Seasonal and annual changes in the macrozoobenthic populations of the Gulf of Gdańsk with respect to hypoxia and hydrogen sulphide*

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Abstract

This study was designed to investigate seasonal and annual changes in the benthic macrofauna in relation to changes in hydrogen sulphide concentration in the sediment and the oxygen content in the water column. Data were collected over a three-year period from 1994 to 1997. The benthic macrofauna inhabiting the sediments of the Gulf of Gdańsk, in which H_2S is permanently present, consists mostly of species with a high tolerance to oxygen deficiency and the presence of H_2S. These species are: *Macoma balthica*, *Harmothoe sarsi*, *Nereis diversicolor*, *Saduria entomon* and *Halicryptus spinulosus*, as well as *Pontoporeia femorata* and *Corophium volutator*, which are more sensitive to these factors. In 1996–1997 a decline in the abundance of almost all benthic species, and especially of the bivalve *M. balthica* at all the stations was observed in comparison to 1994–1995.

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1. Introduction

Baltic benthic fauna is commonly exposed to waters of low oxygen concentration and toxic hydrogen sulphide (H_2S). Oxygen deficiency and the presence of H_2S in the sediments, and even in the water column in the deeper parts of the Baltic Sea, are a natural phenomenon. Hypoxic conditions may also occur in shallow waters, for example, in winter during periods of persistent ice cover, or in summer and autumn as a result of intensive mineralisation of organic matter. Hydrogen sulphide may also appear suddenly in the near-bottom water, where the sediment structure has been broken down, for example, by dredging or trawling. The greater frequency of oxygen deficiency and hydrogen sulphide also in shallower regions has been attributed to increasing eutrophication (Diaz & Rosenberg 1995, HELCOM 1996, Leppäkoski & Mihnea 1996).

Different animal species react differently to the appearance of unfavourable oxygen conditions and toxic hydrogen sulphide in the environment. In conditions of severe hypoxia, death of the most sensitive species occurs (Jørgensen 1980). These species either cannot or do not manage to escape, whereas more mobile organisms are able to move to regions with better oxygen conditions. However, there are many other species capable of surviving in sediments where hydrogen sulphide is permanently present. These organisms exhibit higher resistance to hypoxia, anoxia and the presence of hydrogen sulphide in the environment thanks to their morphological, behavioural and biochemical adaptations (Vismann 1991, Diaz & Rosenberg 1995, Hagerman et al. 1996, Jahn et al. 1997, Normant & Szaniawska 2000).

Nevertheless, even the most resistant species cannot survive prolonged periods of oxygen deficiency. This and the presence of hydrogen sulphide in the environment have given rise to mass mortality of benthic fauna in many regions of the Baltic Sea (Rosenberg & Loo 1988, HELCOM 1990, Weigelt 1991, Diaz & Rosenberg 1995). Such conditions were the cause of the disappearance of all macrofauna from the region of the Gdańsk Deep (Żmudziński & Osowiecki 1991, Osowiecki & Warzocha 1996).

Research into the influence of oxygen conditions and hydrogen sulphide on the species composition and the distribution of the benthic fauna in the Baltic Sea has been carried out for a number of years (Jørgensen 1980, Miron & Kristensen 1993, Gamenick et al. 1996, Janas & Szaniawska 1996, Thiermann et al. 1996, Włodarska-Kowalczuk et al. 1996, Laine et al. 1997).

The aim of the present study was to determine the species composition of the macrozoobenthic community inhabiting areas of the sediments where hydrogen sulphide was permanently present. The study was undertaken in order to examine the influence of the seasonal deterioration of oxygen conditions in the water column immediately above the sea floor, as well as the increase in the hydrogen sulphide concentration in the sediments of the Gulf of Gdańsk, on the seasonal and annual abundance of macrofaunal communities.

2. Material and methods

The macrozoobenthos was investigated monthly from June 1994 to June 1995, from March to April 1996, from September to December 1996, from March to July 1997 and in October 1997 at depths of 37, 51, and 60 m (Fig. 1). The stations were selected according to the H_2S concentrations in the pore water of the sediment.

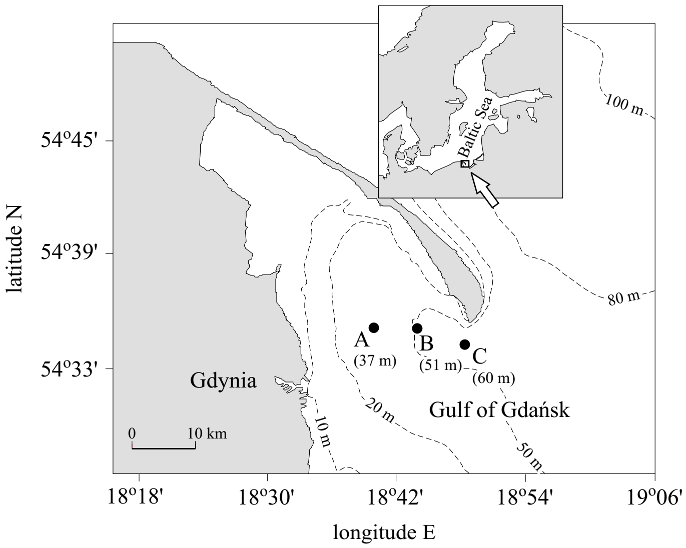


Fig. 1. Location of sampling stations

Seasonal changes in oxygen conditions in the water column were measured about 1 m above the seabed. However, the oxygen available to most bottom-dwelling organisms occurs only in the first few centimetres above the sea floor. This was why oxygen concentrations were measured in the 0–5 cm water layer above the sea floor and were compared with the oxygen content in the layer 1 m above the sea floor. The near-bottom water (about 1 m above the bottom) was sampled with a Nansen bottle. Furthermore, in October, November and December 1996, as well as in March and June 1997, near-bottom water just above the sediment (0–5 cm) was sampled using a hose from a Nemistö sediment corer. The oxygen content was measured by Winkler's method.

The sediment samples were taken with a gravity probe with a pipe diameter of 2.2 cm. Hydrogen sulphide was determined spectrophotometrically in the pore water of the 0–4 and 4–8 cm sediment layers. The H_2S content in the interstitial waters was measured by Cline's method (Cline 1969). The procedure described by Janas & Szaniawska (1996) was followed in this study.

The benthic macrofauna was sampled by taking three van Veen grabs at each station. All samples were passed through a 1 mm mesh sieve and preserved in 10% formalin. The species composition and the abundance of each species were determined. The frequency (the percentage of occurrence in all samples from every station sampled) was calculated for each taxon.

3. Results

The water temperature in the Gulf of Gdańsk was subject to distinct seasonal changes (Fig. 2). The largest variations, from 0.9°C in March to 16.2°C in August 1994, were observed at the shallowest station A (37 m). The highest temperatures, > 8°C in the whole area during the study period, were recorded in the summer-autumn period.

Oxygen was always present in the bottom water at the three stations at concentrations ranging from 1.86 to 8.94 cm^3 dm^{-3} (Fig. 2). The lowest concentration was measured at station B (51 m) in September 1996. Oxygen concentrations during the study period were very similar at all stations. July 1994 and March–April 1996 were exceptions, as were September–December 1996, when the concentrations at the deeper stations were lower.

The oxygen content in the water layer just above the sea floor was usually slightly lower than in the higher water layer (although the differences did not exceed 1 cm^3 dm^{-3}) (Table 1). There were no significant differences in oxygen content between these two depths (Student's t-test, $p < 0.05$). However, in October and November 1996 there was a difference of > 2 cm^3 dm^{-3} in O_2 concentration between the two layers at station B (51 m). At the deepest station the reverse situation obtained, when the concentration in the near-bottom water layer was slightly higher than in the layer above.

At the shallowest station A (37 m) hydrogen sulphide occurred only seasonally in the interstitial waters of the sediments, and its concentration during the whole study period did not exceed 13 μmol dm^{-3} (Fig. 3). However, at the two deeper stations the hydrogen sulphide concentration fluctuated from 0 to 443 μmol dm^{-3} in the shallower layer of the sediments

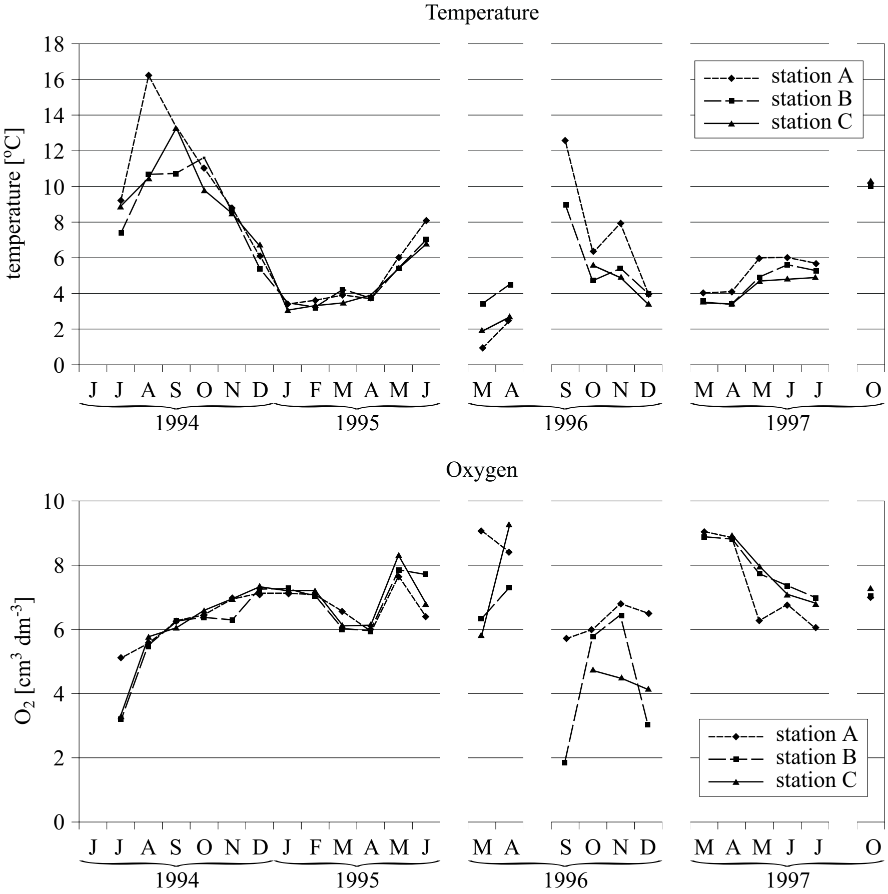
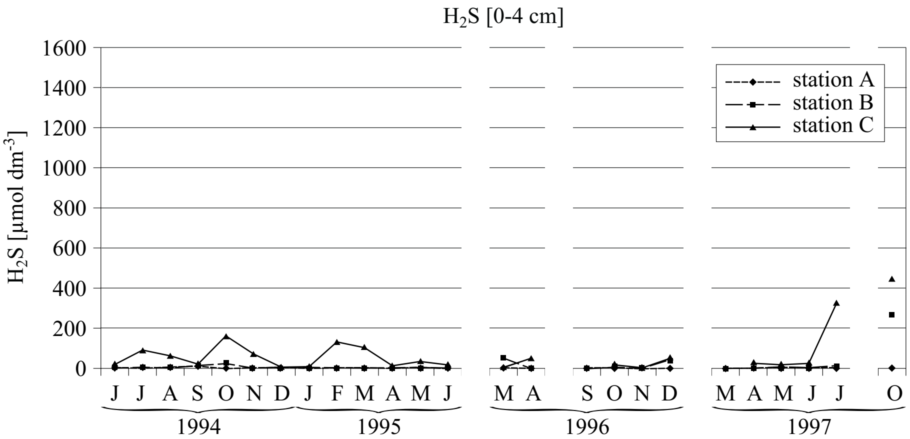


Fig. 2. Temperature [°C] and oxygen concentration [cm^3 dm^{-3}] in near-bottom water in selected months in 1994–1997

Table 1. Comparison of oxygen concentration in near-bottom water [cm^3 dm^{-3}] about 100 cm above the bottom, and 0–5 cm above the bottom

Month	Oxygen concentration [cm^3 dm^{-3}] in near-bottom water					
	Station A		Station B		Station C	
	100 cm	0–5 cm	100 cm	0–5 cm	100 cm	0–5 cm
October 1996	5.99	5.40	5.79	3.45	4.72	5.37
November 1996	6.81	6.70	6.43	4.17	–	–
December 1996	6.51	6.33	3.03	3.57	4.12	4.12
March 1997	9.04	8.95	8.87	8.52	–	–
April 1997	8.89	8.76	8.83	8.94	8.94	9.17



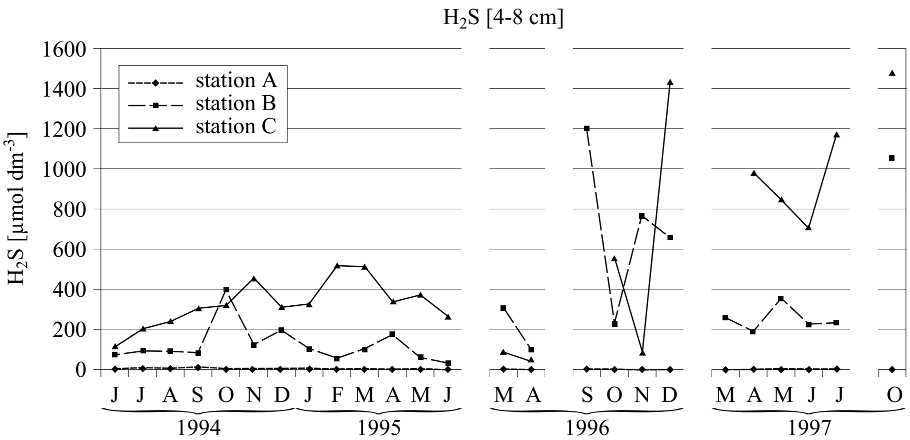


Fig. 3. Concentration of hydrogen sulphide [μmol dm^{-3}] in pore water of 0–4 and 4–8 cm deep layers of sediment in selected months in 1994–1997

(0–4 cm) and from 0 to 1479 μmol dm^{-3} in the deeper layer (4–8 cm). Extremely high concentrations in both layers of sediments (exceeding 200 μmol dm^{-3} in the 0–4 cm layer and 1000 μmol dm^{-3} in the 4–8 cm layer) were recorded in October 1997.

Over the entire study period a total of 25 macrobenthic taxa from the three stations were identified (Fig. 4). 21 taxa were found at the shallowest station A (37 m), 15 at the middle station B (51 m), and 19 at the deepest station C (60 m).

The bivalves *Macoma balthica* and the crustaceans *Pontoporeia femorata* were the only species occurring at all three stations (frequency 100%). Other relatively common taxa (frequency $> 50\%$), occurring at least at one of the deeper stations B and C where hydrogen sulphide was permanently

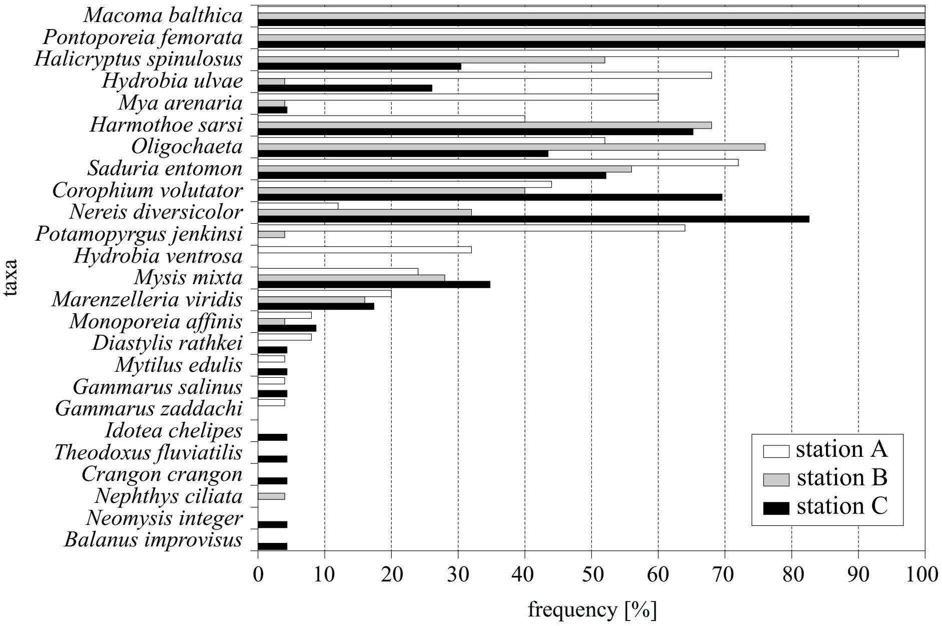


Fig. 4. Frequency of taxa at the 3 stations investigated

present in the sediments, included *Harmothoe sarsi*, *Saduria entomon*, *Nereis diversicolor*, *Corophium volutator* and *Oligochaeta*. Two species – *Hydrobia ulvae* and *Mya arenaria* – were the most common at the shallowest station (frequency $> 50\%$), and *Hydrobia ventrosa* occurred only at this station. Up to 14 taxa of the 25 found at the three stations can be regarded as rare (frequency $< 10\%$).

The highest total macrofauna abundance, 2461 indiv. m^{-2} was recorded in November 1994 at the shallowest station A (37 m), whereas the lowest total abundance 157 indiv. m^{-2} occurred in October 1997 at station B. The average numbers for the whole period were the highest at station A – 924 indiv. m^{-2}, lower at station C – 714 indiv. m^{-2}, and the lowest at station B – 521 indiv. m^{-2}.

The abundance of individual species exhibited considerable spatial and temporal variation (Fig. 5). *M. balthica* had the greatest influence on these changes, as it made up as much as 95% of the entire macrobenthos. Its numbers varied from 120 indiv. m^{-2} to 1633 indiv. m^{-2}. In 1994–1995 its abundance was the highest at the shallowest station and displayed the greatest seasonal changes. At the two deeper stations it occurred in greater numbers during the autumn and winter months, regardless of the increase in hydrogen sulphide concentration in the sediments. In 1996–1997 the

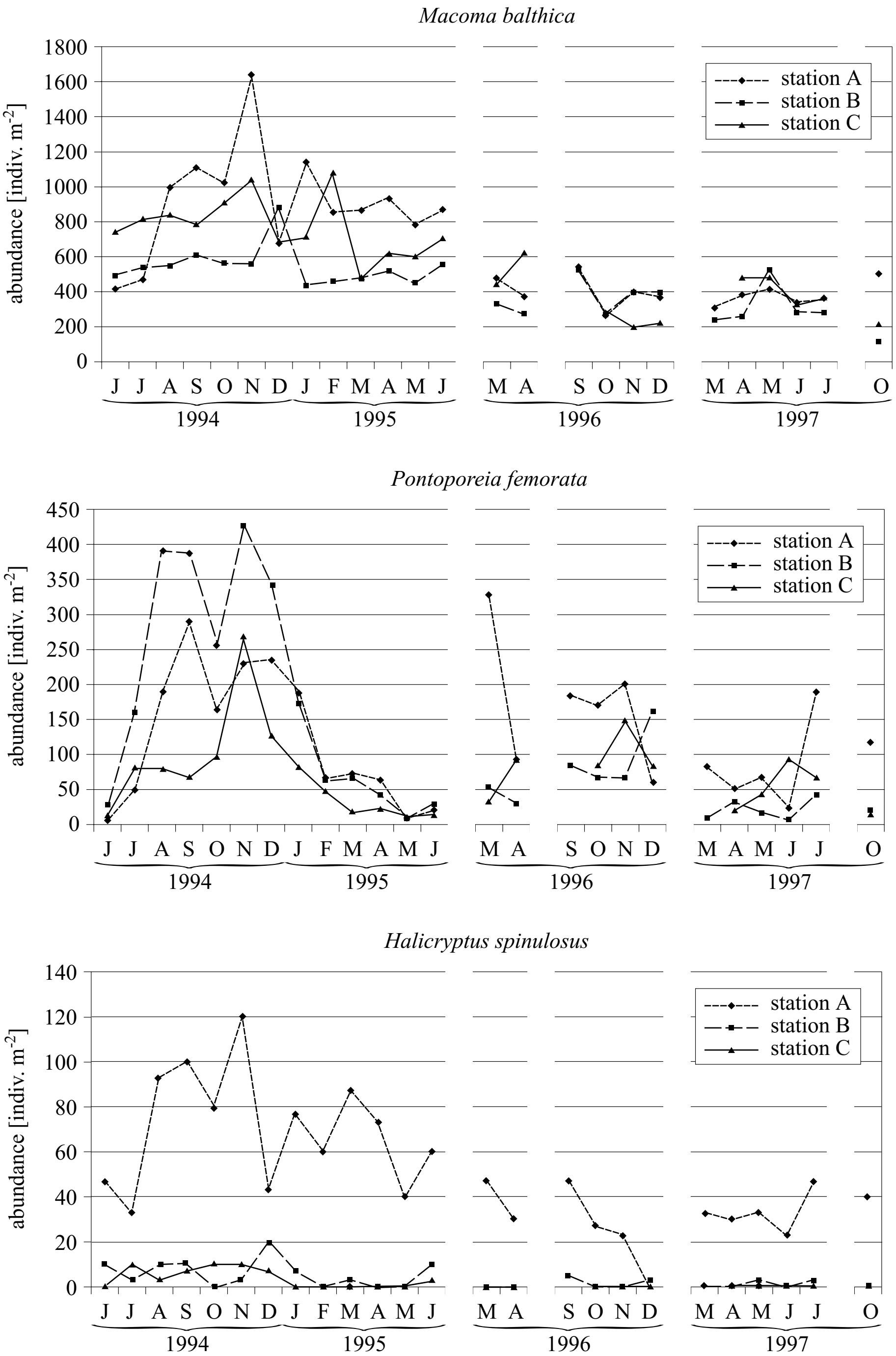
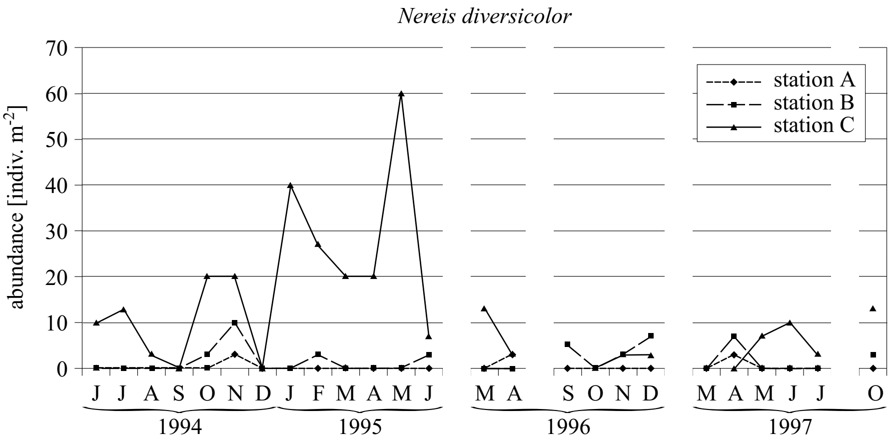
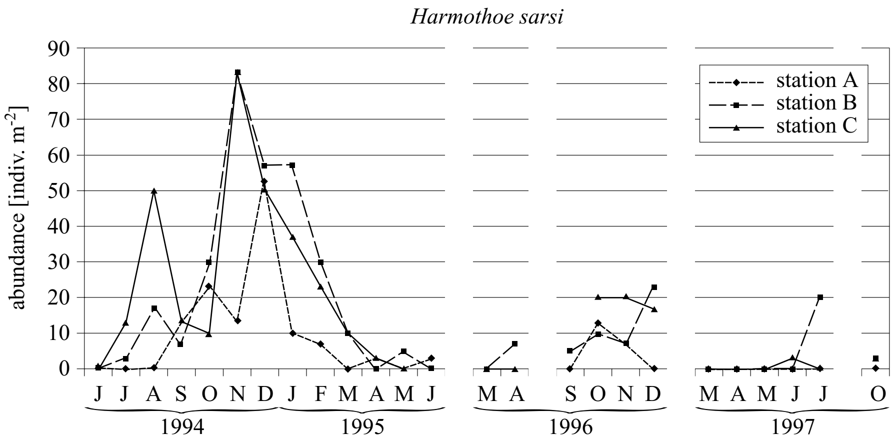


Fig. 5. Seasonal changes in the abundance of macrozoobenthic species in selected months in 1994–1997. Note the different scales





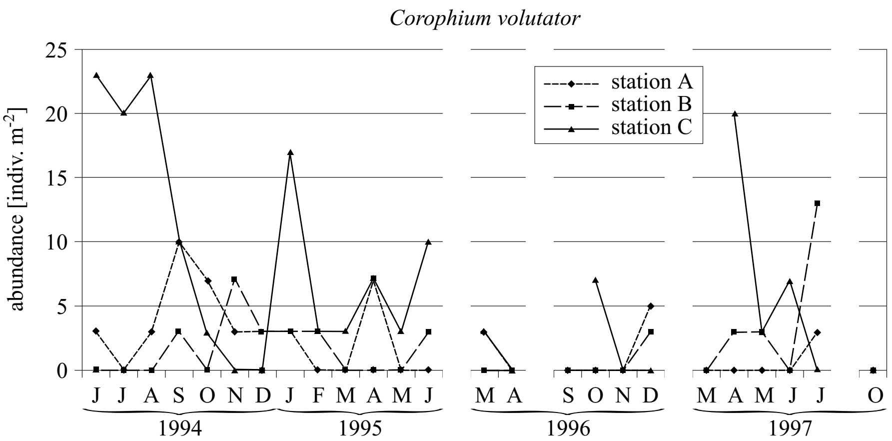


Fig. 5. (*continued*)

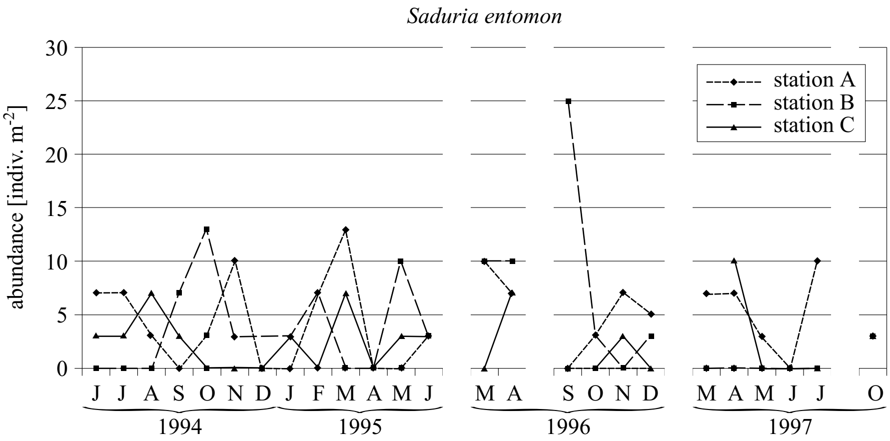


Fig. 5. (*continued*)

abundance at all stations was much lower than in previous years and did not exceed 620 indiv. m^{-2}. It was very low at the two deeper stations in October 1997 (< 21 indiv. m^{-2}), where, at the same time, the hydrogen sulphide concentration in the sediments was extremely high.

The abundance of *P. femorata* was subject to abrupt seasonal changes in 1994–1995, varying from only a couple of individuals to 427 indiv. m^{-2}. The abundance of this species at all stations reached a maximum in autumn and winter. In 1994 its abundance was significantly higher at the middle station B, but this situation was not repeated in subsequent years. During the following study period in autumn-winter 1996, when the oxygen concentration in the water was the lowest recorded during the study and the hydrogen sulphide concentration in the sediments was exceptionally high, numbers were lower, not exceeding 160 indiv. m^{-2}. At other stations they were no higher than 200 indiv. m^{-2}, with the exception of March 1996 when at the shallowest station A they reached 327 indiv. m^{-2}. A very low abundance, 13–20 indiv. m^{-2}, was recorded in October 1997 at the two deepest stations, where an extremely high hydrogen sulphide concentration was noted even in the top 4 cm of the sediment.

The abundance of *H. sarsi* displayed strong seasonal variation, which was similar at all the stations: from 0 to 83 indiv. m^{-2}. The highest values were recorded in the autumn and winter. In the following period, September–December 1996, the abundance at all stations was no higher than 23 indiv. m^{-2}; in October 1997 it was 3 indiv. m^{-2} and then only at the two deeper stations.

The abundance of *N. diversicolor* at the two shallower stations was no greater than 10 indiv. m^{-2}. At the deepest station the highest abundance, 60 indiv. m^{-2}, was recorded in May 1995. During the study periods in 1996–1997 the abundance of this species did not exceed 13 indiv. m^{-2}, but it still occurred occasionally at the deepest station C (60 m).

S. entomon was present irregularly at all the stations and in very small numbers, never more than 15 indiv. m^{-2}; only in September 1996 at station B (51 m) was a larger number of individuals present: 25 indiv. m^{-2}.

Halicryptus spinulosus was the most common at the shallowest station. The highest abundance of 120 indiv. m^{-2} was recorded in November 1994 at the shallowest station A (37 m). At the two deeper stations (B – 51 m and C – 60 m) its abundance did not exceed 20 indiv. m^{-2} during the whole study period, and at the deepest station C its presence was not recorded over the two-year period 1996–1997.

C. volutator was present more often and in greater numbers at the deepest station (C – 60 m), but even there they did not exceed 23 indiv. m^{-2}.

4. Discussion

Living conditions for benthic macrofauna are determined by various factors. The most important of them are oxygen, temperature, salinity, type of sediment, food availability, the presence of toxic substances and biological interactions (Gray et al. 1988, Aschan 1990, Rosenberg et al. 1992, Bonsdorff et al. 1996). Some of the most important factors influencing the species composition of macrofauna are oxygen, and hydrogen sulphide accompanying deteriorating oxygen conditions (Diaz & Rosenberg 1995, Gamenick et al. 1996, Hagerman et al. 1996, Johansson 1997, Laine et al. 1997, Olenin 1997, Rosenberg 2001).

In the Gulf of Gdańsk, seasonal oxygen concentration changes in the near-bottom water were observed above the halocline. Low concentrations of oxygen above the sea bottom were noted in the summer and autumn-winter periods. The lowest recorded concentration of oxygen in the water above the sea floor was 1.86 cm^3 dm^{-3}. There were no significant differences in the oxygen concentrations in the two water layers just above the seabed. According to Jørgensen (1980), the oxygen concentration recorded 50, 20–30 and 5 cm above the sea floor dropped rapidly from 8.4 and 4.1 mg dm^{-3} in the two higher levels to 0.6 mg dm^{-3} near the bottom.

The sediments in the study area were muddy and contained 8–10% of organic matter (Janas & Szaniawska 1996). The conditions in muddy sediments – a high organic matter content and limited diffusion of oxygen into the sediment – are propitious to the formation of hydrogen sulphide (Giere 1992). Hydrogen sulphide was present at depths of 50–60 m during the whole research period in much smaller concentrations in the surface layer than in the deeper layer (4–8 cm), which is in accordance with previous observations (Jørgensen 1983, Janas & Szaniawska 1996). The hydrogen sulphide concentration differed from season to season; this variation was most readily measurable in the deeper layer (4–8 cm). Exceptionally high concentrations were recorded in the summer-autumn period, although at the deepest stations high concentrations were also recorded in spring. One of the reasons for the increase in hydrogen sulphide concentration during summer and autumn may be the temperature rise, which is conducive to a high rate of organic matter production in the water and the greater activity of sulphide-reducing bacteria (Jørgensen 1977). Seasonal hydrogen sulphide concentration changes have also been reported from other Baltic areas and other water basins. The highest concentrations were generally recorded during summer and early autumn, with the lowest concentrations generally occurring during winter (Jørgensen 1983, Hines et al. 1989, Thiermann et al. 1996).

During the study period, environmental conditions at the two deeper stations were worse in 1996–1997 than in 1994–1995. Comparison of the hydrogen sulphide concentration in interstitial waters showed that this had doubled at station C (60 m), and had increased by a factor of 5 at station B (52 m). According to Trzosińska (1997) the oxygen conditions in the near-bottom layers in shallow areas in 1996 were identified as better than the average in 1979–1996. However, in deep-water areas, the conditions were poor: hydrogen sulphide was present in the Gdańsk Deep at the beginning of that year, and high concentrations of hydrogen sulphide near the sea bottom were recorded in the Gotland Deep during the second half of the year.

Despite the presence of hydrogen sulphide in the Gulf of Gdańsk sediments, they were always inhabited by fauna. The group of macrofauna inhabiting the area where hydrogen sulphide was permanently present consisted of *M. balthica*, *S. entomon*, *C. volutator*, *P. femorata*, *H. sarsi*, *N. diversicolor*, *H. spinulosus*, and representatives of the *Oligochaeta*. An interesting fact was the almost constant presence of *C. volutator* at 60 m. Single specimens of this species had also been recorded below 60 m in previous years (Janas & Szaniawska 1996, Warzocha & Gostkowska 1996).

M. balthica is a permanently dominant species in the study area, at times making up 95% of the macrofaunal abundance. The young generation of *M. balthica* is present in the Gulf of Gdańsk throughout the year (Warzocha & Gostkowska 1991). The greater abundance of *M. balthica*, due to the presence of a large number of new individuals, was most obvious in summer and autumn at the shallowest station, and in autumn and winter at the deeper stations. The greater abundance of *P. femorata* in summer and autumn was also due to the appearance of a new generation (Ostrowski 1976, Warzocha & Gostkowska 1991). The decrease in abundance was caused by the mortality of males after fertilisation in the autumn, followed by female mortality after egg-laying in the spring (Segerstråle 1950). No seasonal changes in the abundance of the principal components of the sea-bottom fauna, *M. balthica* and *P. femorata*, which could have been related to the seasonal variations in hydrogen sulphide concentrations in 1994–1995, were observed.

The benthic macrofauna inhabiting the halocline and the waters above it consists mostly of species more tolerant of oxygen deficiency and of hydrogen sulphide in the environment. However, none of these species can survive permanent anoxia. On the basis of the species composition of the macrofauna inhabiting the Gulf of Gdańsk above the halocline, and bearing in mind the resistance capability of each species (Oeschger & Theede 1986, Vismann 1990, Gamenick et al. 1996, Jahn & Theede 1997, Jahn et al. 1997, Johansson 1997, Normant & Szaniawska 2000), it can be stated that in the first half of the 1990s there were no long-lasting periods of anoxia in the near-bottom water. A period of stagnation of a few days' duration, which leads to a shortage of oxygen and the appearance of hydrogen sulphide, is sufficient to bring about the extinction of almost the entire macrofauna (Weigelt & Rumohr 1986). The recolonisation of the area by a similar group of macrozoobenthos is a long-term process, which can last as long as a couple of years (Diaz & Rosenberg 1995).

In 1996 and 1997 the abundance and biomass of macrofauna was found to have decreased in comparison to earlier years. This was true both of the shallowest station, where in the surface sediment layer there was no hydrogen sulphide, and of the deeper stations. That is why these changes cannot be related directly to worsening oxygen conditions near the sea floor, or to the increase in the hydrogen sulphide concentration in the sediments. In spite of the diminishing numbers of macrozoobenthos, no abrupt changes in the structure of the macrofauna occurred. Two species – *M. balthica* and *P. femorata* – were still the dominant components. The lower abundance was most obvious in the case of *M. balthica*, having fallen by at least 50%. The abundance of *H. sarsi*, *N. diversicolor*, *P. femorata* and *H. spinulosus* also decreased. Two species of crustaceans – *S. entomon* and *C. volutator* – appeared very infrequently and then only in small numbers. A similar tendency towards falling numbers, biomass and number of species in those parts of the bottom of the Gulf of Gdańsk lying above the halocline was also observed later, in 2000–2001. The most significant changes, involving the almost complete extinction of macrofauna below 35–40 m, took place in the western part of the Gulf of Gdańsk (Warzocha et al. 2001, Janas et al. in preparation). A significant drop in abundance and biomass in 1998–1999 was also recorded in shallower parts of the Gulf of Gdańsk (31 m) (Osowiecki 1999, 2000).

An ominous fact in the research area lying above the halocline was the diminishing presence of the cold stenothermal species *H. spinulosus*. At present, this species inhabits the bottom at depths of 30–40 m. Although this is an area with better oxygen conditions, the temperature is less stable, which could endanger a species of Arctic origin. As a result of deteriorating oxygen conditions during the 1980s, it disappeared from vast areas below the 80 m isobath (Okołotowicz 1985, Osowiecki & Warzocha 1996); worse still, since 1996 it has not been recorded even at 60 m. Nevertheless, these observations require substantiation through further research efforts covering a wider area. In the Pomeranian Bay, two other relict species – *Monoporeia affinis* and *P. femorata* – have disappeared entirely since 1981, and only a few specimens of the isopod *S. entonom* have been found since 1993 (Kube et al. 1997). Lower numbers of *P. femorata* have been recorded in the western Baltic (Köhn 1990).

It cannot be stated unequivocally that the elevated hydrogen sulphide concentration in the sediments has directly affected the macrozoobenthos inhabiting them. It is well-known, however, that deteriorating oxygen conditions, as well as the presence of high concentrations of hydrogen sulphide can cause bottom-dwelling organisms to rise to the surface of the sediments, thus becoming easy prey for their predators (Jørgensen 1980, Rosenberg & Loo 1988). It is also probable that, owing to the poor oxygen conditions in the deep waters of the Gulf of Gdańsk and the small quantities of food available, the fish feeding on macrozoobethos moved to a shallower zone with better oxygen conditions and more food. This could, in turn, have caused an increase in predator tension in these areas. Fish display avoidance reactions in oxygen saturations of 25–40% (Gray 1992), and such concentrations of oxygen are very often recorded near the sea bottom in water layers located beneath the halocline (Trzosińska 1997). The migration of fish into shallower areas as a result of worsening oxygen conditions was observed in the Gulf of Kiel (Weigelt & Rumohr 1986).

The decrease in the abundance of benthic macrofauna recorded in the second half of the 1990s, which has accelerated in subsequent years, is a very dangerous trend, particularly because it affects the bottom areas of the Gulf of Gdańsk, where changes of a similar drastic nature have never been noted before. It is a warning signal implying that negative changes are taking place in the environment which are giving rise to abnormalities in the functioning of the whole ecosystem.

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