

Long-term changes in the benthic communities of the Pomeranian Bay (Southern Baltic Sea)

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ABSTRACT. Long-term changes in the macrofauna of the Pomeranian Bay were studied by comparing survey data from the 1950s, 1980s, and 1990s. The study area has undergone significant eutrophication during the period of investigation. Biomass of filter-feeding bivalves increased significantly. Spatial distribution patterns of several species have changed. Strong decreases in species richness were caused by oxygen depletion at stations deeper than 15 m. *Saduria entomon*, *Monoporeia affinis*, and *Pontoporeia femorata* vanished entirely between 1981 and 1993. Although a causal relationship between simultaneous increases of nutrient levels and macrobenthic biomass cannot be verified, eutrophication is proposed to be the major process affecting changes in macrofauna assemblages. In addition, changes in hydrography and climate increased frequency and severity of oxygen depletion events in the Pomeranian Bay since the mid 1980s.

INTRODUCTION

Several attempts have been made to explain long-term changes in the macrozoobenthos of the Baltic Sea. Severe biomass reductions or even macrofauna death were often observed below the halocline (Heip, 1995). A general change from bivalve-dominated towards polychaete-dominated communities was documented in the deeper parts of the southern Baltic (Andersin et al., 1978; HELCOM, 1990). The oxygen concentration of the deepest water level had started to decrease by the end of the 19th century and fell to almost negligible concentrations in all deeper basins in the early 1990s. This anoxia has been attributed to both man-made eutrophication and climatic changes (e.g. Fonselius, 1972; Gargas et al., 1978; Gerlach, 1994).

Many authors have also described a significant increase in macrofauna biomass above the halocline as a consequence of higher food supplies (Pearson & Rosenberg, 1978; Cederwall & Elmgren, 1980; Brey, 1986). However, since 1980 oxygen depletion has also caused strong fluctuations in the benthic biomass of several shallow bays during periods of strong stratification (Gosselck & Georgi, 1984; Weigelt & Rumohr, 1986). It is supposed that the observed remarkable changes in community composition were caused by an increase in organic inputs to the sediment due to eutrophication and a change of hydrographic conditions (Weigelt, 1991; Prena, 1994).

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This paper describes long-term changes in the macrozoobenthic communities of the Pomeranian Bay (southern Baltic Sea) by comparing the 1950s with the 1980s and 1990s. The Pomeranian Bay is a shallow transition zone between the Oder Estuary and the deeper Arkona and Bornholm Basins (Fig. 1). Due to its topography and hydrography, recent macrofauna communities are influenced by both an increase in organic riverine loads and severe oxygen depletions in the deeper basins (Powilleit et al., 1995; Kube et al., 1996). The aim of our study is to discuss the long-term changes in the macrozoobenthos in relation to fluctuations and long-term trends in the environmental conditions.

MATERIAL AND METHODS

We compared original data sets from studies carried out from 1955 to 1958 (Löwe, 1963), from 1980 to 1982 (Gosselck, 1985; Warzocha, 1995) and in 1993 (Powilleit et al., 1995). In all studies a heavy, 0.1 m² Van Veen grab, a sieve with 1-mm mesh size, and 4% Formalin for storage were used. All investigators collected three samples at each station and date. Unfortunately, we do not know how much grabs used during different periods of investigation differed regarding the penetration depth and the strength of shock wave.

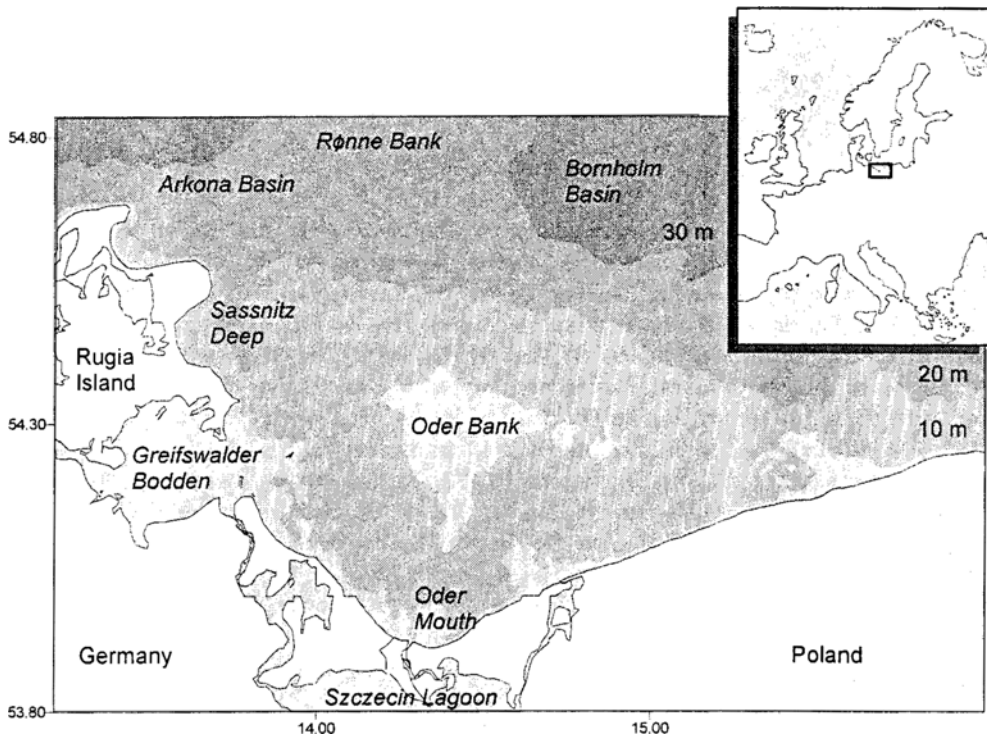


Fig. 1. Map of the area under investigation

Table 1. Number of stations sampled in different habitat types of the Pomeranian Bay during three investigation periods

Depth	Area	Number of stations		
		Löwe (1963)	Gosselck (1985) Warzocha (1995)	Powilleit et al. (1995)
5–10 m	Oder Bank	7	2	3
10–15 m	near shore	5	5	8
10–20 m	off shore	23	7	17
20 m	Sassnitz Deep	11	–	2
20–30 m	Arkona Basin	10	7	5
20–30 m	Bornholm Basin	2	2	–

The data sets compared here are based on 58 stations sampled by Löwe (1963), 23 stations sampled by Gosselck (1985) and Warzocha (1995) and 35 stations sampled by Powilleit et al. (1995). Although all three station grids covered the main habitat types of the study area, sampling sites differed between investigation periods (Table 1, Fig. 5). The border between Germany and Poland runs through the middle of the study area and, therefore, all investigations were restricted either to the German or Polish part of the bay.

Samples were mainly collected outside of the reproduction time in April/May and October/November. About 20% of the samples were taken in July/August. However, the influence of high spat densities on species abundances is almost negligible, because most of the juveniles pass through the meshes of the 1-mm sieve (Powilleit et al., 1995).

The Pomeranian Bay harbours about 40 different macrofauna species (Kube et al., 1996) but abundances of only 14 species could be used for a cluster analysis. The patchily distributed blue mussel, *Mytilus edulis*, and all associated crustaceans were excluded from the cluster analysis because they cannot be sampled precisely with only three replicate grabs. Due to the patchy distribution of *Mytilus*-clumps, relative 95%-confidence limits were greater than 100% of the mean values (Powilleit et al., 1995). We also had to exclude all small polychaetes and the mud snail *Hydrobia ulvae* from the cluster analysis because these species were not counted by Löwe (1963) and Warzocha (1995). Furthermore, three infaunal species (*Hediste diversicolor*, *Marenzelleria viridis*, *Mya arenaria*), burying deeper than 5 cm, were excluded from the cluster analysis.

However, the species that could be used for the cluster analysis are representatives of all major habitat types of the study area, i.e. the deeper parts along the slopes of the adjacent Arkona and Bornholm Basins, the exposed shallow sandy central parts, and the sheltered river mouth (Table 2).

Abundance data were also used to plot species distribution maps. The maps were computed by kriging (Cressie, 1991).

Biomass comparisons were restricted to the bivalves *M. edulis*, *Macoma balthica*, and *M. arenaria*. These species account for more than 90% of the total zoobenthic biomass (Kube et al., 1996). They are characterized by a longevity of more than ten years and a low P/B ratio (Kube, 1996b).

Bivalve biomass data of Löwe (1963) and Powilleit et al. (1995) were recalculated by allometric shell length-ash free dry weight (AFDW) relationships for samples taken

Table 2. Presence (%) and abundance (ind · m⁻²) of macrofauna species and total number of species in the Pomeranian Bay for station assemblages separated by cluster analysis (see Figs 4 and 5 for cluster groups)

	Cluster group (number of stations)																	
	1 (14)		2 (10)		3a (22)		3b (21)		4 (15)		5 (6)		6 (16)		7 (6)		8 (6)	
	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²	%	ind · m ⁻²
<i>Scoloplos armiger</i>	100	1317	10	0	0	0	0	0	0	0	0	0	81	29	17	1	50	4
<i>Terebellides stroemi</i>	86	212	0	0	0	0	0	0	0	0	0	0	25	5	0	0	0	0
<i>Travisia forbesi</i>	0	0	0	0	0	0	0	0	0	0	0	0	19	6	33	9	0	0
<i>Cerastoderma jamarcki</i>	7	0	80	84	100	337	100	278	93	30	83	340	50	10	0	0	0	0
<i>Macoma balthica</i>	100	717	100	457	100	307	100	313	100	276	100	1932	100	450	100	72	100	48
<i>Saduria entomon</i>	71	8	0	0	9	0	9	0	0	0	17	1	50	4	100	7	0	0
<i>Cyathura carinata</i>	0	0	60	58	23	5	0	0	13	1	0	0	0	0	0	0	0	0
<i>Corophium volutator</i>	43	17	100	3242	55	24	32	4	73	601	100	71	50	26	0	0	33	3
<i>Leptocheirus pilosus</i>	0	0	10	9	5	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Diasyllis rathkei</i>	100	248	10	2	14	2	0	0	13	3	17	1	88	52	67	16	0	0
<i>Monoporeia affinis</i>	0	0	0	0	9	1	5	1	13	9	0	0	6	2	100	472	0	0
<i>Pontoporeia femorata</i>	100	990	0	0	0	0	0	0	0	0	0	0	31	14	0	0	0	0
<i>Bathyporeia pilosa</i>	7	1	10	5	64	158	100	3435	13	2	0	1	25	4	50	48	0	0
<i>Halicryptus spinulosus</i>	93	57	0	0	9	4	0	0	7	0	50	14	88	15	100	7	17	1
Total number of species	23		21		20		18		19		11		23		15		11	

in April 1993 (Kube, 1996b). Biomass data of Gosselck (1985) and Warzocha (1995) were excluded from the analysis, because they had not measured the shell length of bivalves.

As already mentioned, the patchily distributed, mobile *Mytilus*-clumps cannot be sampled precisely with less than 10 grab subsamples. The data set of Löwe (1963) provided enough parallel grab samples per cluster group to estimate biomass means. Biomass data from Powilleit et al. (1995) were validated by additional dredge samples and video observations (Kube, 1996b).

Biomass values of *M. arenaria* obtained from Van Veen grab samples represent only about 70% the standing stock (Powilleit et al., 1995).

LONG-TERM VARIABILITY OF ENVIRONMENTAL FACTORS

Oceanography

The water column in the Pomeranian Bay is usually well mixed down to a depth of about 15 m by wind forcing. As a consequence, fresh water supplied by river runoff affects the entire water column (Trzosinska & Cyberska, 1992). There is a strong nega-

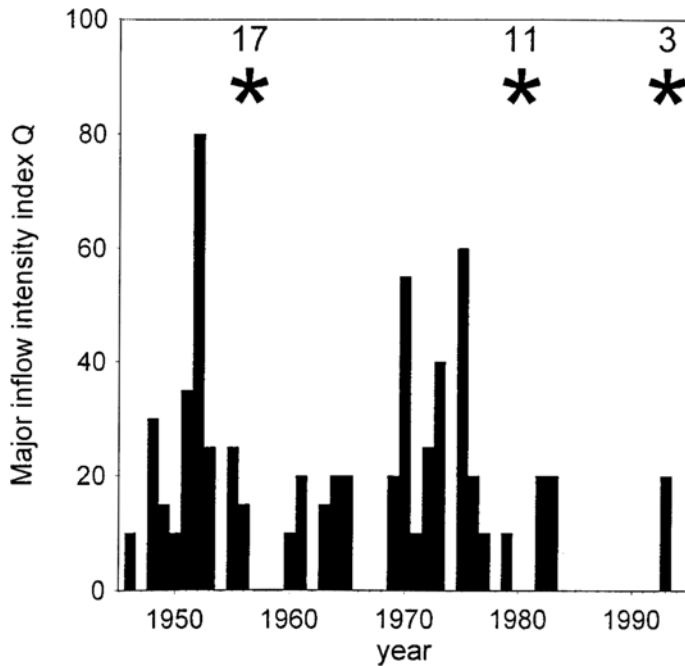


Fig. 2. Intensity index of inflows of highly saline water into the Baltic Sea (annual maximum) between 1946 and 1993 (redrawn from Franck & Matthäus, 1992, see Matthäus & Franck, 1992 for calculation of the index). Asterisks indicate benthos investigations. Values above the asterisks give the total number of major inflow events for the ten year periods preceding each benthos investigation

tive relationship between runoff data of the Oder River and annual salinity means (1950–1992, $r = -0.7$, $p < 0.05$, $n = 41$).

Annual salinity means showed no trend within the last 40 years. Values fluctuated between 6–8‰ near the mouth of the Oder and 7–9‰ on its banks (Nehring, 1990; Cyberski, 1992).

A strong vertical salinity gradient occurs at the steep northern edges of the bay. The 10‰ halocline is known to fluctuate there between 15–35 m depth near the Arkona Basin and 40–60 m depth near the Bornholm Basin. Changes in halocline depth depend mainly on the frequency and intensity of the inflow of highly saline water from the Kattegat into the Baltic Sea (Nehring et al., 1994; Matthäus & Lass, 1995). Occasionally, upwelling-like events are responsible for an uprising of the halocline. As a result, deep water from the Arkona Basin propagates into the bay via the Sassnitz Deep. Such upwelling events sometimes cause strong stratification in the western part of the Pomeranian Bay at depths between 10 and 15 m (Lass, pers. comm.).

The oxygen of the highly saline deep water, inflowing from the North Sea during the winter, is depleted during periods of stagnation. Hence, the oxygen concentration of the deep water below the halocline depends on both, on biological activity and on the frequency and intensity of major inflows. Until the 1970s, major inflows were observed more or less regularly (Fig. 2). Seventeen major inflow events were observed within a period of ten years preceding the investigations of Löwe (1963), and eleven inflows occurred within the ten years before the studies carried out by Gosselck (1985) and Warzocha (1995). A long lasting stagnation period since 1983 resulted in extreme decreases of oxygen concentrations in the Bornholm Basin and, during summer, even in the Arkona Basin (Franck & Matthäus, 1992; Nehring et al., 1994). This stagnation period was interrupted in January 1993 (Matthäus & Lass, 1995).

Temperature

Fluctuations of annual means of water temperature in the Pomeranian Bay are strongly related to the severity of the preceding winter season (Cyberska, 1992). Although the overall trend of the severeness index of winter seasons is negative (1946–1993, $r = -0.21$, $p > 0.05$, $n = 49$), means of severeness indices of a period of ten winter seasons before the beginning of the investigation did not differ (Fig. 3). Differences occurred in the course of the severeness index over the three ten year periods. Whereas the investigations of Löwe (1963), Gosselck (1985), and Warzocha (1995) followed a period of cold winters preceded by a period of mild winters, opposite conditions predated the investigation of Powilleit et al. (1995).

Food supply

The nitrogen input of the Oder River increased from 10000–20000 $t \cdot a^{-1}$ in the 1960s to 70000–80000 $t \cdot a^{-1}$ in the 1990s (Cyberska et al., 1992, 1993; Lampe, 1993). Surface chlorophyll *a* concentrations have doubled in the whole study area between 1970 and 1990 (Schulz & Kaiser, 1986; Nakonieczny et al., 1991; Renk, 1992). The increase in phytoplankton biomass resulted in a decreasing water transparency and a heavy loss of macrophytobenthos in the adjacent Greifswalder Bodden (Messner & Von Oertzen, 1991).

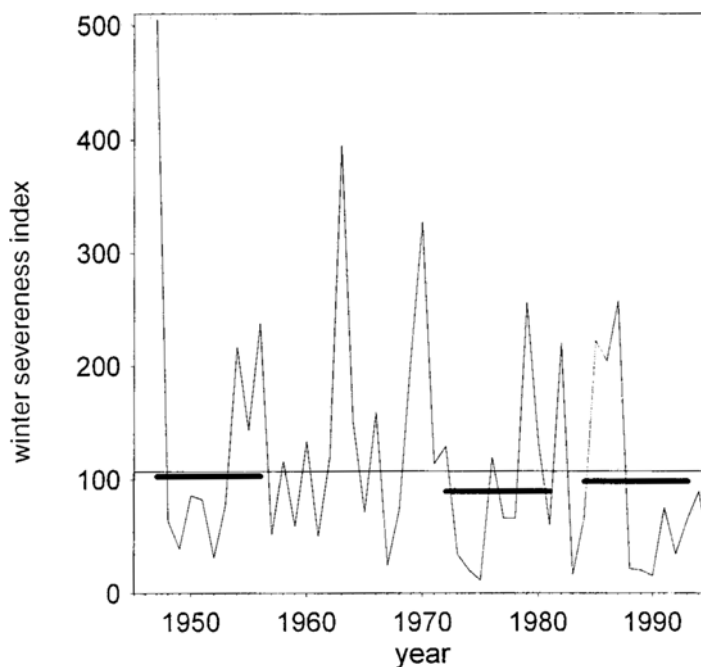


Fig. 3. Index of the severity of the winter seasons between 1946/47 and 1994/95 (sum of minus degrees (daily means) per winter season, data from the Meteorological Station Warnemünde, F.R.G.). Thin horizontal line shows the long-term average. Thick horizontal lines show the average for the ten-year periods preceding each benthos investigation

Furthermore, an increasing accumulation of organic matter was observed in sediments of the sheltered Greifswalder Bodden and in the Sassnitz Deep (Lampe, 1993; Leipe et al., 1995; Nausch, pers. comm.). However, no accumulation of organic matter was found for sandy sediments of the Pomeranian Bay above the 15 m isobath (Neumann & Bublitz, 1969; Koine, 1995).

RESULTS

Long-term changes of the macrozoobenthos assemblages

Eight groups of stations were separated by cluster analysis at a 45% similarity threshold and were computed to spatial distribution maps for all three investigation periods (Figs 4 and 5). The first group combines stations with a high species richness in the southern Arkona Basin. The second group covers shallow coastal locations near the Oder Mouth and near the Greifswalder Bodden. Group three is separated into two main sub-groups 3a and 3b, representing exposed sandy stations on the shallow Oder Bank and its deeper surroundings, respectively. The fourth group contains deeper sites in the southeast of the bay, which are characterised by low densities of characteristic

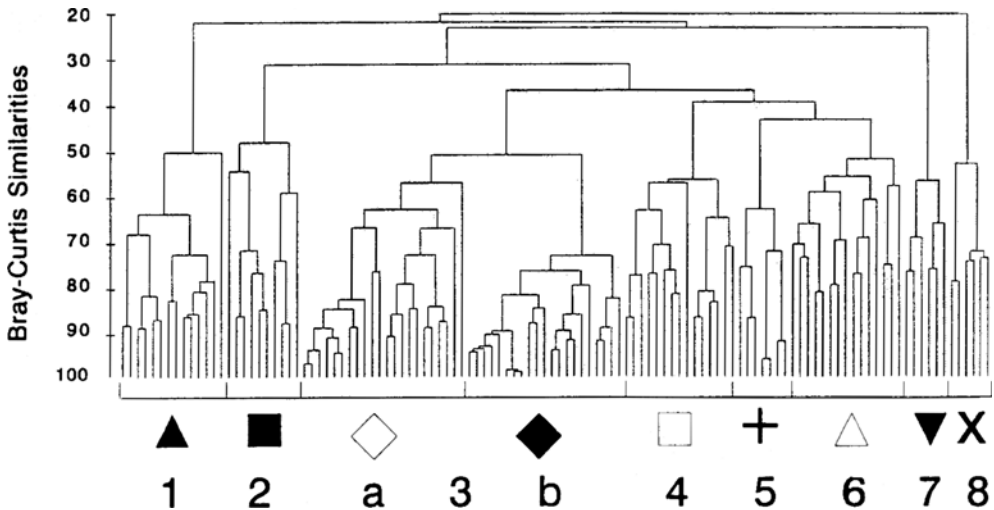


Fig. 4 Dendrogram of the 116 stations using group-average clustering from Bray-Curtis similarities on square root-transformed abundances (presence > 1%). The eight groups of stations separated at a 45% threshold are indicated (symbols and numbers). Additionally, the third station group was divided into the sub-groups 3a and 3b

species of the sand bottom community (*Bathyporeia pilosa*, *Cerastoderma lamarcki*). Group six represents stations in the Sassnitz Deep with a high species richness. Group seven includes stations in the deeper northern part at the slope to the Bornholm Basin. This station group lacks several species typical for the western Baltic Sea. Groups five and eight show a heavily reduced species richness (Table 2).

The spatial distribution maps (Fig. 5) show changes in the areal extension of cluster groups from one investigation period to the next, especially in the western half of the bay. Cluster group one and six, representing diverse macrofauna assemblages in the southern Arkona Basin and in the Sassnitz Deep, almost disappeared between 1957 and 1993. The Oder Bank cluster group (3a) covered the largest part of the Pomeranian Bay in the 1950s. Since 1981 its extension has been restricted to the shallow central parts of the Oder Bank. The deeper sandy areas are now part of the cluster group 3b. Today, a wide range is also covered by cluster group four, as compared with the 1950s when it was restricted to deeper parts in the West near the Isle of Rugia in the 1950s. The cluster groups five and eight represent stations, more than 15 m deep, sampled in 1981 and 1993 in the Sassnitz Deep and along the former Oder River bed. These assemblages were absent during the investigation period of Löwe (1963).

Changes in individual species

Distribution pattern of several species under investigation have changed between 1958 and 1993. The crustaceans *Monoporeia affinis* and *Pontoporeia femorata* vanished entirely since 1981 (Fig. 6). Only a few single individuals of the isopod *Saduria*

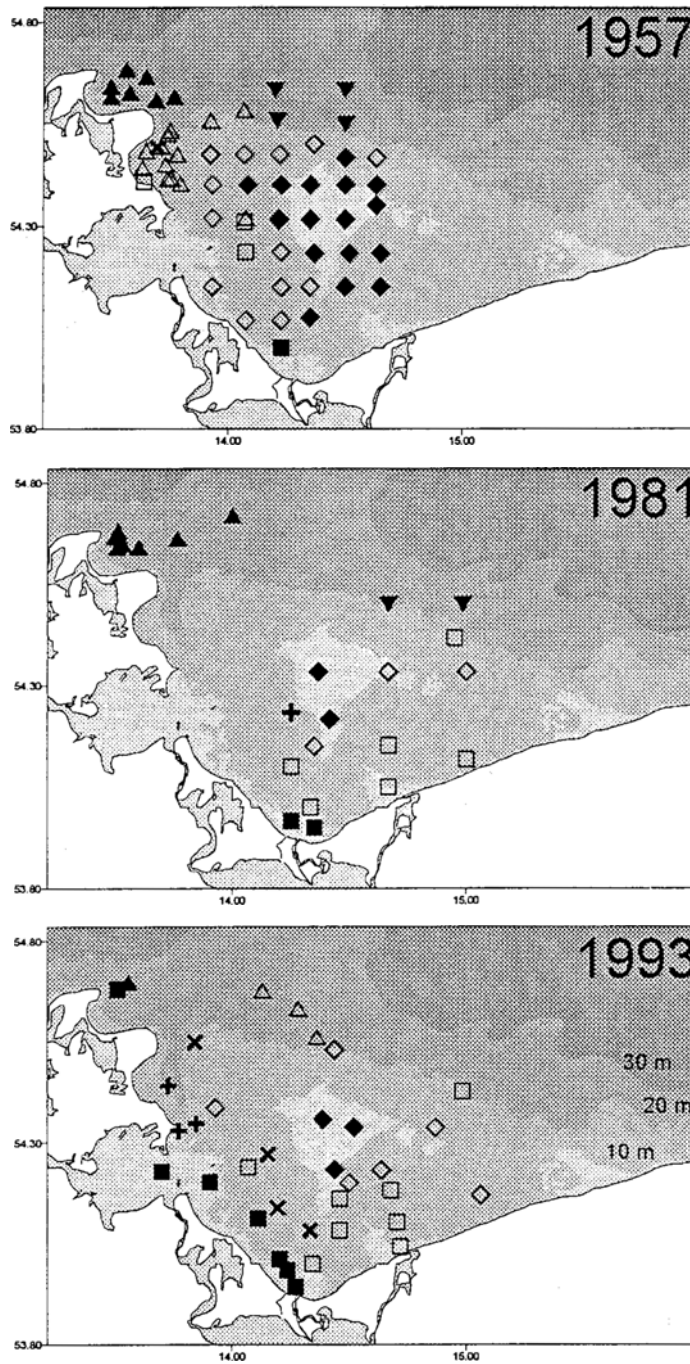


Fig. 5. Maps showing the spatial pattern of different cluster groups during the investigation periods of Löwe (1963), Gosselck (1985), Warzocha (1995), and Powilleit et al. (1995). Symbols are the same as in Fig. 4. See text for further explanations

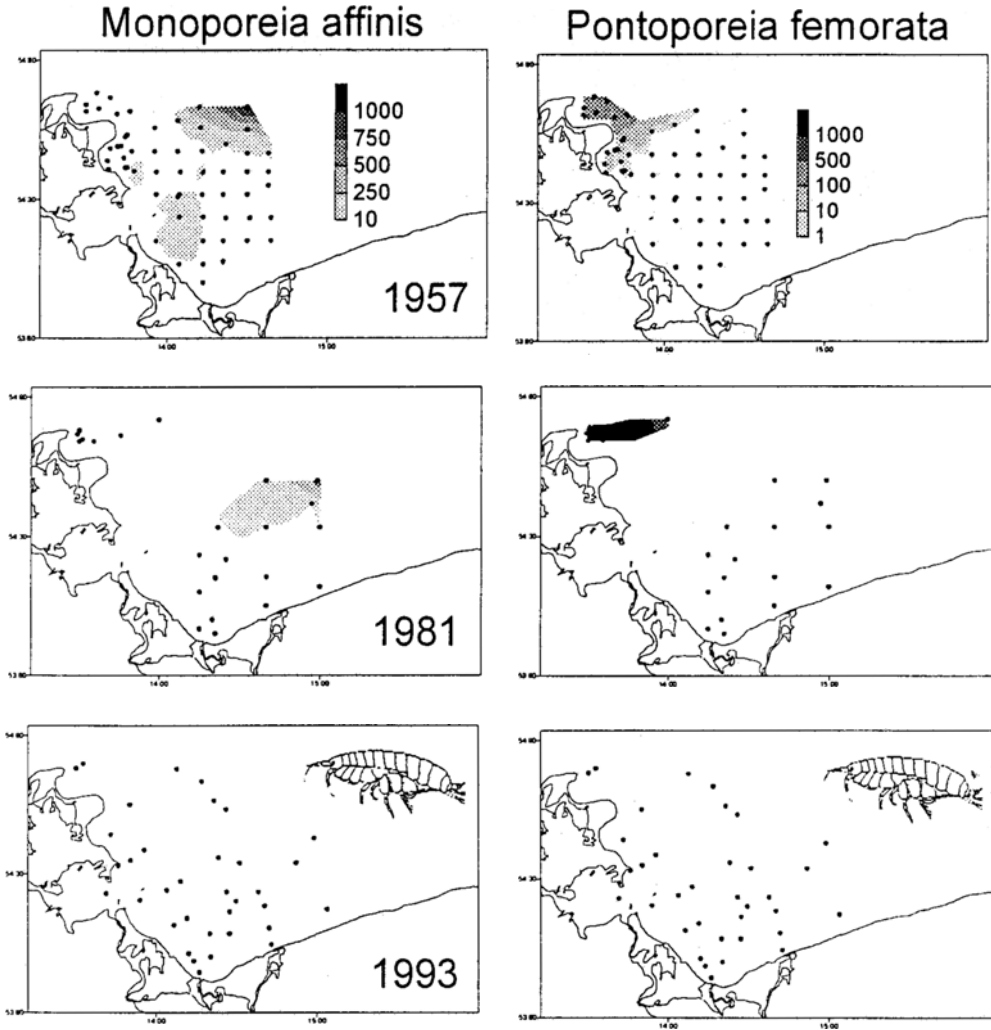


Fig. 6. Distribution of *Monoporeia affinis* and *Pontoporeia femorata* (ind. · m⁻²) during the investigation periods of Löwe (1963), Gosselck (1985), Warzocha (1995), and Powilleit et al. (1995)

entomon were found since 1993. All other species, that were abundant in the southern part of the Arkona Basin and in the Sassnitz Deep between 1955 and 1980 were discovered to be very scarce in 1993. The cockle *C. lamarcki* and the amphipod *B. pilosa* almost disappeared from the southwest of the study area. Their densities remained stable only on the Oder Bank (Fig. 7). Densities of the amphipod *Corophium volutator* have probably increased near the Oder Mouth. No changes were observed for the isopod *Cyathura carinata* and the amphipod *Leptocheirus pilosus* (Fig. 8).

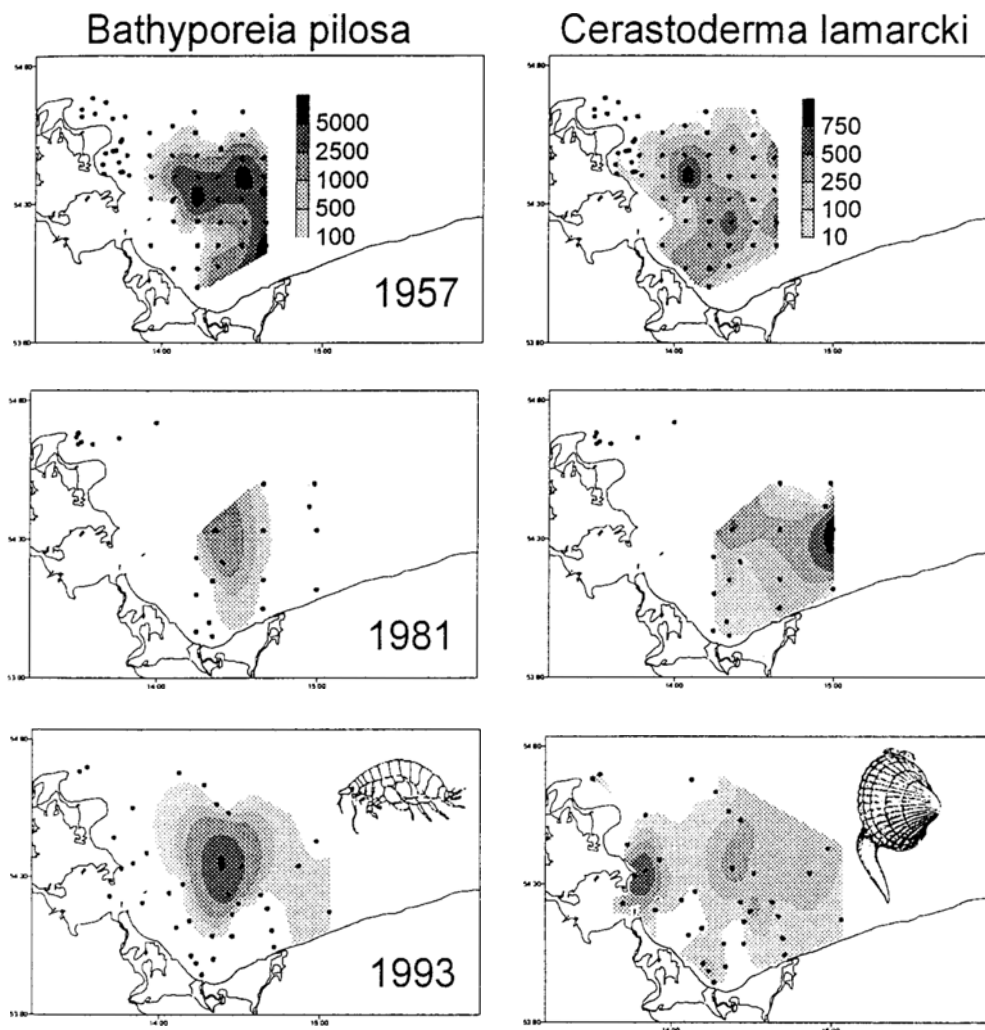


Fig. 7. Distribution of *Cerastoderma lamarcki* and *Bathyporeia pilosa* (ind. · m⁻²) during the investigation periods of Löwe (1963), Gosselck (1985), Warzocha (1995), and Powilleit et al. (1995)

Macrozoobenthic biomass

Changes in the biomass distribution pattern between the 1950s and 1990s are shown for three bivalve species in Fig. 9. The distribution pattern of *M. edulis* and *M. arenaria* have not changed within the past 35 years. The biomass distribution pattern of *M. balthica* in 1993 looked almost like an inverted picture of its 1950s distribution. Biomass values of *M. balthica* have decreased in the southwest and increased north of the Oder Bank.

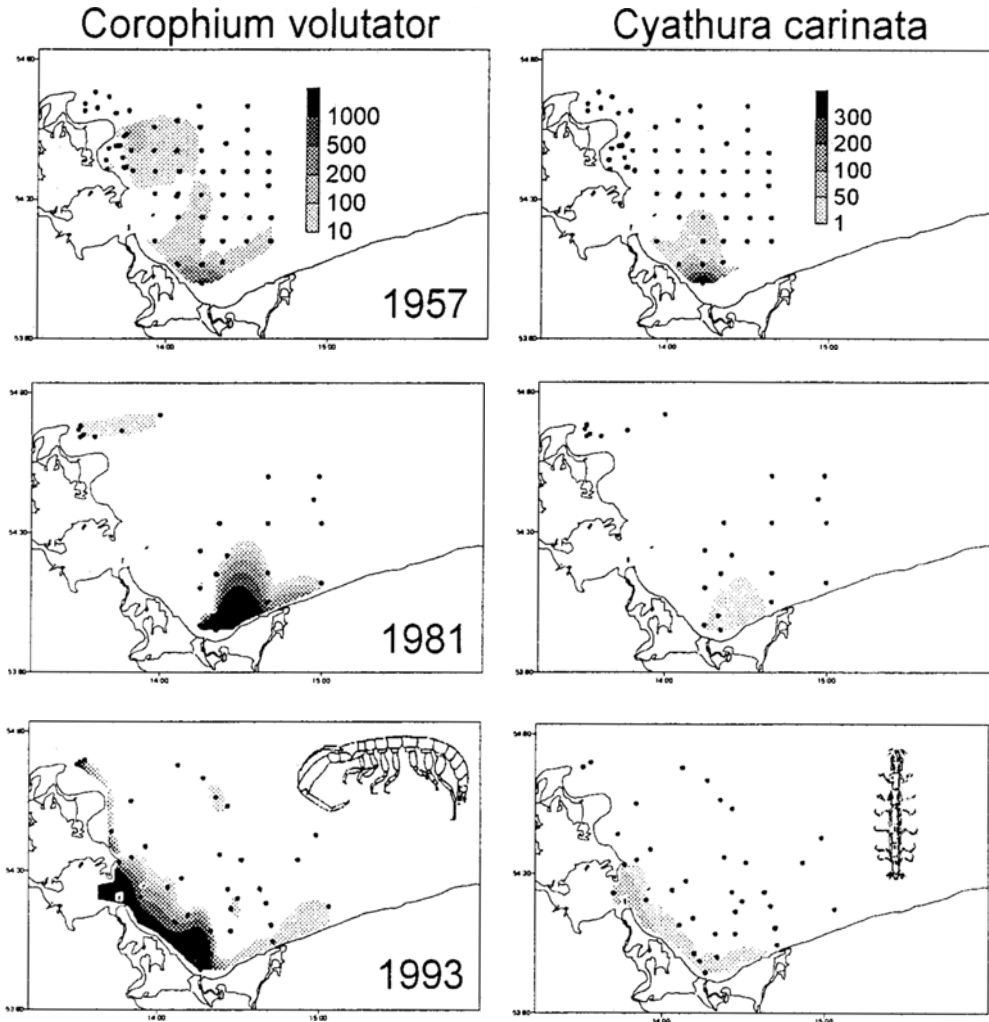


Fig. 8. Distribution of *Corophium volutator* and *Cyathura carinata* (ind. · m⁻²) during the investigation periods of Löwe (1963), Gosselck (1985), Warzocha (1995), and Powilleit et al. (1995)

The mean biomass of *M. edulis* and *M. arenaria* was about eight times higher in 1993 than in the 1950s. The increase is strongly significant. Mean biomass values of *M. balthica* showed no difference between the two investigation periods (Table 3).

To obtain a more detailed view, quantitative changes in bivalve biomasses were also calculated separately for cluster groups 3a, 3b, 4 and 6 (Table 3). Large differences occurred between the cluster groups. Whereas the biomass of *M. edulis* strongly increased in the southwest, biomass values did not increase on the Oder

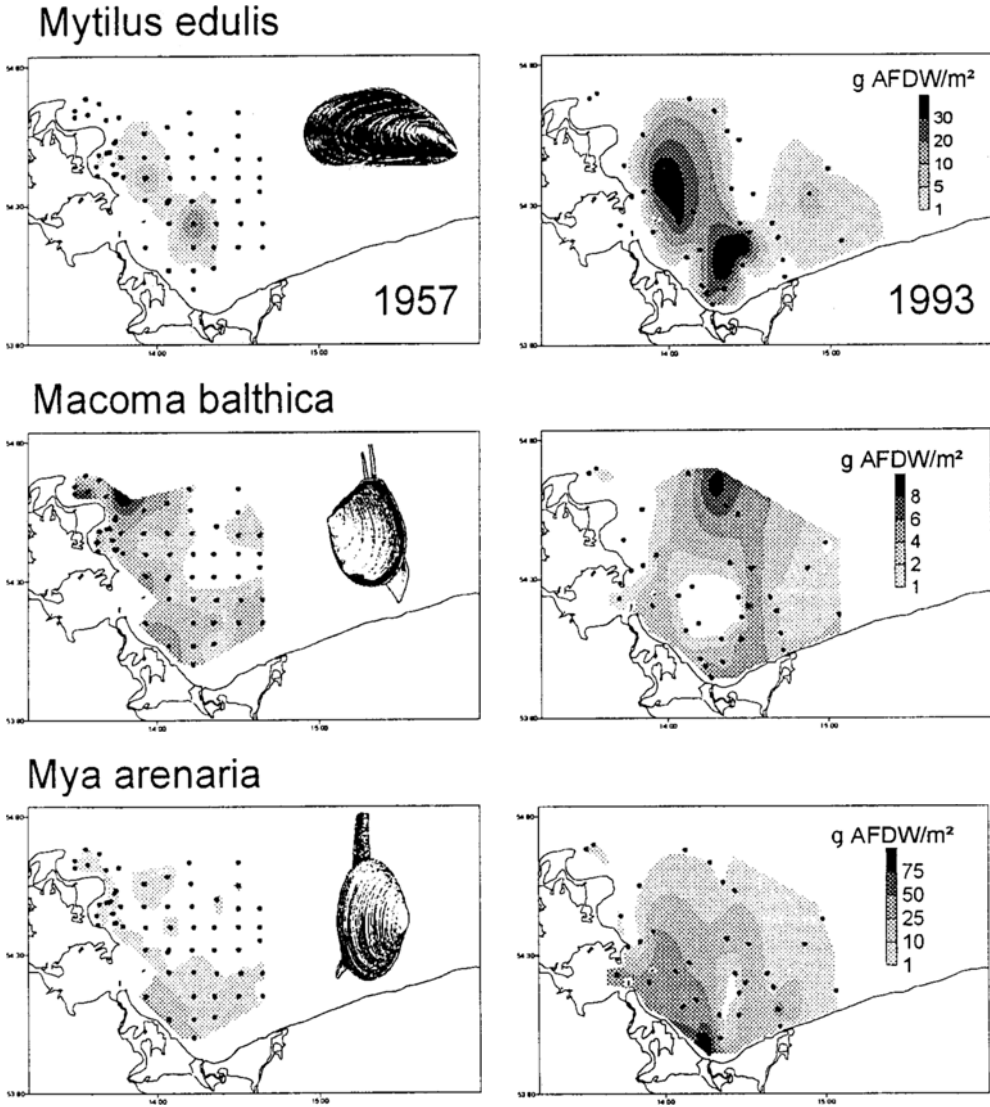


Fig. 9. Biomass distribution of *Mytilus edulis*, *Macoma balthica* and *Mya arenaria* (g AFDW · m⁻²) during the investigation periods of Löwe (1963) and Powilleit et al. (1995)

Bank. The biomass of *M. arenaria* increased in all cluster groups, except for decrease in cluster group 6. However, in all cases sample sizes were too small to obtain significant results.

Table 3. Changes in the biomass values ($g\ AFDW \cdot m^{-2}$) of *Mytilus edulis* (Me), *Macoma balthica* (Mb) and *Mya arenaria* (Ma) in the Pomeranian Bay. Asterisks denote statistical significant changes (***) $p < 0.001$, Mann-Whitney U-test)

Cluster group (n 1955–58/n 1993)	Species	1955–58 (Löwe, 1963)		1993 (Powilleit et al., 1995)		Factor of changes in the mean
		mean \pm se	median	mean \pm se	median	
3a (13/6)	Me	3.4 \pm 1.9	0.4	11.5 \pm 7.3	5.32	3.4
	Mb	2.5 \pm 0.4	2.2	3.1 \pm 0.9	2.1	1.2
	Ma	5.4 \pm 2.5	1.1	12.6 \pm 4.2	8.9	2.3
3b (16/3)	Me	0.3 \pm 0.1	0.2	0.3 \pm 0.2	0.1	0.8
	Mb	1.2 \pm 0.2	1.1	2.5 \pm 1.5	2.3	2.0
	Ma	1.1 \pm 0.2	1.0	9.7 \pm 4.6	12.7	9.0
4 (3/8)	Me	1.9 \pm 1.7	0.3	14.5 \pm 8.1	2.0	7.8
	Mb	1.4 \pm 0.6	1.8	2.2 \pm 0.6	1.9	1.6
	Ma	0.4 \pm 0.2	0.4	13.6 \pm 6.4	5.0	34.6
6 (13/3)	Me	0.8 \pm 0.4	0.0	2.1 \pm 1.2	2.1	2.6
	Mb	3.6 \pm 0.5	4.0	6.1 \pm 2.0	6.9	1.7
	Ma	2.4 \pm 1.0	0.6	0.5 \pm 0.2	0.4	0.2
all samples (58/33)	Me	1.1 \pm 0.5	0.2	9.7 \pm 2.9	2.0	8.5***
	Mb	2.5 \pm 0.3	2.1	2.6 \pm 0.4	2.3	1.0
	Ma	2.4 \pm 0.7	1.0	19.7 \pm 5.0	8.6	8.1***

DISCUSSION

Reliability of data

Comparing data that were gathered by different sampling methods is a general problem in evaluating past and present distribution patterns in the benthos (Reise et al., 1989). Unfortunately, long-term data series are often lacking for sublittoral marine areas, due to the enormous costs of shipboard sampling. As a consequence, almost all documentations of long-term changes in the macrofauna of the Baltic Sea are based on reinvestigations of areas that had been studied intensively several decades ago (Rosenberg & Möller, 1979; Cederwall & Elmgren, 1980; Brey, 1986).

For shallow waters in the western and southern Baltic Sea, we consider it unimportant to resample exactly the same sites in the same season, because:

1. Repositioning the research vessel on exactly the same station that had been sampled decades ago is impossible. Our own examinations of the precision of the navigation system which was used in the 1950s revealed a maximum error of ± 2 km for off shore areas without visible landmarks.
2. Often, there are no great differences in species composition in sandy areas, due to a very low species richness (Kube, 1992; Kube, 1996b; this study).
3. Density variations cannot be related to seasonal oscillations, provided by reproductive cycles. They are super-imposed by stochastic variations in hydrographic conditions (Arntz & Rumohr, 1986; Brey, 1986; Kube, 1992).
4. Abrasion of sediment and bedload transport induced by local winds often cause changes in large-scale patchiness which cannot be covered by taking three parallel grab samples at a single station (Kube, 1996a).

5. The sampling season has no strong effect on estimates of biomass values calculated from standardized length-weight relationships of bivalves with a high longevity and low P/B ratio.

Hence, it seems to us that the coverage of all important habitat types and a large number of samples is more important for a statistical evaluation than spatial and seasonal accuracy. The total number of samples used in this study was much higher than the sample sizes of the investigations of Cederwall & Elmgren (1980) and Brey (1986).

Responses to eutrophication, and fluctuations in hydrography and climate

Eutrophication is usually defined as a complex of phenomena triggered by an increase of limiting nutrients, which leads to increases in benthic abundance, biomass, and number of species but also to anoxic conditions in sediments and massive die-off of benthic animals (Pearson & Rosenberg, 1978; Heip, 1995). Effects of eutrophication are difficult to measure and difficult to explain in a straightforward manner, because benthic communities usually respond in two ways; functionally by increasing their productivity, and structurally by adapting their composition to the higher food supply (Beukema, 1991).

In the Baltic Sea, rates of increase in bivalve biomass above the halocline varied between 5 and 47% of the initial values per year (Table 4). We observed an annual rate of increase of about 20% of the values estimated in the 1950s which corresponds well to the rates of increase in nitrogen input. However, large differences occurred between individual species. The biomasses of the filter-feeders *M. edulis* and *M. arenaria* increased by almost 25% annually. No increase was found for *C. lamarcki* and *M. balthica*, the biomass dominants of the benthic communities in the 1950s. These findings are in accordance with the results reported by Cederwall & Elmgren (1980), who also described that *M. balthica* was replaced by *M. edulis* as the dominant species. The change in dominances seems to be related to a larger complex of causes; competition for food and space, mechanical disturbance by drifting mussel clumps, and shifts in the redox potential in summer due to organic loading.

Table 4. Long-term increase in the biomass of molluscs in shallow sublittoral waters of the Baltic Sea. Initial biomass: biomass at the begin of the investigation period, later biomass: biomass at the end of the investigation period (¹ data from Cederwall & Elmgren, 1980; investigations 1920–23 and 1976/77 around the islands of Öland and Gotland, ² data from Brey, 1986; investigations 1961–65 and 1982–83 in Kiel Bay, and ³ this study)

Species	Initial biomass (g AFDW · m ⁻²)	Later biomass (g AFDW · m ⁻²)	Mean increase (g AFDW · m ⁻²)	Increase rate (% · a ⁻¹ of the initial biomass)
<i>Mytilus edulis</i> ¹	0.09	2.3	0.04	46.5
<i>Cerastoderma spp.</i> ¹	0.03	0.14	0.002	8.5
<i>Macoma balthica</i> ¹	0.61	1.96	0.025	4.1
<i>Mya arenaria</i> ¹	0.003	0.05	0.001	30.3
all Mollusca ²	2.1	12.8	0.54	25.5
<i>Mytilus edulis</i> ³	0.2	2.0	0.05	25
<i>Macoma balthica</i> ³	2.1	2.3	0.006	0.3
<i>Mya arenaria</i> ³	1.0	8.6	0.22	22

Spatial variations in the biomass increase of *M. edulis* demonstrate how strong limitations by other ecological factors can be. In the Pomeranian Bay, motile *Mytilus*-clumps lay attached to *Mya*-shells on the sea floor. Depending on the current situation, single clumps can aggregate to patches of several square meters or disperse. Permanent erosion and strong bedload transports on the shallow Oder Bank prevent a successful settlement of mussel spat and encourage an accumulation of mussel-clumps in the deeper southwest of the bay. As a consequence, distribution patterns of *M. edulis* have not changed considerably during the past 35 years.

Below 15 m, all stations showed a decrease in species richness in the 1990s. These changes were caused by an increase in oxygen depletion events in the Arkona Basin since 1983 and upwelling of deep water with lowered oxygen saturation from the Arkona Basin into the Pomeranian Bay via the Sassnitz Deep. Gosselck (1985) described a rate of increase in macrobenthic biomass of $16\% \cdot a^{-1}$ between the 1950s and 1980s. *M. balthica* dominated macrobenthic biomass in 1980. Its biomass had increased annually by 53% of the initial value. First signs of macrofauna death in the Arkona Basin were noticed in 1984 (HELCOM, 1990). A change in the *M. balthica* population from larger to smaller individuals was observed and its biomass decreased. The total number of species decreased from 40 to 20 between 1980 and 1986. The reduction in the numbers of the crustaceans *P. femorata* and *Diastylis rathkei* was particularly striking.

Changes in the species composition of the macrofauna of the Pomeranian Bay does not result in an increasing proportion of deposit-feeders, as reported previously by other investigators (Heip, 1995). Our analyses rather suggest an increase in the portion of filter-feeders until 1993. A high rate of resuspension of phytoplankton and particulate organic matter in the shallow parts of the bay might be the cause for these findings. This hypothesis is supported by the fact that no organic matter was accumulated in the sediments.

Besides eutrophication, some of the observed phenomena seem also to be triggered by variations in oceanographic and climatic conditions. Although changes due to eutrophication in the benthic communities of the Baltic Sea become more and more obvious, we are still unable to quantify the observed effects.

Events of oxygen depletion were found to increase in the southern Baltic Sea since the 1980s (Weigelt, 1991; Franck & Matthäus, 1992). The large gap of important inflow events since 1983 might have been an important cause for the observed drastic changes in the oxygen regime of the Arkona Basin. Otherwise, the increase in benthic biomass until the 1980s might have accelerated the speed of oxygen depletion below the pycnocline during summer stratification.

Bivalves, the biomass dominants, show highly successful recruitment during summers following a cold winter (Beukema, 1982; Kube, 1996a). This positive effect can establish extraordinarily high biomasses after a series of severe winters due to the long life span of bivalves and, therefore, accelerates the speed of biomass increase (Beukema, 1989). Indeed, the population structure of *M. arenaria* differed strongly between the 1950s and the 1990s. Whereas smaller size classes prevailed during the late 1950s, the population was dominated by large specimens in 1993 (Kube, 1996a). This observation agrees with differences in the time course of the winter severeness index during the ten-year periods preceding both investigations.

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