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Behavioural response of three nereid polychaetes to injection of sulfide inside burrows

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ABSTRACT: The behavioural response (ventilation rate, duration of ventilation bursts, length of pauses between ventilation bursts) of 3 closely related nereid polychaetes (*Nereis virens*, *N. diversicolor* and *N. succinea*) to various levels of sulfide exposure was investigated during spring and summer of 1992. The response to HS^- was species specific. *N. virens* reacted strongly to HS^- by increasing the duration of ventilation bursts. Duration of rest periods was affected less severely while ventilation failed to show any significant variation. The behavioural response of *N. diversicolor* did not show much variation under HS^- exposure. The only significant response was a decreased duration of rest periods at high HS^- concentration. The type of reaction displayed by *N. succinea* was similar to the response of *N. virens*, although less pronounced. *N. diversicolor* removed most HS^- from the burrow in less than 10 min due to the generally high ventilation rate of this species. The slow removal of HS^- by the other 2 species is caused by a slower response and lower ventilation rate. The shape of the HS^- efflux curve indicated that changes in the response during exposure are important in *N. virens* and substantiate a possible toxic effect of HS^-. *N. diversicolor* displayed the fastest recuperation following HS^- exposure (restored ventilation behaviour). For all species, time of recuperation increased with increasing sulfide concentration.

INTRODUCTION

Organic-rich coastal environments are prone to develop hypoxia because of high O_2 demand (Jørgensen 1983, Llanso 1991). Coastal sediments usually contain free O_2 in the upper few mm but they may occasionally be anoxic to the surface with the presence of free sulfide and growth of *Beggiatoa* spp. at the sediment-water interface (Ross 1989, Hall et al. 1990). The survival of benthic invertebrates in hypoxia or anoxia is usually on the order of days to weeks (Theede et al. 1969). Survival under extreme conditions may be extended through behavioural responses which mask the critical limits for tissue responses (Theede et al. 1969). In several marine invertebrates, oxygen uptake is maintained by regulating ventilation rates or the fractional extraction of oxygen (Bayne 1967, 1971, Dales et al. 1970, Kristensen 1983a). Survival is usually considerably reduced by the presence of high concentrations of hydrogen sulfide (HS^-) in the environment (Swanson & Sindermann 1979, Jørgensen 1980, Llanso 1991). Sulfide is known to be toxic to aerobic organisms at low concentrations, often causing the inhibition of metalloenzymes, cytochrome oxydase and blood pigments (Evans 1967). Physiological and biochemical adaptations may improve tolerance and survival in the presence of HS^- (Warren 1984), and studies have shown that *Nereis diversicolor* is capable of active HS^- detoxification (Vismann 1990).

Nereid polychaetes commonly live in the intertidal zone of estuarine and brackish waters, normally in sediments of medium to high organic content (Muus 1967, Kristensen 1988, Miron & Kristensen 1993). Sediment-dwellers, like nereids, face the risk of exposure to sulfide in sediment pore waters, particularly at low tide and when individuals establish new burrows or move within the sediment (Vismann 1991). Physiological tolerance to sulfidic environments is probably important for the spatial distribution of polychaetes. Theede et al. (1973) suggested that ecological differences between

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habitats may result from variations in the tolerance of animals to severe hypoxia or anoxia. In a study on the distribution of 3 closely related nereid species, Miron & Kristensen (1993) showed a high species-specific correlation with pore water HS^-, which probably acted as a controlling factor. The density of *Nereis virens* decreased dramatically with increasing concentration of pore water HS^-. In contrast, *N. diversicolor* and particularly *N. succinea* were more abundant in sulfide-rich sediments. From their study, the latter species also showed higher tolerance toward sulfidic sediments in tank experiments.

The purpose of this study was to investigate the behavioural response (ventilation) of 3 closely related nereid polychaetes, under various levels of sulfide exposure. This should permit better definition of the physiological niches (Spotila et al. 1989) of these species and improve our understanding of nereid distributions in organic-rich estuarine habitats.

MATERIALS AND METHODS

Collection site and handling. *Nereis virens* and *N. succinea* were collected in Kerteminde Fjord/Kertinge Nor (Denmark) in March (Stns 3 & 4 of Miron & Kristensen 1993) and June (Stns 26 & 27) 1992. Individuals of *N. diversicolor* were collected in April 1992 near Kærby Fed in Odense Fjord (Denmark). Only undamaged worms were used. Individuals used in experiments had a mean fresh towel-dried weight of 0.65 ± 0.03 g.

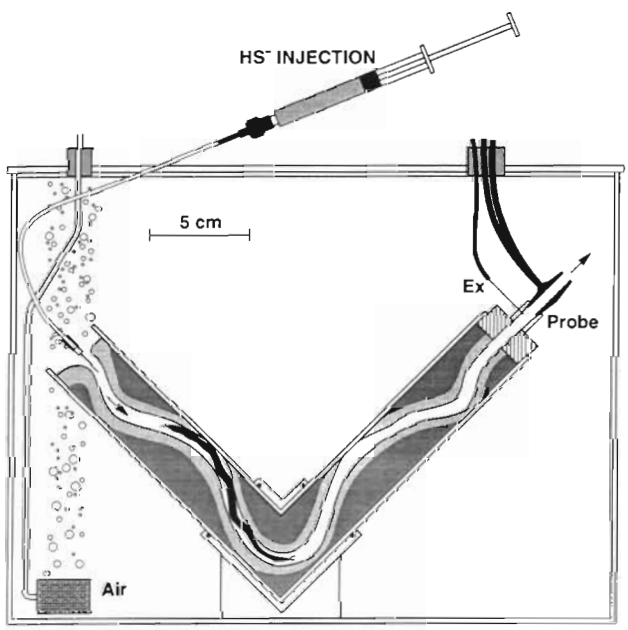

Fig. 1. Experimental set-up for measurement of ventilation currents and excurrent water sampling

For each species, sediment cores (i.d. 3.2 cm) were filled with sieved sediments (1 mm mesh sieve) and assembled using 90° waterpipe fittings to produce experimental V-cores (Fig. 1) (Kristensen et al. 1991). Six V-cores were assembled and placed in a 12 l aerated and darkened aquarium filled with seawater from the collection locality. Seawater was renewed every 2 d for the entire experimental period. The sediment used in the experiments consisted of low-organic (less than 1% particulate organic carbon) well-sorted sand, collected at Fyns Hoved (Denmark). The cores were left for 1 wk to allow the sediment to stabilize before worms were added to cores. After introduction (1 ind. per core), the individuals rapidly dug themselves into the sediment and made burrows from one end of the V-core to the other. The cores were left for 1 wk to allow worms to acclimate to the experimental conditions (15 °C and 20‰).

Ventilation measurements. Ventilation was determined with an electromagnetic flowmeter (Gould SP2202 Blood Flowmeter) equipped with a 2 mm i.d. flowprobe and recorded by a Phillips PM8220 Dual-Pen recorder (Kristensen 1989). A 2 cm polyethylene tube connected the worm burrow to the flowprobe through a single-hole rubber stopper (Fig. 1). The stopper was inserted into one arm of the V-core ('tail end') until it approached the sediment surface such that the tube was continuous with and acted as an extension of the burrow. The flowprobe was calibrated by timed volumetric flow through the probe.

When individuals ventilate their burrows by undulatory movements of the body, they produce a tailward flow of water. Ventilation, presented as ventilation rate (ml min^{-1}), was measured as mean steady flow rate during periods of active ventilation and extrapolated to 1 g wet wt standard worm size (Kristensen 1983b, 1989). During ventilation bursts, the water flow was integrated and averaged. Duration of ventilation bursts (min) and rest periods were timed (measured directly on traces) (Fig. 2). These parameters constituted the behavioural responses of individuals. Data were monitored continuously before sulfide injections, at the time of injections (HS^- exposure) and when the ventilation cycle returned to 'normal' after injection (i.e. ventilation pattern similar to patterns observed before injections) within a period of about 3 h. A total of 24 traces were analysed per species. The mean for each experimental ventilation burst group (e.g. group of bursts before injection, group of bursts under HS^- exposure, and group of bursts in post-injection non-sulfide exposure) was calculated (n = 3 to 5 ventilation bursts per group). The mean durations for the other responses were calculated as for the ventilation rate.

Sulfide injections and excurrent water sampling. Sulfide injections were made using a 1 ml syringe with

the needle just inside the 'head end' burrow opening (Fig. 1). Injections were made at the beginning of an active ventilation burst, 1 h after the start of ventilation monitoring. This period of time was chosen to ensure worm acclimation after handling the V-cores and to have traces of ventilation behaviour under non-sulfide exposure. A volume of 0.4 to 1.0 ml sulfide solution was slowly injected into the 'head end' of the burrow. The volume injected was dependent on the worm reaction, i.e. injections were interrupted when worms ceased all ventilation activity (sulfide cannot enter the burrow without any incurrent water flow). Sulfide solutions were prepared every day by the addition of pH-adjusted Na_2S stock solution (100 mM) to deoxygenated seawater. Concentration of the stock solution was occasionally measured with the methylene blue technique of Cline (1969). Eight different concentration levels were used (approximate concentrations: 5.0, 2.0, 1.0, 0.50, 0.25, 0.10, 0.05 and 0.03 mM). All concentrations injected were measured by the Cline method. The concentrations used in this experiment are within the environmental range (0 to 3 mM) to which nereids may be exposed in Danish estuaries (Fenchel & Riedl 1970, Miron & Kristensen 1993).

For each injected concentration, the 3 most 'successful' cores [i.e. cores with typical U-shape burrows (Reise 1981, Hertweck 1986, Miron et al. 1991) and burrow openings in both ends of the V-cores] were chosen from the pool of 6 V-cores and used for ventilation measurements. These 'successful' cores allowed us to use the flow probe and permitted us to discriminate and measure both incurrent and excurrent water flows. This is not possible if both ends of the burrow are on one side of the core, or if one burrow opening is closed. Individuals exposed to HS^- were replaced. Another set of 3 'successful' V-cores were chosen for the next concentration. Behavioural responses (means) under non-HS^- and HS^- exposures were compared with a *t*-test for each sulfide concentration. Probability intervals are indicated, throughout the text and figures, by $^{\bullet}(0.05 \geq p > 0.01)$, $^{\bullet\bullet}(0.01 \geq p > 0.001)$ and $^{\bullet\bullet\bullet}(0.001 \geq p)$.

Excurrent water samples (0.3 to 1 ml) were taken by syringe from the connecting tube before the flowprobe at the 'tail end' of the V-core. Syringes were previously filled with 0.1 ml of 5% ZnAc to precipitate sulfide (ZnS) in the water samples. Sampling just before the flowprobe, when the ventilation record showed positive flow, ensured that only excurrent water was extracted. Samples were transferred to scintillation vials and subsequently analysed by the Cline method. The term 'sulfide' is here used synonymously for all species of dissolved, reduced inorganic sulfur (H_2S, HS^- and S^{2-}).

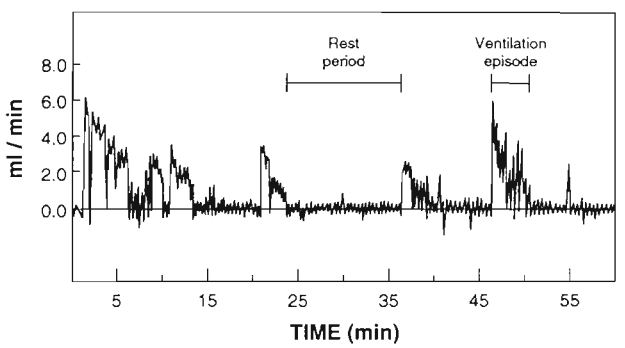

Fig. 2. *Nereis virens*. An example of the ventilation pattern under non-sulfide exposure (60 min) preceding sulfide injection. Duration of record for each experiment is about 3 h

RESULTS

Ventilation pattern

Ventilation patterns under non-sulfide exposure differed from one species to another (Table 1). *Nereis virens* had the lowest ventilation rate and the lowest ventilation frequency (i.e. longest duration and pause between ventilation bursts) of the 3 species. The ventilation rate of *N. diversicolor* was more than 3 times higher than for *N. virens*. Duration of ventilation for *N. diversicolor* was not significantly lower than for *N. virens*, but rest periods between ventilations were less than half (ca 45%). *N. succinea* had intermediate ventilation rates, the shortest duration of ventilation and intermediate length of pauses relative to the other 2 nereids. Variability in the data was always lowest for *N. virens*.

On average, *Nereis virens* used 4 ventilation bursts (5.8 min each) h^{-1} to pump 75 ml of water g^{-1} wet wt worm through burrows. In the same time period, *N. diversicolor* used 7 ventilation bursts (4.8 min each) to pump 366 ml while *N. succinea* needed 8 ventilation bursts (2.9 min each) to pump 112 ml.

Table 1. *Nereis* spp. Ventilation pattern (average) under normal (non-sulfide) conditions. Ventilation rates are presented for a 0.65 g wet wt worm. Results presented as means ± SD

Species	Ventilation rate (ml min^{-1})	Duration of ventilation (min)	Pause between ventilations (min)
Nereis virens	2.1 ± 0.1	5.8 ± 0.3	10.5 ± 0.6
N. diversicolor	7.1 ± 3.2	4.8 ± 1.3	4.6 ± 1.7
N. succinea	3.1 ± 0.7	2.9 ± 0.8	6.1 ± 2.9

Table 2. *Nereis* spp. Total amount of HS^- injected ('Inject') into burrows and the integrated flux of HS^- out of burrows (recovery, 'Rec.') during ventilation periods after injection. Max C_{ex}: highest concentration of HS^- in excurrent water during the first ventilation period. Results presented as means ± SD (n = 3)

N. virens			*N. diversicolor*			*N. succinea*		
Inject (µmol)	Rec. (µmol)	Max C_{ex} (µM)	Inject (µmol)	Rec. (µmol)	Max C_{ex} (µM)	Inject (µmol)	Rec. (µmol)	Max C_{ex} (µM)
5.93 ± 0.75	2.45	70 ± 6	5.18 ± 0.54	2.25	68 ± 5	–	–	–
2.02 ± 0.37	2.25	49 ± 6	2.03 ± 0.73	0.96	58 ± 9	2.43 ± 0.40	2.28	90 ± 45
1.10 ± 0.13	1.02	30 ± 5	1.23 ± 0.43	0.27	16	1.58 ± 0.22	0.73	11 ± 06
0.40 ± 0.00	0.19	12 ± 2	0.60 ± 0.17	0.21	5 ± 0	0.66 ± 0.12	0.75	17 ± 06
0.24 ± 0.07	–	–	0.34 ± 0.05	0.25	4 ± 2	0.24 ± 0.01	0.24	8 ± 02
0.14 ± 0.01	0.08	3 ± 1	0.10 ± 0.02	0.17	3 ± 2	0.10 ± 0.00	0.12	3 ± 01
0.05 ± 0.00	0.04	4 ± 1	0.05 ± 0.01	0.13	1 ± 1	0.03 ± 0.01	0.16	3 ± 01
0.03 ± 0.00	0.03	3 ± 1	0.03 ± 0.06	0.11	1 ± 0	0.02 ± 0.01	0.06	2 ± 00

Sulfide injections

Table 2 shows the amount of sulfide injected ('Inject') inside the V-cores at each concentration level, the integrated amount of HS^- recovered ('Rec.') in the excurrent water (estimated as integrated mass of HS^- in excurrent water during ventilation after injection), and the highest excurrent concentration of HS^- measured at each treatment. The injected sulfide was not the concentration the worms experienced. The correct physiological HS^- concentration is the resulting HS^- concentration in the burrow, best estimated as recovered concentration (determined from the excurrent concentration of HS^-). To study the behavioural responses of nereid species to sulfide, recovered concentrations were used and equal concentrations regrouped into 5 concentration classes (2.0, 1.0, 0.2, 0.1 and 0.05 mM). An interesting result in Table 2 is that at > 1 mM sulfide injected, the recovery for *Nereis diversicolor* was less than 50%.

Ventilation response under sulfide exposure

The ventilation response of the 3 species of *Nereis* to the variable amount of recovered sulfide appeared to be species specific (Fig. 3). *N. virens* reacted to HS^-, at concentration down to 0.10 mM, mainly by increased duration of ventilation periods. Ventilation rates failed to show any significant variation, while the influence of HS^- on the duration of rest periods was less severe than on duration of ventilation bursts. The direction of response was not consistent for the duration of rest periods. Duration changed from positive at low concentrations (0.1 to 1 mM) to negative at high concentration (2 mM). For both duration of ventilation and rest periods, the level of significance increased with increasing recovered sulfide concentrations.

No major response to sulfide exposure was observed for *Nereis diversicolor*. Only the length of rest periods was affected significantly at 2 mM. Results, however, showed that *N. diversicolor* had a tendency to decrease duration of rest periods at all concentrations.

The type of behavioural reaction observed for *Nereis succinea* was similar to that of *N. virens*. No significant sulfide effect was observed on the ventilation rate of this species. Duration of ventilation bursts, on the other hand, increased significantly down to concentration of 0.10 mM, but less dramatically than for *N. virens*. The length of rest periods showed only a significant variation at 1 mM.

The time elapsed from injection until the return of a non-sulfide, 'pre-injection' ventilation cycle (Table 3) varied with sulfide concentration for all nereid species (*Nereis virens* $F_{(7,16)} = 22.73^{***}$; *N. diversicolor* $F_{(7,16)} = 74.29^{***}$; *N. succinea* $F_{(6,9)} = 5.34^{*}$). A Tukey multiple comparison procedure (Table 3) showed that time increased with increasing concentration. For a given HS^- concentration, 'normal' ventilation behaviour, particularly at high concentrations, was restored earlier in *N. diversicolor* than in both *N. virens* and *N. succinea*.

Sulfide discharge from burrows

The temporal pattern of excurrent sulfide concentration following injection was different for the 3 nereid species (Fig. 4). The time response in Fig. 4 represents more than 1 ventilation period; the HS^- concentrations shown are averaged over 2 min time periods when worms ventilate. Thus, the figure represents a time course of excurrent concentrations in about 3 successive ventilation bursts and not the excurrent HS^- concentration during 1 ventilation burst. Data for the 3 highest recovered HS^- concentrations are shown and no discrimination between ventilation and rest periods

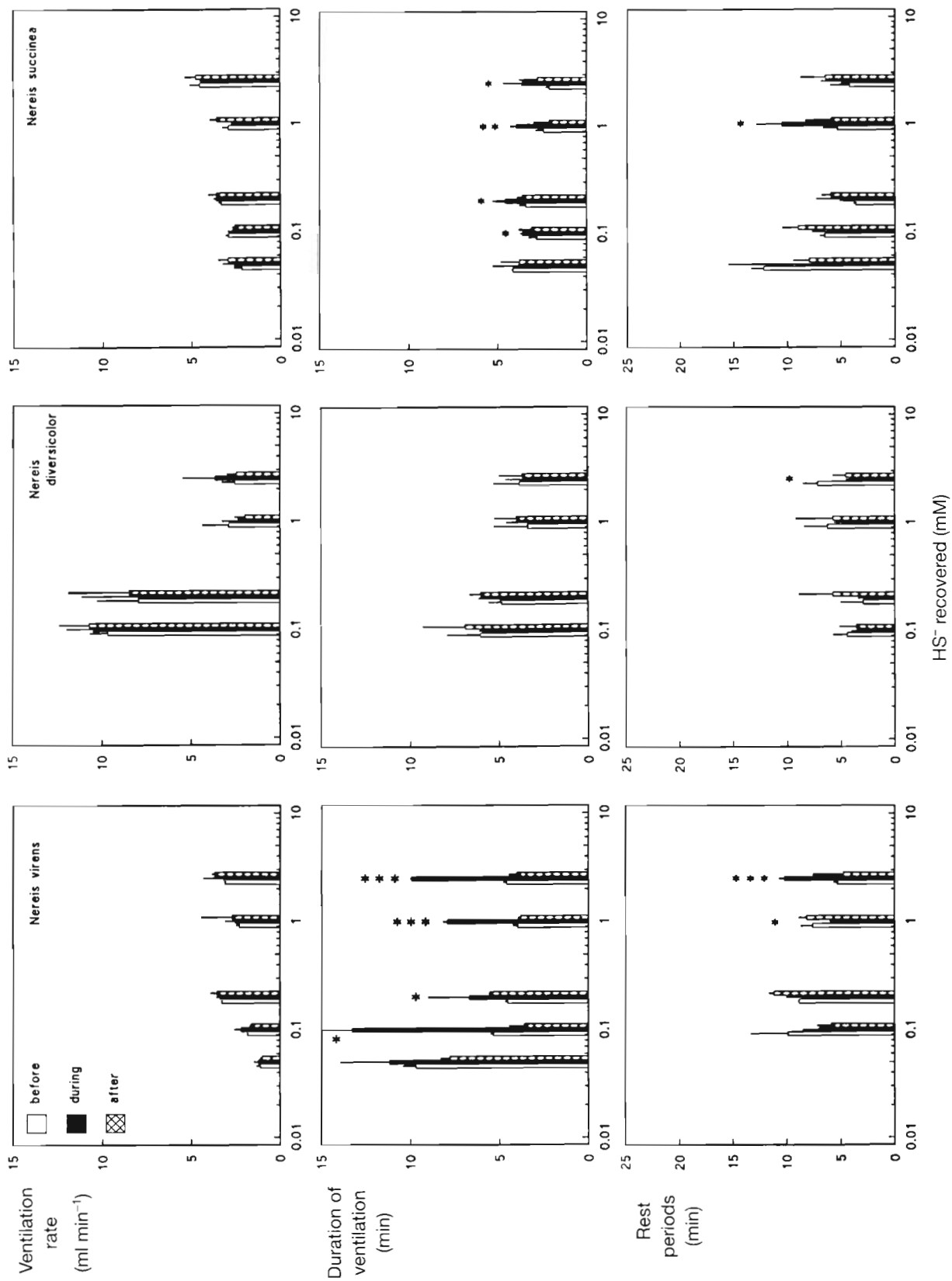

Fig. 3. *Nereis* spp. Ventilation response [ventilation rate (upper panels), duration of ventilation periods (middle) and duration of rest periods (lower)] to variable levels of sulfide recovered. Results are presented as means + SD of measurements (n = 9 to 15 ventilation bursts recorded from 3 individuals). Open bars: results obtained before injection of sulfide; solid bars: data obtained during sulfide exposure; cross-hatched bars: post-injection results after the worms returned to 'pre-injection' behaviour. Asterisks over solid bars indicate that a significant response ($^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$) occurred during sulfide exposure relative to the pre-injection situation

Table 3. *Nereis* spp. Means ± SD of time elapsed between injection and the return to normal ('pre-injection') ventilation cycles. Results (indicated by expt no.) sharing an underline are not significantly different

Expt no.	Approx. conc. injected (mM)	*N. virens* (min)	*N. diversicolor* (min)	*N. succinea* (min)
1	0.03	–	–	15.75 ± 22.27
2	0.05	10.67 ± 9.24	–	39.75 ± 10.96
3	0.10	20.00 ± 4.50	–	38.50 ± 4.95
4	0.25	10.67 ± 9.24	16.00 ± 6.00	18.50 ± 26.16
5	0.50	13.00 ± 11.26	11.50 ± 0.00	54.00 ± 0.00
6	1.00	29.50 ± 9.33	19.38 ± 1.63	>60
7	2.00	42.50 ± 2.75	29.00 ± 9.75	>60
8	5.00	>60	>60	–

Tukey multiple comparison test:

	Expt no.			
N. virens	1 2 4 5	3 6	7	8
N. diversicolor	1 2 3	5 4 6	7	8
N. succinea	1 4	3 2	6 7	

has been made. An initial increase in HS^- concentration was usually observed after 1 to 5 min, corresponding to the time for the front of a HS^- pulse to pass through burrows. The maximum concentration, which was proportional to the injected concentration of HS^- (Table 2), represents the core of the HS^- pulse. Subsequently, the concentration of sulfide decreased due to dilution. For *Nereis virens*, the maximum con-

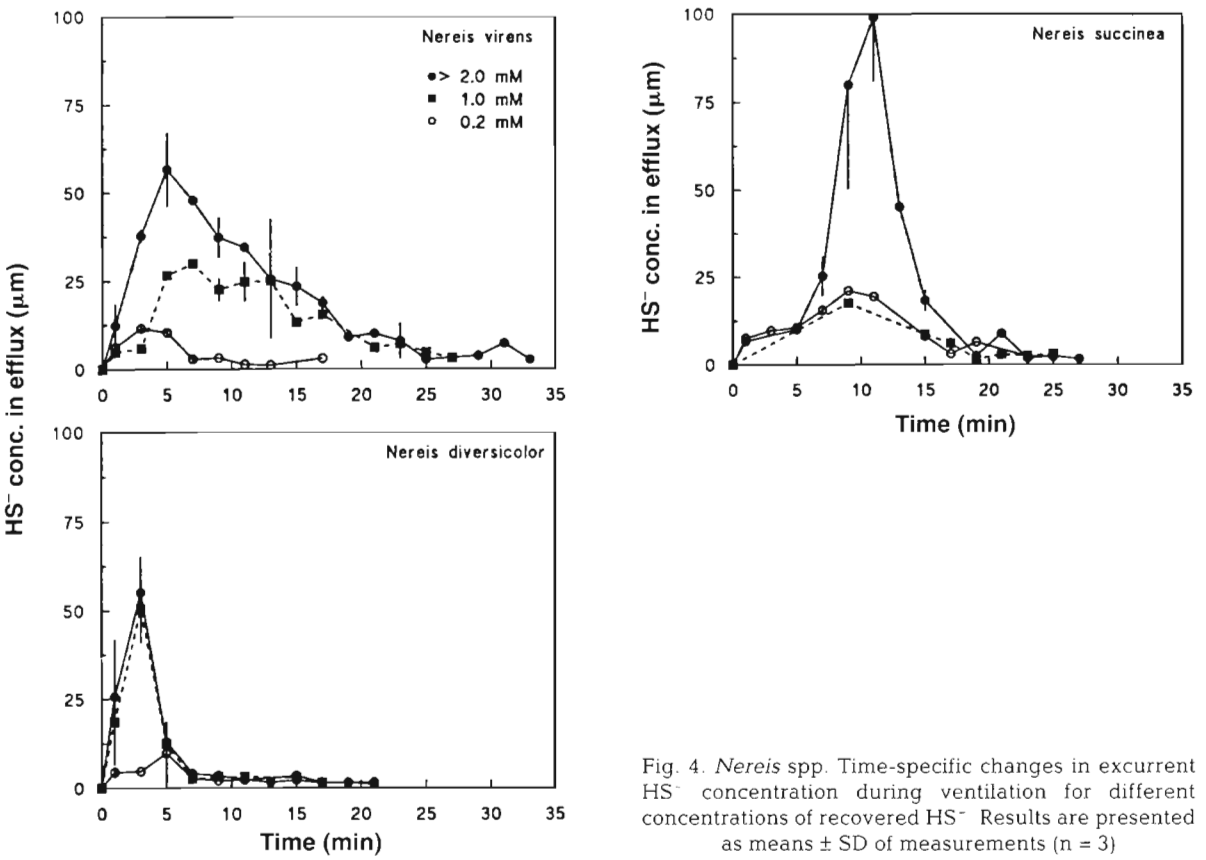

Fig. 4. *Nereis* spp. Time-specific changes in excurrent HS^- concentration during ventilation for different concentrations of recovered HS^- Results are presented as means ± SD of measurements (n = 3)

centration peak was right-sided (peak near the 5 min mark). After 15 to 20 min the HS^- concentration was still above 10% of the maximum concentration. The maximum HS^- concentration for *N. diversicolor* was also right-sided (peak around the 3 min mark), but most sulfide was removed from the burrow in less than 10 min. The shape of the HS^- efflux curve was closer to a normal distribution shape for *N. succinea* than for the other 2 species. A maximum HS^- concentration peak was observed after 10 min, but only 10 min later most HS^- was removed.

DISCUSSION

The ventilation pattern found here for the 3 species, *Nereis virens*, *N. diversicolor*, and *N. succinea*, under 'pre-injection' conditions confirmed the results of Kristensen (1981, 1983a). *N. virens* displayed the longest ventilation periods and the lowest ventilation rate of the 3 species. Ventilation rates of *N. diversicolor* were more than 2 times higher than those of *N. virens* and *N. succinea*. The discrepancy between the ventilation patterns obtained during sulfide exposure in this study and those observed by Kristensen (1983a) during hypoxia probably illustrated toxic effects of HS^-, particularly at high concentrations. Toxicity to sulfide results from the blockage of the respiratory electron transport chain (Torrans & Clemens 1982) which in turn inhibits key enzymes (Evans 1967). The pronounced right-sided tail of the HS^- efflux curve especially for *N. virens* (Fig. 4) indicates a change in response during HS^- exposure and substantiates a toxic effect (shape of the curve would have been closer to a Gaussian distribution curve if worm had failed to show any behavioural response).

Nereis virens appears to be the least tolerant species to sulfide exposure. Duration of rest periods and ventilation were severely affected. The reaction of *N. virens* to sulfide illustrated an increasing stress with increasing concentrations. Longer periods of inactivity (rest periods) for *N. virens* (as well as for *N. succinea*) could, however, be directly related to the increased duration of ventilation with increasing HS^- concentration (recuperation from enhanced physical effort). The absence of behavioural response displayed by *N. diversicolor* might illustrate that this species is least sensitive to sulfide and probably better equipped for sulfide detoxification. Moreover, results from Table 3 also illustrate that the duration of recuperation following HS^- exposure (restored ventilation cycle), which increased with increasing concentration, was shorter for *N. diversicolor* than for *N. virens*. These trends substantiate results from Vismann (1990) which showed that *N. diversicolor* is more tolerant to sulfide than *N. virens*. Responses for *N. succinea* were intermediate between the other 2 nereids. The constant ventilating rate of this species when active (i.e. shape of HS^- efflux curve, close to a normal distribution curve shape, fails to show any acute toxic effect) may indicate that this species is capable of avoiding toxic effects by means of other (physiological) mechanisms.

The inhibitory effects of sulfide on respiration are reversible once sulfide dissipates or is chemically oxidized (Evans 1967). Results from the present study indicate that sulfide is most probably removed from the burrow environment by ventilation processes. An interspecific comparison also indicates that the sulfide response and thus the temporal pattern of removal differ from one species to another. *Nereis* spp. seem to remove sulfide by flushing the burrow. *N. virens* and *N. succinea* react by increasing their ventilatory response to increasing sulfide exposure. The high ventilation capacity of *N. diversicolor* (2 to 3 times higher than the other 2 species), both with and without the presence of sulfide, causes a faster removal rate and could explain the absence of behavioural response. The ventilation response of nereids to sulfide exposure could be considered as a behavioural adaptation to extreme environmental conditions. The importance of this behavioural mechanism is, however, still unknown and has to be compared with other physiological means in future work.

Studies of marine soft-bottom communities have generally revealed that environmental factors are largely responsible for the large-scale distribution of benthic infauna (Fitzhugh 1984, Miron & Desrosiers 1990) while biological interactions, under a variety of forms, usually explain most of the small-scale spatial arrangements (Woodin 1974, Kristensen 1988, Miron 1991). Too little attention has been given to abiotic influences and physiological tolerances on patterns of habitat segregation, especially among closely related species (Dunson & Travis 1991). The field and experimental studies of Miron & Kristensen (1993) suggested that habitat segregation among 3 closely related nereid polychaetes in the same area (an organic-rich estuarine habitat) was in part due to pore water sulfide. The present study suggests that ventilation could be an important mechanism in the adaptation of nereid polychaetes to sulfidic environments. The poor ventilation capacities of *Nereis virens*, combined with low sulfide detoxification capacity (Vismann 1990), may explain the general absence (or low density) of this species in sulfide-rich environments. Those *N. virens* that are usually found in sulfidic sediment are large individuals. The large body-size could increase the survival of *N. virens* in these environments (Miron & Kristensen 1993) since ventilation is proportional to body weight (Kristensen 1983b).

N. diversicolor may benefit from its high ventilation rate which increases its general tolerance toward extreme environmental conditions (see tank experiments in Miron & Kristensen 1993). However, high interspecific competition with other species in Danish estuaries (Kristensen 1988, Miron & Kristensen 1993) does not allow *N. diversicolor* to colonize sulfidic environments inhabited by *N. succinea*. Results from this study do not reveal a ventilation capacity allowing *N. succinea* to colonize sulfidic habitats. The presence of *N. succinea* in mussel beds (Muus 1967, Miron & Kristensen 1993) could, as discussed by Gray (1979), be a consequence of life history strategy (feeding) rather than resistance to sulfide. Studies on sulfide detoxification (physiology) are needed to confirm a sulfide adaptation by *N. succinea*.

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