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Thermochimica Acta 458 (2007) 112–117
thermochimica acta
www.elsevier.com/locate/tca

Fitness and chemical composition of the Baltic clam *Macoma balthica* (Linnaeus, 1758) from sulphidic habitats in the Gulf of Gdańsk (Southern Baltic)

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Abstract

The aims of the study were to determine the contents of glycogen, organic carbon and nitrogen in the Baltic clam *Macoma balthica* tissue and to find out whether there is any difference in fitness and chemical composition between individuals living in sediments with different pore-water hydrogen sulphide concentrations. It was found that hydrogen sulphide permanently present in the sediment at concentrations exceeding 513 μmol dm^{-3} at the middle depths of the Gulf of Gdańsk (60 m) had no adverse influence on the fitness of *M. balthica* and did not reduce the organic compound content in its tissue. This is very probably because of the presence of oxygen in the near-bottom water. Interestingly, animals living in such concentrations of hydrogen sulphide had heavier shells and a greater soft tissue weight. Moreover, the contents of organic matter and glycogen in their soft tissues were significantly higher. Glycogen was 30% higher on average, ranging from 11.1 to 30.3% AFDW during the year. At all the stations during the year, organic carbon in *M. balthica* tissue varied from 50.3 to 55.2% AFDW, and organic nitrogen from 7.7 to 11.7% AFDW.

Keywords: *Macoma balthica*; Glycogen; Organic carbon; Organic nitrogen; Hydrogen sulphide; Hypoxia

1. Introduction

A deficiency of oxygen coupled with the presence of hydrogen sulphide in the sediments of the deeper parts of the Baltic Sea is a natural occurrence, further aggravated by human pressure. Only a few species with a high resistance to such conditions inhabit these waters. Long-term hypoxia or anoxia in the near-bottom water and the presence of hydrogen sulphide in the sediments have been reported as causing changes in the structure and function of benthic communities or even their mass mortality (see the reviews by Bagarinao [1], Diaz and Rosenberg [2], Karlson et al. [3]). Stress in benthic animals can be observed as a change in their behaviour and physiological processes prior to the onset of mortality [4–6]. Despite the abundant literature on the effect of oxygen depletion and hydrogen sulphide on the survival and physiological processes of benthic organisms under laboratory conditions (e.g. [7–9]), little information is available on how these parameters influence the fitness and chemical composition of animals living in such an environment.

The Baltic clam *Macoma balthica* (Linnaeus, 1758) is the principal macrofaunal component in those areas of the Gulf of Gdańsk where hydrogen sulphide is permanently present [10]. It is known that under stressful conditions, like oxygen deficiency, this species uses its reserves of glycogen as the main energy source, but it is likely that lipids and proteins are consumed as well [11–13]. Measurements of the weight and chemical composition of bivalves, including *M. balthica*, could provide information on the overall fitness or condition of the individual animals in a population [14,15].

The aims of the study were to determine the chemical composition of *M. balthica* tissue and to find out whether there is any difference in fitness and chemical composition between individuals of *M. balthica* living in sediments differing in hydrogen sulphide concentration. In the present paper, the expression “fitness” is used in the sense of optimal/maximum tissue weight together with high contents of organic matter and energy reserves.

Information on the organic carbon content in *M. balthica* tissue could also be very valuable for estimating the energy

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0040-6031/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.tca.2007.02.004

resources and calculating the energy budget of the Gulf of Gdańsk, and for constructing a functional model of this ecosystem. To date, only a handful of investigations of the organic carbon and nitrogen contents of benthic marine organisms living in the Baltic Sea have been done (e.g. [16–19]).

2. Experimental

2.1. Study area

The study area was located in the Gulf of Gdańsk, southern Baltic Sea. The relevant parameters were measured at three stations selected to reflect the H_2S gradient in the pore-water of the sediment: (A) at 37 m depth (54°35.00′N, 18°40.00′E), (B) at 51 m depth (54°35.00′N, 18°44.00′E), and (C) at 60 m depth (54°35.15′N, 18°48.6′E).

The hydrogen sulphide concentrations in the sediments increased with the depth of stations in two sediment layers (0–4 and 4–8 cm) during the study period (July 1994–June 1995) (Fig. 1). Less than 13 μmol dm^{-3} was measured in both sediment layers at the shallowest station A. Values were higher at station B: in the 0–4 cm sediment layer they did not exceed 26 μmol dm^{-3}, while in the 4–8 cm layer they ranged from 31 to 392 μmol dm^{-3}. The highest concentrations were recorded in both sediment layers, >162 and >513 μmol dm^{-3}, respectively, at the deepest station C. The oxygen concentration in the near-bottom water varied from 3.2 to 8.3 ml dm^{-3}, the greatest variations being at the two deeper stations B and C. The temperature of the near-bottom water during the study period ranged from 3.1 °C in January to 16.2 °C in August, the highest values being recorded at the shallowest station A [10]. The salinity of the near-bottom water in the Gulf of Gdańsk varied over a very narrow range (7.5–8.0 PSU) in 1994–1995 [20,21]. More detailed measurements (monthly data) of the temperature, oxygen concentration in the near-bottom water and the hydrogen sulphide concentration in the sediment pore-water are given in ref. [10].

2.2. The Baltic clam: sampling and analyses

M. balthica was sampled monthly from July 1994 to June 1995 using a bottom dredge. The individuals were frozen on board ship. On being defrosted, 11–15 individuals ranging in shell length from 14 to 16 mm were chosen from every station and every month. The soft parts of the animals were separated from the shells, and the two parts of the body dried independently at 60 °C (to constant weight) and weighed on a PRECISA 125A automatic electronic balance (±0.001 g). The combined dry tissues from 11 to 15 clams were then homogenised in a mortar.

The glycogen content in *M. balthica* tissue was analysed by a method described in Dubois et al. [22]. Three replications were performed for each sample; the coefficient of variation between them was less than 7%. The glycogen contents given for each month and station are average values. Organic carbon and nitrogen were determined as the difference between their contents in dry mass and in ash with a Perkin-Elmer PE CHNS/O 2400 Series Elemental Analyzer following the procedure given in Gnaiger and Bitterlich [23]. The organic fraction (Ash Free Dry Weight, AFDW) of *M. balthica* tissue was determined as the weight difference before (dry mass) and after combustion (ash) at 450 °C for 12 h. Two replications were performed for each sample, the coefficient of variation between them being less than 0.2% for both carbon and nitrogen.

The organic matter content was expressed as a percentage of dry weight (DW), whereas glycogen, carbon and nitrogen as a percentage of the organic fraction (AFDW).

2.3. Statistical methods

The Shapiro-Wilk test was used to test for normality, and the non-parametric Mann–Whitney *U*-test was used at different levels to determine the significance of the differences between the parameters under examination. The median, the interquartile range containing the middle 50% of values in the sample, and the range of the data from minimum to maximum values are presented.

3. Results

Analysis of *M. balthica* showed that the dry weights of both shell and tissue of individuals in the same size range during almost the whole study period were lowest at the shallowest station A and highest at the deepest station C (Fig. 2). At the

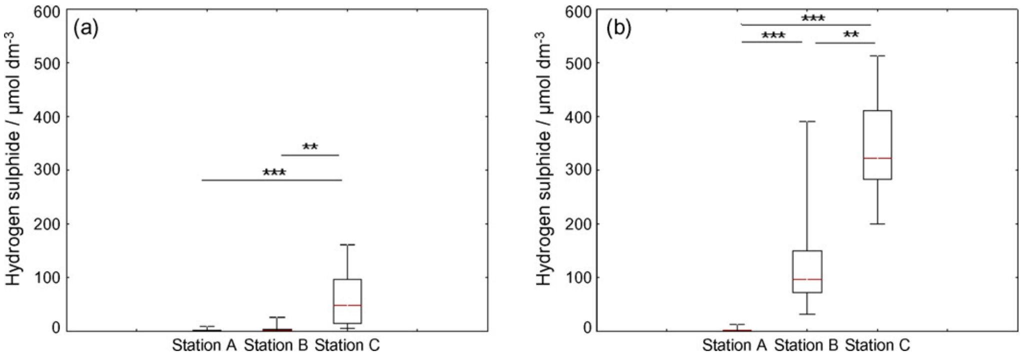

Fig. 1. Hydrogen sulphide concentration in the pore-water of: (a) 0–4 cm and (b) 4–8 cm sediment layers at the three studied stations. The box extends from the 25th percentile to the 75th percentile, with a horizontal line at the median. Whiskers show the range of the data. Eleven or 12 measurements were used for every parameter and station. Significant at $^{**}P < 0.001$ and $^{**}P < 0.0001$.

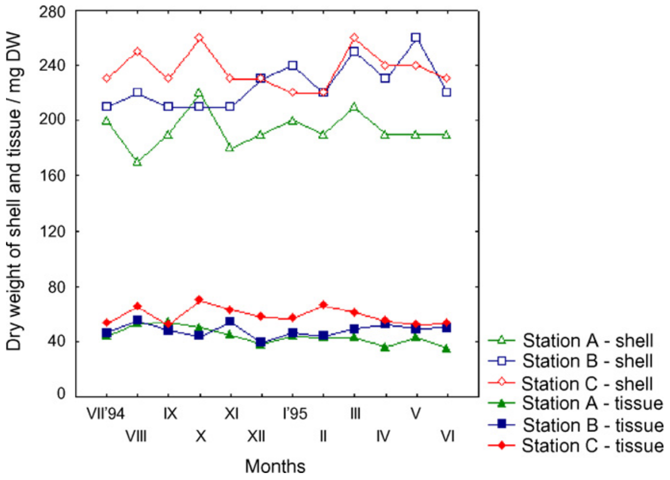

Fig. 2. Seasonal changes in the dry mass of shell and soft tissue (mg) of *M. balthica* at stations A–C.

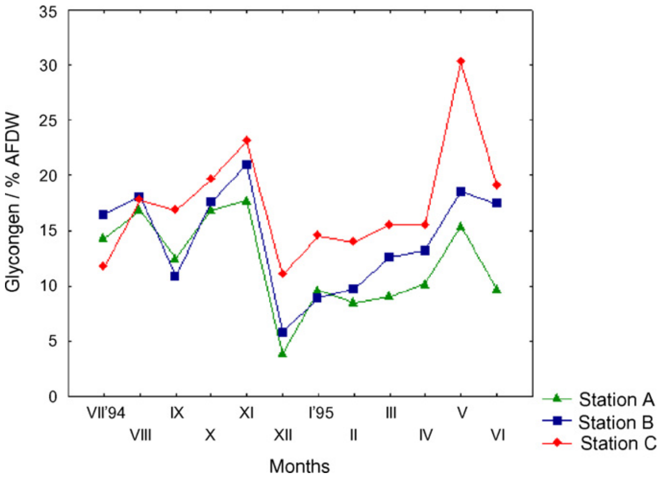

Fig. 4. Seasonal changes in the glycogen content (% AFDW) in the soft tissue of *M. balthica* at stations A–C.

middle depth station B the seasonal pattern of shell dry weight resembled that at station C, but the tissue dry weight more closely resembled that at station A. The shell dry weight at station A varied from 170 to 210 mg and was significantly lower than at station B ($P < 0.001$) and station C ($P < 0.0001$) (Fig. 7a); at C it varied from 220 to 260 mg. The tissue dry weight at station C ranged from 52 to 70 mg and was significantly higher than at stations A and B ($P < 0.001$) (Fig. 7b).

The organic matter content in *M. balthica* tissue varied with depth in a very similar way during the year at the three stations (Fig. 3): the highest values – at station C (from 89.2 to 93.0% DW) – differed significantly from the contents at stations A and B ($P < 0.05$) (Fig. 7c). Organic matter contents were lowest (minimum 86.4% DW) at station A.

Similar changes were recorded in the glycogen content of *M. balthica* tissue at all three depths: it was lowest during winter and highest during spring and autumn (Fig. 4). Except in July and August, values were highest at station C (from 11.8 to 30.3% AFDW). Glycogen contents measured at station C differed significantly from those at station A ($P < 0.05$) (Fig. 7d). Glycogen contents measured at stations A and B were similar to each other ($P > 0.05$) and lower than at C, where they varied from 3.9 to 20.9% AFDW).

The seasonal pattern exhibited by organic carbon in *M. balthica* tissue was much the same at all three stations (Fig. 5): it varied over a very narrow range (50.5–55.2% AFDW) with minimum values during winter. Values recorded at station B were significantly higher than those at stations A and C ($P < 0.05$) (Fig. 7e).

Organic nitrogen in *M. balthica* tissue varied in a very similar way during the year at the three stations (Fig. 6), but the pattern was the reverse of that of organic carbon. This content varied from 7.7 to 11.7% AFDW, with maximum values during winter and minimum during summer. No difference was found in the organic nitrogen content between individuals inhabiting the three stations ($P > 0.05$) (Fig. 7f).

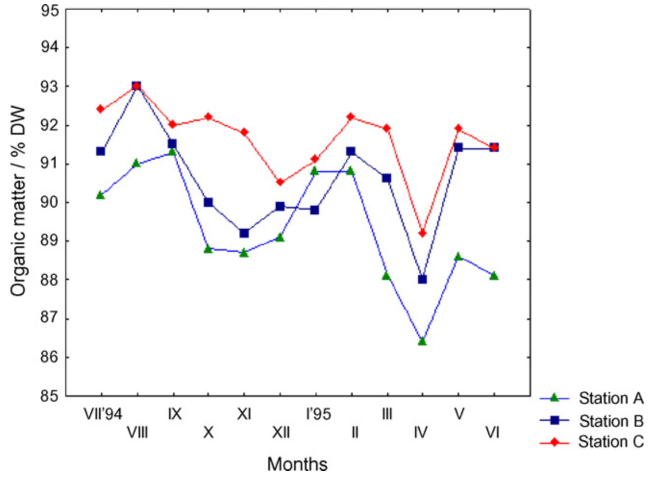

Fig. 3. Seasonal changes in the organic matter content (% DW) in the soft tissue of *M. balthica* at stations A–C.

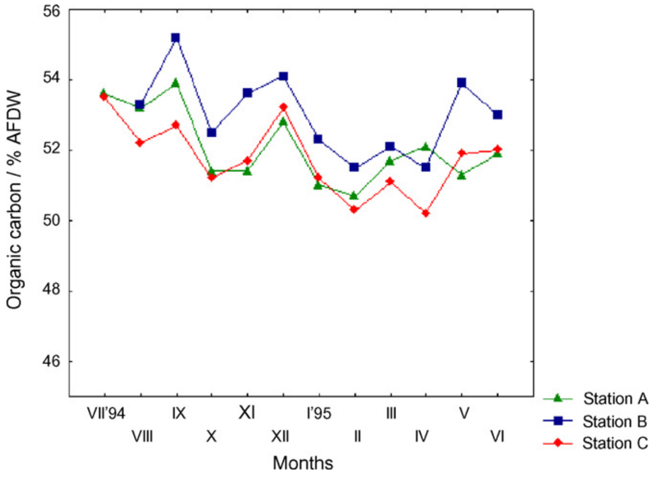

Fig. 5. Seasonal changes in the organic carbon content (% AFDW) in the soft tissue of *M. balthica* at stations A–C.

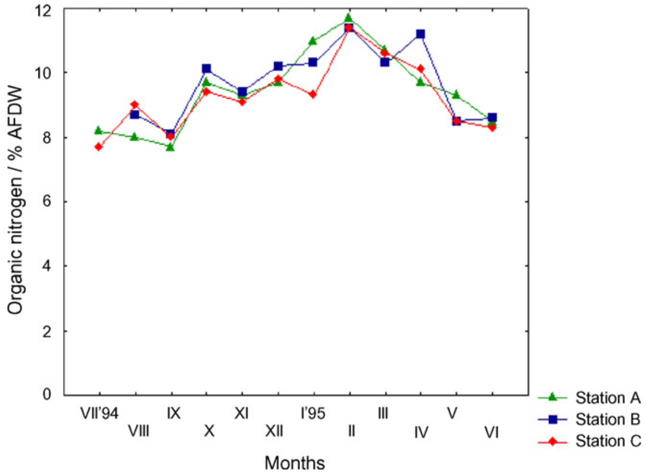

Fig. 6. Seasonal changes in the organic nitrogen content (% AFDW) in the soft tissue of *M. balthica* at stations A–C.

4. Discussion

The earlier literature suggested that the dry weight, organic matter content and chemical composition of *M. balthica* might be influenced by factors such as life cycle, temperature and nutritional condition, and stress [15,24–26].

M. balthica living in sediments with the highest hydrogen sulphide concentrations measured in this study had heavier shells and larger body masses as well as higher soft tissue contents of organic matter and glycogen. Earlier studies of this species had indicated that shell weight increased with increasing depth, a trend reported from the Wadden Sea, the Gulf of Gdańsk and the Åland Archipelago [27–30].

Being a facultative suspension-deposit feeder, *M. balthica* is able to take up particles from both the water column and the surface sediment. Animals from greater depths may well be larger and possess larger energy resources because of the greater

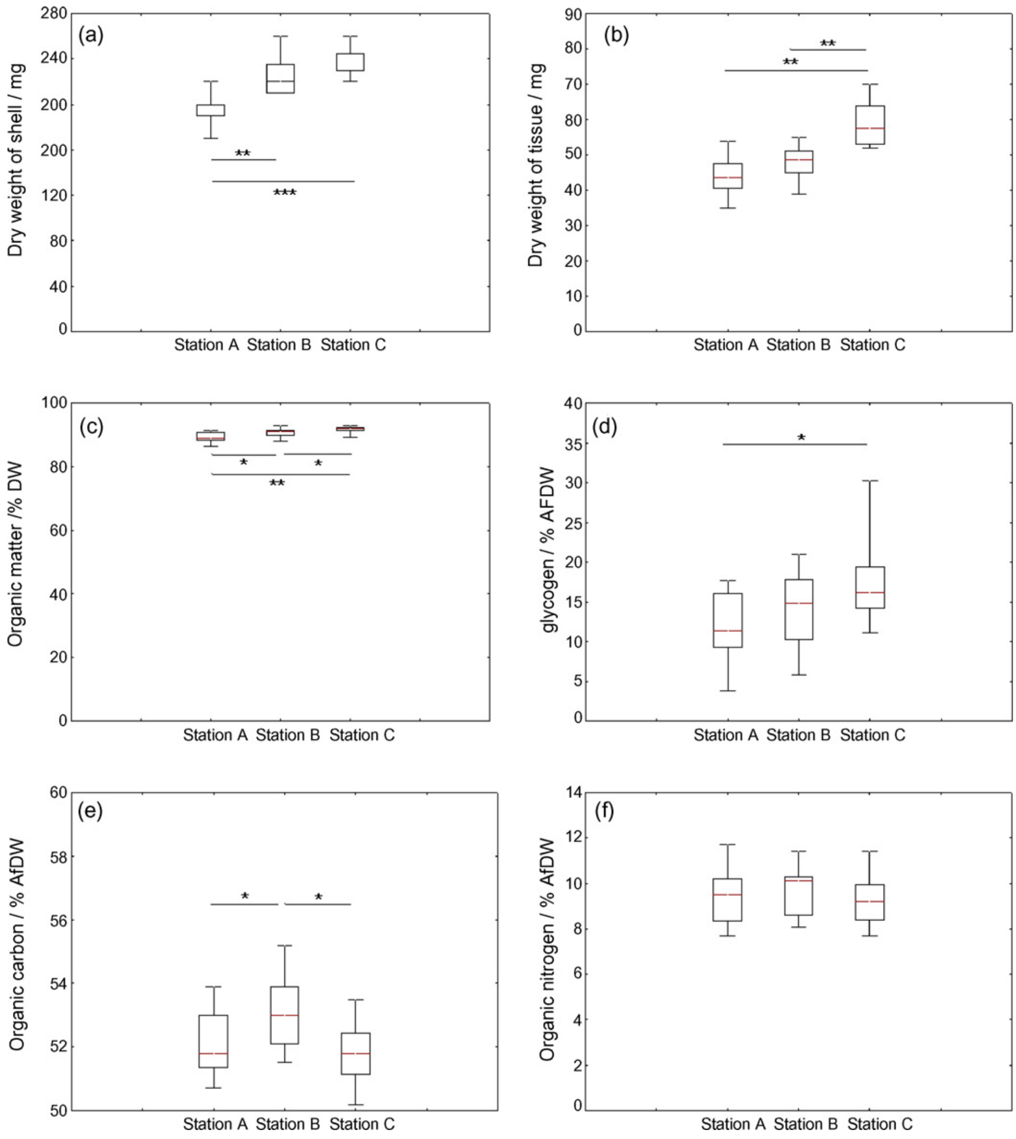

Fig. 7. Pooled data of: (a) dry weight of shell, (b) dry weight of tissue, (c) organic matter (d) glycogen, (e) organic carbon and (f) organic nitrogen content of *M. balthica* tissue. The box extends from the 25th percentile to the 75th percentile, with a horizontal line at the median. Whiskers show the range of the data. Eleven or 12 measurements were used for every parameter and station. Significant at $^{*}P < 0.05$, $^{**}P < 0.001$ and $^{**}P < 0.0001$.

amount of food available to them at those depths. Higher organic matter and organic carbon contents in the sediments at greater depths in the Gulf of Gdańsk were reported by Jankowska [31] and Maksymowska [32]. In the same area, a similar rising trend with depth was found for chlorophyll *a* and phaeophytin in surficial sediments, which indicates an abundance of phytoplankton [32].

Laboratory studies conducted on *M. balthica* have shown that within a few hours of the appearance of anoxic conditions and/or hydrogen sulphide, anaerobic metabolism comes into play [9]. A reduction in glycogen reserves was observed as a result of a few days' exposure to such stressful conditions. After 5 and 15 days of anoxic conditions, glycogen reserves decreased by 14 and 76%, respectively; lipid reserves were depleted more slowly [11]. However, it was observed that the decrease of glycogen could be as high as 38% after 24 h under anoxic conditions (unpublished data). This large fall could be related to the increasing activity of the animals which extend their siphons on emerging on to the sediment surface.

However, this study revealed almost identical seasonal changes of glycogen at stations with differing hydrogen sulphide concentrations in their surficial sediments. The highest glycogen values in *M. balthica* tissue at the deepest station suggest that hydrogen sulphide did not cause the energy reserves accumulated in the form of glycogen to be used up.

A similar seasonal trend was found with respect not only to glycogen in *M. balthica* tissue but also to the organic matter, organic carbon and nitrogen contents. The observed seasonal changes in the components of *M. balthica* body tissue depended mainly on seasonal temperature changes which influence the rates of metabolism and reproductive activity, and on changes in trophic conditions related to phytoplankton blooms.

Our study showed that *M. balthica* accumulates energy reserves twice a year. In April–May, the contents of organic matter, organic carbon and glycogen increased, and in autumn there was a second glycogen peak and a slight increase in organic carbon. Reserves were accumulated when the trophic conditions were the most propitious, i.e. after the algal bloom had sunk to the bottom. The growing season in the Gulf of Gdańsk is relatively long, beginning in the second half of March and lasting until November [33]. During the spring blooms, fresh organic matter is transported very quickly to the bottom; during the autumn bloom, phytoplankton also reaches the bottom, but in a much more advanced state of degradation [34].

The annual cycles of glycogen and organic carbon (which mirror the changes in lipids) are similar to those described for the western Baltic Sea. Graf et al. [24] showed that *M. balthica* from the Kiel Bight commenced the build-up of glycogen and lipid resources immediately following the bloom input in spring and suggested that the autumn peak was also related to the bloom. A similar cycle with two glycogen and lipid peaks was observed in the Gulf of Gdańsk at a depth of around 30 m and also in the Åland area [30]. However, only one spring peak was recorded in the shallow and deep parts of the Gulf of Gdańsk [25,29] and in the shallow part of the Gulf of Finland [13]. The seasonal changes in organic nitrogen, related to protein, with a winter maximum and a summer minimum, resemble those reported earlier from the same area [25], from the Dutch Wadden Sea [12] and the Gulf of Finland [13].

It has been suggested that *M. balthica* inhabiting the Gulf of Gdańsk has only one spawning period per year, beginning in late March–early April [35]. But it does seem that the twice-yearly decrease in organic matter content and organic carbon (in late March–early April and in late September–early October) could be related to spawning periods. Earlier studies also gave indications of a second spawning period. Wenne [35] observed that a considerable number of individuals had gonads ready for spawning in the summer too; Sokołowski [36] found individuals in the reproductive and post-reproductive state in autumn.

Why does hydrogen sulphide present in the sediment not affect the chemical composition of *M. balthica* tissue? Any adverse effect of the presence of toxic hydrogen sulphide in the sediments on the chemical composition of *M. balthica* is countered by the presence of oxygen in the water above the sediments, so long as the periods of anoxia in these waters are of short duration. This has already been demonstrated in studies of macrofaunal associations, and also by the presence in these waters of species more sensitive to the lack of oxygen, e.g. *Corophium volutator* [10]. *M. balthica* is known to be generally independent of the oxygen conditions in the sediment: it usually inhabits the sediment 3–8 cm below the surface, but takes oxygen from above the sediment by means of its inhalant siphon [37]. Additionally, H_2S concentrations in sediments decrease in the immediate vicinity of macrofaunal individuals, thanks to their activity below the surface of the sediment [38]. It has also been demonstrated that this oxic and oxidised zone around their burrows in anoxic sediment are colonised on a large scale by meiofauna [39,40].

Laboratory studies have shown that the Baltic clam is very tolerant towards hypoxia, anoxia and H_2S [9]. Other such studies have indicated that the most resistant individuals are capable of surviving 15–20 days under anoxic conditions [41]. Clams, like other animals having to cope with H_2S, have defensive mechanisms, enabling them to live in the presence of this toxic compound. These involve metal-sulphur precipitation within the vesicles at the mantle edge [42,43]; more importantly, the clams are capable of oxidising hydrogen sulphide to non-toxic thiosulphate [9,44]. The efficacy of this defence mechanism depends, however, on the availability of oxygen in the environment. Deterioration in the oxygen conditions at the bottom and diffusion of H_2S from the sediments could worsen the animals' fitness and lead to their mortality on a large scale. It is probably these very conditions that have brought about a dramatic fall in the biomass of macrofauna, including *M. balthica*, in the Gulf of Gdańsk [10].

Recent studies have revealed disturbing morphological, histological and cytogenetic changes in the *M. balthica* inhabiting especially the deeper waters of the Gulf of Gdańsk, but the causes are still unknown [45–47]. Likewise, the condition and chemical composition of individuals exhibiting these abnormal features are not known. Knowledge of this would help to assess the effect not only on an individual animal but also on the whole population.

Our studies have revealed that even the constant presence of hydrogen sulphide needs not adversely affect the fitness and chemical composition of *M. balthica*. But this is very probably the case only up to a certain concentration of H_2S, and then only if there is sufficient oxygen in the near-bottom water. On the other hand, one cannot rule out the possibility that low concentrations of H_2S could be used by *M. balthica* as a source of energy. This phenomenon was first reported in animals from hydrothermal vents [48], but has also been demonstrated in animals from soft sediments: *Heteromastus filiformis* [8], *Arenicola marina* [49], *Hediste diversicolor* and *Marenzelleria viridis* [50], *Lepidophthalmus louisianensis* and *Callichirus islagrande* [51]. This ability would explain the large sizes and the greatest energy resources of *M. balthica* inhabiting H_2S-rich areas. Further laboratory studies are, however, needed in order to confirm these field observations.

Acknowledgments

We wish to thank Prof. Anna Szaniawska, anonymous referees and the editors for their constructive comments, which have helped to improve the manuscript. We would like also to thank Mrs. Maria Przytarska for performing the CHN analyses at the Department of Chemistry, University of Gdańsk. This research was supported by Grant No. BW 1320-5-0008-3.

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