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ABSTRACT: ^{15}N tracer experiments were conducted to examine the fate of particulate organic nitrogen at the surface of an intact silty sediment community from Narragansett Bay, R.I. (USA). ^{15}N-labelled particulate organic matter (POM, 82.5 atom % ^{15}N excess), obtained from cultured marine diatoms *(Skeletonema costatum)*, was applied to the surface of 10 to 12 cm deep sediment cores and the time course distribution of the tracer was determined in inorganic-N and organic-N compartments in sediment and free water. Tracer experiments were conducted in spring (8 °C) and fall (16 °C). Small amounts of tracer-N were recovered in all sediment and free water compartments after 1.5 d in spring and after 6 h in fall. The initial rates of transport of the tracer downward into the sediment, based on the depth distribution of ^{15}N in cores incubated for less than 2 d, appeared to be anomalously high. Subsequent downward mixing of the tracer in particulate and dissolved forms gave estimates of the sediment vertical mixing coefficient (D_m) of 3 to 5×10^{-6} cm^2 s^{-1}. Net release of NH_4^+ from the cores was suppressed for about 24 h following application of labelled-POM to the sediment surface. This was probably caused by immobilization of nitrogen in a rapidly growing microbial population at the sediment surface. Subsequently, the net rates of $^{15}NH_4^+$ production in the cores averaged 13 (s.d., 5) μmol m^{-2} h^{-1} in spring and 32 (s.d., 12) μmol m^{-2} h^{-1} in fall. The observed rates of NH_4^+ release suggest that 10 to 50 % of the NH_4^+ flux from the sediment was due to rapid nitrogen remineralization at the sediment-water interface. $^{15}NH_4^+$ produced near the sediment-water interface was partitioned between sediment pore waters and exchange sites on sediment solids in ratios (by atoms) of less than 1/1. Rate constants (% h^{-1}, base e) for the decomposition of the labelled organic-N were 0.075 (s.d., 0.030) in spring and 0.14 (s.d., 0.05) in fall. These rates suggest that the 'half-life' of organic nitrogen at the surface of coastal marine sediments is in the order of 1 to 2 mo in spring and of 2 to 3 wk in fall.

INTRODUCTION

As is well known, at least qualitatively, the fertility of the sea is maintained by recycling of essential nutrient elements. Recent estimates of the global inventories and flows of nitrogen – the element most often singled out as limiting primary production in marine ecosystems (Ryther and Dunstan, 1971; Goldman et al., 1973; Thayer, 1974; Smayda, 1974) – show that river-flow, rainfall, and marine nitrogen fixation supply less than 10 % of the nitrogen needed to support annual rates of primary production in the World Ocean (Soderlund and Svensson, 1976; Delwiche, 1977). The inference follows that the deficit must be met by a flux of recycled, i.e. remineralized, nitrogen to the euphotic zone of the sea.

In the deep sea the decomposition of organic matter and remineralization of nutrients goes nearly to completion in the water column (Riley, 1951; Rittenberg et al., 1955; Bender et al., 1977). Unlike offshore systems, a significant portion of the organic matter formed in, or imported to, coastal waters settles out of the water column before pelagic decomposition proceeds very far. This contention is supported by relatively high organic content of nearshore sediments and by the high rates of metabolic activity (as determined by rates of oxygen consumption) reported for coastal marine sediments (e.g. Teal and Kanwisher, 1961; Cary, 1967; Pamatmat, 1971a, b; Smith et al., 1972, 1973; Nixon et al., 1976). Nixon (1981) described a linear relationship between the amount of organic matter produced in, or imported to, these systems and the amount of organic matter respired in the benthos. His regression suggests that 25 to 50 % of the organic matter entering these systems is consumed in the sediments.

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The oxidation of this large amount of organic matter in the nearshore benthos is accompanied by a flux of remineralized nutrients to the overlying water. Recent measurements of the fluxes of nutrients from the sediments to the overlying water have, in fact, shown that this recycling pathway can make significant contributions to the nutrients required to support primary production in the water column (see reviews by Nixon, 1981; Kemp et al., 1982; Nixon and Pilson, in press).

Thus, the picture emerging in marine ecology today shows that subtidal benthic communities function as integral parts of the coastal system: primary production in the water column depends, in part, on nutrients released by the benthos, and secondary production in benthic communities requires organic matter produced in the overlying water. Quantitative annual budgets for nitrogen production and remineralization have provided valuable insights into the balance between nitrogen income and outgo in the coastal environment but many questions, particularly about transformations occurring rapidly at the sediment surface, remain: How much of the detrital nitrogen is immediately remineralized at the sediment-water interface? How much is assimilated by the benthos? How much is ultimately lost to the pelagic system through burial or denitrification?

RATIONALE FOR EXPERIMENTAL DESIGN

The purpose of the experiments described here was to determine the short-term fate of particulate organic nitrogen (PON) at the surface of an intact benthic community. My approach was to simulate the deposition of particulate organic matter (POM) on the sediment surface with a spike addition of organic matter labelled with ^{15}N.

Type of POM. Material collected in sediment traps deployed near the bottom of the Narragansett Bay (Oviatt and Nixon, 1975) consisted of a mixture of intact phytoplankton cells, fecal pellets and detritus. A substantial portion of this material was believed to be resuspended sediment that cannot be taken as representative of freshly deposited material. Although it seems likely that a fraction of the phytoplankton crop must be grazed, evidence that zooplankton fecal pellets convey most of the detrital organic matter to nearshore sediments is equivocal. The data by Knauer et al. (1979) for a sediment trap deployed at 50 m in Monterey Bay (total water depth: 1000 m) show that fecal pellets account for only 10 % or less of the organic matter settling out of the euphotic zone. Studies in meso-scale microcosm tanks (J. Kelley, pers. comm.) have shown that a large fraction of a *Skeletonema* bloom may settle out of the water column under conditions in which the vertical mixing of the water column appears to be more vigorous than in mid-Narragansett Bay (Nixon et al., 1980). Therefore, I assumed that particulate organic matter derived from dead, intact cells of *Skeletonema costatum*, the diatom usually associated with winter-spring and fall diatom blooms in Narragansett Bay (Smayda, 1957; Pratt, 1959, 1965; Martin, 1965; Vargo, 1976), represented a reasonable analog for POM freshly deposited on the sediments surface. As a further attempt to add realism, experiments were conducted in spring and fall when the fallout of POM from *S. costatum* blooms would be expected to be high (Vargo, 1976).

Rate of POM deposition. Ideally, the amount of POM added to the cores would correspond to the natural rate of deposition and would contain tracer-N in quantities sufficient to provide a detectable signal when diluted many times with unlabelled nitrogen in the sediments. The second part of this problem was overcome by using POM highly enriched in ^{15}N. A realistic rate of deposition of fresh detritus cannot be determined directly from the sediment trap data of Oviatt and Nixon (1975). However, it is possible to estimate the maximum amount of carbon needed to support observed rates of oxygen consumption in the sediments using the sediment oxygen uptake *vs.* temperature regression given by Nixon et al. (1976). These calculations, summarized in Table 1, suggest that the addition of ^{15}N-labelled POM corresponding to a rate of deposition of 2 to 2.5 g C m^{-2} would equal the amount of carbon respired in the benthos in 2 to 8 d. Narragansett Bay has been characterized as a plankton-based system (Kremer and Nixon, 1978). Therefore the estimate of primary production the water column of 310 g C m^{-2} yr^{-1} (Furnas et al., 1976) sets an upper limit to the quantity of organic matter available to the benthos, this production in the water column could provide a maximum deposition rate of organic matter to the benthos of 1 to 2 g C m^{-2} d^{-1}. Thus, the addition of 2 to 2.5 g C m^{-2} to the sediments represents the amount of deposition that could occur in 1 to 2 d. I concluded that a single addition of POM corresponding to a rate of deposition of about 2 g C m^{-2} would not be grossly different from conditions in the field and that the POM derived from cultured *Skeletonema costatum* would reasonably simulate the nutritional quality of freshly deposited material in the bay.

METHODS

Description of study site

Sediments used in the tracer experiments were taken from a station (41° 35′ N 72° 22′ W) north of Conanicut Point in mid-Narragansett Bay, Rhode

Island, USA. The sediments in this area of the bay are composed of 60 to 70 % silt with about 20 % each of clay and sand (McMaster, 1960; Hale, 1974), and an organic carbon content of about 1 to 2 % of the sediment dry weight (Hale, 1974; Oviatt and Nixon, 1975).

Water depth at the station (6 m) places the sediments below the 1 % isolume for most of the year (Schenck and Davis, 1972). The macrofaunal community is dominated by polychaetes *(Nepthys incisa, Lumbrinereis fragilis, Mediomastus ambiseta)* and small deposit-feeding bivalves *Nucula annulata, Yoldia limatula)* (Phelps, 1958; Hale, 1974; McCaffrey et al., 1980). Nixon et al. (1976) described the seasonal cycle of benthic metabolism and the fluxes of nutrients from the sediment communities at this site; Oviatt and Nixon (1975) examined the dynamics of sediment resuspension and deposition in the mid-bay region; and McCaffrey et al. (1980) examined the influence of benthic organisms on the fluxes of nutrients and manganese from sediments at the Conanicut Point station.

Source of the ^{15}N-labelled POM

Batch cultures of the marine diatom *Skeletonema costatum* were grown in 15 l carboys using Guillard's (1963) f/2 medium amended with $Na^{15}NO_3$ (99 atom % ^{15}N, Stohler Isotope Chemicals Inc., Waltham, Ma.). After 2 wk of growth under fluorescent light at 15 °C the concentration of cells exceeded $10^6 ml^{-1}$. The cultures were unialgal but not bacteria-free. The labelled cells were harvested by reverse-flow filtration below a membrane filter (Nuclepore N100), concentrated into a pellet by centrifugation (1000 g, 10 min, room temperature), frozen and lyophilized. Carbon and nitrogen content of the lyophilized material was determined by high-temperature combustion (Carlo Erba Model 1100 CHN analyser); phosphorus content was determined by ashing and acid hydrolysis (Andersen, 1976). The elemental composition of the POM on a dry weight basis, 27.4 % C, 3.3 % N, 0.69 % P, gave ratios of nutrients, by atoms, of 102 C : 10.6 N : 1 P. The isotopic composition of nitrogen in the labelled POM, 82.5 ± 0.3 atom % excess, was determined by mass spectrometry using Kjeldahl-Rittenberg procedures (Bremner, 1965c; Fiedler and Proksch, 1975; Garber, 1982).

Experimental

Conditions for the 2 experiments are given in Table 1. Cores of sediment containing 10 to 15 cm of mud with about 1.5 l of overlying water were taken by SCUBA divers from the bay bottom at the Conanicut Point station. Three rectangular box cores (12.5 × 25.5 cm) were taken in spring, 10 round cores (16.6 cm diameter) in fall, 5 of which were treated with labelled POM and 5 were used to determine net flux of NH_4^+ without POM amendment. The coring devices also served as experimental chambers. Cores were brought to the laboratory and held in flowing bay water at ambient bay water temperature before tracer experiments were conducted. Experiments were initiated as follows: the water over the cores was carefully removed and a slurry made by rehydrating an aliquot of the labelled POM with 10 ml of glass-fiber-filtered (Reeve Angel 934 AH) bay water was spread over the surface of the mud. The cores were rocked back and forth to distribute the labelled material as evenly as possible. This procedure resuspended the top 1 to 2 mm of sediment. Glass-fiber filtered bay water was then slowly siphoned onto the cores. The water over the sediment was kept oxygenated and in motion with a stream of air scrubbed through 5 % sulfuric acid and filtered bay water. This treatment had no effect on the pH of the overlying water. The cores were incubated in the dark at ambient bay water temperature. Single cores were sacrificed according to the schedule given in Table 1. In spring the overlying water was replaced with fresh, glass-fiber-filtered bay water on the 4th and 9th days of incubation. The amounts and isotopic compositions of nitrogen in the water removed during the replacements were determined and included in the nitrogen inventories and tracer budgets.

Also in spring, N-remineralization in bay water alone was examined by allowing 0.300 g samples of lyophilized *Skeletonema* POM to decompose in 3 bottles, each containing 1 l of aerated, glass-fiber-filtered bay water. The entire contents of 1 bottle were sam-

Table 1. Experimental conditions for spring and fall ^{15}N-tracer experiments

	Spring	Fall
Time of year	April 1977	October 1977
Water temperature (°C)	8 ± 1	16 ± 1
Sediment coring device and experimental chamber	Box core, 319 cm^2	Round core, 219 cm^2
Estimated rates of benthic metabolism (gC m^{-2} d^{-1})*	0.29	0.80
POM added (g m^2)	9.24	11.4
(gC m^2)	2.5	3.0
(gN m^{-2})	0.325	0.395
Number of daily rations of carbon added to each core	9	4
Incubation time (d)	1.5, 7.3, 17.5	0.25, 0.5, 1, 2, 4

* Based on benthic O_2 uptake *vs.* temperature regression of Nixon et al. (1976). RQ = 1

pled with each spring core, and concentrations of the nitrogeneous fractions determined by the scheme for water shown in Fig. 1. ^{15}N enrichments of these fractions were not determined.

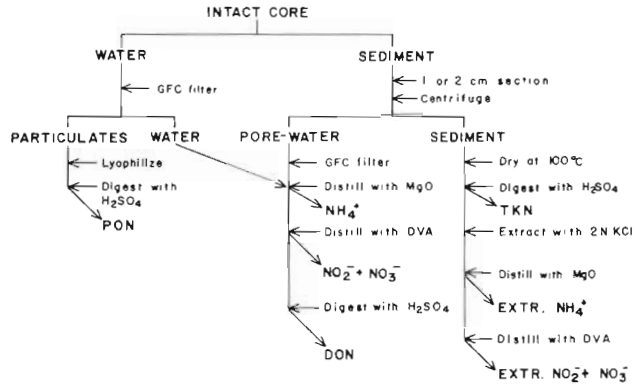

Fig. 1. Flow chart of procedures used to recover various forms of nitrogen from seawater and sediments for $^{15}N/^{14}N$ determinations. GFC: glass fiber; H_2SO_4: analytical reagent grade, low nitrogen, 36 N sulfuric acid; MgO, pre-ignited magnesium oxide powder; DVA: finely powdered Devarda alloy; KCl: potassium chloride; NH_4^+: ammonium; PON: particulate organic-N; TKN: total Kjeldahl-N; DON: dissolved organic-N; $NO_2^- + NO_3^-$: nitrate + nitrite; Extr. NH_4^+: extractable ammonium-N; Extr. $NO_2^- + NO_3^-$: extractable nitrate + nitrite

Forms of inorganic and organic nitrogen in the overlying water, sediments, sediment pore waters and benthic organisms were isolated for isotope determinations by Kjeldahl-Rittenberg procedures (Bremner, 1965a, b, c) following the flow chart shown in Fig. 1. Nitrogen isotope determinations were made using a Micromass 602 C mass spectrometer. Enrichments of the samples are reported in the usual manner as ^{15}N atom % excess. This refers to the enrichment of the sample in ^{15}N over the background levels of naturally-occurring ^{15}N (about 0.37 atom %). The term '^{15}N excess' refers to a quantity (usually in µmoles or nmols) of tracer-N in a particular compartment.

Determination of nutrients in free water and sediment

Overlying water. Samples for nutrient determinations were filtered through glass-fiber filters (Whatman GF/C or Gelman A). The concentration of NH_4^+ was determined using the phenolhypochlorite method (Solórzano, 1969) scaled for 10 ml samples. If the concentration of NH_4^+ exceeded 60 µM the sample was diluted with deionized water to bring the concentration within the linear range of the colorimetric procedure. The concentration of $NO_2^- + NO_3^-$ was determined by a standard automated colorimetric procedure (Strickland and Parsons, 1972). Dissolved organic nitrogen (DON) was determined by Kjeldahl digestion of 500 ml samples after NH_4^+ had been removed from the sample by steam distillation with MgO. Kjeldahl procedures followed Bremner's (1965a) recommendations for the determination of total-N when no nitrate or nitrite is present in the sample. Ammonium-N in the Kjeldahl digest was steam distilled into 5 % boric acid and titrated with 0.005 N sulfuric acid. These procedures have been used in this laboratory for several years and estimates of their precision are given in Table 2.

Sediments. The sediment sampling procedures used in spring and fall differed to accommodate the different designs of the experimental chambers but the strategy used to recover various forms of nitrogen (Fig. 1) was consistent. In spring, the sediment in each rectangular chamber was subsampled 1 time only with

Table 2. Precision of chemical determinations

Chemical form	Method	Precision*	Ref.
Free water			
NH_4^+	Colorimetric	± 0.04 µg-at N l^{-1}	1
$NO_2^- + NO_3^-$	Colorimetric	± 0.1 µg-at N l^{-1}	2, 3
Dissolved organic-N (DON)	Kjeldahl digestion	± 2 µg-at N l^{-1}	4, 5
Particulate organic-N (PON)	Kjeldahl digestion	± 0.25 µg-at N	4, 5
Sediment			
Total Kjeldahl-N (TKN)	Kjeldahl digestion	± 0.4 µg-at N $(gds)^{-1}$	4, 5
Extractable NH_4^+	2N KC1 extraction, direct steam distillation	± 0.1 µg-at N l^{-1}	6, 5
Pore water NH_4^+	Colorimetric	± 0.4 µg-at N l^{-1}	1
	Steam distillation	± 2.5 µg-at N l^{-1}	5
Pore water DON	Kjeldahl digestion	± 4 µg-at N l^{-1}	4, 5

* Standard deviation of at least 4 replicates

1 Solórzano (1969); 2 Strickland and Parsons (1972); 3 Gardner et al. (1976); 4 Bremner (1965a); 5 Garber (1982); 6 Bremner (1965b)

3 acrylic plastic tubes (76 mm diameter). Each subcore was then extruded in air and sectioned at 1 or 2 cm intervals. The water content (% H_2O, by weight) of the sediment was determined by drying sections from 1 subcore at 100 °C. The sections from the other 2 cores were transferred to 250 ml polyethylene centrifuge bottles and centrifuged (3500 g for 20 min at 8 °C). This procedure removed about 40 % of the pore water from each section. The samples of pore water were filtered (Gelman A) and the concentration of NH_4^+ immediately determined using Solórzano's (1969) procedure as described above. The remaining pore water samples from identical sections of the 2 subcores were combined and frozen for subsequent separation of NH_4^+ and DON. The pellets of semi-dry sediment were transferred to glass jars, dried at 100 °C, ground to pass a 40 mesh (250 µm opening) screen and stored, tightly-stoppered, at room temperature. It was not necessary to subcore the sediments in the fall since the entire core could be extruded from the core liner and sliced at 1 cm intervals. The water content of each section was determined by drying a 5 to 10 g subsample at 100 °C. The rest of the sediment from each section was centrifuged, dried, ground, and stored as described above.

The methods used to recover nitrogen from various fractions in the sediment and the preparation of the samples for mass spectrometry were based on Kjeldahl-Rittenberg procedures given in Bremner (1965a, b, c). The fractions are defined as follows:

Total Kjeldahl-N (TKN): nitrogen returned from dried sediment using a standard semi-micro Kjeldahl digestion procedure. This fraction would be expected to include most forms of organic-N in the sediment, extractable NH_4^+, and the dissolved NH_4^+ and DON remaining in the sediment after centrifugation. The procedure does not give quantitative recovery of NO_2^-, NO_3^-, or fixed NH_4^+.

Pore water NH_4^+: NH_4^+ dissolved in the interstitial water. Pore water samples were pressed from the sediments by centrifugation in air. NH_4^+ was recovered by steam distillation with MgO.

Pore water DON: organic forms of nitrogen dissolved in the sediment pore water. Pore water NH_4^+ was first stripped from the sample, then DON was converted to NH_4^+ by Kjeldahl digestion.

Extractable NH_4^+: NH_4^+ recovered by extraction of 10 g samples of the centrifuged, dried, ground sediment with 50 ml of 2 N KCl for 1 h at room temperature. The NH_4^+ released into the KCl solution was then steam distilled into boric acid using MgO. This fraction would be expected to include NH_4^+ reversibly sorbed onto sediment particles ('exchangeable NH_4^+') and the pore water NH_4^+ remaining in the sediment following the centrifugation step.

Extractable $NO_2^- + NO_3^-$: NO_2^- and NO_3^- in the 2 N KCl extracts prepared as described above. These forms were converted to NH_4^+ using Devarda alloy after extractable NH_4^+ had been stripped from the extract by steam distillation.

Macrofauna-N: organic N in the tissues of benthic organisms recovered using standard Kjeldahl digestion procedures.

In addition to the forms given above, NH_4^+ in the sediment may be non-reversibly bound to clay particles, and $NO_2^- + NO_3^-$ may be dissolved in pore waters. 'Fixed' or 'non-exchangeable' NH_4^+ may make significant contributions to the nitrogen inventories in marine sediments (Stevenson and Tilo, 1966; Rosenfeld, 1979). It seemed unlikely that significant enrichment of this compartment would occur during the short duration of the experiments and therefore fixed NH_4^+ was not determined. Tests for the presence of $NO_2^- + NO_3^-$ in pore water by conversion of these forms to NH_4^+ with Devarda alloy were consistently negative.

Calculation of N inventories and budgets

Concentrations of nitrogen in particulate forms (TKN and extractable-N) were based on analyses of known weights of dried sediments. Concentrations of dissolved NH_4^+ and DON were based on known volumes of sediment pore waters. To compute the inventories of N in each of these compartments (and to make direct comparisons of the relative contributions of each of the fractions to the total standing stock of nitrogen in the sediment) the concentration data were transformed to volume-based units, N_s = µg-at N cm^{-3} wet sediment. The equation used to transform the weight-based data was:

$$N_s = N_w (1 - \% H_2O) \varrho \quad (1)$$

where N_w = concentration of fraction N in µg-at N g^{-1} dry sediment; H_2O = water fraction (by weight) of the wet sediment; ϱ = bulk density of wet sediment in g cm^{-3}, which was calculated for each sediment fraction as $2.5/(1 + 1.5\ \% H_2O)$. Similarly, the equations used for the transformation of the volume-based concentration data were of the form:

$$N_s = N_v (\% H_2O) \varrho \quad (2)$$

where N_v = concentration of dissolved fraction N in µg-at N l^{-1}; the other terms were as defined above. Characteristics of the sediments from mid-Narragansett Bay, expressed in these units, are given in Table 3.

'^{15}N inventory' refers to the volume-based concentration of ^{15}N excess in any of the free water and sediment fractions. ^{15}N inventories for sediment fractions were calculated by multiplying the volume-based concentration of N in the fraction (total atoms of

Table 3. Average characteristics and nitrogen inventories in sediment cores from mid-Narragansett Bay. All nitrogen determinations are reported as μg-at N cm^{-3} wet sediment. Table entries: $\bar{x} \pm$ S. D.

	Spring		Fall	
	Field[a]	Experimental[b]	Field[c]	Experimental[d]
Water content (%)	47 ± 7	–	41 ± 2	40 ± 6
Bulk density (g cm^{-3})	1.47 ± 0.09	–	1.55 ± 0.03	1.55 ± 0.04
Total Kjeldahl-N	114 ± 7	113 ± 15	122 ± 13	104 ± 10
Extractable NH_4^+	0.03 ± 0.23	0.93 ± 0.19	–	–
Extractable $NO_2^- + NO_3^-$	0.05 ± 0.1	–	–	–
Pore-water NH_4^+	0.08 ± 0.04	0.17 ± 0.04	0.04 ± 0.01	0.07 ± 0.02
Pore-water DON	0.08 ± 0.05	0.08 ± 0.04	–	0.03 ± 0.01
Pore-water $NO_2^- + NO_3^-$	< 0.01	–	–	–

[a] 2 cores, 6 depth intervals (0 to 10 cm); [b] 3 cores, 6 depth intervals (0 to 10 cm); [c] 1 core, 18 depth intervals (0 to 18 cm); [d] 5 cores, 12 depth intervals (0 to 12 cm)

N cm^{-3}) by their enrichments (atoms ^{15}N/100 atoms N). The sediment ^{15}N inventories were then multiplied by the volume of sediment in each 1 or 2 cm thick layer and these amounts of N were summed to give the total N inventory for each fraction in each core. ^{15}N inventories in the free water fractions were calculated by multiplying the concentrations of nitrogen in each fraction by the appropriate enrichment and then by the volume of overlying water over the core at time of sampling.

RESULTS

The tracer budget for spring experiments shows that measurable amounts of the tracer could be recovered from all sediment and overlying water compartments after 1.5 d of incubation at 8°C (Table 4). In general, net transfers of tracer atoms from ^{15}N-labelled POM into the various compartments took place most rapidly during the first week of the experiment. Tracer budgets for the fall series of cores, also given in Table 4, revealed similar distributions of the tracer. However, the more closely-timed sampling intervals adopted in fall revealed that the release of ^{15}N labelled DON took place during the first 6 h of incubation. A substantial release of DON probably occurred when the freeze-dried POM was rehydrated (Garber, in press). While the net transfer of tracer into the sediment pore-water NH_4^+ compartment proceeded linearly for 2 d ($r = 0.93$) at a rate of about 0.022 percent h^{-1}, the net flux of $^{15}NH_{4+}$ across the sediment-water interface reversed after 6 h and recommenced by the second day. The

Table 4. Recovery of ^{15}N excess in free water and sediment compartments following the application of ^{15}N-labelled PON to the surface of sediment cores. Entries are given as the percent of ^{15}N excess (% of spike) added to each core

	Spring; 8°C; % of spike			Fall; 16°C; % of spike				
	Core S-1 1.5 d	Core S-2 7.3 d	Core S-3 17.5 d	Core F-1 6 h	Core F-2 12 h	Core F-3 1 d	Core F-4 2 d	Core F-5 4 d
Free water compartments								
PON	7.3	0.9	1.8	–	–	–	–	–
DON	8.7	4.4	5.7	9.0	–	7.0	7.2	4.8
NH_4^+	1.8	15	17	0.4	0.0	–	3.9	8.9
Sediment compartments								
TKN								
0–1 cm	26	24	18	62	59	51	60	53
Below 1 cm	2.3	9.9	63	5.8	1.3	5.8	5.0	6.7
Extractable NH_4^+	0.6	1.1	0.7	–	–	–	–	–
Pore water								
DON (0–1 cm)	0.1	0.1	0.0	–	–	–	–	–
NH_4^+	0.6	2.0	1.5	0.6	1.0	0.8	2.1	2.5
Macrofauna*	0.3	1.4	3.3	0.0	0.1	0.2	0.3	0.6
Total recovered	48	59	54	78	61	65	78	76

– Not determined
* Estimated from enrichment of selected individuals (see text)

Table 5. Concentrations and enrichments of nitrogen in the free water over sediment cores following the application of ^{15}N-labelled POM to the sediment surface

Free water sample	Incubation period	PON µM	PON % ^{15}N excess	DON µM	DON % ^{15}N excess	NH_4^+ µM	NH_4^+ % ^{15}N excess	$NO_2^- + NO_3^-$ µM	$NO_2^- + NO_3^-$ % ^{15}N excess
Free water initials, spring cores		0.0	Nat.	13.4	Nat.	0.83	Nat.	0.2	Nat.
Core S–1	0 – 1.5 d	44.2	35.23	69.9	26.68	36.9	10.20	0.5	–
Core S–2	0 – 3.7 d	11.0	14.68	45.3	16.65	159	12.63	1.3	–
	3.7– 7.4 d	12.3	3.23	46.4	5.48	203	7.50	3.6	–
Core S–3	0 – 3.7 d	14.5	21.51	45.8	23.15	113	15.92	1.2	–
	3.7– 9.4 d	15.7	2.94	46.4	5.24	196	7.92	1.2	–
	9.4–17.5 d	28.7	3.20	49.8	2.80	213	3.96	4.2	–
Free water initials, fall cores		–	–	11.9	Nat.	1.42	Nat.	2.06	Nat.
Core F–1	0– 6 h	–	–	60.7	46.3	5.41	22.95	0.20	–
Core F–2	0–12 h	–	–	59.2	–	0.00	–	0.00	–
Core F–3	0–24 h	–	–	58.2	34.4	0.81	–	0.15	–
Core F–4	0–48 h	–	–	52.2	37.0	31.05	33.40	0.00	–
Core F–5	0–96 h	–	–	37.5	26.2	111.6	22.6	2.39	–

Nat. Natural abundance of ^{15}N, assumed to be 0.37 atom % ^{15}N, or 0.00 % ^{15}N excess
– Not determined

reversal of net DIN flux between 6 h and 24 h in fall was also recorded in measurements of total (i.e. labelled plus unlabelled) NH_4^+ and NO_2^- and NO_3^- (Table 5).

Distributions of ^{15}N in particulate and dissolved nitrogen fractions in the sediment are shown in the series of depth profiles in Fig. 2 and 3. As expected, the largest inventories of ^{15}N were found in the TKN fraction in the 0 to 1 cm layer of sediment (Fig. 2a and 3a). However, the initial enrichment of this fraction, about 0.5 and 1.5 atom % ^{15}N excess for Experiments 1 and 2, respectively, was considerably less than the value expected if the total amount of ^{15}N in the labelled POM had been uniformly mixed into the top layer of sediment. The problem of the missing ^{15}N will be addressed later. Here it suffices to point out that one half to two thirds of the tracer atoms added to the cores were not found in the topmost layer of sediment. These deficits carried through the tracer budgets, and are reflected in the totals given in Table 4.

DISCUSSION

Conceptual models of nitrogen dynamics in sediment-water systems are always complex. At any point in the system – and depending on the valence state of the atoms involved and the surrounding redox regime – nitrogen atoms may be (1) assimilated into living biomass, (2) remineralized as NH_4^+, (3) oxidized to NO_2^- or NO_3^-, (4) reduced to N_2O, NH_2OH, NH_4^+ or N_2. In addition to these biological transformations, particle-bound forms may be physically mixed downward into the sediment; dissolved forms may diffuse in any direction along concentration gradients and take part in exchange reactions with mineral phases in the sediment. In the subtidal benthos, this web of chemical and physical processes ultimately depends on organic matter deposited at the sediment surface. The experiments described here examined the processes affecting the fate of freshly-deposited organic nitrogen. The validity of the experiments rests on the assumption that the ^{15}N-labelled PON represented a reasonable analog of detrital material reaching the nearshore benthos. The arguments for this assumption were given earlier. My contention here is that the movement of the ^{15}N tracer from the labelled POM into the overlying water and sediment compartments provided direct evidence that the processes determining the fate of detrital nitrogen include (1) the release of soluble organic-N compounds, (2) remineralization of organic-N as NH_4^+, (3) fluxes of remineralized NH_4^+ upward into the water and downward into the sediment, (4) downward conveyance of particle-bound nitrogen , (5) exchange reactions with sediment particulates, and (6) uptake of some fraction of the detrital-N by benthic fauna.

Release of DON

About 9 % of the labelled PON initially added to the cores appeared in the free water DON compartment immediately after the slurry of *Skeletonema costatum* cells was added to the cores (Table 4). Release of DON

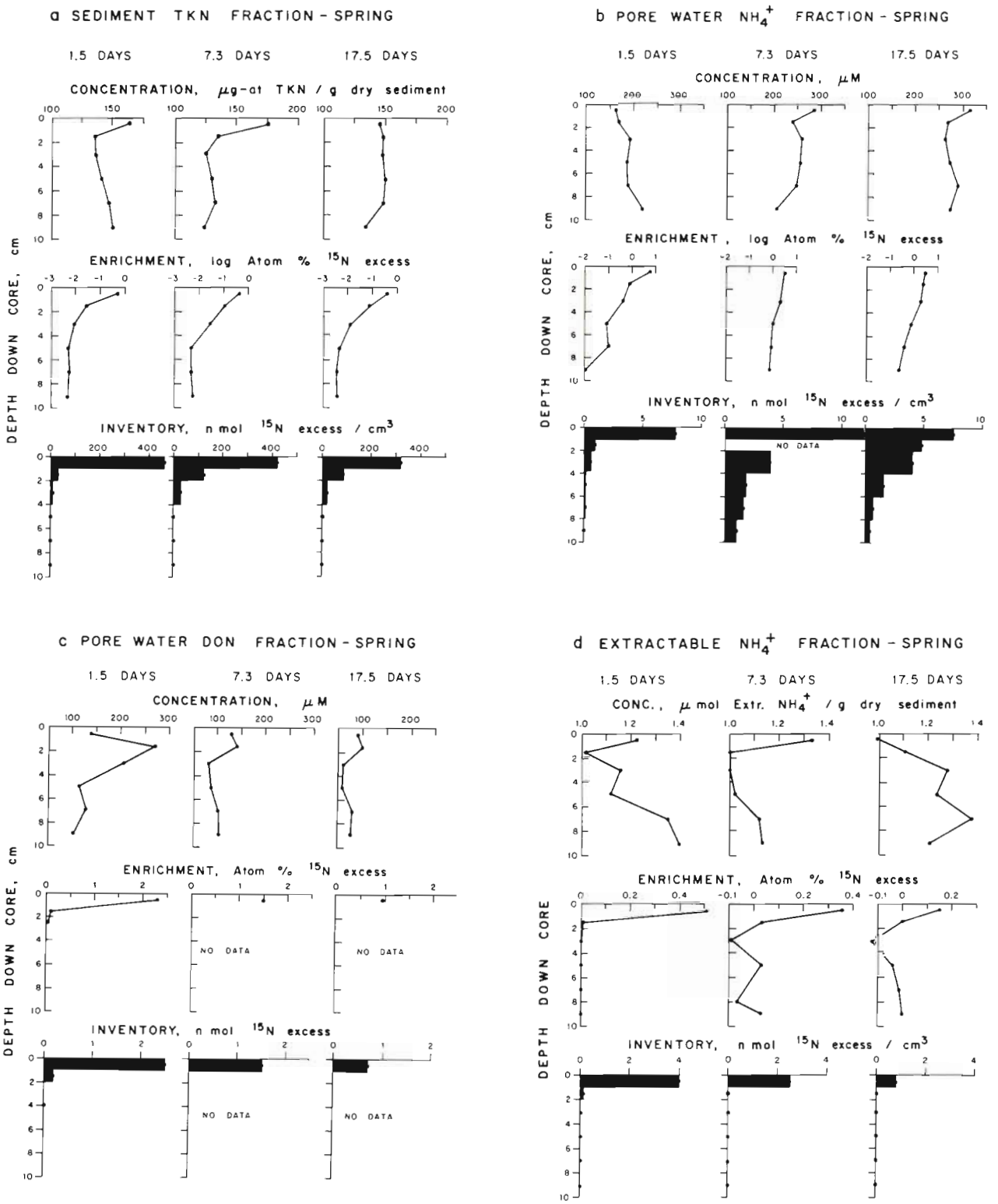

Fig. 2. Spring experiment: profiles of nitrogen concentrations, ^{15}N enrichments, and ^{15}N inventories in sediment TKN (a), pore water NH_4^+ (b), pore water DON (c), and extractable NH_4^+ (d), at various times after cores were treated with ^{15}N-labelled PON

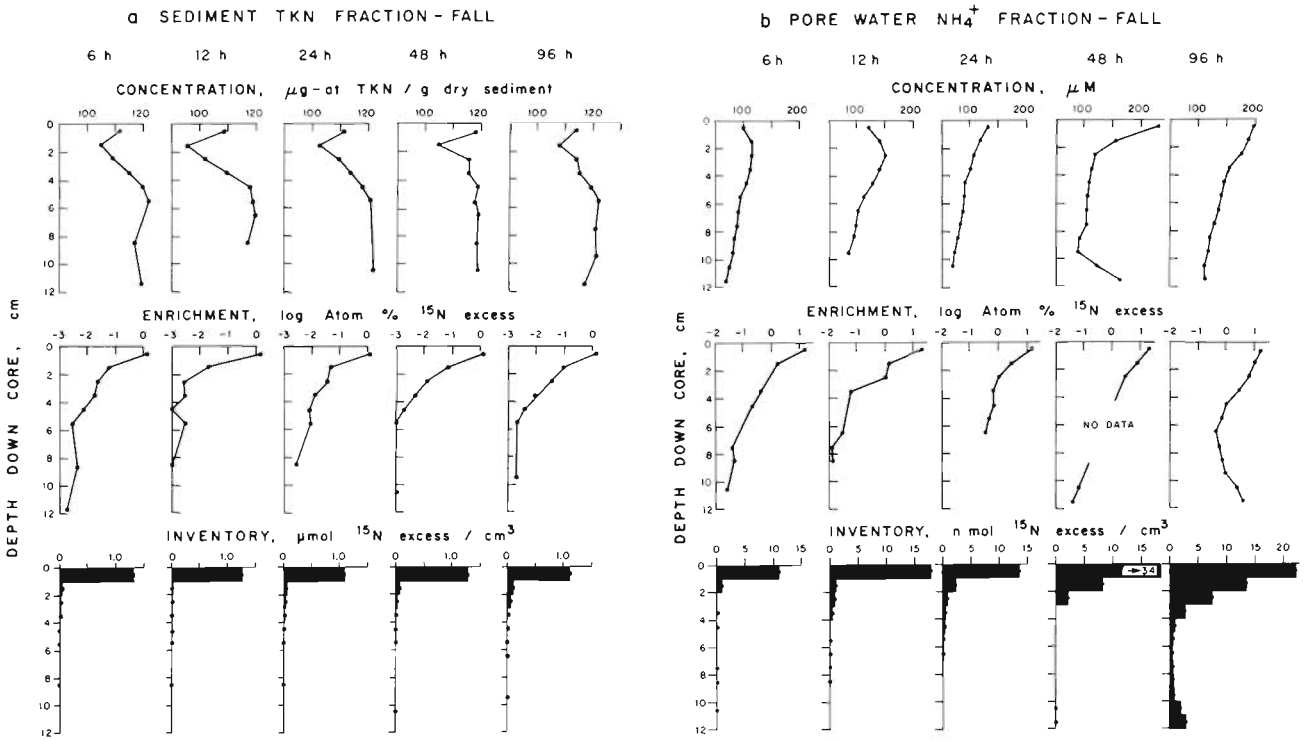

Fig. 3. Fall experiment: profiles of nitrogen concentrations, ^{15}N enrichments and ^{15}N inventories in sediment TKN (a), and porewater NH_4^+ (b), at various times after cores were treated with ^{15}N-labelled PON

also occurred when the labelled cells were allowed to decompose in seawater alone (Fig. 4). The release of DON from lyophilized plankton has been reported in other studies of plankton decomposition (Otsuki and Hanya, 1972; Rajendran, 1978; Garber, in press). Otsuki and Hanya (1972) suggested that the freeze-drying process was responsible for the initial release of soluble cellular components. On the other hand, Golterman (1960) had shown that water soluble forms of organic-N were released when plankton cells die and lyse under a variety of conditions. While lyophilization may have been the least destructive means to kill and preserve the labelled *S. costatum* cells, the initial release of large amounts of DON was probably an artifact of this pre-treatment. Nevertheless, the subsequent fate of the labelled-DON shows that a large fraction, perhaps as much as 50 %, of these compounds were reactive in the sediment-water system Table 4).

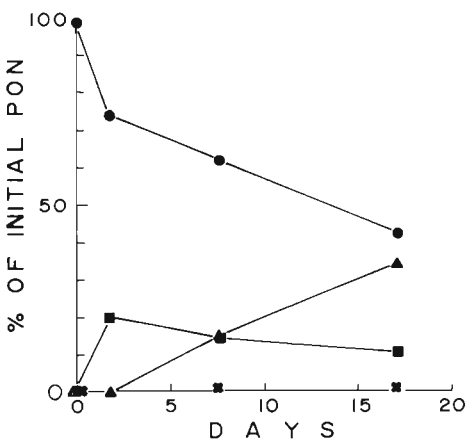

Fig. 4. Dynamics of the aerobic decomposition of ^{15}N-labelled *Skeletonema costatum* cells in glass-fiber-filtered Narragansett Bay water, 8 °C. Initial amount of PON (0.73 mg-at N), identical to that added to sediment cores, was suspended in 1 l of bay water. Circles: PON; squares: DON; triangles: NH_4^+; crosses: $NO_2^- + NO_3$

After the initial release of DON, the concentration of DON in the free water decreased for about 4 d and then, in spring, increased slowly (Fig. 5). In each core the ^{15}N enrichment of the DON compartment decreased with time (Table 5). However, the nearly constant concentration of DON suggests that the disappearance of labelled DON was balanced by a nearly equivalent amount of unlabelled DON.

Rates of N remineralization

In both experiments the primary form of remineralized-N released from the labelled POM was NH_4^+ (Table 5). Although the sediments taken in spring exhibited small positive net releases of $NO_2^- + NO_3^-$ to the overlying water (1 to 2 μmol m^{-2} h^{-1}), nearly

all of the cores taken in fall exhibited net uptakes of $NO_2^- + NO_3^-$ (Table 5). In fall, the net release of NH_4^+ began after a lag of about 24 h during which NH_4^+ and $NO_2^- + NO_3^-$ were removed from the overlying water. This uptake of inorganic-N may have been due to the temporary immobilization of nitrogen in an actively growing population of microbial decomposers. If so, the microbial community at the sediment surface may be remarkably sensitive to the 'quality' of the available organic matter and its activities may determine the direction of nutrient exchanges between sediment and free water. This does not necessarily imply that the same microbial species may take up or release NH_4^+, NO_2^- and NO_3^- depending on the 'quality' of organic matter, but rather that uptake may be due to the dominance of metabolic types different than those responsible for net release.

Net rates of $^{15}NH_4^+$ production (Table 6) were calculated by dividing the total amount of $^{15}NH_4^+$ recovered in each core (free water $^{15}NH_4^+$ + pore water $^{15}NH_4^+$ + exchangeable $^{15}NH_4^+$) by the surface area of sediment in the core and by the duration of incubation. The net rates averaged 13 (s. d. 5) μmol NH_4^+ m^{-2} h^{-1} in spring and 32 (s. d. 12) μmol NH_4^+ m^{-2} h^{-2} h^{-1} in fall. The calculated net rates of NH_4^+ production do not account for the cycling of $^{15}NH_4^+$ through the microbiota and meiofauna and therefore underestimate the instantaneous rates of nitrogen remineralization in the cores (Barsdate et al., 1974; Blackburn, 1979). However, I believe these rates do reflect the *net* rates of NH_4^+ production from the labelled POM in the sediment-water system, and therefore give an indication of the net rate of N-remineralization in an intact benthic system.

If the remineralization of organic-N is assumed to proceed as a first order reaction then the half-lives for organic-N at the sediment surface, based on the net rates of $^{15}NH_4^+$ production in the cores, are in the order of 1 to 2 mo in spring and 2 to 3 wk in fall (Table 6). Even if the remineralization of the organic-N deposited on the sediments were to proceed throughout the entire year at the slower rate found in spring (0.075 % d^{-1}), 99 % of the organic-N would be remineralized in less than 9 mo. These results are consistent with Nixon's (1981) calculations that suggested that only about 1.5 % of the primary production of nitrogen in the surface waters of Narragansett Bay is buried in the sediments annually, and Eadie and Jeffrey's (1973) estimate, based on carbon isotope ratios, that 5 % or less of oceanic POM reaches the deep sea benthos.

Rates of release of total NH_4^+ to the free water over the sediment cores are also given in Table 6. The isotopic composition of the original labelled POM was 82.5 atom % ^{15}N excess. Therefore 1.21 (= 100 ÷ 82.5) moles of total-N were transferred from one compartment to another for each mole of labelled-N recovered in the compartment receiving the transfer. Thus, only 10 to 22 % of the net flux of total NH_4^+ to the overlying water in the spring could be attributed to the decomposition of the labelled POM. The transient depression in the flux of NH^{4+} from the sediments in fall makes similar calculations difficult. However, the net flux of NH_4^+ from sediments in the additional suite of 5 unamended cores was 113 ± 61 μmol m^{-2} h^{-1} (mean ± SD). If this rate of ammonia flux is assumed as a background in the treated cores then the rates of decomposition of the fresh POM at the sediment surface could have been responsible for about 35 % (range 16 to 54 %) of the flux of NH_4^+ associated with these sediments in the fall. These results are consistent with the view that the total flux of remineralized nutrients from subtidal sediments comprises at least 2 components: one originates from the rapid decomposition of freshly deposited material and the other from the, perhaps slower, decomposition of previously deposited material. This results, it seems, in the 'burn-

Table 6. Net rate of production of $^{15}NH_4^+$ and calculated rate constants for the decomposition of ^{15}N-labelled POM in coastal marine sediment-water systems

Temp. (°C)	Core	Net change in total free water NH_4^+ (μmol m^{-2} h^{-1})	Net rate of $^{15}NH_4^+$ production (μmol m^{-2} h^{-1})	Rate constants for N remineralization (% h^{-1}) Linear model (zero order)	Exponential model, base e (1st order)	Half life for fresh organic-N in the sediment-water system (d)
8	S–1	81	13.6	0.073	0.074	39
	S–2	140	17.8	0.096	0.105	27
	S–3	84	7.8	0.042	0.046	62
16	F–1	46	50.2	0.22	0.22	13
	F–2	–7.8	32.4	0.14	0.14	20
	F–3	0.1	15.1	0.066	0.067	43
	F–4	46	35.6	0.16	0.16	18
	F–5	83	29.7	0.13	0.14	20

ing off' of the organic input at a rate that assures that all but a few percent of the organic-N reaching the sediment will be remineralized within a year's time.

Most *in vitro* studies of plankton decomposition report that some fraction of the organic-N is initially present as, or is converted to, refractory organic compounds similar to humic substances in soils (Otsuki and Hanya, 1972). It appears that only a very small fraction of the PON landing on the sediment surface is fated to be converted into refractory substances.

Downward transport of labelled-N

Downward transport of ^{15}N-labelled particulate matter could only be effected by the feeding and burrowing activities of the benthic fauna (bioturbation) whereas labelled ammonium ions could move downward by Fickian diffusion and by advective exchange of pore water driven by the benthic fauna ('biopumping'). Several investigators have used dissolved and particulate radio-tracers to estimate rates of sediment mixing (Aller and Cochran, 1976; Ludke and Bender, 1979; Santschi et al., 1979) and biopumping (Ludke and Bender, 1979). Nitrogen is not an ideal tracer to use for these purposes because it is non-conservative in the sediment system. Denitrification, for example, can lead to the loss of label from the system while ammonification and immobilization can bring about exchanges of tracer between the particulate and dissolved pools both at the sediment-water interface and deeper in the sediment column. Nevertheless, progressions toward log-linear distributions of excess ^{15}N were observed in both the sediment TKN and porewater compartments. I suggest that the depth profiles of ^{15}N in the sediment TKN fraction (corrected for residual pore water $^{15}NH_4^+$) reflect the downward transport of nitrogen associated with particulate phases in the sediment and that the distribution of ^{15}N in the pore water NH_4^+ pool reflects the downward transport of $^{15}NH_4^+$ formed at the sediment-water interface.

Assuming that (1) the sediment-water interface represents a plane source of labelled POM, (2) the sediment below the interface is a uniform (isotropic) diffusive medium, (3) the sediment mixing coefficient (D_m) is constant at all depths in the sediment, and (4) particulate matter can only be mixed downwards, the depth distribution of tracer in the TKN fraction can be described by the equation given by Crank (1975) for diffusion from a plane source in a semi-infinite cylinder:

$$1n\ C = 1n[M/(D_m t)^{1/2}] - (z^2/4D_m t) \quad (1)$$

where C = concentration of ^{15}N (μg-at ^{15}N cm^{-3}) at time t and depth z (measured positively downward from the

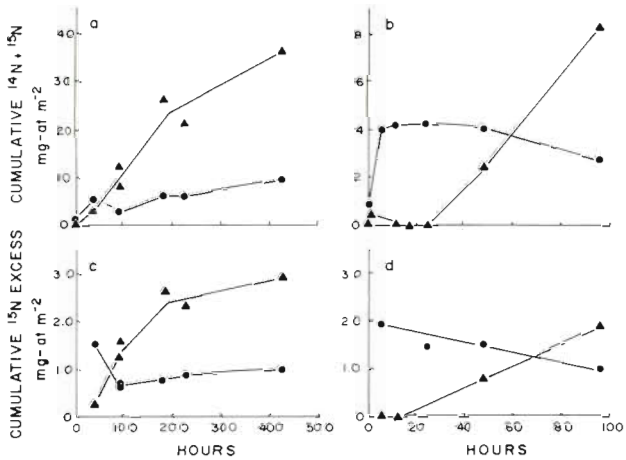

Fig. 5. Dynamics of net release and uptake of total and ^{15}N-labelled DON (circles) and NH_4^+ (triangles) to the free water over sediment cores treated with ^{15}N-labelled PON. Note difference in time scales for spring experiment (Panels a and c) and fall experiment (Panels b and d)

sediment-water interface). By further assuming that (1) the rate of production of labelled ammonium is constant at the sediment-water interface (thus giving a plane source of ammonium at z = 0), (2) ammonium can diffuse both upwards (into the free water) and downwards (into the sediment pore water) and (3) the 'diffusion' constant for ammonium (D_s) is constant at all depths in the sediment, an equation for the distribution of labelled ammonium can be derived that differs from (1) only by a factor of 1/2 in the first term:

$$1n\ C = 1n[M/2(D_s t)^{1/2}] - z^2/4D_s t \quad (2)$$

D_m and D_s can then be estimated from the slope of plots of 1n C vs z^2, z taken as the midpoint of each sediment section. The coefficients D_m and D_s were calculated from the predictive least squares linear regression slopes for the linear portions of plots such as those shown in Fig. 6.

The calculated coefficients ranged over 4 orders of magnitude (Table 7) and the value of the coefficients generally decreases as the length of incubation of the cores increased. D_m values calculated for cores incubated for longer than 1 d showed the best agreement with values determined in other studies (Table 8). These results suggest that either the procedures used to calculate D_m and D_s were not appropriate for short incubation periods or the initial rates of downard mixing of tracer are very much higher than would be predicted based on the results of the longer-term experiments. On the one hand, sediment displacement by the benthic fauna would be most intense near the surface of the core. This could result in rapid conveyance of particulate material to a depth of 1 or 2 cm after which downward mixing would take place more slowly. This interpretation is consistent with inventory

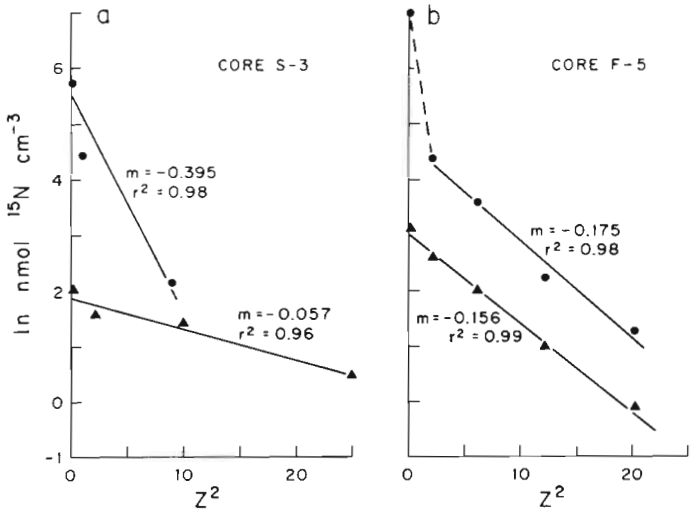

Fig. 6. Examples of plots of ln C *vs* Z^2, where C = inventory of ^{15}N in sediment TKN (circles) and pore water NH_4^+ (triangles); Z = mid-point of each sediment section

data (Table 4). Had the tracer in particulate matter been mixed downward by a process that, on short time scales, was truly analogous to Fickian diffusion, then the inventories of ^{15}N in the TKN fraction below 1 cm would have increased in a regular fashion as the period of incubation increased. Instead, a small fraction of the tracer, amounting to 2 to 5 % of the labelled POM added to the cores, was rapidly conveyed below 1 cm. The possibility that this initial transport of tracer results from the handling of the cores seems remote because great care was taken to avoid cross-contamination of the sediment sections. The values of D_m and D_s in Table 7 suggest that the assumption that the rate of sediment reworking is constant for the entire sediment column is not correct and that the problems stemming from that assumption are particularly troublesome for experiments of short (less than several days) duration. The values of D_m and D_s calculated for the cores incubated for 2 d or more converged on 2 to 5 $\times 10^{-6}$ cm^2 s^{-1}. These sediment mixing coefficients are somewhat higher, but roughly comparable, with the rates reported by other workers (Table 8).

NH_4^+ exchange dynamics

The amount of ammonium reversibly adsorbed onto particulate matter in the sediment was estimated by assuming that centrifugation removed 40 % of the sediment pore water. The inventories of extractable-NH_4^+ were then corrected for the amount of pore water NH_4^+ remaining in the sediment. The calculated concentrations of exchangeable NH_4^+ ranged from 0.5–1.2 µg-at N cm^{-3} (1 to 1.4 µg-at N g^{-1} dry sediment). The isotopic composition of the exchangeable NH_4^+ fraction was then estimated by assuming that the 60 % of the labelled NH_4^+ dissolved in the sediment pore water remained in the centrifuged sediment. The ^{15}N atom % excess in the exchangeable NH_4^+ fraction (R_{ex}) is then

$$R_{ex} = (R_m \cdot N_{ext}) - 0.6\ {}^{15}N_{pw}/N_{exc} \quad (3)$$

where R_m = ^{15}N atom % excess in the exchangeable NH_4^+ pool; N_{ext} = concentration of extractable NH_4^+ in µmol cm^{-3}; $^{15}N_{pw}$ = concentration of excess $^{15}NH_4^+$ in the pore water in µmol cm^{-3}; N_{exc} = calculated concentration of exchangeable NH_4^+ in µmol cm^{-3}.

Significant enrichments of the exchangeable NH_4^+ fraction were found only in the topmost layers of sediment (Fig. 2d). Calculated enrichments of the exchangeable NH_4^+ in the 2 to 4 cm layer were less than 0, that is, the isotopic composition was less than the natural abundance of ^{15}N. Although the apparent depletion of ^{15}N in the tracer experiments may have been caused by discrimination against the heavy

Table 7. Calculated coefficients for sediment mixing (D_m) and NH_4^+ diffusion (D_s) based on the ^{15}N inventories (C) in sediment TKN and pore water NH_4^+ fractions. Table includes least squares regression slopes and coefficients of determination (r^2) for the linear portions of plots of ln C *vs.* Z^2

Core	Δt × 10^5 s	TKN fraction* Interval (cm)	LS slope (r^2)	$D_m \times 10^{-6}$ cm^2 s^{-1}	Pore water NH_4^+ fraction Interval (cm)	LS slope (r^2)	$D_s \times 10^{-6}$ cm^2 s^{-1}
S–1	1.3	0–4	–.428 (.77)	4.4	1–6	–.097 (.99)	19
S–2	6.4	0–4	–.299 (.94)	1.3	1–6	–.048 (.99)	8.2
S–3	15	0–4	–.395 (.98)	0.42	0–6	–.057 (.96)	4.6
F–1	0.22	1–5	–.094 (.88)	123	0–5	–.188 (.82)	62
F–2	0.43	1–5	–.133 (.75)	44	0–5	–.421 (.88)	14
F–3	0.86	1–6	–.061 (.79)	47	0–5	–.144 (.65)	20
F–4	1.7	1–3	–.472	3.1	0–3	–.447 (.96)	3.2
F–5	3.5	1–6	–.175 (.98)	5.2	0–5	–.156 (.99)	4.6

* TKN inventories were corrected for residual pore water $^{15}NH_4$ by assuming that 60 % of the pore water ^{15}N inventories remained in the sediment after centrifugation

Table 8. Comparison of sediment mixing coefficients (D_m) and ammonium diffusion coefficients (D_s) found in this study with values reported in the literature

Location	D_m ($cm^{-2}\ s^{-1} \times 10^{-6}$)	D_s	Reference
Narragansett Bay	0.4–5.2	4.6–8	This study[a]
Narragansett Bay	0.2–0.4		Ludke and Bender (1979)[b]
Narragansett Bay	0.1–0.01		Santschi et al. (1979)[c]
Long Island Sound	1.2–2.5		Aller and Cochran (1976)[d]
Long Island Sound		6.2–7.4	Rosenfeld (1979)[e]
Southern Bight of the North Sea		1–170	Billen (1978)[f]
Roskeeda Bay, Eire		17–86	Raine and Patching (1980)[f]
Free solution molecular diffusivity for NH_4^+, 0–30 °C		9.8–22	Klump and Martins (1981)

[a] Data for cores incubated longer than 24 h
[b] Tracer experiment with ^{141}Ce and ^{59}Fe
[c] Tracer experiments with ^{59}Fe, ^{203}Hg and ^{46}Sc labelled microspheres
[d] Analysis of in situ distribution of ^{234}Th
[e] Laboratory diffusion cells filled with mud
[f] Analysis of pore water profiles

isotope, it is likely that this was an artifact of calculation, caused by uncertainties in the concentrations of the extractable NH_4^+ and the factors used to correct the data for pore water NH_4^+.

Rosenfeld (1979) characterized the dynamics of ammonium absorption in anoxic coastal marine sediments as rapid, reversible and linear with respect to the concentration of ammonium in the sediment pore water. His experiments indicated that the equilibrium between ammonium in the pore water and exchangeable NH_4^+ in the sediment particulate matter was established in 2 h or less. His conclusion, based on the evaluation of a parameter, K, the ammonium absorption coefficient, was that 'of the ammonium produced by organic matter decomposition, one to two times more is associated with the sediment that is dissolved in the interstitial water'. My results, although qualified by the indirect methods used to calculate the concentration and isotopic composition of exchangeable NH_4^+, provide a test of these conclusions. If the NH_4^+ produced during the decomposition of labelled organic matter had been partitioned equally between the exchangeable and pore water NH_4^+ compartments (K = 1), and if the rate of change of the isotopic composition of the pore water NH_4^+ compartment is slow compared to the dynamics of the exchange reactions, then the ratio of the inventories of $^{15}NH_4^+$ in the exchangeable and pore water compartments should be about 1. The data from the sediment sections suggest that this ratio was less than 1 (Fig. 7) and the inventory data (Table 4) show that the ratios of exchangeable $^{15}NH_4^+$: pore water $^{15}NH_4^+$ in the cores fell between 0.5 and 1.0. These results warrant verification, but the conclusion based on the results of the direct measurements of $^{15}NH_4^+$ produced near the sediment water interface is that ammonium may be partitioned between the exchangeable- and pore water-NH_4^+ pools in ratios lower than 1/1.

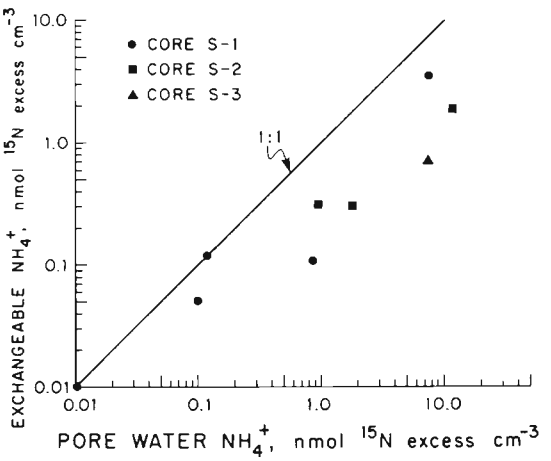

Fig. 7. Relationship between amounts of ^{15}N recovered in pore water NH_4^+ and sediment exchangeable NH_4^+ in spring cores after cores were treated with ^{15}N-labelled PON. Line gives the 1:1 relationship

Incorporation of detrital-N into benthic biomass

The amounts of ^{15}N taken up by the benthic macroinfauna were based on the isotopic compositions of animals captured when the cores were sliced. Rates of uptake (Table 9) were calculated by dividing the ^{15}N enrichments of the animals by the period of incubation of the cores. Therefore the uptake rates represent the

Table 9. Uptake of ^{15}N by benthic infauna following addition of labelled POM to sediment cores

Core	Species (# analyzed)	^{15}N atom % excess	^{15}N uptake rate atom % $h^{-1} \times 10^{-3}$
S–1	*Yoldia limatula* (6)	0.16 ± 0.12	4.35
S–2	*Yoldia limatula* (6)	0.56 ± 0.20	3.16
S–3	*Yoldia limatula* (3)	1.40 ± 0.40	3.3
F–4	*Yoldia limatula* (2)	0.04 ± 0.02	0.8
F–5	*Yoldia limatula* (1)	0.89	7.4
F–2	*Nepthys incisa* (3)	0.016 ± 0.002	1.3
F–3	*Nepthys incisa* (1)	0.015	0.6
F–3	*Maldanopsis* sp. (1)	0.02	0.8
F–5	*Maldanopsis* sp. (2)	0.15 ± 0.06	1.6
F–3	*Nassarius trivittatus* (1)	0.08	3.3

number of ^{15}N atoms incorporated into the tissues of the animal per 100 atoms of N in the animal per hour. The average rates of uptake of ^{15}N for bivalves, gastropods and polychaetes were 0.0044, 0.0033 and 0.011 atom % ^{15}N h^{-1}, respectively. The uptake rates for the 3 groups of organisms appeared reasonably constant (note particularly the uptake rates for *Yoldia limatula*) in the spring series. Since the data were insufficient to estimate the effects of temperature on the uptake rates, I assumed that the rates were constant for the 3 groups in both sets of cores. The amounts of ^{15}N incorporated into benthic biomass given in the tracer budgets (Table 4) were calculated by multiplying the uptake rates by the average concentrations of each group of macrofaunal-N found in replicate sediment cores. These calculations indicate that only a few percent of labelled detritus could have been taken up by the macrofauna in the cores.

Deficits in the N budgets

The deficits in the budgets for the amounts of tracer-N added to the cores averaged 46 % in spring and 28 % in fall. These recoveries, particularly in spring, were dishearteningly low. The improvement in the recoveries of tracer in the second experiment undoubtedly reflects better sampling procedures. Since entire sections of the sediment could be removed from the cores intact, the determinations of sediment inventories were not subject to subsampling errors.

It is possible to account for any fraction of the tracer deficits, or, in fact, for the loss of the entire spike of ^{15}N, by assuming that denitrification in the cores produced N_2 gas that was more or less enriched in ^{15}N. However, if denitrification of the labelled-N were the cause of the loss of significant amounts of the input, I would have expected the deficits in the budgets to increase in some regular fashion with the length of the incubation period. There appeared to be no relationship between the size of the deficit and the length of incubation of the cores. The deficits were relatively constant within each experimental set. This suggests that the losses were the result of sampling or procedural errors, rather than due to a biological process occurring in the cores.

The amount of ^{15}N recovered in the sediment TKN fraction corresponded reasonably well with the amount that would have remained in particulate form if 30 to 40 % of the nitrogen in the input material had been released to the water as DON at the start of the experiment. There can be no doubt that the release of some DON took place when the POM slurry was added to the cores. The problem, however, is that the missing ^{15}N cannot be attributed to uncertainties in the free water DON fraction. Even granting a liberal estimate of the error associated with the determination of the concentration of DON in the free water of ± 10 µg-at N l^{-1} only about 2 % of the input could have been lost in this fraction.

Since none of the sources of error alone can account for a major loss of tracer from the systems, the conclusion seems to be that the losses reflect cumulative errors, each of which contributed to underestimates of the amount of nitrogen in some compartments or to the dilution of labelled-N in the samples. Losses of tracer could also be attributed to processes that are impossible to evaluate quantitatively. These include absorption of labelled-N on the wall and tops of the containers, or the immobilization of N in microbial growth on the walls of the tubes, or leakage of water through the bottom seals of the coring devices.

CONCLUSIONS

The experiments described here represented an attempt to determine the fate of freshly deposited detrital nitrogen at the surface of a heterotrophic benthic community from mid-Narragansett Bay, Rhode Island, USA. The experiments provided direct evi-

dence that nitrogen is remineralized from freshly-deposited POM and the dominant form of remineralized-N leaving the sediments is NH_4^+. Net rates of N-remineralization based on the conversion of labelled PON to NH_4^+ suggest that essentially all but a few percent of detrital-N reaching the sediment surface could be recycled in less than 1 yr.

The tracer experiments also provided evidence that 5 to 10 % of the nitrogen in freshly deposited POM is conveyed to deeper layers of the sediment and that both particulate and dissolved forms of nitrogen are carried downward from the sediment surface. The experiments further provided evidence that freshly remineralized NH_4^+ takes part in exchange reactions with particulate phases in the sediments.

Finally, the recovery of tracer-N in the tissues of a number of benthic organisms demonstrated that the nitrogen originating in the deposited POM was taken up by the benthos. The exact pathway of uptake cannot be determined from the results reported here but it seems clear that only a small fraction, perhaps a few percent, of the organic nitrogen conveyed to the sediment surface in the fallout of detritus is incorporated into benthic biomass, the rest is rapidly remineralized at the sediment surface.

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