

Factors influencing the distribution of nereid polychaetes: the sulfide aspect

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ABSTRACT: A study of the spatial distribution of 3 species of nereid polychaetes (*Nereis virens*, *N. diversicolor* and *N. succinea*) was conducted during fall 1991 in Danish estuarine waters. Results from field data (Kerteminde Fjord/Kertinge Nor and Norsminde Fjord) suggested that pore water sulfide (HS^-) acts on the distribution of these species. *N. virens* was confined to low-sulfidic areas ($< 50 \mu\text{M}$) while *N. succinea* was found in high-sulfidic sediments (from 50 to 2000 μM). *N. diversicolor*, on the other hand, showed a broader distribution with respect to pore water sulfide. Complementary tank experiments indicated that all 3 species preferred non-sulfidic sediments in allopatry, whereas *N. diversicolor* was excluded from the non-sulfidic compartment of tanks in sympatry with each of the other 2 species. Mortality rates indicated that *N. virens* was the least sulfide-tolerant species whereas the other species showed some sort of adaptation with respect to pore water sulfide. Tank experiments and coexistence coefficients from field data indicated that interspecific competition is an important determinant of nereid distribution patterns, particularly for populations of *N. diversicolor*. Field data and results from laboratory tank experiments suggest that *N. succinea* is closely associated with mussel beds.

INTRODUCTION

Studies of marine soft-bottom communities have generally revealed that environmental factors are to a great extent responsible for the large-scale distribution of benthic infauna (Fitzhugh 1984, Hylleberg & Nateewathana 1984, Miron & Desrosiers 1990) while biological interactions, in a variety of forms, usually explain most of the small-scale spatial arrangements (Woodin 1974, Davey & George 1986, Kristensen 1988, Miron et al. 1991a). 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). In this respect, the notion of physiological niche (Spotila et al. 1989) becomes important in explaining the spatial arrangement of species.

Nereid polychaetes commonly live in the intertidal zone of estuarine and brackish waters, normally in sediments of medium to high organic content (Muus 1967). Organically enriched environments are prone to

develop hypoxia and anoxia because of their high O_2 demand (Llanso 1991). The activity of heterotrophic organisms maintains reducing conditions below a thin oxidized surface layer in most coastal sediments (Revsbech & Jørgensen 1986). This stratification provides the basis for bacterial sulfate reduction in the deeper anoxic sediment where sulfate is reduced to toxic sulfide (Jørgensen 1977, Revsbech & Jørgensen 1986, Sampou & Oviatt 1991). Sulfide, the toxicity of which results from inhibition of the electron transport chain in aerobic respiration (Torrans & Clemens 1982), may be important for the distribution (Fenchel 1969) and density variations (Powell et al. 1983) of benthic organisms.

Many studies have examined the tolerance (or resistance) of soft-bottom infauna in relation to sulfide or low O_2 availability (Theede et al. 1969, Swanson & Sinderman 1979, Jørgensen 1980, Degn & Kristensen 1981, Stachowitsch 1984, Jensen 1986, Llanso 1991). However, there is little work on the direct role of sulfide in the distribution patterns or population dynamics of benthic animals. Recently, Vismann (1990) showed that different capacities of HS^- detoxification could explain the distribution of the nereids *Nereis virens* and *N. diversicolor* in the same area.

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The purpose of this study was to investigate the distribution of 3 common species of nereid polychaetes (*Nereis virens*, *N. diversicolor* and *N. succinea*) in relation to pore water sulfide concentration. The effect of sulfide on the distribution pattern of nereid polychaetes is evaluated in terms of interspecific interactions among the 3 species.

MATERIALS AND METHODS

Field study. Study site: The study was carried out in the Kerteminde Fjord/Kertinge Nor system (8.61 km²), a shallow mesohaline estuary situated 10 km east of Odense, on the island of Funen (Fyn), Denmark (Fig. 1). The system is about 7 km long and its width varies from 0.3 to 3 km. The mean water depth is 4 m in the fjord and 2.5 m in the nor. A maximum depth of 8 m is found in a trough in the middle of the fjord. Water temperature varies between -1°C in winter to 20°C in summer (Funen County Council 1991). A small salinity gradient is observed from the southwestern part of the nor (17.7 ‰) to the mouth of the fjord in the

east (20.0 ‰). The gradient is, however, dependent on winds and rainfalls and should play a minor role with respect to the distribution of the nereid species. The water mass of the system, which is affected only by limited freshwater runoff and/or discharges, is exchanged by tides with saline (21 to 24 ‰) water from the Store Bælt entering the fjord through a narrow inlet (60 m). Residence time of water is around 1.5 yr in the nor and 2 to 3 d in the fjord (Fyns Amt 1992). Maximum tidal amplitude is 0.3 m but varies significantly depending on wind direction. Four zones characterized by distinct sediment types dominate the area. A homogeneous zone largely composed of sand is found throughout the fjord and nor system between depths of 0 and 2 m. More heterogeneous sediment is found in a narrow zone in the middle of the fjord at the same depths, while a soft silty sediment zone with a dense mussel bed (*Mytilus edulis*) occurs around a small island near the mouth of the fjord. At depths greater than 2 m in the nor, the sediment is characterized by black anoxic mud covered by a macrophyte mat (Fjordbiologisk Laboratorium 1992). Vegetation in the fjord is scanty and dominated by brown algae

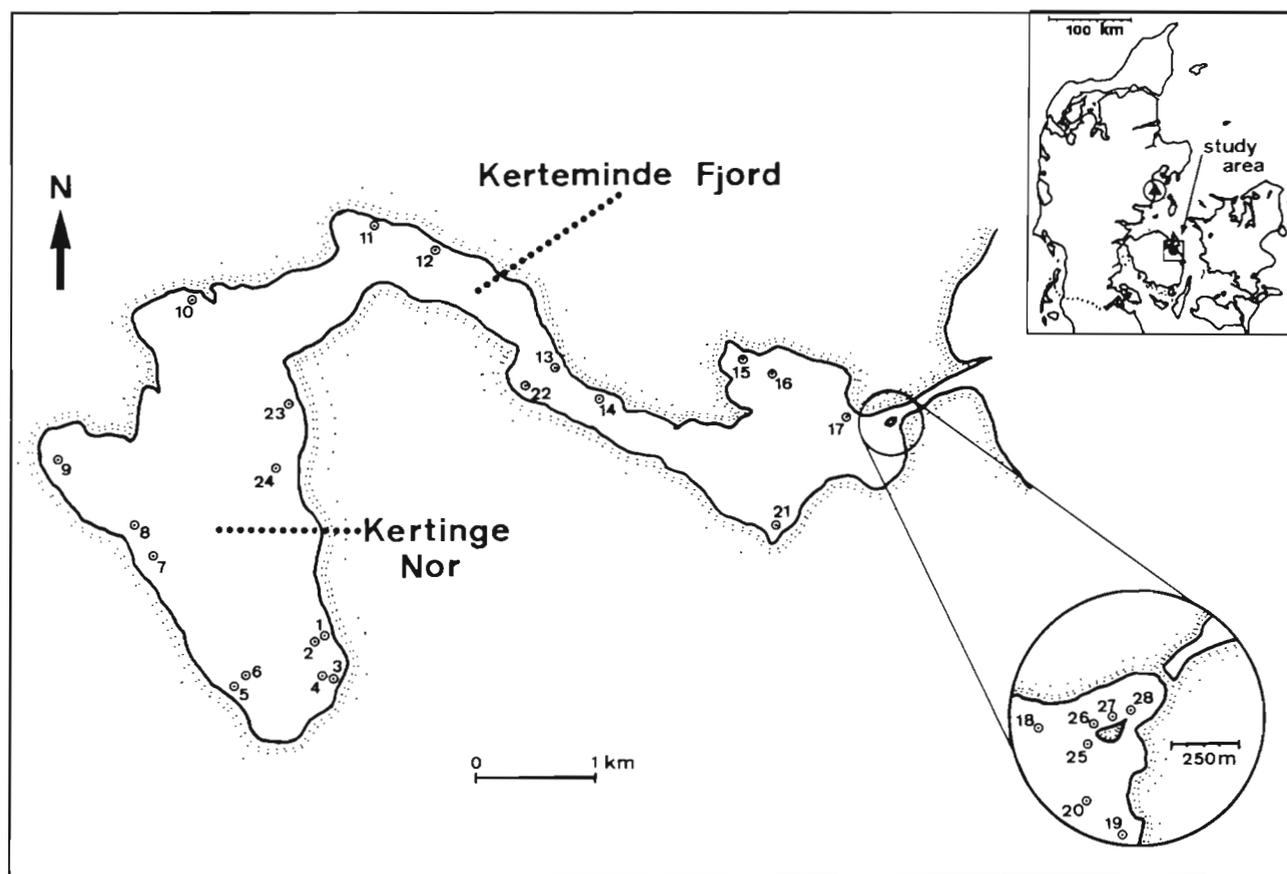


Fig. 1. The Kerteminde Fjord/Kertinge Nor system, Denmark: distribution of sampling stations. Circled triangle in inset shows location of Norsminde Fjord

(*Fucus vesiculosus*). In the nor, a belt of vegetation-free sediment is found between depths of 0 and 2 m. At depths greater than 2 m, vegetation is much more important and is dominated by *Chaetomorpha linum* and *Cladophora sericea* (Fyns Amt 1992). Eelgrass *Zostera marina*, pondweeds *Ruppia maritima* and *R. cirrhosa* and other macrophytes (*Potamogeton pectinarius* and *Zannichellia palestris*) are also important (Fyns Amt 1992). The uppermost edge of the western part of the nor is covered with a small salt marsh dominated by *Phragmites* spp. The entire system is dominated by the ascidian *Ciona intestinalis* and the jellyfish *Aurelia aurita*, which control, almost exclusively, the biomass of phyto- and zooplankton (Riisgård pers. comm.). Polychaetes (mainly nereids) and bivalves (*Macoma balthica* and *Mya arenaria*) are limited to sediments above 2 m depth.

Norsminde Fjord is a similar shallow mesohaline estuary. It is found on the east coast of Jutland (Jylland), 20 km south of Århus (see Fig. 1). A description of Norsminde Fjord is given by Kristensen (1988). The sampling done in the present study showed that the mussel bed had spread toward the north in the entrance of the fjord compared to what was observed in 1978 by Kristensen (1988).

Sampling procedures: Sediments and nereids were collected from Kerteminde Fjord/Kertinge Nor during September and October 1991 from 28 stations distributed between the shoreline and the isobath of 1 m. At each station, 3 to 5 (depending on nereid density) sediment cores of 1/60 m² were taken by a 30 cm long × 15 cm i.d. cylindrical steel corer. Cores were preserved in the field through a 1 mm mesh sieve and all nereids collected. Water temperature and salinity were measured at each station. Worms were fixed in the laboratory with 4 % buffered formalin within 3 h and later counted for density and weighed. Weight was determined using the partial weight method established by Desrosiers et al. (1988) for the first 25 segments.

Data from a transect comprising Stns 28, 27, 26, 25, 18, 17, 16 and 15 in Kerteminde Fjord were compared to results from a similar transect in Norsminde Fjord, where the nereid community has been well studied (Kristensen 1984, 1988). Six of Kristensen's (1988) original stations were sampled (Stns 1, 2, 3, 5, 6 and 8) on 20 October 1991 to examine long-term changes in nereid distribution. The nereid density and distribution at this location were determined as described above.

Coexistence between pairs of species was described for the 2 study areas using a modified version (Kristensen 1988) of the symmetric overlap index formulated by Schoener (1974). According to Kristensen (1988), this index does not necessarily imply competition but should provide some indication of the strength of interspecific interactions.

Sediment characteristics: For each station (Kerteminde Fjord/Kertinge Nor system and Norsminde Fjord), 3 sediment cores were collected with 5.0 cm i.d. acrylic core liners. Pore water sulfide concentrations were determined in the laboratory immediately (within 3 h) following sampling. The term 'sulfide' (also symbolized in the text as HS⁻) refers to all species of sulfide (H₂S, HS⁻ and S²⁻). Pore water was obtained from a 1 cm thick core segment, taken 8 cm below the sediment-water interface. This depth was chosen in order to ensure a measurement from each core within the burrowing depth of nereids, but below the wave resuspension zone. Pore water from sandy sediments was obtained by centrifuging at 3000 rpm for 4 min. In order to increase speed of sampling no attempts were made to prevent loss of pore water sulfides (evaporation, oxidation) during core sectioning and centrifuging. However, no significant difference was observed between samples from Stns 1, 2 and 3 when compared with results from parallel subsamples taken in a glove bag under N₂. Pore water from muddy sediments (fraction of silt and clay > 20 %) was obtained by squeezing them through a Whatman GF/C glass-fiber filter under N₂ (Reeburgh 1967). In all cases, pore water samples were fixed immediately with 5 % ZnAc to precipitate the sulfide as ZnS (Jørgensen et al. 1990). Samples were subsequently analysed photometrically by the methylene blue technique of Cline (1969). A 1-way analysis of variance (ANOVA) was used to compare the density (no. of individuals m⁻²) at different HS⁻ concentrations.

Subsamples of surface sediment from each core were collected and deep-frozen to insure preservation of organic matter. Sedimentary analysis for all samples was performed following a protocol based on the granulometric methods of Rivière (1977). Organic matter was measured as loss-on-ignition (LOI) at 520 °C for 6 h (Kristensen & Andersen 1987).

Tank experiments. The tank experiments (November 1991 to April 1992) were designed to determine the impact of sulfidic sediment and short-term competitive interactions on the distribution of the 3 nereid species in the Kerteminde Fjord/Kertinge Nor system.

Two different sediments were used: (1) pure sand (from Stn 9); (2) a mixture of 10 parts sand (Stn 9) to 1 part highly sulfidic sediment (Stn 27). The mixture was placed in a closed bucket and stored for 1 wk. Each type of sediment was defaunated by sieving through a 1 mm mesh sieve. Experimental tanks (0.07 m²) were divided into 2 equal-sized compartments by a removable PVC partition. One compartment was filled with sandy sediment to a depth of 15 cm and the other with HS⁻ sediment to a similar depth. The experimental tanks were left for one week before the introduction of worms in order to allow the sediment to stabilize. Tanks were supplied with running seawater (20 ‰ S)

under permanent immersion. Water temperature decreased from 11°C (November) to 6°C (February) and again increased to 8°C (April) during the 6 mo experimental period. The partitions were removed 2 d before the introduction of worms. Nereids were introduced randomly in predetermined numbers. No complementary food was provided. After a 30 d period the partitions were reinserted and each compartment was examined for the number and species of nereids. Three cores (per compartment) were also collected for pore water HS^- concentration, mean particle size and organic matter determination. (See Table 1 for sediment characteristics of each compartment.)

A total of 7 tanks were established: 3 with each of the 3 nereid species alone (allopatry); 3 with 2 species (sympatry); and 1 with all 3 species. The initial density for allopatry was 30 ind. tank⁻¹ (426 ind. m⁻²), and for sympatry 2 × 15 and 3 × 10 ind. tank⁻¹. Individuals from all 3 species had a mean fresh towel-dried weight of 0.64 ± 0.14 g. The experiment was repeated 3 times. Comparisons between means in allopatry and sympatry experiments (% of worms present in sand compartment, and mortality) were done with a *t*-test. This test was chosen for its robustness with regard to sample sizes and unequal variances (Zar 1984). Probability intervals are symbolized, throughout the text, by 1 (0.01 < p ≤ 0.05), 2 (0.001 < p ≤ 0.01) or 3 asterisks (p ≤ 0.001).

A complementary tank experiment was done from 18 April to 28 May 1992 and was designed to observe the preference of *Nereis succinea* for the presence of mussels (*Mytilus edulis*) in different types of sediment. A total of 3 tanks were used: one filled with sandy sediment, one filled with HS^- sediment (same mixture as described above), and one divided as in the preceding experiment, with mussels in the HS^- compartment. This experiment was not repeated.

RESULTS

Nereid distribution in Kerteminde Fjord/Kertinge Nor

The distribution of nereids in the studied area is shown in Fig. 2. *Nereis virens* was found throughout the Kerteminde Fjord/Kertinge Nor system except at Stns 19, 21 and 24, which were characterized by large amounts of wood and shell debris. Highest densities (> 500 m⁻²) occurred in the western part of the nor, and lowest densities (< 250 m⁻²) in the eastern part of the fjord (with a small enclave in the eastern part of the nor). Intermediate densities (250 to 500 m⁻²) were found in the western and middle parts of the fjord. In general, densities decreased in the direction of the entrance of the fjord. *N. succinea* was mainly observed

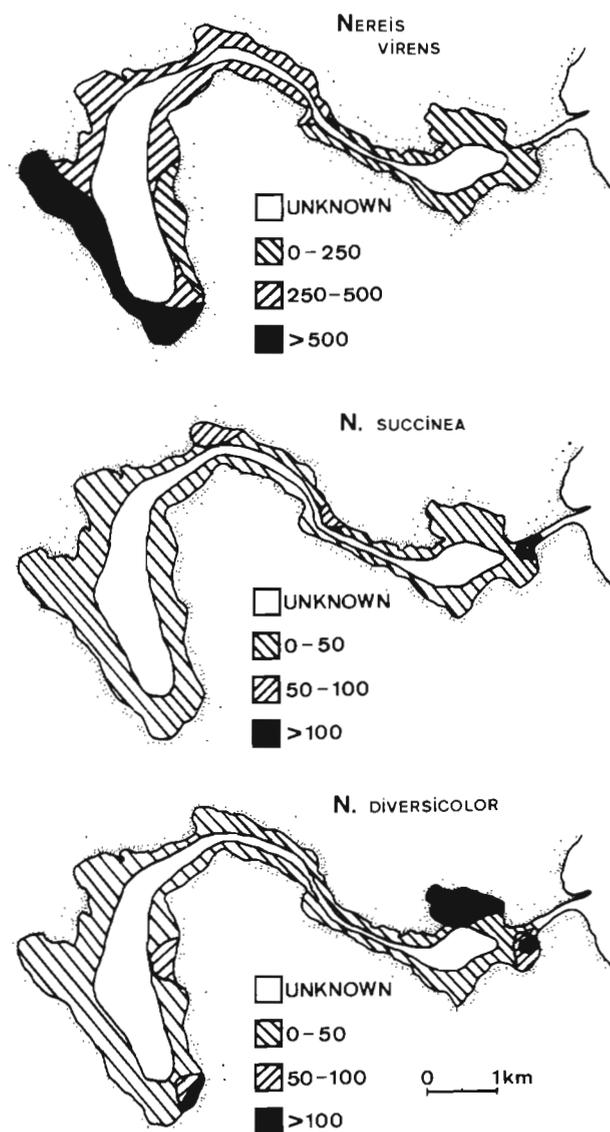


Fig. 2. *Nereis* spp. Distribution of individuals in study area (values are no. of ind. m⁻²)

near the mouth of the fjord in a mussel bed (> 100 m⁻²). Two small enclaves (50 to 100 m⁻²) were also found in the middle part of the fjord. *N. succinea* was absent from all other areas. *N. diversicolor* was observed in the eastern part of the fjord and in small areas on the eastern side of the nor. No individuals were found within stations in the middle and western parts of the fjord and on the western side of the nor.

Sediments

The sedimentary parameters are shown in Table 1. In general, the mean particle diameters (Md) indicate that

Table 1. Mean particle diameter (Md), silt + clay (Md < 63 µm) content, organic carbon (POC) content and sulfide (HS⁻) concentration of sediment from Kerteminde Fjord/Kertinge Nor, and of sediment used in the tank experiment. Values from the field stations are given as means ± SD of 3 measurements

Stn	Md (mm)	Silt + clay (%)	POC (%)	HS ⁻ (µM)
1	0.96 ± 0.91	0.87 ± 1.04	1.25 ± 0.53	42.17 ± 34.02
2	0.32 ± 0.02	2.16 ± 2.64	0.50 ± 0.03	6.54 ± 5.29
3	0.19 ± 0.00	2.45 ± 0.40	0.90 ± 0.14	21.09 ± 8.27
4	0.19 ± 0.01	1.60 ± 1.83	0.87 ± 0.05	10.67 ± 7.36
5	0.36 ± 0.01	1.50 ± 0.86	1.32 ± 0.10	13.60 ± 4.60
6	0.29 ± 0.01	1.52 ± 1.89	1.14 ± 0.11	29.79 ± 10.79
7 ^a	0.70 ± 0.09	0.90 ± 0.28	1.03 ± 0.05	7.71 ± 5.52
8	0.27 ± 0.03	1.28 ± 0.38	0.89 ± 0.08	13.08 ± 5.28
9	0.23 ± 0.02	3.08 ± 2.57	0.75 ± 0.09	12.02 ± 8.59
10	0.45 ± 0.05	4.80 ± 3.30	0.91 ± 0.17	1.66 ± 0.87
11	0.45 ± 0.10	1.73 ± 0.70	1.05 ± 0.05	4.12 ± 1.76
12	0.73 ± 0.07	3.19 ± 2.26	1.06 ± 0.04	2.64 ± 0.98
13	0.96 ± 0.14	2.41 ± 2.18	0.65 ± 0.05	8.89 ± 1.82
14	1.22 ± 1.01	12.06 ± 19.30	0.81 ± 0.04	0.38 ± 0.06
15	0.33 ± 0.01	1.41 ± 0.78	0.83 ± 0.01	6.44 ± 3.47
16	0.27 ± 0.03	1.68 ± 1.20	0.82 ± 0.06	6.77 ± 2.76
17	0.23 ± 0.05	3.36 ± 0.53	1.11 ± 0.05	25.82 ± 19.07
18	0.20 ± 0.02	6.70 ± 1.05	1.32 ± 0.14	42.28 ± 18.21
19	0.19 ± 0.01	4.58 ± 0.53	0.90 ± 0.16	21.00 ± 8.45
20	0.17 ± 0.01	2.58 ± 2.03	1.32 ± 0.18	30.14 ± 13.15
21	0.19 ± 0.01	6.74 ± 8.46	0.62 ± 0.12	32.66 ± 18.33
22	0.49 ± 0.14	4.73 ± 2.52	0.76 ± 0.11	4.49 ± 0.71
23	0.74 ± 0.23	1.38 ± 1.51	0.60 ± 0.09	1.69 ± 1.22
24 ^a	0.34 ± 0.03	2.39 ± 0.02	0.62 ± 0.04	7.78 ± 3.71
25	0.09 ± 0.04	55.97 ± 12.60	11.00 ± 3.86	90.00 ± 103.68
26	0.18 ± 0.07	36.12 ± 9.31	15.49 ± 3.47	550.53 ± 18.71
27	0.05 ± 0.02	67.20 ± 12.45	15.83 ± 4.01	1715.30 ± 1215.11
28 ^a	0.48 ± 0.49	21.92 ± 24.81	4.53 ± 2.39	587.98 ± 37.16
Tank experiment (n = 21):				
Sand	0.50 ± 0.04	0.00 ± 0.00	0.66 ± 0.14	0.85 ± 0.44
HS ⁻ side	0.41 ± 0.01	0.00 ± 0.00	1.17 ± 0.05	208.87 ± 58.09

^aMean ± SD of 2 measurements

sandy sediments dominate the Kerteminde Fjord/Kertinge Nor system. Except for stations in the mussel bed area (25, 26, 27 and 28), percentages of the silt + clay fraction (Md < 63 µm) were usually under 7%. Percentages of particulate organic carbon (POC) were also low (< 1.50%). Differences were most conspicuous with respect to the pore water sulfide concentration. Stations in the mussel bed area (17 to 21, and 25 to 28) have the highest HS⁻ concentrations. At certain stations, the pore water sulfide concentration reached values (mean) greater than 500 µM. Stations in the nor (Stns 1 to 9) had concentrations between 10 and 50 µM while concentrations for the fjord stations (10 to 16 and 22 to 24) were below 10 µM. Variability within each station was generally high. The sedimentary characteristics were pooled in relation to 3 density classes (0–250, 250–500 and > 500 m⁻²) of *Nereis virens* and defined different sedimentary areas (Table 2). Statistical differences (*t*-test)

between each of the studied sedimentary parameters reflected 3 zones. Differences between the sedimentary parameters from the 2 higher density classes (250–500 and > 500) are, however, small and bidirectionally these 2 sedimentary zones could be merged into one main sedimentary area west of Stn 12, with organic-poor sandy sediment. The low-density area (< 250 m⁻²), east of Stn 12, was characterized by sediments with high silt and clay content and pore water HS⁻ concentrations.

Density of *Nereis virens* decreased with increasing pore water HS⁻ concentration ($F_{2,25} = 6.49^{**}$) (Fig. 3). Conversely, the density of *N. succinea* was higher in sediment with > 50 µM ($F_{2,25} = 23.59^{***}$). This species was, however, almost absent from stations in the 2 other concentration classes (0–25 and 25–50 µM). Density of *N. diversicolor* was about the same for the first 2 HS⁻ concentration classes ($F_{2,25} = 0.84$). No individuals were found in stations with sediments having > 50 µM HS⁻.

Results also indicated that the size of individuals (partial weight) varied in relation to the pore water sulfide concentration (Table 3). In spite of a high

variability and a low number of individuals weighed, this trend can be observed particularly for *Nereis succinea* ($t = -4.08^{***}$), where weight (mean) increased by a factor of 6 between the 0–25 µM and the > 50 µM HS⁻ classes. *N. virens* also showed increasing body size between 0–25 µM and 25–50 µM HS⁻ classes ($t = -3.58^{**}$). Results did not indicate any significant changes for *N. diversicolor* in regard to weight distribution ($t = -1.93$). *N. diversicolor* was, however, absent from stations with HS⁻ concentration > 50 µM.

Transects and coexistence

The distribution and density of the nereids along the transect in Kerteminde Fjord are shown in Fig. 4A. The distribution of *Nereis succinea* was related to an area of highly organic and sulfidic sediments within a mussel

Table 2. Mean particle diameter (Md), silt + clay (Md < 63 μm) content, organic carbon (POC) content and sulfide (HS^-) concentration of sediment from Kerteminde Fjord/Kertinge Nor. Data are pooled according to density classes of *Nereis virens*. Values are given as means \pm SE. A: *t*-test between classes 0–250 and 250–500; B: *t*-test between classes 0–250 and >500; C: *t*-test between classes 250–500 and >500

Density (m^{-2})	Md (mm)	Silt + clay (%)	POC (%)	HS^- (μM)
0–250	0.42 ± 0.07	10.61 ± 2.59	2.13 ± 0.51	85.11 ± 41.05
	A: $t = -3.88^{***}$	$t = 21.18^{***}$	$t = 16.12^{***}$	$t = 13.00^{***}$
	B: $t = 4.24^{***}$	$t = 21.52^{***}$	$t = 14.82^{***}$	$t = 12.17^{***}$
	(Stns 1, 2, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28; n = 49)			
250–500	0.48 ± 0.05	2.37 ± 0.51	0.94 ± 0.05	8.43 ± 2.66
	C: $t = 6.55^{***}$	$t = 2.07$	$t = -1.37$	$t = -6.36^{***}$
	(Stns 4, 6, 10, 11, 12; n = 18)			
>500	0.32 ± 0.08	1.91 ± 0.61	0.98 ± 0.10	13.50 ± 1.84
	(Stns 3, 5, 7, 8, 9; n = 14)			
	* $p < 0.05$, ** $p > 0.01$, *** $p < 0.001$			

bed. The other 2 species had higher density outside this area. The same trend was found in Norsminde Fjord (Fig. 4B). *N. succinea* was found in an area characterized by the presence of *Mytilus edulis* (from Stn 1 to 6). Sulfide concentrations and organic matter were, however, lower than in the Kerteminde transect. In both transects, *N. diversicolor* was absent from stations where *N. succinea* was found. In this respect, coefficients of coexistence are given in Table 4. In both study areas, no or only a weak overlap was observed between populations of *N. succinea* and *N. diversicolor*, whereas populations of *N. succinea* and *N. virens* exhibited a high overlap. Populations of *N. virens* and *N. diversicolor*

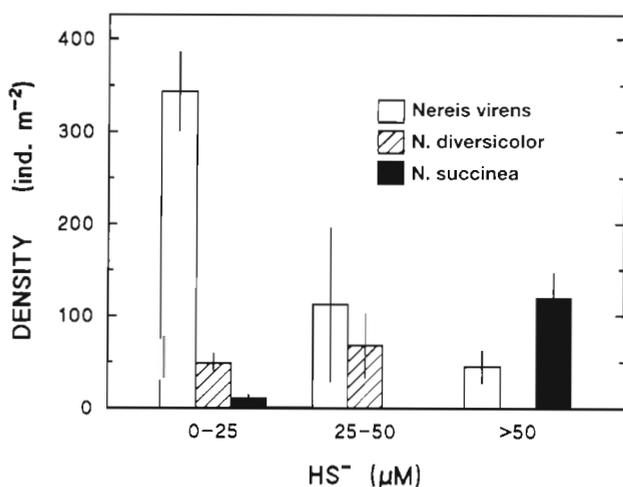


Fig. 3. *Nereis* spp. Distribution of density in relation to pore water sulfide concentrations (error bars: \pm SE)

color showed a partial overlap, which was intermediate between the other 2 population pairs.

Tank experiments

The tank experiments showed that all 3 species preferred non-sulfidic sediments (Fig. 5). *Nereis succinea* did, however, show the lowest preference. Results from both allopatry and sympatry experiments indicated that *N. virens* preferred non-sulfidic sediments in all situations, with no significant change between allopatry and sympatry ($t = -0.77$ with *N. succinea*; $t = -0.71$ with *N. diversicolor*). In sympatry with *N. virens*, both *N. diversicolor* ($t = 3.63^{**}$) and *N. succinea* ($t = 2.93^*$) were found in greater number in the sulfidic sediments compared to allopatry. In sympatry with *N. diversicolor*, *N. succinea* was found more often in non-sulfidic sediments ($t = 2.38^*$). With all 3 species in sympatry, the percentages of individuals present in the sand compartment were about the same for *N. virens* ($t = -1.53$) and *N. diversicolor* ($t = 0.42$) compared to results in the paired sympatry experiments. Results for *N. succinea* were intermediate between those of the other 2 sympatry experiments (pairs), and were comparable to those observed in the allopatry situation ($t = 0.85$).

The mortality of all 3 species was usually lower in allopatry than in sympatry. For *Nereis virens*, mortality increased dramatically from 20% in allopatry to 40 and 60% in situations where *N. succinea* was present ($t = -5.80^{***}$; $t = -5.24^{***}$ with all 3 species together). *N. virens* was not affected ($t = 0.36$) by the presence of *N. diversicolor*. Mortality of *N. diversicolor* was affected by the presence of other species, although not significantly compared to the allopatry situation ($t = -0.93$, -0.36 and -1.63). *N. succinea* was not affected significantly by the presence of *N. diversicolor* ($t = -0.56$ and -0.21). Mortality of *N. succinea* was

Table 3. *Nereis* spp. Weight (partial weight) distribution in relation to sulfide concentration in Kerteminde Fjord. Values are given as means \pm SD

Species	Sulfide concentration (μM)		
	0–25	25–50	>50
<i>N. virens</i>	0.08 ± 0.13	0.20 ± 0.35	0.10 ± 0.07
<i>N. diversicolor</i>	0.06 ± 0.06	0.10 ± 0.08	–
<i>N. succinea</i>	0.03 ± 0.03	–	0.16 ± 0.14

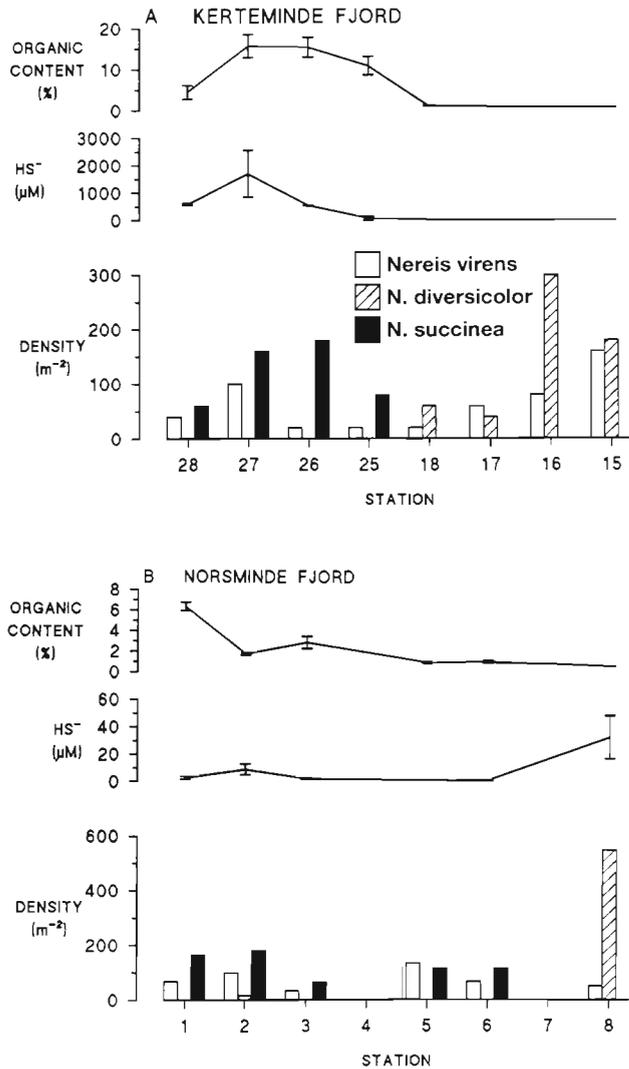


Fig. 4. *Nereis* spp. (A) Distribution of individuals along the Kerteminde transect. (B) Distribution of individuals along the Norsminde transect (see Fig. 1 for location of fjord). Organic content of sediments and pore water sulfide concentrations at the sampling stations are shown (error bars: \pm SE of triplicate cores)

actually lower in sympatry with *N. virens* ($t = 2.40^*$) than in allopatry. The slightly elevated mortality rate for *N. succinea* when in sympatry with *N. diversicolor*, compared to values in the case of the 3 species in sympatry, might have been caused by an interruption of the water circulation which occurred in one of the tanks during the third set of replicates.

The tank experiment with mussels present showed that *Nereis succinea* preferred an association with mussels, whatever the type of sediment used (Fig. 6). The higher preference observed in the sand-mud case, where mussels were positioned on the sulfidic sediment, substantiates this association, since the opposite result was obtained without mussels.

Table 4. *Nereis* spp. Coefficients of coexistence (C_{ij}) in Kerteminde Fjord and Norsminde Fjord

Species combination	Kerteminde Fjord	Norsminde Fjord
<i>N. succinea</i> + <i>N. diversicolor</i>	0.000	0.034
<i>N. virens</i> + <i>N. diversicolor</i>	0.130	0.098
<i>N. virens</i> + <i>N. succinea</i>	0.524	0.614

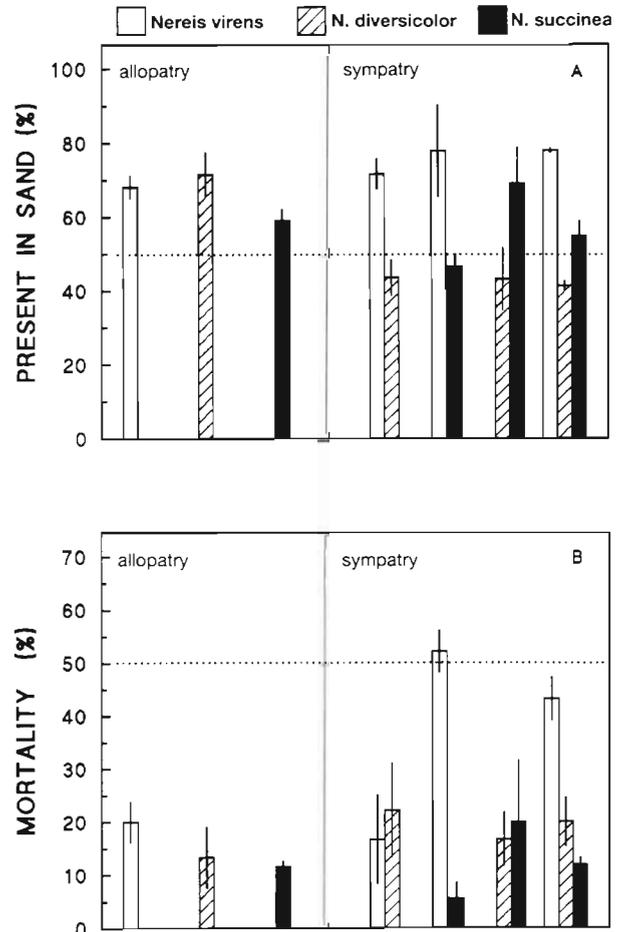


Fig. 5. *Nereis* spp. (A) Final distribution of individuals in the sand (non-sulfide) compartment after 30 d incubation in tank experiments. Values are given as % of the worms present at the end of the experiment. (B) Mortality of individuals after 30 d. Values are given as % of the initial number of worms added (error bars: \pm SE of triplicate experiments)

DISCUSSION

Data obtained in this study indicate that *Nereis virens* is the most common nereid species in the Kerteminde Fjord/Kertinge Nor system. *N. virens* is mainly found in sandy, organic-poor sediments with low levels of pore water sulfides ($< 50 \mu\text{M}$). This is in

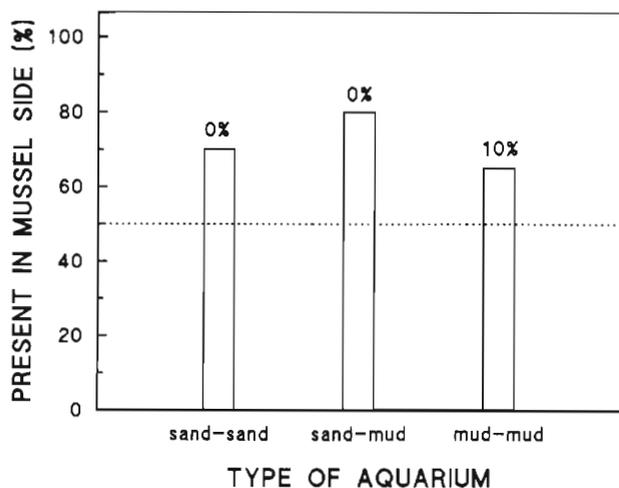


Fig. 6. *Nereis succinea*. Final distribution of individuals in the mussel side of tanks for different types of sediment. Mussels were positioned on the sulfidic mud side in the sand-mud case. Data are given as % of the worms present at the end of the experiment. Values above bars are mortality (%)

accordance with the distribution of *N. virens* found in a similar estuary in Norsminde Fjord (Kristensen 1988), and in mudflats on the northeast coast of North America (Ambrose 1986, Miron & Desrosiers 1990). The *in situ* preference of this species for sandy sediments is in close agreement with results from the tank experiments. The decreasing density toward the more marine habitat (entrance of the fjord) confirms the distribution strategy adopted by *N. virens* in the St. Lawrence estuary (Canada) (Miron & Desrosiers 1990). Our data, however, failed to reveal any clear weight-related segregation although larger individuals were found in highly sulfidic sediments near the mouth of the fjord. The high mortality rates observed in the tank experiments, particularly in sympatry conditions (from 20 to 60 %), illustrate that *N. virens* has a low tolerance to sulfide.

As illustrated in many Danish studies (Muus 1967, Rasmussen 1973, Kristensen 1988), *Nereis succinea* seems to be limited to mussel beds areas, usually characterized by sulfidic muddy sediments (Theede et al. 1969). This is, however, in contrast with the tank experiments, where this species showed a preference for non-sulfidic sediments. In this respect, the mussel tank experiment illustrated that a mussel-related factor may drive this species toward sulfidic sediments in the natural habitat. Faeces from mussels could attract the detritivore *N. succinea* (Goerke 1971, Fauchald & Jumars 1979). In consequence, this species exhibits a high tolerance for HS^- (more than 2000 μM sulfide in pore water) in contrast to the omnivorous *N. virens*. In comparison, results from other studies

(Theede et al. 1969, Maughan 1986, Sampou & Oviatt 1991) indicate that macrofauna is generally excluded from sediments with pore water sulfide concentrations around 1000 μM . The factors that are responsible for the attraction of *N. succinea* toward mussel beds should be explored in future studies.

In the field study, *Nereis diversicolor* did not show any specific sediment preference. This is in accordance with Kristensen's (1988) results in Norsminde Fjord. The tank experiment illustrates, as for *N. succinea*, a preference for sandy sediment. The sympatry experiments also show that *N. diversicolor* is highly tolerant to HS^- . Our data thus confirm the results of Vismann (1990) which indicated that *N. diversicolor* is more tolerant to HS^- than *N. virens*.

Physiological and biochemical adaptations may largely account for the observed differences in the survival ability of polychaetes under hypoxia and anoxia (Warren 1984). The variation in the tolerance of polychaetes to severe hypoxia or anoxia is sometimes reflected in the ecological differences between their habitats (Theede et al. 1973). According to the present results, we must expect a similar or higher rate of HS^- detoxification for *Nereis succinea* relative to *N. diversicolor*. Tolerance to sulfide can thus extend the animal's ecological niche since *N. succinea* seems attracted by mussels rather than HS^- sediments. The fact that *N. virens* and *N. diversicolor* have different rates of HS^- detoxification (sulfide oxidation) illustrates that sulfide is an important factor in determining their distribution. Ventilation rates, which have been well studied in nereids (Kristensen 1981, 1983a, b, c, 1989), may reflect some behavioural or size-specific responses since respiration can be impaired by HS^- exposure (Theede et al. 1969). Since ventilation is directly proportional to body weight (M) and burrow wall area increases according to the surface power law ($M^{0.7}$) (Kristensen 1984), larger worms may be most efficient at removing HS^- from burrow water in sulfidic areas. This is confirmed by the fact that larger *N. virens* individuals were found in the sulfidic mussel bed sediment. Further work is needed in order to determine the precise effect of body size on tolerance to sulfide. Jensen (1986), however, found that nematode species had a higher length/body radius ratio in sulfidic (thiobiotic) habitats.

The field data indicate that competitive interactions are an important determinant for the distribution of nereid species. This is particularly true for populations of *Nereis diversicolor* which do not, or only to a small extent, overlap with populations of *N. virens* and *N. succinea* ($C_{i,j} = 0.13$ and 0.0 respectively). The sympatry tank experiments substantiate this trend, since *N. diversicolor* was forced into the sulfidic sediment. The mortality rates, which were surprisingly low for this species, show that it actually is highly tolerant to

HS⁻. As discussed by Kristensen (1988), the general high tolerance of *N. diversicolor* with respect to many environmental factors has evolved at the expense of competitive ability. In the Kerteminde Fjord/Kertinge Nor system, *N. diversicolor* occupy marginal habitats which, in fact, are refuges from the other 2 species. Aggressive behaviour (territoriality) is important in space-sharing modalities for both *N. virens* (Miron et al. 1991a, b, 1992a, b, c) and *N. diversicolor* (Lambert 1986, Lambert & Retière 1987, Lambert et al. 1992). Work by Reish & Alosi (1968) and Evans (1973) also showed that interspecific aggressive behaviour is frequent and must be considered as a factor determining the distribution of nereid polychaetes. The relatively weak interaction between populations of *N. virens* and *N. succinea* observed in the field ($C_{v,j} = 0.5$ to 0.6) could be related to the high spatial variability of sulfur biogeochemistry (Luther et al. 1991) rather than low aggressive interactions. Patches of low-sulfidic sediments inside the mussel bed could explain the presence of *N. virens* in the habitat of *N. succinea*. Muus's (1967) views on competitive interactions between *N. virens* and *N. diversicolor* are thus confirmed. Differences in interspecific encounters, with respect to aggressiveness and/or territoriality, among all pairs of the studied species should be described in future studies.

Differences of data for 2-species sympatry combinations compared to those for 3-species combinations suggest that there are complex interactions among the 3 species. Results (% present in sand) showed that *Nereis virens* and *N. diversicolor* are unaffected by the addition of *N. succinea*. An intermediate situation is observed for *N. succinea* when present with both *N. virens* and *N. diversicolor*, in contrast to results from the other 2 sympatry situations. These findings suggest that *N. succinea* spatially benefits from the addition of *N. diversicolor*, since more individuals were found in the sand compartment of the tank in comparison to what was observed when *N. virens* was present. In the latter case, *N. succinea* was more evenly distributed throughout the entire tank. Mortality results, however, suggest that *N. succinea* benefits from the addition of *N. virens*.

The idea of tolerance to abiotic factors as a major part of the niche, and the importance of such factors in determining condition-specific competitive abilities, is an old concept (Grinnell 1917, Allee et al. 1949, Odum 1953, Andrewartha & Birch 1954, Hutchinson 1958). When species compete, the outcome will be determined primarily, as discussed by Dunson & Travis (1991), by biotic interactions and the species-specific responses to abiotic factors. According to these authors, physiological responses to abiotic factors could determine the overall conditions of dominance. In the

extreme case, condition-specific intensities of competition can cause a reversal of the competitive dominance such that one species is superior under one subset of abiotic conditions, and another species is superior under another subset (Hutchinson 1961).

This study showed that sulfide concentration in sediments may constitute, as do grain size (Wieser 1959, Gray 1974, Rhoads 1974, Miron & Desrosiers 1990) and salinity (Theede et al. 1973, Kristensen 1988), an important factor in the distribution of soft-bottom communities. *Nereis virens* decreased dramatically in density with increasing pore water HS⁻ concentration. The high mortality rates in the tank experiments corroborated this pattern. A high sulfide tolerance in *N. succinea* (field study) and *N. diversicolor* (tank experiments) allows both of these species to colonize sulfidic sediments. However, low competitiveness forces *N. diversicolor* to inhabit marginal habitats, avoiding interactions with *N. virens* and particularly *N. succinea*. Results from the tank experiments also suggest that a mussel-related factor may be more important than HS⁻ in explaining the distribution of *N. succinea*. We are aware that sulfide is probably correlated with other environmental factors and that these factors play a role in determining the distribution of nereids. Nevertheless, this study should provide interesting field and experimental data for investigating the physiological effect of sulfide exposure, particularly on ventilation behaviour, in nereid individuals (Miron & Kristensen unpubl.). According to Kristensen (1981, 1983a, b, c), ventilation activity, which is related to O₂ regulatory ability, is correlated with preferred sediment type.

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