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Bioturbation effects of the amphipod *Corophium volutator* on microbial nitrogen transformations in marine sediments

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Abstract Microcosms containing different densities of *Corophium volutator,* ranging from 0 to 6000 ind m^{-2}, were incubated in a flow-through system. Benthic fluxes of CO_2, O_2, NO_3^- and NH_4^+ were measured regularly. Thirteen days after setup the microcosms were sacrificed and sediment characteristics, pore water NO_3^-, NH_4^+ and exchangeable NH_4^+ concentrations, and potential nitrification activity were measured. The presence of *C. volutator* increased overall mineralization processes due to burrow construction and irrigation. The amphipods increased the ratio $\Sigma CO_2/O_2$ fluxes from 0.73 to 0.86 in microcosms inhabited by 0 and 6000 ind m^{-2}, respectively. Burrow ventilation removed NH_4^+ from the sediment, which was nitrified in the oxic layer and transported NO_3^- to the burrow sediment, where denitrification potential was enhanced. Nitrification and total denitrification rates (denitrification of NO_3^- coming from the overlying water and of NO_3^- generated within the sediment) were calculated and discussed. Bioturbation by *C. volutator* increased both nitrification and denitrification, but denitrification was stimulated more than nitrification. Denitrification of NO_3^- coming from the overlying water was stimulated 1.2- and 1.7-fold in microcosms containing 3000 and 6000 ind m^{-2} relative to control microcosms. The presence of *C. volutator* (6000 ind m^{-2}) stimulated nitrogen removal from the system, as dinitrogen, 1.5-fold relative to non-bioturbated microcosms. *C. volutator* individuals used in our study were collected from Norsminde Fjord, Denmark, in 1990.

Introduction

Bottom-dwelling organisms transport particles and fluids during feeding, burrowing, tube construction and irrigation activity (Rhoads 1974). These activities affect both physical and chemical processes in the sediments (Aller 1988; Kristensen 1988). Various authors have reported stimulation of carbon and nitrogen mineralization in bioturbated sediments (Kristensen and Blackburn 1987; Hansen and Blackburn 1992b). The purpose of the present paper is to evaluate the effects of bioturbation by *Corophium volutator* on microbial nitrogen transformations and on the transport and build-up of inorganic reactants or products associated with the decomposition of organic matter.

Corophium volutator lives in "U"-shaped burrows 2- to 6-cm deep which are continuously irrigated. Ventilation of surface water into the burrows supplies electron-acceptors (e.g. oxygen, nitrate and sulfate) and removes possibly inhibitory metabolites (e.g. ammonium and sulfide). The infauna has an important effect on the NH_4^+ flux, increasing it considerably by means of direct excretion from the amphipods and by stimulation of microbial nitrogen transformations in the microenvironment around the burrows (Blackburn and Henriksen 1983; Henriksen et al. 1983). Ammonium in burrow walls will either be oxidized by autotrophic nitrifying bacteria or will pass to the burrow water and subsequently to the overlying water by the ventilation current. There is evidence for a high potential nitrification in *C. volutator*'s burrow linings compared to surface sediment (Henriksen et al. 1983). The nitrate produced by nitrification in oxic layers will either pass to the overlying water or enter the anoxic sediment, where it is reduced to free nitrogen gas by denitrification and thereby lost from the ecosystem. Higher nitrification and denitrification activity, due to the presence of *C. volutator*, have been reported by Henriksen et al. (1980, 1983) and Pelegrí et al. (1994). Pelegrí et al. (1994), in an earlier experiment using ^{15}N isotopes, reported that *C. volutator* (19 800 ind m^{-2}) enhanced oxygen uptake, denitrification of NO_3^- from nitrification within the sediment and denitrification of NO_3^- coming from the overlying water by 2-, 3- and 5-fold, respectively. The present paper presents the results of an experiment designed to study the effects of *C. volutator* on nitrogen cycling in a more global context. Inorganic nitrogen pore water profiles, sediment microbial

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activity and fluxes between the sediment and the overlying water were used to describe the importance of benthic animal activity on promoting nutrient exchange.

Materials and methods

Ten plexiglass coring tubes (30 cm long and 7.4 cm inner diameter) were used to hold Norsminde Fjord (Denmark) sediment. This sediment, collected from the upper centimeters layer, had previously been homogenized and sieved through 1-mm mesh on location, in order to remove macrofauna and large particles. The cores, containing 23 cm sediment and a water phase of 7 cm, were closed to avoid air bubbles and kept in the dark at 13 °C, with magnetic stirring. A continuous in situ water (18‰) flow system (63 to 71 $\mathrm{ml\,h^{-1}}$) was installed. The turnover rate of the overlying water was between 4 and 5 h.

After 1 wk, *Corophium volutator* individuals (5 mg wet wt), collected at the same locality in 1990, were added to three cores to a density of 3000 $\mathrm{ind\,m^{-2}}$ (13 ind), three cores to a density of 6000 $\mathrm{ind\,m^{-2}}$ (26 ind), and the remaining four cores were used as controls. The amphipods dug immediately into the sediment after introduction. The *C. volutator* densities used in this experiment are common in Norsminde Fjord. *C. volutator* abundances ranging from 40 $\mathrm{ind\,m^{-2}}$ (Aarhus Amts 1981) to 65000 $\mathrm{ind\,m^{-2}}$ (Thorson 1975) have been reported in Danish estuaries and fjords.

Benthic fluxes were calculated from water samples, collected from the inlet and outlet water, and the flow rates measured for each core. Samples for O_2, CO_2, NH_4^+ and NO_3^- plus NO_2^- concentration measurements were taken every second day. Oxygen was determined by the Winkler method and CO_2 by Gran titration (Talling 1973). The standard autoanalyzer methods described by Grasshoff (1983) for NO_3^- plus NO_2^- and NH_4^+ were used.

Thirteen days after setup, sediment samples were taken to determine sediment characteristics, pore water solute concentrations and microbial activities. The cores were cut into 0 to 0.5, 0.5 to 1.5, 2.5 to 4.5, 4.5 to 6.5 and 6.5 to 8.5 cm sections. Unfortunately, due to the shortage of sediment available, all the analyses were run on single samples. This sediment was used to determine sediment specific density, pore water content (weight loss after 24 h at 105 °C), organic content [loss-on-ignition (LOI) at 500 °C after 12 h], pore water NO_3^- plus NO_2^-, pore water NH_4^+, exchangeable NH_4^+ and potential denitrification rates. Pore water was obtained by centrifuging the sediment for 15 min, at 3000 rpm (1300 *g*), in double centrifuge tubes (Blackburn 1990). The supernatant was collected and frozen. Ammonium attached to sediment particles (exchangeable NH_4^+) was extracted by incubating sediment samples (10 g sediment) in 10 ml 1 *M* KCl solution for 30 min. After the incubation, the samples were centrifuged at 3000 rpm, 130 *g*, for 10 min and the supernatant collected and frozen for NH_4^+ analysis (Blackburn 1980). The concentration of exchangeable NH_4^+ was calculated by subtracting the concentration of NH_4^+ present in pore water from the amount of KCl-extracted NH_4^+.

Potential denitrification was determined in sediment slurries (Kristensen and Blackburn 1987). Acetylene was added to the slurries to block N_2O reduction to N_2 gas (Sørensen 1978). Sediment samples of 2 g were incubated at 22 °C, in 120-ml bottles containing 40 ml seawater, which had previously been enriched with KNO_3^- to 200 μM. The bottles were purged with N_2, to make them anoxic, and subsequently with C_2H_2 to saturation. The bottles were kept closed and shaken throughout the experiment. Gas samples were taken after ≈1, 4, 7 and 10 h and stored in 3.4-ml Venoject blood collection tubes (Terumo Europe N.V.). Gas samples were analyzed for N_2O on a gas chromatographer (model 427; Packard Instr. Co.) equipped with a ^{63}Ni electron capture detector. Solubility coefficients of N_2O were taken from Weiss and Price (1980).

Results

The sediment water content ranged from 15 to 19% (by weight), the organic matter content from 0.4 to 0.6% (by weight) and the sediment specific density from 1.8 to 2.4 $\mathrm{g\,cm^{-3}}$, in the various microcosms. Differences between inhabited and non-inhabited microcosms were masked by differences in compactation of the sieved sediment (data not shown).

Nitrate concentration in pore waters (Fig. 1) was higher in the upper sediment layers and then remained almost constant with depth. The NO_3^- maximum concentration was situated at 2 and 4 cm depth in microcosms containing 0 and 6000 *Corophium volutator* $\mathrm{ind\,m^{-2}}$, respectively. Figs. 2 and 3 show pore water NH_4^+ and exchangeable NH_4^+ concentrations in control and inhabited microcosms. Pore water NH_4^+ concentration in control microcosms increased in the first 2 cm and then remained almost constant at depth, while in *C. volutator*-inhabited microcosms the concentration of pore water NH_4^+ in the sediment decreased continuously (Fig. 2). The concentration of NH_4^+ attached to sediment particles was highest in the surface sediment and then remained almost constant with depth. At the sediment surface, the concentration of exchange-

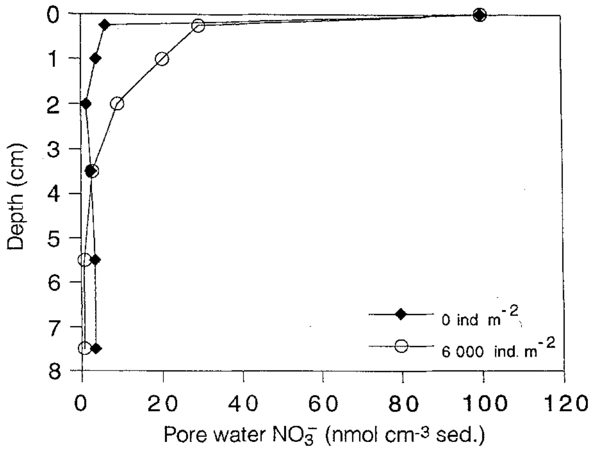

Fig. 1 *Corophium volutator*. Concentration profiles of pore water NO_3^- in microcosms containing 0 and 6000 $\mathrm{ind\,m^{-2}}$. (*sed.* sediment)

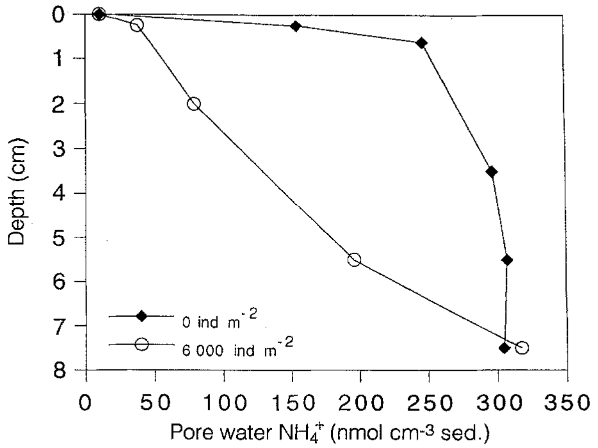

Fig. 2 *Corophium volutator*. Concentration profiles of pore water NH_4^+ in microcosms containing 0 and 6000 $\mathrm{ind\,m^{-2}}$. (*sed.* sediment)

Table 1 Fluxes of O_2, CO_2, NO_3^- and NH_4^+ (in mmol m^{-2}d^{-1}) 13 d after setup in microcosms inhabited by *Corophium volutator* to densities of 0, 3000 and 6000 ind m^{-2}. Enhancement of fluxes due to presence of the amphipods given as % increase relative to non-bioturbated microcosms. Positive fluxes are into the sediment

Amphipod density	NO_3^- fluxes	% increase	NH_4^+ fluxes	% decrease	CO_2 fluxes	% increase	O_2 fluxes	% increase
0 ind m^{-2}	12.0±1.8		1.4±0.1		−20.3±10.3		27.8±3.7	
3000 ind m^{-2}	14.7±6.6	22	0.6±0.5	57	−24.1±12.8	19	30.8±1.7	11
6000 ind m^{-2}	20.2±0.5	68	0.2±0.4	85	−29.0±10	43	33.7±4.5	21

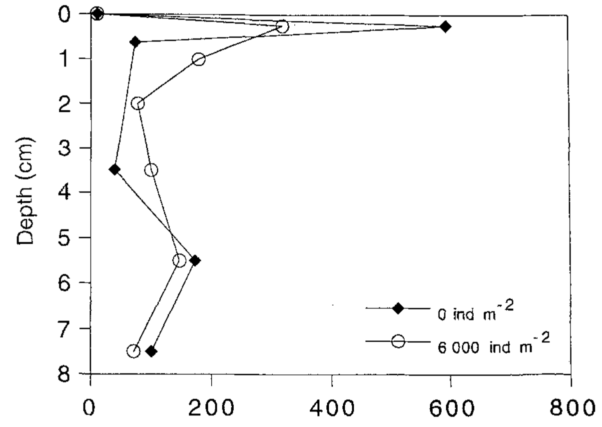

Fig. 3 *Corophium volutator.* Concentration profiles of pore water exchangeable NH_4^+ in microcosms containing 0 and 6000 ind m^{-2}. (*sed.* sediment)

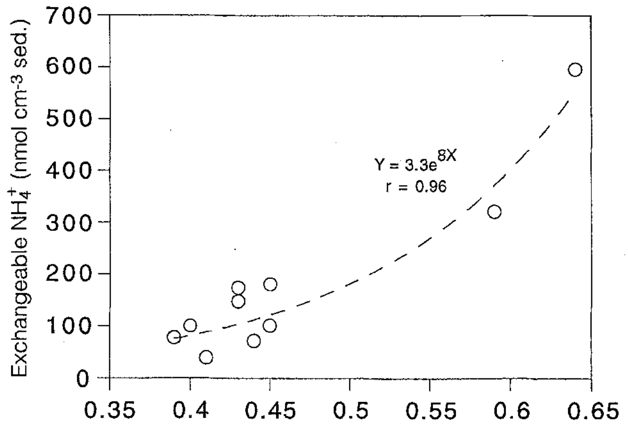

Fig. 4 *Corophium volutator.* Sediment (*sed.*) organic matter content (*LOI*) versus pore water exchangeable NH_4^+. Both parameters were exponencially correlated (r=0.96)

able NH_4^+ was 2-fold higher in non-inhabited relative to bioturbated microcosms (Fig. 3). There was a positive correlation (r=0.96) between exchangeable NH_4^+ concentration and organic matter content in the sediment (Fig. 4).

The sediment-water fluxes reached steady state 6 d after setup (not shown). Table 1 shows the results of the incubation carried out 13 d after setup, before the microcosms were sacrificed. Fluxes of O_2, CO_2, NO_3^- and NH_4^+ for the various microcosms are indicated. Nitrate and NH_4^+ fluxed into the sediment from the overlying water. The amphipods increased O_2 and NO_3^- uptake and CO_2 production by the sediment. *Corophium volutator* decreased the sediment NH_4^+ uptake relative to control microcosms. The ΣCO_2 efflux/O_2 uptake ratio was 0.73, 0.78 and 0.86 in microcosms containing 0, 3000 and 6000 *C. volutator* ind m^{-2}, respectively.

Fig. 5 shows the potential denitrification rates measured in microcosms containing 0 and 6000 ind m^{-2}. The sediment potential denitrification rates were higher in inhabited microcosms until ≈4 cm depth, with a maximum at 2 cm. Potential denitrification rates below 4 cm depth were similar in both bioturbated and non-bioturbated microcosms.

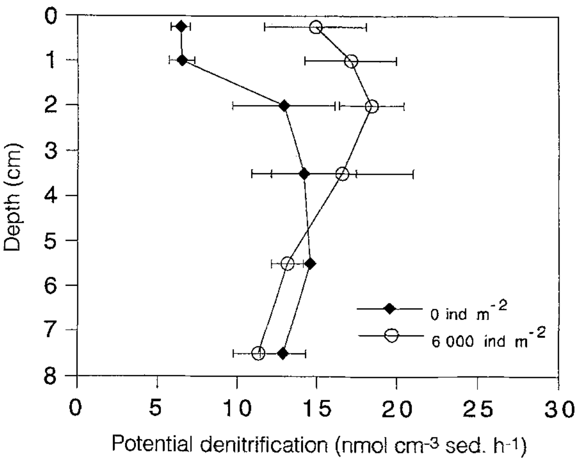

Fig. 5 *Corophium volutator.* Sediment (*sed.*) potential denitrification profiles (±SE) in microcosms containing 0 and 6000 ind m^{-2}

Discussion and conclusions

Corophium volutator increased the overall sediment C-mineralization. Fluxes of O_2 were enhanced by ≈10 and 20%, while CO_2 fluxes were enhanced by ≈20 and 40% in microcosms inhabited by 3000 and 6000 ind m^{-2}, respectively. *C. volutator* densities of approximately 6000 ind m^{-2} have been reported to increase O_2 consumption by 10 to 40% and CO_2 production by 11% (Andersen and Kristensen 1988; Pelegrí et al. 1994). Oxygen consumption rates by *C. volutator*, calculated from the literature (McLusky 1969; Birklund 1977), indicated that the amphipod metabolism accounted for 2 to 3% of the total sediment oxygen uptake in our bioturbated microcosms.

The ratio $\Sigma CO_2/O_2$ fluxes was < 1 in our experiment. This ratio has been reported to lie between 1 and 5 in marine sediments (Hargrave and Phillips 1981; Andersen and Hargrave 1984; Blackburn et al. 1988). Some authors have, however, reported ratios below 1 in sediments collected in Norsminde Fjord (Therkildsen and Lomstein 1993) and Aarhus Bay (Hansen and Blackburn 1991, 1992 a). These authors suggested that these oxygen uptake rates, higher than ΣCO_2 efflux rates, could be explained by chemical oxidation of reduced species in the sediment (e.g. NH_4^+, Mn^{2+}, Fe^{2+}, HS^-). Ratios < 1 are probably due to an uncoupling between anaerobic respiration and the oxidation of reduced compounds. The respiratory quotient ($\Sigma CO_2/O_2$) increased from 0.73 to 0.86 with increasing *Corophium volutator* density from 0 to 6000 ind m^{-2}. Thus bioturbation increased the $\Sigma CO_2/O_2$ ratio to almost 1. This was explained by a greater coupling between anaerobic and aerobic processes in the bioturbated sediment 13 d after setup, when these flux measurements were carried out. Burrowing by the infauna enhances the transport of reduced compounds from deeper anoxic layers to the upper oxic layer where they can be oxidized, while ventilation of the burrow increases the oxygen supply to the sediment. Hylleberg and Henriksen (1980) suggested that the presence of *C. volutator* (6000 ind m^{-2}) enhanced the sediment oxic volume by 100 to 150% by assuming an oxygen penetration of 6 and 2 mm into surface sediment and burrow wall, respectively. Aller (1990) and Canfield et al. (1993) reported that the introduction of oxygen into pore water by infaunal irrigation and reworking activities may cause Fe^{2+} and Mn^{2+} to be oxidized. Hines and Jones (1985), Kristensen and Blackburn (1987) and Thamdrup et al. (in press) indicated that the presence of macrofauna increased sulfide oxidation in the sediments.

Pore water NH_4^+ concentrations revealed a NH_4^+ removal from inhabited microcosms due to burrow irrigation and possibly due to increased rates of nitrification. Henriksen et al. (1993) also reported lower pore water NH_4^+ concentrations in sediment inhabited by an amphipod community (*Ampelisca* spp.) relative to control microcosms, while Henriksen et al. (1980) found 2-fold increased nitrification rates in sediment containing 6000 *Corophium volutator* ind m^{-2}, relative to non-bioturbated sediment. The amount of exchangeable NH_4^+ was proportional to the amount of organic matter present in the sediment, which was highest in the top 2 cm layer. Rosenfeld (1979) reported that NH_4^+ was mostly adsorbed to organic matter in the sediment. Removal of surface organic matter, due to bioturbation, was reflected in the higher amount of NH_4^+ attached to sediment particles in non-bioturbated microcosms.

Nitrate concentration in pore waters was higher in the upper 4 cm of sediment containing *Corophium volutator* (6000 ind m^{-2}). A similar pattern in pore water NO_3^- concentrations was reported by Henriksen et al. (1980, 1983). Higher nitrification rates in the oxic layer of bioturbated sediments were responsible for this NO_3^- accumulation in the upper sediment layer.

The expected N-mineralization fluxes, calculated from ΣCO_2 production rates (assuming that C- and N-mineralization were in proportion to the C:N ratio in the detritus, C:N ratio = 10 from Therkildsen and Lomstein 1993), were 2.0, 2.4 and 2.9 mmol m^{-2} d^{-1} in microcosms inhabited by 0, 3000 and 6000 ind m^{-2}, respectively. The simultaneous influx of NH_4^+ and NH_3^- to the microcosms indicated that the entire net NH_4^+ production was nitrified and that the coupled nitrification-denitrification was close to 100%. From this, we calculated nitrification and total denitrification rates of ≈3.4 and 15.4 mmol m^{-2} h^{-1} in control microcosms. Denitrification of NO_3^- coming from the overlying water and of NO_3^- generated within the sediment represented 79 and 21%, respectively, of the total denitrification.

In order to calculate nitrification rates in bioturbated microcosms in comparison with non-bioturbated microcosms, various sources of NH_4^+ should be taken into account:

(1) Higher N-mineralization rates. The previously calculated N-mineralization rates may have been underestimated due to a higher C:N ratio in bioturbated sediments relative to non-bioturbated sediments. Kristensen and Blackburn (1987) and Hansen and Blackburn (1992 b) found 1.6-fold higher C:N ratios in organic matter taken from sediment inhabited by *Nereis virens* and *Nephthys sp.* relative to amphipod-free sediment. In our experiment, this would lead to N-mineralization rates of 3.8 and 4.6 mmol NH_4^+ m^{-2} d^{-1} in microcosms containing 3000 and 6000 *Corophium volutator* m^{-2}, respectively.

(2) Advection of NH_4^+ generated at deeper layers to the overlying water due to burrow irrigation. Integration of pore water NH_4^+ curves indicated that 13 d after setup ≈10 mmol NH_4^+ m^{-2} was removed from the sediment, in microcosms containing 6000 ind m^{-2} relative to control microscosms. Part of this NH_4^+ was removed shortly after setup, due to burrowing, and the rest was flushed to the water column by the ventilation currents and/or nitrified in the sediment oxic layer. The flux of NH_4^+ from the overlying water into the sediment decreased by ≈60 and 90% in microcosms containing 3000 and 6000 *Corophium volutator* m^{-2}, respectively, relative to control microcosms. This was presumably due to an increased flushing in bioturbated microcosms, which increased the NH_4^+ concentration in the water column and thus decreased the measured NH_4^+ influxes.

(3) The NH_4^+ excreted by the macrofauna. Henriksen et al. (1980, 1983) estimated that macrofaunal excretion constituted 125 to 150% of the increase in NH_4^+ efflux in microcosms containing 6000 *Corophium volutator* ind m^{-2}. In our experiment the calculated excretion rate (1.04 µmol NH_4^+ g^{-1} fresh weight h^{-1}, Henriksen et al. 1983) was 749 µmol NH_4^+ m^{-2} d^{-1} in microcosms containing 6000 ind m^{-2}.

Since no NH_4^+ efflux occurred, we may assume that all NH_4^+ mineralized, excreted by the amphipods and advected from deeper sediment layers (assuming an equal daily removal of NH_4^+) was nitrified in the oxic layer. However, 1.2 mmol NH_4^+ m^{-2} d^{-1} diffused from the sediment to the overlying water in inhabited sediments (6000 ind m^{-2}) relative to control sediments, as deduced from their NH_4^+ influxes. This leads to nitrification rates of 4.9 mmol $N\,m^{-2}\,d^{-1}$, which are 1.4-fold higher than those in control microcosms, but lower than the 2-fold higher rates reported by Henriksen et al. (1980).

Nitrate uptaken by the sediment was 20 and 70% higher in microcosms inhabited by 3000 and 6000 ind m^{-2}, respectively. Henriksen et al. (1980) reported that NO_3^- influxes increased by 65 to 75% in the presence of 6000 *Corophium volutator* ind m^{-2}. These higher NO_3^- consumption rates were reflected in the greater denitrification potential found in the 4 cm upper sediment layer, coinciding with the depth of *C. volutator* burrows. Denitrification in bioturbated sediment was enhanced more than nitrification, as deduced from the increased uptake of NO_3^- relative to the decreased uptake of NH_4^+ in these sediments. If we assume NO_3^- ammonification to be unimportant in our system (Pelegrí et al. 1994), the amphipod increased denitrification rates of NO_3^- coming from the overlying water by 1.2- and 1.7-fold in microcosms containing 3000 and 6000 ind m^{-2}, respectively.

The coupling between nitrification and denitrification, in inhabited microcosms, was very close to 100% as ≈10 mmol $NH_4^+\,m^{-2}$ disappeared from the sediment, but only 0.28 mmol remained as NO_3^- in the sediment and the rest was denitrified. Assuming that all the NH_4^+ which was nitrified in the oxic layer was subsequently denitrified in the adjacent anoxic layer, we calculated denitrification rates of 25.1 $mmol\,m^{-2}\,d^{-1}$ in microcosms containing 6000 ind m^{-2}. Thus denitrification of NO_3^- coming from the overlying water (dw) and of NO_3^- generated within the sediment (dn) increased by 1.7- and 1.4-fold, respectively. Pelegrí et al. (1994) reported a 2.6- and 1.3-fold increase in dw and dn, respectively, in microcosms containing 6600 ind *Corophium volutator* m^{-2}. *C. volutator*'s irrigation mechanism was responsible for this higher stimulation of dw relative to dn (Pelegrí et al. 1994; Pelegrí and Blackburn in press).

Our study has shown that the presence of *Corophium volutator* increased overall C- and N-mineralization processes, taking place in the microcosms, by burrow construction and irrigation. Burrow ventilation removed large amounts of NH_4^+ from the sediment, which was used by nitrifying bacteria in the oxic layer, and transported NO_3^- to the burrow sediment, increasing the possibility of denitrification. The presence of the amphipods increased both nitrification and denitrification, but the latter was stimulated most. The coupling between these two processes was close to 100%. The sediment in our microcosms acted as a net trap for nitrogen, which was removed from the system as dinitrogen. The presence of *C. volutator* (6000 ind m^{-2}) stimulated this nitrogen removal by 1.5-fold relative to non-inhabited microcosms.

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