between Community 5 and Communities 1–4 and 6. Additionally, these species contributed to the high percentage of sand-lickers in this community. Surface deposit feeders were again the dominant feeding mode.

The subtidal community (Community 6) (mean similarity of 17 %) was located within the adjacent channels (Ahne, Vareler Fahrwasser) characterized by 24 h of submergence

time, sediments with high median grain size, low mud, chl *a* and TOC contents. This community was characterized by the highest species richness, Shannon-Wiener diversity and evenness. The mean abundance was relatively low with $3,991 \pm 2,547$ ind./m² similar to Community 3. *S. armiger*, the amphipod *M. maculatus* (Fig. 4d) and the polychaete *Lanice conchilega* were the dominant species. Other species numerically dominating in this community were polychaetes, such as *P. elegans*, *Aricidea minuta*, *Eteone longa* (Fig. 2f) and *Phyllodoce mucosa*, accompanied by *R. obtusa* and the pantopod *Nymphon brevirostre*. Dominant feeding modes were subsurface deposit- and interface feeders, followed by predators. Surface deposit feeders were of minor importance in contrast to the five other communities.

Relationship between spatial distribution and environmental variables

The CCA ordination diagram with stepwise forward selection revealed that submergence time, mud and chl *a* contents were significantly correlated to the variance in species abundance data. The first and second CCA axes together accounted for approximately 81 % of the relations between species and environmental variables. The first axis was most strongly correlated with submergence time followed by median grain size, chl *a* and TOC contents. The second axis was correlated with median grain size and submergence time. The different communities were clearly separated (Fig. 5). Community 6 was characterized by 24 h of submergence time. Community 5, and Community 1 to a lesser degree, were associated with higher median grain size. Community 2 was associated with highest chl *a*, mud and TOC contents, as were Community 3 and 4, but to a lesser degree.

Species (e.g. *L. conchilega*, *M. maculatus*, *S. armiger*, *A. minuta*) related to a longer submergence time were positively correlated to the first axis. Species such as *B. sarsi* and *U. poseidonis*, which were positively correlated to the second axis, related to a higher median grain size. In contrast, species such as *C. volutator*, *T. benedii* and

H. filiformis related to more muddy sediment, were negatively correlated.

Spearman rank correlations between species abundance and environmental variables revealed significant species-specific relationships similar to the CCA presented in Table 2. Macrofauna abundance and species richness were positively correlated to mud, TOC, and chl *a* contents, but negatively to median grain size and submergence time. Especially, the abundance of macrofauna species such as *T. benedii*, *H. filiformis*, juvenile *Nereis* spp., *H. diversicolor* and *R. obtusa* were significantly positively correlated with the mud content, total organic carbon (TOC) and total carbon (TC) contents, but negatively correlated with median grain size and submergence time. In contrast, the abundance of *S. armiger*, *B. sarsi*, *U. poseidonis*, *Arenicola marina* and *Capitella capitata* showed a significantly positive correlation with median grain size, but a significantly negative or no correlation with chl *a* content. Similar results were found for *E. longa* and *Ampharete acutifrons*. Autocorrelations between the environmental variables confirmed negative correlations between submergence time and TOC, chl *a* and mud contents (-0.34 ; -0.60 ; -0.36 , $p < 0.001$), but a positive correlation between submergence time and median grain size (0.37 , $p < 0.001$). Median grain size correlated significantly negative with TOC (-0.79 , $p < 0.001$), chl *a* (-0.78 , $p < 0.001$) and mud contents (-0.80 , $p < 0.001$), but mud content correlated positively with TOC (0.86 , $p < 0.001$) and chl *a* (0.76 , $p < 0.001$) contents.

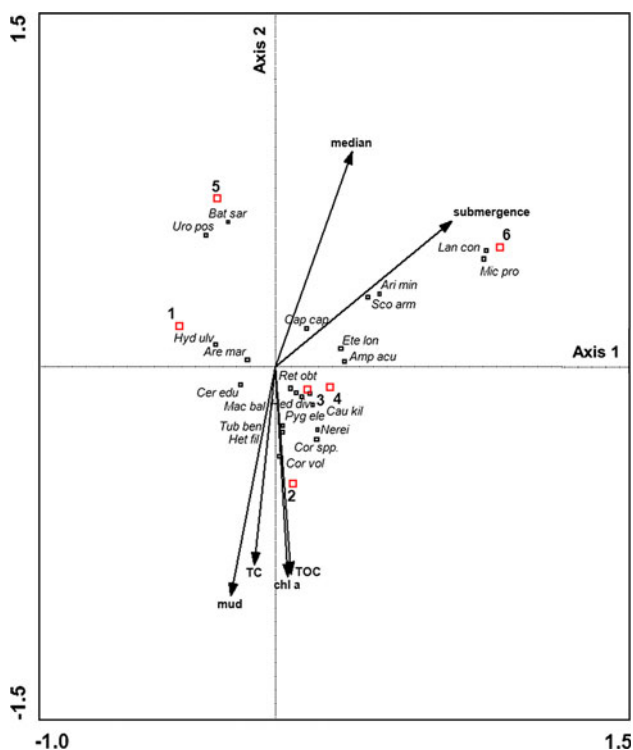


Fig. 5 Species-environmental variables triplot of CCA with different communities, environmental variables selected by the forward selection procedure (indicated by arrows) and selected species. For abbreviation of the macrofauna species names see Appendix Table 5

Discussion

Relationships between spatial distribution of macrofauna communities and environmental variables

The spatial distribution of macrofauna communities in the Jade Bay was best explained by the variability in submergence time, sediment composition (mud content, grain size) and chl *a* content, all following an intertidal gradient. Our results agree with several studies in other areas of the Wadden Sea that sediment characteristics, food availability (expressed as TOC and/or chl *a* contents) and intertidal height (submergence time) are the primary causal factors for the distinct distribution patterns of intertidal macrofauna species resulting in characteristic zonation patterns (Beukema 1988; Junoy and Viéitez 1990; Ysebaert et al. 2003; van Colen et al. 2009). Salinity, which is also a major factor affecting the macrofauna community structure in estuaries (Ysebaert et al. 1998, 2003; Ysebaert and Herman 2002), was of rather minor importance in the whole polyhaline Jade Bay with no major freshwater influence.

Table 2 Spearman rank correlations between species densities and environmental variables (sediment fractions: >63 μm , <63 μm (mud) expressed as percentage, median grain size (μm), total carbon (%), TOC (%), Chl *a* (mg/m^2) and submergence time (h)

Species	>63 μm (%)	<63 μm % (mud)	Median grain size (μm)	Total carbon (%)	TOC (%)	Chl <i>a</i> (mg/m^2)	Submergence (h)
<i>Hydrobia ulvae</i>	-0.12**	0.06	-0.14***	0.25***	0.21***	0.32***	-0.38***
<i>Cerastoderma edule</i>	-0.08*	0.13***	-0.13**	0.10*	0.06 ns	0.21***	-0.28***
<i>Pygospio elegans</i>	-0.19***	0.18***	-0.14***	0.14***	0.13***	0.19***	-0.24***
<i>Tubificoides benedii</i>	-0.59***	0.53***	-0.52***	0.49***	0.45***	0.64***	-0.62***
<i>Scoloplos armiger</i>	0.34***	-0.26***	0.38***	-0.31***	-0.28***	-0.44***	0.44***
<i>Corophium volutator</i>	-0.11**	0.14***	-0.16***	0.07	0.08	0.09	-0.17***
<i>Corophium</i> spp.	-0.21***	0.26***	-0.23***	0.15***	0.15***	0.20 ***	-0.20***
<i>Eteone longa</i>	-0.07	0.09*	-0.02	0.01	-0.02	0.09	-0.15***
<i>Hediste diversicolor</i>	-0.43***	0.34***	-0.35***	0.36***	0.32***	0.52***	-0.44***
<i>Bathyporeia sarsi</i>	0.24***	-0.24***	0.23***	-0.23***	-0.22***	-0.20***	0.08
<i>Caulleriella killariensis</i>	-0.26***	0.19***	-0.25***	0.14***	0.14***	0.18**	0.06
<i>Retusa obtusa</i>	-0.34***	0.31***	-0.24***	0.28***	0.23***	0.38***	-0.28***
<i>Urothoe poseidonis</i>	0.24***	-0.15***	0.13**	-0.26***	-0.25***	-0.15**	-0.03
<i>Ampharete acutifrons</i>	-0.09*	0.12**	-0.05	0.08*	0.03	0.02	0.08*
<i>Arenicola marina</i>	0.11**	-0.09*	0.06	-0.15***	-0.15***	0.001	-0.23***
<i>Heteromastus filiformis</i>	-0.46***	0.44***	-0.42***	0.35***	0.33***	0.42***	-0.30***
<i>Nereis</i> spp.	-0.55***	0.48***	-0.39***	0.43***	0.39***	0.57***	-0.55***
<i>Capitella capitata</i>	0.20***	-0.07	0.11**	-0.21***	-0.21***	-0.01	-0.06
<i>Macoma balthica</i>	-0.37***	0.30***	-0.25***	0.32***	0.29***	0.38***	-0.44***
<i>Scrobicularia plana</i>	-0.35***	0.29***	-0.28***	0.25***	0.22***	0.36***	-0.28***
Species richness	-0.44***	0.37***	-0.33***	0.35***	0.31***	0.46***	-0.53***
Total abundance	-0.24***	0.22***	-0.24***	0.36***	0.32***	0.41***	-0.46***

Significance level $p < 0.001$ is indicated by ***, $p < 0.01$ by ** and $p < 0.05$ by *

Although the Spearman rank correlation coefficients were weakly correlated, results agree well with the species positions in the CCA biplot, which confirms the relationships between the macrofauna communities and the predominant gradients. Similarly, weak relationships were found by van Colen et al. (2009), who explained this with the high small-scale patchiness of benthic organisms. According to their sensitivity to withstand desiccation during increasing times of emersion towards the upper muddy intertidal areas and to cope with increasing hydrodynamics towards the more exposed, lower sandy intertidal areas, species are correlated to the two main gradients in the CCA plot. The general decrease from subsurface deposit and deposit feeders towards interface feeders in terms of abundance with increasing submergence time (decreasing tidal height), reflects also the close relationship between food availability and/or food quality for the macrofauna. Our results (Table 1) confirm that higher sedimentation rates result in nutrient and TOC-rich sediments in the upper intertidal areas, in contrast to the sandflats and subtidal areas, where higher hydrodynamics prevent organic enrichment. These relationships were

previously described by Pearson and Rosenberg (1978) and Hertweck (1994).

The different statistical methods used revealed similar results and divided the Jade Bay into almost the same zones with characteristic macrofauna community compositions corresponding with different habitat types (subtidal vs. intertidal, sandflat, mixed sediments, mudflat, seagrass beds). These results are in accordance with the still common sediment related classification of intertidal flats in the Wadden Sea (see "Introduction").

In addition to the above discussed role of environmental parameters on macrofauna community structure, biological interactions (predation, competition), as well as bio-stabilization, bio-irrigation and bioturbation of species can modify the habitat (Schubert and Reise 1986; Rosenberg 1997; van der Meer et al. 2000; Reise 2002; Orvain et al. 2004, 2006) and, thus, have probably an influence on the distribution patterns of species and the structure of the benthic communities in the Jade Bay. Furthermore, no significant differences in community structure caused by seasonal fluctuations primarily triggered by species-specific differences in the timing of recruitment (ANOSIM

test, unpublished data) were found between spring and early summer.

Comparison of Jade Bay communities with other Wadden Sea areas

In general, the intertidal Jade Bay was characterized by species such as *H. ulvae*, *T. benedii*, *C. killariensis*, *P. elegans*, *S. armiger*, *U. poseidonis*, *R. obtusa*, *C. edule*, *M. balthica*, *C. volutator* and *H. diversicolor*. Although, differences exist in sampling design (area, mesh size), the observed species composition is very similar compared with other areas of the Wadden Sea (e.g. Dörjes 1978; Beukema 1988; Jensen 1992; Hertweck 1994; Reise et al. 1994; van Colen et al. 2009). Reise et al. (1994) found 14 species per sample in Königshafen, while Beukema (1988) for Balgzand and van Colen et al. (2009) for the Zwin nature reserve observed both an average of 11 species per sample. In accordance with these studies, species richness in the Jade Bay revealed an average of 12 species per sample.

The comparison of our six distinct macrofauna communities in the Jade Bay with studies from other areas of the Wadden Sea revealed similar species distribution patterns with respect to their preferred habitat types, but differences in respect to the dominant species were found. The abundances of *H. ulvae* were in an order of magnitude higher than in the western (Beukema 1988) and northern Wadden Sea (Jensen 1992; Reise et al. 1994). This might be caused by the presence of extensive *Z. noltii* seagrass beds in the eastern and south-western Jade Bay at stations of Community 1 (Figs. 1, 4f). In this sandy, generally nutrient-poorer area in the eastern Jade Bay, the occurrence of seagrass beds may increase the rate of sedimentation (Herkül and Kotta 2009) and the presence of macroalgae and microalgae growing on the units, used by *H. ulvae* as food source. Also, seagrass beds decrease the risk of dislodgement by water currents and enable the protection for predation by epibenthic predators, such as crabs, shrimps, fishes and shorebirds (Cardoso et al. 2007). These conditions might have caused the highest abundances (>370,000 ind./m²) of *H. ulvae* in this area. In comparison with other Wadden Sea areas a significant contribution of *H. ulvae* to the total macrofauna abundance (and biomass) is also related to the high proportion of seagrass beds, such as in Königshafen (Tables 3, 4) and the Mondego estuary (Cardoso et al. 2002). The high abundances also observed at stations without seagrass beds probably reflect the high spatial variability of *H. ulvae*, which is quite common due to its active grazing on microphytobenthos (Fenchel et al. 1975; Herman et al. 2000), and migrating and floating behavior (Haubois et al. 2002).

The upper intertidal mudflats (Community 2) were dominated by the pelophilous subsurface-deposit feeding oligochaete *T. benedii*, common for muddy intertidal flats (Dörjes et al. 1969; Vöge et al. 2008). Supported by the significant correlation between abundance and mud content, this opportunistic species with a short life span, high productivity, small body size and an invasive ability (Pearson and Rosenberg 1978) is adapted to these sediments rich in organic carbon and able to tolerate anoxic conditions (Giere et al. 1999). A similar autecological potential has been recorded for the opportunistic *P. elegans*, which is well adapted to survive in moderate hypoxic conditions (Kube and Powilleit 1997). Mud offers a favourable substratum for diatoms (de Jonge 1985), expressed by the highest chl *a* content in this community. This might have explained the high abundance of species such as *H. ulvae*, *P. elegans* and juveniles of *Corophium* spp., which feed on benthic diatoms (Fenchel et al. 1975; Hertweck 1994).

A comparison between different mudflat areas in the Wadden Sea shows that the numerical dominance of various small, r-selected and opportunistic species is common (Table 3). On Balgzand, the upper muddy coastal areas were characterized by a *Corophium volutator*-zone dominated by *C. volutator* and *H. ulvae* (Beukema 1988, Beukema and Cadée 1997). In contrast, *M. balthica*, *Tubificoides pseudogaster*, *P. elegans*, *Tharyx* spp. and *H. filiformis* were dominant species in Königshafen (Reise et al. 1994). However, a *Corophium volutator*-zone had occurred there in the 1930s (Reise et al. 2008), as also described for the Jade Bay in the 1930s (Linke 1939). Erosion and sedimentation processes, which have been linked to sea level rise, are suggested to be major causes of these observed long-term changes (Reise et al. 2008, Schückel and Kröncke submitted). In contrast to Balgzand and Königshafen, the present high densities of *T. benedii* in the Jade Bay were related to the higher areal extent of mudflats (43 % of the intertidal area (Meyer and Ragutzki 1999), Table 4), which contained a mean percentage of 76 % sediment mud content. These regional differences of tidal flats in the Wadden Sea are caused by differences of tidal range (macrotidal vs. mesotidal), which affect morphological characteristics (back-barrier island, land-locked bay or open bay) and sedimentary processes (Bungenstock and Weerts 2010). Sedimentation processes in the tidal flats along the Dutch and the German North Sea coasts are mainly controlled (90 %) by the sediment supply from the North Sea (Beets and van der Spek 2000; Hoselmann and Streif 2004). In contrast, Königshafen is predominated by medium sands originating from surrounding dunes (Reise et al. 1994). However, the comparison between the mesotidal Balgzand (Dutch Wadden Sea) and the macrotidal

Table 3 Comparison of the dominant species ranked according to highest species abundance found per m² on intertidal mudflats, mixed sediments, sandflats and seagrass beds in different areas of the Wadden Sea

Mesh size/season dominant species (ind./m ²)	Jade Bay (present study) 0.5 mm/late spring/early summer 2009	Balgzand (Beukema 1988) 1 mm/early spring	Königshafen (Reise et al.1994) 1 mm/sping and autumn 1990*
Mudflats	<i>Tubificoides benedii</i> <i>Hydrobia ulvae</i> <i>Pygospio elegans</i> <i>Corophium</i> spp. <i>Nereis</i> spp.	<i>Corophium volutator</i> <i>Hydrobia ulvae</i>	<i>Tharyx</i> spp. <i>Macoma balthica</i> <i>Pygospio elegans</i> <i>Heteromastus filiformis</i> <i>Tubificoides pseudogaster</i>
Mixed sediments	<i>Caulerliella killariensis</i> <i>Hydrobia ulvae</i> <i>Pygospio elegans</i> <i>Scoloplos armiger</i>	<i>Hydrobia ulvae</i> <i>Cerastoderma edule</i> <i>Mya arenaria</i> <i>Mytilus edulis</i>	
Sandflats/ <i>Arenicola</i> -sandflats	<i>Hydrobia ulvae</i> <i>Scoloplos armiger</i> <i>Urothoe poseidonis</i> <i>Bathyporeia sarsi</i>	<i>Scoloplos armiger</i>	<i>Hydrobia ulvae</i> <i>Scoloplos armiger</i> <i>Tubificoides benedii</i> <i>Cerastoderma edule</i> <i>Hediste diversicolor</i> <i>Macoma balthica</i>
Seagrass beds	<i>Hydrobia ulvae</i> <i>Cerastoderma edule</i> <i>Tubificoides benedii</i> <i>Pygospio elegans</i> <i>Retusa obtusa</i> <i>Macoma balthica</i>		<i>Hydrobia ulvae</i> <i>Scoloplos armiger</i> <i>Cerastoderma edule</i> <i>Tubificoides benedii</i> <i>Littorina littorea</i>

* Data are combined

Table 4 Comparison of the coverage of intertidal mudflats, mixed sediments, sandflats and seagrass beds of the entire intertidal (area in %) between different areas of the Wadden Sea

Area (in %)	Jade Bay (Meyer and Ragutzki 1999; Adolph 2010)	Balgzand (Beukema 1974)	Königshafen (Reise et al.1994)
Mudflats	43.4	20	9.0
Mixed sediments	16.6	50	
Sandflats	30.9	30	75.9
Seagrass beds	8.1	0	12.4

Jade Bay (German Wadden Sea) mudflat areas reveal that size and mud content varied largely. On Balgzand, only 20 % (Table 4) of the intertidal area contained sediments with a mean percentage of only 10–24 % mud content (Beukema 1974, 1988). This is probably caused by a northward transport of sand brought into the back-barrier basin derived from the fronting barrier (Beets and van der Spek 2000), resulting in the dominance of sandy sediments (Beukema 1988). Higher percentages of mud content in the sediments affect the spatial distribution of macrofauna

species (Sakamaki and Nishimura 2009). An increase in mud content causes an increase in sediment cohesiveness resulting in an impermeable and high organically concentrated sediment layer, which is harmful for sensitive species suffer from anoxic and sulfidic conditions (Sakamaki and Nishimura 2009), but seems to be advantageous for *T. benedii* in the Jade Bay.

Two communities typical for mixed sediments were found in the Jade Bay. According to Beukema (1988) and supported by our results, these areas were defined as intermediate tidal flats characterized by mixed sediments and moderate submergence times, where most species of the mudflat and sandflat areas co-occurred. However, the cluster analysis revealed two significant distinct communities different in terms of species richness, mean abundance and species dominance. Differences were mainly attributed to the presence or absence of *C. killariensis*, *P. elegans*, *H. ulvae* and *S. armiger*. In Community 3 the high abundances of *P. elegans*' biogenic structures may have additionally affected the macrofauna. The increase of the psammophilous orbiinid polychaete *S. armiger* in Community 4 indicated an increase in hydrodynamical

stress, expressed by the somewhat higher median grain size and longer submersion times. Stronger tidal currents at stations of this community are also confirmed by the lower TOC content resulting in the lowest macrofauna densities and species richness.

The intermediate tidal flats on Balgzand were, in a similar manner, numerically dominated by *H. ulvae* (Table 3), but also by suspension-feeding bivalves (*C. edule*, *M. edulis* and *Mya arenaria*) (Beukema 1988), which declined since the 1990s (Beukema and Dekker 2005). As mentioned above for the mudflats, there is evidence that these differences in species composition and abundance between our present and earlier studies (in the Jade Bay and other parts of the Wadden Sea) were related to long-term changes. For instance, several studies discussed the absence of severe winters in the last two decades to be responsible for the lower recruitment success of bivalve species in different areas of the Wadden Sea (e.g. Strasser et al. 2003; Beukema and Dekker 2005; van der Graaf et al. 2009), as well as observed in the Jade Bay (Schückel and Kröncke submitted).

The sandflats (Community 5) located in the central part (Jappensand) and at the margins of the northern entrance of the Jade Bay were dominated by the opportunistic *S. armiger* and mobile amphipods such as *U. poseidonis*, *B. sarsi* and *B. pilosa*. As commonly known from exposed beaches, *S. armiger* and the fast swimming and digging amphipods are typical well-adapted inhabitants of unstable, well oxygenated coarser sandy sediments (pers. observation; Degraer et al. 2003), which is supported by the CCA plot. This explains why corresponding community structures were found at the lower and exposed marginal areas of Balgzand (Beukema 1988) and the Lütetsburger Plate (Steuwer 2002), on the sandflats in Spiekeroog (Grotjahn 1990) and Königshafen (Reise et al. 1994), as well as on the emerging flood delta shoals between the islands of Rømø and Sylt (Lackschewitz and Reise 1998). Especially in Königshafen, the large contribution of sandflats (76 %, Table 4) and the predominance of medium sands might be a structuring factor resulting in higher abundances of *S. armiger* in this part of the Wadden Sea than in the Jade Bay. Higher densities of *Bathyporeia* were also found in the transition area between intertidal and subtidal, as also reported for the Knechtsand by Michaelis (1969).

The subtidal community (Community 6) was dominated by the cosmopolitan *S. armiger* in terms of abundance. Adapted to mobile sediments, this species indicated a higher hydrodynamic stress and tidal currents. Population studies on genetic divergence, reproductive strategies and tolerance to hypoxia of *S. armiger* in subtidal and intertidal areas indicated a sibling species: the intertidal “Type I”

and the subtidal “Type S” (Kruse et al. 2003, 2004). Thus, it might be the case that Community 6 was dominated by the subtidal “Type S”, but Communities 4 and 5 by the intertidal “Type I”. Further genetic studies are necessary to clear this assumption. In addition, the tube-building polychaetes *L. conchilega* and *P. elegans*, as well the amphipod *M. maculatus*, which is common for subtidal flats, occurred in high abundances. Comparing this community structure with other shallow subtidal areas, an almost similar species composition was found in the exposed sandy inlets of the Wichter Ee (Nehmer and Kröncke 2003) and the Otzumer Balje (Reiss and Kröncke 2001) in the East Frisian Wadden Sea.

Of course, our communities revealed a large overlap of dominant species in the different communities (Table 1), which is commonly known from other studies (Reise et al. 1994; Ysebaert and Herman 2002; van Colen et al. 2009; Puls et al. 2011), indicating the wide range of ecological tolerance of these species along the intertidal gradient. However, our results revealed significant differences between the macrofauna communities in the Jade Bay compared with other, more homogenous Wadden Sea areas. The main reason for these differences is the large variation in the proportion of mudflats between areas and the higher sediment mud contents in most of the Jade Bay mudflats resulting, for instance, in the dominance of *T. benedii*. The macrotidal and special bay shaped character of the Jade Bay area seems to cause the regional-specific sedimentation processes that in turn influence the sediment composition, submergence time and food availability for the macrofauna communities, in comparison with other Wadden Sea areas.

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Appendix

See Table 5.

Table 5 List of macrofauna species together with its abbreviations used in the text, tables and figures

Abbreviation	Species name
<i>Amp acu</i>	<i>Ampharete acutifrons</i>
<i>Are mar</i>	<i>Arenicola marina</i>
<i>Ari min</i>	<i>Aricidea minuta</i>
<i>Bat pil</i>	<i>Bathyporeia pilosa</i>
<i>Bat sar</i>	<i>Bathyporeia sarsi</i>
<i>Cap cap</i>	<i>Capitella capitata</i>
<i>Cau kil</i>	<i>Caulleriella killariensis</i>
<i>Cer edu</i>	<i>Cerastoderma edule</i>
<i>Cor spp.</i>	<i>Corophium spp.</i>
<i>Cor vol</i>	<i>Corophium volutator</i>
<i>Cum goo</i>	<i>Cumopsis goodsir</i>
<i>Ete lon</i>	<i>Eteone longa</i>
<i>Hed div</i>	<i>Hediste diversicolor</i>
<i>Het fil</i>	<i>Heteromastus filiformis</i>
<i>Hyd ulv</i>	<i>Hydrobia ulvae</i>
<i>Lan con</i>	<i>Lanice conchilega</i>
<i>Mac bal</i>	<i>Macoma balthica</i>
<i>Mic mac</i>	<i>Microprotopus maculatus</i>
<i>Nep hom</i>	<i>Nephtys hombergii</i>
<i>Nep spp.</i>	<i>Nephtys spp.</i>
<i>Nerei</i>	<i>Nereis spp.</i>
<i>Nym bre</i>	<i>Nymphon brevivirostre</i>
<i>Phy muc</i>	<i>Phyllodoce mucosa</i>
<i>Pyg ele</i>	<i>Pygospio elegans</i>
<i>Ret obt</i>	<i>Retusa obtusa</i>
<i>Ret spp.</i>	<i>Retusa spp.</i>
<i>Sco arm</i>	<i>Scoloplos armiger</i>
<i>Scr pla</i>	<i>Scrobicularia plana</i>
<i>Tub ben</i>	<i>Tubificoides benedii</i>
<i>Uro pos</i>	<i>Urothoe poseidonis</i>

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