The influence of hydrogen sulphide on macrofaunal biodiversity in the Gulf of Gdańsk^{*}

OCEANOLOGIA, No. 38 (1) pp. 127–142, 1996. PL ISSN 0078–3234

> Hydrogen sulphide Sediment Zoobenthos

URSZULA JANAS, ANNA SZANIAWSKA Institute of Oceanography, Gdańsk University, Gdynia

Manuscript received October 8, 1995, in final form November 11, 1995.

Abstract

Investigations into the occurrence and concentrations of hydrogen sulphide in sediments of the Gulf of Gdańsk were carried out in September 1994. It was found that the concentration of H₂S increased with basin and sediment depths. The highest concentration (1244 μ mol dm⁻³) was recorded in the 4–8 cm sediment layer at the deepest of the stations investigated (station 14; 82 m depth). The studies demonstrated that numerous species belonging to the macrozoobenthos are exposed to H₂S concentrations from several to several hundred μ mol dm⁻³. These are both deep-water species – Macoma balthica, Harmothoe sarsi, Saduria entomon, Pontoporeia femorata – and shallow-water species – Corophium volutator, Mya arenaria. High concentrations of hydrogen sulphide, *i.e.* > 1000 μ mol dm⁻³, caused the number of different macrozoobenthos species to decrease, even though abundance and biomass levels remain high. The studies indicated that the presence of hydrogen sulphide is best tolerated by two species – Macoma balthica and Harmothoe sarsi.

1. Introduction

In recent years, a series of unfavourable changes brought about by human activities have been observed in the Baltic Sea area. One of the most alarming is the process of eutrophication (Cederwall and Elmgren, 1990). The natural stratification of Baltic waters and the increasing sedimentation of organic matter at the bottom of this sea has led to the formation of extensive areas where oxygen deficiency and the presence of hydrogen sulphide

 $^{^{*}}$ This research was supported by grant No. 0344/P2/93/05 from the State Committee for Scientific Research, Republic of Poland.

have been recorded. Such conditions have a direct, unfavourable impact on the bottom fauna.

Hydrogen sulphide is widespread in the marine environment, and its occurrence in bottom sediments has been determined and described by many researchers (Bagarinao, 1992; Fenchel and Riedl, 1970; Jørgensen, 1977, 1988; Jørgensen et al., 1990; Millero, 1991). Even nano- and micromolar concentrations of this compound are toxic to the majority of aerobic organisms (National Research Council, 1979). It is therefore a significant factor influencing the biodistribution (Theede, 1981; Miron and Kirstensen, 1993), species composition (Fenchel and Riedl, 1970), and biotic processes of bottom fauna (Hagerman and Visman, 1993; Levitt and Arp, 1991; Oeschger and Storey, 1993). Now, a number of laboratory investigations have demonstrated the increased resistance of certain species to H_2S (Theede et al., 1969; Theede 1973), and the ability of some species, e.g. Saduria entomon (Visman, 1991a), Arenicola marina (Groenendaal, 1981; Völkel and Grieshaber, 1992) and *Halicryptus spinulosus* (Oeschger and Vetter, 1992), to develop special adaptive mechanisms. In order to emphasise the importance of hydrogen sulphide as an environmental factor, Visman (1991b) has suggested that animals be divided into H_2S -tolerant and H_2S -non-tolerant species, in the same way that they are already divided into steno- and eurythermal or steno- and euryhaline ones.

Studies of the macrozoobenthos in the Gulf of Gdańsk (Herra and Wiktor, 1985; Legeżyńska and Wiktor, 1981; Wiktor *et al.*, 1980; Wołowicz, 1994; Żmudziński, 1976) and the geochemical parameters of the bottom sediments in this area (Jankowska, 1993, Kępińska *et al.*, 1990; Pęcherzewski, 1974) have been carried out for many years. Although the literature on the above subjects is extensive, there are no publications dealing with H₂S occurrence and its impact on animal distribution in the Gulf of Gdańsk. The existing reports concern only the occurrence of H₂S in near-bottom waters (Trzosińska and Cyberska, 1992) or in the interstitial waters of the sediments from the coastal zone of the Hel Peninsula (Bolałek *et al.*, 1994). Therefore, it seems important to pinpoint the regions of the Gulf of Gdańsk where H₂S is present and to determine its concentrations in the sediments, especially in the layer inhabited by the macrozoobenthos, as well as to find out by both quantitative and qualitative analysis of the macrofauna composition which species occur in and dominate H₂S-rich areas.

2. Materials and methods

Material for the studies was collected from on board r/v 'Oceanograf II' in September 1994. The H₂S content in the interstitial waters of the bottom sediments was determined down to a depth of 8 cm at 16 sampling

The influence of hydrogen sulphide on macrofaunal biodiversity ...



Fig. 1. Location of sampling stations

stations in the Gulf of Gdańsk (Fig. 1). The sediment samples were taken with a gravity probe with a pipe diameter of 2.2 cm. Immediately after collection, the cores were sectioned into 4 cm segments (in the case of stations 7, 11 and 92A into 1 cm segments) and centrifuged at 3700 rpm for 3 min to recover interstitial water. The water samples obtained were mixed with N,N-dimethyl-p-phenylene diamine dichloride and ferric chloride solution. Concentrations of H₂S below 40 μ mol dm⁻³ were determined spectrophotometrically (Cline, 1969). Samples containing higher H₂S concentrations were diluted prior to the addition of the reagents. The terms hydrogen sulphide and H₂S used in this paper refer to all forms of hydrogen sulphide, *i.e.* H₂S, HS⁻ and S²⁻.

At stations 7, 11, 14 and 92A, the following near-bottom water parameters were also determined: temperature (°C), oxygen content (ml O₂ dm⁻³) and H₂S (μ mol dm⁻³) concentration. The oxygen content was measured by Winkler's method (UNEP, 1988). In addition, bottom sediment cores (10 cm long) were collected with the aid of a corer to assay the type of sediment and the organic matter it contained. Organic matter was determined as a loss during ignition for 4 h at 500°C (Dybern *et al.*, 1976). Sediment type was analysed granulometrically on sieves. Zoobenthos was collected with a Van Veen grab (three grabs at stations 7, 11, 92A and two at station 14). Each sample was sifted through a sieve of 1 mm mesh. The organisms that remained after sifting were preserved in 10% formalin and used to determine the species composition, and the abundance and biomass of the macrobenthos (the bivalve biomass included shells). The results presented below are the mean values of abundance and biomass obtained for all collections at a given station recalculated per square metre of bottom surface.

3. Results

3.1. The occurrence of H_2S in the interstitial waters of bottom sediments

The presence of hydrogen sulphide in the surface layers of the bottom sediments from the Gulf of Gdańsk was confirmed at sampling stations below 28 m depth (Figs. 2 and 3). A gradual increase in H₂S concentration with depth was observed in both layers studied, *i.e.* 0–4 and 4–8 cm (Figs. 2 and 3). In the 0–4 cm sediment layer, H₂S levels were rather low, from 0 to $35 \ \mu$ mol dm⁻³; only at station 14 was a higher concentration of 1072 μ mol dm⁻³ recorded (Fig. 2). Concentrations of H₂S in the 4–8 cm sediment layer were several or even several hundred times higher (Fig. 3).

The vertical distribution of H_2S content in the 0–8 cm sediment layer analysed at stations 7, 11 and 92A showed that its concentration increased with sediment depth (Fig. 4). Slight discrepancies in the vertical gradient were observed only in the 1–3 and 6–8 cm layers at station 92A and in the 6–7 cm layer at station 11.

Four sampling stations were selected for detailed study: 7, 11, 14 and 92A (Fig. 1), which differ with respect to H₂S concentration in the interstitial waters of the bottom sediments. Tab. 1 sets out the characteristics of the environmental parameters at these stations. The H₂S concentrations in the interstitial waters at station 92A were relatively low $-8.7 \ \mu$ mol dm⁻³ and 12.7 μ mol dm⁻³ for the 0–4 cm and 4–8 cm sediment layers respectively. At stations 7 and 11 the respective figures for the surface sediment layers were fairly low -13.1 and 20.4 μ mol dm⁻³, but high for the deeper sediment layers $-83.5 \ \mu$ mol dm⁻³ at station 7 and 304.6 μ mol dm⁻³ at station 11.



Fig. 2. H₂S concentration [μ mol dm⁻³] in the pore waters of bottom sediments in the 0–4 cm layer

At station 14, H₂S levels were highest in both sediment layers studied – 1072.9 μ mol dm⁻³ in the 0–4 cm layer and 1224.3 μ mol dm⁻³ in the 4–8 layer.

3.2. Determination of the macrozoobenthos species dominant in areas of H_2S occurrence

Analysis of the macrozoobenthos composition revealed the presence of 9 species at station 92A: Macoma balthica, Pontoporeia femorata, Halicryptus spinulosus, Harmothoe sarsi, Mya arenaria, Corophium volutator, Hydrobia ulvae, Hydrobia ventrosa, Potamopyrgus jenkinsi, and 7 species at stations 7 and 11: Macoma balthica, Pontoporeia femorata, Halicryptus spinulosus, Harmothoe sarsi, Mya arenaria, Corophium volutator, Saduria entomon (Tab. 2). In addition, some representatives of the taxon Oligochatea



Fig. 3. H₂S concentration [μ mol dm⁻³] in the pore waters of bottom sediments in the 4–8 cm layer

were found at station 7. Only 3 species were found at the deepest of the stations with the highest concentration of H₂S (station 14): *Macoma balthica, Pontoporeia femorata, Harmothoe sarsi.* The crustaceans *Mysis mixta,* found at stations 14 and 92A, are not typical representatives of the benthos, and because of their mode of life they are considered to be a part of the nectobenthos. Accordingly, their abundance and biomass was not taken into account in the calculations. The largest number of animals (1676 indiv. m⁻²) was found at station 92A, the smallest (913 indiv. m⁻²) at station 11. The highest total biomass (270.25 g m⁻²) was measured at station 7, the smallest (195.65 g m⁻²) at station 11. Relatively high levels of abundance -1362 indiv. m⁻² – and biomass -261.94 g m⁻² – were recorded at station 14, where the H₂S concentration was the highest. The above results are



Fig. 4. Vertical distribution of $\rm H_2S$ in the pore waters of bottom sediments at stations 92A, 7 and 11

Tab	\mathbf{le}	1.	Environmental	parameters at	the	stations	investigate	ed
-----	---------------	----	---------------	---------------	-----	----------	-------------	----

Parameters	Station				
	92A	7	11	14	
longitude N	$54^{\circ}35.0'$	$54^{\circ}35.0'$	$54^{\circ}34.15'$	$54^{\circ}38.0'$	
latitude E	$18^{\circ}40.0'$	$18^{\circ}44.0'$	$18^{\circ}48.6'$	$18^\circ 58.3'$	
depth [m]	37	51	60	82	
overlying bottom wa	ater:				
temperature [°C]	13.3	10.7	13.3	_	
oxygen [ml $O_2 dm^{-3}$]	6.3	6.3	6.1	_	
$H_2S \ [\mu mol \ dm^{-3}]$	0	0	0	_	
bottom sediment (la	ayer 0–10	cm):			
organic matter [%]	8.07	8.84	9.55	20.26	
sediment type	fine silty	sandy silt	sandy silt	_	
· -	sand	·	·	_	
concentrations of H_2S in surface sediment layers:					
0–4 cm	8.7	13.1	20.4	1072.9	
4–8 cm	12.7	83.5	304.6	1224.3	

Table 2. Species composition, abundance and biomass of each taxon, and number of taxa at the stations investigated (abundance (ind. m^{-2}), [] – biomass (g m^{-2}), [+] – biomass < 0.01 g m^{-2})

Taxon	Station			
	92A	7	11	14
Macoma balthica	$1107 \\ [180.34]$	607 $[263.65]$	783 [191.85]	$1260 \\ [258.50]$
Mya arenaria	$ \begin{array}{c} 40 \\ [6.18] \end{array} $	$13 \\ [0.11]$	$30 \\ [1.01]$	0 0
Hydrobia ulvae	$100 \\ [0.44]$	0	0	0
Hydrobia ventrosa	$10 \\ [0.02]$	0	0	0
Potamopyrgus jenkinsi	$ \begin{array}{c} 3 \\ [0.02] \end{array} $	0	0	0
Halicryptus spinulosus	$100 \\ [7.84]$	$10 \\ [3.55]$	7[2.26]	0
Harmothoe sarsi	$13 \\ [0.05]$	7 [0.02]	$\begin{array}{c} 13 \\ [0.04] \end{array}$	$100 \\ [3.44]$
Oligocha et a	0	${3 \atop [+]}$	0	0
Saduria entomon	0	$7 \\ [0.77]$	$\begin{array}{c} 3 \\ [0.06] \end{array}$	0 0
Pontoporeia femorata	$290 \\ [1.83]$	387 [2.11]	$67 \\ [0.43]$	5 [+]
$Corophium \ volutator$	$13 \\ [0.15]$	$ \frac{3}{[0.04]} $	$10 \\ [+]$	0
Total	$1676 \\ [196.87]$	1037 [270.25]	913 $[195.65]$	$1365 \\ [251.94]$
Number of taxa	9	8	7	3

given in Tab. 2, together with determinations of abundance and biomass of individual taxa.

Macoma balthica turned out to be the most abundant species at station 14 (up to 1260 indiv. m⁻²), where the H₂S concentration exceeded 1000 μ mol dm⁻³. The lowest abundance of this species (607 indiv. m⁻²) was recorded at station 7. However, its biomass distribution did not follow this pattern. The peak biomass of Macoma balthica (263.65 g m⁻²) was recorded



at station 7, the smallest (180.34 g m⁻²) at station 92A. In the case of three species – Halicryptus spinulosus, Mya arenaria, Pontoporeia femorata – the frequency of occurrence was found to decrease with increasing basin depth and H_2S concentration; the last of these species was most abundant at station 7. A tendency for the abundance to increase with depth, despite the rising H_2S concentration, was observed only in the case of one species – Harmothoe sarsi. Two species – Corophium volutator and Saduria entomon - as well as representatives of two higher taxa - Oliqochaeta and Hydrobi*idae* – occurred only sporadically and in small numbers. The percentages of individual species in the total abundance at the stations investigated are presented in Fig. 5. Species the proportions of which were below 1% at a given station were placed in the 'other' group. At all stations, the bivalve Macoma balthica turned out to be the clearly dominant species, the highest percentage of which (92%) was recorded at station 14. Another species occurring relatively frequently was Pontoporeia femorata, the maximum percentage of which (37.3%) was found at station 7. The percentage of Harmothoe sarsi increased with depth and, at station 14, reached 7.3%.

4. Discussion

Hydrogen sulphide is a naturally-forming compound widespread in the aquatic environment. The most spectacular H₂S-rich sites are hydrothermal vents (Fisher, 1990; Tunnicliffe, 1991). H_2S is also present worldwide in marine sediments, where it is formed as a result of the bacterial oxidation of organic matter (Fenchel and Riedl, 1970). Moreover, the dumping of organic carbon of anthropogenic origin as well as the increasing productivity of water basins resulting from their eutrophication have undoubtedly contributed to the rising H₂S levels in the aquatic environment. Concentrations of H_2S vary from micromolar in coastal waters to several hundred micromolar in the vicinity of hydrothermal springs or even to millimolar in salt marshes and sewage outlets (Bagarinao, 1992). Some H_2S diffuses from sediments into water. Fenchel (1969) recorded a maximum H₂S concentration of $ca \ 20 \text{ mmol dm}^{-3}$ at a depth of 12 cm below the sediment surface and 600 μ mol dm⁻³ in the water above this sediment. In the Black Sea, a water basin 2000 m deep, hydrogen sulphide is always present in the water column below 150-200 m (Sorokin, 1972). The H₂S concentration in the interstitial waters of the bottom sediments in the Gulf of Gdańsk tends to increase with depth. In deeper parts of this basin, organic matter accumulates at the bottom owing to the sorptive properties of alcuritic and pelitic sediments (Jankowska, 1993). The intensive mineralisation of organic matter in sediments consumes oxygen, while further decomposition of organic matter leads to the formation of H_2S . Water stratification is yet another factor

causing the oxygen conditions in the sediments and the near-bottom water below the halocline to deteriorate. The oxygenation of near-bottom waters takes place only during inflows of water from the North Sea. This is probably one of the reasons for the very high H₂S concentration (*ca* 1000 μ mol dm^{-3}) at station 14 (Tab. 2). Part of the hydrogen sulphide diffuses to the sediment surface and into the surrounding water, thereby forming a gradient with depth of both sediment and near-bottom water (Fenchel, 1969; this paper). Our studies have shown that no H_2S was present in the water 1 m above the sea bed. Measurements carried out during the period 1985–1989 revealed the presence of H_2S in the near-bottom waters of the outer Gulf of Gdańsk (Trzosińska and Cyberska, 1992). In autumn its concentration was 44 μ mol dm⁻³. During the same period, H₂S was also found to be present in the near-bottom waters of the inner part of this basin (Trzosińska and Cyberska, 1992). The H_2S concentrations measured in the Gulf of Gdańsk are not very high compared to other aquatic basins. Only in the sediments of deep-water regions does the hydrogen sulphide content reach dangerous and alarming levels.

Even in nano- or micromolar concentrations, H_2S is toxic towards the majority of aerobic organisms. Its toxicity is due to the inhibition of enzymes containing a metal, cytochrome c oxidase in particular, which causes oxygen metabolism to be blocked (Evans, 1967). The presence of H_2S in the marine environment may upset the natural balance in the infauna and even the epifauna and nekton biocenoses.

The somewhat sparse data from previous years concerning the occurrence and concentration of H_2S in the waters of the Gulf of Gdańsk, as well as the total lack of data in the case of sediments, make it impossible to assess the role of H_2S in shaping the biocenosis of this basin. It is known, however, what damage has been caused by this compound in the Gdańsk Deep. A deficiency of oxygen together with the presence of H_2S were responsible for the gradual impoverishment of the bottom fauna until it almost vanished from this area. In 1925 the Gdańsk Deep was inhabited by a group of 9 species of biomass 25.6 g m⁻² (Hagmeier, 1926). In August 1951, only 5 species were found with a total biomass of 3.71 g m^{-2} (Demel and Mulicki, 1954). During the period 1980–1983 just one single species was recorded, namely Harmothoe sarsi (Okołotowicz, 1985). At the present time too, *Harmothoe sarsi* is the only species occurring from time to time in this region (Witek, 1993). The implication of the results of this study is that the occurrence of only three benthic species at a depth of 82 m is due to the high concentration of H₂S of > 1000 μ mol dm⁻³ at this depth. Such conditions, however, do not seem to be detrimental to the bivalve Macoma balthica, as both its abundance and biomass were high. The Macoma balthica biomass at the station investigated was 40 times as high as that recorded at station 17 (78 m depth) in 1981 (Okołotowicz, 1985). The animals living at a depth of 56–60 m are exposed to hydrogen sulphide concentrations of the order of several hundred μ mol dm⁻³. These include deep water species – Macoma balthica, Harmothoe sarsi, Saduria entomon, Pontoporeia femorata – as well as shallow-water species: the Oligochaeta, Mya arenaria and Corophium volutator. In recent years, the biomass of Corophium volutator and the depth of its occurrence have increased (Wiktor, 1992). Resistant to pollution, this crustacean prefers muddy bottoms, and during our studies was found even at a depth of 62 m. The species composition at stations 50–60 m deep has not changed since the 1980s, but its biomass has decreased twofold (Okołotowicz, 1985; this paper). A H_2S concentration in the several-micromolar range has no unfavourable impact on the biocenosis at depths of 30–40 m. At station 92A, 9 species were recorded whose total biomass amounted to 197 g m⁻². Similar values were obtained during determinations carried out in previous years (Herra and Wiktor, 1985; Witek, 1993).

Species	H_2S concentration $[\mu mol dm^{-3}]$	Source
Macoma balthica	max. 500 max. 1224	Jahn <i>et al.</i> (1993) this paper
Mya arenaria	max. 305	this paper
Halicryptus spinulosus	$2-49, \max. 665$ max. 305	Oeschger and Vetter (1992) this paper
Nereis diversicolor Nereis virens Nereis succinea Arenicola marina	< 50 < 50 50-2000 max. 340	Miron and Kristensen (1993) Miron and Kristensen (1993) Miron and Kristensen (1993) Völkel and Grieshaber (1992)
Harmothoe sarsi Saduria entomon Pontoporeia femorata Corophium volutator	about 1000 about 20 max. 1224 about 20	this paper this paper this paper this paper

Table 3. Concentrations of H_2S at sites where benchic species have been recorded

The bivalve Macoma balthica and the polychaete Harmothoe sarsi are the least sensitive to H_2S in the environment. Macoma balthica has been a dominant species in the area, studied for many years (Żmudziński, 1967; Okołotowicz, 1985; Wiktor, 1992; this paper). Bivalves of this species live buried in the sediment, most often at a sediment depth of 8 cm (Reise, 1981; Medsen and Jensen, 1987); however, they extract oxygen from the water above the sediment by means of a siphon. Under unfavourable conditions, they can temporarily close their shells (Theede, 1973). This, as well as its well-developed adaptive mechanism, enables the species to inhabit regions which are rather unattractive to most other organisms. Another species occurring in regions with high H₂S concentrations is *Harmothoe sarsi*: its semi-pelagic mode of life and active dislocation capability are factors that help it survive in such an environment. *Harmothoe sarsi* was the only species occurring in the Gdańsk Deep between January and April and in October 1987, when the oxygen concentration in the near-bottom water was >2 ml dm⁻³ (Witek, 1993). During the other months of that year, when the oxygen content was lower, not a single benthic species was to be found in this region (Witek, 1993). Tab. 3 lists some benthic species and the H₂S concentrations in their natural environment. For comparison, information concerning benthic organisms from other parts of the Baltic Sea is also given.

Laboratory investigations done by other authors (Theede *et al.*, 1969, Theede, 1973; Oertzen, 1972) have revealed the increased resistance to H_2S displayed by some species of bottom fauna. These organisms have developed special adaptive and detoxification mechanisms. The existence of such mechanisms has also been confirmed in *Saduria entomon* (Visman, 1991a), *Halicryptus spinulosus* (Oeschger and Vetter, 1992), *Arenicola marina* (Völkel and Grieshaber, 1992), to name but a few examples. The occurrence of *Macoma balthica* and *Harmothoe sarsi* in the sediments of the Gulf of Gdańsk with such a high H_2S concentration suggests that these organisms also possess certain adaptive mechanisms.

This study indicates that if oxygen conditions continue to deteriorate and H_2S concentrations increase, the environment will suffer impoverishment and the natural balance in the biocenosis of the Gulf of Gdańsk will be upset. As in the deep parts of this basin, the number and diversity of species will decline, and only the more resistant ones, *i.e. Macoma balthica* and *Harmothoe sarsi*, will remain.

References

- Bagarinao T., 1992, Sulfide as an environmental factor and toxicant: tolerance and adaptations in aquatic organisms, Aquat. Toxicol., 24, 21–62.
- Bolałek J., Jankowska H., Lęczyński L., Falkowska L., 1994, Investigating the source of hydrogen sulphide in sediments of the Puck Bay in the vicinity of Hel port, Stud. i Mater. Oceanol., 67, 73–81.
- Cederwall H., Elmgren R., 1990, Biological effects of eutrophication in the Baltic Sea. Particularly the Coastal zone, AMBIO, 19, 109–112.

- Cline J. D., 1969, Spectrophotometric determination of hydrogen sulfide in natural waters, Limnol. Oceanogr., 14, 454–458.
- Demel K., Mulicki Z., 1954, Quantitative investigations on the biological bottom productivity of the South Baltic, Pr. Mor. Inst. Ryb., 7, 75–109, (in Polish).
- Dybern B. I., Ackeford H., Elmgren R. (eds.), 1976, Recommendations on methods for marine biological studies in the Baltic Sea, Baltic Mar. Biol., 1, 98.
- Evans C. L., 1967, The toxicity of hydrogen sulphide and other sulphides, Q. J. Exp. Physiol., 52, 231–248.
- Fenchel T. M., 1969, The ecology of the marine microbenthos IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa, Ophelia, 6, 1–182.
- Fenchel T. M., Riedl R. J., 1970, The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms, Mar. Biol., 7, 255–268.
- Fisher C. R., 1990, Chemoautotrophic and mathanotrophic symbioses in marine invertebrates, Rev. Aquat. Sci., 2, 399–436.
- Groenendaal M., 1981, The adaptation of Arenicola marina to sulphide solutions, Netherl. J. Sea Res., 15 (1), 65–77.
- Hagerman L., Visman B.,1993, Anaerobic metabolism, hypoxia and hydrogen sulphide in the brackish water isopod Saduria entomon (L.), Ophelia, 38 (1), 1–11.
- Hagmeier A., 1926, Die Arbeiten mit dem Petersenschen Bodengreifer auf der Ostseefahrt April 1925, Ber. Deutsch. Komm. Meeresforsch. N. F., 2, 4, 92–95.
- Herra T., Wiktor K., 1985, Composition and distribution of bottom fauna in coastal zone of the Gulf of Gdańsk Proper, Stud. i Mater. Oceanol., 46, 115–142, (in Polish).
- Jankowska H., 1993, The bottom deposits of Puck Bay, Stud. i Mater. Oceanol., 64, 163–171.
- Jahn A., Theede H., Oeschger R., 1993, Different capacities of hydrogen sulphide detoxification in populations of Macoma balthica, Verh. Deutsch. Zool. Gesell., Short Communications, 86. Jahresversammlung 1993 in Salzburg, (in press).
- Jørgensen B. B., 1977, The sulfur cycle of coastal marine sediment (Limfjorden, Denmark), Limnol. Oceanogr., 22, 814–831.
- Jørgensen B. B., 1988, Ecology of the sulphur cycle: oxidative pathways in sediments, [in:] The nitrogen and sulphur cycles, J. M. Cole and S. J. Ferguson (eds.), 42nd Symp. Soc. Gen. Microbiol., Univ. of Southampton, Cambridge Univ. Press, Cambridge, 31–63.
- Jørgensen B. B., Bang M., Blackburn H., 1990, Anaerobic mineralization in marine sediments from the Baltic Sea – North Sea transition, Mar. Ecol. Prog. Ser., 59, 39–54.
- Kępińska U., Wypych K., 1990, Bottom sediments, [in:] The Gulf of Gdańsk, A. Majewski (ed.), Wyd. Geol., Warszawa, 55–64, (in Polish).

- Legeżyńska E., Wiktor K., 1981, *Bottom fauna in Puck Bay Proper*, Zesz. Nauk. UG, Oceanografia, 8, 63–77, (in Polish).
- Levitt J. M., Arp A. J., 1991, The effects of sulfide on the anaerobiosis metabolism of two congeneric species of mudflat clams, Comp. Biochem. Physiol., 98B (2/3), 339–347.
- Medsen P. B., Jensen K., 1987, Population dynamics of Macoma balthica in the Danish Wadden Sea in an organically enriched area, Ophelia, 27 (3), 197–208.
- Millero F. J., 1991, The oxidation of H₂S in Chesapeake Bay, Estuar. Coast. Shelf Sci., 33, 521–527.
- Miron G, Kristensen E., 1993, Factors influencing the distribution of nereid polychaetes: the sulfide aspect, Mar. Ecol. Prog. Ser., 93, 143–153.
- National Research Council, 1979, *Hydrogen sulfide*, Division of Medical Science, Subcommittee on Hydrogen Sulfide, Univ. Park Press, Baltimore, 183 pp.
- Oertzen J. A., 1972, Abiotic potency and physiological resistance of shallow and deep water bivalves, OIKOS Suppl., 15, 261–266.
- Oeschger R., Vetter R. D., 1992, Sulfide detoxification and tolerance in Halicryptus spinulosus (Priapulida): a multiple strategy, Mar. Ecol. Prog. Ser., 86, 167–179.
- Oeschger R., Storey K. B., 1993, Impact of anoxia and hydrogen sulphide on metabolism of Artica islandica L. (Bivalvia), J. Exp. Mar. Biol. Ecol., 170, 213–226.
- Okołotowicz G., 1985, Macrozoobenthos biomass values in the Polish Fisheries Zone in the Baltic as an indicator of its pollution, Biul. Mor. Inst. Ryb., 16, 5–6, 27–40, (in Polish).
- Pęcherzewski K., 1974, The content and distribution of organic C in the superficial layer of bottom sediments in the southern Baltic, Zesz. Nauk. UG, Oceanografia, 2, 7–21 (in Polish).
- Reise K., 1981, High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea, Helgoländ. Wiss. Meeresunters., 34, 413–425.
- Sorokin Y. I., 1972, The bacterial population and process of hydrogen sulphide oxidation in the Black Sea, J. Cons. Internat. Explor. Mer., 34, 423–455.
- Theede H., Ponat A., Hiroki K., Schlieper C., 1969, Studies on the resistance of marine bottom invertebrates to oxygen – deficiency and hydrogen sulphide, Mar. Biol., 2, 325–337.
- Theede H., 1973, Comparative studies on the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates, Netherl. J. Sea Res., 7, 244–252.
- Theede H., 1981, Studies on the role of benthic animals of the Western Baltic in the flow of energy and organic material, Kieler Meeresforsch., 5, 434–444.
- Trzosińska A., Cyberska B., 1992, Oxygen and hydrogen sulphide, Stud. i Mater. Oceanol., 61, 93–106.
- Tunnicliffe V., 1991, The biology of hydrothermal vents: ecology and evolution, Oceanogr. Mar. Biol. Ann. Rev., 29, 319–407.

- UNEP/IOC/IAEA, 1988, Standard chemical methods for marine environmental monitoring. Reference methods for marine pollution studies, 50, 50.
- Wenne R., Wiktor K., 1982, Benthic fauna of the inshore waters of Gdańsk Bay, Stud. i Mater. Oceanol., 39, 137–171, (in Polish).
- Wiktor K., Skóra K., Wołowicz M., Węsławski M., 1980, The near-bottom stocks of crustaceans in the inshore waters of Gdańsk Bay, Zesz. Nauk. UG, Oceanografia, 7, 135–160, (in Polish).
- Wiktor K., 1992, Bottom fauna, Stud i Mater. Oceanol., 61, 194–198.
- Wiktor K., Pliński M., 1992, Long term changes in the biocenosis of the Gulf of Gdańsk, Oceanologia, 32, 69–79.
- Witek Z. (ed.), 1993, Structure and function of marine ecosystem in the Gdańsk Basin on the basis of studies performed in 1987, Stud. i Mater. Oceanol., 63, 124.
- Wołowicz M., 1994, Long-term changes of the molluscan fauna in Puck Bay (S. Baltic) as a result of human activity, Haliotis, 23, 43–50.
- Visman B., 1991a, Physiology of sulfide detoxification in the isopod Saduria (Mesidotea) entomon, Mar. Ecol. Prog. Ser., 76, 283–293.
- Visman B., 1991b, Sulfide tolerance: physiological mechanisms and ecological implications, Ophelia, 34 (1), 1–27.
- Völkel S., Grieshaber M. K., 1992, Mechanisms of sulphide tolerance in the peanut worm, Sipunculus nudus (Sipunculidae) and in the lugworm, Arenicola marina (Polychaeta), J. Comp. Physiol. B., 162, 469–477.
- Zmudziński L., 1967, Zoobenthos of Gdańsk Bay, Pr. Mor. Inst. Ryb., 14 A, 49–80, (in Polish).
- Zmudziński L., 1976, Bottom fauna as an indicator of the advancing eutrophication of the Baltic, Stud. i Mater. Oceanol., 15, 97–306, (in Polish).