

Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes

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ABSTRACT: The impact of suspension-feeding *Nereis diversicolor* and non-suspension-feeding *N. virens* on C and N dynamics in an organic-poor sediment was investigated in a controlled laboratory study simulating periods of high and low phytoplankton (*Rhodomonas* sp.) concentration. High phytoplankton concentration resulted in a 30-fold higher deposition (clearance) of particulate C and N to the sediment inhabited by *N. diversicolor* than to *N. virens* and defaunated sediment. Concurrently, O₂ consumption and NH₄⁺ + NO₃⁻ release were increased by a factor of 3 in sediment with *N. diversicolor*, but only by a factor of about 1.5 in *N. virens* and defaunated treatments. Steady-state porewater concentrations of TCO₂ and NH₄⁺ decreased exponentially with increasing ventilation activity of nereids. Ventilation activity was highest for suspension-feeding *N. diversicolor* and lowest for deposit-feeding *N. virens*. About 30% of the deposited algal C and N in the *N. diversicolor* sediment were lost rapidly as excess CO₂ or NH₄⁺ + NO₃⁻ flux to the water column. Incorporation into *N. diversicolor* tissues accounted for 2/3 of the retained C and N. In the case of *N. virens*, where no net phytoplankton deposition occurred, organic matter removal due to mineralization resulted in a net loss of both sedimentary C and N. Accordingly, the biology and behaviour of infaunal species are important determinants for sediment biogeochemistry and element cycling in marine areas.

KEY WORDS: Carbon · Deposit-feeding · Fluxes · *Nereis diversicolor* · *Nereis virens* · Nitrogen · Sandy sediment · Suspension-feeding

INTRODUCTION

Fluxes across the sediment-water interface and transformation of carbon and nitrogen substances within the sediment are important processes in the biogeochemical element cycling of marine environments. Deposition of organic particles onto coastal sediments is basically controlled by plankton dynamics and hydrography, but the intensity of physical and biological resuspension, infaunal particle mixing and biodeposition are important factors determining net incorporation into sediments (Aller 1982, Wheatcroft et al. 1994, Graf & Rosenberg 1997).

Settling of organic particles can be accelerated considerably by the activities of suspension-feeding infauna (Meadows et al. 1990, Miller et al. 1992). They meet their nutritional demands by extracting sus-

pended particles (e.g. phytoplankton) from ventilation currents (Gerritsen et al. 1994, Riisgård & Larsen 1995), thus enhancing the deposition at the sediment surface directly in the form of biodeposited fecal pellets (Vedel et al. 1994, Graf & Rosenberg 1997). Deposit-feeding infauna may increase deposition indirectly by creating a stagnant boundary layer between densely packed tubes (Rhoads et al. 1978) or by enhancing passive deposition into feeding pits (Yager et al. 1993). The infauna may also enhance resuspension with subsequent lateral advection by ejection of particles into the overlying water (Bender & Davis 1984, Rowden & Jones 1994) or by destabilization of the sediment surface during feeding and tube building (Eckman et al. 1981).

Removal of organic matter from coastal marine sediments is, in addition to resuspension events, mediated largely by aerobic and anaerobic microbial mineralization processes with a significant macrobenthic component (Hansen & Blackburn 1992, Aller 1994). Burrow-

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dwelling animals are known to stimulate decomposition processes in sediments (Andersen & Kristensen 1991, Marinelli & Boudreau 1996). Irrigation and burrowing create steeper solute gradients, enhance fluxes and impart a multidimensional heterogeneity to the sediment matrix in both time and space (Martin & Banta 1992, Krager & Woodin 1993, Aller 1994). Infaunal burrows in coastal areas can thus be viewed as microbially dynamic extensions of the sediment surface with oxidized walls and a short distance between aerobic and anaerobic layers (Reichardt 1988, Fenchel 1996).

The widely distributed and closely related marine polychaetes *Nereis diversicolor* and *N. virens* are known as important bioturbators of shallow coastal sediments (e.g. Kristensen 1988, Hansen & Kristensen 1997). Although they both live in more or less U-shaped burrows and are often found in coexistence, the former has an affinity for relatively organic-rich sediments whereas the latter prefer more sandy, organic-poor sediments (Miron & Kristensen 1993). Both are omnivores (detritivores), but *N. diversicolor* also has the ability to live solely as a suspension-feeder (Vedel & Riisgård 1993, Nielsen et al. 1995). It spins and attaches a mucus net near the entrance of the burrow and pumps water through the net by undulating body movements. The net, containing trapped food particles, is then swallowed and a new cycle is started. Above a certain threshold of phytoplankton concentration in the water column (1 to $3 \mu\text{g chl a l}^{-1}$) *N. diversicolor* conducts its suspension-feeding cycle repeatedly (Riisgård 1991, Vedel et al. 1994). No such suspension-feeding has been observed in *N. virens*.

The purpose of this experimental study was to investigate the role of suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*Nereis virens*) nereid polychaetes for carbon and nitrogen fluxes in a shallow coastal sediment. Controlled laboratory experiments with microcosms inhabited by the 2 nereid species were conducted with and without an excess phytoplankton food source in the overlying water. Based on the downward flux of phytoplankton carbon and nitrogen and upward flux of dissolved inorganic carbon and nitrogen, budgets for the sediment environment were established and the role of polychaete feeding mode was evaluated.

MATERIALS AND METHODS

Sediment and worm collection. Sediment and worms were collected in March from the innermost part of the shallow cove Kertinge Nor, Denmark. For a detailed description of the study area consult Riisgård et al. (1995). The study site was characterized by non-

vegetated sandy sediment inhabited by populations of *Nereis diversicolor* and *N. virens* at densities of 500 to 1000 ind. m^{-2} (Miron & Kristensen 1993). Water depth, salinity and temperature were 1 m, 18‰ and 5°C, respectively. Sediment, which consisted of well-sorted low-organic sand, was gently sieved through a 1 mm mesh to remove larger macrofauna and homogenized by hand. Sediment microcosms were established by transferring the homogenized sediment into 25 cm long and 8 cm i.d. plexiglass core liners to a depth of ~14 cm. The sediment was then allowed to stabilize in the cores for 8 d. Although the process of sieving and sediment mixing disturbs the original chemical gradients and obstructs any direct extrapolation to *in situ* conditions (van Duyl et al. 1992), it is preferred here for comparative purposes.

Intact and healthy specimens of *Nereis diversicolor* and *N. virens* were collected in the sampling area by gentle sieving and were acclimated to the experimental temperature (15°C) for 1 wk.

Experimental set-up. Three nereid worms (~400 mg wet wt each) were added to each of 12 cores (equivalent to a density of 600 ind. m^{-2}), i.e. 6 with *Nereis diversicolor* and 6 with *N. virens*. An additional 6 cores were used as defaunated controls. The worms were allowed to establish in the sediment for a period of 12 d under experimental conditions by placing the cores in 2 darkened tanks, each containing 400 l of seawater (18‰ and 15°C). Subsequently, the experiment was initiated by replacing the tank water with 0.2 μm filtered, phytoplankton-free seawater. Phytoplankton (*Rhodomonas* sp.) was added to 1 tank containing half of the cores (AC, AD and AV cores representing control, *N. diversicolor* and *N. virens* treatments, respectively) at a concentration of 10 000 cells ml^{-1} , while the other tank with the remaining cores (C, D and V cores representing control, *N. diversicolor* and *N. virens* treatments, respectively) was maintained algal-free. The concentration of phytoplankton in the former tank was kept constant during the entire experiment by daily adjustments. To ensure homogeneous distribution of algae, the water was vigorously aerated and circulated. Each core was supplied with an internal magnetic stirrer rod driven by external rotating magnets (~80 rpm) to assure continuous exchange of water between core tubes and the surrounding tank.

Clearance measurements. Once every week for a period of 27 d, the clearance of algae from the water phase above the sediment was determined in all core types from the tank with phytoplankton. Clearance was measured by elevating the cores above the water surface and supplying them with air diffusers to completely stir the water phase without resuspending the sediment surface, and subsequently following algal disappearance in a time series of samplings. A coulter counter (Elzone-

80XY) was used to determine algal concentrations. For determination of particulate C and N content, *Rhodomonas* sp. cells were concentrated by centrifugation (3000 rpm; 1200 × *g*) of 10 ml samples from a batch culture of known cell concentrations. Carbon and nitrogen content of the pre-weighed and dried (105°C, 24 h) algal material were analyzed on a Carlo Erba CHN-analyzer according to Kristensen & Andersen (1987).

Flux measurements. Fluxes of O₂ and DIN (NO₃⁻ and NH₄⁺) were measured every third day by sealing the cores with Plexiglas lids. The incubations were terminated before oxygen concentration decreased more than 20% to ensure a linear change in solute concentrations of the enclosed water volume. Initial and final water samples were GF/C filtered before further handling. Oxygen samples were measured immediately by the standard Winkler technique. Samples for DIN were frozen and analyzed as soon as possible. NH₄⁺ was determined manually using the salicylate method according to Bower & Holm-Hansen (1980). NO₃⁻ (NO₂⁻ was insignificant and is included in NO₃⁻) was analyzed by the standard autoanalyzer method of Armstrong et al. (1967).

Core sectioning. At the end of the experiment all cores were sectioned into the following depth intervals: 0 to 0.5, 0.5 to 1, 1 to 2, 2 to 3, 3 to 4, 4 to 6, 6 to 8 and 8 to 10 cm. The sediment fractions were analyzed for porewater and solid phase characteristics. Porewater samples for TCO₂ and DIN were extracted by centrifugation at 1800 rpm (450 × *g*) for 10 min. Subsamples of 1.8 ml were analyzed immediately for TCO₂ by the flow injection/diffusion cell technique (Hall & Aller 1992) on a Kontron Ion Liquid Chromatograph, while the rest was frozen for later analysis of DIN as described above.

The solid phase was analyzed for water content as loss of weight after drying at 105°C overnight. Subsamples of the dried sediment were subsequently used for determination of organic content measured as particulate organic carbon (POC) and nitrogen (PON) on a Carlo Erba EA 1108 elemental analyzer. The concentration of chl *a* in the sediment was determined by extracting 2 g wet subsamples in 5 ml of 100% acetone overnight at 5°C. The extract was centrifuged at 3000 rpm (1200 × *g*) for 10 min and the supernatant analyzed spectrophotometrically at 665 and 750 nm before and after adding 2 drops of 2 M HCl according to Parsons et al. (1984).

Worms recovered during sectioning were collected and weighed. Worm growth rates were calculated as the difference between mean initial and final weights according to Vedel & Riisgård (1993).

Worm ventilation, respiration and NH₄⁺ excretion. Ventilation activity, O₂ respiration and NH₄⁺ excretion were measured on individual worms of both species.

The worms were placed in U-shaped glass tubes in 2 separate 20 l aquaria at 15°C; 1 without and 1 with algal additions (10000 *Rhodomonas* sp. cells ml⁻¹). Ventilation activity was continuously monitored by attaching a flow probe (2 mm i.d.) connected to an electromagnetic flowmeter on the excurrent opening of the tubes (Kristensen 1989). Ventilation is presented as pumping rate during active periods (*V_w*), and duration of ventilation periods as the percentage of total measured time, *D_v* (%), and as the average duration in minutes, *D_v* (min).

Oxygen respiration of actively ventilating worms was determined simultaneously as oxygen extraction during water passage through the glass tube. Samples of excurrent burrow water were continuously siphoned through an oxygen electrode (Radiometer, Copenhagen) at a known rate. Output signals from both ventilation and oxygen systems were recorded on a Phillips PM8220 dual-pen recorder. Calibrations of the system and calculation of ventilation activity and oxygen respiration were done according to Kristensen (1989). Ammonium excretion was determined as the difference in ammonium concentration of incurrent and excurrent water samples taken at short intervals during active ventilation.

RESULTS

Visual observations

Both types of control sediment (C, AC) exhibited a smooth surface throughout the experiment with a brownish oxidized zone down to 1.5 cm depth in treatments without, and 0.6 to 0.8 cm with, phytoplankton in the water column. In sediment containing *Nereis diversicolor* (D, AD), the surface became irregular and rough after a few days, with an oxidized zone of about 2 cm depth. Burrows of *N. diversicolor* had chimney-like openings extending 0.5 to 1 cm above the sediment surface when phytoplankton were present in the water column, whereas these structures were missing in the absence of algae. *N. virens* never produced such chimney-like structures. The sediment in the *N. virens* treatments (V, AV) was oxidized to 1–2 cm depth. The surface was rather smooth without phytoplankton, but was more irregular with feeding traces when phytoplankton was present in the water column. Burrows of both species extended to 9 cm without, and 11 to 13 cm depth with, phytoplankton in the overlying water. Sediment surrounding worm burrows of *N. diversicolor* was generally more oxidized (7 to 11 mm layer) than those of *N. virens* (<2 mm layer). The oxidized zones around *N. diversicolor* burrows were deepest in the algal-treated systems.

Clearance, ventilation and growth

The presence of phytoplankton in the water column affected the ventilation pattern of the 2 nereids in opposite directions. The time-integrated ventilation of *Nereis diversicolor* individuals was enhanced almost 4-fold in the presence of algae (AD) compared with the non-algae (D) situation (Table 1). This was due to increases in the ventilation amplitude and the total duration of ventilation activity. For *N. virens* individuals the time-integrated ventilation rate was reduced to $\frac{1}{3}$ in the presence of algae (AV) due to both decreasing

amplitude and duration of ventilation periods. The ventilation activity of *N. diversicolor* was always considerably higher than *N. virens*, i.e. 44 (AD:AV) and 4 (D:V) times. In the tank with phytoplankton, high ventilation and filtration activity of the *N. diversicolor* (AD) population (600 ind. m^{-2}) resulted in a 30-fold higher clearance than for both the non-suspension-feeding *N. virens* (AV) population (600 ind. m^{-2}) and the defaunated control (AC) (Table 1). Thus, passive sedimentation of algae in the AV and AC treatments was nearly similar. Since carbon and nitrogen content of *Rhodomonas* sp. were similar in all treatments, $3.9 \times 10^{-6} \text{ mol C cell}^{-1}$ and $7.1 \times 10^{-7} \mu\text{mol N cell}^{-1}$ (equivalent to a molar C:N ratio of 5.5), the downward transport of organic C and N was also enhanced 30-fold by the *N. diversicolor* population.

The presence of phytoplankton in the water column allowed *Nereis diversicolor* and *N. virens* to sustain positive growth with rates of 3.46 and 0.29% d^{-1} , respectively. When no phytoplankton was present in the water column, the growth was negative with rates of -0.36 and $-0.89\% \text{ d}^{-1}$, respectively.

Sediment-water fluxes

Addition of algae to the water phase affected sediment O_2 consumption rates most when *Nereis diversicolor* was present (Fig. 1). After an initial increase, O_2 uptake by the AD sediment stabilized after Day 7 at a level which was about 3 times higher than in the D treatment. The algal-treated AV and AC sediments both consumed about 40% more O_2 than their algal-free counterparts (V, C).

Unfortunately, measurements of CO_2 release from the sediment failed due to storage and analytical problems. For use in carbon budgets, CO_2 fluxes were therefore estimated from O_2 fluxes by the use of respiratory quotient (RQ) values of 1.1 to 1.3 as found previously in our laboratory for this sediment type (Hansen & Kristensen 1997). The use of a theoretical RQ of 1.1 to 1.3 to convert O_2 to CO_2 fluxes is debatable, but justifiable. Flux studies using organic-poor and sandy sediments from the same region as here have found comparably low RQ values (i.e. 0.8 to 1.6; Kristensen et al. 1992, Kristensen 1993). A low RQ is characteristic of a sediment showing anaerobic respiration (e.g. sulfate reduction) with simultaneous oxidation of reduced metabolites (e.g. sulfide) (Andersen & Kristensen 1998). Accordingly, the low pool sizes of total iron (1 to $2 \mu\text{mol cm}^{-3}$) and reduced sulfides (2 to $5 \mu\text{mol cm}^{-3}$) found in these organic-poor sands (unpubl. data) indicate a low capacity for storage of reducing equivalents.

NH_4^+ release by the sediments was affected in a pattern similar to O_2 , except for a more rapid initial in-

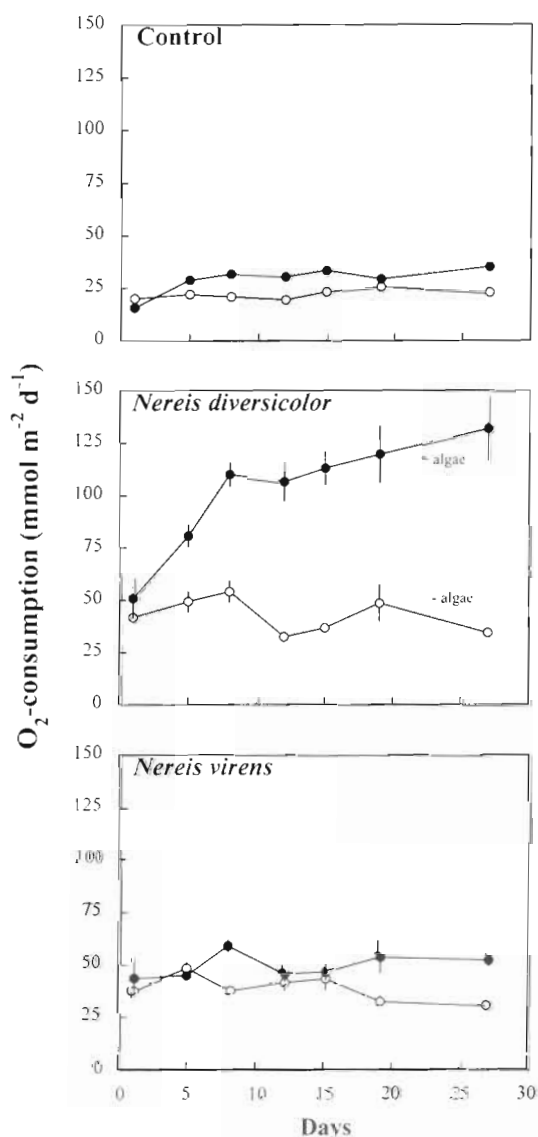


Fig. 1. Oxygen uptake in control, *Nereis diversicolor* and *N. virens* sediment with (●) and without (○) addition of *Rhodomonas* sp. (algae) in the overlying water throughout a 27 d experimental period. Values are presented as mean \pm SD ($n = 3$)

Table 1. Ventilation activity of individual worms placed in glass tubes (see 'Materials and methods' for further details). V_w : ventilation amplitude for 1 average sized (~400 mg) worm. Duration of ventilation is given as average period-length in minutes (D_v [min]) and as percentage of total elapsed time: (D_v [%]). Time- and area-integrated ventilation is estimated as: $V_w \times D_v$ [%] $\times d$, where d is the population density of nereids m^{-2} . Average daily clearance is presented as the water volume cleared of algae. Corresponding removal of algal C and N from the water phase is determined by relating the change in concentration of algae cells ml^{-1} with their carbon and nitrogen content. AC, AD and AV: control, *Nereis diversicolor* and *N. virens* treatments with algae in the water column, respectively, whereas D and V: worm treatments without algae. Values for ventilation and D_v are given as mean \pm SE ($n = 3$)

	AC	AD	D	AV	V
Ventilation					
Amplitude, V_w ($ml\ min^{-1}$)	–	3.7 ± 0.3	2.4 ± 0.3	0.4 ± 0.1	0.8 ± 0.0
D_v (min)	–	5.9 ± 1.1	0.7 ± 0.9	7.1 ± 0.7	9.6 ± 2.4
D_v (%)	–	85 ± 2	54 ± 19	42 ± 17	39 ± 3
Integrated ($l\ m^{-2}\ d^{-1}$)	–	2704 ± 185	754 ± 80	62 ± 9	179 ± 8
Clearance ($l\ m^{-2}\ d^{-1}$)	137	3711	–	125	–
C removed ($mmol\ m^{-2}\ d^{-1}$)	5.3	144.7	–	4.9	–
N removed ($mmol\ m^{-2}\ d^{-1}$)	0.97	26.3	–	0.89	–

crease in the AD treatment (Fig. 2). The average NH_4^+ release by the AD sediment from Day 7 onwards was 3.5 times higher than by the algal-free D sediment. The algal-treated AV sediment produced 50% more NH_4^+ than the algal-free V sediment. There was no significant difference in NH_4^+ release between control sediments with and without phytoplankton added to the overlying water. The exchange of NO_3^- was directed out of the sediment in all treatments (Fig. 3). The flux varied considerably during the first 15 d in AD sediment, but appeared to stabilize towards the end at a level 3 times higher than in the D sediment. Rates remained relatively constant in all other treatments. The average release of NO_3^- from Day 7 onwards was about 70 and 200% higher in AV and AD sediment, respectively, than in the equivalent systems devoid of algae. Molar CO_2 :DIN flux ratios (average, Day 7 onwards) based on converted CO_2 fluxes and measured DIN ($NH_4^+ + NO_3^-$) fluxes ranged between 6 and 11 in all treatments; lowest in *Nereis diversicolor* with algae (AD) and highest in *N. virens* without algae (V) (Table 2).

Oxygen uptake by *Nereis diversicolor* and *N. virens*, which was extrapolated from single worms in glass tubes to the population density ($600\ ind.\ m^{-2}$) used in the core experiment (Table 3), accounted for about 15% of the total sediment O_2 demand in the algal-free treatments, but changed by the presence of algae to about 30 (AD) and 10% (AV). Excretion of NH_4^+ by the worms (Table 3) accounted for about 20 (D) and 50% (V) of the total DIN release in the algal-free treatments,

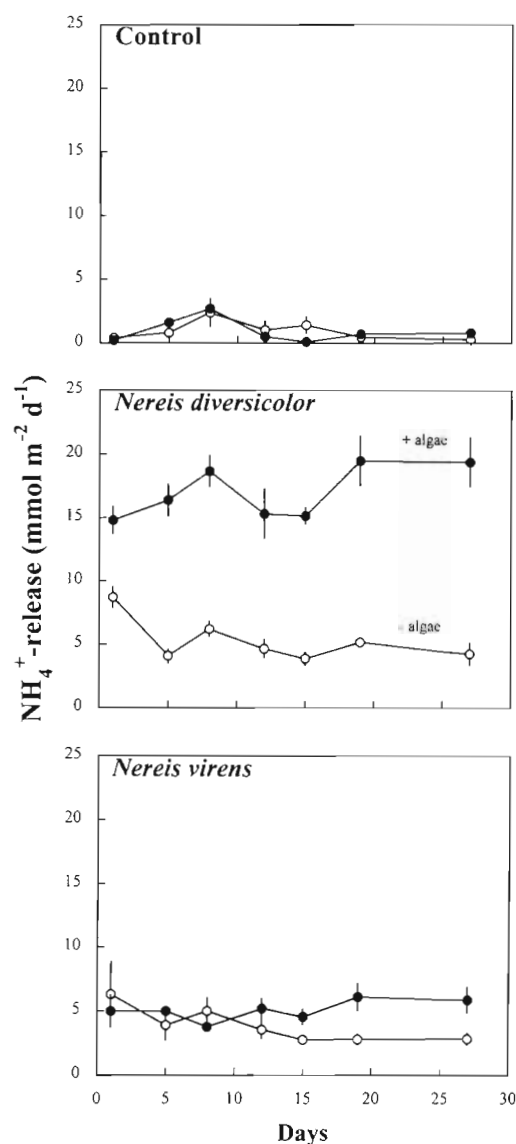


Fig. 2. Ammonium release in control, *Nereis diversicolor* and *N. virens* sediment with (●) and without (○) addition of *Rhodomonas* sp. (algae) in the overlying water throughout a 27 d experimental period. Values are presented as mean \pm SD ($n = 3$)

Table 2. C:N stoichiometry of fluxes after Day 7 with and without worm contribution given as $\Delta\text{CO}_2:\Delta\text{DIN}$ flux ratios, where ΔCO_2 is estimated from ΔO_2 using a RQ of 1.1 to 1.3 (see 'Results' for details). The final (Day 27) reaction stoichiometry (R_C/R_N) of net mineralization in the sediment is derived from slopes of porewater plots: TCO_2 versus NH_4^+ ($\Delta\text{TCO}_2:\Delta\text{NH}_4^+$, Fig. 8). Estimated R_C/R_N values for faunated sediment are presented as a range determined by the possible transport coefficient ratios ($D_C/D_N = 0.6$ to 1.0)

	AC	C	AD	D	AV	V
$\Delta\text{CO}_2:\Delta\text{DIN}$ (+worms)	7.8–9.2	6.6–7.8	5.8–6.9	7.3–8.6	8.5–10.0	9.5–11.2
$\Delta\text{CO}_2:\Delta\text{DIN}$ (–worms)	7.8–9.2	6.6–7.8	5.2–6.1	7.2–8.5	10.2–12.1	15.1–17.8
C:N porewater (R_C/R_N)	4.5	4.8	2.7–4.5	3.7–6.1	4.3–7.2	4.0–6.6

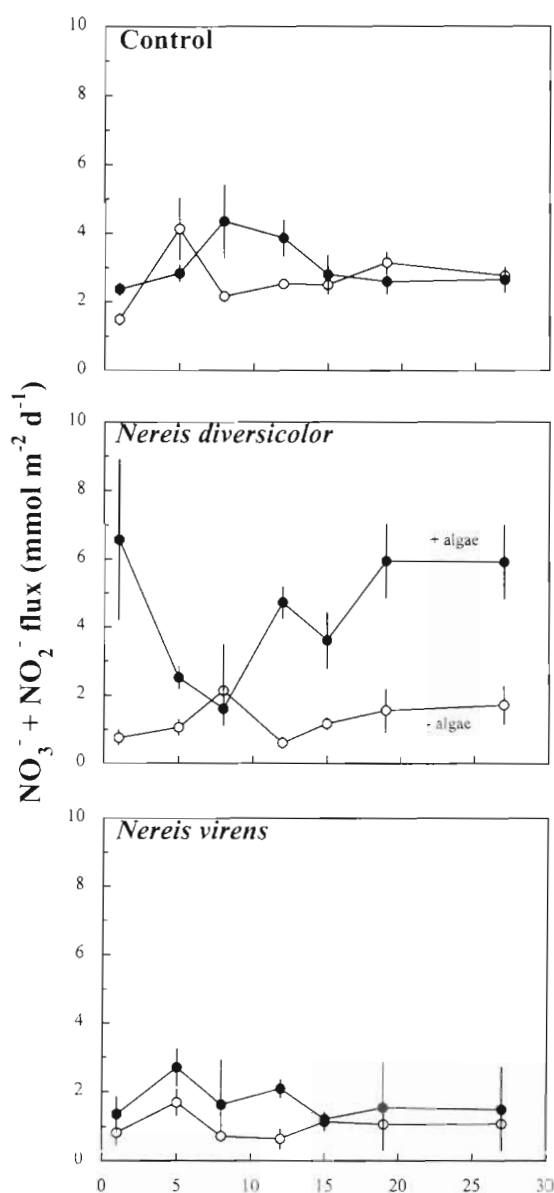


Fig. 3. Nitrate and nitrite release in control, *Nereis diversicolor* and *N. virens* sediment with (●) and without (○) addition of *Rhodomonas* sp. (algae) in the overlying water throughout a 27 d experimental period. Values are presented as mean \pm SD ($n = 3$)

whereas the worm contribution was about 20% for both species when phytoplankton was added. CO_2 release by worms was estimated from O_2 uptake by applying a RQ of 1.2 (Kristensen 1989). The C:N ratio of excretion products was 8 to 9 in *N. diversicolor* and about 3.5 in *N. virens*. After subtracting the direct worm contribution from the total fluxes in faunated sediment, the estimated microbially derived $\text{CO}_2:\text{DIN}$ flux ratios became considerably higher in sediment containing *N. virens* (V, AV) (Table 2). Subtraction of the faunal contribution in *N. diversicolor* (D, AD) treatments had only limited impact on C:N flux ratios due to the similarity of sediment and animal C:N flux ratios.

Porewater profiles

Profiles of dissolved TCO_2 and NH_4^+ increased steeply with depth in both types of control sediment (Fig. 4). TCO_2 concentrations increased from about 2 mM in the water column to 24 (AC) and 29 mM (C) at 10 cm depth, whereas NH_4^+ concentrations increased from about 0.2 mM to 3.0 (AC) and 3.6 mM (C). Most solute profiles were affected considerably by animal activities. In the presence of actively suspension-feeding *Nereis diversicolor* (AD), the porewater concentration of TCO_2 and NH_4^+ hardly increased from the sediment surface to 10 cm depth and exhibited a level around 2 and 0.3 mM, respectively. When no phytoplankton was added to the water overlying *N. diversicolor*

Table 3. Measured O_2 consumption and NH_4^+ excretion by nereid worms in glass tubes. Data are given as area-specific rates ($\text{mmol m}^{-2} \text{d}^{-1}$) by extrapolating to the population density (600 ind. m^{-2}) applied in the core experiment. Values are mean \pm SE ($n = 3$)

	AD	D	AV	V
Worm O_2 consumption	33.8 ± 2.3	7.6 ± 0.8	4.4 ± 0.6	5.5 ± 0.2
Worm NH_4^+ excretion	4.4 ± 0.3	1.1 ± 0.1	1.6 ± 0.2	2.0 ± 0.2

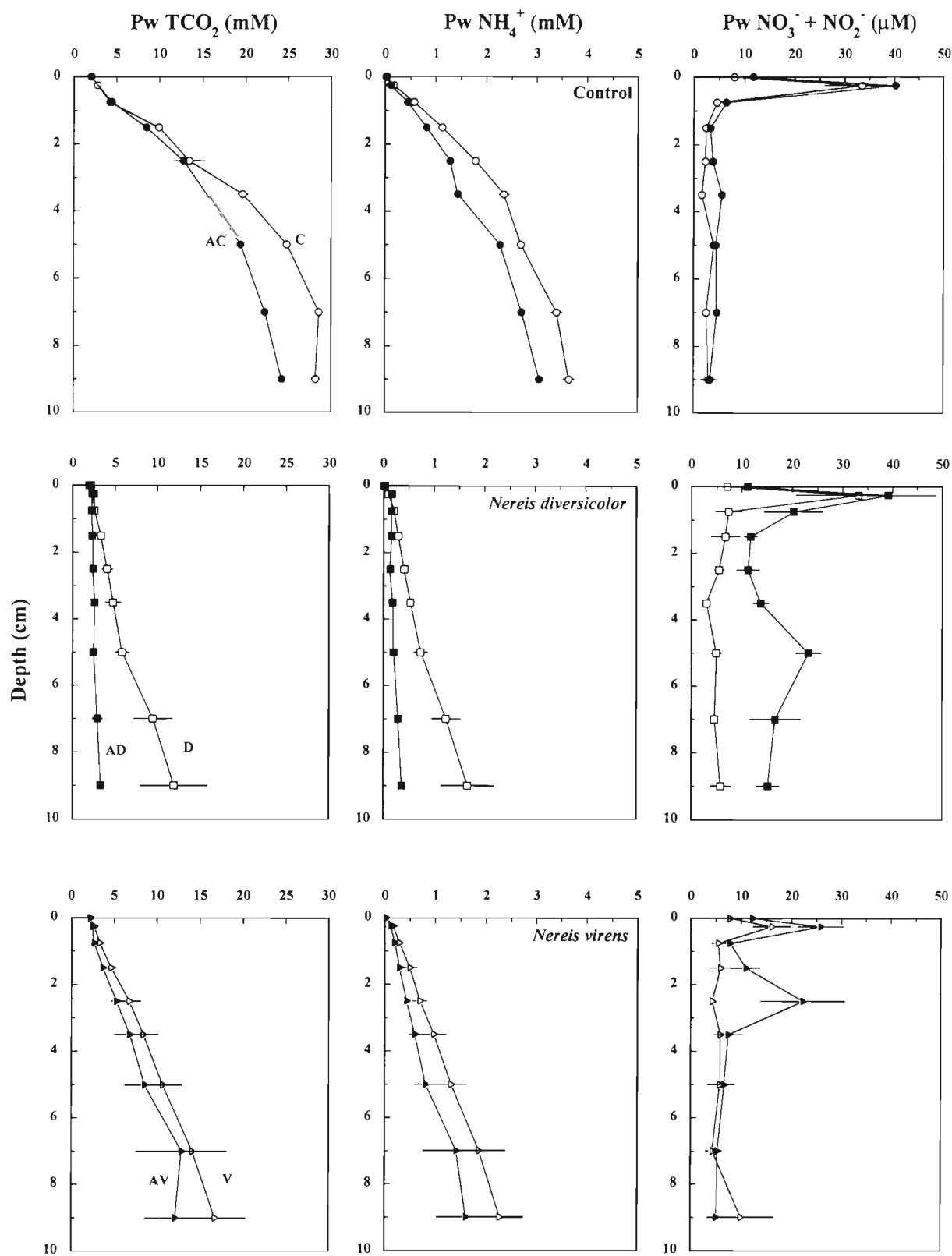


Fig. 4. Vertical profiles of porewater TCO_2 , NH_4^+ and NO_3^- in control (AC, C), *Nereis diversicolor* (AD, D) and *N. virens* (AV, V) sediment with (solid symbols) and without (open symbols) addition of *Rhodomonas* sp. (algae) in the overlying water. Values are presented as mean \pm SD ($n = 3$). Data from the control treatment with algae (AC) are only based on 1 determination

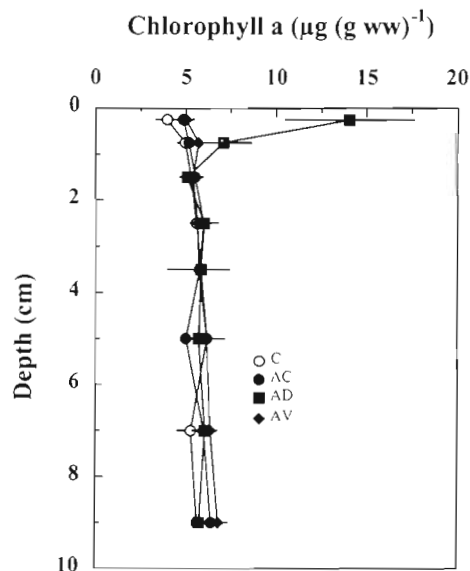


Fig. 5. Vertical profiles of chl *a* in control sediment with (AC) and without (C), and *Nereis diversicolor* (AD) and *N. virens* (AV) sediment with addition of *Rhodomonas* sp. (algae) in the overlying water. Values are presented as mean \pm SD ($n = 3$). Data for the AC treatment are only based on 1 determination

color sediment (D) the porewater concentration of TCO_2 and NH_4^+ increased gradually with depth to 12 and 2 mM, respectively. Porewater profiles of TCO_2 and NH_4^+ from sediment containing *N. virens* both without (V) and with (AV) algae were comparable to those of the D sediment. There was no significant difference between *N. virens* treatments (AV, V) for any of the measured porewater solutes.

Porewater profiles of NO_3^- generally showed depth patterns of similar shape regardless of treatment (Fig. 4). In all cases there was a peak at 0.5 cm depth with concentrations of 30 to 40 μM in both types of control (C, AC) and *Nereis diversicolor* (D, AD) sediment. However, somewhat lower peak values (15 to 25 μM) were detected in *N. virens* (V, AV) sediment. Below 0.5 cm the concentrations decreased to a constant level of 2 to 5 μM in all treatments devoid of algae (C, D, V) and the control treatment with algae (AC). A subsurface peak of about 20 μM was evident at 2 to 3 cm depth in *N. virens* (AV) sediment with algae. The concentrations of NO_3^- below 0.5 cm in algal-treated *N. diversicolor* (AD) sediment remained between 10 and 20 μM with a subsurface peak around 5 cm depth.

Sediment characteristics

The chl *a* content of the sediment was almost constant, around 5.5 $\mu\text{g g}^{-1}$ wet wt with depth in all treatments. The only exception was a 3-fold increase in

the upper 0.5 cm of *Nereis diversicolor* sediment when phytoplankton was present in the water column (Fig. 5).

Pools of POC in the upper 0.5 cm of the sediment ranged from 167 to 183 $\mu\text{mol g}^{-1}$ dry wt, and those of PON from 15 to 19 $\mu\text{mol g}^{-1}$ dry wt, except for a significant 36 and 42% increase, respectively, in the presence of both *Nereis diversicolor* and algae (AD). Bulk sediment C:N ratios in all treatments were about 8.8.

DISCUSSION

The 2 closely related nereid species *Nereis diversicolor* and *N. virens* are widely different with respect to their impact on transport processes and chemical reactions in sediments. The present experiments demonstrate that the suspension-feeding capacity of *N. diversicolor* may enhance phytoplankton deposition by more than 1 order of magnitude and benthic metabolism several-fold compared with the deposit-feeding *N. virens*. However, since only situations with 1 density of animals in allopatry subjected to a constant phytoplankton concentration under a well-stirred water column were applied for comparative purposes, direct extrapolations of the experimental results to natural conditions in the field should be made with caution.

Feeding modes

The chimney-like extensions of *Nereis diversicolor* burrows when phytoplankton is present in the overlying water appear to be indicators of active suspension-feeding by this species. Clearance estimated for *N. diversicolor* (Table 1) is comparable to *in situ* values previously obtained for populations of this species (4.6 to $9.8 \times 10^3 \text{ l m}^{-2} \text{ d}^{-1}$) (Riisgård 1991, Vedel & Riisgård 1993). The concentration of 10000 *Rhodomonas* sp. cells ml^{-1} corresponds to 12.5 $\mu\text{g chl a l}^{-1}$ (Vedel & Riisgård 1993), which is within the range of chl *a* in the water column of Kertinge Nor during productive periods (particularly spring and autumn with 10 to 50 $\mu\text{g chl a l}^{-1}$; Riisgård et al. 1995). A phytoplankton concentration of this magnitude is known to support a growth rate of *N. diversicolor* around 3.9% d^{-1} (Vedel & Riisgård 1993), which is almost identical to the growth found here for suspension-feeding individuals of this species. The retention of particulate carbon and nitrogen by suspension-feeding *N. diversicolor* was evident in the upper 0.5 cm of the sediment, where the organic content was about 40% higher than in the other treatments. The phytoplankton origin of the excess organic matter is substantiated by an almost 3-fold increase in chl *a* content near the sediment surface (Fig. 5). It may

be argued, however, that natural populations of *N. diversicolor* rarely experience high phytoplankton concentrations. Recent studies have demonstrated that suspension-feeding by dense *N. diversicolor* populations may reduce phytoplankton concentrations by up to 50% in the near-bottom water layer (5 to 10 cm) on calm days (Riisgaard et al. 1996, Vedel 1998). Thus, effective vertical mixing by waves and currents is extremely important for dense populations of this worm to realize their great suspension-feeding potential.

The disturbed sediment surface in the *Nereis virens* system with phytoplankton in the overlying water indicates that this species acted as a surface deposit feeder on passively deposited algae. The substantial reduction in ventilation activity when algae were present also indicates that individuals of this species spent more time as active deposit feeders at the surface than in the situation without algae. However, *N. virens* was only able to sustain a growth rate of less than 10% of *N. diversicolor* due to limited food supply even when phytoplankton was present in the system. Both nereid species lost weight when phytoplankton was absent in the water column due to exhaustion of food resources. The higher ventilation activity of *N. diversicolor* than *N. virens* in this situation (Table 1) may be an inherent mechanism that triggers the former species to conduct frequent suspension-feeding cycles to test for available phytoplankton, and thus increases water transport above the level needed for maintaining living conditions in the burrow (Nielsen et al. 1995). A sufficient and variable food supply is usually available for a deposit feeder, like *N. virens*, in the natural environment. The high abundance of microphytobenthos and macroalgal detritus, as well as live and dead invertebrates found in shallow coastal sediments, represents a sufficient food source for this species and also for *N. diversicolor* during phytoplankton-poor periods (Goerke 1971).

Benthic metabolism

The activities of *Nereis diversicolor* and *N. virens* considerably enhance the sediment-water exchange of O_2 (CO_2) and NH_4^+ . The faunal stimulation of benthic metabolism in the algal-free situation (O_2 uptake by a factor of 2 and NH_4^+ release by a factor of 4 to 5) is comparable to previous values reported from organic-poor sediment inhabited by *N. diversicolor* (Hansen & Kristensen 1997) or *N. virens* (Kristensen & Blackburn 1987). The worms themselves also contribute to the total benthic metabolism by feeding, assimilation and respiration. The respiratory requirement and NH_4^+ excretory capacity of the polychaetes accounted for a minor (10 to 20%) part of the total sediment O_2 uptake

and DIN release, but generally up to half of the faunal-induced flux enhancement. The remainder of the enhanced fluxes was due to stimulated microbial processes in the sediment surrounding burrows (Marinelli & Boudreau 1996). Other studies have also reported that the contribution of *Nereis* spp. to total benthic metabolism is around 20% (Andersen & Kristensen 1988, Kristensen et al. 1992). A number of mechanisms have been suggested as being responsible for the faunal-induced enhancement of microbial metabolism and capacity for organic matter degradation in sediments, e.g. redistribution of particles, enhanced pore-water transport, and secretions of labile mucus along burrow walls (Wheatcroft et al. 1994, Marinelli & Boudreau 1996, Aller & Aller 1998).

The stronger impact of suspension-feeding *Nereis diversicolor* than deposit-feeding *N. virens* on benthic metabolism after addition of phytoplankton to the water phase (Figs. 1 to 3) is partly caused by high microbial activity in burrow walls associated with enhanced deposition of algae and fecal pellets. Accordingly, we have found higher organic content and microbial decomposition rates in burrow linings of *N. diversicolor* than those of *N. virens* from a natural environment with phytoplankton in the overlying water (unpubl. data). However, the abundant supply of nutritious food for *N. diversicolor* also increased the worms' own metabolism considerably (Table 3). The nutritional state therefore appears to be an important endogenous factor influencing the metabolism of polychaetous annelids (Cammen 1987, Kristensen 1989), and thus total benthic metabolism.

The generally high NH_4^+ excretion by *Nereis virens* was probably caused by utilization of body proteins for the metabolism (Regnault 1981), because this deposit-feeding worm was in a more or less starved condition irrespective of algal presence in the overlying water. The relatively higher NH_4^+ excretion of starved *N. virens* than of suspension-feeding *N. diversicolor* was expected, but the low excretion of starved *N. diversicolor* is puzzling. Starved individuals of this species may, to a larger extent than *N. virens*, lose excess nitrogen in dissolved organic form (e.g. urea; O'Malley & Terwilliger 1975) or via secretion of protein-rich mucus for filter construction.

Porewater relations

The impact of nereid polychaetes on transport conditions in the sediment is evident as significantly displaced porewater profiles in systems with animals (Fig. 4). A similar strong influence of infaunal ventilation on the concentration and transport of porewater solutes have been observed frequently in coastal

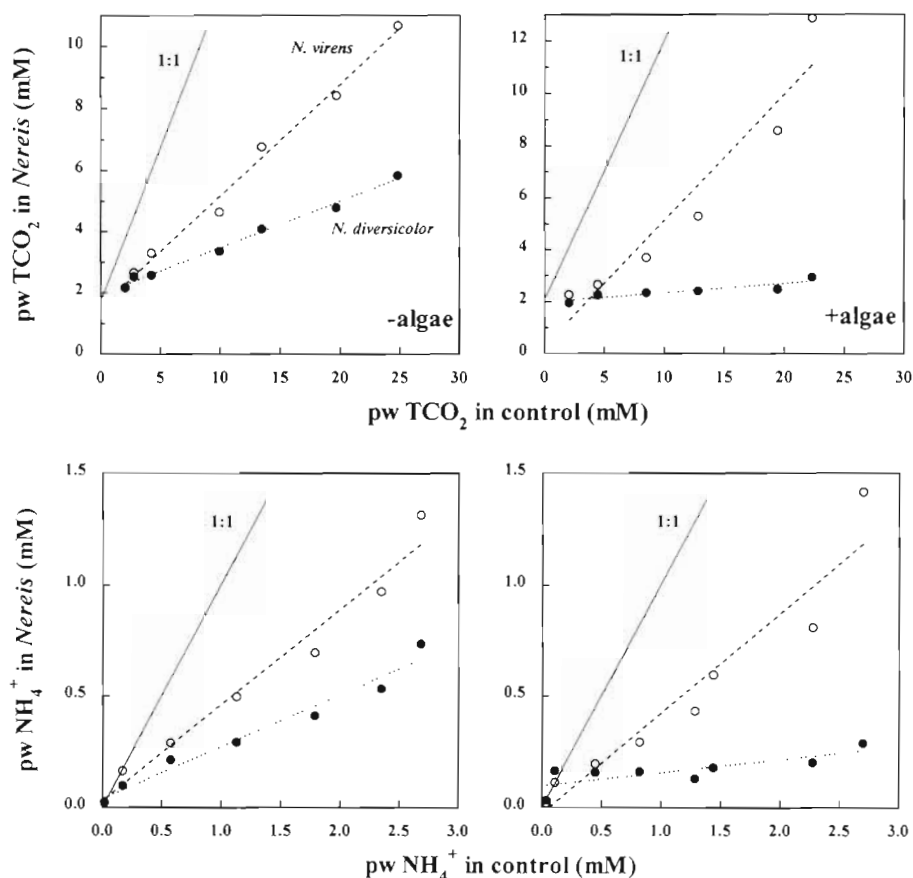


Fig. 6. Relationship between solute concentration (TCO_2 and NH_4^+) in the porewater of control sediment and the corresponding *Nereis diversicolor* (.....) or *N. virens* (-----) treated sediment. Left panels: systems without (-algae); right panels: with (+algae) phytoplankton in the overlying water. Lines are drawn according to least-squares linear regression. 1:1 lines are shown for comparison (displaced 2 mM upward in the TCO_2 plots)

marine sediments (Aller & Yingst 1985, Huettel 1990, Kristensen & Hansen 1999). The lower concentrations of TCO_2 and NH_4^+ found in the algal-treated, compared with the non-algal-treated, controls may be caused by a stimulated growth and activity of bioturbating meiofauna and small polychaetes in the surface layer of sediments underlying a phytoplankton-rich water column (Aller & Aller 1992). Enhanced solute transport in the uppermost sediment layer will always be reflected as displaced porewater profiles deeper in the sediment.

Porewater profiles of diagenetically active solutes in sediments are basically controlled by a balance between microbially derived reaction rates and the prevailing transport conditions (Aller 1982). The solute profiles in the present experiment were clearly affected by diffusion down to at least 6 to 8 cm depth in control sediments, and by *Nereis*-induced transport to at least 10 cm depth in faunated sediments. The upper 6 to 10 cm of the sediment can therefore be considered an open, diffusion-dominated zone approaching steady state (Aller & Mackin 1989, Kristensen & Hansen 1999). Although the absolute concentrations are different, the basic shape of porewater profiles of TCO_2 and NH_4^+ should be independent of infaunal activity within the bioturbated zone when reaction and

transport rates are assumed constant with depth (Kristensen & Hansen 1999). Transport conditions in the examined depth interval (0 to 10 cm) should be depth-independent in the *Nereis*-inhabited sediment as suggested by a burial depth of about 10 cm. Because the sediment was initially homogenized in the present study, the reaction rates (or CO_2 and NH_4^+ production) are also approximated as depth-independent and constant. This was shown in a similar experiment by Kristensen & Hansen (1995). The above assumptions are substantiated by the more or less linear relationship between porewater (TCO_2 and NH_4^+) profiles in *Nereis*-inhabited and control sediment (Fig. 6). Slopes lower than unity indicate a faster removal of solutes due to ventilation transport via burrows than by molecular diffusion. The minor curvature observed for some *N. virens* cases in Fig. 6 is probably caused by a slight decrease in ventilation activity, and thus reduced solute transport in the deepest part of the examined depth interval.

The average porewater concentration in bioturbated sediments is generally considered to depend on the size and abundance of infauna (Aller 1982). However, the ventilation activity varies considerably between infaunal species (Kristensen 1988) and may

depend on the feeding mode within a single species, as observed here for both *Nereis diversicolor* and *N. virens* (Table 1). The buildup of porewater solutes may therefore, in addition to size and density, also be a function of total population ventilation activity. The direct relationship between ventilation rate of our nereid populations of a fixed size and porewater concentrations is clearly demonstrated in Fig. 7. Slopes of porewater (TCO_2 and NH_4^+) plots between bioturbated and control sediments (from Fig. 6) decrease exponentially with population ventilation rate of the 2 nereid species studied here. The relationship was similar for both examined solutes at a fixed *Nereis* density of 600 ind. m^{-2} (porewater ratio(TCO_2) = $-0.122 \ln(\text{ventilation}) + 0.99$, $r^2 = 0.99$; porewater ratio(NH_4^+) = $-0.109 \ln(\text{ventilation}) + 0.94$, $r^2 = 0.95$) and possibly also for other porewater constituents subject to zero order kinetics. Aller (1982) has shown similar relationships by a modelling approach, but he used population density as the independent variable instead of total population ventilation rate. However, future studies of infaunal impacts on solute transport in sediments should consider population ventilation as a key parameter when species composition, abundance and environmental conditions change in time and space (Webster 1992, Marinelli 1994).

Carbon and nitrogen stoichiometry

It has been shown that the C:N ratio of the mineralized organic matter may be ascertained from vertical steady-state porewater profiles of TCO_2 and NH_4^+ if simple stoichiometric decomposition following first-order kinetics occurs (Berner 1977, Kristensen & Hansen 1995). More specifically, the slope of TCO_2 versus NH_4^+ plots ($\Delta\text{TCO}_2/\Delta\text{NH}_4^+$) multiplied with the ratio of sediment transport coefficients for TCO_2 and NH_4^+ (D_C/D_N) provides an estimate of net carbon and nitrogen reaction stoichiometry (R_C/R_N) within the sediment according to:

$$R_C/R_N = (\Delta\text{TCO}_2/\Delta\text{NH}_4^+) \times (D_C/D_N)$$

The ratio D_C/D_N is 0.6 in defaunated sediment where molecular diffusion is the only transport process, and 1.0 when the transport is generated solely by porewater advection. Kristensen & Hansen (1999) showed that solute transport in sediments inhabited by actively ventilating infauna is driven by a combination of diffusion (i.e. non-local exchange; Emerson et al. 1984) and biogenic porewater turbulence (i.e. effective diffusion, Berner 1980). Diffusion dominates in non-permeable muds, whereas both diffusion and porewater advection are important in permeable sandy sediments (Kristensen & Hansen 1999). For the present sandy sediment

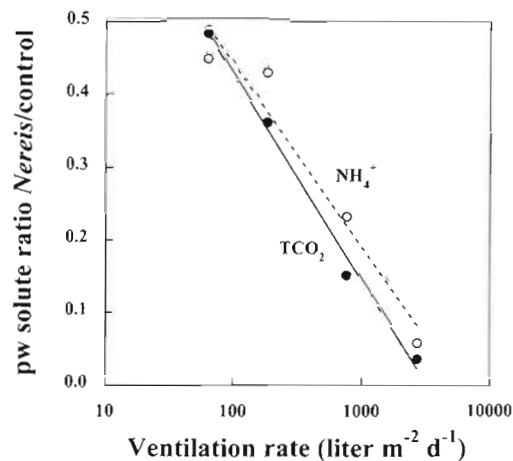


Fig. 7. Slopes of the relationship between porewater solute concentrations in control and *Nereis*-treated sediment as a function of nereid population ventilation rate. Lines are drawn according to least-squares linear regression. (—) TCO_2 ; (-----) NH_4^+ . Note the logarithmic ventilation scale

the effective ratio of transport coefficients (D_C/D_N) is 0.6 in the control sediment and within a range of 0.6 and 1.0 in the faunated treatments. However, the exact value for the bioturbated sediment is unknown and depends on the ventilation activity of the worms.

A significant linear relationship between porewater TCO_2 and NH_4^+ is evident for all treatments (Fig. 8) providing slopes ranging from 4.4 (AD) to 8.0 (C). By assuming steady-state and no porewater advection, the C:N reaction stoichiometry in defaunated sediments varies from 4.5 to 4.8 (Table 2). For the faunated sediments with an unknown degree of porewater advection, the C:N reaction stoichiometry must range from 2.7 – 4.3 ($D_C/D_N = 0.6$) to 4.5 – 7.2 ($D_C/D_N = 1.0$). Low C:N ratios such as those found here (3 to 7) have been observed in a number of studies (Berner 1977, Klump & Martens 1987, Kristensen & Hansen 1995), and indicate a preferential microbial degradation of organic nitrogen, since the bulk sediment C:N ratio usually is between 8 and 10 (8.8 in the present study). The rate and stoichiometry of organic matter decomposition in sediments are generally considered to be controlled by the size and chemical composition of the organic pool actually being degraded and not by the bulk sediment composition (Westrich & Berner 1984, Kristensen & Blackburn 1987). Particularly in the *Nereis diversicolor* treatment with algae, a sufficient source of labile protein was available from the retained algal cells (C:N = 5.5) to provide the very low C:N reaction stoichiometry in this sediment.

The C:N stoichiometry of net organic matter mineralization within the sediment was always lower than

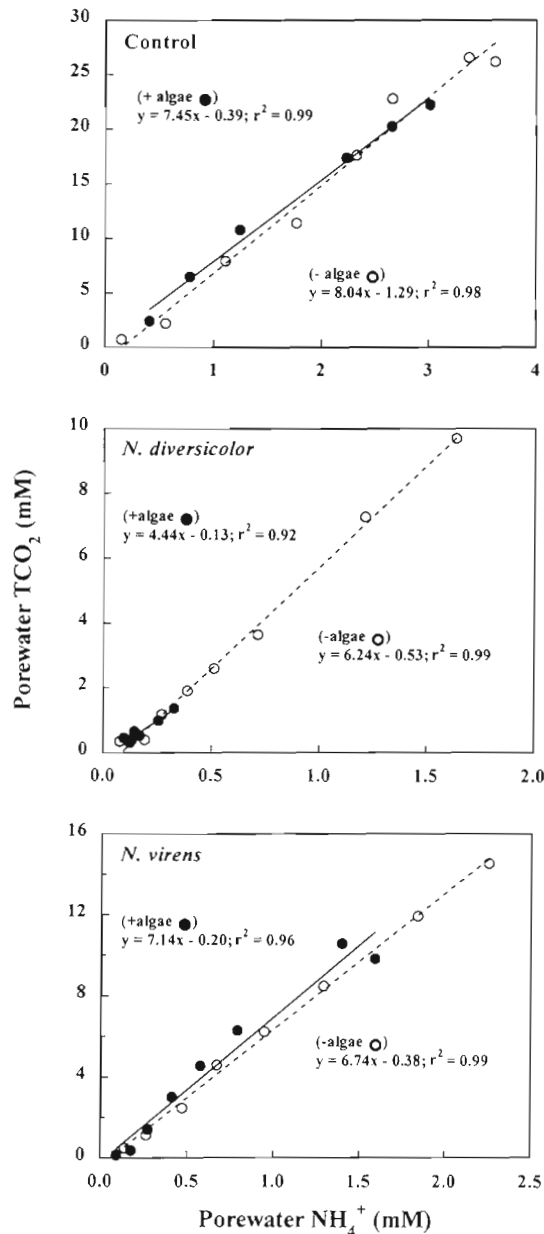


Fig. 8. Plots of porewater NH_4^+ versus TCO_2 in all treatments. Lines are fitted by least-squares linear regressions according to the equations given

for sediment-water fluxes (Fig. 9), indicating a net loss or retainment of nitrogen within the sediment. The missing nitrogen may either be lost as N_2 via denitrification (Seitzinger 1988, Joye et al. 1996) or incorporated into the organic pool by bacterial assimilation (Blackburn 1988). The loss was apparently proportional to benthic metabolism as depicted from the almost constant deviation from the 1:1 line in the flux versus porewater C:N relationship (Fig. 9). The nitrogen loss in the algal-treated systems accounted

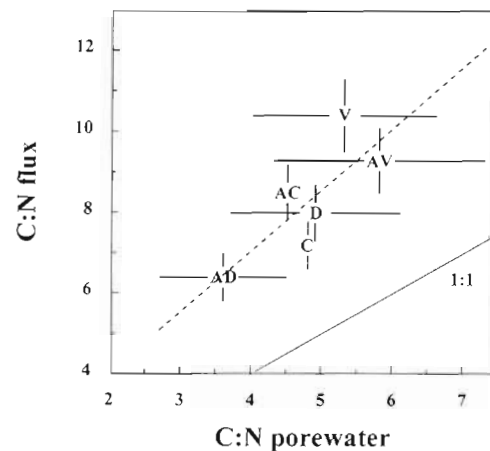


Fig. 9. Relationship between C:N stoichiometry of fluxes after Day 7 ($\Delta\text{CO}_2/\Delta\text{DIN}$ flux ratios) and C:N stoichiometry of the final (Day 27) reaction stoichiometry (R_C/R_N) of net mineralization in the sediment derived from slopes of porewater plots: TCO_2 versus NH_4^+ ($\Delta\text{TCO}_2/\Delta\text{NH}_4^+$, Fig. 8). Letter symbols indicate the different treatments. Vertical error bars represent the range obtained when ΔCO_2 is estimated from ΔO_2 using RQs of 1.1 and 1.3. Horizontal error bars represent the range obtained when R_C/R_N values for faunated sediment are estimated using transport coefficient ratios (D_C/D_N) of 0.6 to 1.0. The 1:1 line is shown for comparison

for 60 to 80% of the measured DIN efflux; proportionally highest in the control and lowest in the *Nereis diversicolor* treatments. A much wider range is apparent in the systems devoid of algae, ranging from 30% in the control to 100% of the DIN efflux in the *N. virens* treatments. Although the present data provide no quantitative differentiation between the various nitrogen sinks, it is generally accepted that denitrification is the most important scavenger of combined inorganic nitrogen in marine sediments (Seitzinger 1988).

Ecological implications

Based on fluxes and transformations determined in this study, the potential impact of *Nereis diversicolor* and *N. virens* for sedimentary carbon and nitrogen dynamics in shallow coastal sediments can be evaluated in the presence and absence of phytoplankton in the overlying water (Table 4). It should be noted, however, that the present laboratory experiment does not include other autochthonous (i.e. benthic microalgae) and allochthonous (i.e. drifting seaweeds) sources of organic matter. Ingestion by animals and incorporation into sediments of these organic sources under natural conditions may affect fluxes and transformations of carbon and nitrogen compared with the laboratory-based budgets presented here.

Most of the organic carbon and nitrogen captured by suspension-feeding *Nereis diversicolor* are lost as excess flux to the water column via metabolic processes by bacteria and the worms themselves, but about 30% are retained within the sediment (Table 4). About $\frac{2}{3}$ of the retained carbon and nitrogen is incorporated into living tissue by the growing worms. The remainder is either assimilated into microbial biomass, lost as N_2 via denitrification, or stored as undecomposed algal remains within the sediment. It appears therefore that organic carbon and nitrogen accumulates in sediments inhabited by *N. diversicolor* during periods of high phytoplankton availability (e.g. spring and fall bloom periods). A net loss of sedimentary carbon and nitrogen always occurs in the presence of *N. virens* irrespective of phytoplankton concentration in the overlying water (and for *N. diversicolor* without algae, Table 4). Both animals and bacteria enhance the overall benthic metabolism despite the lack of any organic input. Most of the excess carbon loss is due to microbial mineralization processes, whereas NH_4^+ excretion by animals appears to be more important for nitrogen. Accordingly, populations of suspension-feeding *N. diversicolor* are potential net increasers of sedimentary organic matter during periods with sufficient phytoplankton in the overlying water, but net decreasers when no phytoplankton is present. Populations of *N. virens*, on the other hand, are always net decreasers of organic matter in sediments.

Surface deposit-feeding polychaetes, like nereids, may have territorial struggles resulting in disturbances of the feeding activity or increased emigration (Evans 1973). In some cases it may lead to complete spatial separation of populations of different species (Miron & Kristensen 1993). The ability to change feeding mode may, however, reduce competitive interactions (Levin 1982, Taghon 1992). Thus, *Nereis diversicolor* spends less time at the surface when suspension feeding, which reduces the chance of confrontation with neighboring individuals. The adaptation of *N. diversicolor* to part-time suspension feeding creates a competitive release and allows species like *N. diversicolor* and *N. virens* to coexist. The enrichment of surface sediments with labile organic matter caused by suspension-feeding *N. diversicolor*, which is a nutritious food source for deposit feeders like *N. virens*, may contribute further to reducing competition and promoting coexistence. Nevertheless, these 2 co-occurring and congeneric polychaete species have very different impacts on sediment biogeochemistry due to their different feeding behaviour. This fact must be considered when the role of these and other related infaunal species on sediment processes are evaluated, i.e. the feeding biology and behaviour of infaunal organisms are important for their influence on element cycling in coastal marine environments.

Table 4. Budgets of carbon and nitrogen fluxes ($mmol\ m^{-2}\ d^{-1}$) in sediments inhabited by *Nereis diversicolor* (AD, D) and *N. virens* (AV, V) in the presence and absence of phytoplankton in the water column. Values are given as the difference between systems with and without nereids and are averaged from Day 7 onwards (20 d). The CO_2 efflux is estimated from measured O_2 uptake by applying a mean RQ of 1.2 for both sediment fluxes and worm respiration. Microbial respiration (resp.) and mineralization (min.) are estimated as the difference between total rates and worm contribution. Growth of nereids is transformed into carbon and nitrogen units using appropriate conversion factors (Vedel & Riisgård 1993, Nielsen et al. 1995). Positive values indicate input to, and negative values indicate loss from, the sediment system

	AD-AC	D-C	AV-AC	V-C
POC captured	139.4	0	-0.4	0
CO_2 efflux				
Worm resp.	-40.6	-9.1	-5.3	-6.6
Microbial resp.	-60.6	-13.7	-18.5	-11.4
C-retained				
Worm growth	26.5	-2.8	1.2	-3.7
Sediment	11.7	-20.0	-25.4	-21.7
PON captured	25.4	0	-0.1	0
DIN efflux				
Worm excr.	-4.4	-1.1	-1.6	-2.0
Microbial min.	-13.1	-1.4	-0.6	1.4
N-retained				
Worm growth	5.1	-0.6	0.3	-0.7
Sediment	2.8	-1.9	-2.6	0.1

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