Marine Biology 66, 59–65 (1982)

MARINE BIOLOGY

Ammonium Regeneration and Assimilation in Eelgrass (*Zostera marina*) Beds

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Abstract

Regeneration and assimilation of ammonium in the water column and in sediments of eelgrass (*Zostera marina* L.) beds of Izembek Lagoon and Crane Cove, Alaska, USA and Mangoku-Ura, northeastern Japan, were investigated by using a ^{15}N isotope dilution technique. In the water column of Mangoku-Ura, ammonium was regenerated at a rate of 12 nmol l^{-1} h^{-1} and assimilated at a rate of 74 nmol l^{-1} h^{-1}. The ammonium regeneration rate in sediments ranged from 2 to 150 nmol g^{-1} h^{-1}, and with one exception, exceeded ammonium assimilation in sediments (0.3 to 77 nmol g^{-1} h^{-1}). The ammonium regeneration in the water column was of little significance for the nitrogen supply to the eelgrass bed ecosystem. Net ammonium production (regeneration minus assimilation) in the sediment of Izembek Lagoon met nitrogen demand for eelgrass growth, suggesting that ammonium regeneration in the sediments was very important for the nitrogen cycle in the eelgrass bed ecosystem.

Introduction

The importance of ammonium regeneration in the nitrogen cycle of coastal waters has been emphasized since the nitrogen requirement for sustaining their high productivity sometimes exceeds nitrogen influx from river runoff, precipitation and deep-water advection (Haines, 1975). Recent studies (Harrison, 1978; Caperon *et al.*, 1979) revealed that ammonium regeneration is nearly in balance with the requirement by autotrophs in inshore waters. Using a large experimental container, Hattori *et al.* (1980) demonstrated that ammonium regeneration rate in the surface layer is about 60% of the rate of ammonium uptake by phytoplankton populations. Thorstensen and MacKenzie (1974) and Rowe *et al.* (1975) noted that ammonium regenerated in sediments and diffusing into overlying water forms the major source of nitrogen for phytoplankton in coastal waters.

Seagrass beds are highly productive among coastal waters (McRoy and McMillan, 1977). A fertilization experiment (Orth, 1977) demonstrated that the eelgrass (*Zostera marina*) productivity in the Chesapeake Bay, USA is nutrient-limited. It was not shown, however, which nutrient among ammonium, nitrate, phosphate, and potassium had the most significant effect. The productivity of cordgrass (*Spartina alterniflora*) has been shown to be limited by nitrogen availability (Sullivan and Daiber, 1974; Patrick and Delaune, 1976). Since seagrasses are rooted vascular plants and can absorb nitrogen from their roots as well as from leaves (Iizumi and Hattori, in press), nitrogen regeneration in sediments is expected to be significant in supporting high nitrogen demand by seagrasses.

Berner (1974) computed ammonium regeneration rate in sediments from the vertical ammonium distribution in interstitial water of marine sediments using a one-dimensional diffusion-advection model. This method, however, is difficult to apply to coastal regions where physical and biological turbulences are substantial at the surface sediments. Another method for estimating ammonium regeneration is to follow the change in ammonium content in sediments during incubation under simulated conditions (Billen, 1978). Hartwig (1976) and Rowe *et al.* (1975) measured ammonium release or uptake from the sediments using a bell jar set over the sediment surface. Their methods give information on the sum of production and consumption of ammonium, but not on the respective processes.

An isotope dilution technique was introduced by Kirkham and Bartholomew (1954, 1955) for the determination of ammonium regeneration in soil, and by Blackburn (1979) for that in marine sediments.

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0025-3162/82/0066/0059/$ 01.40

This paper reports on experimental studies of ammonium regeneration and assimilation in eelgrass beds of Izembek Lagoon and Crane Cove, Alaska, and of Mangoku-Ura, northeastern Japan, by using the isotope dilution technique. Emphasis was placed on the processes occurring in the sediments.

Materials and Methods

Study Site (Table 1)

Izembek Lagoon is located at the western end of the Alaska Peninsula (Lat. 55°15′N, Long. 163°50′W). Eelgrass (*Zostera marina* L.) beds cover about 55% of the total area of the lagoon (116 km², McRoy, 1966). A detailed description of Izembek Lagoon is given elsewhere (Iizumi *et al.*, 1980).

Crane Cove is located on Baranof Island (Lat. 65°51′N, Long. 135°22′W) in Southeast Alaska. The cove is 300 m diameter and ca 5 m deep at the center. At the center of the cove, bare sites were patchily scattered among eelgrass beds.

Mangoku-Ura is located in northeastern Japan (Lat. 38°25′N, Long. 141°23′E). The entire bay was covered by eelgrass except the mouth which had sand flats. The bay consists of two parts; a deep basin (ca 5 m) at the far end from the mouth of the bay and a shallow part (ca 2 m).

Incubation Experiments (Sediments)

Incubation experiments were conducted on 2–3 September 1976 in Mangoku-Ura, on 29–30 July 1977 in Izembek Lagoon and on 26–27 August 1977 in Crane Cove.

Sediment samples were collected with Plexiglas tubes (3.5 to 5.0 cm in diameter) by hand, and sectioned to 1–6 cm thick sediments. Incubations were started within 5 h after the sampling. Subsamples of the sediments (15 to 50 g wet wt) were placed in Erlenmeyer flasks (100 to 200 ml). ^{15}N-labelled ammonium (98.8 to 99.0 atom% ^{15}N: Hikari Kogyo Co., Tokyo) was added together with 10 to 150 ml of Millipore HA filtered seawater. Quantities of ammonium added were selected to give final concentrations of ammonium as near as possible to those of interstitial waters. Flasks were flushed with N_2 for ca 5 min to remove O_2, capped with rubber stoppers and incubated at approximately *in situ* temperatures (Table 1). Sediment samples from the surface layer were incubated aerobically. The samples treated with chloroform (5 ml per flask) served as controls.

At intervals, the flasks were shaken vigorously and portions (1 to 10 ml) of the incubated samples were removed with a large-mouthed pipette and frozen immediately.

Incubation Experiment (Seawater)

A seawater sample, collected at Station M-10 on 7 May 1975, was placed in a 5-l glass bottle together with ^{15}N-labelled ammonium (1 μmol of 50 atom% ^{15}N-enriched ammonium per 5 l), and incubated outdoors at 14° to 16° C. At intervals, 1-l aliquots were removed and filtered through a Whatman GF/C glass fiber filter. For preservation, $HgCl_2$ was added to the filtrate to give a final concentration of 2×10^{-4} M.

Table 1. Study site

Station		Type of eelgrass	Water temperature
Izembek Lagoon			11° to 15 °C
I-1	Upper edge of an intertidal zone	Tide pool type with short (< 60 cm) and narrow (< 2 mm) leaves, distributing sparanely and patchy	
I-4	Middle of an intertidal zone	Tidepool type same as at Station I-1 but covering the bottom evenly	
I-10	Subtidal zone (water depth, ca 2 m)	Subtidal type with long (> 1 m) and wide (> 2 mm) leaves, covering the bottom evenly and densely	
Crane Cove			13° to 17 °C
C-4	Center of the cove (water depth, ca 5 m)	(no eelgrass)	
C-5	Center of the cove	Subtidal type, covering the bottom evenly	
Mangoku-Ura			20° to 22 °C
M-7	Innermost basin (water depth, ca 5 m)	Subtidal type, covering the bottom sparsely	
M-10	Center of the bay (water depth, ca 2 m)	Subtidal type, covering the bottom densely	

^{15}N-Content Determination

Total (free plus adsorbed) ammonium in the sediment samples was extracted by the microdiffusion method of Greenfield *et al.* (1970) and collected in 1.0 ml of 0.1 N HCl. The yield of ammonium extraction was ca 100%.

The HCl solution containing 0.2 to 0.3 μmol of ammonium was transferred to a glass capillary (1.3 mm inner diameter (ID), 20 mm long) and dried under an IR lamp. The capillary was placed into a Pyrex discharge tube (2 mm ID, 15 cm long) together with a briquette of CaO-CuO (1 : 1 mixture, ca 30 mg). The tube was evacuated below 10^{-2} Pa and sealed off with a hand torch. The tube was heated at 590 °C for 12 h to convert ammonium nitrogen to N_2. ^{15}N-content was determined by emission spectrophotometry using a JASCO NIA-1 ^{15}N analyzer. Calibration was made using standard N_2 samples with known ^{15}N-contents (provided by Hikari Kogyo Co., Tokyo). ^{15}N-content was expressed as atom% ^{15}N; $^{15}N/(^{15}N+^{14}N) \times 100$. Relative sensitivities of the determination were 1 and 3% at 20 and 1 atom% ^{15}N levels, respectively.

Kirkham and Bartholomew (1954, 1955) and Blackburn (1979) calculated the ammonium assimilation rate from the changes in the quantity and the ^{15}N-content of total ammonium. We determined the ammonium assimilation rate directly from an increase of the ^{15}N-content of organic nitrogen.

The sediment samples from which ammonium had been extracted were further flushed with steam to remove traces of ammonium. Organic nitrogen in the sediment samples was converted to ammonium by Kjeldahl digestion, followed by steam distillation. The ^{15}N-content of the ammonium nitrogen was determined by the hypobromite oxidation method with a Hitachi RMU-6 mass spectrometer. Sensitivity of the ^{15}N-determination by the mass spectrometry was 10^{-4} atom% ^{15}N.

Ammonium was extracted from seawater samples by vacuum distillation. The sample, acidified to pH 2.5, was reduced in volume to about one-third with a rotary evapolator. After raising pH to ca 10, ammonium was distilled for 48 h by introuding NH_3-free air at a rate of 180 ml min^{-1}, and collected by two cascade-connected traps containing 50 ml of 1 N HCl each. The recovery of ammonium was 100%. The HCl solutions in the traps were combined and ^{15}N-content was determined by the mass spectrometer.

The ^{15}N-content in particulate nitrogen collected on the filter was determined mass-spectrometrically by the Dumas' method described by Wada *et al.* (1977).

Sediment Analysis

Interstitial waters were extracted by the method of Reeburgh (1967), except those of Crane Cove where the equilibrators as described by Hessline (1976) were used. Ammonium concentration in the interstitial water was determined by the method of Koroleff (1976) after dilution with deionized water. The water content was calculated from the weight loss after drying at 90° C for 2 d. Specific gravity was determined with a Gay-Lussac pycnometer. Organic nitrogen content in the dry sediment was determined with a Yanagimoto MT-500 CN analyzer. The quantity of total (free plus adsorbed) ammonium in sediments was calculated by the following equation;

$$A_{total} = A_{add}\,(R_{add} - R_0)/(R_0 - r),$$

where A_{total} denotes the quantitiy of total (free plus adsorbed) ammonium in the sediments; A_{add}, the quantity of added ammonium; R_{add}, the ^{15}N-content of added ammonium; r, the ^{15}N-content of the total ammonium before the addition of the ^{15}N-labelled ammonium ($r=0.00366$); R_0, the ^{15}N-content in ammonium immediately after the addition of the ^{15}N-labelled ammonium to the sediments. By extrapolating the regression line in Fig. 1 to $t=0$, R_0 was estimated. The value of total ammonium obtained by this method might be somewhat overestimated if there was irreversible adsorption of the isotope (T. H. Blackburn, personal communication).

Kinetic Model of Ammonium Regeneration

Ammonium is regenerated by the decomposition of organic nitrogen, and at the same time, assimilated by organisms. The following equations are introduced;

$$dN/dt = V_r - V_a \tag{1}$$

$$dn/dt = v_r - v_a, \tag{2}$$

where N denotes the sum of labelled and nonlabelled ammonium nitrogen; V_r, the regeneration rate of N; V_a, the assimilation rate of N; n, the quantity of the ^{15}N-labelled ammonium nitrogen; v_r and v_a, the regeneration and assimilation rates of n, respectively. The following relations also hold;

$$v_r = V_r\,R_{org} \tag{3}$$

$$v_a = V_a\,R_a \tag{4}$$

$$R_a = n/N, \tag{5}$$

where R_{org} denotes the ^{15}N-content of organic nitrogen, and R_a, the ^{15}N-content of ammonium.
From Eq. (1) to (5), we obtain;

$$dR_a/dt = V_r\,(R_{org} - R_a)/N. \tag{6}$$

Then we find;

$$-\ln\,[R_a - R_{org})/(R_0 - R_{org})] = V_r/(V_r - V_a)\ln\,[1 - (V_r - V_a)\,t/N_0], \tag{7}$$

where N_0 denotes initial ($t=0$) quantity of N. We assume that R_{org} is constant ($=0.0037$) and that variation of N, $(V_r - V_a)\,t$, is small when compared to the initial quantity of ammonium, N_0. This will be valid during the initial short incubation period because the quantities of nitrogen

transferred from ammonium to organic nitrogen and vice versa are small compared to the quantities of ammonium and organic nitrogen. Thus, we obtain;

$$-V_r\, t/N_0 = \ln\left[(R_a - R_{org})/(R_0 - R_{org})\right]. \quad (8)$$

The ammonium regeneration rate, V_r, is calculated from the tangent of $\ln(R_a - R_{org})$ *vs* time plots.

Results

Sediment characteristics are summarized in Table 2.

When the sediment samples taken from Station I-10 of Izembek Lagoon were incubated with ^{15}N-labelled ammonium, the ^{15}N-content ammonium decreased with time (Fig. 1). Samples treated with chloroform showed no decreasing trend, indicating that biological reactions were primarily responsible for ammonium regeneration.

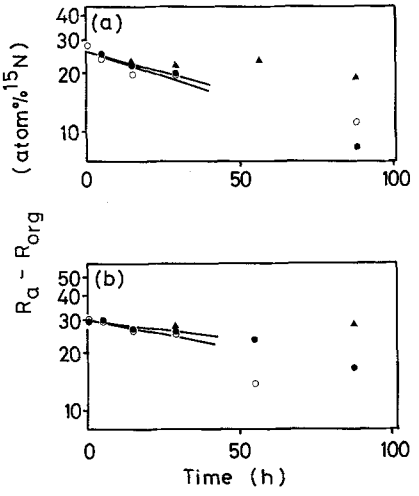

Fig. 1. Time variations in the ^{15}N-content of ammonium ($R_a - R_{org}$) in sediment samples collected from Station I-10, Izembek Lagoon. (a) 0–3 cm, (b) 3–8 cm. Duplicate experiments were conducted (○ and ●); ▲, chloroform-treated. ($R_a - R_{org}$) is plotted in a logarithmic scale. Regression lines fitted for initial 29-h incubation are also shown.

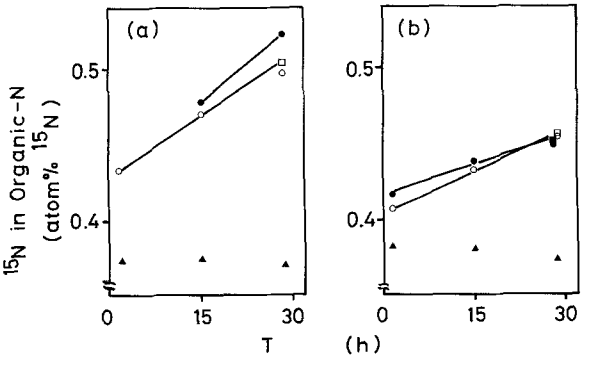

Fig. 2 Time variations in the ^{15}N-content of organic nitrogen (R_{org}) in the same samples as in Fig. 1. Symbols are also the same as in Fig. 1. (a) 0–3 cm, (b) 3–8 cm. The ^{15}N-content of ammonium decreased during the incubation. Therefore, the ^{15}N-content of organic nitrogen was corrected for this decrease (shown by □)

Table 2. Sediment characteristics

Location	Depth cm	Water content %	Specific gravity g cm^{-3}	Organic nitrogen % w/w
Izembek Lagoon				
I-1	0 – 2	38.1	2.56	0.14
	2 – 4	48.5	2.60	0.34
	4 – 7	52.3	nd	0.27
	20 – 25	37.9	(2.60)[a]	0.10
I-4	0 – 2	32.2	2.60	0.11
	2 – 4	36.2	2.74	0.09
	4 – 7	30.4	nd[b]	0.07
	15 – 20	nd[b]	2.66	0.02
I-10	0 – 2	77.5	2.37	0.50
	2 – 4	72.5	2.49	0.37
	4 – 7	68.3	nd[b]	0.32
	20 – 25	53.0	2.41	0.18
Crane Cove				
C-4	0 – 3	67.5	2.29	0.72
	10 – 15	55.7	2.42	0.43
C-5	0 – 3	71.7	2.43	0.90
	10 – 15	52.4	nd[b]	0.31
Mangoku-ura				
M-7	0 – 3	nd[b]	2.29	0.44
	9 – 12	nd[b]	2.10	0.25
	15 – 20	nd[b]	2.05	0.26
M-10	0 – 3	nd[b]	2.32	0.35
	6 – 12	nd[b]	2.45	0.15
	18 – 24	nd[b]	nd	0.07

[a] the specific gravity of 15 – 20 cm stratum
[b] no data

The ^{15}N-content of organic nitrogen in sediments increased with time (Fig. 2). Chloroform-treated samples again showed no increase. The ^{15}N-content of organic nitrogen, corrected for the variation of the ^{15}N-content of ammonium is also shown in Fig. 2. The ammonium assimilation rate was calculated from a regression line fitted to the corrected values.

Time variation in the ^{15}N-contents of ammonium and organic nitrogen in sediments from Crane Cove and Mangoku-Ura were similar to those observed with the Izembek Lagoon sediments. Regression lines fitted to the data during initial 29, 27 and 59 h of incubation were used for calculation of rates of ammonium regeneration and assimilation in sediments of Izembek Lagoon, Crane Cove and Mangoku-Ura, respectively. During these periods, $\ln(R_a - R_{org})$ decreased, and R_{org} increased, almost linearly with time. Calculated regeneration and assimilation rates are summarized in Table 3.

The sediment samples contained detrital material, such as dead roots, rhizomes and fragmented leaves, which prevented uniform distribution of added ^{15}N-labelled ammonium and even sampling. This could be cause of fluctuation in the data. Average standard deviations of

Table 3. Ammonium regeneration and assimilation in eelgrass sediments

Station	Depth	Regeneration $[V_r]$	Assimilation $[V_a]$	Net accumulation $[V_r - V_a]$	Assimilation: Regeneration $[V_a/V_r]$	Total ammonium $[A_{total}]$
	cm	nmol g^{-1} h^{-1}				μmol g^{-1}
Izembek Lagoon						
I-1	0 – 3	58	72	– 14	1.24	2.0
	3 – 8	9.8	8.3	+ 0.6	0.85	1.7
I-4	0 – 3	46	39	+ 7	0.85	0.19
	3 – 8	14	5.6	+ 8	0.40	0.77
I-10	0 – 3	49	38	+12	0.78	3.7
	3 – 8	26	13	+13	0.50	2.6
Crane Cove						
C-4	0 – 3	120	50	+70	0.42	11
	10 – 15	13	3.7	+ 9	0.28	4.3
C-5	0 – 3	150	77	+70	0.51	19
	10 – 15	6.8	3.2	+ 3.6	0.47	4.6
Mangoku-ura						
M-7	0 – 1	35	11	+24	0.31	4.2
	9 – 12	6.0	bd[a]	nd[b]	nd[b]	8.5
	18 – 24	3.2	0.71	+ 2.5	0.22	14
M-10	0 – 1	24	21	+ 3	0.88	3.5
	6 – 12	2.0	0.46	+ 1.5	0.23	1.6
	18 – 21	2.2	1.4	+ 0.8	0.64	1.9

[a] below the detection limit (0.3 nmol g^{-1} h^{-1}).
[b] no data

duplicate experiments of ammonium regeneration and assimilation were 26 and 24%, respectively.

From the time variation of the ^{15}N-content of ammonium and particulate nitrogen in the seawater sample collected at Station M-10 of Mangoku-Ura and incubated with ^{15}N-labelled ammonium (Fig. 3), the rates of ammonium regeneration and assimilation in the water column were calculated to be 0.012 and 0.074 μmol l^{-1} h^{-1}, respectively. The same correction as in Fig. 2 for the ^{15}N-content of organic nitrogen was made. Ammonium concentration in the overlying water of eelgrass beds of Izembek Lagoon and Crane Cove were so low that the addition of ^{15}N-labelled ammonium would change nutrient conditions in the samples. Therefore, no attempt was made to estimate ammonium regeneration rate in the water column at those locations.

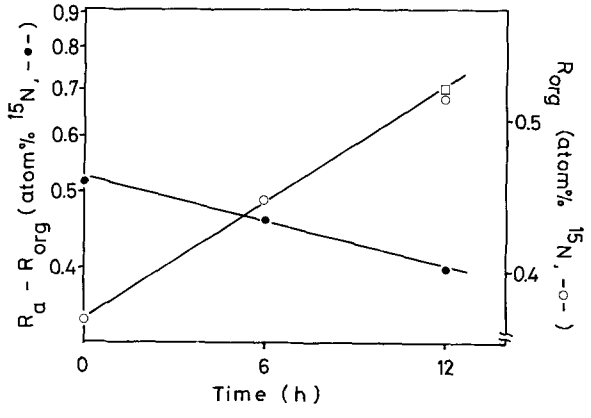

Fig. 3. Time variations in the ^{15}N-contents of ammonium (●, $R_a - R_{org}$) and of particulate organic nitrogen (○, R_{org}) in the seawater sample collected at Station M-10, Mangoku-Ura. The same correction was made for the ^{15}N-content of particulate nitrogen (□) as in Fig. 2

Discussion

A high assimilation : regeneration ratio (6.2) of the ammonium in the water column of the Magoku-Ura eelgrass bed indicated that the supply of ammonium from outside of the bay or from the bottom sediment is necessary to maintain the ammonium concentration in the water column at the level of 0.3 to 10.0 (average 3.4) μmol l^{-1}. Caperon *et al.* (1979) reported that the ammonium regeneration is roughly in balance with the ammonium uptake in coastal waters of Kaneohe Bay, Hawaii. On the other hand, the data obtained by Harrison (1978) show that the ratio is higher than unity in inshore water off the California coast and that it decreases with distance from the coast. The high assimilation rates in inshore waters seem to be closely related to high concentrations of particulate organic matter, including living organisms.

The water samples used in our experiments were taken about noon. There might be less zooplankton than at night because they usually hide in the shade of eelgrass leaves

and of bottom detritus during the day. The significance of zooplankton in ammonium regeneration has been documented (Jawed, 1973; Harrison, 1978; Caperon *et al.*, 1979). Therefore, the ammonium regeneration rate in the Magoku-Ura water column would be somewhat underestimated. If the ammonium regeneration proceeds at a constant rate of 0.012 μmol l^{-1} h^{-1} over the 2-m depth, the ammonium regeneration is calculated to be 0.58 mmol m^{-2} d^{-1}.

Ammonium regeneration rates of surface sediments of eelgrass beds, calculated on a volume basis, ranged from 7.2 to 59 nmol cm^{-3} h^{-1}, which are high, relative to the values reported by Blackburn (1979), 1.2 to 1.5 nmol cm^{-3} h^{-1}. This indicates high ammonium regeneration in eelgrass bed sediments.

The ammonium regeneration in the sediments was higher in the surface strata (0 to 1 cm or 0 to 3 cm) than in the subsurface strata at all stations (Table 3). Relatively high ammonium regeneration in the surface strata of coastal sediments have been observed by Billen (1976) and Blackburn (1979). The deeper strata (3 to 8 cm) of Station I-10, which had higher organic matter content, exhibited a high regeneration rate relative to those of other stations of Izembek Lagoon.

Regeneration rates of the Crane Cove sediments were generally higher than those of other locations. In Magoku-Ura, the ammonium regeneration rates at Station M-7 were higher than at Station M-10. At Station M-7, water was stagnant and oyster culture was carried out, resulting in a high organic matter content in the sediment as this station. We could conclude that ammonium regeneration is high where the content of organic matter or biologically decomposable organic nitrogen compounds is high.

However, this inference cannot be applied to the Crane Cove sediments. The concentration of total ammonium in the 10 to 15 cm stratum at the eelgrass bed (Station C-5) was slightly higher than at the bare site (Station C-4) but the ammonium regeneration rate at the same depth at the bare site was twice that at the eelgrass bed. The reason for this is unknown. Why and how bare sites are formed within the eelgrass beds need to be investigated.

The assimilation : regeneration ratio in the sediments ranged from 0.22 to 1.24 (average 0.57), except one (< 0.05) at the 9 to 12 cm stratum of Station M-7 (Table 3). This ratio is higher than that reported by Blackburn (1979). The ammonium assimilation rate in the sediments tended to increase with an increase in the standing stock of eelgrass at the Mangoku-Ura and Izembek Lagoon stations. In our experimental systems, ammonium might be taken up not only by microorganisms, but also by excised roots. The extent of contribution of ammonium uptake by the excised roots is unknown. The averaged assimilation : regeneration ratio (0.35) at Station C-4, where there was no eelgrass, was ca 70% of that at Station C-5 (0.49), which was located near Station C-4 but had eelgrass populations (Table 3). If we assume that the difference (30%) is due to the root uptake

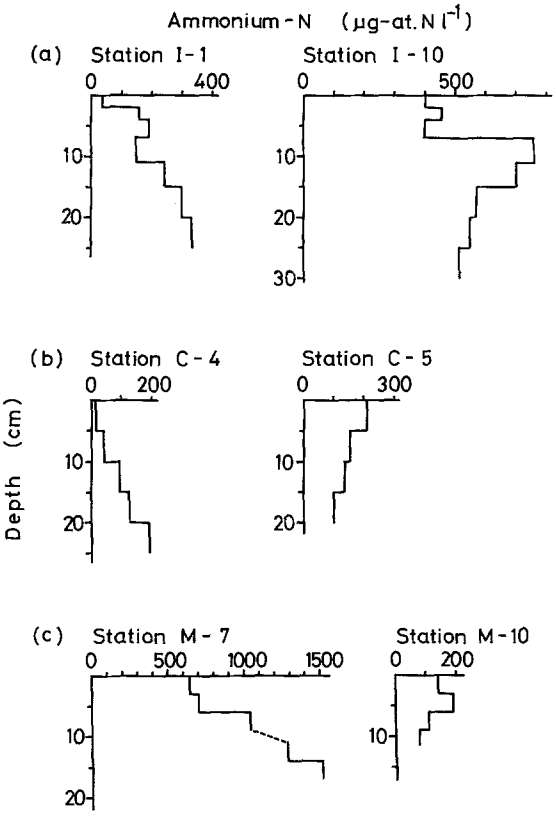

Fig. 4. Vertical profiles of ammonium in interstitial water of eelgrass bed sediments. (a) Izembek Lagoon (19 and 27 July 1977), (b) Crane Cove (2 September 1977), (c) Mangoku-Ura (15 April 1976)

and we apply this figure to the other stations, 41% of the regenerated ammonium is estimated to be assimilated by microorganisms in the sediments.

The excretion of oxygen from eelgrass roots into sediments (Iizumi *et al.*, 1980) might give rise to a high ammonium assimilation : regeneration ratio.

The amount of nitrogen required for eelgrass production in Izembek Lagoon estimated from the growth rate is 0.30 and 0.45 g N m^{-2} d^{-1} at Stations I-4 and I-10, respectively (Iizumi, 1979). To estimate total net ammonium production, we assume that biological reactions decrease exponentially with depth. We also assume that 41% of the regenerated ammonium is assimilated by microorganisms in the sediments and that the rest (59%) is available for eelgrass and other organisms in the eelgrass beds. Total net ammonium production rates were calculated to be 0.51 and 0.32 g N m^{-2} d^{-1} at Stations I-4 and I-10, respectively. These values are nearly identical to those of nitrogen demands by eelgrass. In July, eelgrass grew most actively, and thus took up ammonium intensively. This was reflected in the profile of interstitial ammonium at Station I-10, which shows an apparent decrease in the upper 7 cm of the sediment, probably due to the uptake by eelgrass populations (Fig. 4). In Crane Cove, total net ammonium production rates are estimated to be 0.66 and 0.29 g N m^{-2} d^{-1} at Stations C-4 and C-5, respectively, using the

same assumptions. The eelgrass populations at Station C-5 took up ammonium nitrogen at a rate of 0.03 g N m^{-2} d^{-1} (Iizumi, 1979). This rate is rather low when compared with the estimated total net ammonium production in the sediments. This would be due to the fact that the experiments were conducted in late August when the standing stock and the growth rate of eelgrass declined. Ammonium probably accumulates in the sediments during late summer and winter when ammonium uptake activity of eelgrass is low.

To assess the contribution of the regenerated ammonium to the eelgrass bed productivity, information is needed on seasonal changes in regeneration and assimilation rates and the total ammonium content in the sediments. However, the rough calculations presented above serve to illustrate the importance of ammonium regeneration from organic nitrogen in the sediments for the eelgrass bed productivity.

The regenerated ammonium is partially oxidized to nitrite and nitrate at the rhizosphere of eelgrass roots (Iizumi *et al.*, 1980), but its rate is about one-hundredth of the ammonium assimilation rate. A part (41%) of the ammonium is reassimilated by microorganisms. The rest of the regenerated ammonium is partially absorbed by eelgrass roots, and partially diffuses out from the sediment surface to the overlying water where it can be taken up by benthic algae, epiphytes and eelgrass leaves. The mechanisms of ammonium regeneration from organic nitrogen in sediments form a main pathway for supplying nitrogen to the whole ecosystem associated with eelgrass beds.

Acknowledgements. The authors wish to thank M. J. Klug, Kellogg Biological Station, Michigan State University, T. McConnaughey, F. T. Short, Institute of Marine Science, University of Alaska, and H. Mukai, Ocean Research Institute, University of Tokyo, for their kind help in field sampling, and T. H. Blackburn, Institute of Ecology and Genetics, University of Aarhus, for his critical review. Thanks are also due to crew of R/V "Acona", University of Alaska, for the cruise to Crane Cove. This work was supported by grants (012005, 111307, 210507) from the Ministry of Education, Culture and Science, Japan, and by the US National Science Foundation, Office of the International Decade of Ocean Exploration (OCE 77-27050) as a part of the Seagrass Ecosystem Study.

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Date of final manuscript acceptance: October 28, 1981.
Communicated by T. Fenchel, Aarhus