

## Muskrat (*Ondatra zibethicus*) Disturbance to Vegetation and Potential Net Nitrogen Mineralization and Nitrification Rates in a Freshwater Tidal Marsh

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**ABSTRACT.**—The muskrat (*Ondatra zibethicus*) is a wetland mammal whose disturbance activities include grazing, burrowing and lodge construction. We evaluated the effects of these disturbances on plant biomass, species richness and diversity, stem density and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh on the Hudson River in New York. We hypothesized that muskrats increase floristic richness and diversity by decreasing the biomass of narrowleaf cattail (*Typha angustifolia*) and that muskrats increase potential net nitrogen mineralization and nitrification rates through aeration and reduced plant uptake because of herbivory. Because muskrats commonly build lodges on or close to creek banks, we separated the disturbance effects of muskrats from the disturbance effects of the creek bank by sampling quadrats along transects placed perpendicular to creek banks at lodge sites. Muskrats decreased biomass, particularly of cattail, but had no measurable effect on stem count, species richness or species diversity. Muskrats increased potential net nitrogen mineralization and nitrification rates; however, this effect was limited to active sites. Creek bank disturbance increased stem count but had no effect on the other variables. Although muskrats did not significantly affect floristic diversity in this study, their disturbance activities did influence soil nitrogen dynamics, which is an important component of wetland function.

### INTRODUCTION

Disturbance influences all levels of ecological organization (Connell, 1978; Pickett and White, 1985; Reice *et al.*, 1990). Burrowing animals, as agents of disturbance, can profoundly affect their environment, principally through increases in soil aeration and water infiltration, and by altering development of plant and animal communities (Meadows and Meadows, 1991; Hansell, 1993; Butler, 1995; Johnston, 1995). Much research has been conducted on the impact of invertebrate burrows in marine and terrestrial ecosystems (Pickett and White, 1985; Meadows and Meadows, 1991) and mammal burrows in terrestrial ecosystems (Huntly and Inouye, 1988; Swihart, 1991; Swihart and Picone, 1991; English and Bowers, 1994), but little study of mammal burrows in wetland ecosystems has been conducted. The muskrat (*Ondatra zibethicus*) is a common wetland mammal that influences soil, plant and animal communities through grazing, burrowing and lodge construction, and possibly increases the diversity of its habitat (Danell, 1977; Kangas, 1985; Berg and Kangas, 1989; Nyman *et al.*, 1993). We expected narrowleaf cattail (*Typha angustifolia*) marsh ecosystems

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to be influenced by the muskrat at many levels, but this has been quantified only in a limited manner. Thus, understanding ecological dynamics in freshwater wetlands may require quantifying the role of the muskrat. In this study we examined the effects of muskrat disturbance on soil and vegetation in a freshwater tidal marsh on the Hudson River at Tivoli, New York.

Muskrat lodges are conical or irregular mounds of plant material 0.3–1.2 m above water and 1–2 m in diameter with internal chambers used for shelter from weather, flooding and predators (Alexander, 1956). Burrows are tunnels 13–15 cm in diameter and up to 13 m long that have underwater entrances (Rezendes, 1992). Burrows below the water table often provide access to lodges whereas burrows above the water table serve as a substitute for lodges. Runways are trails of trampled vegetation and soil, and canals are underwater trails created for efficient swimming. Feeding platforms are small piles of plant material on which muskrats eat, groom and sleep in the open. Push-ups are structures intermediate between feeding platforms and lodges and serve as covered feeding stations in winter. Young are reared in lodges and bank burrows as well as in open nests. In freshwater tidal marshes muskrats typically build all the structures described (Smith, 1938).

Tidal marshes, including freshwater tidal marshes such as Tivoli North Bay, have a characteristic plant zonation pattern along the creek bank (Odum *et al.*, 1978; Mitsch and Gosselink, 1993). This zonation pattern is a result of many environmental influences including substrate elevation and duration of tidal inundation, shade, soil chemistry and ice scouring. A collection of environmental influences causing a gradual spatial change in vegetation can be considered an *environmental gradient* (Gauch, 1982). In tidal marshes one key environmental gradient is the lateral gradient of vegetational diversity with respect to distance from the tidal creek, the creek-bank effect (Fig. 1a).

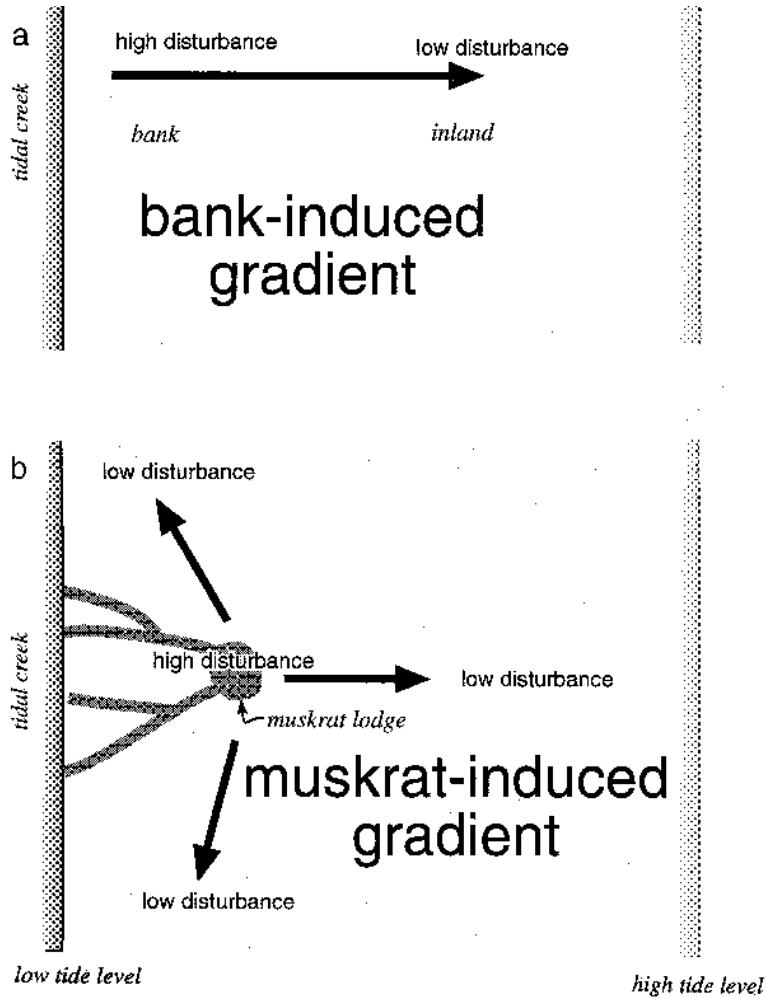
In contrast to the creek-bank effect, a muskrat lodge is potentially a point disturbance that may produce a radial gradient of biotic diversity around the lodge location (Fig. 1b). Because muskrats typically build lodges near banks, this point disturbance is commonly superimposed on the edge disturbance of the creek-bank effect. To quantify any disturbance gradient of the muskrat it is necessary to distinguish effects of muskrats from the environmental gradient of the creek bank.

We quantified the effects of muskrat disturbance on the marsh ecosystem by measuring plant species richness, plant species diversity, aboveground total biomass, stem density and potential net nitrogen mineralization and nitrification rates of soil. These measurements encompass interactions spanning three trophic levels (herbivore, vegetation and nutrient remineralizers) and are of value because most studies generally address interactions within one trophic level. Narrowleaf cattail is the dominant species in this marsh and is favored by muskrats for food and lodge building. Therefore, we expected muskrats to decrease *Typha* biomass and, hence, total biomass. Consequently, we hypothesized that muskrat activities increase vegetational species richness and diversity due to the decrease in the dominant species. We also hypothesized that muskrats increase potential net nitrogen mineralization rates by (1) increasing aeration of the soil, which increases microbial activity and (2) reducing plant uptake of nitrogen through herbivory. With increased microbial activity and reduced plant uptake of nitrogen there would be more ammonium available in the soil for transformation to nitrite. Therefore, we further hypothesized that muskrat activity also increases nitrification rates, as there would be more nitrite available for the transformation of nitrite to nitrate.

#### METHODS

Tivoli North Bay, a component of the Hudson River National Estuarine Research Reserve, is a ca. 150-ha freshwater tidal marsh on the east bank of the Hudson River in New York

FIG. 1.—Diagrammatic representations of: a. Environmental gradient due to the edge disturbance of a tidal creek in a freshwater tidal marsh and b. Disturbance gradient due to muskrat activities along the bank of a freshwater tidal marsh. The marsh is completely covered at high tide

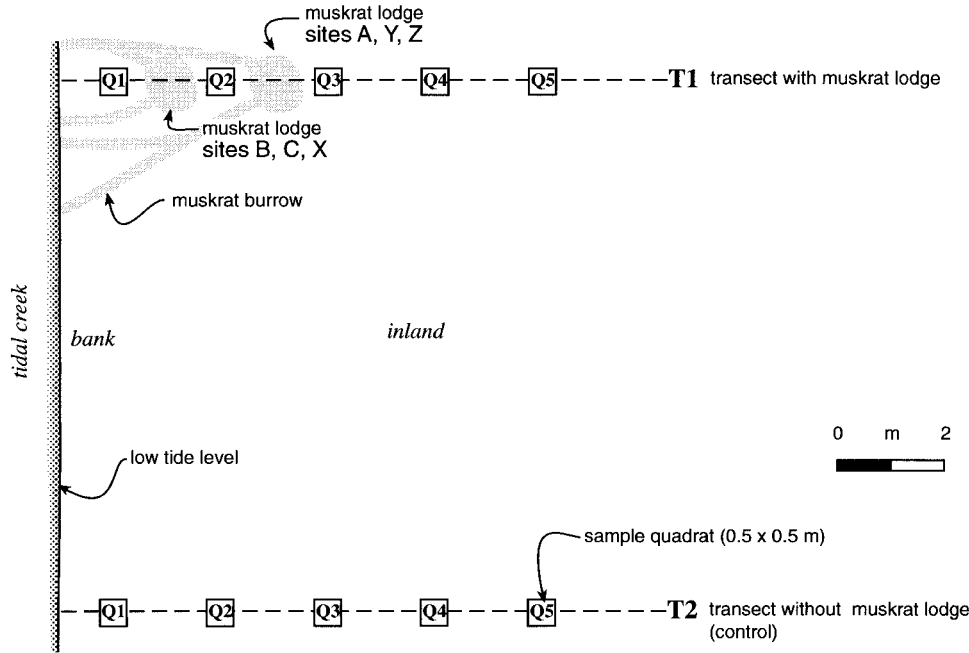


State ( $73^{\circ}55'30''\text{W}$ ,  $42^{\circ}2'55''\text{N}$  to  $73^{\circ}55'0''\text{W}$ ,  $42^{\circ}2'30''\text{N}$ ). Two alternating low and high tides occur every 25 h. Water levels fluctuate approximately 1.2 m vertically, with water covering the entire marsh at high tide (E. Kiviat, pers. obs.).

In Tivoli North Bay muskrats build lodges and feeding stations primarily from narrowleaf cattail, usually in stands of cattail or cattail mixed with other plants. Lodges are built or rebuilt in late summer or fall and often destroyed in Feb. or Mar. by floods (E. Kiviat, pers. obs.). Consequently, lodges typically last only 6–18 mo. All lodges sampled were located on creek banks, not in the creek itself, and were inundated at high tide. At low tide lodges are completely drained.

We sampled three active (A, B, C) and three abandoned (X, Y, Z) muskrat lodge sites

FIG. 2.—Two sampling designs were used so that the bank effect and muskrat effect could be adequately represented. The sampling design was fixed with respect to distance from bank (at low tide level). Lodges near the creek bank (B, C, X) lie between quadrats 1 and 2, whereas lodges farther from the bank (A, Y, Z) lie between quadrats 2 and 3. Control=reference in text



along creek banks in the fall of 1994. Active lodges were built the previous fall and were approximately 10–12 mo old. Abandoned lodge sites had a flattened mound of detritus from the lodge. These lodges were probably 12–18 mo old. Similar areas of apparently older muskrat activity existed, but it became difficult to verify that the area was a lodge without knowing its history, thus areas such as these were not included in the study.

We sampled two transects at each site (Fig. 2). Sample units were five  $0.5 \times 0.5$  m square quadrats (de la Cruz, 1978) spaced 2 m apart on-center along the transects. Transect one (T1) intersected the lodge perpendicular to the creek bank and represented muskrat disturbance combined with the creek-bank effect. We placed quadrats on both sides of the lodge, each 1 m from lodge center along the transect. Lodges varied slightly in distance from the bank. Lodges close to the bank had one quadrat between the lodge and creek and four quadrats extending from the lodge into the intercreek marsh. Lodges inland from the bank had two quadrats between the lodge and the creek and three quadrats extending from the lodge into the intercreek marsh.

Transect two (T2) was placed parallel to, and 8 m from, transect one and represented a reference with respect to muskrat disturbance, sampling only the bank effect (Fig. 2). Observations of muskrat activity (scat, tracks and cuttings), along with preliminary sampling of two lodges, showed current muskrat activity limited to a zone within 4 to 6 m of the lodge. Placement of the reference transect to the right or left of the lodge transect was randomized when possible. Three sites with lodges close to the junction of two tidal creeks

did not have space for a randomly placed reference transect. In these cases we placed the reference transect away from the channel junction.

Vegetation was sampled from 29 Aug. through 26 Sept. 1994. In each quadrat we identified plants, counted stems and clipped them at ground level. Samples were dried at 93 C to constant weight and weighed to the nearest 0.1 g by species. Plants are senescing in Sept., but we found no correlation between sampling date and biomass.

Soil samples (15 cm deep and 15 cm across) were taken 27 and 28 Sept. 1994 from the edge of each quadrat and stored in sealed plastic bags at room temperature. Within 2 d of collection percent moisture and potential net nitrogen mineralization and nitrification rates were quantified as the amounts of ammonium-nitrogen plus nitrate-nitrogen ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ , respectively) and nitrate alone, produced during a 10 d incubation at 25 C and ambient moisture content (Duncan and Groffman, 1994). Ammonium and nitrate were measured with an AlpKem TFS 300 rapid flow analyzer.

We performed a separate three-way factorial analysis of variance (ANOVA), setting  $\alpha = 0.0071$  (see discussion of multiplicity below), and examined all two-way interactions for each of seven dependent variables: stem count, species richness, species diversity, total plant biomass, *Typha* biomass and potential net nitrogen mineralization and nitrification. Species diversity was evaluated by computing a Shannon index of diversity based on stem count for each quadrat along each transect. The independent variables were quadrat (distance from the bank), transect (lodge or reference) and age of lodge (active or abandoned). We treated all independent variables as discrete fixed variables (Bennington and Thayne, 1994). Any statistically significant difference among quadrats should represent the bank-imposed gradient, whereas any difference among transects should represent muskrat activity. The seven ANOVAs present a potential multiplicity effect. To control this Type I error we used the Bonferroni correction (Samuels, 1989) and therefore adjusted  $\alpha$  to  $\alpha = 0.05/7 = 0.0071$ . We analyzed all data using Data Desk (Velleman, 1988).

All data except the Shannon diversity index violated the ANOVA assumption of normality. Stem count and species richness were transformed to  $\log_e(x + 1)$  before analysis, and total plant biomass, *Typha* biomass and potential net nitrogen mineralization and nitrification were transformed to square root  $(x + 0.5)$  to reduce deviations from normality.

We measured the height of water above ground surface at high tide (relative elevation) of each quadrat to determine any within-site variation in elevation between the muskrat and reference transects. With our ANOVA design, any difference among transects should represent muskrat activity. However, we could not attribute this difference to muskrats if elevations between transects were not equal. A paired *t*-test comparing each matched quadrat along the two transects showed no difference ( $P > 0.05$ ) in relative elevation between matched quadrats at each site. Therefore, differences between T1 and T2 at each site were not due to elevation. We also normalized the relative elevation measurements to a water depth sensor in Tivoli South Bay (Paul Barten, School of Forestry and Environmental Studies, Yale University, pers. comm.) to compare elevations among sites.

## RESULTS

Muskrat activity had a highly significant effect on total biomass ( $F = 13.24$ ,  $df = 1$ ,  $P = 0.0007$ ) and *Typha* biomass ( $F = 26.10$ ,  $df = 1$ ,  $P < 0.0001$ ), both being significantly lower in transects through muskrat lodges than in reference transects (Table 1). The effect of distance from the bank was not significant for total biomass, but there was a significant increase in *Typha* biomass with distance from the bank ( $F = 10.84$ ,  $df = 4$ ,  $P < 0.001$ ). Age of lodge was also a significant determinant of total biomass ( $F = 12.67$ ,  $df = 1$ ,  $P = 0.0009$ ) and *Typha* biomass ( $F = 15.95$ ,  $df = 1$ ,  $P = 0.0002$ ), with greater biomass in active sites

TABLE 1.—Summary of P-values from 3-way ANOVAs for each dependent variable. Significant values are in bold type ( $P < 0.0071$  with Bonferroni correction)

Independent variable	Log stem count	Log species richness	Square root biomass	Square root <i>Typha</i> biomass	Square root mineralization	Square root nitrification	Species diversity Shannon, H'
Transect	0.3204	0.0899	<b>0.0007</b>	$\leq$ <b>0.0001</b>	0.9686	0.6438	0.4721
Quadrat	<b>0.0010</b>	0.0118	0.0093	$\leq$ <b>0.0001</b>	0.9290	0.0130	0.0927
Age	0.8720	0.2747	<b>0.0009</b>	<b>0.0002</b>	<b>0.0001</b>	$\leq$ <b>0.0001</b>	0.2972
Trt*Qdr	0.3284	0.6411	0.3877	0.4371	0.7529	0.5558	0.4024
Trt*Age	0.2353	0.1191	0.9311	0.3389	0.1153	0.1654	0.0793
Qdr*Age	0.2565	<b>0.0046</b>	0.3134	0.3831	0.1042	0.3520	0.0117

(Table 1). For ease in interpreting the statistical results, please refer to Table 2 which gives means and standard errors of the raw data.

We identified 13 plant species in the sampling units using nomenclature from Gleason and Cronquist (1991): *Bidens* sp., *Echinochloa walteri* (Pursh) Heller, *Iris pseudacorus* L. or *I. versicolor* L., *Impatiens capensis* Meerb., *Leersia oryzoides* (L.) Swartz, *Lythrum salicaria* L., *Peltandra virginica* (L.) Schott & Endl., *Pilea pumila* (L.) A. Gray, *Polygonum punctatum* Elliott, *Sagittaria latifolia* Willd., *Scirpus fluviatilis* (Torr.) A. Gray, *Sparganium eurycarpum* Engelm. and *Typha angustifolia* L. The number of species per lodge site ranged from 5 to 10. There was no significant difference in the number of species between transects with muskrat activity and reference transects ( $F = 3.01$ ,  $df = 1$ ,  $P = 0.09$ ; Table 1). With the Bonferroni correction the effect of distance from the bank on species richness also was not significant ( $F = 3.65$ ,  $df = 4$ ,  $P = 0.01$ ), however there was a significant interaction between age of lodge and distance from the bank affecting species richness ( $F = 4.37$ ,  $df = 4$ ,  $P = 0.005$ ).

Neither muskrat activity nor bank effect had a significant effect on species diversity ( $H'$ ). The interaction between quadrat and age ( $F = 3.66$ ,  $df = 4$ ,  $P = 0.01$ ), while not significant

TABLE 2.—Raw data summary showing means-standard errors for each dependent variable. Each transect, quadrat and whether active or abandoned is shown separately for efficient comparison of the raw data

Independent variable	Species richness		Biomass (g)	Typha biomass (g)	Mineralization ( $\mu\text{g N g}^{-1} \text{d}^{-1}$ )	Nitrification ( $\mu\text{g N g}^{-1} \text{d}^{-1}$ )	Relative elevation (m)
	Stem count (per 0.25 m <sup>2</sup> )	richness (per 0.25 m <sup>2</sup> )					
Transect 1	39/41	3/1	123.9/141.4	65.2/100.0	9.42/6.09	0.45/0.56	0.31/0.12
Transect 2	39/43	4/2	201.1/116.1	149.0/124.4	10.05/9.45	0.55/0.86	0.31/0.17
Quadrat 1	89/69	5/1	110.7/60.8	40.4/48.2	10.74/12.37	0.84/1.10	0.22/0.05
Quadrat 2	28/19	3/1	149.8/179.0	63.5/98.8	8.91/6.09	0.72/0.66	0.33/0.16
Quadrat 3	20/16	3/1	108.1/113.9	74.0/109.4	10.89/0.47	0.47/0.47	0.34/0.17
Quadrat 4	32/19	3/2	239.4/168.2	196.9/170.6	8.66/5.92	0.14/0.22	0.33/0.15
Quadrat 5	27/11	3/1	204.5/68.0	160.9/59.1	9.50/7.25	0.33/0.73	0.33/0.16
Active sites	36/31	3/2	214.8/151.2	147.6/139.8	13.74/8.76	0.86/0.83	0.33/0.20
Abandoned	41/51	4/1	110.2/89.6	66.7/78.6	5.74/4.10	0.14/0.32	0.29/0.05

with the Bonferroni correction, suggests a gradient in diversity in either occupied or abandoned lodges, but not both.

Stem count was quite variable in Quadrat 1, but significantly higher than other quadrats ( $F = 5.58$ ,  $df = 4$ ,  $P = 0.001$ ). Muskrat activity did not affect stem count, as there was no difference between transects ( $F = 1.01$ ,  $df = 1$ ,  $P = 0.320$ ) or age ( $F = 0.03$ ,  $df = 1$ ,  $P = 0.872$ ).

There was no difference in potential net nitrogen mineralization or nitrification rates between muskrat and reference transects or among quadrats. However, potential net nitrogen mineralization and nitrification rates were significantly higher in soil at active than abandoned lodges (Table 1). Because both the transect factor (T1 vs. T2) and the age factor (current vs. former muskrat activity) represent contrasts between presence and absence of muskrats, but gave conflicting results, we explored whether the significant age effect may have been caused by differences in elevation between sites. However, differences in elevation did not cause the difference in mineralization and nitrification between the active and abandoned transects.

#### DISCUSSION

As we expected, muskrat activity reduced total plant biomass and *Typha* biomass. The reduction was seen in both active and abandoned sites and was greatest closest to the lodge. *Typha* is the dominant plant in this freshwater marsh, so we expected a reduction of its biomass to provide space for competitively inferior, or secondary, species thereby increasing total stem count and plant species richness and diversity. Muskrat effects on stem count and plant species richness and diversity, however, were not statistically significant. Muskrat reduction of cattail biomass was concentrated near the lodge (quadrats two and three). Muskrats feed on aboveground stalks and often pull the rhizomes out for food. This disturbance activity creates open spaces around the lodge, but there was no significant increase in species richness as a result of these open spaces. The environmental conditions around the lodge may not be as favorable to secondary species as the conditions on the bank despite decreased competition.

We observed a significant interaction between quadrat and age of site affecting species richness; yet, neither age (hence muskrat presence) nor distance from the bank separately affected species richness. There was no gradient of increasing or decreasing species richness along the quadrats when analyzing the total data set. However, when we separated the data set into active and abandoned sites the active sites had higher species richness at quadrats one, two and three, which are the quadrats closest to the bank and to the lodges on transect one. Therefore, in active sites, the muskrats did significantly increase species richness but this was only measurable in combination with the bank effect. Nyman *et al.* (1993) found that plant species richness and muskrat activity were positively correlated in a brackish Louisiana marsh.

Although muskrat effects on *Typha* biomass were seen in both active and abandoned sites, *Typha* biomass was higher overall in the active sites. If conditions at the sites disturbed by muskrats are not suitable for secondary species to colonize (as postulated above), it seems logical that *Typha* biomass should be higher in abandoned sites that are no longer being denuded by muskrats. The decaying detrital mat at the abandoned sites may inhibit regrowth for a time. For example, site Z was located along an interior inlet which had a low tidal flushing force compared to other areas in the marsh. This site also had the largest detrital mat and the lowest amount of regrowth in the disturbed area. Another possible contribution to decreased *Typha* growth in abandoned sites is that disturbance by cutting

cattail shoots decreases its productivity in the following growing season. Jordan and Whigham (1988) found that cutting or bending dead cattail shoots lowered aboveground production and flowering in the following growing season because cutting and bending resulted in lower oxygen concentrations in the rhizomes.

We found no significant results for muskrat or bank effect on species diversity ( $H'$ ). It should be noted, however, that without our conservative approach with the Bonferroni correction there would have been a significant interaction between quadrat and age of site, as explained above, for species richness. The interaction between quadrat and age for species diversity is interesting given the significant interaction between quadrat and age for species richness, and is worthy of further attention.

Although muskrats reduced the cattail biomass in Tivoli North Bay, we did not observe a concomitant increase in other plant species stem count, richness or diversity. Perhaps the density of muskrats, and hence muskrat disturbance, was not substantial enough to cause a shift from the dominant cattail due to the short time lodges exist in this tidal marsh. A follow-up study documenting revegetation of more lodge sites over a greater time period would determine the long-term biotic response to muskrat disturbance in a freshwater tidal marsh.

We expected muskrats to increase potential net nitrogen mineralization and nitrification, yet there was no difference between transect one (muskrat) and two (reference). However, age of lodges (which tested current versus old muskrat activity) significantly affected mineralization and nitrification rates suggesting muskrat impact. The two major differences between sites were elevation and age (presence or past presence of muskrats). We then considered whether elevation was confounding the age effect on soil mineralization and nitrification rates. For example, lower sites would be less aerobic and would have lower rates of potential net nitrogen mineralization and nitrification. Sites A, B and Z were located in secondary stream channels and were lower in elevation than C, X and Y. Therefore, we expected sites A, B and Z to have lower potential net nitrogen mineralization and nitrification rates. However, we found no correlation between elevation and potential net nitrogen mineralization and nitrification rates in these sites. The active sites (A, B, C) had the highest potential net nitrogen mineralization and nitrification rates. Scatterplots of mineralization vs. nitrification show a better correlation in active sites than in abandoned sites. This correlation was seen in both transect one and two, which was why there was no significant difference for the transect factor in the ANOVA.

Although we saw no visible sign of muskrat activity beyond 8 m, the lack of a significant difference in the transect factor suggests to us that transect two was inadequate as a reference for soil nitrogen mineralization and nitrification rates. Errington (1961) found muskrats foraged within 45 to 92 m of their lodge or burrow. We suspect that the muskrats in these Tivoli North Bay lodges were active beyond 8 m but that their activity was obscured by tidal action.

Several types of muskrat disturbance activities could increase the nitrogen mineralization and nitrification rates of soil such as reduced plant uptake due to herbivory, lodge decomposition, fecal accumulation and aeration of the soil. The first two activities listed are not likely to cause the significant effect seen with mineralization and nitrification rates because the effect is only seen in active lodge sites. For example, reduced plant uptake is unlikely because *Typha* biomass was higher in active lodge sites. We expected areas where *Typha* was denuded to have higher mineralization and nitrification rates because the nitrogen was not being taken up by the plants, but abandoned lodge sites had lower mineralization and nitrification rates. Likewise, lodge decomposition is not the source of the difference in mineralization and nitrification rates between sites because



abandoned lodges had lower rates. Fecal accumulation is also unlikely because the sites are inundated and drained twice a day. This tidal action would flush away or at least move around any fecal pellets, thereby eliminating fecal pellets as a source of increased mineralization and nitrification rates.

We hypothesized that aeration of the soil may increase potential net nitrogen mineralization and nitrification rates of soil. Muskrats aerate the soil through burrowing and treading activities. It is possible that the muskrat burrow system is extensive enough to influence aeration of soils at 8 m. Tivoli North Bay muskrat burrows can persist for many years after abandonment of a lodge site (E. Kiviat, pers. obs.). However, if these burrows were the source of aeration and increased mineralization and nitrification rates, then abandoned sites would have had rates as high as active sites. Thus burrows are not important in modification of the mineralization and nitrification rates of soils.

It is important to remember that plants are important in the sediment aeration in tidal freshwater wetlands because live plant roots leak oxygen and other oxidized substances (Howes *et al.*, 1981). The more aerobic soil conditions stimulate nitrogen mineralization and nitrification (Bowden, 1987). The lower rates of nitrogen mineralization and nitrification in the abandoned lodge sites could be associated with the lower plant biomass on these sites. However, the ANOVA results did not support this conclusion. In both active and abandoned lodge sites biomass was significantly higher in the reference transect than in the muskrat transect, yet there was no difference in nitrogen mineralization and nitrification rates between the two transects.

Muskrat treading activities may create small aerobic zones that stimulate mineralization and allow nitrification. The muskrat is a lightweight animal (about 1 kg) whose tracks do not compact the saturated wetland soils found in Tivoli North Bay. The soil probably redistributes with each step, and tracks allow air and water to infiltrate. Since treading is the only disturbance activity that solely affects active sites in this study we interpret the increased potential net nitrogen mineralization and nitrification rates of soil in the active sites as a temporary effect related to active muskrat disturbance.

This study showed that muskrat disturbance effects in a freshwater tidal wetland increase potential net nitrogen mineralization and nitrification rates of soil, most likely through soil aeration. Most wetland sediments have low nitrite and nitrate concentrations due to low oxygen tensions that favor denitrification (Bowden, 1987). Denitrification is important as a potential sink for excess nitrate, which can cause eutrophication in marine ecosystems (Ryther and Dunstan, 1971). Our data indicate that muskrats can increase nitrate levels, at least in small areas of the marsh. This increase may foster the occurrence of certain plant species that favor nitrate and may increase nitrate losses from the marsh.

A number of rodent species are known to have dramatic effects on the availability of resources to other species. For example English and Bowers (1994) found that woodchuck (*Marmota monax*) activity increases plant species richness at intermediate distances from burrows and decreases plant species richness both near and distant from burrows. Pocket gopher activity increases the heterogeneity of the soil surface by creating patches of high and low soil fertility (Johnston, 1995). Schiffman (1994) found giant kangaroo rat (*Dipodomys ingens*) activity increases the diversity of exotic grass species while decreasing the diversity of native species in a California grassland and the North American beaver (*Castor canadensis*) is notable for its extensive alteration of resources (Naiman, 1988). Our study establishes the muskrat as modifier of potential net nitrogen mineralization and nitrification rates of soil and previous studies (Danell, 1977; Kiviat, 1978; Weller, 1987; Nyman *et al.*, 1993) suggest that the muskrat affects diversity of both vegetation and animals. Therefore, the impacts of muskrats are likely to influence wetland restoration and management.

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