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ORIGINAL ARTICLE

Benthic macrofauna communities of the submersed Pleistocene Elbe valley in the southern North Sea

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Abstract Macrozoobenthic community structure was studied in two surveys along a transect of 13 stations following the submersed Pleistocene Elbe valley in the south-eastern North Sea during May to June 2000 and March 2001. Two replicates of bottom samples were taken with a van Veen grab of 0.1 m² sampling size. In order to analyse the benthic macrofauna communities, the animals obtained were identified and counted, and MDS and cluster analysis were performed. Out of 200 taxa identified, 84 were polychaetes, 46 molluscs, 40 crustaceans, 15 echinoderms, and 15 belonged to other groups. Mean abundance was 4,860 individuals per m², mean biomass 32.9 g ash free dry mass per m². Mean diversity was 1.76 and mean evenness 0.54. The macrofauna of the Pleistocene Elbe valley is composed of three associations according to the cluster analysis. Each association is described by a combination of characterizing and discriminating species. An *Amphiura-brachiata*—*Tellinomya-ferruginosa*-association was found in the south-eastern part of the depression, whereas a transitional association with elements of both assemblages lead to an *Amphiura-filiformis*—*Galathowenia-oculata*—*Nuculoma-tenuis*-association in the north-western part of the valley. In the context of the entire southern North Sea, both associations are small-scale substructures, and as such are

contained in the *Nucula-nitidosa*-community and the *Amphiura-filiformis*-community, respectively. A north-westward shift of the community of the southern Elbe valley was found and discussed as a possible consequence of warm winters of the last decades.

Keywords Benthic communities · Macrozoobenthos · North Sea · Pleistocene Elbe valley

Introduction

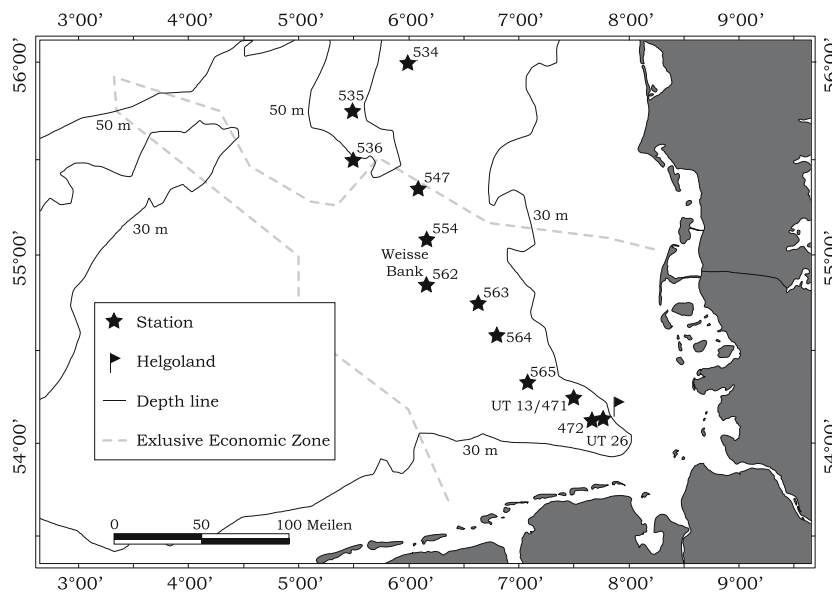
The macrozoobenthos of the offshore North Sea has been the subject of scientific studies since the end of the 19th century. The first quantitative work was conducted by Petersen (1914) and Hagmeier (1925). The main objects of these early studies were related to fish biology. Later studies aimed at creating detailed pictures of the biotic community structure of the seafloor and its connections to biotopes, pollutions, and nature conservation (e.g. Caspers 1939; Stripp 1969; Salzwedel et al. 1985; Duineveld et al. 1991; Heip et al. 1992; Künitzer et al. 1992; Rachor and Nehmer 2003). Gear and methods employed have constantly been improved, and with the introduction of computers the possibility arose to analyse vast amounts of data from exhaustive surveys with statistical methods (Salzwedel et al. 1985).

Unusual, geographically limited structures such as the Pleistocene Elbe Valley and the Helgoland Deep Trench with their special hydrographical characteristics were of particular interest for scientific studies (Caspers 1939; Figge 1980; Rachor and Albrecht 1983; Büsselberg 1985; Berberich 1989; Künitzer 1990). The valley is a depression in the seafloor,

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Fig. 1 Macrozoobenthos study sites in the Pleistocene Elbe valley (southern North Sea); positions of stations 471 and U13 are identical



where cold bottom water can be advected along the valley into the German Bight. Furthermore, during the years from 1981 to 1983, low oxygen was recorded in bottom waters of the valley, which led to damaged fauna of the neighbouring seafloor (Rachor and Albrecht 1983).

The analysis of the macrozoobenthos of the Pleistocene Elbe valley carried out in 1984 was limited to the south-eastern and central parts of the valley from west of the island of Helgoland to east of the Weisse Bank (Büsselberg 1985). In 1990, the valley was investigated along its whole length, but the emphasis of that study was on seasonal variability of environmental parameters in the central North Sea (Künitzer 1990).

The aim of the present study is to describe the macrozoobenthic community structure of the whole Pleistocene Elbe valley in order to evaluate possible changes in the communities of the area by a comparison with the above previous studies. Another aim is the evaluation of the valley, its habitats, and communities with respect to their role in nature protection concepts. The valley is important in netting soft bottom habitats with the rocky habitats off Helgoland, as the eastern slope includes pebbles, stone fields, and erratic blocks. In this area, communities are tightly interlocked and display high-species diversity. Furthermore, in deeper habitats of the valley, salinity is relatively stable and the fluctuation of temperature is less intensive than in shallow waters near the coast. Thus, the valley serves as a retreat and an area of regeneration for some species (Rachor and Nehmer 2003).

Methods

Study area

During the last European glaciation until about 15,000 years ago, most of the present seafloor of the North Sea was above the waterline. Many structures in seabed morphology can be tracked back to that time (Becker 1990). The Pleistocene Elbe valley, situated in the south-eastern North Sea (Fig. 1), is the most conspicuous relict from that period. The former riverbed of the Elbe can still be distinguished from the surrounding seafloor as a channel ~25–40 km wide extending from the Southeast (including the Helgoland Deep Trench, which is also influenced by tectonic processes) to the Northwest of the German Bight up to the Dogger Bank. As such, it has peculiar hydrographical features, which have attracted much attention of various investigations in the past (Caspers 1939; Figge 1980; Rachor and Albrecht 1983; Büsselberg 1985; Berberich 1989; Künitzer 1990).

Sampling of macrozoobenthos

Macrozoobenthos was sampled at 13 stations in the Pleistocene Elbe valley using a van Veen grab of 0.1 m² sampling size during cruises onboard RV “Heincke” in May and June 2000 and onboard RV “Uthörn” in March 2002, respectively (Fig. 1, Table 1). Sampling during summer 2000 took place in the setting of the project “Erfassung und Bewertung ökologisch wertvoller Lebensräume in der Nordsee” of the German Federal Agency for Nature Conservation (BfN) (Rachor

Table 1 Sampling and boitic data of the macrozoobenthic communities of the Pleistocene Elbe valley (southern North Sea)

Cluster/station	Position		Depth (m)	Sediment	Species number	H'	J'	S (90%)	Abundance (ind m ⁻²)	Biomass (g ⁻²)
	Latitude (N)	Longitude (E)								
Southeast					76	2.26 (2.45)	m 0.67 (0.69)	m 15 (22)	4575 (2705)	m 42.47 (24.12)
UT26	54°08.04'	07°45.92'	38	s FS	43	0.9 (2.74)	0.24 (0.73)	3 (19)	9920 (1940)	99.71 (15.17)
UT13	54°14.87'	07°30.56'	40	m FS	40	1.41 (2.14)	0.38 (0.58)	6 (16)	7110 (2700)	66.65 (43.15)
472	54°08.10'	07°40.07'	40	m FS	39	2.58	0.71	16	5700	57.85
471	54°15.09'	07°30.00'	41	FS	34	2.67	0.76	18	1945	27.09
565	54°34.90'	06°47.97'	41	m FS	27	2.2	0.67	10	3450	18.97
564	54°19.96'	07°05.19'	39	m FS	34	2.32	0.66	15	2710	21.14
Central					49	2.17	m 0.62	m 14	3528	m 21.51
563	54°45.09'	06°38.00'	41	m FS	40	2.17	0.59	11	5200	28.28
562	54°51.94'	06°09.91'	40	m FS	29	2.17	0.64	12	1855	14.74
Northwest					82	1.62	m 0.44	m 11	6528	m 22.7
554	55°04.92'	06°09.76'	47	m FS	40	1.44	0.39	4	6945	26.80
536	55°29.98'	05°29.94''	53	fs M	42	1.79	0.48	11	6110	28.59
535	55°45.11'	05°30.21'	54	fs M	46	1.66	0.43	7	7090	18.59
534	56°00.00'	05°59.07'	48	fs SI	34	1.57	0.45	12	3440	12.46
Single station										
547	50°20.98'	06°04.96'	49	s M	21	1.33	0.44	5	1700	7.37

Values in brackets were calculated with *Phoronis* spp. excluded, H' diversity (Shannon and Weaver 1949), J' evenness (Pielou 1966), m median, *ind* individuals, sediment types: *FS* fine sand, *M* mud, *SI* silt, *fs* fine sandy, *m* muddy, *s* sandy

2006). Two replicates were taken at each station. Samples were sieved over 1 mm meshes and preserved in 5% buffered formalin. Biomass is given in ash free dry mass and calculated from wet mass using conversion factors provided by Brey (2001).

Community analysis

Differences in the structure of the benthic fauna of the valley were elaborated by running cluster analysis as well as MDS. Juvenile animals were removed from the species list before running the community analysis to exclude seasonal effects caused by different times of sampling during the years 2000 and 2001. Stations were grouped according to the results of the cluster analysis as well as MDS. The similarity matrix of both methods was calculated with Bray–Curtis-Index (Bray and Curtis 1957); after a fourth root transformation, the group average method was applied. Analyses were carried out with the programme Primer (Version 5.1.2).

Characterization of station groups

Diversity H' (Shannon and Weaver 1949), evenness J' (Pielou 1966), and S (90%) that gives the number of species, which represent 90% of the individuals, were calculated to characterize station groups obtained from cluster analysis and MDS. For further description of the communities, characterizing species (Salzwedel et al. 1985) as well as discriminating species (Clarke and Warwick 1994) were identified.

After Salzwedel et al. (1985) characterizing species are determined out of those with a numerical dominance greater than 1% within a certain station group, if they satisfy at least three of the following conditions:

- numerical dominance within the station group higher than 5%,
- presence within the station group higher than 80%,
- fidelity of abundance (FA) (degree of association regarding individuals DAI) higher than 66%, or
- fidelity of presence (FP) (degree of associations regarding stations DAS) higher than 66%.

The expressions of DAI and DAS introduced by Salzwedel et al. (1985) were renamed by FA and FP (Rehm 2002).

Discriminators were calculated as shown by Clarke and Warwick (1994). A suitable discriminator is a species k , which shares as much dissimilarity δ_k as possible of the dissimilarity δ of two station groups. In addition, the species should be distributed evenly over the station group, which means the standard deviation $SD(\delta_k)$ should be low. Therefore, suitable discriminators are characterized by high values of $\delta_k/SD(\delta_k)$.

Results

Macrobenthic community structure

As shown in Fig. 2, there are three clusters at a similarity level of 45% and a single outgrouping station (547).

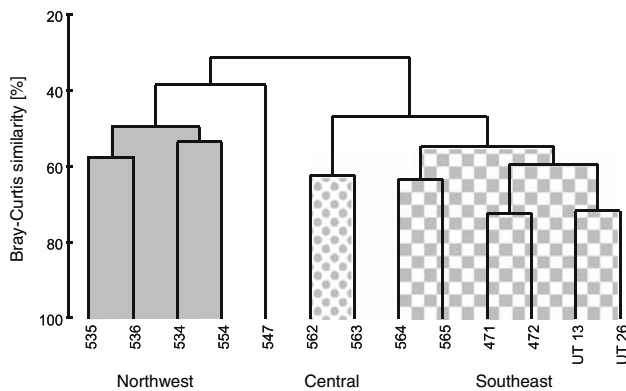


Fig. 2 Cluster analysis of macrozoobenthic abundance calculated with Bray–Curtis similarity; forth root transformation and group average method were applied

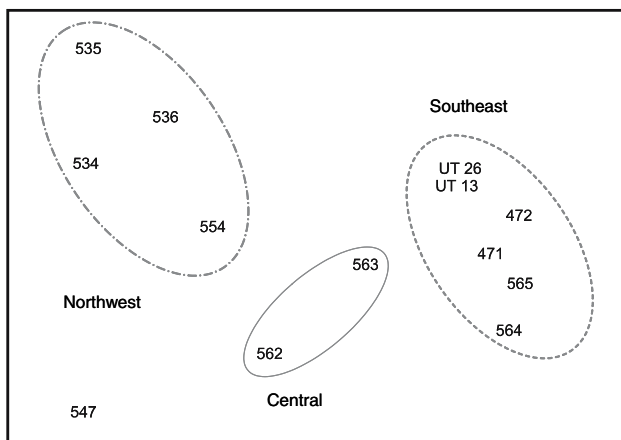


Fig. 3 MDS plot on macrozoobenthic abundance calculated with Bray–Curtis similarity and fourth root transformation; stress = 0.07

According to the geographic arrangement along the Elbe valley, the clusters were named Northwest, Central, and Southeast. At a similarity level of 30%, the Pleistocene Elbe valley is divided into two clusters only, the first containing the station groups Central and Southeast, the second Northwest, now joined with the single station 547.

No distinct station groups are visible from the MDS (Fig. 3). Only stations of cluster Southeast are closer to each other than most of the other stations and confirmed by the MDS, while station 547 is again separated from all other stations. The distance between the stations of groups Northwest and Central is similar; however, the arrangement of the stations again roughly resembles the geographical arrangement along the Pleistocene Elbe valley. Evenly distributed stations along the valley display a gradual change of macrobenthic communities.

Characterization of the communities

Differences in biotic features between the station groups for species number, diversity, evenness, and S (90%) are shown in Table 1. Species number is lowest in the central group, where only four grabs were taken. Diversity, evenness, and S (90%) decrease from coastal stations towards the open sea. Exceptions of this trend are stations UT13 and UT26, due to mass occurrences of *Phoronis* spp. in 2001. After the exclusion of *Phoronis* spp., the values of diversity, evenness, and S (90%) correspond with those of the remaining stations of station group Southeast.

The variation in biomass is very high. However, biomass at stations UT13, UT26, and 472 is noteworthy, as the values are exceptionally high. Again, for UT26, this is due to the mass occurrence of *Phoronis* spp, which does not, however, apply for stations UT13 and 472 (Table 1).

Salzwedel et al. (1985) picked characterizing species out of those which had dominances within an association of at least 1%. In station group Northwest, three characterizing species were identified, and seven in station group Southeast (Table 2). In contrast to the high number of characterizing species in the latter group, in station group Central no species fulfilled the criteria.

Unlike characterizing species, discriminators are important for separation of two station groups. Dominance is less important than the contribution of species to the average dissimilarity δ . Generally, discriminators and characterizing species do not have to be identical. Most important discriminators for the station group Southeast are the ophiurid *Amphiura brachiata* and the bivalve *Tellimya ferruginosa* (Table 3). Station group Central is mainly characterized by two discriminators, the amphipod *Harpinia antennaria* and the bivalve *Abra nitida*. Important discriminators of station group Northwest are *Amphiura filiformis*, *H. antennaria*, and the cnidarian *Cerianthus lloydii*. All these discriminators are characterized by their contribution to dissimilarity against both the other station groups or by complete absence in at least one station group.

Based on the analysis of community characterizing species, a north-western *Amphiura-filiformis*–*Galat-howenia-oculata*–*Nuculoma-tenuis*-association was identified. The central association is a transitional one with elements of both the other associations and without characterizing species. Considering the high number of characterizing species in station group Southeast, the association in the southern part of the Pleistocene Elbe valley was named by species which were

Table 2 Characterization of species, which occurred with dominance $\geq 1\%$ in the associations of the Pleistocene Elbe valley (southern North Sea)

Cluster/species	Taxon	ind	med	mean	min	max	dom	pre	FA	FP
Southeast										
Phoronis spp.	Ten	13870	688	2312	30	7980	50.4	100.0	98.1	54.5
Nucula nitidosa	Biv	3185	550	531	55	1075	11.6	100.0	75.5	60.0
Owenia fusiformis	Pol	1980	75	330	10	1275	7.2	100.0	88.9	60.0
Abra alba	Biv	1406	23	234	0	1240	5.1	83.3	100.0	100.0
Scalibregma inflatum	Pol	1090	80	182	0	760	4.0	83.3	99.9	83.3
Amphiura brachiata	Ech	630	105	105	70	155	2.3	100.0	100.0	100.0
Phaxas pellucidus	Biv	460	40	77	25	205	1.7	100.0	87.3	60.0
Tellimya ferruginosa	Biv	435	70	73	35	125	1.6	100.0	95.6	85.7
Nephtys hombergii	Pol	370	58	62	25	105	1.3	100.0	64.9	50.0
Corbula gibba	Biv	326	33	54	0	140	1.2	83.3	10.0	50.0
Mysella bidentata	Biv	335	60	56	0	115	1.2	66.7	33.0	40.0
Central										
Amphiura filiformis	Ech	1780	890	890	625	1155	36.6	100.0	15.9	22.2
Nucula nitidosa	Biv	1000	500	500	45	955	20.5	100.0	23.7	20.0
Corbula gibba	Biv	540	270	270	125	415	11.1	100.0	16.6	20.0
Phoronis spp.	Ten	220	110	110	60	160	4.5	100.0	1.6	18.2
Owenia fusiformis	Pol	220	110	110	0	220	4.5	50.0	9.9	10.0
Nephtys hombergii	Pol	105	53	53	35	70	2.2	100.0	18.4	16.7
Polinices pulchellus	Gas	100	50	50	40	60	2.1	100.0	27.0	20.0
Spiophanes bombyx	Pol	85	43	43	30	55	1.7	100.0	20.0	18.2
Pholoe baltica	Pol	85	43	43	40	45	1.7	100.0	14.4	18.2
Magelona filiformis	Pol	80	40	40	30	50	1.6	100.0	52.6	33.3
Phaxas pellucidus	Biv	65	33	33	15	50	1.3	100.0	12.3	20.0
Corystes cassivelaunus	Cru	55	28	28	25	30	1.1	100.0	40.1	25.0
Thyasira flexuosa	Biv	55	28	28	0	55	1.1	50.0	20.7	12.5
Northwest										
Amphiura filiformis	Ech	8345	2053	2086	1270	2970	48.0	100.0	74.6	44.4
Galathowenia oculata	Pol	3211	105	803	1	3000	18.5	100.0	100.0	100.0
Corbula gibba	Biv	2085	10	521	0	2065	12.0	50.0	63.9	20.0
Mysella bidentata	Biv	635	158	159	25	295	3.7	100.0	62.5	40.0
Pholoe baltica	Pol	390	73	98	35	210	2.2	100.0	66.0	36.4
Lanice conchilega	Pol	305	68	76	0	170	1.8	50.0	68.8	25.0
Lagis koreni	Pol	222	11	56	1	200	1.3	100.0	75.0	33.3
Nuculoma tenuis	Biv	186	30	47	1	125	1.1	100.0	100.0	100.0
Diplocirrus glaucus	Pol	186	20	46.5	1	145	1.1	100.0	91.6	57.1

Ind individuals m^{-2} , *med* median, *min* minimum numbers of species, *max* maximum numbers of species, *dom* numerical dominance (%), *pre* presence (%), *Biv* bivalvia, *Cru* crustacea, *Ech* echinodermata *Gas* gastropoda, *Pol* polychaeta, *Ten* tentaculata, *FA* fidelity of abundance, *FP* fidelity of presence, characterizing species after Salzwedel et al. (1985) are printed in bold letters

both characterizing and discriminating: *Amphiura brachiata*—*Tellimya ferruginosa*-association.

Discussion

In general, the benthic biomass in the southern North Sea decreases with increasing distance from the coast (Rachor 1982; Kröncke and Rachor 1992; Künitzer et al. 1992). A negative correlation of biomass with latitude was found by Heip et al. (1992), which holds true also for the macrozoobenthic community of the Pleistocene Elbe valley. Duineveld et al. (1991) stated a more complex image of biomass distribution; nevertheless, they also found an increased biomass in the area of the island of Helgoland. The values reported in the present study for stations near Helgoland are up to three times higher than those recorded by other authors (Salzwedel et al. 1985; Büsselberg 1985; Duineveld et al. 1991). Towards the northern end of the

Pleistocene Elbe valley, however, biomass values were comparable to those formerly measured. In 1995, correspondingly high biomasses were found to the East off Helgoland (Thatje and Gerdes 1997). At the border of the muddy-sandy area south of Helgoland, biomass reached a maximum of $2,470 \text{ gm}^{-2}$ wet mass, which was ascribed to a mass occurrence of the polychaete *Lanice conchilega*. As the high biomasses of this study are ascribed to mass occurrences of *Phoronis* spp., differences with other studies should not be overestimated. Rachor (1990) stated an increased biomass in 1975 due to eutrophication in comparison to the survey carried out by Hagmeier (1925) in 1923. It is supposed that the trend of increased eutrophication has continued until nowadays (Kröncke and Rachor 1992; Rachor and Nehmer 2003). Recent observations from long term community data off Helgoland (Schröder 2003) support the suggestion that the ecosystem of the inner German bight showed a trend back towards the state of the 1970s (Radach 1998).

Table 3 Discriminating species of the clusters of the Pleistocene Elbe valley (southern North Sea)

Compared clusters/species	Taxon	Average abundance (m ⁻²)		Ind dom	δ_k	$\delta_k/SD(\delta_k)$	Share of δ (%)
		(a)	(b)				
Southeast (a) and Northwest (b), $\delta = 70.71$							
<i>Amphiura filiformis</i>	Ech	3.5	2086.3	48.0	3.94	5.72	5.6
<i>Amphiura brachiata</i>	Ech	105.0	0.0	2.3	2.02	13.14	2.9
<i>Tellimya ferruginosa</i>	Biv	72.5	0.0	1.6	1.82	8.13	2.6
<i>Harpinia antennaria</i>	Cru	0.0	41.3	0.9	1.49	4.74	2.1
Southeast (a) and Central (b), $\delta = 53.36$							
<i>Amphiura filiformis</i>	Ech	3.5	890.0	36.3	3.31	4.68	6.2
<i>Amphiura brachiata</i>	Ech	105.0	0.0	2.3	2.14	11.25	4.0
<i>Abra nitida</i>	Biv	46.7	17.5	1.0	1.36	9.63	2.6
<i>Harpinia antennaria</i>	Cru	0.0	15.0	0.6	1.33	5.29	2.5
<i>Ophiodromus flexuosus</i>	Pol	1.7	1.0	0.0	0.65	6.27	1.2
<i>Cylichna cylindracea</i>	Gas	7.5	1.0	0.2	0.60	5.22	1.1
Northwest (a) and Central (b), $\delta = 58.04$							
<i>Mysella bidentata</i>	Biv	158.8	0.5	3.7	1.91	4.03	3.3
<i>Phoronis</i> spp.	Ten	0.5	110.0	4.5	1.82	3.98	3.1
<i>Magelona filiformis</i>	Pol	0.3	40.0	1.6	1.57	3.41	2.7
<i>Abra nitida</i>	Biv	0.0	17.5	0.7	1.37	11.81	2.4
<i>Cerianthus lloydii</i>	Cni	11.5	0.0	0.3	1.18	3.25	2.0

Ind dom dominance of individuals in compared clusters (%), δ_k share of dissimilarity of species *k*, δ average dissimilarity, *SD* standard deviation, *Biv* Bivalvia, *Cni* Cnidaria, *Cru* Crustacea, *Ech* Echinodermata, *Gas* Gastropoda, *Pol* Polychaeta, *Ten* Tentaculata

Within the valley, diversity and evenness decreased with increasing distance to the coast (towards the northern end of the valley). This is in contradiction to other investigations (Heip et al. 1992; Kröncke and Rachor 1992), but shows a good correlation to the data from the intermediate part of the Pleistocene Elbe valley presented by Salzwedel et al. (1985). For the southern part of the valley, no such trend was recorded (Büsselberg 1985; Salzwedel et al. 1985).

The three associations (station groups) of the Pleistocene Elbe valley are distinguished by their characterizing and discriminating species. The method of calculating discriminators has a major disadvantage, as presence within a station group is not considered sufficiently. Also in our case, fidelities of presence of the discriminating species of station groups Northwest and Centre are low. Therefore, only characterizing species were taken into consideration for the description of the association of station group Northwest. Station group Centre lacks both characterizing species and discriminators with high fidelity of presence, since the elements of its fauna are represented too strongly within both the other associations. The only species that was found exclusively in this association was the polychaete *Podarkeopsis helgolandica*, of which only two specimens were found. Therefore, this association is regarded as a transitional one, situated around a depth of 40 m, connecting the north-western and the south-eastern associations. The 40 m depth line was also described as a border between the two fine sediment

communities of the inner and the outer Exclusive Economical Zone of Germany (Rachor and Nehmer 2003). In the report of the Study Group on the North Sea Benthos Project (ICES SGNSBP Report 2006), the boundary of the two muddy communities of the southern North Sea is 35 m. The transitional association is marked by a low number of species compared to the other associations, which is probably only due to the much lower number of grab samples taken in this association. For the description of station group Southeast, the seven characterizing species were reduced by selecting those species, which are both characterizing and discriminating. Only the two species *A. brachiata* and *Tellimya-ferruginosa* meet both criteria.

Consequently, two main associations along the Pleistocene Elbe valley were found. The *Amphiura-brachiata*–*Tellimya-ferruginosa*-association is located in the south eastern part of the submersed valley, whereas the *Amphiura-filiformis*–*Galathowenia-oculata*–*Nuculoma-tenuis*-association is located in the north western valley. In between, there is a transitional association with elements of the faunas of both other associations.

When the structure of the macrozoobenthic community described above is viewed in the context of the entire study conducted by Rachor and Nehmer (2003), there is no evidence for additional associations within the Pleistocene Elbe valley. Thus, the associations found in this study have to be considered small-scale structures within the *Nucula-nitidosa*-community and

the *Amphiura-filiformis*-community (see Rachor and Nehmer 2003). In the ICES SGNSBP Report (2006), two communities are described for muddy sediments of the Exclusive Economical Zone of Germany as well, but the intermediate part of the Pleistocene Elbe valley is inhabited by both communities, which might reflect the transition recorded in the present study.

Nevertheless, in the years 1983–1988, three associations within the submersed Pleistocene Elbe valley were found by Künitzer (1990), which correspond very closely with the associations of the present study. The characterizing species of the *Amphiura-filiformis*–*Galathowenia-oculata*–*Nuculoma-tenuis*-association appeared with constant dominance in the northern association during these years. The polychaete *Spiophanes bombyx* was the only dominant species of the intermediate part of the valley, which occurred in both studies. Dominant species of the southern part of the Pleistocene Elbe valley which were found by Künitzer (1990) as well were *Phoronis* spp., *Nucula nitidosa*, *Scalibregma inflatum*, *Nephtys hombergii*, and *Mysella bidentata*. As stated by Künitzer, the most dominant species was *Ophiura albida*, which was not among the dominant species in the *Amphiura-brachiata*–*Tellimya-ferruginosa*-association of the present examination.

In the study of the southern Pleistocene Elbe valley of Büsselberg (1985), the benthic community was even more different from the present study. The *Amphiura-filiformis*-association with species of the *Nucula-nitidosa*-association found in 1984 comprised an area, which contained the stations 471/UT13 and 472 of the present study. *Chaetopterus variopedatus*, *Gattyana cirrosa*, *Ampharete* sp., *Lagis (Pectinaria) koreni*, and *S. inflatum* were characteristic representatives of this association. During our study, *Ch. variopedatus* was limited to the northern-most part of the Pleistocene Elbe valley, *G. cirrosa* occurred in the central and northern part, *Lagis koreni* was found in almost all samples with a maximum in the northern part of the area, and *S. inflatum* was recorded in the entire southern part of the valley. Characteristic species found during our study were *A. filiformis* and *Magelona filiformis*.

The *Amphiura-filiformis*/*Tellina-fabula*-association mentioned by Büsselberg (1985) is situated in the area of stations 563, 564, and 565 during 2000. Typical species of the association were *A. filiformis*, *Magelona johnstoni*, *Magelona minuta*, *Fabulina (Tellina) fabula*, and *Perioculodes longimanus*. In 2000/2001, *A. filiformis* was only recorded at station 563, which was the southern border of its distribution. *M. johnstoni* occurred only at station 471 and *M. minuta* was only found at station 562. *F. fabula* was recorded from stations 564, 563, and the southernmost area of the Pleis-

tocene Elbe valley. *P. longimanus*, however, occurred in the entire area and north of it.

The northern-most and most specious association of the year 1984 was the *Amphiura-filiformis*-association, which corresponded with our stations 554 and 562. Most important faunistic elements of this association were *Eulima alba*, *Pectinaria (Amphictene) auricoma*, *H. antennaria*, and *Diastylis rathkei*. The only one species recorded again in the years 2000 and 2001 was *H. antennaria*. *A. auricoma* was found northward only.

The present study shows that serious changes in the community of the Pleistocene Elbe valley have taken place over the past two decades. Of the characteristic species of 1984, *M. johnstoni* and *M. minuta* were only found with a few specimens in 2000; others such as the polychaetes *Amphictene auricoma*, *G. cirrosa*, and *C. variopedatus* drew back into deeper areas of the Pleistocene Elbe valley. *Chamelea gallina* occurred along the entire southern Pleistocene Elbe valley in 1984, while in 2000 it was found only at one station. The most important change we recorded was the substitution of the characterizing species *Amphiura filiformis*, which was formerly an important element along the total Pleistocene Elbe valley. During the present study, the southern association was characterized by *A. brachiata* instead of *A. filiformis*.

Both are important species of the community of muddy sediments of the Bay Biscay. *A. brachiata* and *Clymene oerstedii* are characteristic in the “Infralittoral Étage”; the “Étage du large” is characterized by *A. filiformis* and *Tellina serrata* (Glémarec 1973). Both ophiurids are most important characterizing species of the associations of the submersed Pleistocene Elbe valley, too. Obviously, there was some kind of shift of the community of the Pleistocene Elbe valley towards a community comparable to that of the Bay of Biscay. After Kröncke et al. (2001), a shift of the macrozoobenthic community off Norderney since 1988 is connected to the increase of the North Atlantic Oscillation Index (NAOI). A positive value of the NAOI indicates a warm and moist winter. Since 1971, no period with negative values in at least three consecutive years was recorded (Hurrell 1995, also compare http://www.jisao.washington.edu/data_sets/naoi/).

A consequence of this seemingly recent warming could be a shift of the southern North Sea towards conditions of Atlantic waters. In this case, the Helgoland Deep Trench could prove to be a refuge for formerly common boreal species. Here, stratification of the water column is possible due to a comparatively high depth (up to 60 m) and the special current of the trench. Thus, independent of season cold high-saline bottom water can persist in the trench (Caspers 1939).

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