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Oxygen and Inorganic Nitrogen Exchange in a *Nereis virens* (Polychaeta) Bioturbated Sediment-Water System[1]

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ABSTRACT

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The significance of *Nereis virens* bioturbation on exchange of oxygen and inorganic nitrogen (ammonium and nitrate) across the sediment-water interface was determined in two laboratory systems: (1) Entire sediment systems, with and without *Nereis*, and (2) individual worm + burrow systems. Sediment oxygen uptake and ammonium release was augmented 43 and 79%, respectively, by the burrow habit of this polychaete (density 600 m^{22}). This effect was not due purely to worm metabolism, that only accounted for 11 and 33%, respectively. The residual exchange was promoted by stimulation of microbial metabolism and mineralization in the burrow wall, apparently by mucus secretion serving as a new reactive substrate. The stimulation, however, was reduced by the low oxygen concentration predominating in the sparsely ventilated burrows, reducing aerobic metabolism. Another consequence of the low oxygen conditions was a net nitrate consumption in the burrows by nitrate reduction processes, like denitrification, whereas the oxic surface sediment released a considerable amount of nitrate by net nitrification. The high rate of denitrification was evident from a high O/N ratio in burrow fluxes (23 to 24) compared to surface sediment (16), indicating a loss of nitrogen in the burrow environment.

ADDITIONAL INDEX WORDS: *Benthic metabolism, benthic processes, Nereis virens, O/N ratio, worm burrows.*

INTRODUCTION

The exchange of biogenic elements between bottom sediments and overlying water has been recognized as one of the principal factors regulating chemical and biological cycles in coastal and estuarine systems (NIXON *et al.*, 1976; FENCHEL and BLACKBURN, 1979; BOYNTON *et al.*, 1980; KLUMP and MARTENS, 1981). Release of nutrients from sediments is largely regulated by the rates at which organic detritus reaches the sediment, and the rates at which nutrients released to pore waters are transported to the overlying water by diffusion and bioturbation. The quantitative importance of benthic animals in the cycling of elements like carbon, nitrogen, and phosphorus has been recognized rather recently (ALLER and YINGST, 1978; BLACKBURN and HENRIKSEN, 1983; HENRIKSEN *et al.*, 1983; KRISTENSEN, 1984a). Bioturbation occurs whenever macro- and meiofauna inhabit benthic sediment; it takes the form of both particle reworking and exchange of sediment pore water with overlying water by ventilatory pumping. Bioturbation is especially important in coastal ecosystems that are densely populated by infaunal deposit feeders (ALLER, 1982; RHODES and BOYER, 1982).

Burrowing animals increase the water exchange and thereby also the oxygen and inorganic nitrogen over the sediment-water interface. Additionally the animals consume oxygen and excrete ammomium, which contributes to the total benthic metabolism. The aim of the present study was to determine the significance of the infaunal polychaete *Nereis virens* Sars on the exchange of oxygen and inorganic ni-

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trogen between sediment and overlying water in an estuarine system. This was attempted by flux measurements of individual *Nereis* inhabited burrows and worms removed from the sediment, together with tank experiments on whole sediment systems, both with and without worms. The effect of nereid activities on microbial metabolism was evaluated by comparing exchange figures for individual worms, burrow walls and surface sediment

MATERIALS AND METHODS

Sediment and specimens of *Nereis virens* were collected in Norsminde (Kysing) Fjord, Denmark, during August and September 1983. This is a shallow mesohaline estuary covering an area of 1.9 km^2. The average water depth is 0.6 m, with a tidal amplitude of 0.2 m (MUUS, 1967). Water temperature and salinity at the sampling site near the entrance was 18 to 20°C and 20°/oo S.

Bulk Exchange of Oxygen and Inorganic Nitrogen in Tanks

The experiment was performed in 40 l seawater tanks (area 0.08 m^2) containing sediment to a depth of about 15 cm. The sediment was first sieved through a 1.5 mm mesh to remove the larger macrofauna. Organic content was 2% measured as loss on ignition (500°C). The sieved sediment was allowed to settle for one week before addition of the worms. The density, determined at the end of experiment, was 600 m^{-2} in the *Nereis* tank. This is in the normal range for Norsminde Fjord (KRISTENSEN, 1984b). Another tank without worms served as a control. The worms were allowed to establish themselves in circulating seawater for about two weeks before measurements. Water temperature and salinity during experiments was 16°C and 20 to 25 °/oo S.

Oxygen uptake (J_{O_2}) and exchange of inorganic nitrogen (J_{NH_4}, J_{NO_3}, and J_{NO_2}) across the sediment-water interface was measured by trapping a volume of water above the sediment in plexiglass cylindrical chambers (diameter, 19.6 cm and volume, 2.4 l). The darkened chambers were equipped with magnetic stirrers to stimulate natural water movements. The stirring speed was kept well below the resuspension limit. Samples for oxygen and inorganic nitrogen were taken by a syringe through a rubber stopper. Replacement of the sampled water was assured by a 50 cm tube opened to the ambient water. Oxygen concentration was measured immediately by a Radiometer P_{O_2}—electrode. Samples for ammonium, nitrate, and nitrite were quickly frozen and analyzed as soon as possible by autoanalyzer (Chemlab. Instr. Ltd.), using the automated methods of SOLÓRZANO (1969) for ammonium and ARMSTRONG *et al.* (1967) for nitrate and nitrite. Concentration changes ($\mu M\ h^{-1}$) in the water were measured over time (t = 0, ½, 1, 2, 3, 5, and 7 hours). Exchange rates (J_x, $\mu mol\ m^{-2}h^{-1}$) were calculated from concentration changes, using the volume of water trapped above the sediment after insertion of the chambers. The measurements were made in four independent series.

Oxygen and Inorganic Nitrogen Exchange of Individual Burrows

Exchange measurements of individual burrows of *Nereis virens* were performed using V-shaped sediment cores, as described by KRISTENSEN (1984a). The sediment was similar to that used in tank experiments. Five days before measurements, one individual of *N. virens* was introduced into each V-core. Of ten attempts seven were successful, *i.e.* the worms rapidly dug themselves into the sediment and made continuous and permanent burrows from one end to the other in the $\dot{V}$-cores.

Oxygen uptake ($\dot{V}_{bO_2}$) during water passage through a burrow was determined by measuring the water current ($\dot{V}_w$) produced by the worm during active ventilation periods; simultaneously, inspiratory and expiratory water samples were taken from the burrow for oxygen analysis. Ventilation ($\dot{V}_W$, lh^{-1}) was monitored with an electromagnetic flowmeter (Micron. Instr. Corp.), equipped with a 0.5 cm i.d. flowprobe, and recorded continuously (KRISTENSEN, 1981). The samples for oxygen analysis passed directly from the burrow via tubing to a P_{O_2}—electrode at a constant rate (ca. 1 ml min^{-1}). Oxygen extraction was recorded continuously. Oxygen uptake ($\dot{V}_{bO_2}$, $\mu mol\ h^{-1}$) was calculated as:

$$(C_{iO_2} - C_{eO_2}) \cdot \dot{V}_w$$

where C_{iO_2} and C_{eO_2} are incurrent and excurrent oxygen concentration in μM. Exchange of inorganic nitrogen between worm burrows and overlying water was determined by monitoring the ventilation of the worms and relating this to the difference in nutrient concentration in μM before and after water passage through the burrow. Inorganic nitrogen flux (B_x, $\mu mol\ h^{-1}$) of individual burrows was calculated by methods similar to those for oxygen uptake measurements. The subscript x stands for the actual solute of interest (*i.e.* ammonium, nitrate, and nitrite).

Oxygen and Ammonium Exchange of Individual Worms

Oxygen uptake ($\dot{V}_{O_2}$) and ammonium excretion ($\dot{V}_{NH_4}$) by individual worms removed from the sediment were determined by the experimental technique previously described, except that the worms inhabited artificial burrows (polyethylene tubes) instead of natural sediment. This method simulates natural conditions in contrast to the use of common respirometers (KRISTENSEN, 1983). Oxygen concentration was recorded continuously and water samples for ammonium were taken at short intervals.

RESULTS

Oxygen Uptake

The sediment oxygen uptake was considerable in the tank experiment. Oxygen in the chambers showed linear decrease over time ($r = 0.997$ to 0.999), indicating constant uptake rates down to at least 60% air saturation (Figure 1). A significant difference was observed between the control (no worms added) and the tank containing 600 *Nereis virens* m^{-2}. Oxygen uptake was about 74% higher in the *Nereis* tank, suggesting that 523 μmol $m^{-2}h^{-1}$ was consumed by the worm+burrow system (Table 1).

During water passage through burrows of *N. virens* (1.6 g individuals) ca. 44% of the oxygen was extracted. By applying a ventilation rate ($\dot{V}_w$) of 36.0 ml h^{-1} a worm+burrow system would consume ($\dot{V}_{bO_2}$) 4.9 μmol O_2h^{-1} (Table 2). Experiments with worms in polyethylene tubes revealed that 1.3 μmol O_2 h^{-1} or 26.5% was due to the worm ($\dot{V}_{O_2}$). These figures did not represent purely active periods, but they were corrected for the duration of ventilation periods, *i.e.* the rates during active ventilation periods (normally 20 to 30% of the time for this species) were integrated over the total time measured. From the natural density of this species in Norsminde Fjord (600 m^{-2}) the worm+burrow system estimated from individual uptake rates would consume 632 μmol O_2m^{-2} h^{-1}, which is close to the figure found in tank experiments (Figure 3A).

Exchange of Inorganic Nitrogen

Changes in ammonium, nitrate, and nitrite concentrations with time in the tank experiment are shown on Figure 2. The concentration changes were fairly linear over time ($r = 0.789 - 0.999$). Only slight exchange of nitrite occurred, and since no significant difference was observed between the control and *Nereis* tanks, nitrite was subsequently included with nitrate data. A low rate of ammonium release to the overlying water was found in the control tank ($J_{NH_4} = 21$ μmol $m^{-2}h^{-1}$). The *Nereis* tank, however, showed a flux that was 5 times higher ($J_{NH_4} = 100$ μmol $m^{-2}h^{-1}$). The worm+burrow system apparently produced 79% of the total flux (Table 1).

The ammonium exchange measurements of individual worm+burrow systems (1.6 g individuals) showed release rates (B_{NH_4}) of 0.46 μmol h^{-1} (Table 2). The worm excretion ($\dot{V}_{NH_4}$) made up 41% or 0.19 μmol h^{-1}. The residual 0.27 μmol h^{-1} was possibly produced by mineralization processes in the burrow wall. At normal densities, the worm+burrow system was responsible for an efflux of 59 μmol NH_4^+ $m^{-2}h^{-1}$) This was in the same order of magnitude as found by the tank experiment (79 μmol $m^{-2}h^{-1}$) (Figure 3B).

Table 1. Exchange of oxygen, ammonium, nitrate, and total dissolved inorganic nitrogen (DIN) between sediment and overlying water in the tank experiment. all values are in μmol $m^{»2}h^{»1}$, except O/N ratio. Positive values are release to, and negative values represent loss from the water column.

	J_{O_2}	J_{NH_4}	J_{NO_3}	J_{DIN}	O/N
600 m^{-2}	−1227	100	32	132	18.6
Control	−704	21	66	87	16.2
Worm + burrow	−523	79	−34	45	23.2

Nitrate exchange measured in the tank experiment showed an opposite pattern to the ammonium exchange (Table 1). A high release rate ($J_{NO_3} = 66$ μmol $m^{-2}h^{-1}$) was observed in the control. The *Nereis* tank, on the other hand, showed a reduced efflux ($J_{NO_3} =$ μmol $m^{-2}h^{-1}$). A surprisingly unlikely exchange of nitrate was observed for individual burrows. Here a slight efflux of nitrate occurred ($B_{NO_3} = 0.02$ μmol $m^{-2}h^{-1}$), suggesting a net nitrification of 2.5 μmol $m^{-2}h^{-1}$ when related to the normal density (Table 2). In the tank experiment, however, the burrows showed an apparent net nitrate reduction of 34 μmol $m^{-2}h^{-1}$ (Table 1).

DISCUSSION

Oxygen uptake by marine sediments is the result of aerobic metabolism of benthic organisms and of the reaction of oxygen difussing into the sediment with reduced compounds diffusing out. Previous reports on bulk sediment oxygen uptake, using *in*

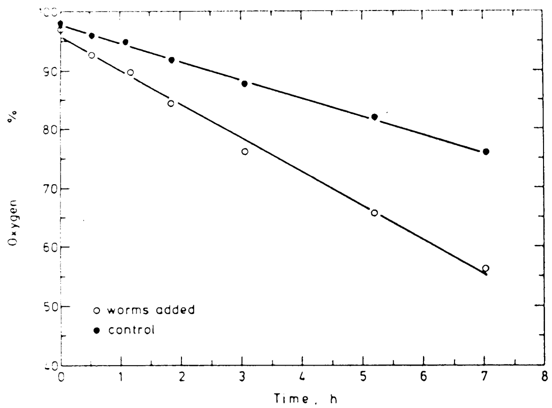

Figure 1. A plot of oxygen saturation (%) in overlying water over time in representative tank experiments. The control tank has sediment only. The other tank has sediment plus 600 *Nereis virens* m^{-2}.

situ or laboratory techniques on coastal and estuarine sediments, have showed a wide range of values: 0.18 to 2.83 mmol $m^{-2}h^{-1}$ (HARGRAVE, 1969; PAMATMAT, 1971; SMITH *et al.*, 1972; BOYNTON *et al.*, 1980; REVSBECH *et al.*, 1980; NEDWELL *et al.*, 1983). Total benthic oxygen consumption in Norsminde Fjord sediment were within the range of these reports, thus 1.23 mmol $m^{-2}h^{-1}$ in September (16°C)(Figure 3A). About 0.70 mmol $m^{-2}h^{-1}$ was respired at the sediment surface, the rest was consumed by the worm+burrow system, primarily by microbial respiration in the burrow walls, since the worms only consumed 0.14 mmol $m^{-2}h^{-1}$. Many attempts have been made to separate the benthic respiration into major components, such as: (1) chemical oxidation, (2) microbial (+meiofaunal) respiration, and (3) macrofaunal respiration (SMITH, 1973). The chemical oxygen demand is a result of the oxidation of reduced compounds formed by anaerobic metabolism and gives some indications of anaerobic activity. Sediment chemical oxidation has not been measured here, but it was found to be less than 10% of the total oxygen uptake in a sediment type similar to the present, though a wide range of values have been reported; 5 to 78% (PAMATMAT, 1971; SMITH, 1973; BOYNTON *et al.*, 1980). The microbial respiration is normally believed to be responsible for more than half the benthic total (SMITH, *et al.*, 1972) and it has been generally accepted that the macrofauna should be minor contributors to total sediment respiration (2 to 27%; SMITH, 1973).

Table 2. Exchange of oxygen, ammonium, nitrate, and total dissolved inorganic nitrogen (DIN) between individual burrows of 1.6 g Nereis virens and overlying water. All values are in μmol h$^{»1}$, except O/N ratio. Positive values are release to, and negative values represent loss from the water column.

	O_2	NH_4^+	NO_3^-	DIN	O/N
Worm + burrow	−4.9	0.46	0.02	0.48	20.4
Worm	−1.3	0.19	—	0.19	13.7
Burrow	−3.6	0.27	0.02	0.29	24.8

The burrowing and ventilatory activities of infaunal species like *Nereis* sp., exert a significant influence on the decomposition of organic matter in sediments. The activities of *Nereis virens* accounted for 43% of the total benthic respiration (Table 3), although only 11% was worm respiration, the rest was apparently microbial and chemical uptake by the burrow walls. According to KRISTENSEN (1984a), burrows of *Nereis virens* increase the sediment-water interface by about 136% at a density of 600 m^{-2}. The microbial and chemical oxygen uptake, however, only increased 55%, suggesting low oxygen conditions or low degradability of organic matter in the burrows (Table 3). The oxygen level in burrows was apparently low, since 44% of the oxygen was extracted during water passage through the burrows. This evidence, together with the fact that *N. virens* only ventilated its burrow 20 to 30% of the time indicated (assuming a constant microbial oxygen uptake at all concentrations) that oxygen was more or less depleted 6 to 7 minutes after the onset of resting periods, with anoxic conditions prevailing during long such periods (Figure 4). Similar low oxygen conditions with high concentrations of reduced compounds, such as H_6S, have

Table 3. Relative importance of sediment surface, burrow walls, and individuals of Nereis virens on the exchange of oxygen and inorganic nitrogen. Values are in % of total.

	O_2	NH_4^+	DIN
Sediment surface	57.4	21.0	65.0
Burrow wall	31.3	46.3	19.9
Nereis virens	11.3	32.7	14.2
Σ	100.0	100.0	100.0

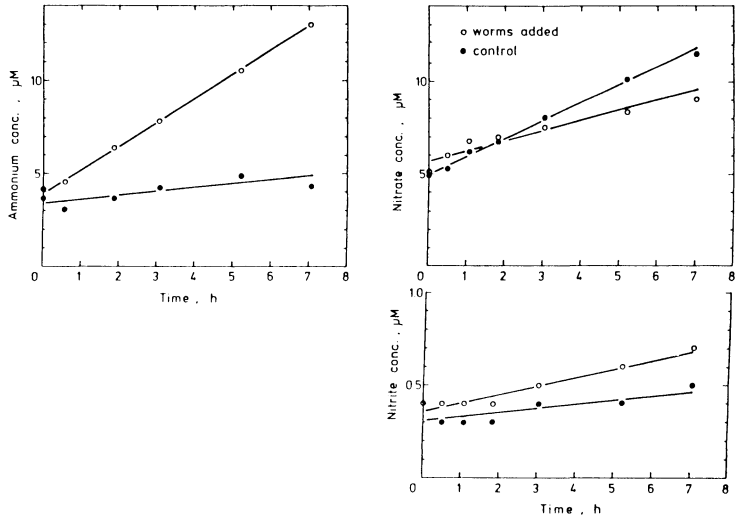

Figure 2. Examples of ammonium, nitrate, and nitrite concentration pattern (µM) in overlying water during time in tank experiments.

been reported for burrowing shrimps (KOIKE and MUKAI, 1983; WASLENCHUK *et al.*, 1983). The oxygen uptake by 1 m^2 burrow walls during active ventilation periods, on the other hand, appeared quite high; 1.5 mmol $m^{-2}h^{-1}$ (2.2 times that consumed by surface sediment), suggesting a relatively high potential for oxygen uptake by the walls. Aside from changing the distribution of microbial activity by redistributing particles and mechanically increasing the area of sediment-water interfaces, the worms apparently stimulated the rates of microbial mediated decomposition reactions.

The great variability in oxygen consumption commonly found in benthic respiration studies may partly be a consequence of the experimental techniques employed, especially stirring rate, since microbial and chemical oxygen demands are positively affected by stirring of the overlying water (REVSBECH *et al.*, 1980). The abundance of macrobenthos, however, may also influence the uptake rate due to their effect on microbial respiration. Obviously slight changes in macrofaunal abundance would significantly affect the total respiration.

Coastal sediments are generally sites for significant mineralization and export of inorganic nitrogen. Ammonium is commonly the major constituent of nitrogen release from sediments (BLACKBURN and HENRIKSEN, 1983). The ammonium efflux of 100 µmol $m^{-2}h^{-1}$ in bioturbated Norsminde Fjord sediment was comparable to previous reports (NIXON, *et al.*, 1976; HOPKINSON and WETZEL, 1982; HENRIKSEN *et al.*, 1983). The presence of *N. virens* apparently increased the ammonium flux 5 times compared to defaunated sediment (Figure 3B). Excretion by the worms was an important part of the observed increase (41%), and it has been found as high as 63% (HENRIKSEN *et al.*, 1983). Ammonium flux from the burrow walls, which was 46% of the total benthic flux (Table 3), was derived from aerobic and anaerobic mineralization in the wall, plus diffusion from the surrounding sediment. The burrow wall is a site of high bacterial activity, similar to the oxic surface layer (ALLER and YINGST, 1978). This stimulation of sediment metabolism occurs by providing new reactive substrate, such as *Nereis* mucus secretion associated with a high percentage of adsorbed fine particles by decreasing metabolic buildup and by supplying electron acceptors (ALLER *et al.*, 1983; KRISTENSEN *et al.*, 1985).

Nitrate release from the sediment to the overlying water was relatively high in Norsminde Fjord, 66 µmol $m^{-2}h^{-1}$. Other studies on similar sediment types have showed quite variable results, thus efflux by some and influx by others (NIXON *et al.*, 1976; BOYNTON *et al.*, 1980; CALLENDER and HAMMOND, 1982; HENRIKSEN *et al.*, 1983). These discrepancies may partially be related to dif-

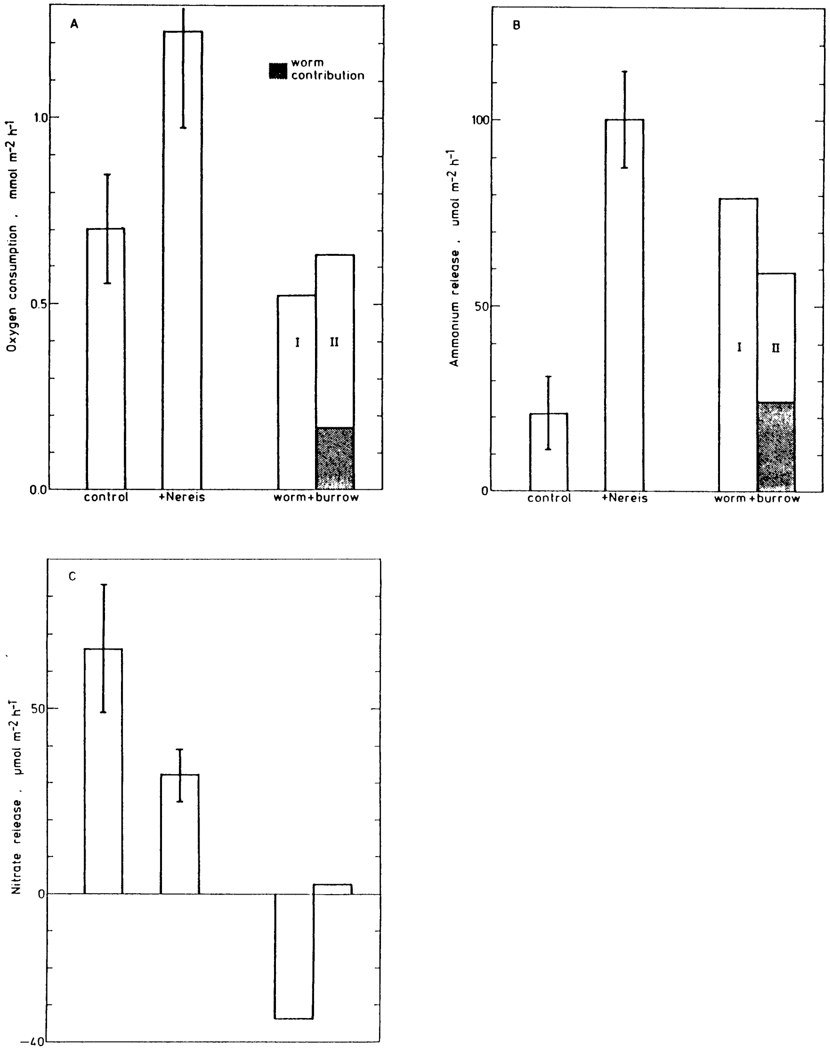

Figure 3. Exchange rates of (A) Oxygen (mmol $m^{-2}h^{-1}$), (B) Ammonium, and (C) Nitrate (μmol $m^{-2}h^{-1}$) in control and *Nereis* tanks. Worm+burrow contribution was obtained by: (I) Subtracting control from *Nereis* tank exchange rates, (II) Integrating individual measured rates to the natural density (600 m^{-2}). The hatched areas indicate worm contribution. Error bars indicate S.D. of 4 measurements.

ferent microbial conditions in the sediment. The major determinant of nitrate exchange is the balance between aerobic nitrification and anaerobic nitrate reduction (primarily denitrification) (VANDERBORGHT and BILLEN, 1975). Such processes are affected by the activities of *Nereis virens* (HENRIKSEN *et al.*, 1983; KRISTENSEN *et al.*, 1985). Two factors commonly influence the nitrate flux; depth of oxygen penetration in the sediment and nitrate concentration in the overlying water. The 50% reduction of nitrate flux in the presence of *Nereis* indicated a relatively high rate of nitrate reduction in the burrow walls, which possibly was affected by the apparent low oxygen concentration. HENRIKSEN *et al.* (1983) reported that different infaunal species show different nitrate flux patterns; *Nereis* is, as observed here, described as a nitrate flux decreaser, and species like the amphipod,

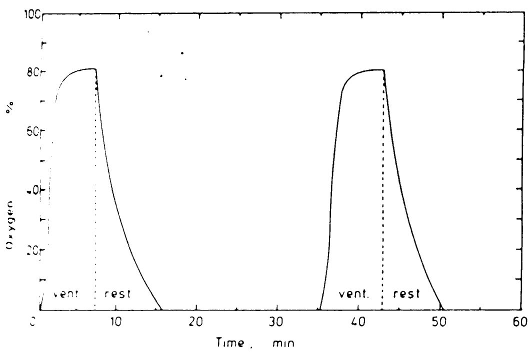

Figure 4. A hypothetical representation of oxygen concentration changes in the center of a *Nereis virens* burrow. *N. virens* ventilates the burrow ca. 7 min., where about 44% oxygen is extracted from the water, followed by a 25 to 30 ,min. rest period, where oxygen is depleted. *Vent.* indicate ventilation and *Rest* indicate start of resting periods.

Corophium volutator are nitrate flux increasers. Generally the nitrate flux increasers have high ventilation activities and large burrow volume compared to body size, promoting good oxygen conditions, while the opposite is true for the nitrate flux decreasers. Nitrate concentration in the overlying water is important for the concentration gradient in the uppermost sediment layers and thereby is an important determinant of nitrate reduction rate (KRISTENSEN, 1984a). However, the apparent differences in nitrate flux between burrows in tank experiments and individual burrows at similar ambient nitrate concentrations (Figure 3C), may be due to the time of acclimation; 5 days for individual burrows and 14 days for tank experiments, promoting different microbial conditions in the burrows.

In terms of the amount of oxygen consumed, the inorganic nitrogen (ammonium and nitrate) released was low in the *Nereis* tank, yielding an O/N atomic ratio of 18.6, compared to 16.2 in the control (Table 1). These values are within the expected range, based on sediment C/N ratios of 7 to 10 based on (BLACKBURN, 1980), when oxygen is assumed to to oxidize carbon preferentially. Algal cells of a low C/N ratio (ca. 6.6)(REDFIELD, 1934) are commonly deposited and decomposed at the sediment surface, with preferential decomposition of protein and nucleic acids, liberating ammonium. The partially decomposed cells, rich in structural materials of high C/N ratio, gradually mixed downwards are responsible for the commonly observed bulk C/N ratios approaching 10 in sediments (BLACKBURN, 1980). High O/N or low N/P ratios of elements exchanged across the sediment-water interface are often observed in decomposing sediments (NIXON *et al.*, 1976; BOYNTON *et al.*, 1980; HOPKINSON and WETZEL, 1982) and argued to be a result of nitrification-denitrification processes, producing a considerable loss of nitrogen as N_2. This was confirmed by the very high O/N ratio found in burrows (20.4 to 23.2) suggesting a higher rate of denitrification, consistent with the high loss of nitrate in this environment (Table 1). The burrow walls were apparently responsible for the loss, since O/N ratio for the worms alone was as low as 13.7 (Table 2).

The present study clearly shows that the life habit of macrobenthos, such as burrow dwellings, has to be considered when the significance of faunal elements on benthic processes is evaluated. The role of *N. virens* on sediment oxygen consumption is 3 times higher than the aerobic respiration of the worms themselves. They stimulate microbial processes, such as oxygen and nitrate respiration and overall mineralization by their burrowing and ventilatory activities.

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