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THE RESPONSE OF INTERSTITIAL AMMONIUM IN EELGRASS (*ZOSTERA MARINA* L.) BEDS TO ENVIRONMENTAL PERTURBATIONS¹

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Abstract: Natural and human-induced perturbations of eelgrass (*Zostera marina* L.) beds were used to examine the interaction between the sediment interstitial ammonium pool and nitrogen uptake by the plants. Eelgrass colonization of unvegetated areas was accompanied by a substantial decrease in the interstitial ammonium pool over a 4-yr period. The changes in interstitial ammonium and shoot density during colonization support an already determined relationship between shoot density and ammonium pool measurements. In field perturbation experiments, removing eelgrass leaves and sealing the sediment surface altered the flux of ammonium from the interstitial ammonium pool, and resulted in a rapid increase in interstitial ammonium concentrations. Measurements of ammonium accumulation under the various perturbation conditions and a control permitted calculation of the sediment ammonium flux. These estimates include uptake by eelgrass roots, regeneration in the root zone, and diffusion from the sediments. Nitrogen limitation was observed in some eelgrass beds.

INTRODUCTION

Seagrasses, submerged marine angiosperms, inhabit most of the shallow coastal waters of the world (Den Hartog, 1970; McRoy & Helfferich, 1977; Phillips & McRoy, 1980). The dominant seagrass in northern temperate oceans is eelgrass, *Zostera marina* L. Numerous descriptive studies of its distribution and seasonal occurrence have suggested processes relating eelgrass abundance to various environmental conditions, some suggesting the influence of nutrient resource availability (Philip, 1936; Short, 1981; Kenworthy *et al.*, 1982; Short, in press; McRoy, unpubl.). An understanding of the extent to which these processes interact in eelgrass beds can be approached through manipulation of the environment, perturbing a specific process and observing the system's response. This approach has been used in enrichment studies of eelgrass beds by altering the nutrient resource in the sediments (Orth, 1977) and the water column (Raymont, 1947; Harlin & Thorne-Miller, 1981).

Nutrient supplies for eelgrass growth are available in both sea water and the upper layers of the sediments. Uptake of nitrogen by aquatic roots and leaves was measured using ¹⁵N-labelled ammonium and nitrate (McRoy & Goering, 1974; Toetz, 1974; Short, 1981; Iizumi & Hattori, 1982). Similarly, uptake of phosphorus by leaves and roots of eelgrass and other aquatic plants was demonstrated using ³²P-labelled

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phosphate (McRoy & Barsdate, 1970; Carignan & Kalff, 1980; Penhale & Thayer, 1980).

Ammonium, NH_4^+ , is produced in anoxic sediments primarily by the decomposition of organic matter and accumulates in the interstitial water and on sediment particles. In highly reduced eelgrass sediments, ammonium is lost from the interstitial pool by diffusion into the thin oxidized sediment surface layer and the overlying water column, by uptake by eelgrass roots, by adsorption onto sediments, and by incorporation into bacterial cells. Adsorbed ammonium in the sediments is present in two forms: fixed and exchangeable (Rosenfeld, 1979). Fixed ammonium is adsorbed into the clay structure and its interaction with the interstitial water is negligible. However, exchangeable ammonium is easily released by ion exchange and exceeds the amount present in the interstitial ammonium pool. The amount of exchangeable ammonium is dependent on the texture, mineralogy, and organic content of the sediments.

The objective of this research was to examine the removal of ammonium from the interstitial water by eelgrass roots and determine how the interstitial ammonium pool might affect the plants. The studies involved monitoring interstitial ammonium concentrations in four perturbations: (1) a natural destruction of an eelgrass bed by ice damage (scouring), followed by recolonization by eelgrass; (2) colonization of introduced foreign substratum by eelgrass; (3) leaf removal; and (4) sealing the sediment surface. Ammonium flux associated with the sediment interstitial pool was calculated from ammonium regeneration measured in perturbations 3 and 4. Rates of eelgrass root uptake of ammonium and phosphate were also estimated from these perturbation experiments.

MATERIALS AND METHODS

These experimental studies were part of an investigation of the nitrogen requirements of eelgrass and the plants' utilization of available ammonium resources (Short, 1981) in Izembek Lagoon, located on the north side of the Alaska Peninsula (Fig. 1). Seagrass meadows in this lagoon represent one of the most extensive stands of eelgrass, *Zostera marina*, in the world. The specific study sites were intertidal eelgrass beds located north of Grant Point where the mean depth was 1.0 m, and south of the point along a transect where the mean depth varied from 0.2 to 1.4 m.

Eelgrass is distributed over a large area of the lagoon, forming vast meadows of varying shoot density. Sampling was restricted to areas within the meadow comprising relatively homogeneous beds; disturbed areas and bare patches were avoided.

Samples of eelgrass leaf material were collected within a 6.25 cm² area; for rhizome and root material, a 16-cm diameter core sampler was used. Shoot density was estimated by counting the number of shoots in leaf samples and by in situ counts in the experimental areas. Plant biomass samples were washed free of sediments in the field and dried at 90 °C for 24 h. The weight ratios of carbon and nitrogen in eelgrass plants were measured on dry plant samples using a Perkin Elmer CHN analyzer.

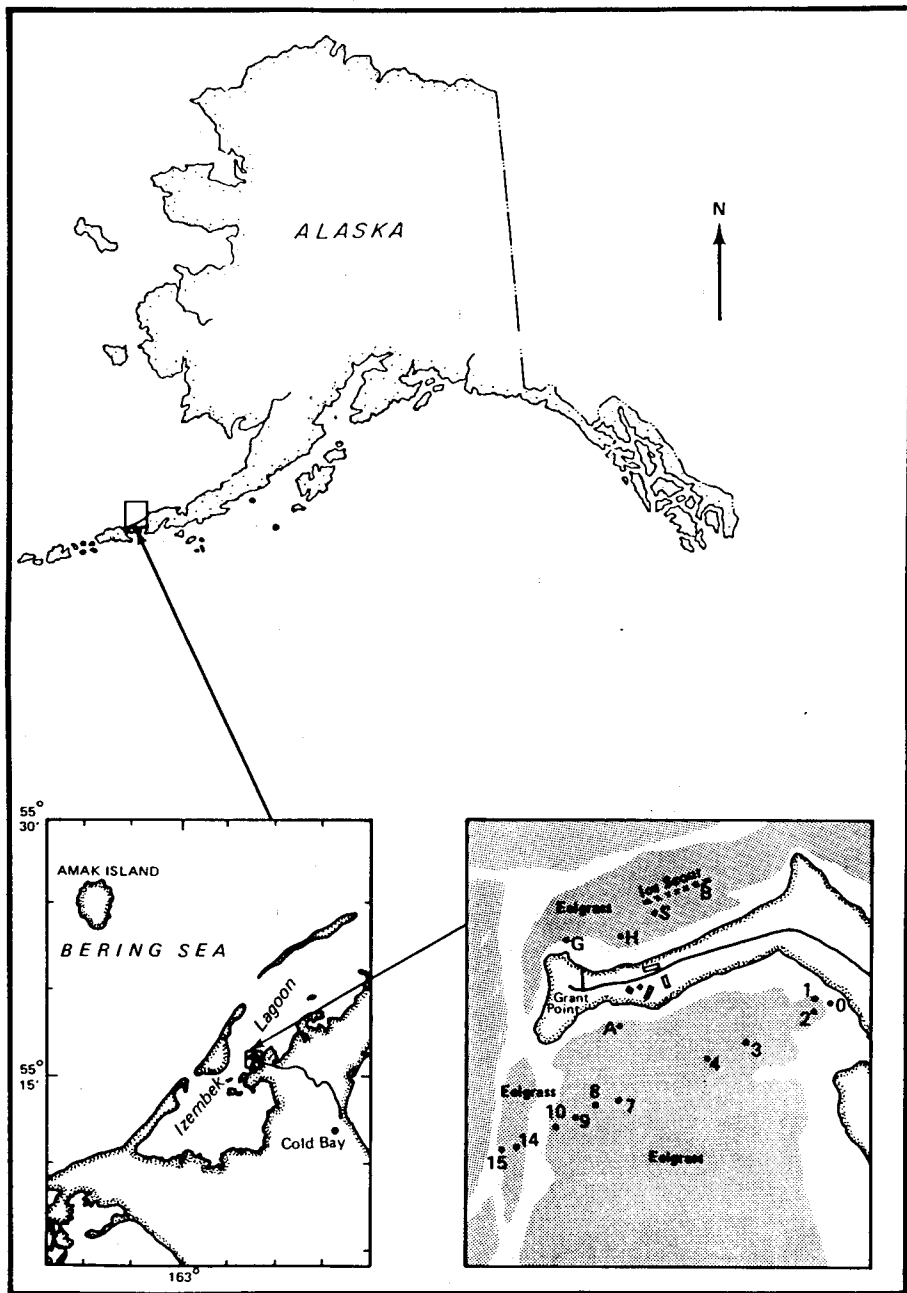


Fig. 1. Map of Alaska showing locations of Izembek Lagoon and Grant Point: the area of continuous eelgrass meadow (shading), an ice scour area, and the sampling stations are shown.

Interstitial nutrient profiles were determined from replicate 4.7 cm diameter cores. Core depths of 15 cm included 89% of the eelgrass root system (McRoy, unpubl.); cores to a depth of 20 cm were collected at times to obtain extended profiles. The core samples were sliced into 5-cm sections directly into a sediment squeezer (Reeburgh, 1967) and the interstitial water was filtered through a glass fiber filter into a sealed Vacutainer. Samples for ammonium analysis were diluted and analyzed colorimetrically (Koroleff, 1976). Estimates of the interstitial ammonium pool were determined from the product of concentration, moisture, and density for each sediment section and the integration of this measured quantity of ammonium to a depth of 15 cm. This calculation provided an estimate of the total amount of dissolved ammonium available to the plants per unit area of bottom. Phosphate concentrations were also measured in the interstitial water samples (Strickland & Parsons, 1972). The fraction referred to as organic matter in the squeezed sediment core samples was calculated by dividing the total dry weight into the ash-free dry weight after combusting the samples for 24 h at 500 °C.

PERTURBATION EXPERIMENTS

Colonization studies were designed to investigate the response of the interstitial ammonium pool to the invasion and growth of eelgrass in unvegetated marine substratum. An area of unvegetated substratum (≈ 1 m wide and 30 m long), created by ice gouging during the severe winter of 1974–75, was monitored each summer for 3 ice-free yr starting in 1976. This scour probably resulted from the folding of an ice sheet which then gouged the lagoon bottom, scraping off the upper 3–5 cm layer of sediment. The gouging completely disrupted the eelgrass bed by removing all the leaves and rhizomes and thus made a large area of substratum available for eelgrass colonization by both vegetative growth from adjacent beds and by seed germination. Three 0.25-m² areas of the ice scour were marked off with cylindrical steel collars extending from the surface to 20 cm into the sediment, providing a permanent area for sampling. This did not disrupt the vegetative expansion since the eelgrass rhizomes grew up and over the edge of the collars. The effect of sediment type on colonization was examined by establishing collars (0.25 m²), containing beach sand and organic-rich terrestrial soil (land-fill material), within the scour area.

In the leaf removal experiment all the eelgrass shoots were clipped at the sediment surface leaving the root and rhizome undisturbed in a 0.25 m² portion of an eelgrass bed. The sediment isolation experiment consisted of an equal area of substratum within this eelgrass bed that was clipped free of shoots and then sealed with a steel barrel lid, leaving the roots and rhizomes in the sediment. In both cases a control plot within the same eelgrass bed was marked for sampling so that the extent of change in nutrient pools could be measured.

RESULTS

Interstitial dissolved ammonium profiles in undisturbed eelgrass beds were characterized by low concentrations of ammonium in the upper 10 to 15 cm zone (Fig. 2), the

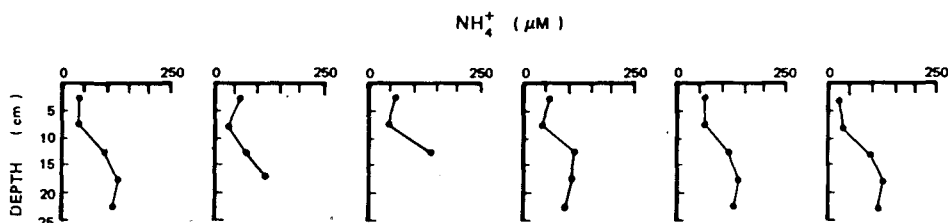


Fig. 2. Profiles of interstitial ammonium concentration vs. depth in the sediments at Station S, Izembek Lagoon: six replicate cores collected within 1 m² on 30 June, 1976.

depth in the sediments of maximum eelgrass root biomass. The average coefficient of variation for these initial ammonium profiles at Station S was 20% representing typical spatial variation at most stations. Seasonal and diurnal variations in the ammonium profiles were observed in relation to plant activity; however, they do not substantially affect these results.

COLONIZATION

The ice scour area was first colonized by a few plants during the second summer (1976) by both vegetative growth and seedlings. Seeds from the previous year had germinated by mid-June, but the vegetative invasion from the bordering eelgrass bed did not begin until July. Substantial revegetation was seen in 1977, the third summer after the ice scour; the area had recovered by the fourth summer (Figs. 3, 4). A change in the size of the interstitial ammonium pool was evident through the years in the three replicate areas of organic rich marine substratum (5.3% organic content; Fig. 4). Interstitial ammonium profiles from one of these ice scour areas show high concentrations in the second summer and reduced levels during subsequent years, coinciding with an increase in eelgrass shoot density (Fig. 3a).

Colonization was slower in the foreign substrata than in the natural marine sediment (Fig. 3). Seedling abundance for the second and third summers was low in the foreign substratum, with 110 seedlings · m⁻² in sand (0.9% organic content) and 54 seedlings · m⁻² in soil (5.8% organic content), compared to an average density in Izembek Lagoon of 400 seedlings · m⁻². The concentration of ammonium in these foreign substrata increased from the first through the third summers but decreased in the fourth summer when shoot densities increased sharply.

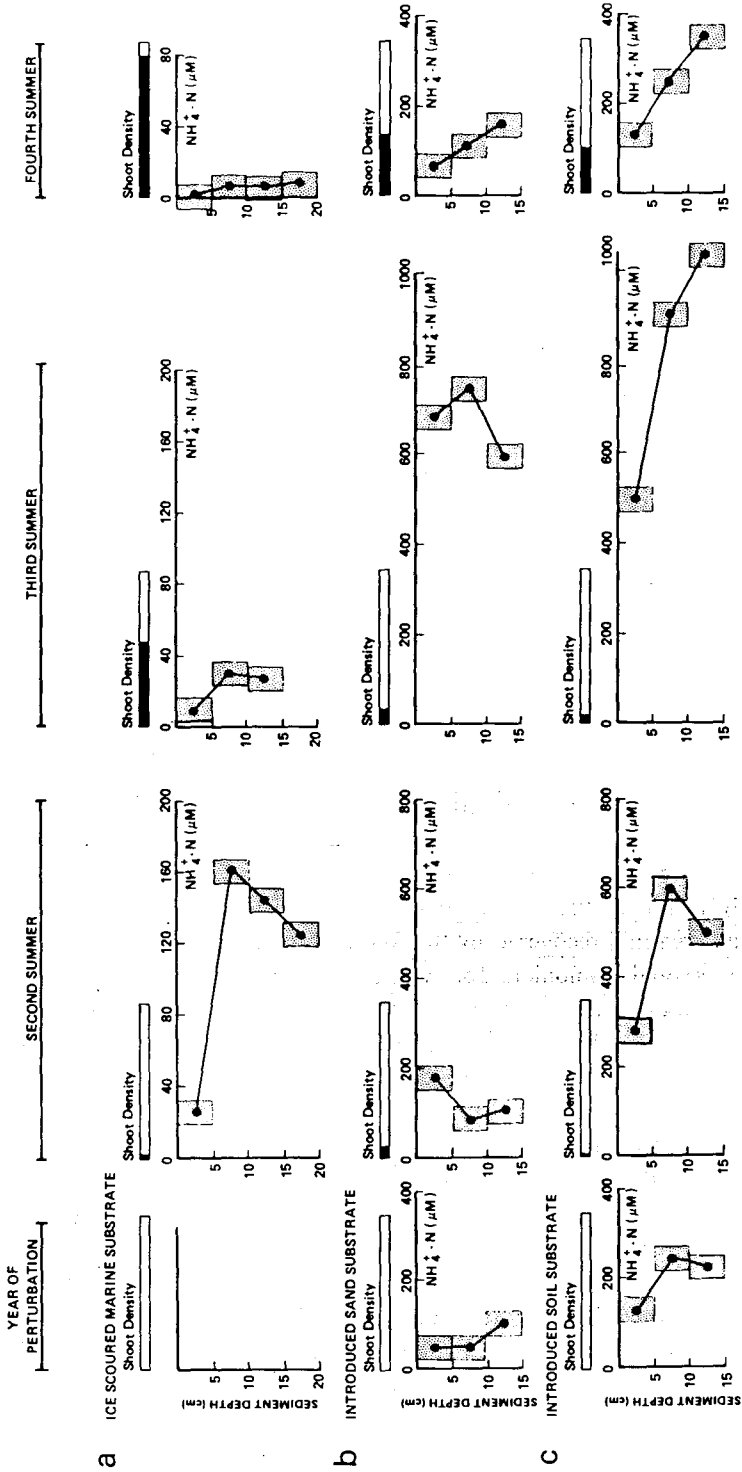


Fig. 3. Three colonization experiments showing interstitial ammonium profiles from single cores are presented with observed eelgrass shoot densities (open bar showing the maximum density of 5400 shoots · m⁻² for the bordering eelgrass bed); the shaded blocks indicate the sediment section that is represented by the plotted concentration; a, ice scour perturbation of high organic marine substratum; b, introduced substratum of low organic beach sand; c, introduced substratum of high organic non-marine soil.

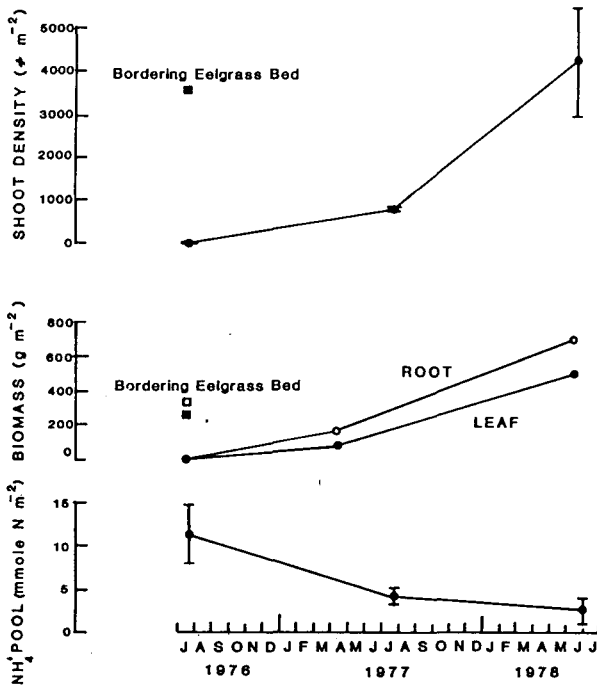


Fig. 4. Eelgrass colonization of ice scour area, mean and standard error for shoot density and the 0 to 15 cm integrated interstitial ammonium pool for the three replicate areas; also leaf and root biomass in the ice scour area and data for the bordering eelgrass beds are shown.

EAF REMOVAL AND SEDIMENT ISOLATION

The results of these experiments were expressed as the difference in ammonium concentrations (ΔNH_4^+) between the experimental sampling area and the control area (Figs. 5, 6). In July 1977, the removal plots and control at Station S (Table I) differed only slightly in interstitial ammonium concentrations (ΔNH_4^+) at the initial clipping (Day 0). Three days after leaf removal, ΔNH_4^+ had increased in the upper 5 cm, and on Day 9 ΔNH_4^+ had increased throughout the entire 15-cm section (Fig. 5a). However, eelgrass regrowth from the clipped stems was observed on Day 12 and by Day 16 the ammonium concentration in the experimental area was lower, resulting in negative values for ΔNH_4^+ . The eelgrass did not survive the winter in the experimental area and with no sign of regrowth 294 days after the leaf removal, ammonium concentrations greater than those of the control plot (ΔNH_4^+) were observed. The rate of accumulation of ammonium in the upper 15 cm of sediment between 3 and 9 days after plant removal was calculated to be $51 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$.

Ammonium regeneration and desorption were estimated from changes in concentration at Station S where the sediment surface was sealed to prevent vertical diffusion across the sediment-water interface. Throughout the same 16-day period ammonium

TABLE I

Environmental data for leaf removal experiments in Izembek Lagoon showing the interstitial nutrient concentrations for the control plots, organic content of the sediments and plant data.

Station		Interstitial concentration (μM)			<i>n</i>	Organic matter (%)	Shoot density (m^{-2})	Total biomass ($\text{g} \cdot \text{m}^{-2}$)
		$\bar{X}_{0-5 \text{ cm}} \pm \text{SE}$	$\bar{X}_{5-10 \text{ cm}} \pm \text{SE}$	$\bar{X}_{10-15 \text{ cm}} \pm \text{SE}$				
S	NH_4^+	137 ± 38	118 ± 40	68 ± 20	10	5.0	3552	600
9	NH_4^+	45 ± 21	132 ± 67	147 ± 70	4	6.6	1570	1090
	PO_4^{3-}	28 ± 15	21 ± 18	8 ± 4	4			
4	NH_4^+	27 ± 9	32 ± 13	20 ± 12	4	3.1	9308	1770
	PO_4^{3-}	7 ± 1	4 ± 4	4 ± 4	4			

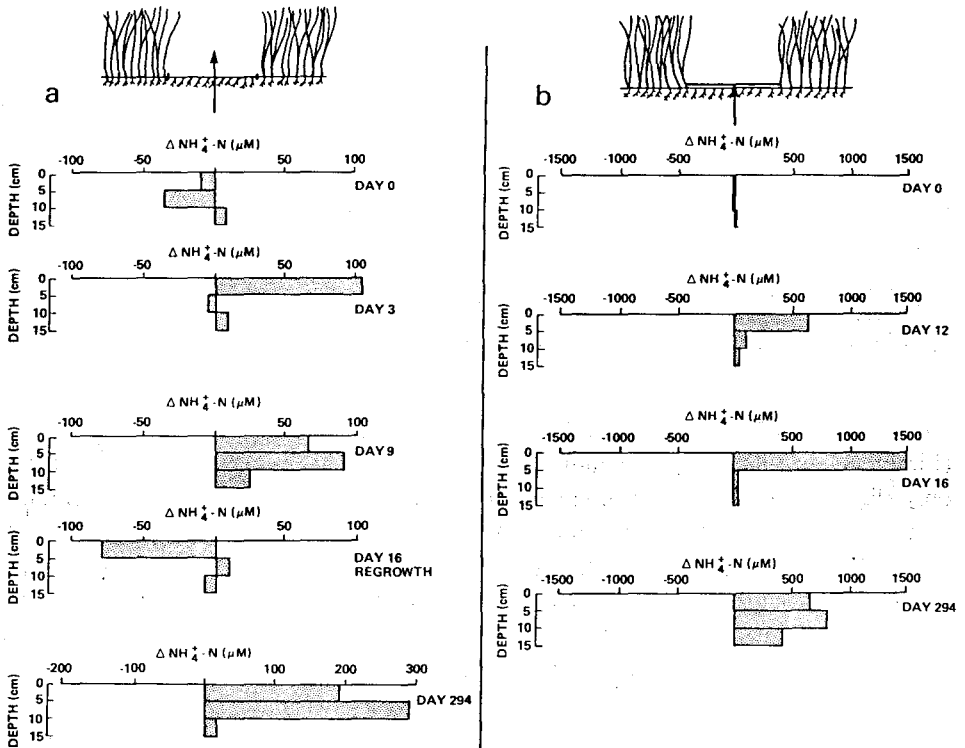
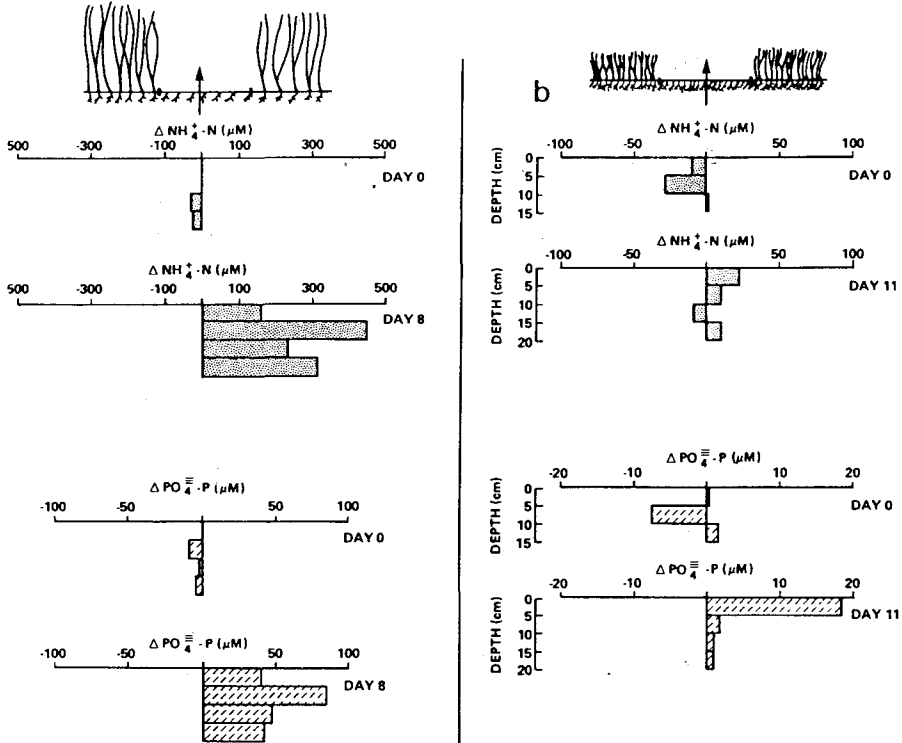


Fig. 5. Leaf removal and sediment isolation experiments: ammonium profiles vs. depth plotted as the difference between the experimental conditions and a control (ΔNH_4^+); Day 0 indicates the natural variation between experimental area and control; experiment at Station S Izembek Lagoon initiated 21 July, 1977; a, leaf removal experiment allowing flux from the sediment; regrowth of eelgrass was observed on Day 16 but the following summer, Day 294, no eelgrass was evident; b, sediment isolation experiment sealing the sediment surface preventing nutrient flux.

entrations were much higher (Fig. 5b) than in the leaf removal experiment. During following summer, the surface remained sealed, and elevated concentrations were uniformly distributed over the upper 15 cm (Fig. 5b). The calculated ammonium use in this 15-cm zone for the period from Day 3 to Day 12 was $139 \mu\text{mol m}^{-2} \cdot \text{h}^{-1}$. Ammonium diffusion was calculated by difference between the sealed bed experiments and the leaf removal experiments, indicating a diffusion rate of $\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$.



Leaf removal experiment allowing flux from the sediments: ammonium (ΔNH_4^+) and phosphate (ΔPO_4^{3-}) profiles plotted as the experimental conditions minus a control; Day 0 indicates natural variation in experimental area and control; initiated 4 June, 1978 in Izembek Lagoon; a, high organic sediment and low eelgrass shoot density, Station 9; b, low organic sediment and high eelgrass shoot density, Station 4.

Similar experiments were conducted in June 1978 to examine changes of both ammonium and phosphate in sediments of two different eelgrass beds (Stations 9 and 4, sites I and II). Substantial increases in ammonium and phosphate concentrations were evident 8 days after leaf removal in the eelgrass bed having higher organic sediment (a). Little evidence of ammonium buildup was observed in the lower organic sediments at Station 4 even after 11 days; however a significant increase in phosphate was seen in the upper 5 cm of sediment (Fig. 6b).

DISCUSSION

The dissolved ammonium pool in these sediments is an important interactive part of an eelgrass bed, as interstitial nutrients are directly available to the plants through the root/rhizome system. Nitrate and nitrite are minor components of available nitrogen resources (Iizumi *et al.*, 1980) and nitrogen fixation measured in these eelgrass beds is insignificant compared to ammonium production from decomposition (McRoy, unpubl.). Losses of ammonium from the interstitial pool are replaced by desorption from the sediments and microbial regeneration, but can these processes meet the demand for ammonium by eelgrass roots?

The revegetation experiment showed that eelgrass modified the size of the dissolved interstitial ammonium pool (Fig. 3). As eelgrass colonized the disturbed area, the ammonium pool size decreased and eelgrass shoot density and biomass increased (Fig. 4). Additional evidence for the effect of plant density on the ammonium pool size is provided by the leaf removal experiments in which ammonium concentrations increased in the interstitial water only 3 days after the shoots were clipped (Fig. 5).

COLONIZATION

Depletion of ammonium concentrations with increased shoot density and biomass in colonization experiments supplies evidence of the interaction between eelgrass and sediment nitrogen resources. The return of eelgrass to its former density was complete only 4 yr after a major natural perturbation had destroyed a portion of the eelgrass bed.

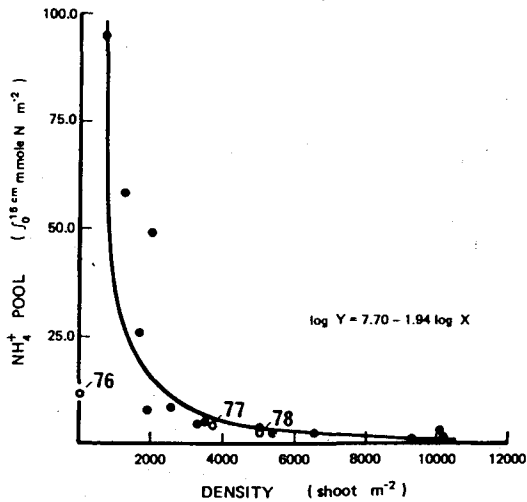


Fig. 7. Shoot density vs. integrated interstitial ammonium (replotted from Short, in press): undisturbed eelgrass beds (●) and the colonization samples (○) in an ice scour from 1976, 1977, and 1978, indicating increasing density; logarithmic transformation of density and ammonium indicating a correlation coefficient of 0.94 and the calculated regression line and equation.

Rapid regrowth was facilitated by available seed stock and the actively growing dense eelgrass bed bordering the disturbed area (Fig. 4). In the second summer after the ice scour, there was little regrowth, and the interstitial ammonium concentrations were much higher than in the surrounding eelgrass bed (Fig. 3). By the third summer, the smaller ammonium pool and increased shoot density of this eelgrass bed were similar to those of beds characterized by a density-ammonium relationship (Short, in press; Fig. 7). During the fourth summer, the ammonium pool had further decreased and shoot density was as high as surrounding eelgrass beds. The colonization study of this eelgrass bed confirms the correlation between shoot density and the ammonium pool (Short, in press), and illustrates the effect of eelgrass on interstitial ammonium concentrations.

Eelgrass colonization of both introduced foreign substrata was slower than in the area of natural marine sediment. However, there was little difference in colonization rate between the organic-poor sand substratum and the organic-rich soil substratum (Figs. 3b and c). Interstitial ammonium profiles in the sediments decreased after substantial eelgrass density was established, but the ammonium concentrations were still much higher than in the marine substratum. Similarity between the high ammonium concentrations in the sand substratum and the soil substratum was unexpected, due to the difference in particulate organic matter. The reasons for slow colonization by eelgrass in these introduced substrata and the high ammonium concentrations in the sediments remain unresolved.

AMMONIUM FLUX

The genesis of ammonium in the interstitial water was assumed to result primarily from the decomposition of organic matter. In sediments associated with eelgrass, ammonium replenishment in the interstitial water was balanced primarily by removal through uptake by the roots and diffusion into the overlying water. The regeneration and desorption of ammonium in these sediments and the flux of ammonium from the sediments were measured to estimate cycling through the interstitial pool. The experiments involving leaf removal provided time course measurements of interstitial ammonium, from which rates of ammonium removal by roots were calculated (Fig. 5a). This rough calculation does not allow for the increase in diffusion and absorption with increased concentration, which would underestimate uptake, or include increased ammonium regeneration from decomposing eelgrass roots, which would result in elevated uptake rates. The sediment isolation experiment was used to calculate an ammonium regeneration rate in the upper 15 cm of sediment and the diffusive flux of ammonium through the interstitial pool (Fig. 6b). The estimated ammonium regeneration rate of $139 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ is low compared to estimates for net ammonium reduction in similar eelgrass beds at Izembek Lagoon of $950\text{--}1520 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Iizumi *et al.*, 1982) but comparable to rates for non-seagrass sediments of $180\text{--}230 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Blackburn, 1979). The rate of ammonium removal by the plants, $51 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, in late July was less than the total regenerated ammonium, giving, by

difference, an estimate of diffusion of $88 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$. This is a valuable estimate for eelgrass sediments since it is difficult to calculate the diffusive flux from inverted ammonium profiles (Fig. 2). This ammonium diffusion rate is within the range of that measured in non-seagrass marine sediments of -4 to $276 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Hale, 1976) and up to $400 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ (Nixon *et al.*, 1976).

Both ammonium and phosphate removal during the next summer's maximum growth period were examined in clipping experiments to determine if the results were repeatable and to assess nutrient uptake by roots of actively growing plants (Fig. 6). The calculated ammonium and phosphate uptake by roots was greater in these highly organic substrata than in the sandy organic-poor substratum. The highest calculated uptake rate by roots (greatest accumulation in the sediments) was measured in mid-summer at Station 9 in sediments with greatest organic matter (Table 1). Ammonium uptake by eelgrass roots was estimated to be $450 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, and phosphate uptake was estimated to be $30 \mu\text{mol P} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ for this 8-day leaf-removal experiment. The N:P atomic ratio for uptake was 15:1 compared to a plant composition ratio of 23:1 (McRoy, 1970), indicating that the nitrogen requirement could be satisfied if phosphate were taken up from the sediments in excess. Surplus phosphate uptake by roots and leakage from leaves into surrounding water was previously demonstrated by McRoy & Barsdate (1970). The uptake rates estimated for organic-poor substratum (3.1% organic matter) were $3.0 \mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ for ammonium and $2.5 \mu\text{mol P} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$ for phosphate at Station 4 (Table II). The N:P ratio for uptake in these organic-poor sediments was 1.2:1, and the low nutrient concentrations indicate the lack of ammonium in the interstitial water and insufficient nitrogen available for plant growth.

TABLE II

Nitrogen uptake rates calculated from the leaf removal experiment at two stations in Izembek Lagoon during June 1978 (Fig. 6) presenting the eelgrass carbon to nitrogen ratio, calculated eelgrass requirement and ammonium uptake rates by eelgrass roots calculated from the buildup of nitrogen and phosphate in the sediments.

Station	C/N	Eelgrass requirement ^a		Root uptake		Additional uptake requirement (% of total)
		NH_4^+ ^b	N:P	NH_4^+ ^b	N:P	
9	21.8	1290	23:1	450	15:1	65
4	25.5	1793	23:1	3	1.2:1	99.8

^a Based on average production of $0.31 \text{ mg C} \cdot \text{g}(\text{dry})^{-1} \cdot \text{h}^{-1}$ and plant data in Table I.

^b $\mu\text{mol N} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$.

The extent of ammonium change (ΔNH_4^+) in the three stations examined was associated directly with the organic content of the sediments and so presumably with the rate of nutrient regeneration. Thus the ability of organic-rich sediments to replenish the nutrients depleted by uptake may be sufficient to satisfy plant requirements.

However, in the organic-poor sediments, it appears that regeneration is inadequate to supply the nitrogen required by eelgrass. Therefore these experimental manipulations suggest that nitrogen resources are limiting in some eelgrass beds.

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REFERENCES

- BLACKBURN, T. H., 1979. Method for measuring rates of NH_4^+ turnover in anoxic marine sediments, using a $^{15}\text{N-NH}_4^+$ dilution technique. *Appl. Environ. Microbiol.*, Vol. 37, pp. 760-765.
- CARIGNAN, R. & J. KALFF, 1980. Phosphorus sources for aquatic weeds: water or sediment? *Science*, Vol. 207, pp. 987-989.
- DEN HARTOG, C., 1970. *The seagrasses of the world*. North-Holland, Amsterdam, 275 pp.
- HALE, S. S., 1976. The role of benthic communities in the nitrogen and phosphorus cycles of an estuary. ERDA Symposium Series 1975, edited by F.G. Howell, J.B. Gentry & M.H. Smith (CONF-740513), pp. 291-308.
- HARLIN, M. M. & B. THORNE-MILLER, 1981. Nutrient enrichment of seagrass beds in Rhode Island coastal lagoon. *Mar. Biol.*, Vol. 65, pp. 221-229.
- IZUMI, H. & A. HATTORI, 1982. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. *Aquat. Bot.*, Vol. 12, pp. 245-256.
- IZUMI, H., A. HATTORI & C. P. MCROY, 1980. Nitrate and nitrite in interstitial waters of eelgrass beds in relation to the rhizosphere. *J. Exp. Mar. Biol. Ecol.*, Vol. 47, pp. 191-201.
- IZUMI, H., A. HATTORI & C. P. MCROY, 1982. Ammonium regeneration and assimilation in eelgrass (*Zostera marina*) beds. *Mar. Biol.*, Vol. 66, pp. 59-65.
- KENWORTHY, J. S., J. C. ZIEMAN & G. THAYER, 1982. Evidence for the influence of seagrass on the benthic nitrogen cycle on a coastal plain estuary near Beaufort, North Carolina. *Oecologia (Berlin)*, Vol. 54, pp. 152-158.
- KOROLEFF, F., 1976. Determination of NH_4^+ -N. In, *Methods of seawater analysis*, edited by K. Grasshoff, Verlag Chemie, Weinheim, pp. 127-133.
- MCROY, C. P., 1970. On the biology of eelgrass in Alaska. Ph.D. thesis, University of Alaska, Fairbanks, 138 pp.
- MCROY, C. P. & R. J. BARSDATE, 1970. Phosphate absorption in eelgrass. *Limnol. Oceanogr.*, Vol. 15, pp. 6-13.
- MCROY, C. P. & J. J. GOERING, 1974. Nutrient transfer between the seagrass *Zostera marina* and its epiphytes. *Nature (London)*, Vol. 228, pp. 173-174.
- MCROY, C. P. & C. HELFFERICH, 1977. *Seagrass ecosystems: a scientific perspective*, M. Dekker Inc., New York, 314 pp.

- NIXON, S.W., C.A. OVIATT & S.S. HALE, 1976. Nitrogen regeneration and the metabolism of coastal marine bottom communities. In, *The role of terrestrial and aquatic organisms in decomposition processes*, edited by J.M. Anderson & A. MacFayden, Blackwell Scientific Publ., Oxford, pp. 269–283.
- ORTH, R.J., 1977. Effect of nutrient enrichment on growth of eelgrass in the Chesapeake Bay, Virginia, U.S.A. *Mar. Biol.*, Vol. 44, pp. 187–194.
- PENHALE, P.A. & G.W. THAYER, 1980. Uptake and transfer of carbon and phosphorus by eelgrass (*Zostera marina* L.) and its epiphytes. *J. Exp. Mar. Biol. Ecol.*, Vol. 42, pp. 113–123.
- PHILIP, G., 1936. An enalid plant association in the Humber Estuary. *J. Ecol.*, Vol. 26, pp. 205–219.
- PHILLIPS, R.C. & C.P. MCROY, 1980. *Handbook of seagrass biology; an ecosystem perspective*. Garland STPM Press, N.Y., 353 pp.
- RAYMONT, J.E.G., 1947. A fish farming experiment in Scottish Sea lochs. *J. Mar. Res.*, Vol. 6, pp. 219–227.
- REEBURGH, W.S., 1967. An improved interstitial water sampler. *Limnol. Oceanogr.*, Vol. 12, pp. 163–165.
- ROSENFELD, J.K., 1979. Ammonium adsorption in nearshore anoxic sediments. *Limnol. Oceanogr.*, Vol. 24, pp. 356–364.
- SHORT, F.T., 1981. Nitrogen resource analysis and modelling of an eelgrass (*Zostera marina* L.) meadow in Izembek Lagoon, Alaska. Ph.D. thesis, University of Alaska, Fairbanks, 173 pp.
- SHORT, F.T., in press. The seagrass, *Zostera marina* L.: plant morphology and bed structure in relation to sediment ammonium in Izembek Lagoon, Alaska. *Aquat. Bot.*
- STRICKLAND, J.D. & T.R. PARSONS, 1972. A practical handbook of seawater analysis, *Bull. Fish. Res. Board Can.*, No. 167, 310 pp.
- TOETZ, D.W., 1974. Uptake and translocation of ammonium by freshwater hydrophytes. *Ecology*, Vol. 55, pp. 199–201.