

Two annual maxima of nitrate reduction and denitrification in estuarine sediment (Norsminde Fjord, Denmark)

Kirsten Schannong Jørgensen, Jan Sørensen*

Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, DK-8000 Aarhus C, Denmark

ABSTRACT: In situ rates of NO_3^- reduction and denitrification were measured in the sediment of a Danish estuary during 3 annual cycles. The acetylene inhibition technique was used with undisturbed sediment cores. A reproducible seasonal pattern was obtained for both total NO_3^- reduction and denitrification rates. Both processes showed maximal activity in the spring and fall. High benthic primary production and subsequent degradation of the algal biomass seemed responsible for the spring maximum (May). In early spring, a diel denitrification pattern with low activity during the day was due to O_2 production during benthic photosynthesis; the effect was most significant (up to 60% inhibition) when algal biomass was at a maximum (March–April). Low NO_3^- concentrations during summer (June–September) were followed by higher NO_3^- concentrations in the overlying water and seemed responsible for the second maximum in the fall (October–December). Temperature was the limiting factor for denitrification during winter (January–February). Over an annual cycle, NO_3^- reduction rates ranged from 10 to 40 $\text{mmol N m}^{-2} \text{d}^{-1}$ and denitrification rates from 2 to 10 $\text{mmol N m}^{-2} \text{d}^{-1}$. The annual activities of NO_3^- reduction and denitrification were 6.7 and 1.8 $\text{mol N m}^{-2} \text{yr}^{-1}$, respectively, averaged over a 3 yr period.

INTRODUCTION

In coastal marine waters, NO_3^- input from run-off and groundwater discharge (Capone & Bautista 1985) may locally support high planktonic and benthic algae production. Elevated primary production may in turn cause higher decomposition rates in the bottom layers and frequently lead to significant O_2 deficits in both the bottom waters and sediments. Among the decomposition processes, bacterial denitrification contributes to both the mineralization of organic matter and to sedimentary nitrogen cycling. The NO_3^- transformation to gaseous N_2 thus comprises a natural nutrient sink and may mitigate the increasing NO_3^- discharge and primary productivity in coastal environments.

In spite of the apparent role of denitrification in marine eutrophication, only few long-term studies have dealt with the natural regulation of the process in coastal waters (Sørensen 1984, Jørgensen & Sørensen 1985, Seitzinger & Nixon 1985, Smith et al. 1985, Jen-

sen et al. 1988 [companion article]). In estuaries, where the external NO_3^- input sometimes exceeds the endogenous NO_3^- production from nitrification in the sediment (Smith et al. 1985, King & Nedwell 1987), the NO_3^- level in the surface water may primarily determine the denitrification activity. Smith et al. (1985) reported a year-round relationship between denitrification and NO_3^- availability in a subtropical estuary where summer rains gave a high allochthonous NO_3^- input from May to September. Locally, however, temperature, availability of O_2 and NO_3^- , accumulation of organic matter, etc., may all contribute to complicated denitrification patterns in the sediments (Andersen et al. 1984, Jensen et al. 1984, Sørensen 1984, Jørgensen & Sørensen 1985, Jensen et al. 1988). In such cases, it is of prime importance to study the regional, seasonal and diel variations at short sampling intervals. The purpose of the present study, which involved a small NO_3^- -polluted estuary in Denmark, was to obtain a detailed pattern for the temporal variation of sediment denitrification during 3 annual cycles and to determine the role of a variety of controlling factors for the process.

* Addressee for correspondence

MATERIALS AND METHODS

Study site. The study site was a small estuary (Norsminde Fjord) on the east coast of Jutland, Denmark (Fig. 1). The sampling site, a subtidal mudflat near the river outlet, was described previously (Station 4) by Jørgensen & Sørensen (1985). The water depth was about 0.5 m; ice cover was typically from January to March. Due to the high discharge of riverine water in late winter, salinity varied from 0.5‰ (winter) to 12‰ (summer). Both temperature and salinity were determined regularly during the investigation. The sediment was a soft mud with a water content of about 60% and an organic content of about 5 to 15% (ignition loss); the latter reflected a seasonal variation. The surface zone of the sediment was oxidized and brown-colored (Fe hydroxides) to a depth of about 4 cm in winter, but only to about 0.5 cm depth in late summer. In the early spring, a dark-brown layer of benthic microalgae (mostly diatoms) could be observed on the sediment surface. The benthic fauna of polychaetes (*Nereis* sp.), tubificid worms and crustaceans (*Corophium* sp.) was scarce compared to the marine part of the estuary (Sørensen & Glob 1987).

Sampling and core incubation. Water samples were taken in glass bottles and intact sediment cores in acrylic tubes at 2 to 4 wk intervals during 3 annual cycles. The 15 cm long and 3.6 cm wide tubes were equipped with a vertical series of silicone-filled holes (0.5 cm depth intervals), which served as injection ports for the acetylene inhibitor used in the denitrification

assay (see below). All samples were brought to the laboratory within 3 h. Water samples were frozen (-20°C) for later analysis of NO_3^- and cores were stored at in situ temperature under aerated and circulating water from the sampling site.

Water contents, densities and organic contents (ignition loss at 550°C) were determined in 0.5 to 1 cm depth intervals of some of the cores. In other cores, the acetylene inhibition technique was used for the determination of both denitrification (Sørensen 1978b, Andersen et al. 1984) and total NO_3^- reduction (Jørgensen & Sørensen 1985); C_2H_2 blocks N_2O reduction to N_2 in denitrifying bacteria (Balderston et al. 1976, Yoshinari & Knowles 1976) and analysis of N_2O accumulation is therefore considered a measure of in situ denitrification activity. Furthermore, since C_2H_2 also inhibits NH_4^+ oxidation in the nitrifying bacteria (Walter et al. 1979, Hynes & Knowles 1982), a determination of the consumption rate for NO_3^- plus NO_2^- should express the overall NO_3^- -reducing activity in the cores (Jørgensen & Sørensen 1985, Sørensen 1987).

In cores receiving C_2H_2 , the sediment surface was first adjusted to a fixed position, about 6 cm from the upper edge of the tube. Water and gas phases corresponding to 30 ml volumes (3 cm height in the tubes) were included in the cores. C_2H_2 -saturated, distilled water (200 μl) was then injected by syringe through each of the silicone-filled holes; the inhibitor was spread homogeneously into the sediment. The water and gas phases also received C_2H_2 so that the final C_2H_2 concentration in both the sediment, water and gas phase was about 10% of saturation. After injection, the cores were immediately closed with gastight, light-permeable acrylic caps. A magnetic bar mounted inside the cap could be moved by a larger external magnet and served to stir the water phase. All cores were incubated at the in situ temperature in a thermostatted water bath and half of them were exposed to light through the caps. The light source was a 400 W mercury lamp (Osram HQI-T, Stuttgart, FRG) placed 60 cm above the sediment surface (light intensity $200 \mu\text{E cm}^{-2} \text{s}^{-1}$).

Extraction procedure and determination of activity.

For both dark and light incubations, 4 cores were sacrificed for NO_3^- , NO_2^- and N_2O analyses after 0, 1, 2, and 3 h, respectively. First, 3 ml of the gas phase was injected into pre-evacuated 'Venoject' tubes (Terumo Europe N.V., Leuven, Belgium) for later analyses of N_2O . The core was then uncapped and 10 ml of the water phase quickly transferred to a 60 ml glass beaker. The uppermost cm of the sediment was cut into 0.5 cm segments followed by 1 cm segments down to 4 cm depth. Each segment was placed in a 60 ml beaker containing 10 ml of 2 N KCl solution. After the transfer of a sample, the beaker was immediately capped with a rubber stopper and shaken vigorously by

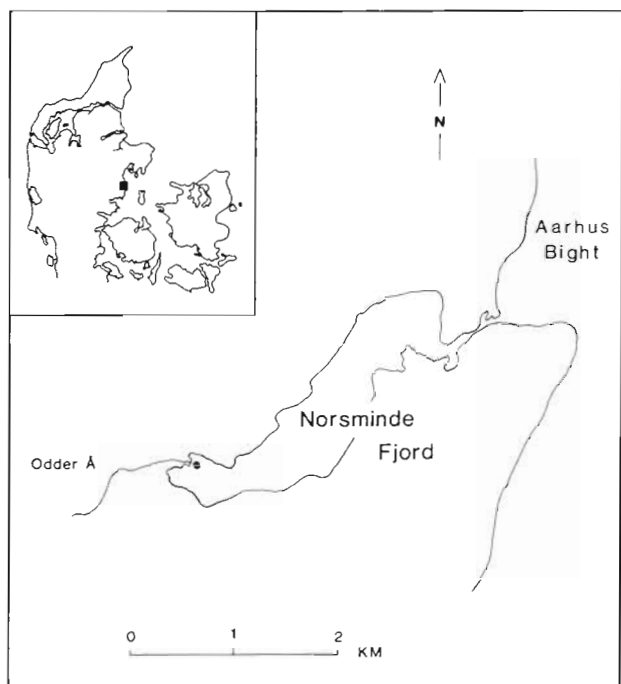


Fig. 1. Study site in Norsminde Fjord, Denmark

hand for 2 min. A gas sample of 3 ml was then withdrawn from the headspace and injected into a pre-evacuated glass vial for storage. Finally, both the water samples and the suspensions were centrifuged ($2000 \times g$, 10 min) and the supernatants frozen (-20°C).

The N_2O content in the gas samples were determined on a Packard model 427 gas chromatograph installed with a ^{63}Ni electron capture detector (320°C). The gas chromatograph was equipped with a 2 m long Porapak Q column to separate the sample components and a backflush system (Parkin et al. 1984) to avoid C_2H_2 contamination of the detector. Pure N_2 served as the carrier gas (15 ml min^{-1}) and oven temperature was 80°C . This configuration allowed a gas sample to be injected every 3 min.

The concentration of N_2O in sediment and water samples was obtained from the measured N_2O content in the gas sample and the Bunsen solubility coefficients for N_2O in KCl solution or seawater (Markham & Kobe 1941, Weiss & Price 1980). Water content and density of the sediment were used to convert the measured concentrations into appropriate dimensions. The N_2O accumulation was usually linear for the whole incubation period of 3 h, but in a few cases with low NO_3^- concentrations, the production rate was only constant

for 1 h (late summer); here, the rate of N_2O accumulation decreased during the incubation, and the initial rate (first h) was used as an estimate of denitrification activity. The N_2O recovered in the water and gas phases of the cores was anticipated to originate from activity in the upper 0.5 cm of the sediment (Andersen et al. 1984).

The NO_3^- and NO_2^- contents in the water phase and the supernatants were determined on a Chemlab auto-analyser using the method of Armstrong et al. (1967). Water contents and densities of the sediment were used to calculate the total NO_3^- plus NO_2^- content in each of the C_2H_2 -treated cores. The rate of NO_3^- consumption during the whole incubation period of 3 h was used to calculate the total NO_3^- reduction in the sediment.

RESULTS

NO_3^- concentrations in the water and sediment

Temperature and salinity varied predictably from February 1985 to February 1986 (Fig. 2). As indicated by low salinities, river discharge was generally highest

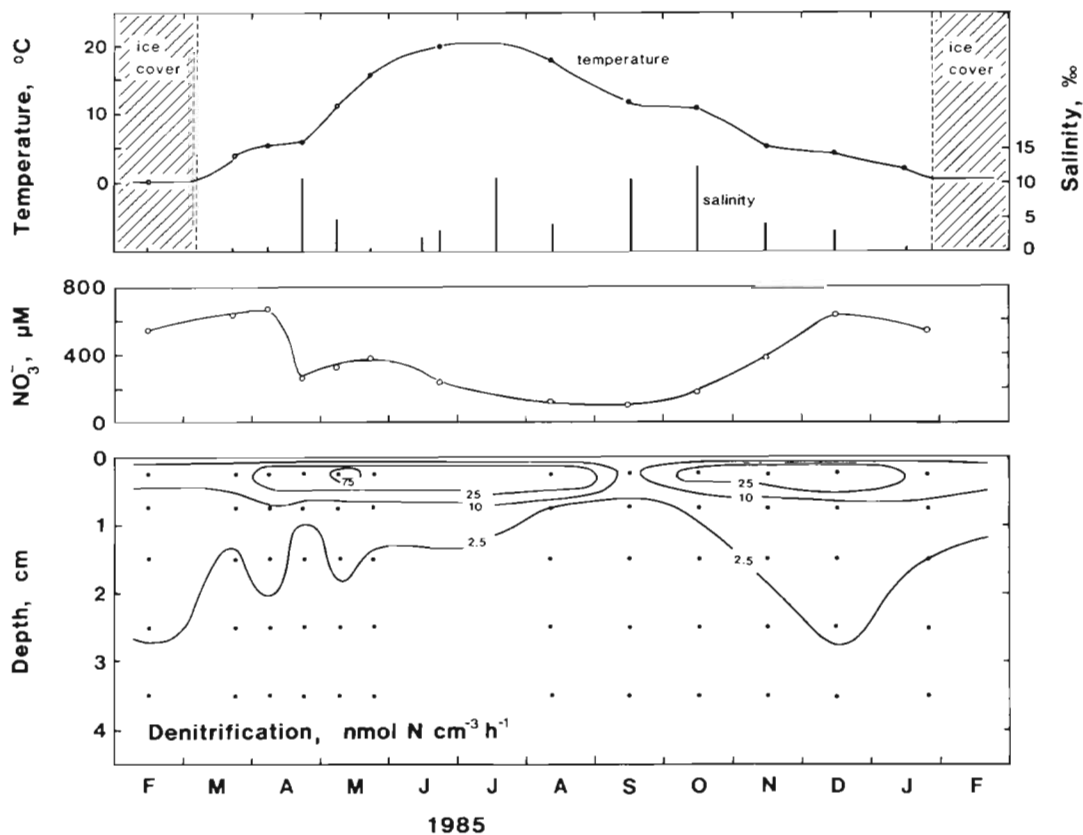


Fig. 2. Upper panel: Seasonal variation of salinity (columns) and temperature in Norsminde Fjord (February 1985 to February 1986). Middle panel: NO_3^- concentrations in the water. Lower panel: Distribution of denitrification activity in the sediment (isopleths)

in the winter and early spring. Nutrient input was also maximal at this time, when more than $500 \mu\text{M}$ NO_3^- could be observed in surface waters. The lower NO_3^- concentrations of 100 to $250 \mu\text{M}$ during summer resulted from both lower water discharge and the rapid nutrient consumption in the spring (Jørgensen & Sørensen 1985). Throughout the year, NO_3^- concentrations in the sediment seemed largely controlled by the load of NO_3^- in the overlying water phase of the estuary. In the upper 0.5 cm depth interval, which contained the highest NO_3^- concentration in the sediment, about $300 \mu\text{M}$ was observed in winter (January 1986) and $10 \mu\text{M}$ in summer (September 1985) (data not shown). Thus, as judged from the concentration gradient at the sediment-water interface, there was always a transport of NO_3^- from the water into the sediment.

Denitrification in the sediment

The depth of the denitrification zone is indicated in Fig. 2 (lower panel). Little activity was found below the uppermost cm and between 50 and 90 % of the measured denitrification was located within the uppermost 0.5 cm segment. The profiles also reveal 2 annual maxima of denitrification activity in the surface layer, one in the spring (May) and one in the fall (October to

December). A minimum of activity thus appeared in late summer (September) when the temperature was relatively high, but the NO_3^- concentrations had decreased to $100 \mu\text{M}$ in the overlying water and about $10 \mu\text{M}$ in the surface layer of the sediment. Finally, when the temperature decreased in the winter, the second minimum of denitrification activity appeared, even though NO_3^- concentrations were again relatively high.

In spite of the variation expected from heterogeneity in the sediment, the spring and fall denitrification maxima could be discerned for all 3 yr of the investigation (Fig. 3). The range of activities was also similar from year to year; peak values in the spring and fall were about $10 \text{ mmol N m}^{-2} \text{ d}^{-1}$ and minimum values in the summer and winter about $2 \text{ mmol N m}^{-2} \text{ d}^{-1}$.

The inhibition of denitrification by light was most pronounced in early spring (March–April) when the activity was 60 % lower in the light-incubated cores than in the dark-incubated ones (Fig. 4, upper panel). Strongest inhibition was thus observed 1 to 2 mo before the appearance of the denitrification maximum in May and was best correlated with development of a benthic algal mat. The increase of organic content at the surface, from about 5 % in winter to about 15 % in early spring, illustrated the elevated production and biomass of the benthic micro-algae (Fig. 4, lower panel).

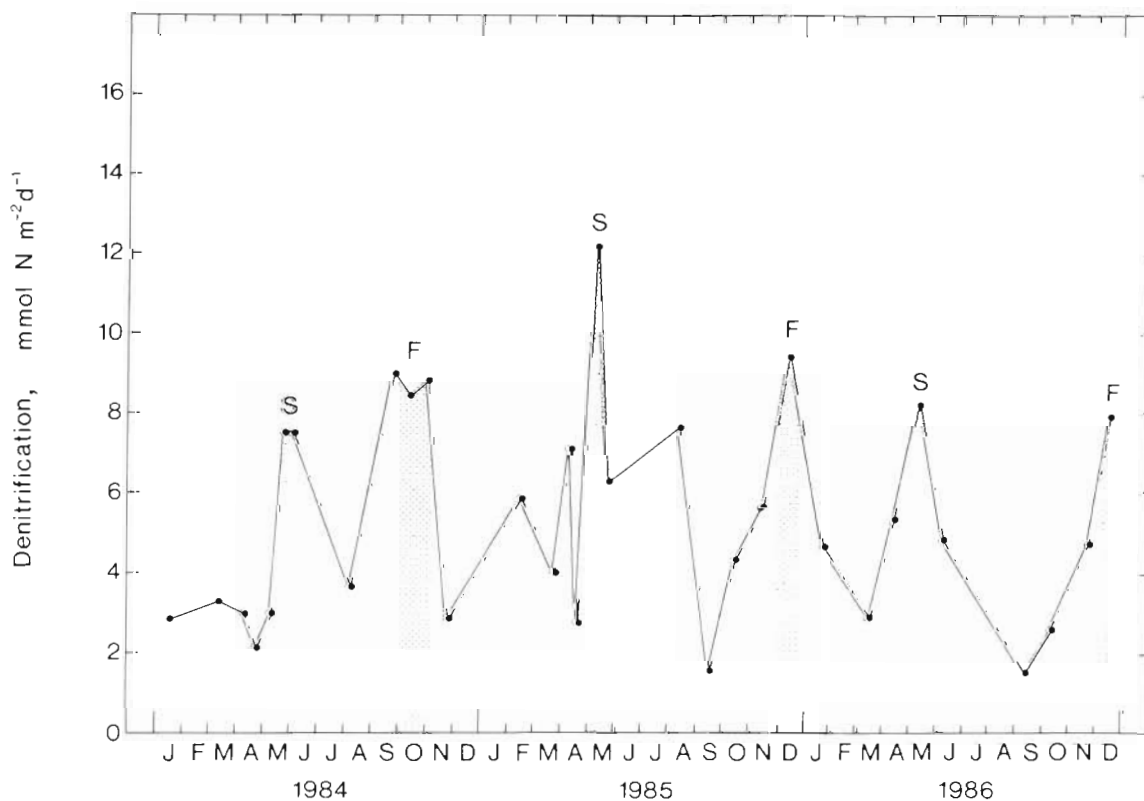


Fig. 3. Seasonal variation of the denitrification activity in the Norsminde Fjord Sediment (1984 to 1986). Shaded areas indicate periods of high denitrification activity in spring (S) and fall (F)

NO₃⁻ reduction in the sediment

The annual patterns for total NO₃⁻-reducing activity also show a marked seasonal variation with 2 consistent maxima, one in the spring (May) and one in the fall (October to December) (Fig. 5). Peak values of NO₃⁻ reduction (spring and fall) were about 40 mmol N m⁻² d⁻¹ and minimum values (summer and winter) about 10 mmol N m⁻² d⁻¹.

Except for 2 occasions in late summer and early fall (September 1985 and October 1986), the concurrent measurements of denitrification and total NO₃⁻ reduction showed that total NO₃⁻ reduction was from 1.5 to 7 times higher than denitrification (Fig. 6). For the 2 exceptions, denitrification accounted for less than 10% of the total NO₃⁻ reduction; in these instances the sediment was highly reduced and contained only about 10 μM NO₃⁻ in the uppermost 0.5 cm segment. Otherwise, there was no apparent correlation between the sampling time (NO₃⁻ level) and the ratio of denitrification to total NO₃⁻ reduction.

DISCUSSION

Seasonal and diurnal variation of denitrification

A consistent seasonal pattern of in situ denitrification was found in the Norsminde Fjord estuary; during 3 yr of investigation, from 1984 to 1986, maxima were found in mid-spring (May) and in fall (October to December). The spring maximum was previously observed in an earlier study (Sørensen 1984, Jørgensen & Sørensen 1985), but this is the first report of the fall maximum.

The increasing temperature in early spring should generally stimulate the activity in the sediment, but temperature and denitrification from February to May, 1984 to 1986, were not correlated by an Arrhenius equation (data not shown). Other factors such as increased availability of organic substrate due to decomposition of benthic algae seemed to be more important. For example, the spring denitrification maximum was correlated with a rapid decline of sediment organic content in May (Fig. 4). The decline in organic content was probably a result of intensive grazing and decomposition of the surface microalgal mat. During this period, a general increase of heterotrophic activity has previously been observed from the rates of O₂ uptake in the sediment (Jørgensen & Sørensen 1985). It is important to note that NO₃⁻ concentrations in the estuarine water were still relatively high in May. The subsequent decrease of denitrification in the summer could thus be a response to limited NO₃⁻ availability (lower concentrations and smaller penetration depth in the sediment). As judged from the high rates of O₂

uptake (Jørgensen & Sørensen 1985) it seems unlikely that availability of organic substrate would be a limiting factor during summer. The regulation of denitrification by NO₃⁻ availability in the summer was further supported by the appearance of a denitrification maximum in the fall when NO₃⁻ concentrations increased. The minimum in the winter was most likely controlled by low temperature.

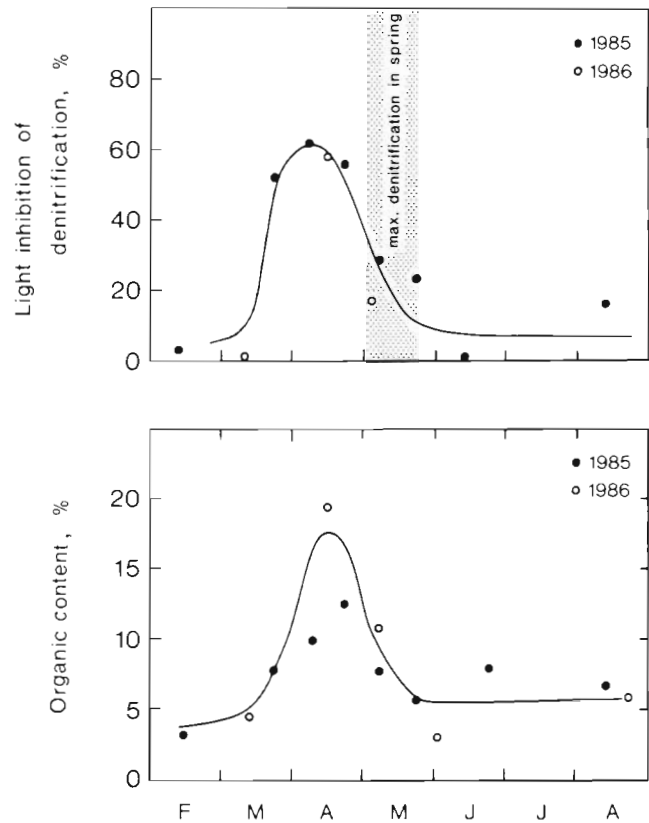


Fig. 4. *Upper panel:* Seasonal variation of light inhibition of denitrification activity. Shaded area indicates period of maximum denitrification in spring. *Lower panel:* Seasonal variation of organic content (ignition loss) in the uppermost cm of the Norsminde Fjord sediment

The effect of light-and-dark cycles on denitrification activity was pronounced in early spring (March–April), when a dense population of microalgae appeared on the sediment surface. Benthic photosynthesis may increase the O₂ penetration into the sediment (Sørensen et al. 1979, Revsbech et al. 1981, Jensen et al. 1984, Baillie 1986) and thus result in significant inhibition of the surface-located denitrification. Andersen et al. (1984) demonstrated such a diel denitrification pattern, with low activities in the daytime, during a period of intensive benthic primary production in April. The present study demonstrates light inhibition of denitrification during the whole spring period of elevated benthic productivity.

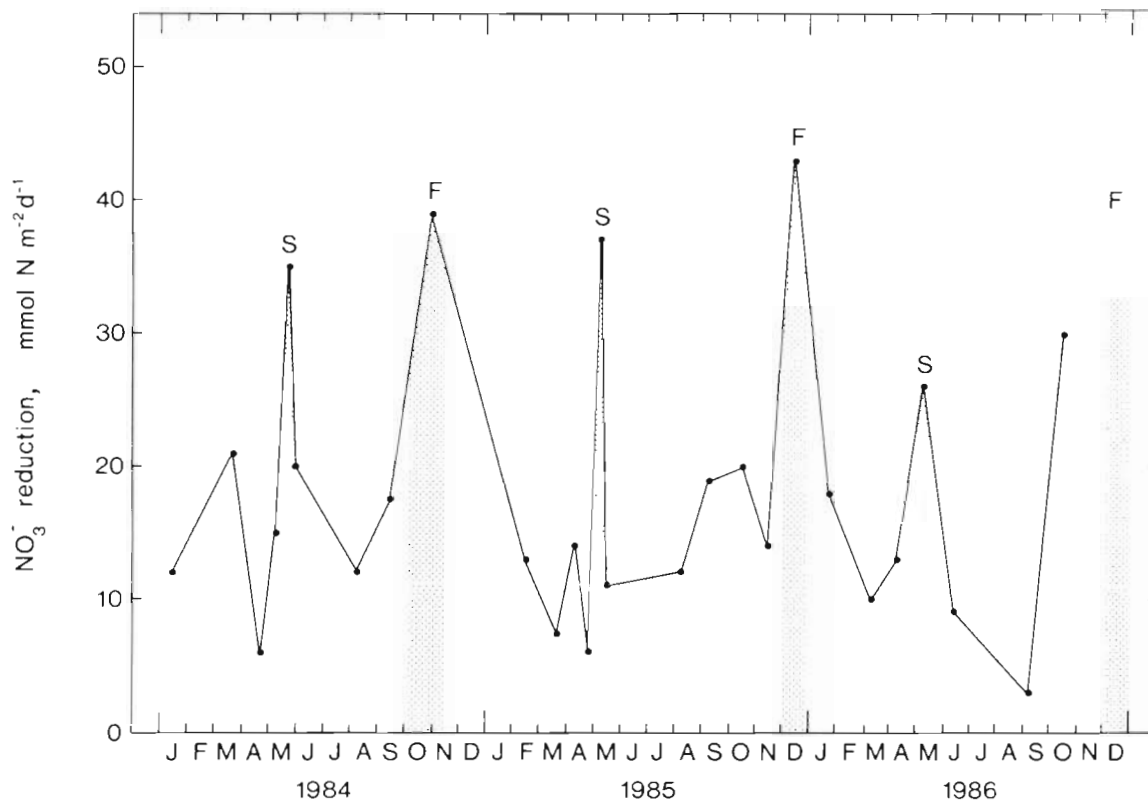


Fig. 5. Seasonal variation of total NO_3^- -reducing activity in the Norsminde Fjord sediment (1984 to 1986). For a comparison of the seasonal patterns of denitrification and total NO_3^- reduction, periods of high denitrification activity in spring (S) and fall (F) are indicated (shaded areas)

Significance of denitrification and other NO_3^- -reducing activity

The seasonal cycle of total NO_3^- reduction showed the same maxima in the spring and fall as found for denitrification. This indicated that the 2 processes were controlled by similar environmental factors. For single measurements, denitrification accounted for a most variable fraction, from 15 to 70%, of the total NO_3^- reduction; for a whole year, however, the fraction was surprisingly constant, about 30% for 1984, 1985 and 1986 (see below). Nishio et al. (1982) also observed in an estuarine sediment that denitrification accounted for about 30 to 60% of the overall NO_3^- reduction. Jørgensen & Sørensen (1985) attributed the difference between NO_3^- reduction and denitrification to bacterial ' NO_3^- ammonification' (dissimilatory NO_3^- reduction to NH_4^+). ' NO_3^- ammonification' can be readily demonstrated in $^{15}\text{NO}_3^-$ -amended sediments (Koike & Hattori 1978, Sørensen 1978a, Enoksson & Samuelsson 1987, K. S. Jørgensen unpubl.), but it has been most difficult to determine its in situ significance even at low NO_3^- concentrations. From current evidence, however, it seems that a NO_3^- -reducing activity other than denitrification (probably ' NO_3^- ammonification') may some-

times comprise a major fraction of the overall NO_3^- reduction in estuarine sediments. Alternatively, it has also been argued that incomplete blockage by C_2H_2 may sometimes lead to an underestimate of denitrification. Incomplete C_2H_2 blockage has been reported in relatively reduced sediments with low NO_3^- concentrations (Kaspar 1982, Oremland et al. 1984), but only twice (in 3 yr) was the NO_3^- concentration as low as $10 \mu\text{M}$ in the uppermost depth interval (both occurring in late summer). At these times the sediment was indeed relatively reduced after a period of complete anoxia in the bottom water. The 2 occasions were the only ones with extraordinarily low rates of denitrification relative to NO_3^- reduction; denitrification may have been underestimated in these cases. One possible explanation for this problem could be the alleviation of the C_2H_2 blockage by sulfide (Tam & Knowles 1979, Sørensen et al. 1987).

The annual rates of NO_3^- reduction, measured in dark-incubated cores, were 7.0 , 6.0 and $6.1 \text{ mol N m}^{-2} \text{ yr}^{-1}$ (Table 1). Denitrification rates were 1.8 , 2.0 and $1.4 \text{ mol N m}^{-2} \text{ yr}^{-1}$ for 1984, 1985 and 1986, respectively, after correction for light inhibition during spring. Denitrification thus accounted for about 30% of total NO_3^- reduction in all 3 yr. The areal NO_3^- load of the

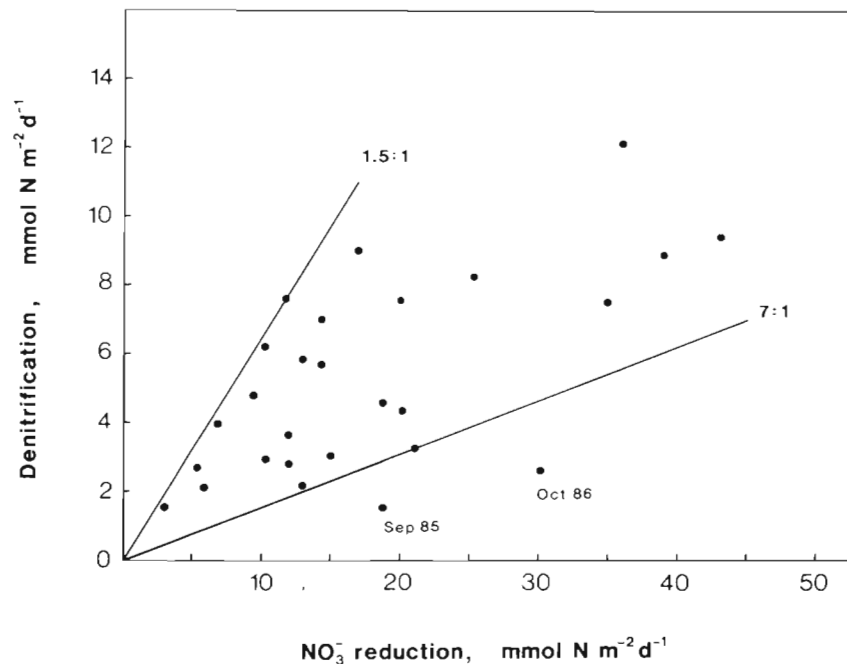


Fig. 6. Denitrification versus total NO_3^- reduction in the Norsminde Fjord sediment (1984 to 1986). Two data points (September 1985 and October 1986) had very low NO_3^- concentrations (about $10 \mu\text{M}$) in the uppermost cm of the sediment

estuary (Table 1) was calculated from the riverine nutrient discharge and the total area of the estuary (1.9 km^2). The percentage of the external NO_3^- input which could potentially be removed by denitrification was 25 %, assuming that the measured denitrification was representative for the whole estuary. Actually, the activity decreases towards the marine part of the estuary (Jørgensen & Sørensen 1985) and the denitrified fraction of the input must be lower. Nitrate not lost during denitrification is either trapped by sedimentation in the estuary or exported to the sea as plankton or suspended detritus (Jørgensen & Sørensen 1985).

Table 1. Annual NO_3^- load and activities of NO_3^- reduction and denitrification (all $\text{mol N m}^{-2} \text{ yr}^{-1}$) in Norsminde Fjord estuary

Year	NO_3^- load ^a	NO_3^- reduction ^b ($\text{mol N m}^{-2} \text{ yr}^{-1}$)	Denitrification ^b
1984	10.0	7.1 (ND)	1.8 (1.8)
1985	9.9	6.2 (5.8)	2.1 (2.0)
1986	5.7	6.1 (ND)	1.6 (1.4)

^a Calculated from riverine discharge of NO_3^- and area of estuary
^b Numbers in parentheses indicate activity corrected for inhibition by light in the daytime
 ND: not determined

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