Hydrogen sulphide and other factors influencing the macrobenthic community structure in the Gulf of Gdańsk\*

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Gulf of Gdańsk Macrofaunal communities Hydrogen sulphide Biodiversity

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#### Abstract

Three stations in the Gulf of Gdańsk were sampled monthly for one year with regard to macrozoobenthos composition, oxygen content and temperature of near-bottom waters, granulometry, organic matter content and  $H_2S$  concentration in sediments. The differences in  $H_2S$  concentrations at the stations were most conspicious. The presence and concentrations of  $H_2S$  appeared to be the decisive factor for the grouping of samples in the Bray-Curtis Similarity Index-based ordination. Even seasonality was of secondary importance. The number of species and the Shannon Indices decreased, and the dominance of the predominant species – *Macoma balthica* – increased in accordance with the  $H_2S$  gradient between the stations. The community was dominated by detritus-feeders.

# 1. Introduction

The impact of hydrogen sulphide on marine animals has been studied intensively by marine biologists for the last 20 years. Because of its high toxicity (Evans, 1967) high concentrations of this compound in the marine

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environment may result in the mass mortality of fauna (Brongersma-Sanders, 1957). On the other hand rich benthic communities well adapted to  $H_2S$  exist in the vicinity of hydrothermal vents (Southward, 1983). There are a number of papers concerning the toxicity of  $H_2S$  and the mechanisms of physiological adaptations to its presence including its detoxification (*e.g.* Theede *et al.*, 1969; Vismann, 1991a; Somero *et al.*, 1989). Less attention has been paid to environmental studies of the  $H_2S$  impact on benthic fauna composition and distribution (Fenchel and Riedl, 1970; Miron and Kristensen, 1993).

Hydrogen sulphide is a significant environmental factor for benthic fauna inhabiting highly polluted and eutrophicated areas. It is omnipresent in marine sediments (Fenchel and Riedl, 1970), but its presence is usually restricted to the deeper anoxic sediment layers below the Redox-Potential-Discontinuity layer (Fenchel, 1969). The constant, strong input of organic carbon, observed in eutrophicated regions, results in high rates of sulphate reduction, uplift of the RPD layer, hypoxia, and H<sub>2</sub>S concentrations exceeding 1 mM in near-bottom waters, and hence the mortality of macrofauna (Sampou and Oviatt, 1991). Elimination of species or entire communities due to hypoxia and H<sub>2</sub>S has been reported in different parts of the Baltic - e.g. in the coastal waters of the south-east Kattegat (Baden *et al.*, 1990), in the Bornholm and Gdańsk Deeps (Żmudziński, 1968).

The qualitative and quantitative composition, as well as the patterns of seasonal variations of macrofauna in the Gulf of Gdańsk have been studied by Zmudziński (1967), Wenne and Wiktor (1982), Herra and Wiktor (1985), Legezyńska and Wiktor (1981); its trophic structure has been described by Wiktor (1985). With regard to environmental factors, these papers analysed the depth, sediment granulometry, temperature and salinity of near-bottom waters. The influence of these factors and oxygen conditions on the distribution of selected species was described by Mulicki (1957, 1958). However, none of these papers dealt with  $H_2S$  as an environmental factor.  $H_2S$  concentrations in this region have been measured by Trzosińska and Cyberska (1992) in near-bottom waters and by Bolałek *et al.* (1994) in the interstitial waters of sediments. The first report on the impact of  $H_2S$  on the macrofaunal composition in the Gulf of Gdańsk was presented recently by Janas and Szaniawska (1996). The present study aims to examine the impact of  $H_2S$ and the other environmental factors traditionally considered in this region (temperature and oxygen content in near-bottom waters, granulometry and organic matter content in sediments) on the macrobenthic community structure as described by its qualitative and quantitative composition, diversity and trophic structure.

# 2. Material and methods

Material was collected at 3 stations situated in the Gulf of Gdańsk: 92A (depth 37 m), 7 (51 m) and 11 (60 m) (Fig. 1). Samples were taken from on board r/v 'Oceanograf 2' every month from February 1994 to February 1995, excluding July and August 1994. Because of navigational difficulties, samples were not taken in February 1994 at station 11 or in May 1994 at station 92A.



Fig. 1. Location of sampling sites

The near-bottom waters were sampled with a Nansen bottle, while temperature was measured on board using a thermistor. Oxygen content was determined by Winkler's method in the laboratory the same day. Sediment cores 8 cm in length were taken using a gravity probe with a pipe diameter of 2.2 cm. The H<sub>2</sub>S content in interstitial waters was measured by Cline's method (Cline, 1969). The procedure described by Janas and Szaniawska (1996) was followed in this study. The organic matter content was determined as an ignition loss after 4h at 500°C. For granulometric analysis the sediment was dried and sifted on sieves of 0.5, 0.25 and 0.065 mm mesh size. The macrofauna was sampled with the use of a Van Veen grab of  $0.1 \text{ m}^2$  sampling area size. Three samples were taken at each station, sifted through a sieve of 1 mm x 1 mm mesh diameter and preserved in 4% formaldehyde solution. Species composition, abundance and biomass of each species were determined for each sample. Molluscs were weighed with shells (wet mass).

Frequency (the percentage of occurence in all samples), percentage in the total abundance and in the total biomass were calculated for each taxon. Dominants were determined as taxons contributing more than 10% to the total abundance. The number of species per sample and the Shannon Index were used as measures of diversity. Both were correlated to the environmental factors measured at stations. The trophic structure of the community was analysed. With regard to their feeding preferences, species were classified into 4 groups: deposit feeders, suspension feeders, predators and facultative suspension-deposit feeders according to information provided by Wiktor (1985).

Classification and ordination procedures (hierarchical cluster analysis and multidimensional scaling (MDS)) were applied to species/abundance data in order to distinguish groups of samples of similar faunal composition<sup>1</sup>. The data were double-root transformed. Group average linking of Bray-Curtis similarities was performed. The results were presented in the form of a dendrogam and a two-dimensional MDS-plot. To evaluate the influence of environmental factors on the taxonomic composition of samples, a visual technique of superimposition of environmental factors on faunal ordination was used. The symbols, scaled in size according to the values of the environmental factors measured, were superimposed onto the MDS configuration. Formal testing of this visual approach was performed by regressing each environmental factor on the x and y co-ordinates of sample location on the MDS (multiple linear regression) (Clarke, 1993).

## 3. Results

The near-bottom water temperature was lowest in February 1994 (2.0°C) and highest in September (13.2°C). The oxygen content varied from 5.61 ml dm<sup>-3</sup> to 8.98 ml dm<sup>-3</sup>, the differences between stations being small and rarely exceeding 1 ml dm<sup>-3</sup>. The mean values for the stations were: 92A – 7.43 ml dm<sup>-3</sup>, 7 – 6.98 ml dm<sup>-3</sup>, 11 – 6.80 ml dm<sup>-3</sup>. Oxygen deficiency conditions in near-bottom waters were not observed at any station in the period studied. The organic matter content in sediments rarely exceeded 10%

<sup>&</sup>lt;sup>1</sup>The cluster, MDS and superimposing of environmental data analysis were performed with the use of programs of the PRIMER package kindly provided by Plymouth Marine Laboratory.

and was on average 8.58% at station 92A, 8.82% at station 7 and 8.86% at station 11. Granulometric analysis classified sediments as fine muds containing 35% sand. No significant difference in sediment type was noted between stations. H<sub>2</sub>S concentrations in the interstitial waters of the sediment increased in accordance with the depth gradient: in all months values were highest at station 11, lower at station 7 and lowest at station 92A. On average there was 2.3  $\mu$ mol dm<sup>-3</sup> H<sub>2</sub>S at station 92A, 104  $\mu$ mol dm<sup>-3</sup> at station 7, and 167.9  $\mu$ mol dm<sup>-3</sup> at station 11.

The representatives of 17 taxa were found in the macrofaunal samples. Macoma balthica, Pontoporeia femorata and Halicryptus spinulosus were the most frequent species in the study area, occurring in more than 75% of samples. Saduria entomon and Harmothoe sarsi were common species (50-74%). Corophium volutator, Mya arenaria, Nereis diversicolor, Hydrobia ulvae and Hydrobia ventrosa and Oligochaeta representatives occurred with a frequency of between 25 and 49%. Six other species occurred in less than 24% of the samples, so they can be treated as accidental in the material analysed.

Two species -M. balthica and P. femorata – were found to be dominants at station 7, and one -M. balthica – at stations 92A and 11 (Tab. 1). In all samples M. balthica made up from 50 to 95% of the total faunal abundance. The ratios of this species to the total biomass were even higher – in excess of 90% in all samples. On average it made up 90% of the total faunal biomass on at station 92A, 96% at station 7 and 98% at station 11.

The numbers of species per sample and the Shannon Indices are presented in Tab. 2. The maximum number of taxa (12) was recorded at station 92A in October, the minimum (3) at station 7 in June. On average 9 taxa were found in samples taken at station 92A, and 6 each at stations 7 and 11. The Shannon Indices ranged from 0.37 (May, station 11) to 1.24 (November, station 92A). In most months these indices were highest at station 92A (mean -1.04), lower at station 7 (mean -0.84), and lowest at station 11 (mean -0.65). Among the environmental variables only H<sub>2</sub>S was significantly correlated with the Shannon Index at p < 0.05 (r = 0.40, p = 0.046) (Tab. 3).

The community consisted of representatives of 4 trophic types (Fig. 2). Most taxa were classified as detritus feeders: *N. diversicolor, Diastylis rathkei, P. femorata, Pontoporeia affinis, C. volutator, H. ulvae, H. ventrosa, Potamopyrgus jenkinsi, Theodoxus fluviatilis* and Oligochaeta. They made up about 1% of the total faunal biomass. Only 1 suspension feeding species – *Mytilus edulis* – was observed in the study area; its contribution to the total biomass did not exceed 1% at stations 92A and 7, and was absent at station 11. The predators of this region are *S. entomon, H. spinulosus,* 

Taxon	F%	Station 92A		Station 7		Station 11	
		D%	B%	D%	B%	D%	B%
Macoma balthica	100	71.36	90.39	69.66	96.41	84.00	97.82
Pontoporeia femorata	97	9.72	0.81	22.06	0.87	9.02	0.51
Halicryptus spinulosus	84	5.63	3.71	1.3	1.18	0.74	0.68
$Saduria\ entomon$	66	0.23	0.44	0.72	1.35	0.37	0.64
Harmothe sarsi	63	0.94	0.03	3.16	0.04	2.43	0.04
$Corophium \ volutator$	47	0.24	0.01	0.24	0.01	0.63	0.02
Oligochaeta	41	0.27	+	2.3	+	0.3	+
Hydrobia ulvae	38	6.31	0.17	_	_	0.66	0.01
Mya arenaria	38	3.06	3.61	0.2	0.01	0.33	0.05
Nereis diversicolor	31	0.11	+	0.28	0.01	1.33	0.24
Hydrobia ventrosa	25	1.5	0.04	_	_	_	_
Potamopyrgus jenkinsi	22	0.36	0.01	_	_	_	_
Diastylis rathkei	13	0.08	0.01	_	_	0.04	+
Pontoporeia affinis	13	0.03	+	0.04	+	0.07	+
Mytilus edulis	6	0.19	0.76	0.04	0.13	_	_
Crangon crangon	3	_	_	_	_	0.04	+
Theodoxus fluviatilis	3	_	_	_	_	0.04	+

**Table 1.** Frequency in all samples (F%), average percentage in the total abundance (dominance, D%) and average percentage in the total biomass (B%) at stations for the taxa determined (– not observed, + percentage < 0.01%)

**Table 2.** Number of species per sample (n) and Shannon Indices (H) for all samples and average at stations (– samples not taken)

Station		1994 Feb.	Mar.	Apr.	May	June	Sept.	Oct.	Nov.	Dec.	1995 Jan.	Feb.	Mean
92A	n H	9 1.00	8 0.96	6 1.02	_	7 0.75	9 1.15	12 1.17	12 1.24	$9 \\ 1.2$	9 0.93	9 0.96	9 1.04
7	n H	$\begin{array}{c} 5 \\ 0.80 \end{array}$	4 0.60	$5 \\ 0.55$	$\begin{array}{c} 4 \\ 0.46 \end{array}$	3 0.46	7 0.93	6 1.12	9 1.16	$7\\1.00$	7 1.18	7 1.00	$\begin{array}{c} 6 \\ 0.84 \end{array}$
11	n H	_	$5 \\ 0.65$	$5 \\ 0.53$	$\begin{array}{c} 4 \\ 0.37 \end{array}$	$5 \\ 0.41$	7 0.68	$\begin{array}{c} 6 \\ 0.60 \end{array}$	$8 \\ 0.92$	$7\\0.82$	$\begin{array}{c} 6 \\ 0.85 \end{array}$	8 0.69	$\begin{array}{c} 6 \\ 0.65 \end{array}$

*H. sarsi* and *Crangon crangon*. Their ratios to the total biomass decreased from 4% at station 92A to 3% at station 7 and 1% at station 11. The community was dominated by facultative suspension-detritus feeders – *M. balthica* and *M. arenaria* – the percentage of which in the total biomass exceeded 90% and increased from station 92A to station 11.

**Table 3.** Correlation matrix for environmental variables and diversity measures (n – number of species per sample and H – Shannon Indices)

	Temperature	Oxygen	Organic matter	Hydrogen sulphide
n H	$\begin{array}{c} 0.30\\ 0.39 \end{array}$	$0.26 \\ 0.31$	$\begin{array}{c} 0.16 \\ 0.07 \end{array}$	$0.37 \\ 0.40^*$

\* p < 0.05



Fig. 2. The ratios of organisms of different trophic types to the total biomass at stations

Both clustering and multidimensional scaling showed two distinct groups of samples: the group of samples from station 92A and those from stations 7 and 11 (Figs. 3 and 4). Within each of them two subgroups could be distinguished: spring samples and autumn-winter samples. In Fig. 5 the values of the water temperature and oxygen content, sediment organic matter content and hydrogen sulphide concentrations were superimposed onto the MDS configuration plot. If these factors influence the configuration to any degree, the samples with similar values of these variables, and hence symbols of similar size, should cluster together (Warwick and Clarke, 1993). The temperatures (Fig. 5a), oxygen contents (Fig. 5b) and organic matter contents (Fig. 5c) are distributed quite randomnly, hence we assume that these factors did not determine the differences in sample species composition. On the other hand the symbols representing  $H_2S$  concentrations display a very clear distribution pattern (Fig. 5d) – they form two groups: one of very low  $H_2S$  values (which fits the group of samples at station 92A) and one of higher  $H_2S$  values (fitting the group of samples at

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Fig. 3. Dendrogram resulting from the clustering of all samples. Stations: a – 92A, b – 7, c – 11. Months of sampling: 2 – February 1994, 3 – March 1994, ..., 1' – January 1995, 2' – February 1995



Fig. 4. MDS-plot resulting from the ordering of all samples. Stations: a - 92A, b - 7, c - 11. Months of sampling: 2 - February 1994, 3 - March 1994, ..., 1' - January 1995, 2' - February 1995



Fig. 5. MDS configuration from Fig. 4 with symbols scaled to show the values of the environmental factors measured at the sampling sites: water temperature (a), oxygen content of the water (b), organic matter in the sediment (c), hydrogen sulphide concentrations in sediment interstitial waters (d); r – multiple regression coefficient resulting from regressing the environmental factor at the sample location coordinates on MDS; \* p < 0.05

stations 7 and 11). Hence the H<sub>2</sub>S concentration in the interstitial waters of sediments appears to be the factor best correlating with the species composition differences between samples, which is confirmed by the multiple regression results (shown in Fig. 5). Only the H<sub>2</sub>S values are significantly correlated with the sample location coordinates on the MDS at p < 0.05 (r = 0.51, p = 0.015).

### 4. Discussion

The species composition of the material analysed is similar to that found during the investigations carried on in the same region by Zmudziński (1967). The only major difference is the lack or very scarce presence of D. rathkei in our samples. According to Zmudziński's (1967) classification, stations 92A, 7 and 11 are situated in the deep-water part of the Gulf of Gdańsk. The community is therefore dominated by deep-water, cold-water species, although significant quantities of typically shallow water species (e.g. H. ulvae) were present as well. Most species common in the study area have been described as characteristic of eutrophicated waters, tolerating high levels of organic pollution or oxygen deficiency, and  $H_2S$  resistant. Pearson and Rosenberg (1978) included M. balthica, M. arenaria, H. ulvae, C. volutator and N. diversicolor in their list of species typical of areas polluted by organic material. Resistance to a relatively high oxygen deficiency and to  $H_2S$  in *M. balthica* and *M. arenaria* was observed under experimental conditions by Oertzen and Schlungbaum (1972). Mechanisms of  $H_2S$  detoxication for S. entomon were described by Vismann (1991b), for H. spinulosus by Oeschger and Vetter (1992) and for N. diversicolor by Vismann (1990).

Both clustering and ordination of samples revealed 2 basic groups of samples – one taken at station 92A, the other from stations 7 and 11. Among the environmental factors measured, differences in the hydrogen sulphide concentration in sediment interstitial waters were the most conspicious differences between stations. Whereas  $H_2S$  was absent or present only in small quantities at station 92A, its concentrations were found to be relatively high at stations 7 and 11. Among the factors considered  $H_2S$  was best correlated with species composition differences between samples, which the MDS plots with superimposed environmental factors show up very clearly. Hence we assume that  $H_2S$  is the factor controlling the macrofaunal composition and distribution in this region. The similarity of samples taken at sites with similar  $H_2S$  concentrations was even higher than the similarity of samples taken in the same seasons. Therefore,  $H_2S$  turned out to be more important than seasonality for the species composition at the stations analysed. Herra and Wiktor (1985) suggested that sediment granulometry was the factor determining macrofaunal distribution in the coastal waters of the Gulf of Gdańsk. The bottom type is very important for the invertebrates inhabiting it, providing as it does a specific habitat, (e.g. because of the degree of hardness, and the presence and extent of the interstitial space system), and may influence the availability of food (Wieser, 1967). The granulometric analysis of the sediment showed this to be very similar at the stations studied, so this factor could not have been responsible for any differences

in faunal composition. Rosenberg et al. (1992) stated that in eutrophicated brackish waters like Baltic Sea coastal waters there are three main factors structuring the macrofaunal communities: oxygen conditions, salinity and temperature. The salinity was not measured during the present study, but Nowacki (1993) reported the near-bottom waters in this region as being homogeneous with regard to salinity, their PSU values ranging from 7.75 to 8. The water temperature fluctuated during the year according to seasonality, but no significant differences in monthly values or in amplitudes were noted between stations. Nevertheless, the seasonal changes in temperature must have influenced the secondary grouping of samples - into a subgroup of spring samples and a subgroup of autumn-winter samples. In eutrophicated areas the oxygen conditions are a very important factor, as the development of hypoxic conditions may result in significant reductions among benthic organisms (Rosenberg et al., 1992). At all three stations the oxygen conditions were favourable, the minimum  $O_2$  concentration recorded being 5.61 ml  $dm^{-3}$ ; no significant differences between stations were noted, and this factor did not influence the benthic distribution in the study area.

The numbers of species in samples were much lower at stations 7 and 11 (on average 6 taxa) than at station 92A (on average 9 taxa). The seasonal migrations of species caused their number to increase in autumn. The differences in the number of species per sample are similar to the differences in Shannon Indices. The values of this index recorded were usually the highest at station 92A, lower at station 7, and the lowest at station 11. Biodiversity, a measure both of the number of species present (species diversity) and of the quantitative relations between species – how equally or unequally the species divide the sample (dominance diversity; Whittaker, 1965), is a reflection of the complexity of biological interactions, the stage of community development, and the diversity and stability of the habitat. According to Sanders' (1968) 'time-stability hypothesis', a high diversity is characterisic of biologically accommodated communities living in stabilised environments, where the physical conditions have been stable and physiological stresses have been low for a long period of time. When physiological stress increases, resulting from increasing fluctuations in physical conditions or from increasingly unfavourable physical conditions, the nature of the community gradually changes into a physically controlled one (Sanders, 1968). A number of species which are unable to adapt to the new conditions are eliminated, the most resistant species become more abundant, and a few of them become predominant in the community. A situation like this seems to be occurring in the study region: the number of species is relatively low, the number of dominants never exceeded 2, but one of them -M. balthica - is absolutely predominant in the community

– making up from 50 to 95% of the total abundance and from 80 to 99% of the total biomass. These three factors – the number of species, the Shannon diversity index and the degree of domination of the 'superdominant'– M.balthica – change gradually from station 92A to station 11; presumably, they can be related to the H<sub>2</sub>S concentration gradient. Among the environmental factors studied H<sub>2</sub>S is the only one significantly correlated with the Shannon Index. At station 92A, where H<sub>2</sub>S was absent or present in only very small quantities, the number of species and the Shannon Indices were the highest and the ratios of M.balthica to the total abundance and biomass the lowest. At station 11, where the H<sub>2</sub>S concentrations were the highest and have reached 322  $\mu$ mol dm<sup>-3</sup>, the number of species and the Shannon Indices were the lowest, and M. balthica dominated the community to the greatest extent. At station 7 both H<sub>2</sub>S concentrations and the diversity and dominance factors were intermediate.

The trophic structure of the community was analysed according to Wiktor's (1985) classification. Our analysis showed facultative suspensiondetritus feeders to be dominating the community, something that Wiktor had also observed at similar depths. Wiktor classified 2 taxa into this feeding type group: M. balthica and M. arenaria. Olafsson (1986) reported that M. balthica changed its feeding preferences and behaviour in accordance with the bottom sediment type, filtering suspensions when living on sands, but becoming a detritus feeder on muds. This phenomenon was observed under both laboratory and environmental conditions. From these findings, together with the results of granulometric analysis of sediments from all three stations, one would expect M. balthica to feed on detritus in the study region; it could then be included in the detritus feeder group, which would thus make up from 95% of the total biomass at station 92A to 99% at station 11. The other significant group was formed by predators, the ratios of which to the total biomass ranged from 4% at station 92A to 1% at station 11. Such a trophic structure of this community may have resulted from both the bottom type and the organic pollution level. Long and Lewis (1987) found the relative proportion of detritus feeding and suspension feeding to be correlated significantly to sediment grain size, and hence deposit feeders increasing and suspension feeders decreasing as the ratio of sand to pelite decreases. A high level of eutrophication can influence the trophic structure of a benthic community as well. Pearson and Rosenberg (1978) described the progressive simplification of trophic variety in response to increasing organic enrichment, the elimination of filtrators, and under high organic pollution input levels the development of a community composed almost entirely of deposit feeders with a small proportion of carnivores.

Despite the increasing eutrophication of this region of the Gulf of Gdańsk, Wenne and Wiktor (1982) did not record any changes in the species composition reported by Żmudziński (1967). However, they did observe a significant increase in the total biomass, from 111 g m<sup>-2</sup> in 1962/63 to 187 g m<sup>-2</sup> in 1977/78 (Tab. 4). The average biomass at the stations studied in the same region in 1994/95 was 206 g m<sup>-2</sup>. Such a relatively slow increase in macrofaunal biomass during the last 17 years compared to the rapid increase during the previous 15 years could signify a retardation in the trends observed by Wenne and Wiktor (1982). On comparing their results with those of Zmudziński (1967), Wenne and Wiktor did not observe the changes in benthic community structure characteristic of the shallow water part of the Gulf of Gdańsk, namely, the increase in bivalve biomass and the decrease in the biomass of the other components of the community, especially crustaceans (Legeżyńska and Wiktor 1981). In both Żmudziński's and Wenne and Wiktor's samples Bivalvia made up ca 85% of the total biomass, and Crustacea 11–13%. The results of the present study -95% of bivalves and 1.55% of crustaceans – show the increasing role of Bivalvia and decreasing importance of crustaceans in the deep-water part of the Gulf of Gdańsk in recent years. Theede (1973) found lamellibranches to be more resistant to oxygen deficiency and H<sub>2</sub>S than are gastropods, polychaetes, crustaceans and echinoderms. He attributed this to their ability to reduce their contact with the ambient medium by closing their shells and to reduce their mechanical and metabolic activity by responses of the whole animal as well as by cellular reactions. It is not possible to evaluate the role of  $H_2S$ in the temporal changes in community structure described in the present

Taxon	1962/63		1977/	'78	1994/95		
	$[g m^{-2}]$	%	$[{\rm g}~{\rm m}^{-2}]$	%	$[g m^{-2}]$	%	
Oligochaeta	_	_	0.01	+	0.01	+	
Polychaeta	0.1	0.09	0.01	+	0.12	0.12	
Priapulida	0.5	0.45	3.17	1.69	3.6	1.91	
Gastropoda	_	_	0.01	+	0.13	0.07	
Crustacea	15.5	13.93	21.31	11.37	3.19	1.55	
Bivalvia	95.2	85.53	162.84	86.92	195.8	95	
Total	111.3		187.35		206.1		

**Table 4.** The average biomass of the main macrofaunal components in the deep-water part of the Gulf of Gdańsk (below 30 m) in 1962/63 (after Żmudziński, 1967), in 1977/78 (after Wenne and Wiktor, 1982) and in 1994/95 (present study) (– not observed, + percentage < 0.01%)

paper since we do not have any information on its presence or quantities in the Gulf of Gdańsk from before 1992, but Theede's (1973) observations suggest that it could have been one of factors responsible for the changes in the relative proportions of the principal community components in its total biomass.

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