Long term changes of macrozoobenthos in the Arkona Basin (Baltic Sea)

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In 2001–2004 extensive studies of the macrozoobenthos community within the German Arkona Basin were undertaken. The results with consideration of the habitat conditions prevailing in different depth zones are presented. By multidimensional scaling we distinguished two separate macrozoobenthos communities (global $r = 0.758$, $p = 0.1$), one predominant in a habitat with sandy sediment or gravel and stones at water depths < 35 m (8–11 psu) and the other preferring a muddy habitat with higher salinity (11–23 psu) at water depths > 35 m. Additionally, long-term changes in selected benthic species of the Arkona Basin are described by comparing the recent macrozoobenthic data with data sets of the last 80 years. Special emphasis was placed on the use of historical data as a tool of assessment of changes of macrozoobenthic communities with respect to different habitat conditions. While the distribution patterns of several species under investigation have changed between the different time periods, nevertheless, with few exceptions no consistent changes from the past to present days were observed. The species composition of the macrozoobenthic community in the shallower area was very similar during all time periods. Only in deeper waters did we find differences, which may be explained by past changes in hydrography (e.g. salinity, oxygen). In both depth ranges a 3–10-fold increase of abundance from the past to the present has been observed that might have been caused by eutrophication.

Introduction

The definition and identification of reference areas with pristine conditions is a main target of the EU Water Framework Directive (WFD). One possible approach is the analysis of historical data sets, in this particular case quantitative and qualitative data on distribution of macrozoobenthic species. A few years ago the authors established a database of all literature on macrozoobenthos in German Baltic waters (Zettler and Röhner 2004). For the Arkona Basin approximately 2500 data on 130 species were published in 80 papers from 1873 to 2001. Furthermore some HELCOM (Helsinki Commission, Baltic Marine Environment Protection Commission) monitoring stations with long time series observations/data/measurements exist (e.g. Cederwall et al. 2002). Therefore the Arkona Basin may be considered as a well investigated area with both historic and recent data. This is the first approach using the complex data set of recent investiga-
tions (131 stations) and historical data (Zettler and Röhner 2004) to study the changes of the macrozoobenthos communities in the Arkona Basin.

The water quality of the Baltic Sea shows a general trend of increasing nutrient concentrations in most regions and eutrophication has been an increasing ecological threat during the past 50 years (HELCOM 1996, Karlson et al. 2002). Several papers have dealt with the effects of eutrophication on macrozoobenthic communities (e.g. Cederwall and Elmgren 1980, Kube et al. 1997, Laine et al. 1997, Cederwall et al. 2002, Karlson et al. 2002, Perus and Bonsdorff 2004). The zoobenthic succession model of Rumohr et al. (1996) distinguished the supra-halocline area (< 30 m depth), the intermediate depths of 40 to 50 m and the sub-halocline area (> 50 m depth) for the southern Baltic. The community is gradually impoverished with increasing depth. Differences in successional sequences between basins and vertical zones are documented (Rumohr et al. 1996).

During the last years, extensive studies of the benthic habitat within the German Arkona Basin were accomplished. The present paper describes long-term changes in the benthic communities of the Arkona Basin by comparing these recent macrozoobenthic data with historical data of the last 80 years. The analysis of a long-term data set (the last 10 to 20 years) of two HELCOM monitoring stations has also flown into the comparison. Special emphasis is placed on the use of historical data comparison as a tool for the assessment of changes of macrozoobenthic communities with respect to different depth zones (sediment compositions and salinity conditions). In contrast to long-term studies of macrozoobenthos in areas stressed by e.g. eutrophication (Perus and Bonsdorff 2004) or by stagnation periods (Laine et al. 1997), we show that the variability and changes of benthic communities in the Arkona Basin are probably due to natural conditions.

Fig. 1. Maps showing the pattern of stations during the four investigation periods compared. Thulin (1922) and Hertling (1928) for the period between 1921 and 1926; Löwe (1963) for 1954 to 1958; Gosselck (1985) for 1980 and own data between 2001 and 2004 (★ = monitoring stations, KF = Kriegers Flak, AG = Adlergrund). The scale bar is in nautical miles. Bottom right the water depth of 35 m is indicated by the dotted line. Deeper waters are situated to the North of the line.
Material and methods

Study area

The Arkona Basin is regarded as a part of the transitional zone between the Kattegat and the deep basins of the Baltic Proper. It covers an area of about 19 000 km². The long-term average flow is about 21 000 m³ s⁻¹ with salinities between 14 and 14.6 psu in bottom waters (Gustafsson 2001). About a quarter of this area is deeper than 40 m (maximum 53 m). Only the marginal zones (like Adlergrund or Kriegers Flak) are shallower than 20 m (Fig. 1). Adlergrund is a glacial morphological structure and a part of the Rönnebank system. It is situated in the southeastern part of the Arkona Basin. It divides this Basin from the more easterly lying Bornholm Basin. Kriegers Flak has the same genesis and is located northwest of the investigation area. The Arkona Basin is Swedish and Danish territory in the North and German in the South. The main sediment type > 35 m is mud. The shallower areas, e.g. a sand plateau in the West, are characterized by well sorted sandy substrates. Gravel, stones and boulders are typical for the glacial banks mentioned above.

Macrozoobenthos

The present study on macrozoobenthos of the Arkona Basin covers almost all literature sources that have dealt with some aspects of benthic studies within this investigation area (Zettler and Röhner 2004). Altogether approximately 80 literature sources were included. Most of these papers contain only little information on macrozoobenthos. Others provide only qualitative data on the distribution of species. Only few works are suitable for the analysis of the historical and recent development of macrozoobenthic communities of the Arkona Basin. We compared data sets from studies carried out from (a) 1921 to 1926 (Thulin 1922, Hertling 1928), from (b) 1954 to 1958 (Löwe 1963), in (c) 1980 (Gosselck 1985) and from (d) 2001 to 2004 (own data). In these studies a 0.1 m² Petersen grab (a), a 0.1 m² box corer and a 0.2 m² van Veen grab (c) or a 0.1 m² van Veen (b, d) was used (see Table 1). The sieving procedure and sample fixation of Hertling (1928) was not described, Thulin (1922) used 0.8 mm mesh size and during the latter three investigations sieves with 1 mm mesh size were used. The preservation of the samples by Thulin (1922) and during the latter three periods with formalin was done. Hertling (1928) probably analysed unfixed samples onboard. We know that between the different investigation periods some parameters e.g. the penetration depth of grabs have changed and the handling and fixing of the samples may have also been different. Nevertheless in our opinion these studies contain quantitative data suitable as a basis for a comparative analysis.

<table>
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<tbody>
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<td>Gosselck (1985)</td>
<td>this study</td>
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<td>Van Veen 0.1 m²</td>
<td>Van Veen 0.2 m²</td>
<td>Van Veen 0.1 m²</td>
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<td>yes</td>
<td>no</td>
<td>yes</td>
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<td>1</td>
<td>2–3</td>
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<td>Sieve (mm)</td>
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<td>1.0</td>
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<td>Fixation</td>
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<td>72</td>
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<td>No. of stations at depth &gt; 35 m</td>
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<td>30</td>
<td>21</td>
<td>59</td>
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<td>Bottom salinity (psu)</td>
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<td>7–20</td>
<td>15–17 (max. 23)</td>
<td>7–22.5</td>
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Table 1. Methods and number of stations sampled in two depth ranges of the Arkona Basin and the bottom water salinity during four investigation periods. * = During the study of Gosselck (1985) only depths between 20 and 40 m were sampled. Thus the measured salinity range is slightly higher than in the other time periods.
The data sets compared here are based on 18 stations sampled by Thulin (1922) and Hertling (1928), 62 stations sampled by Löwe (1963), 32 stations sampled by Gosselck (1985) and 131 stations sampled in this study. Although all four station grids covered the two depth ranges (deeper and shallower than 35 m), sampling sites differed between investigation periods (Table 1 and Fig. 1). Another major problem is the change of taxonomical expertise or motivation. The older investigations focused mainly on nutritional species for fishes. Small polychaetes or snails were not always counted. Some infauna species (e.g. bigger polychaetes or soft-shell clams) burrow deeper than the regular catching depth (5–10 cm, depending on substrate) of the grabs. Most epibenthic species show a patchy distribution, the success of counting depends on the replication number of sampling. Some nomenclature has changed during the last 100 years; in some cases an exact nomenclatorial classification is impossible (e.g. Pholoe sp., Ampharete sp., Harmothoe sp., Gammarus sp.). Unfortunately, especially in the older studies we had no information on the whole macrozoobenthic community but rather on selected “interesting” species. From the present point of view we assume that at least the papers of Thulin (1922) and Hertling (1928) do not reflect the complete macrozoobenthic community.

We decided to analyse the results for two separate depth ranges (deeper and shallower than 35 m), because of the substantial change of sediment conditions, from sandy or gravel and stones in the shallow to muddy in the deeper waters (own results by video imaging and sediment analysis), and higher salinity in deep water in consequence of inflowing near bottom water and a formation of a halocline (see also Rumohr et al. 1996). Multidimensional scaling (PRIMER software) pointed to two separate communities (Fig. 2). The global $R$ arising from analysis of similarities (ANOSIM) was 0.758 with a significance level of 0.1%.

Hence for each depth range we chose 6 species, for which we guess that the scientists were able to identify the species, they were big and interesting enough for detection, the species were or are common and all species are listed in each checklist. Consequently for the depth range shallower than 35 m we chose the bivalves Mytilus edulis and Macoma balthica, the gastropod Hydrobia ulvae, the polychaetes Pygospio elegans and Scoloplos armiger and the amphipod Pontoporeia femorata. In the deeper waters of the Baltic basins distinct benthic assemblages were dominated by only a few species (Laine 2003). For the comparison of the depths > 35 m we selected the priapulid Halicryptus spinulosus, the bivalve Macoma balthica, the polychaetes Terebellides stroemi and Scoloplos armiger, the amphipod Pontoporeia femorata and the cumacean Diastylis rathkei. This species group was very similar to the assemblage described by Laine (2003) for the deep open Baltic Sea.

**Results**

**Salinity, sediment and oxygen conditions**

Own measurements showed that the water column in the shallow areas of the Arkona Basin was well mixed down to a depth of about 20 m. The mean bottom salinity ranged between 7 and 10 psu. Below 30–35 m the salinity depends mainly on marine water inflow from the Kattegat region which occasionally can raise salinity to a maximum of 23 psu. During the observations reported here mean values were between 15 and 18 psu (measurements 3 to 6 times per year, Table 1).
In the shallow depth interval sediment conditions vary between well sorted sand, mixed sand, and gravel to stony and boulder grounds. The sediment at water depths > 35 m is distinctly different from that in shallower areas. The characteristic substrate type is mud with high water and organic content (own data, not shown in figure). The oxygen conditions during earlier sampling occasions were not well documented (Thulin 1922, Hertling 1928). Löwe (1963) documented oxygen concentrations in the bottom water of the Arkona Basin ranging between 2.8 and 4 ml l\(^{-1}\). Gosselck (1985) observed low oxygen values in the summer time (about 0.2 ml l\(^{-1}\)) but not hydrogen sulphide in water. In our study (2001–2004) we measured between 2.2 and 9.4 ml l\(^{-1}\) in the bottom water layer.

At two monitoring stations (< and > 35 m water depth) investigations on macrozoobenthos and hydrographic parameters have been carried out by the Baltic Sea Research Institute for two decades. Station 109 (K4) lies in the muddy central Arkona Basin at 45 m water depth. During the last 20 years the mean bottom water salinity varied between 14.4 and 18.7 psu (Fig. 3a) with a minimum of 11 psu (February 1985) and a maximum of 23.1 psu (February 1993). The mean oxygen content in the near bottom water layer varied between 3.4 and 6.9 ml l\(^{-1}\) (Fig. 3b) with a minimum of 0.7 ml l\(^{-1}\) in August 1988. Another low content with 0.9 ml l\(^{-1}\) was observed in August 2003. All other measured values were > 1 ml l\(^{-1}\) in this period. The second monitoring station (152 or K3) in the southern Arkona Basin is characterised by 31 m water depth and sandy sediment. The time series dates back 13 years. The mean salinity of bottom water varied between 7.7 and 10.4 psu (Fig. 4a). A minimum of 7.6 psu (several times in 1991, 1993, 2001, 2003) and a maximum of 11.2 psu (November 1992) were measured. The oxygen content of the bottom water reached values between 4.5 and 8.0 ml l\(^{-1}\) (Fig. 4b). While a minimum of 4.1 ml l\(^{-1}\) was measured in October 1994, further oxygen depletion was never observed during the period considered.

**Biodiversity, abundance and biomass of macrozoobenthos**

After analysis of all literature sources and own observations, 153 taxa were observed in the Arkona Basin (Fig. 5). Polychaeta showed the highest biodiversity with 50 species, followed...
by the crustaceans with 36 species. Molluscs (20 species), cnidarians (13), oligochaeta (9) and bryozoa (7) had lower biodiversity. The miscellaneous group consists of nemerteans (5), ascidians (3), priapulids (2) and single taxa of several other taxonomical groups (insects, arachnids, hirudineans, echinoderms, poriferans, pycnogonids, turbellarians).

Between 2001 and 2004, 131 stations at different depths of the Arkona Basin were sampled (Fig. 1 and Table 1). The results of this study are summarised in Table 2. Altogether 109 taxa were observed.

In the depth range shallower than 35 m we found 79 taxa at 72 stations (Table 2) alto-

Table 2. Presence, mean abundance and mean biomass (ash-free dry weight, Afdw) of all species (in- and epifauna) found at least at 50% of all the stations < or > the 35 m water depth in the investigation period between 2001 and 2004. Indicative species (presence > 70%) of both depth intervals are set in boldface; species which are common in both depth intervals are also listed. Number of species, Shannon diversity, total abundance and biomass are given at the bottom of the table. x = only qualitative records.

<table>
<thead>
<tr>
<th>Presence (%)</th>
<th>Ind. m⁻²</th>
<th>Afdw mg m⁻²</th>
<th>Taxon</th>
<th>Presence (%)</th>
<th>Ind. m⁻²</th>
<th>Afdw mg m⁻²</th>
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<td>&lt; 35 m</td>
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<td>16160</td>
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<td>132</td>
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<td>92</td>
<td>51</td>
<td>120</td>
<td><em>Gammarus salinus</em></td>
<td>19</td>
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<td></td>
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<tr>
<td>90</td>
<td>100</td>
<td>335</td>
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<td>26</td>
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<tr>
<td>88</td>
<td>x</td>
<td></td>
<td><em>Electra crustulenta</em></td>
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<td>79</td>
<td>160</td>
<td>19</td>
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<tr>
<td>79</td>
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<td>5</td>
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<td>294</td>
<td>25</td>
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<tr>
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<td>1191</td>
<td>159</td>
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<td><em>Scoloplos armiger</em></td>
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Total for species above 1653 7097

Total for all taxa 59 stations 1720 7947

Shannon diversity (H') 73 taxa 2.62
gether. The Shannon diversity (calculated from infauna species only) for this zone averaged 2.16 (± 0.53).

Only 21 species (in- and epifauna) showed presence of more than 50% within all stations and again only 9 species indicated this depth zone. The characteristic and typical species were the molluscs *Mytilus edulis* and *Hydrobia ulvae*, the crustaceans *Gamarus salinus* and *Jaera albilfrons*, the polychaetes *Hediste diversicolor*, the oligochaetes *Tubifex costatus* and *Tubificoides benedeni* and the bryozoans *Electra crustulenta* and *Alyonidium polyoum*. Other species were common too, but their presence was not as strongly correlated with this depth range. These species (e.g. *Pygospio elegans*, *Macoma balthica*, *Crangon crangon* and *Diastylis rathkei*) were very often found in both depth ranges. The total mean abundance and biomass were approx. 6000 ind. m⁻² and 22.7 g m⁻² (ash-free dry weight), respectively. The highest mean abundance was reached by the blue mussel *M. edulis* with about 3000 ind. m⁻², followed by the spionid *P. elegans* with approx. 1200 ind. m⁻² and the hydrobiid snail *H. ulvae* with approx. 450 ind. m⁻². With respect to biomass the bivalve species *M. edulis* (about 16 g m⁻²) and *M. balthica* (approx. 3.5 g m⁻²) dominated this community. A third bivalve species, the soft shell clam *Mya arenaria*, was ranked 3 and reached 1.3 g m⁻². Due to the mainly coarse sands and gravel it occurred only at fewer than half of all stations (not shown in Table 2).

Deeper than 35 m (59 stations) altogether 73 taxa were observed (Table 2). The Shannon diversity averaged 2.62 (± 0.36), only infauna species were considered.

Thirteen species (in- and epifauna) were observed at more than 50% of all the stations. Only 6 species were indicative for this depth zone. These species were the priapulids *Halicyrtus spinulosus* and *Priapulus caudatus*, the polychaetes *Terebellides stroemi*, *Ampharete balthica* and *Scoloplos armiger* and the amphipod *Pontoporeia femorata*. Other very common species were the cumacean *Diastylis rathkei*, the bivalve *Macoma balthica* and the polychaete *Bylgides sarsi*. The total mean abundance and biomass were approx. 1700 ind. m⁻² and 7.9 g m⁻², respectively. The highest mean abundance was reached by the bivalve *M. balthica* with approx. 400 ind. m⁻² followed by the polychaetes *P. elegans* and *S. armiger* with approx. 350 ind. m⁻² each and the cumacean *D. rathkei* with 140 ind. m⁻². The biomass was dominated by the bivalve *M. balthica* (5.4 g m⁻²) and the polychaetes *S. armiger* and *T. stroemi* (about 0.3 g m⁻² each).

The species number per station varied between 9 and 42 (Fig. 6a). Mean species numbers at stations shallower or deeper than 35 m were 25 and 20, respectively. No significant correlation between water depth (with its increasing salinity) and species number was found. Conversely the Shannon diversity increased with increasing water depth (Fig. 6b). The highest indices were observed at depths > 35 m. Both the abundance and the biomass were highest in the depth range shallower than 35 m (Fig. 6c and d). The abundance varied enormously especially due to the presence or absence of *M. edulis*. For example, at two stations we observed abundances of about 30 000 and 50 000 ind. m⁻² with ash-free dry weight values reaching 139 and 212 g m⁻², respectively.

### Long-term changes of macrozoobenthos

#### Monitoring stations

The macrozoobenthos at station 109 (water depth = 45 m) showed large interannual variability with respect to abundance and biomass (Fig. 7a). The abundance varied between 18 ind. m⁻² in 1989 and 1075 ind. m⁻² in 1991. Increasing abundance and all peaks were caused by high densities of the polychaete *S. armiger* (not shown). This species reached values between 64% and 93% of total abundance in years with high total abundance (e.g. 1985, 1988, 1991–1993, 1998, 2002). The biomass (fresh weight) without the ocean quahog *Arctica islandica* ranged between 0.7 g m⁻² and 59 g m⁻² (Fig. 7a). Due to the patchy occurrence of *A. islandica* (biomass range between 0 and 64 g m⁻²) and the large individual weights we decided to exclude it from the whole biomass values. In these years (1984, 1985, 1986, 1987, 1991, 1995, 1998, 2000) *A. islandica* dominated the biomass with 70% to 97% of
total biomass. Other “co-affecting” species are the bivalves \textit{M. balthica} (1980, 2003 and 2004) and \textit{Astarte elliptica} (1986) with high biomass values as well.

Until the end of the 1980s and the beginning of the 1990s a decreasing trend in species number and Shannon diversity was observed (Fig. 7b). The species number declined from about 10 (maximum 12 in 1982) to only 3–5. At the same time the diversity index dropped from about 3.3 to 0.52. Later both the species number and the Shannon diversity increased rapidly to 23 and 2.9 respectively.

At the shallower monitoring station 152 (water depth = 31 m) total abundance increased, too, due to a strong increasing abundance of the spionid \textit{P. elegans} until the mid 1990s (not shown). A maximum of about 12 000 ind. m$^{-2}$ (1995) was observed (Fig. 8a). Except for 2001 and 2002, \textit{P. elegans} dominated the community with a relative abundance between 55% and 77% (300 to 9500 ind. m$^{-2}$). Subdominant species were the bivalves \textit{M. balthica} and \textit{M. edulis}. The latter occurred very patchily. Its abundance ranged between 12 ind. m$^{-2}$ (1991) and 1800 ind. m$^{-2}$ (1999). In some years the cumacean \textit{D. rathkei} reached remarkable abundances (e.g. 600 ind. m$^{-2}$ in 1995). Total biomass was mainly affected by the density of \textit{M. balthica}, which dominated the biomass in all years with values of about 50% of total biomass. Only \textit{M. edulis} reached similar high values during some years. Both in abundance and biomass we observed increasing amounts to the mid 1990s. Afterwards both parameters decreased again. Both values are significantly correlated with the population dynamics of \textit{P. elegans} and \textit{M. balthica} (not shown).

Since the beginning of the macrozoobenthic investigations in 1991, we observed no significant trend at station 152 in both the number of taxa and the diversity index of Shannon (Fig. 8b). In 1991 and 1992 the species number counted was 9 and the diversity was about 1.5. Afterwards the species number and diversity increased with moderate variability. In 1997 both parameters dropped again, similarly to abundance, but only one year later the species number
(25) recovered. Afterwards the number varied between 20 and 27. The values of diversity ranged between 1.5 and 2.1 and diversity was at its maximum in 2002.

Comparison of different investigation periods

Data sets of 4 different time periods (Fig. 1) were compared separately for two depth ranges (Figs. 9 and 10) with respect to 6 common and representative species.

At water depths > 35 m the species T. stroemi, M. balthica, S. armiger, P. femorata, D. rathkei and H. spinulosus were taken into account (Fig. 9). In the 1920s the polychaete T. stroemi had an abundance of 220 ind. m\(^{-2}\) and dominated the community with 67%. S. armiger and H. spinulosus only reached about 20 ind. m\(^{-2}\) in this period. Similar to the depth range < 35 m the species composition in the deeper areas was more balanced during the investigation period of the 1950s. With the exception of H. spinulosus all characteristic species (Table 2) were dominant. In 1980 and during our studies the highest abundances were observed in the bivalve M. balthica. Subdominant species were the polychaete S. armiger, and the cumacean D. rathkei. H. spinulosus was represented during all periods in the same order of magnitude and reached abundances between 10 ind. m\(^{-2}\) and 60 ind. m\(^{-2}\).

The total abundance increased up to an order of magnitude when the first two time periods and 1980 are compared. In the recent study the mean abundance decreased to half of the value from 1980.

At water depths shallower than 35 m the species M. edulis, P. elegans, S. armiger, H. ulvae, P. femorata and M. balthica were taken into account (Fig. 10). In the 1920s this selected group became dominated by the bivalves which reached 82% of the relative abundance. The blue mussel M. edulis represented the largest fraction of about 72%. In the 1950s the ratio between these selected species was more bal-
anced. The bivalves amounted to about 11% whereby the hydroboid snail *H. ulvae* became dominant and reached the highest relative abundance with 37%. The relative abundance of *M. edulis* decreased to 7%. With approximately 34% the polychaetes *P. elegans* (21%) and *S. armiger* (13%) were subdominant. The fraction of the amphipod *P. femorata* was about 3%. In 1980 the polychaetes reached a relative abundance of 37% (*P. elegans* 1100 ind. m$^{-2}$ and *S. armiger* 1800 ind. m$^{-2}$ respectively). Among the bivalves (15%) *M. edulis* became less important (1%). With about 1120 ind. m$^{-2}$ (14%) *M. balthica* reached its highest abundance in this comparison. With about 400 to 500 ind. m$^{-2}$ and a relative abundance between 6% and 7% *H. ulvae* showed similar distribution patterns during the last two investigation periods. Only in 1980 the amphipod *P. femorata* occurred in a noteworthy abundance. During the years 2001 to 2004 the relative abundance again was dominated by *M. edulis* (51%). Since the 1920s the abundance of the polychaete *P. elegans* has increased constantly until the 1980s. Only a few individuals were observed in the 1920s and a couple of hundred in the 1950s. Since the 1980s *P. elegans* has belonged to the dominant faunistic elements of sandy bottoms < 35 m depth of the Arkona Basin. Usually its abundance has been higher than 1000 ind. m$^{-2}$. In this depth zone, *S. armiger* showed highest abundances during the investigation periods of the 1950s and in 1980. Whereas the total abundance of the first two time periods ranged around 2000 ind. m$^{-2}$, about 8000 and 6000 ind. m$^{-2}$ were observed in 1980 and in 2001–2004, respectively.
Discussion

The Arkona Basin in view of 100 years of benthic studies

In the late 19th century benthological studies were carried out in the Arkona Basin (Möbius 1873, Michaelsen 1897) resulting in qualitative data only. About 30 species were found during these early studies. Some common examples are the molluscs *Astarte borealis*, *H. ulvae* and *M. balthica*, the cumacean *D. rathkei* and the polychaete *Scoloplos armiger*. Within the first decades of the 20th century only few studies were carried out. Some of these works were Reibisch (1902), Thulin (1922), Hagmeier (1926, 1930) and Hertling (1928). Especially the quantitative data in the papers by Thulin and Hertling are comparable with recent data. During the next 20 years a couple of investigations by Polish scientists were published (Demel and Mańkowski 1951, Demel and Mulicki 1954, 1958, 1959, Mulicki 1957, 1962, Mulicki and Zmudziński 1969). It is difficult to compare recent results, especially quantitative ones, with older data. This is due to different methods, different geographical areas and a mixture of qualitative and quantitative data. The extensive study in the 1950s by Löwe (1963) supplied a data set suitable for a comparison with recent data. In 1980 investigations of Gosselck (1985) were done within the Arkona Basin. These data were also used for comparison. All historical and recent sampling occasions represent similar salinity conditions and are comparable in this respect (Table 1). In the Arkona Basin we did not find any long-term hypoxic or anoxic conditions in the past two decades. However, significant reductions in mean species numbers, biomass and abundance have occurred until the end of the 1980s and the beginning of the 1990s. These results are very similar to the results of Swedish and Danish investigations (DMU 1998, Cederwall et al. 2002) but we were not able to identify reduced oxygen concentrations as the cause for the reduced fauna. The hypoxic events of the Arkona Basin indicated by Karlson et al. (2002) from 1960 to 2002 were found very sporadically in the past two decades. From 123 measurements (5 to 9 per year) of oxygen in bottom waters only 11 were < 2 ml l⁻¹ and only three < 1 ml l⁻¹. Maybe even short-term hypoxic events affect the macrozoobenthic community. Effects on the benthic community due to duration and strength of hypoxic/anoxic events have been proven in many parts of the Baltic (e.g. Andersin and Sandler 1991, Laine et al. 1997, Powilleit and Kube 1999, Karlson et al. 2002, Janas et al. 2004).

Overall species spectrum

In consideration of historical data and our own collections for the Arkona Basin, altogether 153 macrozoobenthic taxa were described. In the Baltic Sea the richness of species decreased following the salinity gradient from about 764 species in the Kiel Bight (western Baltic) to 358 in the Mecklenburg Bight and 153 in the Arkona Basin, to only 90 species in the Pomeranian Bay (Gerlach 2000, Zettler and Röhner 2004). During our recent studies in the Arkona Basin 109 (96 without bryozoans and cnidarians) taxa were determined. In the 1920s 39 (38) taxa, during the 1950s 23 (22) taxa and in 1980 39 (37) taxa were observed (Thulin 1922, Hertling 1928, Löwe 1963, Gosselck 1985).

Comparing both depth ranges regarding the species richness an approximately equal high diversity of the polychaetes and the molluscs was observed. Only in shallow water areas with strong physical structures (e.g. boulder grounds) did crustaceans rise in high species numbers, too (Zettler 2001). At depths shallower than 35 m crustaceans showed an approx. 40% higher species number than within the deeper range and they were the species-richest taxonomical group in the comparison period with the exception of 1980 (Gosselck 1985). The predominantly epibenthic crustaceans found better living conditions on the more diverse bottom structures located mainly in shallow waters than those at depths > 35 m that were more affected by sedimentation.

Comparing data that were gathered by different sampling methods is a general problem in evaluating past and present distribution patterns in the benthos (Kube et al. 1997). The strongly varying species diversity found in the different investigation periods is on the one hand related
to the different number of examined stations (Table 1), on the other hand the individual investigations were conducted with partially different motivations and goals (see also Material and methods). However, some general features of the present situation can be compared with observations from the past.

**Long-term changes in macrozoobenthos**

In general changes in the composition of the macrozoobenthic community of the Arkona Basin were particularly affected by the varying influx of salt- and oxygen-rich water from the Kattegat and the western Baltic Sea (e.g. Andersin et al. 1990, Cederwall et al. 2002). Of course, the composition of the species, the distribution pattern, the productivity etc. depended among other things on these two major abiotic factors. During the last 24 and 13 years, at the two monitoring stations deeper and shallower than 35 m, respectively, no significant correlation between the variability of salinity or oxygen and the variability of biotic parameters (abundance, biomass, species number, diversity index) of the macrozoobenthic community was detected.

Since the beginning of benthic studies in the 1920s no significant changes have been observed when considering the benthic assemblage characterized by the selected species and two different depth ranges. While the distribution patterns of several species under investigation have changed between the different time periods, no consistent changes from the past to present days could have been stated. On the other hand a 3–10-fold increase in total abundance between the first two time periods and more recent studies (1980 and 2000s) were observed and could not be satisfactorily explained. Maybe disregarding small, epibenthic or mobile species in the past is the reason for this difference. Although these four time periods are only snapshots over 80 years, the comparison of these data gave us an opportunity to have more than two “time spots” with possibly large differences. It showed us that community structures were subject to large-scale or marginal changes. The biological variability driven by e.g. stagnation periods and salt-rich water inflow, masked possibly visible consequences of eutrophication. Only in deeper waters did we find differences, which may be explained by “eutrophication”. For instance filter and suspension feeding organisms like *M. balthica* seem to increase in their number and biomass, at least temporarily. A replacement of *M. balthica* by *M. edulis* reported by Cederwall and Elmgren (1980) and Kube et al. (1997) was not observed. The comparability of the occurrence and distribution of *M. edulis* is limited by the sampling methods used and the sites investigated during the different time periods. The sampling of *M. edulis* is strongly coincidence conditioned because of their patchy distribution on the coarse sand and gravel predominant in depths shallower than 35 m. An estimation of the actual distribution is therefore possible only with a very high sampling density, which is practically not feasible covering the whole surface area(s). The high individual densities on the Adlergrund, which were already found during the 1920s (Thulin 1922, Hertling 1928) are remarkable and similar to results of the recent time. In the 1950s and 1980s this special subarea with dense blue mussel banks, however, was not at all or less studied as compared with other stations with a smaller areal extent. Excluding the patchy distributed *M. edulis* during the 1920s from the average, 17.7 g fresh weight (fw) per m² was left (Thulin 1922). During the 1950s, Löwe (1963) observed 31.5 g m⁻², whereas in 1980 about 194 g m⁻² (Gosselck 1985) and for the recent time period 107 g m⁻² were assessed. The abrupt increase of the productivity of the macrozoobenthos in several water bodies of the Baltic Sea during the last decades was explained by eutrophication (e.g. Cederwall and Elmgren 1980, Laine et al. 2003, Perus and Bonsdorff 2004). This seems plausible since mainly filter feeding and deposit feeding organisms benefit from higher nutrition load. However, in the Arkona Basin a causal relationship between increases of nutrient levels (not analysed) and macrobenthic biomass cannot be verified. Eutrophication effects could only be suspected and it would be speculative to reduce all changes to this general process. Dramatic changes in hydrography will have major impacts on the distribution and composition of macrozoobenthic species (Laine 2003). In the time periods considered, no such changes or impacts could be observed in the studied area.
In conclusion, the macrozoobenthic community showed a high variability during the last 80 years, but the changes were not consistent and did not indicate a clear trend. However, in both depth ranges a 3–10-fold increase of total abundance from the past to present was noticed. In the Arkona Basin no precise correlation with changing abiotic conditions could be seen due to limitations of the methods used. Especially in consideration of different time periods and their zoobenthic assemblages a recurrence of similar faunistic inventory could be observed. Only with respect to a few single species (e.g. *Pygospio elegans*) and only for specific depth zones did we find some changes. Finally, this paper suggests a connection of the changes in benthic communities to natural processes and/or eutrophication in the Arkona Basin.

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References


Michaelsen W. 1897. Die Polychaetenfauna der deutschen Meere einschließlich der benachbarten und verbinden-


