Biogeochemistry **45:** 147–168, 1999.

Transport of carbon dioxide and ammonium in bioturbated (*Nereis diversicolor*) coastal, marine sediments

KRIK KRISTENSEN & KIM HANSEN
Institute of Biology, Odense University, DK-5230 Odense M, Denmark

Accepted 29 July 1998

Key words: bioturbation, effective diffusion, *Nereis diversicolor*, nonlocal exchange, sediment permeability, transport enhancement

Abstract. Two identical experiments with sieved and homogenized sandy and muddy sediment were conducted to determine transport enhancement of porewater solutes (TCO_2 and $NH_4{}^+$) by the presence of the polychaete *Nereis diversicolor* (1000–1500 m^{-2}). Flux measurements showed that *N. diversicolor* enhanced the release of CO_2 and $NH_4{}^+$ 1.5–5 times. Accordingly, porewater concentrations of these compounds were reduced considerably in the bioturbated zone of both types of sediments. Two different diagenetic models, "effective (eddy) diffusion" and "nonlocal exchange", were used to describe solute profiles in the bioturbated sediments. In permeable sandy sediments advective porewater movements may occur more readily than in more cohesive muddy sediments. The "effective diffusion" model (with $D_e = 1.6$–$2.0\ cm^2\ d^{-1}$) provided an excellent fit to the measured concentrations of both solutes below the bioturbated zone in permeable sandy sediment, whereas this model overestimated the concentration in the bioturbated zone. However, in the less permeable muddy sediment the "effective diffusion" model overestimated the $NH_4{}^+$ profile considerably at all depths. The "nonlocal exchange" model (with $\alpha = 0.17$–$0.29\ d^{-1}$), on the other hand, provided an excellent fit in the less permeable muddy sediment, suggesting that solute profiles here were controlled by molecular diffusion, even in the presence of burrow irrigation. For the permeable sediment, the "nonlocal exchange" model (with $\alpha = 0.14\ d^{-1}$) underestimated the measured $NH_4{}^+$ profile. Accordingly, linear slopes from plots of porewater TCO_2 as a function of porewater $NH_4{}^+$ revealed that eddy diffusion (or advective porewater movements) was important in the bioturbated zone of this sediment type. However, combined with the generally more realistic shape of profiles derived by the "nonlocal exchange", these evidences suggest that both eddy and molecular diffusion must operate in the bioturbated zone of permeable sediments.

Introduction

The activities of benthic infauna have profound impacts on transport conditions and diagenetic processes in aquatic sediments. Sediment reworking and water irrigation (or ventilation) redistributes both particles and porewater

(Aller 1982; Matisoff 1982). By volume, the amount of water moved is much larger than that of particles, and burrows act as channels for the direct communication between porewater and overlying water (Aller 1977). The animal stimulation of solute exchange between subsurface porewaters and overlying water, therefore, redistributes dissolved reactants and products of microbial reactions (Aller 1982; Christensen et al. 1984; Archer & Devol 1992).

Several attempts have been made to quantify irrigation rates of infaunal animals directly and to describe the irrigation impact on porewater solutes. Among techniques to measure irrigation rates directly, electromagnetic flowmeters (Kristensen et al. 1991), microthermistors (Aller & Yingst 1978) and infrared phototransducers (Vedel & Riisgård 1993) have provided new knowledge on temporal activity patterns of benthic infauna and exchange rates of dissolved compounds and particulate matter between the sediment and overlying water. In the context of biogeochemistry, however, sediment irrigation rates have usually been quantified by a class of indirect techniques. With respect to effects of bioturbation on porewater solute distribution in the sediment, primarily three basic types of transport-reaction models have been described. The first, an "effective diffusion" type, assumes that irrigation can be modelled as an increased effective transport (e.g. eddy diffusion) of solutes within the sediment (e.g. Vanderborght et al. 1977; Goldhaber et al. 1977). The second, a "radial diffusion" type, assumes that changes in porewater solutes due to irrigation is caused by a two-dimensional (radial) diffusion geometry and flushing of solutes in the presence of burrows and tube structures (Aller 1980). The third is a one-dimensional "nonlocal exchange" model with a single nonlocal transport parameter (Emerson et al. 1984; Martin & Sayles 1987). Under certain conditions, the latter model is equivalent to the "radial diffusion" model (Boudreau 1984). The models have been verified more or less succesfully by fitting either steady state distributions of naturally occurring solutes (substrates and metabolites of microbial reactions or radioisotopic tracers) with a known reaction rate or transient state distributions of added radioisotopic tracers.

It is generally accepted that the "radial-diffusion" and "nonlocal exchange" models provide the most realistic characterization of the geochemistry of irrigated sediments (Aller 1982; Boudreau 1997). Basically, in these models it is assumed that solutes move through the porewaters only by molecular diffusion and can enter or leave the sediment both at the sediment-water interface and along the burrow wall. The role of irrigation is therefore to increase the surface area available for exchange. The models have usually been applied to relatively impermeable sediments where eddy diffusion is negligible. In recent years, however, a number of studies have demonstrated that advective porewater movements can occur in permeable, sandy sediments when exposed to pressure gradients induced by water currents (Huettel & Gust 1992; Glud et al. 1996). Since many burrow dwelling invertebrates living in shallow sandy sediments irrigate their burrows vigorously (Kristensen 1988; Vedel & Riisgård 1993), porewater advection (eddy diffusion) may be an important process, in excess of molecular diffusion, for the transport of solutes in permeable sediments.

The purpose of the present work was to evaluate the applicability of the "effective diffusion" and "nonlocal exchange" models in describing solute distribution in bioturbated coastal, marine sediments of different permeability. By the use of homogenized microcosms containing either permeable sandy or cohesive muddy sediment, transport stimulation of solutes by irrigation was determined for the polychaete *Nereis diversicolor*. The models were evaluated based on the relationship between porewater profiles of two solutes (total CO_2 and NH_4^+) with different molecular diffusion coefficients.

Materials and methods

Sediment collection and handling

Organic-poor, sandy sediment used in experiment 1 (sand-exp) was collected in June 1992 from the shallow (0–1 m) marine lagoon, Fallesstrand, on the northeast coast of Fyn, Denmark. Annual range in water temperature and salinity in the area is 2–22 °C and 16–23‰, respectively. The sediment consisted of homogeneous quartz sand (median particle size about 0.2 mm and 0.5% silt+clay content) with an organic content of 0.4–0.8% Loss-on-Ignition (LoI). Most of the primary production in the lagoon is due to benthic diatoms. The macrophyte vegetation is poor and dominated by the seagrass, *Ruppia maritima*. The benthic macrofauna are numerous, but low in diversity and dominated by 3 species of surface deposit-feeders: the polychaete *Nereis diversicolor*, the gastropod *Hydrobia neglecta*, and the crustacean *Corophium volutator*. For further details consult Kristensen (1993).

Organic-rich sediment for experiment 2 (mud-exp) was obtained in March 1993 from the inner region of the shallow lagoon, Kertinge Nor, on the east coast of Fyn, Denmark. Temperature and salinity conditions are similar to those at Fællesstrand. The sediment at the sampling site is muddy (median particle size <0.15 mm and 10–20% silt+clay content) and of relatively high organic content (5–14% LoI). At present, primary production is dominated by benthic diatoms. In the recent past (i.e. before 1992), however, the sediment had been covered by thick mats of the floating macroalgae *Chaetomorpha linum* and *Cladophora serica*, which were the origin of the high content of sedimentary organic matter (Hansen & Kristensen 1997). The benthic macrofauna was sparce during sampling, consisting of a few scattered individuals of *N. diversicolor*. For further details consult Riisgård et al. (1995).

At each sampling occasion, the uppermost 5–10 cm of the sediment was dredged and sieved through a 1.5-mm mesh to remove macrofauna and larger particles. In the laboratory, the sediment was homogenized before it was transferred into 6 acrylic core liners (30 cm long and 5.2 cm i.d. in sand-exp, 25 cm long and 8 cm i.d. in mud-exp) to a depth of about 15 cm. Cores were kept at 15 °C in darkness using an incubator with circulating seawater (Kristensen 1993). Salinity was 14 ‰ in sand-exp and 16 ‰ in mud-exp. After 2 days of stabilization in sand-exp, and 17 days in mud-exp, a number of 3 (sand-exp) or 6 (mud-exp) medium sized (200–400 mg wet wt.) individuals of the polychaete *Nereis diversicolor* were added to 3 of the cores (N-cores). The remaining 3 cores were kept as defaunated controls (C-cores).

Experimental procedures

All cores were maintained in the seawater incubator with open tops for 32–45 days interrupted by 2 incubations of 2 randomly chosen cores of each type (sand-exp: day 24 and 30 and mud-exp: day 23 and 33) for determination of O_2, total CO_2 ($TCO_2 = H_2CO_3 + HCO_3^- + CO_3^{2-}$) and NH_4^+ flux across the sediment-water interface. During flux incubations the seawater flow was temporarily disconnected, and the cores were sealed with magnetic stirrer motors as the lid. Stirring was kept below the resuspension level. Water samples for O_2, TCO_2 and NH_4^+ were taken at the start (before inserting the motors) and at the end (after removing the motors). Incubation time was 2–5 h depending on treatment. Concentration changes during incubations are assumed linear, because O_2 rarely decreased below 60% of air saturation (previous tests have confirmed the linearity). Samples for O_2 and TCO_2 were analyzed within 12 h of sampling. Those for NH_4^+ were frozen immediately and analyzed as soon as possible.

At the end, i.e. day 32 (sand-exp) and day 45 (mud-exp), all cores were sectioned by slicing into 1 cm intervals to 12 cm depth in sand-exp and to 10 cm depth in mud-exp. Subsamples of the sediment slices were examined for wet density (weight of a known volume), water content (weight loss after drying at 130 °C for 6 h), and particulate organic carbon (POC) and nitrogen (PON). Filtered porewater for TCO_2 and dissolved NH_4^+ analysis from the sandy sediment in sand-exp was isolated by centrifugation at 1800 rpm for 5 min in double centrifuge tubes containing GF/C filters. Porewater from the muddy sediment in mud-exp was extracted by squeezing it through GF/C filters under N_2 pressure. Samples for TCO_2 were analyzed within 12 h and those for NH_4^+ stored frozen for later analysis.

Chemical analysis

POC and PON content of 130 °C pre-dried sediment subsamples were analyzed on a Carlo Erba EA1108 CHN Elemental Analyzer according to the procedure of Kristensen and Andersen (1987). TCO_2 was determined by the flow injection/diffusion cell technique of Hall and Aller (1992) using a Kontron Ion Chromatograph. Interfering sulfides were precipitated before analysis by adding $ZnCl_2$. The standard Winkler technique was used for O_2 analysis (Strickland & Parsons 1972). NH_4^+ in sand-exp was determined by the standard autoanalyzer technique of Solorzano (1969), whereas the manual salicylate hypochlorite method of Bower and Holm-Hansen (1980) was used in mud-exp.

Results

Sediment description

The defaunated control cores had a more (sand-exp) or less (mud-exp) well defined upper oxidized brown zone of 0.5–0.7 cm thickness. Deeper in the sandy sand-exp cores the sediment gradually changed color to grey and greyish-black. The deep sediment in control cores of mud-exp, on the other hand, was brownish-black. In *Nereis* cores the upper oxidized zone was 1–2 cm deep with irregular extensions deeper down caused by ventilated worm burrows in the greyish-black (sand-exp) or brownish-black (mud-exp) subsurface sediment. Worm burrows extended to 6–8 cm depth in sand-exp and 5–6 cm in mud-exp. In sand-exp the recovery of worms was 67%, while 88% of the added worms remained at the end in mud-exp. Lost worms had either died (although no dead individuals were noticed) or escaped from cores. Accordingly, the density of worms must have ranged from 1500 to 1000 m^{-2} in sand-exp, and from 1200 to 1000 m^{-2} in mud-exp.

Sediment porosity (calculated from water content and wet density) was 0.32–0.35 in sand-exp and 0.75 in mud-exp. Initially the sediment in sand-exp contained about 200 μmol POC cm^{-3} and 20 μmol PON cm^{-3}, providing a C:N ratio of 10. In the mud-exp sediment, POC and PON was about 2000 and 190 μmol cm^{-3}, respectively, providing a C:N ratio of 10–11.

Core fluxes

Rates of O_2 and CO_2 flux were of the same order of magnitude in both experiments (Table 1) with no significant (two-tailed t-test, $p < 0.01$) temporal difference between the two incubations (all data are therefore pooled here).

Table 1. Fluxes of oxygen, carbon dioxide and ammonium across the sediment-water interface in cores with and without *Nereis diversicolor* from sand-exp and mud-exp. Rates are given as mean (mmol m^{-2} d^{-1}) ± S.D. of 4 cores.

	O_2	CO_2	NH_4^+
Sand-exp:			
Nereis	54.6 ± 16.6	45.0 ± 1.7	5.4 ± 0.5
Control	39.6 ± 2.6	35.1 ± 8.8	-1.2 ± 0.1
Mud-exp:			
Nereis	60.9 ± 4.3	85.1 ± 4.1	9.7 ± 2.0
Control	27.4 ± 1.1	36.1 ± 4.9	2.0 ± 0.1

The impact of worms on fluxes was somewhat higher in mud-exp (a factor of 2.2–2.4, $p < 0.01$) than sand-exp (a factor of 1.3–1.4, $p > 0.05$). The flux of NH_4^+ in control cores behaved inconsistently with uptake in sand-exp and release in mud-exp of similar magnitude. However, worms stimulated the efflux of NH_4^+ considerably in both experiments (a factor 4.9 in mud-exp, $p < 0.01$) attaining a flux in mud-exp at a rate about double of that in sand-exp. The CO_2:NH_4^+ flux ratio in mud-exp was reduced from 18.1 to 8.8 by the presence of worms. For comparison, the CO_2:NH_4^+ flux in the bioturbated cores of sand-exp was 8.3.

Porewater solutes

The products of organic carbon and nitrogen mineralization, TCO_2 and NH_4^+, generally accumulated with depth in the sediment (Figure 1), except for a deflection of TCO_2 in the upper 1 and 2 cm of control and *Nereis* cores, respectively, in sand-exp. In control cores, TCO_2 otherwise increased rapidly to about 17–18 mm at 6 cm followed by a slow or no increase deeper down. Porewater profiles of NH_4^+ in control cores were similar to those of TCO_2, although less deflected in the uppermost layers in sand-exp, and attained concentrations around 2 (mud-exp) and 3 (sand-exp) mM below 6 cm depth. No accumulation of dissolved organic carbon (DOC) occurred in any of the experiments (data not shown).

The influence of *Nereis diversicolor* was evident in all experiments as a lower concentration level and a slower increase in concentrations of both solutes with depth in the sediment. The vertical distribution of burrows was clearly reflected in the porewater profiles from sand-exp and mud-exp. The

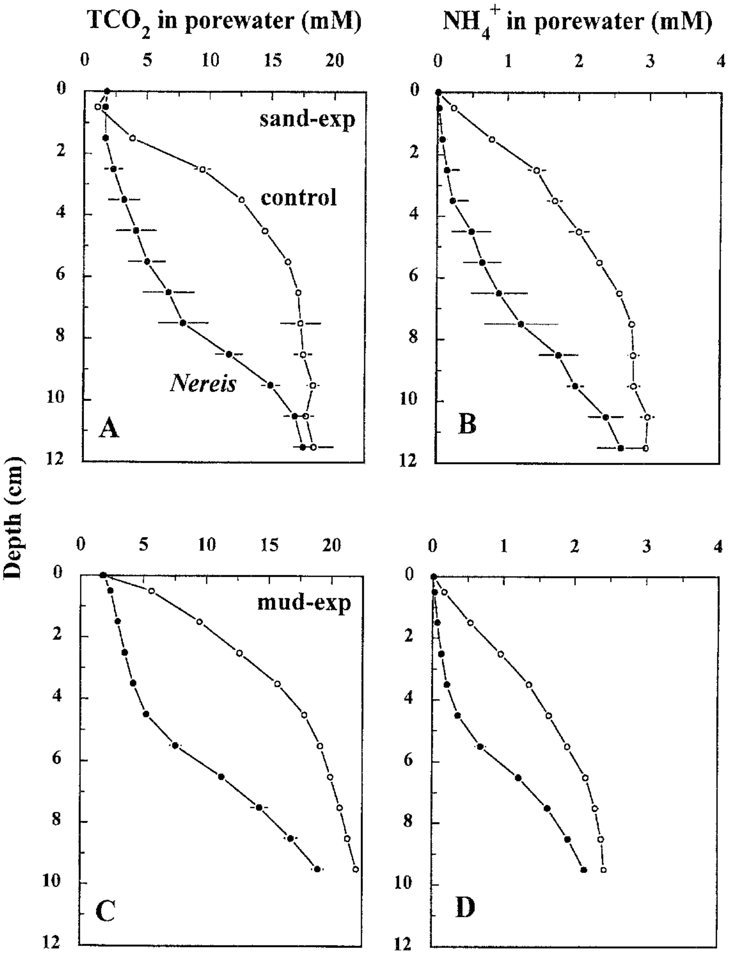

Figure 1. Vertical profiles of porewater TCO_2 (A, C) and NH_4^+ (B, D) in sand-exp and mud-exp. Profiles from non-bioturbated control sediment are indicated by the symbol ○, while *Nereis* bioturbated sediment is represented by ●. Error bars are ± 1 standard error of the mean.

solute concentrations remained low in the burrowed zone (6–8 cm in sand-exp and 5–6 cm in mud-exp) and increased steeply below, almost reaching the level of the control sediment in the deepest layer.

Transport-reaction models

Solutes consumed or generated in sediments by diagenetic reactions are subject to transport by molecular diffusion, advection and mixing processes caused by physical or biological activity. In the absence of sedimentation and compaction, the concentration of any solute, C(x,t), in the porewater can be described by the classic one-dimensional diffusion-reaction model of Berner (1980). However, in the presence of bioturbating infauna the model must be modified to account for the enhanced transport induced by irrigating animals. Two transport-reaction models with modifications for use in bioturbated sediments will be used here. In both models a two-layer formalism (Aller 1982) is applied with an upper bio-irrigated zone ($0 \leq x \leq L_1$) and a lower diffusion controlled zone ($L_1 \leq x \leq L_2$).

The first model ("effective diffusion") assumes that the impact of irrigating macrobenthos on porewater solutes can be described one-dimensionally by an increased "effective" diffusion coefficient (Vanderborght et al. 1977; Berner 1980). The second model ("nonlocal exchange") suggests that irrigation can be accounted for by a source/sink term that permits the exchange of porewater from any depth with the overlying water (Emerson et al. 1984; Boudreau 1984). The solute profiles can be described as one-dimensional diffusion with a nonlocal term and reaction. The transport terms of both models are here, for simplicity, assumed constant with depth in the bioturbated zone, although they ideally may decrease with depth (Martin & Banta 1992). Solute transport in the underlying sediment can be described for both models by simple one-dimensional molecular diffusion.

The steady state vertical distribution of solutes is then:

Zone 1 ($0 \leq x \leq L_1$), "Effective diffusion":

$$\frac{\partial C_1}{\partial t} = D_e \frac{\partial^2 C_1}{\partial x^2} + R = 0 \tag{1}$$

Zone 1 ($0 \leq x \leq L_1$), "Nonlocal exchange":

$$\frac{\partial C_1}{\partial t} = D_s \frac{\partial^2 C_1}{\partial x^2} - \alpha(C_1 - C_t) + R = 0 \tag{2}$$

Zone 2 ($L_1 \leq x \leq L_2$), common:

$$\frac{\partial C_2}{\partial t} = D_s \frac{\partial^2 C_2}{\partial x^2} + R = 0 \tag{3}$$

Boundary conditions for both cases are:

1. $x = 0, \quad C_1 = C_t$

2. $x = L_1, \quad D_e \frac{\partial^2 C_1}{\partial x^2} = D_s \frac{\partial^2 C_2}{\partial x^2} \quad \text{or} \quad D_s \frac{\partial^2 C_1}{\partial x^2} = D_s \frac{\partial^2 C_2}{\partial x^2}$

Table 2. Constants used to obtain the best fit of model profiles to measured profiles. C_t is measured concentration in overlying water; D_s is porosity corrected molecular diffusion coefficients in sediment (Li & Gregory 1974); R is reaction rate determined from the best fit below the bioturbation zone for carbon and estimated for nitrogen based on the reaction stoichiometry found in control cores; D_e and α are found from the best fit of the modelled profiles to the measured profiles in the bioturbated zone.

	C_t (mM)	R (mM d^{-1})	D_s (cm^2 d^{-1})	D_e (cm^2 d^{-1})	α (d^{-1})
CO_2					
Sand-exp	1.78	0.118	0.266	1.600	0.085
Mud-exp	1.82	0.207	0.532	2.000	0.172
NH_4^+					
Sand-exp	0.009	0.025	0.448	1.600	0.143
Mud-exp	0.014	0.043	0.896	2.000	0.290

3. $x = L_1, \quad C_1 = C_2$

4. $x = L_2, \quad \dfrac{\partial^2 C_2}{\partial x^2} = 0$

where t is time, x is depth in sediment, L_1 is depth of bioturbated zone (7.5 cm in sand-exp and 6 cm in mud-exp), L_2 is total depth of sediment column (15 cm), C is solute concentration in sediment (model output), C_t is measured solute concentration in the overlying water (Table 2), D_s is whole sediment molecular diffusion coefficient (Table 2), D_e is the “effective diffusion” coefficient (Table 2), α is the “nonlocal exchange” coefficient (Table 2), and R is reaction rate (Table 2). Solutions to the model equations are given in the Appendix.

Because the sediment was initially homogenized in the present study, the reaction rates (or CO_2 and NH_4^+ production) (R) is approximated as depth-independent and constant. This was shown in a similar, but non-bioturbated, experiment by Kristensen and Hansen (1995). Any changes in reaction rate caused by *N. diversicolor* bioturbation (Kristensen & Blackburn 1987) is ignored here and the reaction rate is assumed similar in all treatments and depths within each sediment type. However, chemoautotrophic oxidation of, e.g., HS^- and NH_4^+, caused reactions in the upper 1–2 cm of the sediment in sand-exp to be different both with respect to rates and direction from those in the deeper more reduced sediment as indicated especially by deflections of TCO_2 profiles (Figure 1; Kristensen & Hansen 1995).

The "effective diffusion" coefficient, D_e, in the first model is analogous to eddy transport coefficients used to describe physical mixing events, and in the present case should illustrate porewater movements. Accordingly, the same D_e applies to all porewater solutes within the bioturbated zone irrespective of their molecular diffusion coefficients. The "nonlocal exchange" coefficient, α, in the second model represents any mode of transport that is capable of exchanging material between nonadjacent points in the sediment. The nonlocal exchange coefficient is fundamentally different from the effective (eddy) diffusion coefficient. Eddy diffusion operates on the gradient whereas nonlocal exchange is strongest where the difference in concentrations between porewater solutes and overlying water is greatest (Boudreau 1997).

Nonlocal transport will be viewed here as a pure diffusional process, which means that the transport coefficient is solute specific and directly related to the diffusion coefficient of the solute of interest. Two solutes with different molecular diffusion coefficients, like TCO_2 and NH_4^+ in the present study, can then be related according to definitions involved in nonlocal transport as: $\alpha_N = \alpha_C D_N/D_C$, where the subscripts C and N denote HCO_3^- and NH_4^+, respectively. The diffusion coefficient of HCO_3^- was used here, because in marine sediments with a pH around 8 this compound accounts for about 95% of TCO_2.

The model fit to the measured data was first performed empirically for TCO_2 by varying transport coefficients (D_e and α) and reaction rates (R) until the best possible agreement between measured TCO_2 concentrations and the model output (C) was obtained. Subsequently, the model fit to the measured NH_4^+ data was done by applying the empirically derived model parameters for TCO_2 after conversion to NH_4^+ units (Table 2). The transport coefficients for NH_4^+ were converted from those of TCO_2 as mentioned above, and rates of NH_4^+ production were converted from CO_2 production by the C:N stoichiometry given for these sediments by Kristensen and Hansen (1995) and Hansen and Kristensen (1997), i.e. 4.7 (sand-exp) and 4.8 (mud-exp).

The model fit to the TCO_2 data in both sand-exp and mud-exp are generally good (Figure 2). The "effective diffusion" model provides an excellent fit below the bioturbated zone. In the bioturbated zone, however, this model overestimates the measured concentrations considerably. The "nonlocal exchange" model, on the other hand, fitted the measured data very well. The slight discrepancy in the upper 3 cm of sand-exp may be due to chemoautotrophic CO_2 consumption or depth dependent changes in the "nonlocal exchange" coefficient. When converted to NH_4^+ data, the fit of the "effective diffusion" model in sand-exp is as good as for TCO_2 with an overestimate in the bioturbated zone and an excellent fit below this depth (Figure 2). However, in mud-exp this model results in a very poor fit to

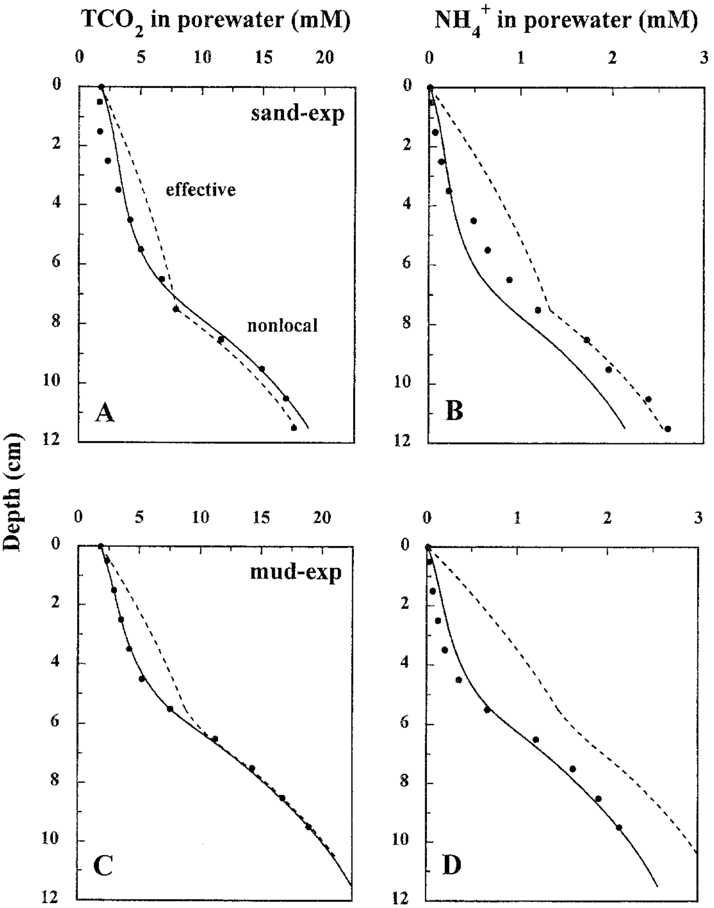

Figure 2. Vertical profiles of porewater TCO_2 (A, C) and NH_4^+ (B, D) in bioturbated sediment from sand-exp and mud-exp. Measured data are indicated by the symbol ●. Profiles fitted by the "effective diffusion" model (eqs. 1 & 3) is represented by the broken line. Profiles fitted by the "nonlocal exchange" model (eqs. 2 & 3) is represented by the full line.

NH_4^+ with considerable overestimates at all depths. Conversely, the "nonlocal exchange" model underestimates the measured NH_4^+ profile below 4 cm depth in sand-exp, but provides almost as good a fit in mud-exp for NH_4^+ as for TCO_2.

Discussion

Since the purpose of this study was to evaluate the impact of bioturbation on solute transport within coastal sediments, the experimental set-up was designed to remove the natural variability of the sediment system. Mixing and homogenization may temporarily destroy the natural chemical, physical and biological structure of sediments, but the effects are generally believed to be short-term (days) relative to an incubation time of 1–2 months (Sun et al. 1991). Accordingly, the measured fluxes of CO_2 and NH_4^+ in the *Nereis* cores are similar to those obtained for undisturbed and bioturbated sediment from the same locations, i.e. between 50 and 100 mmol CO_2 m^{-3} d^{-1} and about 5 mmol NH_4^+ m^{-2} d^{-1} (Kristensen 1993; Hansen & Kristensen 1997). However, full steady state with respect to reaction and transport could not be assumed here because the distance significantly influenced by diffusion in defaunated cores after 30–40 days will only be 5–7 cm (Aller 1978), as also indicated by the vertical shape of profiles in control cores below this depth (Figure 1). The faunated cores, on the other hand, are assumed to be at steady state within the measured depth range.

Faunal induced flux enhancement

The irrigation activity of *Nereis diversicolor* clearly enhances the solute flux out of the sediment (Table 1), as also indicated by the much lower porewater concentrations in bioturbated than in non-bioturbated sediment (Figure 1). A similar pattern has been observed frequently for a variety of bioturbated sediments (e.g., Kristensen & Blackburn 1987; Huettel 1990; Kristensen et al. 1992). Most of the reported flux enhancement factors determined for a variety of solutes from both laboratory experiments and in situ data using sediments from coastal zones to the continental margin are within a range of 1.2 to 7 (Aller 1978; McCaffrey et al. 1980; Andersen & Helder 1987; Archer & Devol 1992). However, the flux enhancement obtained here and by Andersen and Kristensen (1988); (1.2–2.1) for populations of *Nereis diversicolor* are low compared to most other faunal assemblages. The uptake of NH_4^+ in control cores of sand-exp suggests that this compound is consumed by nitrification in the oxic surface of this sediment. The lower CO_2:NH_4^+ flux ratio in bioturbated sediment, on the other hand, indicates that the action of worms creates a more direct passage of reduced compounds from anoxic production sites deep in the sediment to the overlying water.

Porewater models

Bioirrigation effects on porewater TCO_2 parameterized as "effective diffusion" works well below the zone of bioturbation, but is less accurate within this zone. The effective diffusion coefficients obtained here (1.6–2.0 cm^2 d^{-1}; Table 2) are in the low end of the range previously reported for a variety of infaunal assemblages and sediments with D_e values in the range of 0.9 to

8.6 cm^2 d^{-1} (Vanderborght et al. 1977; Aller 1978; McCaffrey et al. 1980; Martin & Sayles 1987; Forster et al. 1995). The excellent fit of the NH_4^+ "effective diffusion" model, after conversion from TCO_2 to measured NH_4^+ data below the bioturbated zone in the permeable sediment of sand-exp, indicates that all solutes in the bioturbated zone of this sediment are subjected to similar transport rates. Eddy diffusion or advective porewater transport is a mechanism which affects all solutes similarly (Aller 1982). However, in the less permeable sediment of mud-exp, where eddy diffusion must be of limited importance, the fit of the NH_4^+ converted "effective diffusion" model to the measured data was, as expected, very poor. The convex shape of modeled profiles in the bioturbated zone of sediments instead of the measured concave profiles suggest that other transport mechanisms in addition to vertical eddy diffusion certainly must control porewater profiles.

The "effective diffusion" coefficients from sand-exp and mud-exp were 4–6 (TCO_2) and 2–4 (NH_4^+) times higher than molecular diffusion coefficients, which is higher than the enhanced TCO_2 flux and comparable to the enhanced NH_4^+ flux in sand-exp caused by *N.diversicolor* (Table 1). However, a comparison between faunal induced changes in transport coefficients and net sediment-water fluxes is hampered by the impact of consumption processes (e.g., nitrification and other chemoautotrophic processes) on fluxes at the aerobic sediment surface.

Profiles of porewater TCO_2 obtained by fitting with the "nonlocal exchange" model are in excellent agreement with measured data and support the radial diffusion theory of Aller (1980) for bioturbated sediments. A comparison of "nonlocal exchange" coefficients with results from the literature is complicated due to the solute specificity of α and the general lack of reports on TCO_2 and NH_4^+. However, Martin and Sayles (1987) estimated a maximum (α_0) value of 0.46 d^{-1} for ^{222}Rn; Martin and Banta (1992) found a range of 0.02–0.28 d^{-1} for ^{222}Rn and 0.02–0.82 for Br; and Emerson et al. (1984) listed values converted from other transport parameters in the range of 0.005–0.86 d^{-1} for a variety of solutes. The values found here for TCO_2 and NH_4^+ (0.09–0.29 d^{-1}) are well within the range given above. After conversion to NH_4^+, the "nonlocal exchange" model provided a better fit in the less permeable (mud-exp) than the permeable (sand-exp) sediment, substantiating the possible role of eddy diffusion in the latter.

Stoichiometric evaluation of transport models

Berner (1977) has shown that if simple stoichiometric decomposition following first-order kinetics occurs, the C:N ratio of the mineralized organic matter may be ascertained from vertical steady state porewater profiles of SO_4^{2-} and NH_4^+ from anoxic sediments using the ratio between one-dimensional diffusion-reaction models for the two solutes. Kristensen and Hansen (1995) showed that the stoichiometry of carbon and nitrogen regeneration can be expressed directly from TCO_2 and NH_4^+ profiles in non-bioturbated sediments by a modification of the Berner (1977) approach when no accumulation of dissolved organic carbon (DOC) occurs. Since the solute profiles in the present non-steady state control cores clearly were affected by diffusion down to 5–7 cm depth, the upper part of the sediment can be considered an open, diffusion dominated zone approaching steady state (Aller & Mackin 1989). As no sedimentation and compaction occurred, and reaction rates are assumed constant with depth below ca. 1 cm, the reaction stoichiometry in the diffusion dominated zone of non-bioturbated sediment can be described by:

$$\frac{R_c}{R_n} = \frac{D_{sc}}{D_{sn}} \frac{dC_c}{dC_n} \tag{4}$$

where subscripts c and n denotes TCO_2 (HCO_3^-) and NH_4^+, respectively; R is the reaction rate; dC_c/dC_n is the slope of a porewater TCO_2 vs. NH_4^+ plot (Figure 3); and D_s is sediment diffusion coefficient. The ratio of TCO_2 and NH_4^+ production rate (C:N ratio of organic matter being mineralized) is then approximately equal to the slope of the relationship between vertical porewater profiles of TCO_2 and NH_4^+ multiplied by the ratio (r) between sediment transport coefficients of the major ions, i.e., for molecular diffusion: $r = D_{sc} / D_{sn} = 0.59$.

Dissolved porewater TCO_2 and NH_4^+ from the diffusion dominated zone of defaunated control sediment in both experiments show a good linear relationship (Figure 3; Table 3). By applying the molecular diffusion correction (r), the C:N stoichiometry of organic matter decay is estimated to 4.6 in both sand-exp and mud-exp. This value is similar to those previously obtained from other anoxic marine sediments (Berner 1977; Aller & Yingst 1978; Klump & Martens 1987; Andersen & Kristensen 1988; Kristensen & Hansen 1995). C:N ratios of 4–5 for mineralization products during decomposition in the sediment indicate that nitrogen was mineralized preferentially to carbon since the C:N ratio of the bulk sediment organic pool was around 10. This is a common feature of many coastal sediments (e.g. Klump & Martens 1987; Boudreau et al. 1992; Kristensen 1993). Although sediment-water fluxes appeared to be somewhat higher in the organic-rich (mud-exp) than the organic-poor (sand-exp) sediment, the accumulation and C:N stoichiometry of both fluxes and porewater solutes were similar in both sediments types, implying that comparable organic substrates have been degraded in each case. Aerobic microbial biomass (including benthic diatoms) is probably a significant source of labile and nitrogen-rich material in the present experiments

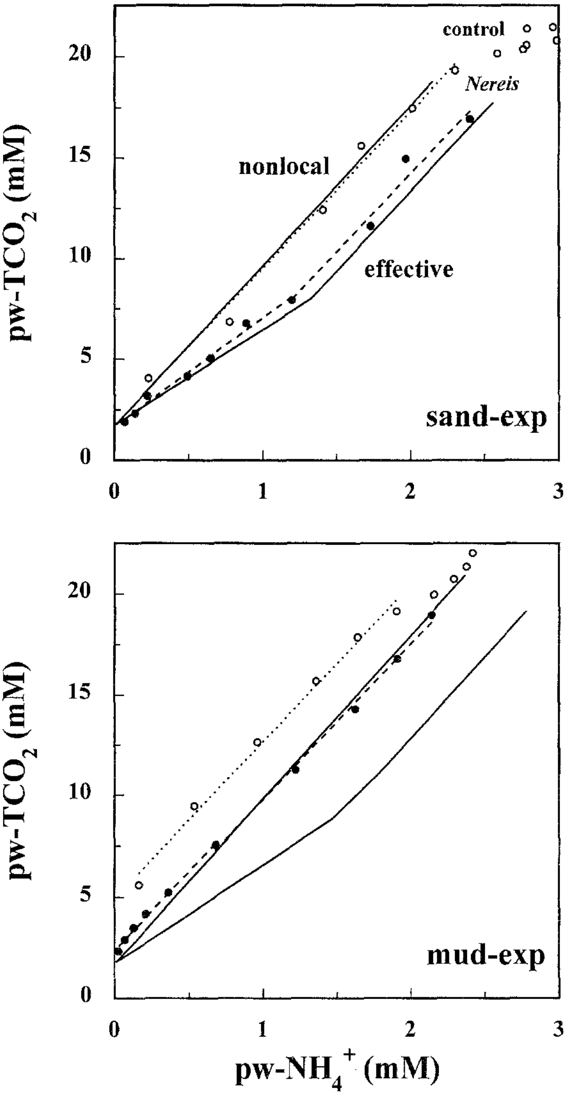

Figure 3. Relationships between porewater profiles of TCO_2 and NH_4^+ in sand-exp and mud-exp. The symbol ○ and dotted line represent non-bioturbated control sediment, while ● and broken line represent *Nereis* bioturbated sediment. The upper full line is the relationship derived from the "nonlocal exchange" model (eqs. 2 & 3), and the lower full line is derived from the "effective diffusion" model (eqs. 1 & 3). Dotted and broken lines are drawn according to linear regression with constants as presented in Table 3. The relationships based on measured data and those derived from the "effective diffusion" model are divided into the upper bioturbation zone and the lower non-bioturbated zone. The relationships from the non-bioturbated sediment based on measured data only include the diffusion controlled upper zone, excluding the data points outside the regression line. The regression from the non-bioturbated sediment in sand-exp is displaced 3 mM TCO_2 upwards for clarity.

Table 3. Regression output from plots of porewater TCO_2 versus dissolved NH_4^+ in sand-exp and mud-exp according to the equation: $y = ax + b$. Results from modelling using the "effective diffusion" and the "nonlocal exchange" approach are shown for comparison. The correlation coefficients, r^2, are shown for measured profiles. For *Nereis* cores the measured data and the "effective diffusion" output are separated in the bioturbated (upper) and the non-bioturbated (lower) zone.

	a	b	r^2
Sand-exp			
Nereis (upper)	5.35	1.69	0.989
Nereis (lower)	7.76	–1.29	0.970
Effective (upper)	4.72	1.74	—
Effective (lower)	7.95	–2.54	—
Nonlocal	7.95	1.71	—
Control	7.77	1.76	0.989
Mud-exp			
Nereis (upper)	7.73	2.40	0.993
Nereis (lower)	7.75	2.03	0.996
Effective (upper)	4.81	1.75	—
Effective (lower)	8.11	–3.39	—
Nonlocal	8.11	1.71	—
Control	7.77	4.90	0.993

(Kristensen & Hansen 1995). After being mixed into the sediment during the pre-experimental homogenization procedure, the displaced microbial biomass was degraded rapidly by the anaerobic microbial community. The large detritus pool originating from past macroalgal depositions in the organic-rich sediment was relatively refractory (Hansen & Kristensen 1997) and therefore without any significant contribution to the parameters determined here.

The relationship between porewater TCO_2 and NH_4^+ in the faunated sediments is different in sand-exp and mud-exp (Figure 3). In the upper 6 cm bioturbated zone of sand-exp, the slope is significantly lower than in the undisturbed zone below (two-tailed t-test, $p < 0.01$) and in the defaunated control sediment ($p < 0.05$); (Table 3). In mud-exp, however, no significant differences are evident between the upper bioturbated and the lower undisturbed zones of the faunated sediments or between both these zones and the defaunated control sediment. These patterns of porewater solutes within the bioturbated zone points to fundamental differences in transport conditions within the two sediment types.

The relationships between measured porewater TCO_2 and NH_4^+ can be compared with those obtained from fitted profiles based on the two transport models (eqs. 1 & 2). The "effective diffusion" model provides two linear relationships, one in the eddy diffusion dominated bioturbated zone with slopes (4.7–4.8) equivalent to the C:N reaction stoichiometry, and one in the molecular diffusion dominated zone below with slopes (8.0–8.1) similar to those obtained in control sediments (Table 3). When based on the diffusion controlled "nonlocal exchange" model only one linear relationship is obtained over the entire depth interval with slopes similar to those of the deep zone of the "effective diffusion" model. Since the relationship in the bioturbated zone of faunated sand-exp sediment approaches that of the "effective diffusion" model, the transport in this zone of the permeable sand-exp sediment must have a significant eddy diffusion component (e.g., from eq. 4, $D_{sc}/D_{sn} \rightarrow 1$). However, since the sand-exp slope is significantly different from both the "effective diffusion" ($p < 0.05$) and the "nonlocal exchange" ($p < 0.01$) slopes, an intermediate situation with both eddy and molecular diffusion control must prevail in this permeable sediment. In mud-exp, on the other hand, the slope of the porewater relationship in the bioturbated zone is not significantly different from that determined from the "nonlocal exchange" model. This implies that all transport within the bioturbated zone of the less permeable mud-exp sediment was driven by molecular diffusion. In the deep zone of faunated sediments in both sand-exp and mud-exp, the slopes are similar to those found for the "nonlocal exchange" and for the deep zone of the "effective diffusion" model, indicating that molecular diffusion was the only transport process here.

Biogenic advection, as observed in the permeable sediment from Fællestrand (sand-exp), has previously been suggested as an important solute transport mechanism between relatively well-mixed and distinct reservoirs within bioturbated sandy sediments and the overlying water (McCaffrey et al. 1980; Aller 1982; Waslenchuk et al. 1983). A classic example of biogenic advection is the burrow system of the polychaete *Arenicola marina*, where respiratory water, drawn into the sediment via the J-shaped burrow, is pressed into the feeding pocket and percolates upward in the sediment-filled head shaft and emerges from the sediment in the feeding funnel (Newell 1979). This upward directed water flow rapidly exchanges porewater and associated solutes in the head shaft with overlying water (Huettel 1990).

In the case of *N. diversicolor*, conditions are somewhat different. This species inhabits U- or Y-shaped burrows with at least two openings to the surface, allowing free passage for irrigated water (Davey 1994). The eddy diffusion or biogenic porewater advection created by irrigation currents (0.3 cm s^{-1}; Riisgård et al. 1992) of this species in permeable sediments (like in sand-exp) may be driven by small-scale pressure gradients along the irregular burrow structure. In comparison, Huettel and Gust (1992) found that the surface roughness of permeable sandy sediments exposed to unidirectional water flow (friction velocity of 0.5 cm s^{-1}) creates pressure gradients large enough to drive porewater out of the sediment. They determined that surface currents similar to those typically found in *N. diversicolor* burrows could enhance the solute flux across the sediment-water interface several fold and influence the concentration of porewater solutes down to several cm depth. Porewater movements across burrow walls, however, may be hampered by the presence of mucus linings of low permeability (Aller 1983). The enhanced solute transport by *N. diversicolor* in less permeable sediments (like in mud-exp) is caused by molecular diffusion across the burrow wall with subsequent flushing to the overlying water by the irrigation current. In this case only limited porewater advection will occur. The degree of transport enhancement is then directly related to the burrow wall area and thus to the increase in sediment-water contact zone (Davey & Watson 1995).

Conclusions

Based on experimental evidence, it was shown here that transport conditions of porewater solutes in the *Nereis diversicolor* bio-irrigated zone was dependent on the permeability of the sediment. A "nonlocal exchange" model generally fitted measured porewater profiles of TCO_2 and NH_4^+ better than an "effective diffusion" model. In less permeable sediment, the molecular diffusion stoichiometry of the former model provides an excellent fit to the profiles of both solutes within and below the bioturbated zone, which the latter did not. It can therefore be concluded that the transport enhancement by *Nereis diversicolor* in less permeable sediments is controlled by nonlocal transport driven by molecular diffusion and directly related to the increase in sediment-water contact zone created by burrows. When the "nonlocal exchange" model is applied to permeable sediments a reasonable fit is achieved, but molecular diffusion corrected (i.e., $r = 0.59$) stoichiometry appears not to be adequate. Here the "effective diffusion" model with an eddy diffusion corrected (i.e., $r = 1$) stoichiometry provides a good fit of both solutes, especially below the bioturbated zone. Although the fit by this model was poor in the bioturbated zone, a plot of measured porewater TCO_2 versus NH_4^+ gave a slope which approached that predicted by the "effective diffusion" model. Based on these evidences, it must be concluded that eddy diffusion (or advective porewater movements) is important in bioturbated, permeable sediments. However, the better fit of the "nonlocal exchange" model with measured profiles, combined with the fundamentally different shapes of profiles fitted by the "effective diffusion" model suggests that both eddy and molecular diffusion operates in the bioturbated zone of permeable sediments. Accordingly, the otherwise most recognized "nonlocal exchange" models must consider both forms of transport to describe bio-irrigation more accurately in such sediments.

Acknowledgements

We thank H. Brandt valuable assistance in the laboratory. Our gratitude is also due to B.P. Boudreau and R.C. Aller for constructive discussions. This work was supported by the Centre for Strategic Environmental Research in Marine Areas, Grant no. 4.22 and SNF Grant # 9601423.

Appendix

The solution to the "effective diffusion" model (eq. 1 & 3) with the boundary conditions given is:

Zone 1:

$$C_1(x,t) = C_t - \frac{R}{2D_e} \times (x - 2L_2)$$

Zone 2:

$$C_2(x,t) = C_t - \frac{R}{2D_s} \times (x - 2L_2) + RL_1\left(\frac{1}{2D_s} - \frac{1}{2D_e}\right)(L_1 - 2L_2)$$

The solution to the "nonlocal exchange" model (eq. 2 & 3) with the boundary conditions given is:

Zone 1:

$$C_1(x,t) = C_t + A_1 \sinh(\beta x) + \frac{R}{\alpha}(1 - \cosh(\beta x))$$

Zone 2:

$$C_2(x,t) = C_t + A_2 + \frac{Rx}{2D_s}(2L_2 - x)$$

where:

$$\beta = \sqrt{\frac{\alpha}{D_s}}$$

$$A_1 = \frac{R}{\alpha}\tanh(\beta L_1) + \frac{R}{D_s}\frac{(L_2 - L_1)}{\beta\cosh(\beta L_1)}$$

$$A_2 = A_1\sinh(\beta L_1) + \frac{R}{\alpha}(1 - \cosh(\beta L_1)) - \frac{RL_1}{2D_s}(2L_2 - L_1)$$

References

Aller RC (1977) The influence of macrobenthos on chemical diagenesis of marine sediments. Ph.D. dissertation, Yale University, Connecticut, 600 pp

Aller RC (1978) Experimental studies of changes produced by deposit feeders on pore water, sediment, and overlying water chemistry. Am. J. Sci. 278: 1185–1234

Aller RC (1980) Quantifying solute distributions in the bioturbated zone of marine sediments by defining an average microenvironment. Geochim. Cosmochim. Acta 44: 1955–1965

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL & Tevesz PJS (Eds) Animal-Sediment Relations (pp 53–102). Plenum, New York

Aller RC (1983) The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. J. Mar. Res. 41: 299–322

Aller RC & Mackin JE (1989) Open-incubation, diffusion methods for measuring solute reaction rates in sediments. J. Mar. Res. 47: 411–440

Aller RC & Yingst JY (1978) Biogeochemistry of tube-dwellings: A study of the sedentary polychaete *Amphitrite ornata* (Leidy). J. Mar. Res. 36: 201–254

Andersen FØ & Helder W (1987) Comparison of oxygen microgradients, oxygen flux rates and electron transport system activity in coastal marine sediment. Mar. Ecol. Prog. Ser. 37: 259–264

Andersen FØ & Kristensen E (1988) The influence of macrofauna on estuarine benthic community metabolism: a microcosm study. Mar. Biol. 99: 591–603

Archer D & Devol A (1992) Benthic oxygen fluxes on the Washington shelf and slope: A comparison of in situ microelectrode and chamber flux measurements. Limnol. Oceanogr. 37: 614–629

Berner RA (1977) Stoichiometric models for nutrient regeneration in anoxic sediments. Limnol. Oceanogr. 22: 781–786

Berner RA (1980) Early Diagenesis, A Theoretical Approach. Princeton University Press, New Jersey, 291 pp

Boudreau BP (1984) On the equivalence of nonlocal and radial-diffusion models for porewater irrigation. J. Mar. Res. 42: 731–735

Boudreau BP (1997) Diagenetic Models and Their Implementation. Springer-Verlag, Berlin, 414 pp

Boudreau BP, Canfield DE & Mucci A (1992) Early diagenesis in a marine sapropel, Mangrove Lake, Bermuda. Limnol. Oceanogr. 37: 1738–1753

Bower CE & Holm-Hansen T (1980) A salicylate-hypochlorite method for determining ammonia in seawater. Can. J. Fish. Aquat. Sci. 37: 794–798

Christensen JP, Devol AH & Smethie WM (1984) Biological enhancement of solute exchange between sediments and bottom water on the Washington continental shelf. Continental Shelf Res. 3: 9–23

Davey JT (1994) The architecture of the burrow of *Nereis diversicolor* and its quantification in relation to sediment-water exchange. J. Exp. Mar. Biol. Ecol. 179: 115–129

Davey JT & Watson PG (1995) The activity of *Nereis diversicolor* (polychaeta) and its impact on nutrient fluxes in estuarine waters. Ophelia 41: 57–70

Emerson S, Jahnke R & Heggie D (1984) Sediment-water exchange in shallow water estuarine sediments. J. Mar. Res. 42: 709–730

Forster S, Graf G, Kitlar J & Powilleit M (1995) Effects of bioturbation in oxic and hypoxic conditions: a microcosm experiment with a North Sea sediment community. Mar. Ecol. Prog. Ser. 116: 153–161

Glud RN, Forster S & Huettel M (1996) Influence of radial pressure gradients on solute exchange in stirred benthic chambers. Mar. Ecol. Prog. Ser. 141: 303–311

Goldhaber MB, Aller RC, Cochran JK, Rosenfeld JK, Martens CS & Berner RA (1977) Sulfate reduction, diffusion and bioturbation in Long Island Sound sediments: Report of the FOAM group. Am. J. Sci. 277: 193–237

Hall POJ & Aller RC (1992) Rapid, small-volume flow injection analysis for ΣCO_2 and NH_4^+ in marine and freshwaters. Limnol. Oceanogr. 37: 1113–1118

Hansen K & Kristensen E (1997) The impact of macrofaunal recolonization on benthic metabolism and nutrient fluxes in a shallow marine sediment previously overgrown with macroalgal mats. Estuar. Coast. Shelf Sci. 45: 613–628

Huettel M (1990) Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sand flat sediments. Mar. Ecol. Prog. Ser. 62: 241–248

Huettel M & Gust G (1992) Impact of bioroughness on interfacial solute exchange in permeable sediments. Mar. Ecol. Prog. Ser. 89: 253–267

Klump JV & Martens CS (1987) Biogeochemical cycling in an organic-rich coastal marine basin. 5. Sedimentary nitrogen and phosphorus budgets based upon kinetic models, mass balances, and the stoichiometry of nutrient regeneration. Geochim. Cosmochim. Acta 51: 1161–1173

Kristensen E (1988) Benthic fauna and biogeochemical processes in marine sediments: Microbial activities and fluxes. In: Blackburn TH & Sørensen J (Eds) Nitrogen Cycling in coastal Marine Environments (pp 275–299). John Wiley, Chichester

Kristensen E (1993) Seasonal variations in benthic community metabolism and nitrogen dynamics in a shallow, organic-poor Danish lagoon. Estuar. Coast. Shelf Sci. 36: 565–586

Kristensen E & Andersen FØ (1987) Determination of organic carbon in marine sediments: a comparison of two CHN-analyzer methods. J. Exp. Mar. Biol. Ecol. 109: 15–23

Kristensen E & Blackburn TH (1987) The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. J. Mar. Res. 45: 231–257

Kristensen E & Hansen K (1995) Decay of plant detritus in organic-poor sediment: Production rates and stoichiometry of dissolved C and N compounds. J. Mar. Res. 53: 675–702

Kristensen E, Jensen MH & Aller RC (1991) Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete (*Nereis virens*) burrows. J. Mar. Res. 49: 355–377

Kristensen E, Andersen FØ & Blackburn TH (1992) Effects of benthic macrofauna and temperature on degradation of macroalgal detritus: the fate of organic carbon. Limnol. Oceanogr. 37: 1404–1419

Li Y-H & Gregory S (1974). Diffusion of ions in seawater and in deep-sea sediments. Geochim. Cosmochim. Acta 38: 703–714

Martin WR & Banta GT (1992) The measurement of sediment irrigation rates: A comparison of the Br^- tracer and $^{222}Rn/^{226}Ra$ disequilibrium techniques. J. Mar. Res. 50: 125–154

Martin WR & Sayles FL (1987) Seasonal cycles of particles and solute transport processes in nearshore sediments: $^{222}Rn/^{226}Ra$ and $^{234}Th/^{238}U$ disequilibrium at a site in Buzzards Bay, MA. Geochim. Cosmochim. Acta 51: 927–943

Matisoff G (1982) Mathematical models of bioturbation, In: McCall PL & Tevesz MJS (Eds) Animal-Sediment Relations (pp 289–330). Plenum, New York

McCaffrey RJ, Myers AC, Davey E, Morrison G, Bender M, Luedtke N, Cullen, D, Froelich P & Klinkhammer G (1980) The relation between porewater chemistry and benthic fluxes of nutrients and manganese in Narragansett Bay, Rhode Island. Limnol. Oceanogr. 25: 31–44

Newell RC (1979) Biology of Intertidal Animals. Elsevier, New York, 781 pp

Riisgård HU, Christensen PB, Olesen NJ, Petersen JK, Møller MM & Andersen P (1995) Biological structure in a shallow cove (Kertinge Nor, Denmark) – control by benthic nutrient fluxes and suspension feeding ascidians and jelly fish. Ophelia 41: 329–344

Riisgård HU, Vedel A, Boye H & Larsen PS (1992) Filter-net structure and pumping activity in the polychaete *Nereis diversicolor*: effects of temperature and pump-modelling. Mar. Ecol. Prog. Ser. 83: 79–89

Solorzano L (1969) Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801

Strickland JDH & Parsons TR (1972) A practical Handbook of Sea-Water Analysis. Fish. Res. Bd. Can. Bull. 167 (2nd ed.)

Sun M, Aller RC & Lee C (1991) Early diagenesis of chlorophyll-a in Long Island Sound sediments: a measure of carbon flux and particle reworking. J. Mar. Res. 49: 379–401

Vanderborght JP, Wollast R & Billen G (1977) Kinetic models of diagenesis in disturbed sediments. Part 1. Mass transfer and silica diagenesis. Limnol. Oceanogr. 22: 787–793

Vedel A & Riisgård HU (1993) Filter-feeding in the polychaete *Nereis diversicolor*: growth and bioenergetics. Mar. Ecol. Prog. Ser. 100: 145–152

Waslenchuk DG, Matson EA, Zajac RN, Dobbs FC & Tramontano JM (1983) Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. Mar. Biol. 72: 219–225