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Effects of *Tubifex tubifex* (Oligochaeta: Tubificidae) on N-mineralization in freshwater sediments, measured with ^{15}N isotopes

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ABSTRACT: Sediment cores containing different densities of *Tubifex tubifex*, ranging from 0 to 70000 ind. m^{-2}, were incubated in the laboratory. Rates of O_2 and NO_3^- uptake, NH_4^+ production, nitrification and denitrification were determined from sediment-water fluxes. Pore water NH_4^+ was measured at the end of the experiment. At natural densities, ~50000 ind. m^{-2}, there were increased rates of O_2 consumption (×2), denitrification of water phase NO_3^- (×3) and NH_4^+ efflux (×26). Nitrification was stimulated at low worm densities, but inhibited at higher worm densities. The transport of reduced compounds and organic matter, with the fecal pellets, to the sediment surface stimulated anoxic conditions in the inhabited microcosms. These anoxic conditions led to increased rates of denitrification and were responsible for the decrease in nitrification at higher worm densities. Approximately 25% of the NO_3^- produced by nitrification within the sediment was subsequently denitrified. Denitrification was responsible for 25% of the NO_3^- disappearance from the system. The higher rates of denitrification were counterbalanced by higher rates of NH_4^+ flux from the sediment. It is likely, however, that the presence of *T tubifex* resulted in a net loss of nitrogen that could otherwise have been used by the primary producers.

KEY WORDS: Bioturbation · Nitrification · Denitrification · Sediments

INTRODUCTION

Macrobenthos, through their burrowing, feeding, locomotive, respiratory and excretory activities, play an important role in mediating both physical and chemical processes near the sediment-water interface (Fisher 1982, McCall & Tevesz 1982). Tubificid worms are often, along with chironomid larvae, the most abundant macrofauna species in eutrophied stream and lake sediments. Population densities can be as high as millions of individuals per m^2 (Palmer 1968). Many studies concerning the effect of these worms on the physical properties of the sediment have been carried out (McCall & Fisher 1980, Fisher 1982, McCall & Tevesz 1982). However, their role in nutrient cycling, specifically nitrogen cycling, has received less attention (Kikuchi & Kurihara 1977, 1982, Chaterpaul et al. 1979, 1980).

Tubificid worms feed primarily in the top 2 to 8 cm of sediment (McCall & Tevesz 1982), adjusting their feeding depth to lower strata at higher worm densities (Robbins et al. 1979, McCall & Fisher 1980). Tubificid worms are 'conveyor belt' feeders (Rhoads 1974). They typically live and feed head down in the sediment. Some portion of the posterior of the worms may project above the sediment-water interface. The worms selectively ingest silt and clay particles at depth and digest the attached microflora, primarily bacteria (Davis 1974). Fecal pellets are deposited at the sediment-water interface, where they may form a pelletized layer.

Studies of the effect of bioturbation by marine infauna on nitrification and denitrification processes

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(Kristensen et al. 1991, Pelegrí et al. 1994, Pelegrí & Blackburn 1995) have shown that the particular feeding and burrowing strategies of the various animals can lead to variable stimulation of aerobic respiration, nitrification and denitrification. The aim of this study is to clarify the effect of tubificid worms on nitrogen metabolism and on fluxes across the sediment-water interface.

MATERIAL AND METHODS

Undisturbed sediment cores (19.5 cm long and 3.5 cm inner diameter), containing no visible macrofauna, were collected in Giber Å stream (Denmark). This stream is dominated by runoff from agricultural areas and receives fluctuating amounts of NO_3^- and organic matter (Nielsen et al. 1990). *Tubifex tubifex* Müller (Oligochaeta: Tubificidae), collected from sieved (500 µm) Universitetsparken Lake sediment, were added to these cores (n = 11) at densities ranging from 0 to 70 ind. $core^{-1}$ (70000 ind. m^{-2}). The worms dug immediately into the sediment. The cores were placed in a reservoir containing well-aerated tap water, and kept in darkness at 10.8 ± 0.8°C. An atmospheric NH_4^+ trap, consisting of 3 gas washing bottles containing 0.1 M H_2SO_4, 50 mM K_2HPO_4 and distilled water connected in line, was installed in the aerating circuit between the air pump outlet and the reservoir. Ammonium concentrations in the reservoir water ranged from 0.3 to 1.1 µM during the experiment.

Experimental procedure. Every second day O_2, NH_4^+ and NO_3^- + NO_2^- fluxes were measured in order to determine when steady state was reached. This was done by closing the cores for 2 h, after which samples from the overlying water were collected and immediately frozen. Eleven days after setup, when steady state was reached, $^{15}NO_3^-$ (5 mM $K^{15}NO_3^-$, 99% ^{15}N stock solution) was added to the reservoir water to a final concentration of 38.3 µM NO_3^- (69.7% $^{15}NO_3^-$). After 2 d, the cores were stoppered and incubated for 4 to 5 h, which resulted in less than 20% O_2 depletion. At the end of the incubation the stoppers were removed and water samples were taken and stored. Samples for analysis of dissolved N_2 gas were stored in 6 ml glass vials (Exetainer, Labco Ltd, Buckinghamshire, UK), containing 2% $ZnCl_2$ in order to stop microbial activity. Nitrogen gas was extracted from these water samples with 0.9 ml helium, and analyzed by mass spectrometry. Samples for analyzing NH_4^+, NO_3^- + NO_2^- and $\%^{15}NO_3^-$ enrichment were collected in plastic vials and immediately frozen.

In order to test the applicability of the denitrification assay in our bioturbated sediment, the water in the reservoir was exchanged with water containing 73 µM NO_3^- (83% $^{15}NO_3^-$) and the cores were incubated again following the same procedure as described above. Two days later a final incubation took place (reservoir water containing 62.1 µM NO_3^-, 81% $^{15}NO_3^-$).

At the end of the experiment the cores were cut into 0–0.5, 0.5–1, 1–2, 2–3 and 3–5 cm sections. Pore water was obtained by centrifuging the sediment for 10 min, at 3000 rpm (2000 × *g*) in double centrifuge tubes (Blackburn 1980). The supernatant was immediately collected and frozen for later analysis. Unfortunately, due to the small volumes of pore water, the analyses were run on single samples.

Analysis. Oxygen was measured directly in the microcosms with an oxygen microsensor provided with a guard cathode (Revsbech et al. 1989). NO_3^- + NO_2^- was measured by standard methods (Grasshoff et al. 1983) in a flow injection analyzer (Tecator, Höganäs, Sweden) and analyses of NH_4^+ were done by the salicylate hypochlorite method (Bower & Holm-Hansen 1980). The formation of ^{15}N labeled dinitrogen pairs ($^{14}N^{15}N$ and $^{15}N^{15}N$) by denitrification was measured on an isotope ratio mass spectrometer as described by Nielsen (1992). The concentration of the dinitrogen pairs in the samples was calculated by multiplying their ratio ($^{14}N^{15}N$ or $^{15}N^{15}N$/total N) by the N_2 concentration in the water (Weiss 1970). The $\%^{15}NO_3^-$ enrichment was analyzed on a mass spectrometer after using denitrifying bacteria cultures to transform NO_3^- to gaseous N_2 (Risgaard-Petersen et al. 1993).

Calculations. Rates of denitrification were measured using the isotope pairing technique (Nielsen 1992). The formation rates of single- ($^{14}N^{15}N$) and double-labeled ($^{15}N^{15}N$) dinitrogen pairs were used to calculate the denitrification of NO_3^- coming from the overlying water (*dw*) and of NO_3^- generated within the sediment by nitrification (*dn*):

$$d_{15} = (^{14}N^{15}N) + 2(^{15}N^{15}N) \quad \text{(Koike \& Hattori 1978)};$$

$$d_{14} = d_{15}\frac{(^{14}N^{15}N)}{2(^{15}N^{15}N)},$$

$$dw = d_{15}\frac{100}{e_{15}},$$

$$dn = d_{14} + d_{15} - dw \quad \text{(Nielsen 1992)}$$

where e_{15} is the $\%^{15}NO_3^-$ enrichment of the reservoir water.

Nitrification was calculated by a modification of the equation described by Blackburn (1993) for $^{15}NH_4^+$ turnover in sediments:

$$d = (d - i)\frac{\ln(e_0 - 0.003663) - \ln(e_t - 0.003663)}{\ln\frac{c_t}{c_0}} + dn$$

where *d* is the nitrification rate, *i* is the NO_3^- consumption rate, *e* is the $\%^{15}NO_3^-$ enrichment, *c* is the NO_3^-

concentration in the water phase (0 = initial, t = final) and 0.003663 is the natural abundance of ^{15}N in nature.

The rates of *dw* and NO_3^- uptake are dependent on the NO_3^- concentration in the water column, which was different in the various incubations. These rates were normalized to 50 µM NO_3^- concentration in the overlying water for all incubations.

RESULTS

Oxygen consumption (Fig. 1A), NH_4^+ fluxes (Fig. 1B) and NO_3^- consumption (Fig 1C) were stimulated by the presence of the worms.

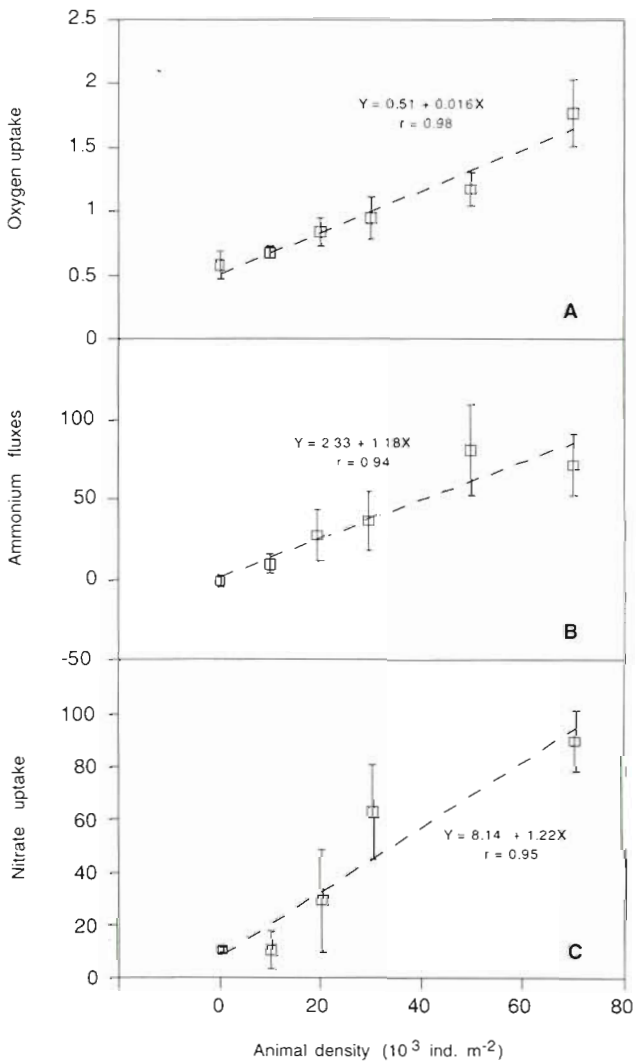

Fig. 1. *Tubifex tubifex*. (A) Oxygen uptake (mmol m^{-2} h^{-1}), (B) ammonium effluxes (µmol m^{-2} h^{-1}) and (C) nitrate uptake (µmol m^{-2} h^{-1}) corrected to 50 µM NO_3^- in the water phase, versus tubificid worm density. Each data point is the average of 6 replicates, except for microcosms containing 10000 ind. m^{-2} with only 3 replicates. Error bars represent standard errors

The isotope pairing technique assumes that the increase in concentration in the water by the addition of $^{15}NO_3^-$ does not influence denitrification of the sediment-produced $^{14}NO_3^-$ and that the NO_3^- species ($^{15}NO_3^-$ and $^{14}NO_3^-$) are uniformly mixed in the denitrification zone. Since the production of unlabeled N_2 ($^{14}N^{14}N$) is not measured directly but estimated from the production of single- ($^{14}N^{15}N$) and double-labeled ($^{15}N^{15}N$) dinitrogen pairs, changes in the ratio of *dw* (denitrification of NO_3^- coming from the overlying water) to *dn* (denitrification of NO_3^- generated within the sediment oxic layer) due to bioturbation may underestimate the *dn* values. This can be tested by incubating with different concentrations of $^{15}NO_3^-$. Thus at higher $^{15}NO_3^-$ levels more $^{14}NO_3^-$ will be paired with $^{15}NO_3^-$ to form measurable $^{14}N^{15}N$ and less $^{14}N^{14}N$ is formed. Rates of *dn*, measured with NO_3^- concentrations in the overlying water ranging from 38.3 to 73 µM, were not significantly different ($p < 0.001$). Thus the addition of 38.3 µM NO_3^- to the overlying water was sufficient to avoid underestimation of *dn* rates. Rates of nitrification and *dn* (Fig. 2A) increased significantly ($p < 0.05$) by increasing the worm density from 0 to 20000 ind. m^{-2}. However, nitrification rates decreased significantly ($p < 0.05$) when worm density increased from 20000 to 70000 ind. m^{-2}. Around 25% of the total NH_4^+ nitrified was subsequently denitrified in the suboxic sediment layer.

Denitrification of NO_3^- coming from the overlying water (*dw*) was stimulated by the presence of the worms (Fig. 2B). An average of 25% of the NO_3^- uptake by the sediment was removed from the system by denitrification. Rates of *dw* represented from 20 to 90% of the total denitrification rates in microcosms containing worm densities ranging from 0 to 70000 ind. m^{-2}.

Ammonium concentrations increased with depth, but the increase, compared with the control, was less with < 20000 ind. m^{-2} and greater with > 20000 ind. m^{-2} (Fig. 3).

DISCUSSION

In our experiments, oxygen uptake was increased 3-fold at a tubificid density of 70000 ind. m^{-2}, whereas McCall & Fisher (1980) reported a 2-fold increase at 100000 ind. m^{-2}, 20% of which was due to worm respiration. Our results indicated that the worms (20000 ind. m^{-2}) increased denitrification of NO_3^- coming from the overlying water by 175%. Chaterpaul et al. (1980) reported that *Limnodrilus hoffmeisteri* and *Tubifex tubifex* (12000 to 16000 ind. m^{-2}) increased denitrification rates by only 80%, in spite of NO_3^- concentrations

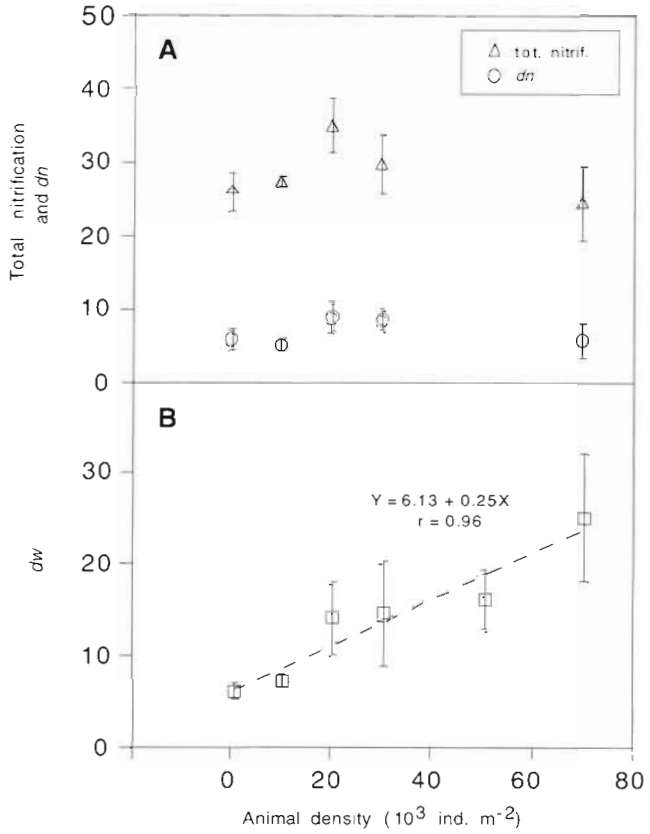

Fig. 2. *Tubifex tubifex*. (A) Total nitrification and denitrification of NO_3^- generated within the sediment (*dn*) and (B) denitrification of NO_3^- coming from the overlying water (*dw*), corrected to 50 µM NO_3^- in the water phase, versus tubificid worm density. Each data point is the average of 6 replicates, except for microcosms containing 10000 ind. m^{-2} with only 3 replicates. Error bars represent standard errors. Units: µmol m^{-2} h^{-1}

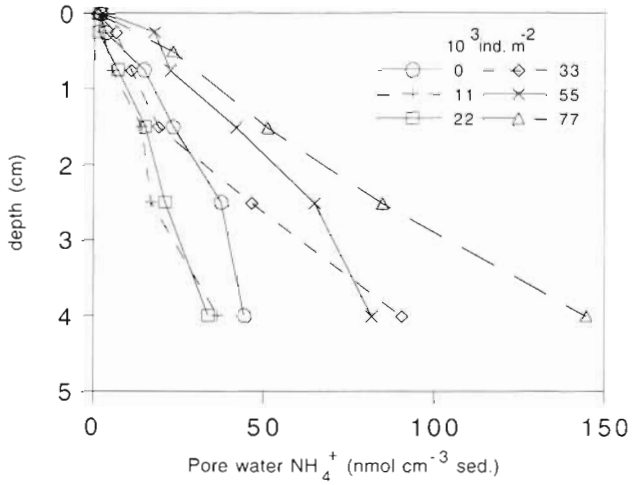

Fig. 3. *Tubifex tubifex*. Sediment concentration profiles of pore water NH_4^+ in microcosms containing tubificid worm densities ranging from 0 to 70000 ind. m^{-2}

in the overlying water 4 times higher in their experiment.

The increase in oxygen consumption rates and in nitrate uptake, in bioturbated microcosms, could be associated with a change in the characteristics of the surface sediment, due to the particular feeding strategy of *Tubifex tubifex* or to active irrigation of the burrow by the worms (Pelegrí et al. 1994). Tubificid worms are capable of affecting many sediment properties by the formation of a stable layer of fecal pellets at the sediment surface. Egested material is packaged into mucus-bound pellets which may maintain their integrity for some time after deposition on the sediment surface (Fisher 1979). McCall & Fisher (1980) reported increases in sediment porosity of 80% at the 0–1.5 cm layer due to fecal pellets (*Limnodrilus hoffmeisteri* and *T. tubifex*, 3000 ind. m^{-2}). They believed that changes in sediment porosity were responsible for an increased diffusion of chloride tracer in sediment containing *T. tubifex* (100000 m^{-2}). Wood (1975), however, attributed an increased diffusion of rhodamine B into sediment to irrigation by tubificid worms. Increased porosity and/or diffusivity results in a deeper penetration by oxygen (Davis 1974, Fukuhara 1987) and NO_3^-, but the transport of reduced material to the sediment surface and the accumulation of organically enriched fecal pellets can result in increased rates of oxygen and NO_3^- utilization. McCall & Fisher (1980) reported a 2-fold increase in organic content at the 0–1.5 cm layer, probably attributable to the higher organic content in fecal pellets compared to bulk sediment (35%; Brinkhurst et al. 1972).

The pore water NH_4^+ content increased in sediments at worm densities >20000 ind. m^{-2}. Similar increases occurred in the 0–5 cm layer of rice-field soil containing *Limnodrilus hoffmeisteri* and *Branchyura sowerbyi* (Kikuchi & Kurihara 1977) and in sediment with mixed populations of *L. hoffmeisteri* and *L. cervix* (Fisher 1982). This increased NH_4^+ might have been due either to animal excretion or to enhanced microbial activity (Matisoff et al. 1985). Certainly, tubificids excrete NH_4^+ at quite high rates, 0.6 nmol NH_4^+ $ind.^{-1}$ h^{-1} (Gardner et al. 1983), and this occurs well below the sediment surface (Wisniewski & Planter 1985). It is probable that most of the increased NH_4^+ in our sediments could be attributed to direct worm excretion, rather than to increased microbial activity. Increases in porosity and/or diffusivity at the sediment surface due to *Tubifex tubifex* may lead to enhanced NH_4^+ fluxes out of the sediment, compared to non-inhabited microcosms. Our measurements showed indeed increased NH_4^+ fluxes in the presence of the worms.

Nitrification rates increased by 23% from 0 to 20000 ind. m^{-2}, and decreased by 30% from 20000 to 70000

ind. m^{-2}. This accords well with increased rates of nitrification as organic degradation increases up to the highest organic loading rates, at which an inhibition of nitrification took place (Blackburn 1990, Blackburn & Blackburn 1993, Caffrey et al. 1993). As the rate of organic degradation increased, the quantity of NH_4^+ increased, but the availability of O_2 decreased resulting in a compression of the zone of nitrification into a thinner band, closer to the sediment surface. Eventually, even though NH_4^+ concentrations might be high, the rate of loss of NH_4^+ by diffusion exceeds the rate at which it could be oxidized. This scenario fits the observed data: NH_4^+ concentrations increased with worm density and this was coupled to higher rates of O_2 uptake. The NH_4^+ was probably mostly produced by the worms and at least some of the increased O_2 uptake was also attributed to worm uptake. It is likely, however, that O_2 penetration into the sediment surface decreased with increased worm population densities, partially due to the microbial activity in the fecal pellet layer at the sediment surface. The relatively low degree of coupling between nitrification and denitrification (~25%) also suggests that nitrification was close to the sediment-water interface and that nitrate could escape by diffusion into the overlying water. Chaterpaul et al. (1980) found that the presence of *Limnodrilus hoffmeisteri* and *Tubifex tubifex* (12000 to 16000 ind. m^{-2}) increased sediment nitrification rates by 40% during a substantially longer incubation period.

CONCLUSION

The presence of *Tubifex tubifex* enhanced O_2 and NO_3^- uptake, associated with changes in surface sediment diffusivity, due to their feeding behavior and/or to irrigation activity of the worms. Nitrification was stimulated at low worm densities (20000 ind. m^{-2}) but was inhibited at higher densities (70000 ind. m^{-2}). It is likely that the O_2 penetration depth decreased with increasing worm density, due to the transport of reduced compounds and organic matter, with the fecal pellets, to the sediment surface. These anoxic conditions led to increased rates of denitrification and were responsible for the decrease in nitrification at higher worm densities. An average of 25% of the NO_3^- uptake by the sediment was removed from the system by denitrification. There was some evidence for the reduction of NO_3^- to NH_4^+ at a population density of 70000 ind. m^{-2} (data not shown). This process was not measured at other worm densities. It is most likely that the discrepancy between the rate of NO_3^- uptake and the rate of denitrification was due to NO_3^- assimilation by micro-organisms. The detritus in freshwater systems often has a high C:N ratio, because of its origins in plant structural material. Micro-organisms utilizing this material can be nitrogen-starved (Fenchel & Blackburn 1979). The higher rates of denitrification were counterbalanced by higher rates of NH_4^+ flux from the sediment, due mainly to worm excretion. It is likely, however, that the presence of bioturbating worms, stimulating rates of denitrification, resulted in a net loss of nitrogen that could otherwise have been used by the primary producers.

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