Significance of body size in sulphide detoxification in the Baltic clam *Macoma balthica* (Bivalvia, Tellinidae) in the Gulf of Gdańsk

Andreas Jahn[1,*], Urszula Janas[2], Hans Theede[1], Anna Szaniawska[2]

[1]Institut für Meereskunde an der Universität Kiel, Abteilung Meereszoologie, Düsternbrooker Weg 20, D-24103 Kiel, Germany
[2]Institute of Oceanography, University of Gdańsk, Al. Marsz. Piłsudskiego 46, 81-378 Gdynia, Poland

ABSTRACT: The Baltic clam *Macoma balthica*, a predominant species of macrofauna in the Gulf of Gdańsk (Poland), is exposed to high concentrations of hydrogen sulphide at many locations in this bay. When oxygen is available, the species is able to detoxify penetrating sulphide mainly by oxidizing it to non-toxic thiosulphate. Sulphide influx rate can be quantified by calculation of the diffusion coefficient for total sulphide. A relatively low apparent diffusion coefficient of about 2×10^{-6} cm^2 s^{-1} indicates that *M. balthica* is able to reduce sulphide diffusion by temporary valve closure. During oxic-sulphidic incubation, an equilibrium between sulphide diffusion and detoxification is established at a specific internal sulphide concentration, c_i, which can be calculated by the following equation: $c_i = c_0\, e^{-k\, r_a^2 /3D}$ where c_i = internal sulphide equilibrium concentration, c_0 = external sulphide concentration, k = apparent detoxification constant, r_a = effective radius, and D = apparent diffusion coefficient. The amount of accumulated sulphide in the tissues is strongly dependent on individual size. This is confirmed by experiments as well as by field studies. After specific sulphide incubations, only low internal sulphide concentrations are found in large clams, whereas small clams accumulate much more sulphide in the tissues. Field studies show a distinct reduction in numbers of small clams in high sulphidic areas. We conclude that efficient sulphide detoxification seems possible only if the body size exceeds a certain minimal value.

KEY WORDS: *Macoma balthica* · Hydrogen sulphide · Apparent diffusion coefficient · Apparent detoxification constant · Macrofauna · Baltic Sea · Gulf of Gdańsk

INTRODUCTION

The Baltic clam *Macoma balthica* (L.) is one of the most common macrozoobenthic species of the Baltic Sea. It was observed in the Gulf of Gdańsk that it can settle in poorly oxidised sediments with high concentrations of hydrogen sulphide in the pore water (Janas & Szaniawska 1996). (Note: In this study, reference is made to 'sulphide' as the sum of S^{2-}, HS^-, and undissociated H_2S). Hydrogen sulphide is known as being strongly toxic to eukaryotic organisms (Evans 1967, National Research Council 1979), and is also recognised as an important ecological factor in marine coastal sediments (Somero et al. 1989, Vismann 1991b, Bagarinao 1992, Giere 1992, Grieshaber et al. 1992)

Physiological studies have shown that sulphide can be detoxified in many marine invertebrates by oxidation to non-toxic compounds like thiosulphate, sulphite or elemental sulphur (Vismann 1991a, Jahn et al. 1992, 1993, 1996, Oeschger & Vetter 1992, Völkel & Grieshaber 1992, Hagerman & Vismann 1993, Jahn & Theede 1997b, Johns et al. 1997).

Hydrogen sulphide penetrates into the tissues by diffusion. The ratio of sulphide influx to oxidation is crucial for successful detoxification. However, only few data are available with reference to these rates due to the difficulties of making direct measurements. Powell (1989) gave mathematical models for sulphide diffusion into worm-like 'thiobiotic' meiofauna. Julian & Arp (1992) isolated the body wall of the echiuran worm *Urechis caupo* and measured the permeability coefficients of H_2S and HS^- in artificial diffusion chambers.

*E-mail: ajahn@ifm.uni-kiel.de

Völkel & Grieshaber (1992) estimated the diffusion coefficient for undissociated H_2S for the body wall of the peanut worm *Sipunculus nudus* by using a non-differential form of Fick's first law. Organisms like clams or ostracods, which possess shells, are able to reduce sulphide diffusion into their tissues temporarily by different degrees of shell closure. Direct measurement of sulphide diffusion through the body wall is not possible in these organisms. Therefore, the determination of an apparent diffusion coefficient for total sulphide for the ostracod *Cyprideis torosa* was proposed using measured concentrations of sulphide and its oxidation products in the tissues (Jahn et al. 1996).

The purpose of this study was, firstly, to investigate the distribution of *Macoma balthica* in the Gulf of Gdańsk in relation to the concentration of hydrogen sulphide in the sediment and, secondly, to find out the significance of sulphide diffusion and possible consequences for the efficiency of detoxification, with emphasis on relation to body size.

MATERIAL AND METHODS

Field study. Four stations located in the Gulf of Gdańsk were studied in September 1994: Stn 1 (54°35.0' N, 18°40.0' E; 37 m depth), Stn 2 (54°35.0' N, 18°44.0' E; 51 m depth), Stn 3 (54°34.2' N, 18°48.6' E; 60 m depth), and Stn 4 (54°38.0' N, 18°58.3' E; 82 m depth) (Fig. 1). Sulphide content in the interstitial water of sediment layer at 0 to 8 cm depth was measured photometrically according to Cline (1969). The detailed procedure is described in Janas & Szaniawska (1996). In order to determine species composition, macrofauna was collected with a Van Venn grab, sifted through a sieve with 1 mm mesh size, and preserved in 10% formalin. Biomass of each taxon was determined after drying for 3 d at 60°C (bivalve biomass without shell). Samples for length-frequency distribution of *Macoma balthica* consisted of more than 100 specimens. Shell length of individuals was measured to 0.1 mm.

Physiological studies. Specimens of *Macoma balthica* were collected in Gdańsk Bay from depths of 37 m (Stn 1) and 60 m (Stn 3) in August 1993 and September 1994. Average shell lengths of the clams were 15.3 ± 1.5 mm (n = 20). Prior to experiments, the bivalves were kept in aquaria with sediment and well-oxygenated seawater (5°C, 9‰ S). One day before the start of the experiments, the clams were acclimatized to the experimental temperature of 10°C.

Oxic-sulphidic incubations (200 µM sulphide; O_2 > 167 µM; 9‰ S; 10°C; pH 8.0) were carried out by using
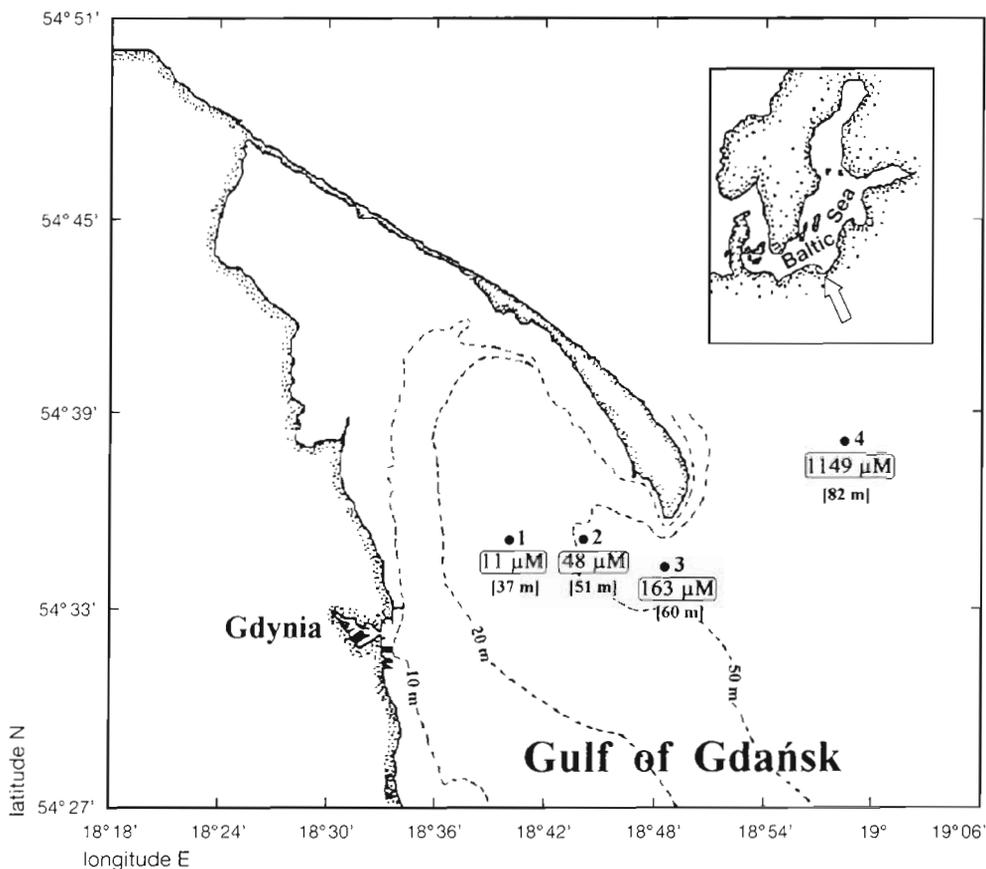

Fig. 1. Location of sampling stations in the Gulf of Gdańsk and sulphide concentrations in the pore water of sediment layer in 0–8 cm depth in September 1994

a flow-through system as described in Jahn (1997) and Jahn & Theede (1997b). During the experiments, pH, oxygen (according to Ingvorsen & Jørgensen 1979), and sulphide concentrations (according to Cline 1969) were regularly monitored.

After incubation, concentrations of sulphide, thiosulphate, and sulphite in the tissues (without shells) were analysed by High-Performance Liquid Chromatography (HPLC) by derivatization with monobromobimane (Newton et al. 1981, Vetter et al. 1989, Jahn et al. 1996, Jahn 1997). Concentration of elemental sulphur (cyclic octamer S_8) was analysed according to Lauren & Watkinson (1985), Jahn (1997), and Jahn & Theede (1997b).

Data were analysed by using the nonparametric U-test of Mann & Whitney with a significance level of 5%.

Apparent diffusion coefficient. The apparent diffusion coefficient for total sulphide was calculated according to a model which assumes that accumulation of internal sulphide concentration c at a given external sulphide concentration c_0 follows Michaelis-Menten kinetics (Jahn et al. 1996, Jahn 1997)

$$c(t) = \frac{c_0 t}{\tau + t} \tag{1}$$

where t is time and τ, analogous to the Michaelis-Menten constant, indicates the time after which $c_0/2$ is attained inside (half-saturation time).

The model describes the animal's body as a sphere. For a sphere Fick's second law is given according to Berg (1993) as

$$\frac{\partial c}{\partial t} = D \frac{1}{r^2} \frac{\partial}{\partial r}\left(r^2 \frac{\partial c}{\partial r} \right) \tag{2}$$

where D is the diffusion coefficient and r the radius of the sphere.

By using the differential equation (Eq. 2), it is possible to determine with measurable values, the effective radius (r_e) and the half-saturation time (τ), an apparent diffusion coefficient for total sulphide (D), summing up all diffusion barriers in the tissues (Jahn et al. 1996, Jahn 1997):

$$D = \frac{r_e^2}{3\tau} \tag{3}$$

The effective radius (r_e) can be calculated from the volume (V) by using the tissue water content (w), the fresh mass of the animal (m), and the density of water (ρ):

$$r_e = \sqrt[3]{\frac{3}{4} \frac{wm}{\rho\pi}} \tag{4}$$

The half-saturation time (τ) can be estimated by using the reciprocal form of Eq. (1) as linear curve fitting (Lineweaver-Burk-Plot):

$$\frac{1}{c} = \frac{\tau}{c_0} \frac{1}{t} + \frac{1}{c_0} \tag{5}$$

Total sulphur concentration (c) in the tissues was measured after different incubation times (t) under sulphidic conditions $(c_0 = 200\ \mu M)$. Total sulphur concentration is the sum of sulphide ($H_2S + HS^- + S^{2-}$), thiosulphate ($S_2O_3^{2-}$), sulphite (SO_3^{2-}), and elemental sulphur (S_8) by consideration of stoichiometric ratios and control values $(t = 0)$.

Apparent detoxification constant. Hydrogen sulphide that has entered will be detoxified by oxidation to thiosulphate, sulphite, and elemental sulphur. This detoxification starts immediately at the beginning of sulphide influx. Thus, detoxification has first order kinetics (Powell 1989), which means that the decrease of the internal sulphide concentration (c) during the time (t) is proportional to the actual sulphide concentration in the tissues:

$$-\frac{\partial c}{\partial t} = kc \tag{6}$$

The proportionality constant (k) is the apparent detoxification constant which describes the rate of sulphide detoxification. Comparable to the apparent diffusion coefficient, this constant sums up all detoxification processes in the tissues.

Both processes, diffusion and detoxification, occur simultaneously. Therefore, a certain internal sulphide concentration at equilibrium between diffusion and detoxification will be established. This equilibrium concentration determines the effectivity of detoxification. For equilibrium the combination of Eqs. (2) & (6) gives:

$$D \frac{1}{r^2} \frac{\partial}{\partial r}\left(r^2 \frac{\partial c}{\partial r} \right) = kc \tag{7}$$

Substitution with

$$u = r^2 \frac{\partial c}{\partial r}$$

and integration between 0 and $u(r)$ or between 0 and r_e respectively gives:

$$\Rightarrow D \int_0^{u(r)} du = kc \int_0^{r_e} r^2\, dr$$

$$\Leftrightarrow D r^2 \frac{\partial c}{\partial r} = kc \frac{1}{3} r_e^3$$

The limits of the second integration are the beginning of the diffusion distance at the surface $(r = 0)$ with the external sulphide concentration (c_0) and the end of diffusion distance at the centre $(r = r_e)$ with the equilibrium concentration (c_i):

$$\Rightarrow \quad D \int_{c_0}^{c_i} \frac{1}{c} \partial c = \frac{1}{3} k r_e^3 \int_0^{r_e} r^{-2} \partial r$$

$$\Leftrightarrow \quad D \ln \frac{c_i}{c_0} = -\frac{1}{3} k r_e^3 \frac{1}{r_e}$$

$$\Leftrightarrow \quad \ln \frac{c_i}{c_0} = -\frac{k r_e^2}{3D} \tag{8}$$

$$\Leftrightarrow \quad k = \frac{3D}{r_e^2} \ln \frac{c_0}{c_i} \tag{9}$$

Eq. (3) in Eq. (9) gives:

$$k = \frac{1}{\tau} \ln \frac{c_0}{c_i} \tag{10}$$

The apparent detoxification constant (k) can be calculated from Eq. (10) with the measured sulphide equilibrium concentration (c_i) at a given external concentration (c_0) and the determined half-saturation time (τ) (Eq. 5). Eq. (8) gives:

$$c_i = c_0\, e^{-k\, r_e^2 / 3D} \tag{11}$$

By using Eq. (11), it is possible to estimate the sulphide equilibrium concentration (c_i) in the tissues as a function of the effective radius (r_e) (Eq. 4).

RESULTS

Sulphide concentration in bottom sediments in the Gulf of Gdańsk

Hydrogen sulphide concentrations in interstitial water of sediment layers at 0 to 8 cm depth are presented in Fig. 1 The lowest sulphide concentration of 11 µM was found at the shallowest station, Stn 1, while the highest concentration of 1149 µM occurred at the deepest station, Stn 4. At Stns 2 and 3 concentrations were 48 and 163 µM, respectively.

Community structure of macrozoobenthos

At the sampling stations in the Gulf of Gdańsk *Macoma balthica* (L.) (Mollusca, Bivalvia, Tellinidae) was the predominant species (Fig 2). Its proportion of the total biomass varied from 89% (Stn 1) to 97% (Stn 3). The following were the main species which also occurred: Stn 1: *Halicryptus spinulosus* v. Siebold (Priapulida), *Mya (Arenomya) arenaria* (L.) (Mollusca, Bivalvia, Myidae), *Pontoporeia femorata* Krøyer (Arthropoda, Crustacea, Amphipoda, Haustoriidae); Stn 2: *H. spinulosus, P. femorata*; Stn 3: *H. spinulosus*; Stn 4: *Harmothoe (Antinoella) sarsi* (Kinberg) (Annelida, Polychaeta, Polynoidae).

Population structures of *Macoma balthica* varied at the sampling stations (Fig. 3). At Stn 1, which had the lowest sulphide concentration in the sediment, the highest proportion of young clams with shell lengths less than 6 mm could be found, whereas at the other stations young specimens were rather seldom. At Stn 4, which had the highest sulphide concentration, individuals from 10 to 12 mm in size were dominant.

Physiological studies

Oxic-sulphidic incubation caused a slow increase of sulphide in the tissues of *Macoma balthica* (Fig. 4). Sulphide concentration was already significantly higher than in the control after 3 h and reached its highest level with 41 ± 23 nmol g^{-1} fresh mass (fm) after 5 d. *M. balthica* was able to oxidize sulphide to thiosulphate ($S_2O_3^{2-}$) very quickly. After 3 h, thiosulphate concentration had already increased significantly and reached a maximum (68 ± 80 nmol g^{-1} fm) after 1 d of incubation. As a further oxidation product, elemental sulphur (S_8) appeared, but the content had increased significantly only after 6 d of incubation (35 ± 12 nmol g^{-1} fm). No sulphite (SO_3^{2-}) could be found in the tissues.

Due to oxidation of sulphide, which therefore was eliminated from the diffusion equilibrium, more sulphide penetrated into the tissues, resulting in an in-
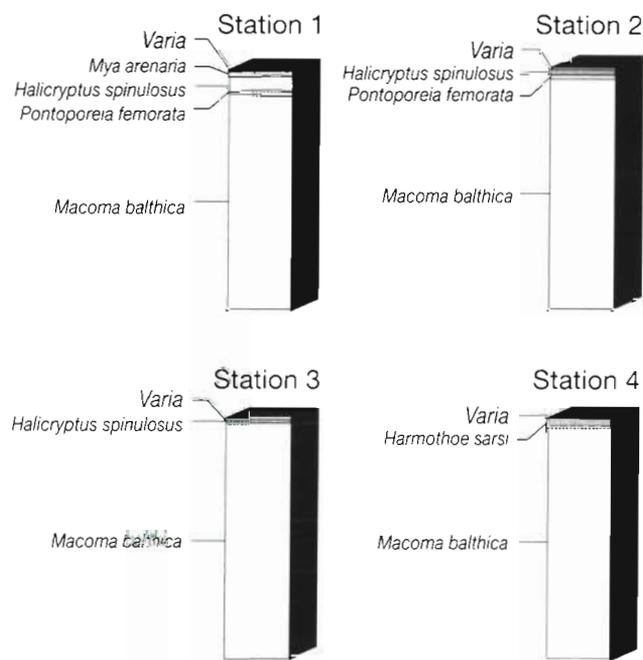

Fig. 2. Benthic community structure in terms of biomass at the sampling stations. 'Varia' corresponds to species with mass fractions <1 % of biomass. For location and depths of stations see Fig. 1
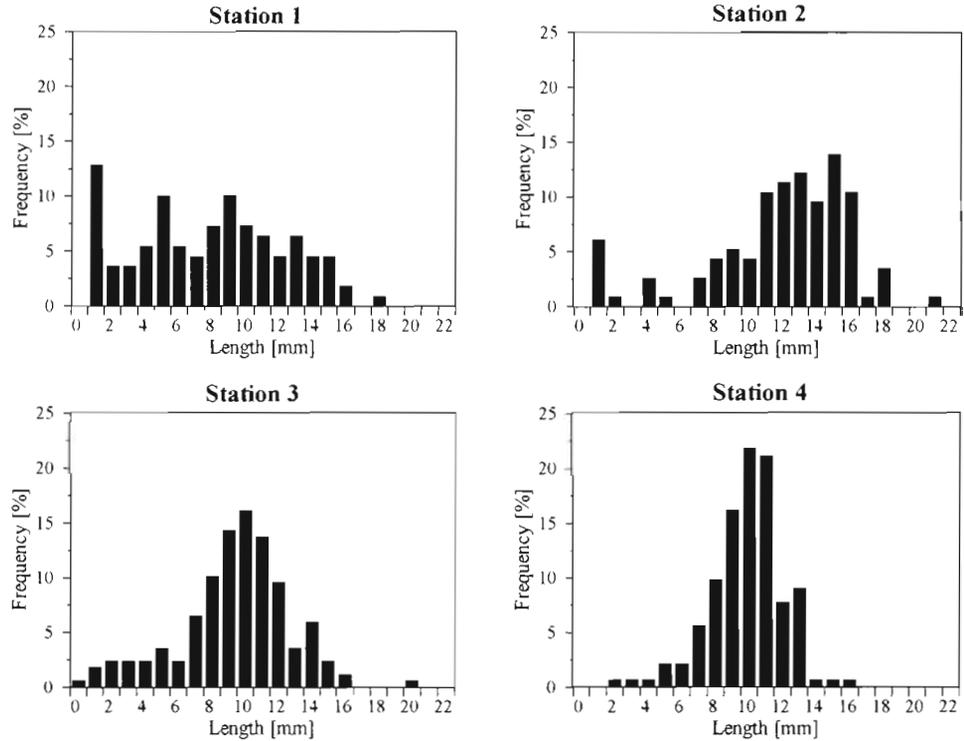
Fig. 3. *Macoma balthica*. Length-frequency distribution at the sampling stations. For location and depths of stations see Fig. 1

crease of total sulphur concentration c (sum of H_2S, $S_2O_3^{2-}$, S_8; Fig. 4). In order to determine the half-saturation time τ, the reciprocal value of the total sulphur concentration $1/c$ was plotted against the reciprocal value of the incubation time $1/t$ (Fig. 5) The corresponding linear equation is:

$$f(x) = 0.0257x + 0.0048 \qquad (12)$$

The intersection with the abscissa, or fitting Eq. (12) into Eq. (5), led to a half-saturation time τ of 5.4 h.

The average fresh mass of one clam without shell was $m = 188 \pm 75$ mg (n = 35). Placing this value in Eq. (4), together with the tissue water content $w = 0.84$ (Bordin et al. 1992) and the density of water $\rho \approx 1$ g cm^{-3}, gave the effective radius $r_e = 0.335$ cm. These data led to a diffusion coefficient for total sulphide for *Macoma balthica* from the Gulf of Gdańsk of $D = 1.9 \times 10^{-6}$ cm^2 s^{-1} (Eq. 3).

During sulphidic incubation ($c_0 = 200$ µM), sulphide tissue concentration of 41 nmol g^{-1} fm was found in *Macoma balthica* after 5 d (Fig 4). After subtraction of sulphide tissue concentrations of control animals (1 nmol g^{-1} fm) and taking into account the water content ($w = 0.84$), the internal equilibrium concentration
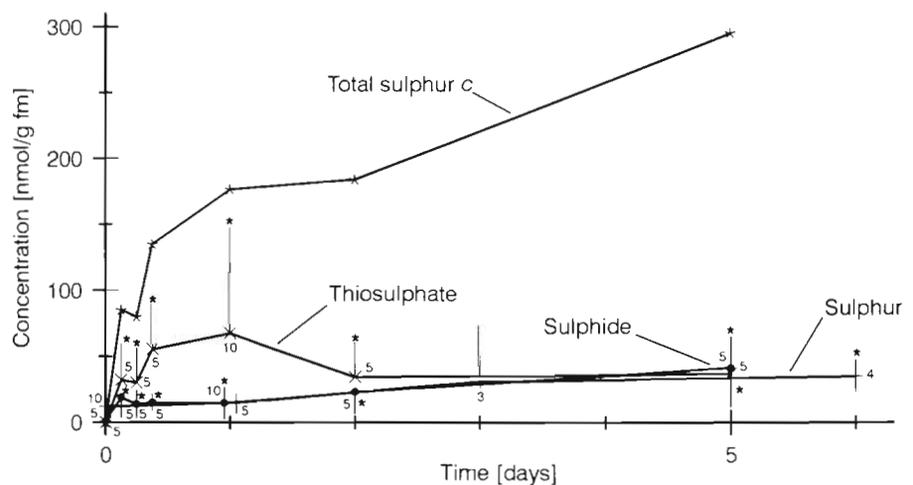

Fig. 4. *Macoma balthica* (Stns 1 and 3). Concentrations of sulphide, thiosulphate, elemental sulphur, and total sulphur c in the tissues after oxic incubation at 200 µM sulphide (10°C; 9‰ S). Total sulphur is the sum of sulphur species, taking account of stoichiometric ratios, minus control values. Data are given in nmol g^{-1} fresh mass $\pm$ SD (number of replicates). *Significant difference to control (p ≤ 0.05)

$1/c$ [nmol^{-1} g fm]

$$c(t) = \frac{c_0\, t}{\tau + t}$$

$$\Leftrightarrow \quad \frac{1}{c} = \frac{\tau}{c_0}\frac{1}{t} + \frac{1}{c_0}$$
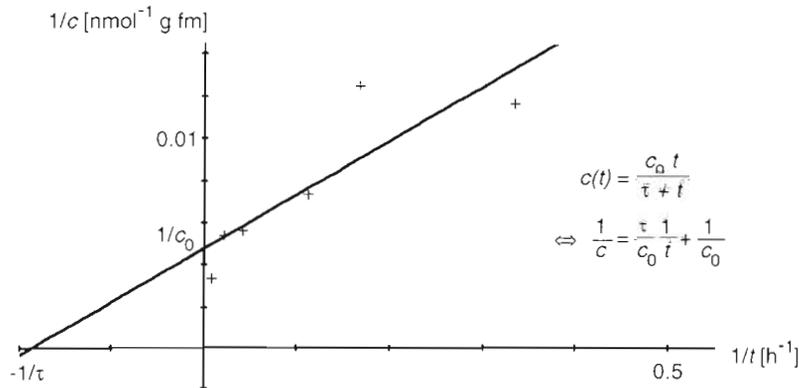
Fig. 5. *Macoma balthica* (Stns 1 and 3). Determination of half-saturation time by Lineweaver-Burk-Plot. Reciprocal total sulphur concentration $1/c$ after oxic incubation at 200 µM sulphide (10°C, 9‰ S) is plotted against reciprocal incubation time $1/t$. The intersection with the abscissa gives the reciprocal half-saturation time $-1/\tau$

was c_i = 48 µM. Therefore, the detoxification constant for *M. balthica* was calculated as $k = 7.3 \times 10^{-5}$ s^{-1} (Eq. 10).

In order to study the role of body size for sulphide detoxification, specimens of different size classes of *Macoma balthica* were incubated for 1 d under oxic-sulphidic conditions, and tissue concentrations of sulphide and thiosulphate were analysed. Sulphide concentrations of only 2 ± 2 nmol g^{-1} fm were measured in the tissues of large clams with shell lengths of more than 16 mm and fresh masses higher than 200 mg after the incubation (Fig. 6). Correspondingly, thiosulphate production in the tissues was also very low (14 ± 8 nmol g^{-1} fm). In contrast, in small specimens with shell lengths less than 12 mm and fresh masses lower than 100 mg, sulphide entered more quickly within the same amount of time, resulting in higher concentrations of sulphide (50 ± 27 nmol g^{-1} fm) and thiosulphate (463 ± 114 nmol g^{-1} fm) in the tissues. The size class with shell lengths between 12 and 16 mm showed intermediate values (sulphide: 31 ± 23 nmol g^{-1} fm; thiosulphate: 237 ± 119 nmol g^{-1} fm).
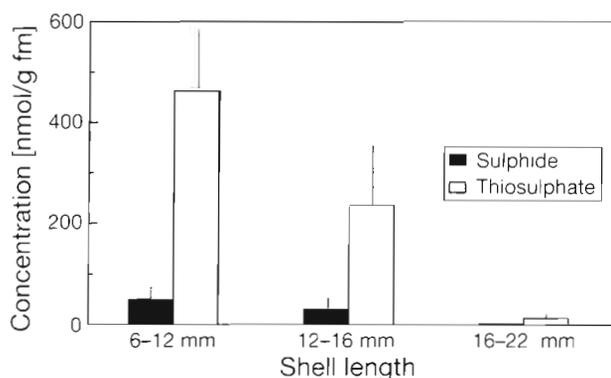

Fig. 6. *Macoma balthica* (Stns 1 and 3). Concentration of sulphide and thiosulphate in the tissues in small (6–12 mm shell length; n = 5), medium (12–16 mm shell length; n = 9), and large (16–22 mm shell length; n = 13) individuals after 1 d of oxic incubation at 200 µM sulphide (10°C, 9‰ S). Data are given in nmol g^{-1} fresh mass + SD

DISCUSSION

The Baltic clam *Macoma balthica* is the predominant species of macrofauna in the Gulf of Gdańsk (Żmudziński 1967, Okołotowicz 1985, Wiktor 1992, Janas & Szaniawska 1996, Włodarska-Kowalczuk et al. 1996). The clams live buried in the sediment, mostly at sediment depths of 3 to 8 cm (Reise 1981, Madsen & Jensen 1987). There, they can be exposed to high concentrations of hydrogen sulphide in the pore water. *M. balthica* show a distinct tolerance to oxygen deficiency (von Oertzen 1973, Dries & Theede 1974), and, particularly in populations from sulphidic habitats such as the Gulf of Gdańsk, a high tolerance to hydrogen sulphide as well (Jahn et al. 1993, Theede et al. 1995, 1996, Jahn 1997, Jahn & Theede 1997b). The results of our field study demonstrate the importance of *M. balthica* in the Gulf of Gdańsk, especially at the high sulphide contaminated sampling stations, Stns 3 and 4 (Figs. 1 & 2).

One of the most important protection mechanisms against penetrating hydrogen sulphide is oxidation to non-toxic compounds. By means of a siphon, *Macoma balthica* is able to pump water from above the sediment through its gills and extract oxygen from it. If oxygen is available, *M. balthica* produces high amounts of thiosulphate (Fig. 4), comparable to several other marine species (Vismann 1991a, Jahn et al. 1992, 1996, Oeschger & Vetter 1992, Völkel & Grieshaber 1992, Hagerman & Vismann 1993, Johns et al. 1997). However, the ratio between sulphide influx and sulphide detoxification in the tissues has not yet been analysed sufficiently (cf. Dubilier et al. 1995)

The rate of sulphide diffusion into the tissues is crucial for sulphide detoxification. Therefore, sulphide influx data were used for an estimation of the diffusion coefficient as well as the detoxification constant for total sulphide. The calculation used in this study takes into account not only sulphide diffusion through the body wall but also through all diffusion barriers inside the whole organism. Therefore, the value D is called
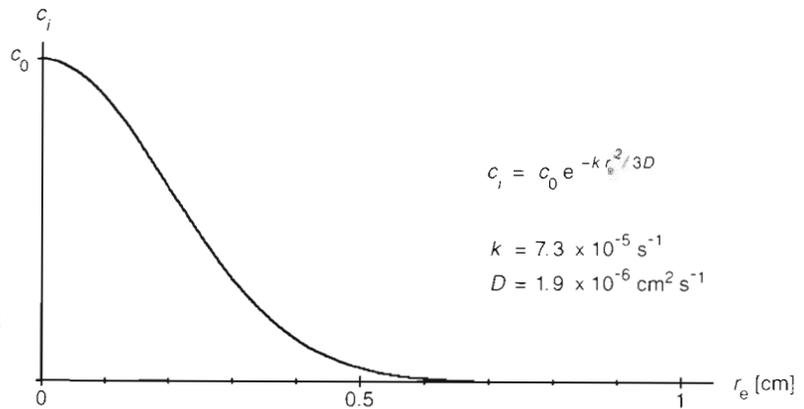
Fig. 7. *Macoma balthica*. Internal sulphide equilibrium concentration c_i plotted against the effective radius r_e of the clams. Data resulted from oxic incubation at 200 µM sulphide (10°C, 9‰ S). For further explanation see text. (From Jahn & Theede 1997a)

$$c_i = c_0 e^{-k r_e^2 / 3D}$$

$$k = 7.3 \times 10^{-5} \text{ s}^{-1}$$
$$D = 1.9 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$$

the 'apparent' diffusion coefficient (cf. 'apparent' Michaelis-Menten constant). This apparent coefficient has some advantages in comparison to direct measurements of diffusion into a specific tissue. Protection strategies like shell closure will result in a decrease of the apparent coefficient. Moreover, differences between internal and external pH are included by using total sulphide data (sum of S^{2-}, HS^-, and undissociated H_2S, which is considered as the primary diffusion species). Therefore, the apparent coefficient is an index for the sum of protection strategies like shell closure or reduction of the internal pH, which will result in a lower rate of sulphide influx (Groenendaal 1981, Völkel & Grieshaber 1992, Zimmermann & Jahn 1996). Elimination of penetrated sulphide by oxidation to thiosulphate, sulphite, and elemental sulphur are also included. Treating the animal's body as a sphere is appropriate because diffusion depends on surface area to volume ratio and a sphere is the geometrical body with the lowest area to volume ratio. Therefore, this calculation represents the most conservative case for the estimation of a maximum diffusion coefficient. However, the 'effective' radius of the theoretical sphere was calculated from the fresh mass of the animal, which is independent of its geometrical shape.

In comparison to diffusion coefficients for other species, the apparent diffusion coefficient for *Macoma balthica* of 1.9×10^{-6} cm^2 s^{-1} is significantly low. Julian & Arp (1992) found a sulphide permeability of 0.068 cm h^{-1} for the body wall of the echiuran worm *Urechis caupo*. Assuming a diffusion distance of 0.2 cm, this value leads to a diffusion coefficient of 3.8×10^{-6} cm^2 s^{-1} Powell (1989) assumed the diffusion coefficient of undissociated H_2S to be equal to that of oxygen in water ($D_{H_2S} \approx D_{O_2} \approx 5 \times 10^{-6}$ cm^2 s^{-1}). An even higher diffusion coefficient of 4×10^{-5} cm^2 s^{-1} was given by Völkel & Grieshaber (1992) for the body wall of the peanut worm *Sipunculus nudus*. However, these authors used a non-differential form of Fick's first law.

For the ostracod *Cyprideis torosa* an apparent diffusion coefficient of only 8.1×10^{-7} cm^2 s^{-1} was found (Jahn et al. 1996), which is even lower than the coefficient for *M. balthica*. Obviously, species with shells, like *M. balthica* and *C. torosa*, are able to reduce sulphide diffusion by temporary valve closure or reduction of valve opening. However, it has to be considered that behavioural changes will result in a change in the apparent diffusion coefficient, too. In our study, periods and degrees of shell opening and closure, for instance, were not measured. In addition, the influx of sulphide and hence the apparent diffusion coefficient also depends on convection by pumping of sulphidic water through the gills. Therefore, comparisons of the apparent diffusion coefficient of *M. balthica* with diffusion coefficients of other species are only possible in a limited sense.

The equilibrium between sulphide diffusion and detoxification results in a specific internal sulphide concentration within the tissues. In Fig. 7 this equilibrium concentration is plotted against the effective radius of *Macoma balthica* (Eq. 11). In spite of limitations in the determination of the apparent diffusion and detoxification constants (e.g. variable shell opening), the decisive role of body size for the internal equilibrium sulphide level is obvious. At large radii, the internal equilibrium concentration approaches 0. This implies that large animals are more easily able to detoxify penetrated sulphide at a given rate of diffusion and detoxification. With decreasing radius the internal sulphide equilibrium concentration approaches the external concentration. For example, a value of r_e lower than 0.23 cm results in $c_i > c_0/2$. As the ratio between effective radius and shell length in the clams is about 1:5, only those animals which are longer than 1 cm will be able to reduce internal sulphide to about 50%. In smaller specimens with lengths of only a few mm, internal sulphide concentration will approach external concentration. Then, effective sulphide detox-

ification will no longer be possible. Lower diffusion coefficients (e.g. resulting from longer shell closure periods) or higher detoxification constants (e.g resulting from stimulated metabolism) would shift the curve to the left but would reduce the internal sulphide concentration of small organisms (<1 mm) only slightly. Therefore, reducing sulphide diffusion or stimulating the detoxification metabolism seems to be an effective strategy only for larger individuals but not for small ones like larvae or meiofauna. For meiofauna this was also postulated by Powell (1989) and experimentally confirmed for the ostracod *Cyprideis torosa* (Jahn et al. 1996). In contrast to larger animals, small individuals do not seem to be able to detoxify hydrogen sulphide effectively enough but rather can only survive in sulphidic habitats due to their anaerobic capacity. In this matter, a qualitative difference between macro- and meiofauna, which are normally separated only by the quantitative feature of body size, can be seen.

The decisive role of body size for sulphide detoxification was also demonstrated experimentally for *Macoma balthica* (Fig 6). After oxic-sulphidic incubations, low sulphide and thiosulphate concentrations were found in large clams, whereas sulphide entered much more quickly into small specimens within the same amount of time, followed by higher thiosulphate production. Therefore, small specimens seem to be more easily negatively affected when environmental conditions become more sulphidic. High external sulphide concentration may then lead to the occurrence of older specimens in the population, which was confirmed by our observations in Gdańsk Bay (Fig. 3). Only at Stn 1, which had a low sulphide concentration in the sediment, was a substantial proportion of small clams found. A similar situation, avoidance of sulphidic sediments by smaller animals, was also shown for polychaetes (Jørgensen 1980), especially for *Neanthes (Nereis) succinea* and *Neanthes (Nereis) virens* (Miron & Kristensen 1993). The additional decrease of larger or older animals of *M. balthica* at the sulphidic Stns 3 and 4 may be correlated with higher parasite infection (Wenne & Klusek 1985). It is known that infection rate by the trematode *Parvatrema affinis* increases with increasing shell length of *M. balthica* (Lauckner 1983).

In conclusion, at least adult specimens of *Macoma balthica* are able to detoxify penetrated sulphide by oxidation to thiosulphate. However, efficient sulphide detoxification seems impossible if the body size falls below a certain size threshold. Thus, young animals and especially larvae may be affected by hydrogen sulphide. Therefore, hydrogen sulphide could lead to population structures with an excessive proportion of older individuals and has to be considered as an important factor for colonisation of new habitats.

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