

Distribution of adsorbed ammonium pools in two intertidal sedimentary structures, Marennnes-Oléron Bay, France

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ABSTRACT: The 1-step and multiple-step KCl extraction technique was used to evaluate quantitatively the distribution of adsorbed NH_4^+ in the 0–5 cm strata of 2 intertidal muddy structures from Marennnes-Oléron Bay, France. KCl extraction efficiency was higher in the reconstituted sediment slurries and decreased significantly in the presence of porewater ions, leading to underestimations of the size of the pool of adsorbed, easily desorbed NH_4^+ . Various pools of adsorbed NH_4^+ were displaced from the sediment after reaction with KCl in multiple steps. Pools of tightly bound NH_4^+ were much larger in runnels as opposed to ridges, and accounted for up to 32% (ridge) and 40% (runnel) of the NH_4^+ desorbed from the sediment. These pools have important implications for the calculation of the K_D value, the dimensionless NH_4^+ distribution coefficient. Differing relationships between easily desorbed NH_4^+ or tightly bound NH_4^+ , on the one hand, and the sediment grain size, CaCO_3 and N content, on the other, suggest multiple origins for particulate matter in the sediment.

KEY WORDS: Ammonium · Adsorption · Mudflat · Ridge · Runnel

INTRODUCTION

An important fraction of the organic matter produced in coastal ecosystems is deposited and decomposed in sediments. Ammonium, which is regenerated by deamination of this organic matter, can be found dissolved in pore water, adsorbed onto the surface of clay particles and organic matter, or fixed within the clay structure. There is a dynamic equilibrium between NH_4^+ pools and, in addition, there is a rapid exchange between the adsorbed pool and the porewater pool. Ammonium which is not nitrified in the oxic layers of sediment is ultimately released to the overlying water and may influence primary production (Boynton et al. 1982). As the adsorbed pool may represent a substantial part of total NH_4^+ in sediments, the adsorption process must be considered when model-

ling nitrogen diagenesis in coastal sediments (Rosenfeld 1979). Indeed, Berner (1976, 1977) established the importance of including an adsorption term in his stoichiometric model of nitrogen regeneration, and Blackburn (1980) showed that the assessment of this exchangeable NH_4^+ is necessary for studying nitrogen turnover.

The assessment of adsorbed NH_4^+ is usually achieved through KCl extraction, but Laima (1992b,c) has shown that a 1-step procedure protocol is not sufficient to release the total adsorbed pool and that it is necessary to proceed through a multiple KCl extraction method of up to 6 or 7 successive steps. Thus, he found that 1-step extractions removed only 29 to 77% of the total adsorbed NH_4^+ pool, depending on the sediment type and season. This 'tightly bound NH_4^+ ' (the sum of additional KCl extractions), as opposed to the 'easily exchangeable NH_4^+ ' fraction (the amount released by a 1-step KCl extraction minus porewater NH_4^+), can

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represent the dominant form of NH_4^+ and may strongly influence the calculation of the sediment exchange capacity and the NH_4^+ turnover rate. Therefore, it is of prime importance to assess this pool quantitatively and to appraise the effect of the factors controlling it.

Intertidal mudflats are areas of intensive organic matter production and deposition, and thus also of mineralization. These mudflats play an important role in benthic regeneration in estuaries and associated bays. Although their importance in primary productivity (Pinckney & Zingmark 1993) and as a food source for benthic invertebrates (Montagna et al. 1995, Riera et al. 1996) has been recognized, their role in the whole ecosystem is not fully understood. Such mudflats are frequently characterized by major sedimentary structures known as 'ridges and runnels', i.e. a parallel succession of crests and troughs normal to the shore (Dyer 1998). These features are likely to act as a prominent structuring spatial factor, however, and their influence on the distribution of most geochemical and biological variables is still unknown.

It is therefore our goal (1) to test the methodology for the measurement of the different adsorbed NH_4^+ pools and (2) to show that the 'ridges and runnels' structures strongly influence the distribution of sediment ammonium pools and the efficiency of ammonium extractability. Finally, we shall provide a budget of ammonium distribution as a function of these intertidal sedimentary structures.

MATERIALS AND METHODS

Study area. Marennes-Oléron Bay is an estuarine zone occupying an area of about 170 km² between Aix Island and the Maumusson Channel in south-west France (Fig. 1). Bedforms extend over most of the mudflat, and they represent permanent structures in which ridges occupy $\frac{2}{3}$ and runnels $\frac{1}{3}$ of the surface area (Sauriau et al. 1997). There is a major contribution of autochthonous material to the sediments, essentially composed of microphytobenthos (Cariou-Le Gall & Blanchard 1995), of which the most abundant are

diatoms (particularly *Navicula*, *Nitzschia* and *Gyrodinium*). Macrofauna assemblages on Brouage mudflats belong to the *Macoma balthica* community (Thorson 1957). However, there is some difference between the species abundances on ridges and runnels (Sauriau & Gouleau unpubl. data). Thus, *Hydrobia ulvae* is more numerous in the runnels. This is a surface and/or a subsurface deposit feeder that can easily crawl on and dig into the fluid mud of runnels. In contrast, *Scrobicularia plana*, a deposit-feeder, is more numerous on ridges: its biomass can be over 30 g ash-free dry weight (AFDW) m⁻². Polychaetes species are also more numerous in ridges as against runnels. *Tubificoides benedini*, *Tharyx marioni*, *Streblospio shrubsolii* benefit from the more stable conditions on the ridges compared to runnels. *M. balthica*, a suspension/deposit-feeder bivalve, and *Nereis ombergii*, a carnivorous polychaete, are equally distributed over both bedforms. The hydrobiological characteristics of the bay have been described elsewhere (Héral et al. 1983). Recent work has studied the role of the microtopography on diffusive NH_4^+ and NO_3^- fluxes (Gouleau

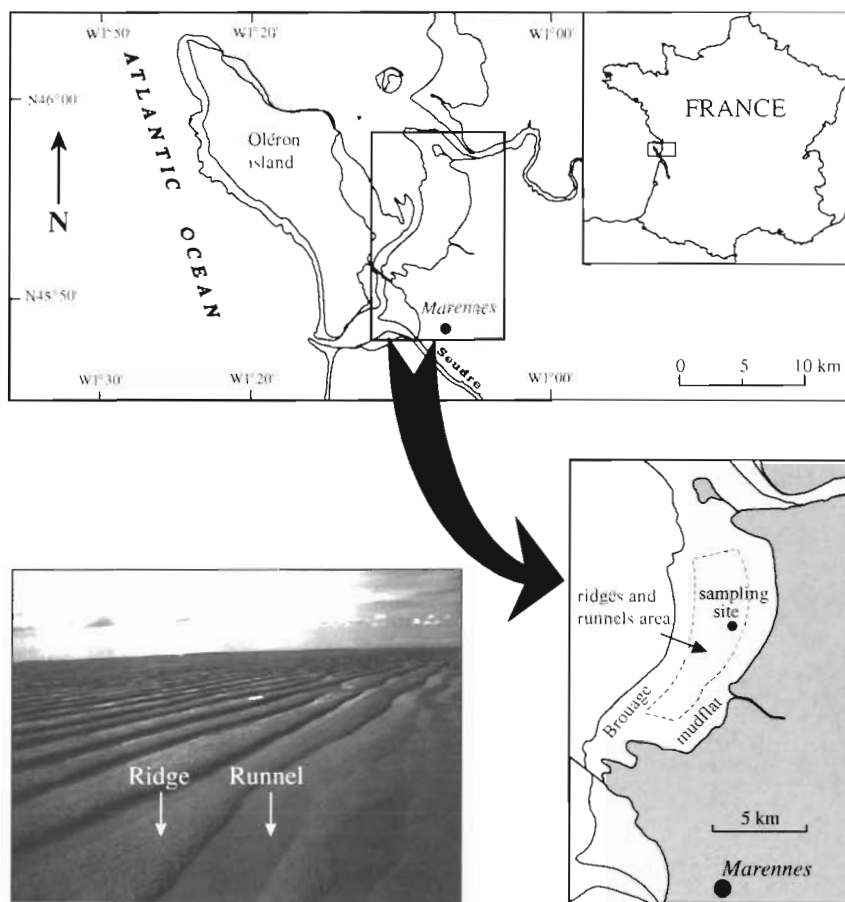


Fig. 1. Photograph of ridges and runnels at the study site, and maps showing the site location in the middle of an intertidal mudflat in Marennes-Oléron Bay, France

unpubl. data) and on its ability to trap nutrients and to regulate geochemical fluxes (Feuillet-Girard et al. 1988, 1997).

Sampling protocol and extraction procedures. Sampling took place in the upper part of the middle slikke where the ridge-and-runnel system spreads over a 30 km² area of the mudflat, see Fig. 1 and Germaneau & Sauriau (1996). Twelve sediment cores (5.4 cm diam., 20 cm long) were collected randomly by hand at low tide (tidal coefficient = 36) on April 16, 1997, 6 covering about 3 m² of surface area on a ridge and similarly a further 6 in an adjacent runnel. Based on previous tests on site variability of porewater nutrient concentration, this sampling strategy was found to give a good representation of the study area (Feuillet-Girard unpubl. data). Sediment cores were stored at 0°C and quickly transported to the laboratory. Overlying water was carefully discarded, the sediment was then cut into five 1 cm thick slices. Samples were sieved through a 1.5 mm mesh to remove gross detritus and macrofauna. Specific density was measured gravimetrically in triplicate. A portion of wet sediment was sieved (50 µm mesh); some coarse fraction was used for grain size determinations and some was dried and decarbonated with HCl for the determination of the CaCO₃ content. Water content was measured as weight loss after drying for 72 h at 60°C and corrected for salt effects. The C-N composition of sediment organic matter was determined in duplicate using a CHN analyzer Carlo Erba 1500 using acetanilide (N = 10.39% and C = 71.09%) as standard. Prior to the C-N analysis, 100 mg of sediment were acidified with HCl 1 N to remove carbonates. This decarbonation was increased by sonification. Then the samples were dried under vacuum to eliminate HCl vapours, after which 1 ml of Milli-Q H₂O was added and the samples were homogenized by sonification and freeze-dried.

Some sediment characteristics are shown in Table 1.

Collection of porewater and KCl extracts. Moderate to intensive extraction assays were designed to point out the likely effect of porewater ions on KCl efficiency for displacement of NH₄⁺ from the sediment, and to desorb at least 3 exchangeable NH₄⁺ pools. In Series A (Fig. 2, left-hand side) slices from different depths were purged in N₂ and centrifuged in gas-tight containers. Porewater extracts were filtered through GF/C Whatman filters (0.45 µm pore size), and stored at -20°C for further treatment. Sediment pellets from which pore water had been removed (about 30% remained) were mixed together with de-ionized H₂O in a double wash, and left on ice. The suspension was centrifuged and NH₄⁺ was measured in the supernatant. This procedure was repeated until the NH₄⁺ concentration in the supernatant was below 5 µmol l⁻¹. When necessary, de-ionized H₂O was added to these pellets to regain the original H₂O content. Reconstituted sediments were pooled and extracted at 0°C with 2 M KCl which was bubbled with pure N₂ immediately before use (Laima 1994). In Series B (Fig. 2, right-hand side), slices from each level were pooled together, and KCl extracts incorporating both pore water and the easily desorbed pool were obtained as before. Finally, pellets were weighed and new equivalent amounts of KCl were added, always keeping the sediment to extractant ratio constant. Multiple extractions were carried out until 6 additional supernatants were obtained from each depth.

Analyses and calculations. Salinity was measured using a microprocessor conductivity meter LF 320 WTW and a standard conductivity cell Tetracon 325. Ammonium was measured using the salicylate method with minor modifications (Laima 1992a). Reagents were added to 10- to 20-fold diluted water samples, and absorbance units (AU) were read in a Uvikon 722 LC spectrophotometer fitted with a quartz halogen

Table 1. Some characteristics of ridge and runnel structures. Marennes-Oléron Bay, April 1997

Layer (cm)	H ₂ O (ml g ⁻¹)	Porosity (ml cm ⁻³)	Salinity ^a (‰)	N (µg mg ⁻¹ dw)	C (µg mg ⁻¹ dw)	Grain > 50 µm (%)	CaCO ₃ ^b (%)
Ridges							
0-1	0.57	0.71	44.7	1.7	11.5	1.9	21.3
1-2	0.51	0.58	45.0	1.6	10.8	4.3	16.9
2-3	0.49	0.61	40.0	1.6	10.6	4.7	15.1
3-4	0.54	0.68	39.0	2.0	12.6	2.2	16.9
4-5	0.56	0.70	37.7	1.6	10.7	1.9	25.5
Runnels							
0-1	0.66	0.81	35.3	1.7	12.0	1.9	48.9
1-2	0.66	0.85	35.7	1.9	14.2	2.8	55.8
2-3	0.62	0.79	35.3	2.2	15.2	1.8	59.1
3-4	0.61	0.80	35.0	2.1	12.8	1.9	53.7
4-5	0.60	0.80	32.8	1.8	12.1	5.6	39.8

^aPorewater data. ^bMeasured in the coarse fraction (>50 µm)

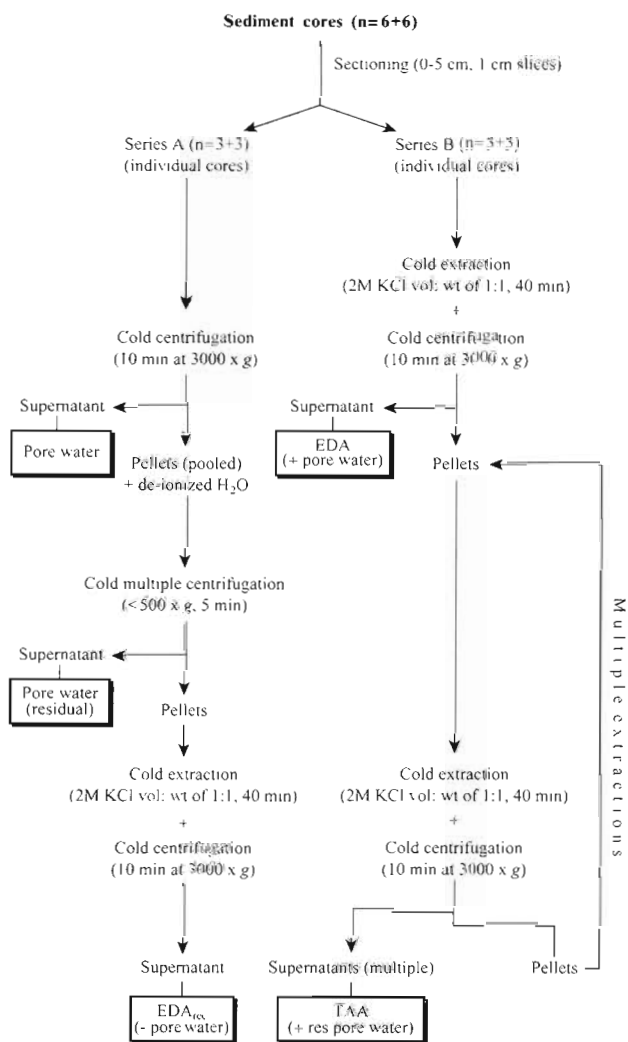


Fig. 2. Extraction scheme for removal of porewater, easily desorbed NH_4^+ (EDA), reconstituted EDA (EDA_{rec}) and tightly adsorbed ammonium (TAA) pools. All steps were performed under a stream of N_2 .

lamp and a R 928 PM detector. Detection limits lie in the -0.3 to 4 AU range, the photometric accuracy is better than ± 0.004 AU at 1 AU. Unknown factors present in extracts from marine sediments are known to interfere with colour development of the salicylate method (Ngo et al. 1982). We tested these effects by calculating NH_4^+ recovery in 10- to 20-fold diluted samples that were spiked with internal standards. A good recovery ($\sim 99\%$) was obtained, so possible interfering factors on colour development were absent in the used dilution range. Adsorbed, easily desorbed NH_4^+ (EDA) is the pool desorbed in the normal 1-step extraction of fresh sediment (Series B), minus the NH_4^+ dissolved in pore water. Reconstituted, easily desorbed NH_4^+ (EDA_{rec}), is the fraction desorbed after 1-step KCl

extraction of reconstituted sediment (Series A). Total adsorbed NH_4^+ is obtained by subtracting porewater NH_4^+ (as measured in Series A) from the total NH_4^+ in multiple KCl extractions (Series B), after correction for residual pore water and residual KCl. Tightly adsorbed ammonium (TAA) is obtained by subtracting the EDA pool from the pool desorbed in 6 residual extractions. Analyses of variance and correlation analysis at 95% confidence interval were performed using STATISTICA (StatSoft Inc. 1993).

RESULTS AND DISCUSSION

Pool sizes of easily desorbed NH_4^+ depended on whether or not pore water had been removed prior to addition of KCl. Fig. 3 shows relationships between EDA and EDA_{rec} in the 0–5 cm strata of ridges and runnels. In both structures, measurements of the reconstituted pool yielded more NH_4^+ compared to the original pool. It is not likely that the higher NH_4^+ yield found in EDA_{rec} is due to exposure of new organic binding sites to added K^+ since we did not observe more coloured waters in these rinses. An explanation for a lower NH_4^+ yield in EDA compared to EDA_{rec} is a K^+ effect in the presence of porewater (pw) ions, in moving the equilibrium $\text{NH}_4^+_{\text{pw}} \rightleftharpoons \text{NH}_4^+_{\text{exch}}$ towards sites with poor access to cation exchange (exch). Depressive effects of K^+ on NH_4^+ exchange have also been reported in other coastal environments (Laima 1994) and in soil studies (Nõmmik & Vahtras 1982). This hypothesis is further supported by Fig. 4, where cumulative NH_4^+ concentration data obtained from multiple extractions of intact sediments (pore water included) are plotted against the number of

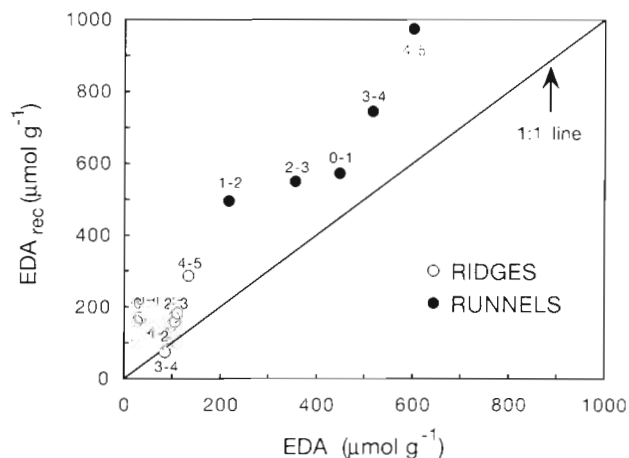


Fig. 3. Effect of the extraction procedure on the measurement of the EDA pool

Table 2. Average distribution of NH_4^+ pools in the 0–5 cm strata of ridge and runnel structures and linear relationships between dissolved and adsorbed NH_4^+

	NH_4^+ (nmol g^{-1})	NH_4^+ (% total)	Linear regression (r^2)	p
Ridges				
Pools				
Pore water	51	22		
EDA _{rec} (1-step KCl extraction)	108	46		
TAA (6 extra KCl extractions)	74	32		
Total extractable pool	233	100		
Relationships				
Pore water vs EDA _{rec} (n = 20)			0.92	<0.05
Pore water vs TAA (n = 20)			0.73	>0.05
Runnels				
Pools				
Pore water	80	7		
EDA _{rec} (1-step KCl extraction)	587	53		
TAA (6 extra KCl extractions)	447	40		
Total extractable pool	1114	100		
Relationships				
Pore water vs EDA _{rec} (n = 20)			0.17	>0.05
Pore water vs TAA (n = 20)			0.09	>0.05

extractions. Extraction of NH_4^+ increased initially, following a progressive dilution of the porewater pool and a simultaneous increase of excess K^+ concentration. However, if the NH_4^+ yield were only a result of volumetric effects, dilution curves would be comparable. This was not the case. It is more likely that NH_4^+ , which moved towards non-exchangeable pools during the first extraction step, had re-entered the exchangeable pool. The decrease in yield during the remaining extractions was probably caused by exhaustion of NH_4^+ adsorbed to the sediment matrix. It is clear that the TAA pool represented a substantial fraction of NH_4^+ in these intertidal sediments: 32% in ridges and 40% in runnels (Table 2).

Differences between ridges and runnels were also found in the porewater NH_4^+ distribution along the sedimentary profile (Table 3). Variation among cores was high (CV up to 56%). Porewater salinity was higher in ridges (mean [\pm SE] = $41 \pm [3]$ PSU) than in runnels (mean [\pm SE] = $35 \pm [1]$ PSU) (Table 1). However, pooled salinity and porewater NH_4^+ (n = 30) were inversely correlated (Fig. 5A). A salinity rise in the upper horizons of ridges is likely due to water losses through evaporation during emersed conditions. On the other hand, when the tide is in, flushing due to gravitational drainage may also induce NH_4^+ losses in these horizons. Exposure to rain and wave-pumping can also alter salinity and porewater NH_4^+ concentrations. Essentially, runnels represent waterlogged micro-environments in which nutrients are better retained than in the ridges.

The dimensionless NH_4^+ distribution coefficient K_D is calculated as (Krom & Berner 1980):

$$K_D = (1 - \Phi/\Phi) p_s K^* \quad (1)$$

where Φ is porosity (porewater volume/sediment volume), p_s is dry sediment density (assumed 2.65 g ml^{-1}) and $K^* = C_N^*/C_N$, where C_N^* is the rapidly exchangeable NH_4^+ concentration in $\mu\text{mol g}^{-1}$ dry wt sediment and C_N is the porewater concentration in mM relative to porewater volume. Usually, K_D values range from 1 to 20 in marine sediments (Seitzinger et al. 1991, Raaphorst & Malschaert 1996). The term C_N^* in Eq. (1) was improved to account for the multiple-extractable pool. The adsorbed pool obtained in this way undoubtedly gives a better estimate of this coefficient (Table 2) and therefore should be used in models of NH_4^+ adsorption (Boatman & Murray 1982).

Plots of adsorbed NH_4^+ (in 1-step or multiple-step extraction protocols) against porewater NH_4^+ were not significantly correlated ($p > 0.05$), except the relationship NH_4^+ pw versus EDA_{rec} that correlated significantly in ridges (Table 2). Some inverse correlations were found between porewater NH_4^+ and the improved K_D values (Fig. 5B). Indeed, both consistency and non-consistency in these relationships have been reported (Mackin & Aller 1984, Simon & Kennedy 1987). Mayer & Rice (1992) suggest that this inverse correlation is due to saturation of high-energy sorption sites with

Table 3. Porewater NH_4^+ data (mM) and calculated distribution coefficients (K_D) using Eq. (1). Rapidly exchangeable NH_4^+ (C_{ex}^*) is given by the EDA_{rec} pool. C_{tot}^* is obtained by adding the TAA pool to C_{ex}^* . NH_4^+ pw: porewater NH_4^+ ; K_{D1} : data from using EDA_{rec} in Eq. (1); K_{D2} : data from using (EDA_{rec} + TAA) in Eq. (1)

Section (cm)	NH_4^+ pw	K_{D1}	K_{D2}
Ridges			
0–1	0.095 ± 0.03	1.2 ± 0.4	1.3 ± 0.4
1–2	0.037 ± 0.01	2.9 ± 0.9	10.7 ± 0.9
2–3	0.087 ± 0.06	2.1 ± 1.5	3.8 ± 2.5
3–4	0.085 ± 0.01	1.9 ± 0.3	2.5 ± 0.4
4–5	0.166 ± 0.02	1.0 ± 0.1	1.0 ± 0.1
Runnels			
0–1	0.127 ± 0.05	2.4 ± 0.4	6.0 ± 2.5
1–2	0.148 ± 0.04	1.3 ± 0.3	2.6 ± 0.6
2–3	0.074 ± 0.02	4.8 ± 1.2	8.5 ± 2.1
3–4	0.121 ± 0.01	3.7 ± 0.4	6.7 ± 0.7
4–5	0.171 ± 0.03	3.4 ± 0.6	3.9 ± 2.6

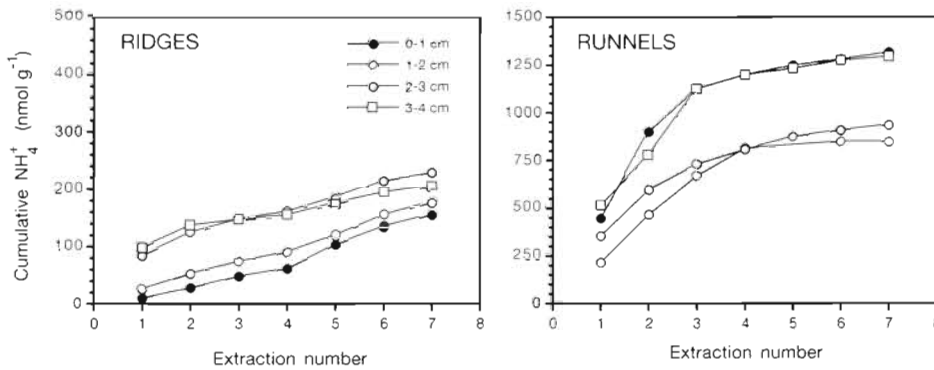


Fig. 4. Cumulative NH_4^+ content plotted against number of KCl extractions. The 4–5 cm stratum was omitted to avoid overlapping lines

increasing porewater NH_4^+ concentrations. We extend this explanation to complex K^+ effects and possibly to ion-pairing processes affecting NH_4^+ exchange.

Ridges and runnels are both silt type sediments with similar low contents of C (1.1 and 1.3%) and N (0.2 and 0.2%) and similar grain sizes, but differing in CaCO_3

content (Table 1). In ridges, grain size fractions ($<50 \mu\text{m}$) did not significantly correlate with EDA_{rec} ($r^2 = 0.55$, $p > 0.05$) but were inversely correlated with TAA ($r^2 = 0.77$, $p < 0.05$). CaCO_3 did not significantly correlate with EDA_{rec} ($r^2 = 0.50$, $p > 0.05$) or with TAA ($r^2 = 0.56$, $p > 0.05$). In runnels, grain size fractions ($<50 \mu\text{m}$) did not correlate significantly with TAA ($r^2 = 0.66$, $p > 0.05$) or with EDA_{rec} ($r^2 = 0.62$, $p > 0.05$). The same was the case for CaCO_3 and organic N. These differences suggest that adsorbed NH_4^+ has a different source in these structures and that organic N plays a minor role in the dynamic behaviour of adsorbed NH_4^+ pools.

Bioturbation effects may also account for a higher NH_4^+ yield in runnels compared to ridges. Indeed, in the 0–5 cm strata, *Hydrobia* sp. averaged 35 ind. cm^{-2} in runnels but only 2 ind. cm^{-2} in ridges, and accounted for over 90% of total fauna present in the cores. They eat benthic diatoms, so their higher populations in runnels may reflect higher sediment activity in that zone (Laima et al. unpubl.). They can thus enhance NH_4^+ regeneration and alter NH_4^+ concentrations in sediment pore water by means of excretion including fecal pellets and bioturbation (Jönsson et al. 1993).

In summary, these results clearly highlight the following points:

(1) Preliminary experiments involving analysis of the reconstituted pool in 1-step extractions of ridge and runnel sediments showed that it is important to check whether current extraction techniques correctly assess the adsorbed NH_4^+ pool. These data are in agreement with earlier observations that the KCl technique, when applied to coastal muddy sediments, should be used with caution (Laima 1994).

(2) Ridges and runnels are sedimentary structures placed side by side in the mudflat. They exhibit enormous differences with respect to NH_4^+ extraction efficiency, adsorption to their particulate phases, and relationships with sediment parameters. Results clearly show that runnel bedforms contain high, multiple pools of adsorbed NH_4^+ . The turnover rate of these adsorbed pools, their influence on diffusive NH_4^+

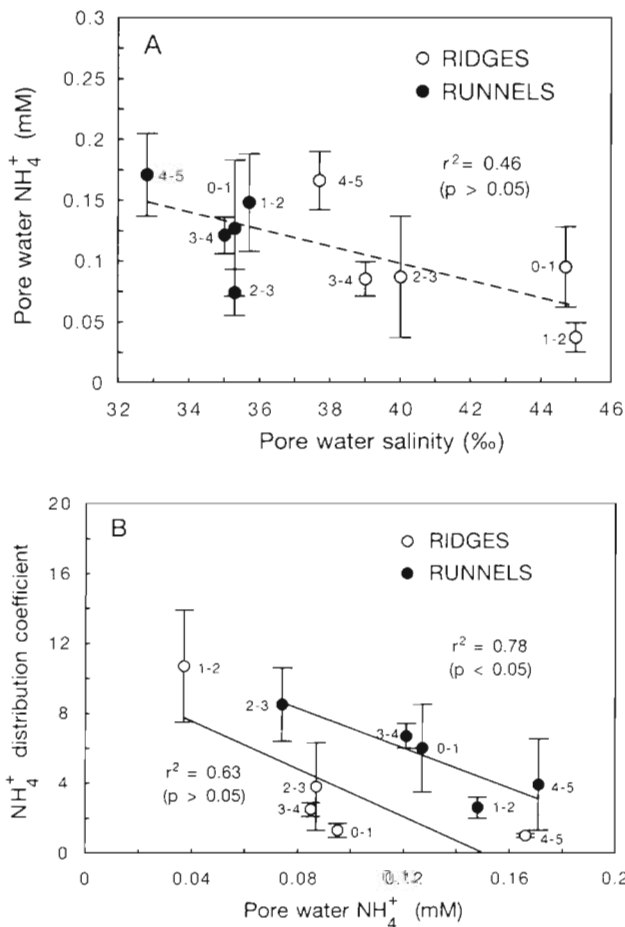


Fig. 5. (A) Relationship between porewater salinity and porewater NH_4^+ concentrations ($n = 3$) in ridges (o) and runnels (●). Regression analysis was performed using pooled data from ridges and runnels. (B) Relationship between average ($n = 3$) porewater NH_4^+ concentration and K_D values obtained from using KCl in multiple extractions

fluxes at the sediment-water interface, and possible influence on the N cycle, are unknown. Therefore, they should be the subject of further research.

(3) Spatial heterogeneity is an important issue when nutrient budgets are calculated for a particular environment. This study was restricted to the effect of 2 sedimentary structures on the spatial distribution of NH_4^+ pools. As other complex sedimentary forms are present in the bay, distribution patterns of NH_4^+ pools may be even more complex.

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LITERATURE CITED

- Berner RA (1976) Inclusion of adsorption in the modelling of early diagenesis. *Earth Planet Sci Lett* 29:333–340
- Berner RA (1977) Stoichiometric models for nutrient regeneration in anoxic sediments. *Limnol Oceanogr* 22:781–786
- Blackburn TH (1980) Seasonal variations in the rate of organic-N mineralization in anoxic marine sediments. In: Dumas R (ed) *Biogéochimie de la matière organique à l'interface eau-sédiment marin*. Centre National de Recherche Scientifique, Paris, p 173–183
- Boatman CD, Murray JW (1982) Modelling exchangeable NH_4^+ adsorption in marine sediments: process and control of adsorption. *Limnol Oceanogr* 27:99–110
- Boynton WR, Kemp WM, Keefe CW (1982) A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In: Kennedy VS (ed) *Estuarine comparisons*. International estuarine research conference 6. Academic Press, New York, p 69–90
- Cariou-Le Gall V, Blanchard GF (1995) Monthly HPLC measurements of pigment concentration from an intertidal muddy sediment of Marennes-Oléron Bay, France. *Mar Ecol Prog Ser* 121:171–179
- Dyer KR (1998) The morphological development of intertidal mudflats. 2nd Annual Report, European Commission, Directorate General XII, MAST III, Contract MAS 3-CT95-0022 Univ Plymouth
- Feuillet-Girard M, Héral M, Sornin JM, Paoli MD, Robert JM, Mornet F, Razet D (1988) Éléments azotés de la colonne d'eau et de l'interface eau-sédiment du bassin de Marennes-Oléron: influence des cultures d'huîtres. *Aquat Living Resour* 1:251–265
- Feuillet-Girard M, Gouleau D, Blanchard G, Joassard L (1997) Nutrient fluxes on an intertidal mudflat in Marennes-Oléron Bay, influence of the emersion period. *Aquat Living Resour* 10:49–58
- Germaneau J, Sauriau PG (1996) La mer des Pertuis: un système topographique filtrant les agents météo-océaniques. *Bull Soc Sci Nat Ouest France (nouv sér)* 18:53–68
- Héral M, Razet D, Deslous-Paoli JM, Berthome JP, Garnier J (1983) Caractéristiques saisonnières de l'hydrobiologie du complexe estuarien de Marennes-Oléron (France). *Rev Trav Inst Pêches Marit* 46:97–119
- Jönsson B, Sundbäck K, Nilsson P, Nilsson C, Lindström Swanberg I, Ekeboom J (1993) Does the influence of the epibenthic predator *Crangon crangron* L. (brown shrimp) extend to sediment microalgae and bacteria. *Neth J Sea Res* 31:83–94
- Krom MD, Berner RA (1980) Adsorption of phosphate in anoxic marine sediments. *Limnol Oceanogr* 25:797–806
- Laima MJC (1992a) Evaluation of the indophenol method to measure ammonium in extracts from coastal marine sediments. *Mar Chem* 39:283–296
- Laima MJC (1992b) Extraction and seasonal variation of ammonium pools in different types of coastal marine sediments. *Mar Ecol Prog Ser* 82:75–84
- Laima MJC (1992c) Recovery of $^{15}\text{NH}_4^+$ in labelling experiments on coastal marine sediments. *Mar Chem* 44:31–42
- Laima MJC (1994) Is KCl a reliable extractant of $^{15}\text{NH}_4^+$ added to coastal marine sediments? *Biogeochemistry* 27:83–95
- Mackin JE, Aller RC (1984) Ammonium adsorption in marine sediments. *Limnol Oceanogr* 29:250–257
- Mayer LM, Rice DL (1992) Early diagenesis of protein: a seasonal study. *Limnol Oceanogr* 32:280–295
- Montagna PA, Blanchard GF, Dinet A (1995) Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *J Exp Mar Biol Ecol* 185:149–165
- Ngo TT, Pan APH, Yam CF, Leenhoff HM (1982) Interference in determination of ammonia with the hypochlorite-alkaline phenol method of Berthelot. *Anal Chem* 54:46–49
- Nömmik H, Vahtras K (1982) Retention and fixation of ammonium and ammonia in soils. In: Stevenson FJ (ed) *Nitrogen in agricultural soils*. American Society of Agronomy, Madison, WI, p 123–171
- Pinckney JL, Zingmark G (1993) Modelling the annual production of intertidal benthic microalgae in estuarine ecosystems. *J Phycol* 29:396–407
- Raaphorst WV, Malschaert JFP (1996) Ammonium adsorption in superficial North Sea sediments. *Cont Shelf Res* 16:1415–1435
- Riera P, Richard P, Grémare A, Blanchard G (1996) Food source of intertidal nematodes in the Bay of Marennes-Oléron (France), as determined by dual stable isotope analysis. *Mar Ecol Prog Ser* 142:303–309
- Rosenfeld JK (1979) Ammonium adsorption in nearshore marine sediments. *Limnol Oceanogr* 24:356–364
- Sauriau PG, Germaneau J, Morin K, Robert S (1997) Zonation scheme of bedform structure from Brouage mudflat in the Marennes-Oléron bay (Atlantic coast, France) in the morphological development of intertidal mudflats. 1st Annual Report, European Commission Directorate General XII, Mast III, Intrmud, Contract MAS 3-CT95-0022, Univ Plymouth
- Seitzinger SP, Gardner WS, Spratt AK (1991) The effect of salinity on ammonium sorption in aquatic sediments: implications for benthic nutrient cycling. *Estuaries* 14:167–174
- Simon NS, Kennedy MM (1987) The distribution of nitrogen species and adsorption of ammonium in sediments from the tidal Potomac River and Estuary. *Estuar Coast Shelf Sci* 25:11–26
- Thorson G (1957) Bottom communities (sublittoral or shallow shelf). *Treatise on marine ecology and paleoecology*. Geol Soc Am Mem 67:461–534