The role of muskrats (Ondatra zibethicus) as ecosystem engineers in created freshwater marshes

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Introduction

The role of muskrat (Ondatra zibethicus) populations in wetland succession is widely recognized (Danell, 1979; Kangas, 1985; Berg and Kangas 1989; Nyman et al., 1993; Clark, 1994). These resident herbivores influence hydrology, substrate properties, and ecosystem biota through grazing, burrowing, and lodge construction (Wilcox and Meeker, 1992; Taylor and Grace, 1995; Hewitt and Miyonshi, 1997; and Gough and Grace, 1998; Connors et al., 2000). During winter, muskrats use vegetation to build lodges for shelter. These lodges are commonly constructed from above-ground portions of sturdy vegetative species such as Typha spp. and Phragmites spp. Berg and Kangas (1989) found removal of biomass to be as high as 20% of the cover in a Czechoslovakian marsh.

Muskrat populations function as part of wetland ecosystems and can have profound effects. Mitsch and Gosselink (2000) illustrate that muskrats play an important role in the development of spatial patterns in wetlands. Wilcox and Meeker (1992) argued that foraging and lodge building increased interspersion in dense vegetated stands, causing a positive effect on invertebrates and avian populations. Taylor et al. (1997) challenged the assumption that herbivory reduces neighbor competition, and concluded that intense small mammal herbivory has neither positive nor negative effects on neighboring species. In this study we intend to examine the consequences of muskrat eat-outs and herbivory on vegetative regrowth in wetlands.

Muskrat activity and its effect on ecosystem development were compared, over two years (2000 and 2001) in planted and naturally colonized created wetlands. A significant immigration of muskrats was beginning in these two wetlands as the study began. The goal of this study was to determine what effects the removal of large amounts of plant biomass by muskrat eat-out would have on macrophyte recovery, productivity, and macrophyte species diversity in freshwater marshes. The objectives to meet these goals were: (1) to compare macrophyte biomass in eat-out areas and non-eat-out areas in the growing season following winter lodge building, and (2) to isolate the effect of herbivory during the study period by building enclosure structures, and comparing enclosure areas to open areas. Meeting these objectives permitted the testing of the following hypotheses.

Hypothesis 1: Areas where muskrats remove most of the vegetation for lodge building will show a greater short-term decrease in macrophyte biomass than undisturbed areas.

Hypothesis 2: Muskrat herbivory will not significantly affect macrophyte biomass in eat-out areas during the growing season following lodge building.

Methods

Vegetation recovery after muskrat eat-out

In early January 2000, areas where muskrats had removed vegetation for lodge building were outlined on site maps. Missing vegetation and the presence of chewed-off shoots made eat-out areas easy to identify. Total eat-out area was calculated in wetlands 1 and 2 using a planimeter to measure the individual eat-out areas sketched on the scaled map. Plots were randomly chosen throughout the eat-out with larger areas containing more plots and smaller areas containing fewer plots. This method of plot selection was done to equally represent all eat-out areas throughout the two marshes; 47 eat-out plots resulted (Table 1). The southeast corner of each plot was marked with PVC pipe and orange flagging. Control areas, where vegetation had not been eaten-out, were established in a paired order with study plots, resulting in 94 total, eat-out and control plots (Figure 1). Each eat-out plot was paired with a non eat-out, or control, plot in a corresponding vegetation zone.

Biomass estimation

During spring 2000, the map with previously recorded eat-out areas was updated to show vegetation that had been removed for lodge upkeep and repair. On June 24-26, 2000 biomass data were recorded, using nondestructive methods. A square 0.25 m²-pipe assembly was used to define the plot boundary, so that only vegetation inside the square was counted and recorded. Number of each species, stem length, number of leaves, number of flowers, and water
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Equation 3, from a study by Ahn and Mitsch (2002) was used to calculate the dry weight for *Schenoplectus tabernaemontani*.

A nested ANOVA was created using SAS (1996) to statistically compare the amount of biomass in planted versus naturally colonizing wetland and in eat-out versus non eat-out plots.

Muskrat herbivory effects

Twenty plots were established with temporary exclosures surrounding each plot. Ten of the plots were located in eat-out areas, and ten of the plots were located in corresponding control areas. The purpose of the exclosure structures was to keep muskrats out of the plots so that vegetation could grow unaltered by future muskrat herbivory, thereby determining what potential effects muskrat herbivory may have on the recovery of vegetation in eat-out and control plots.

Stakes made of PVC pipe were used to define the four corners of each 0.25 m² plot (Figure 2). The perimeter of each plot was trenched and plastic coated wire fencing (openings = 38 cm²) was inserted into the marsh soil. The fencing extended approximately 1.2 m above ground, and 8.0 cm below ground. Each plot was completely surrounded by fencing, and secured with plastic fasteners. Openings in the wire mesh surrounding the exclosure plots were 6.0 cm², and not likely to inhibit plant growth.

Biomass

Number of each species, number of leaves, stem length and number of flowers were recorded in each exclosure and open plot. Regression equations for *Typha*, *Schenoplectus*, and *Sparganium* were used to calculate dry weight for vegetation in the exclosure plots (Equation 3.1, 3.2 and 3.3). Exclosures were closely monitored for signs of intrusion during the data collection period.

Figure 2. Diagram of muskrat exclosure

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**Figure 1.** Scaled diagram of the two experimental marshes with eat-out areas caused by muskrats in spring 2000 outlined in black. Eat-out plots (white) and control plots (black) are shown. Open plots are circular, exclosure plots are rectangular.

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Figure 2. Diagram of muskrat exclosure
A nested ANOVA was created using SAS (1996) to compare the amount of biomass in planted versus naturally colonizing wetland and eat-out versus non eat-out plots, and grazed versus not grazed plots.

**Results**

**Vegetation Recovery after Muskrats**

In the 2000 growing season following muskrat invasion, biomass recovery was significantly less in eat-out areas than in control areas for both wetland 1 and wetland 2 (Figure 3). The areas where muskrats removed large amounts of vegetation, for lodge building during winter 1999-2000, grew 87% less biomass on average than control areas in summer 2000. Control areas, where muskrats removed little to no vegetation for mound building, recovered similar amounts of biomass relative to pre-invasion years at the same marsh. The results of a nested ANOVA support the findings that biomass in eat-out versus control plots within wetlands is significantly different (r = 0.0039) (Table 2). As hypothesized, the data show a reduced recovery of macrophyte biomass in the growing season following intense muskrat eat-out.

**Muskrat herbivory after invasion**

Biomass of macrophytes on exclosure plots was not different from that on open plots in July 2000 for either wetland (Figure 4). Isolated muskrat herbivory, independent of eat-out effects, had no effect on biomass in either wetland.

The data from plots in wetland 1 revealed more biomass in open plots than in exclosure plots for June, 2000. Significantly more vegetation returned in open plots for June, and is probably because of a greater number of open plots (n=38) than exclosure plots (n=10) (the open plots encompassed more area for possible plant regrowth). In July, as more vegetation returned the data show no significant difference between open and exclosure plots in wetland 1. No significant difference was found between open and exclosure plots in wetland 2. The results of a nested ANOVA show no significant difference in the comparison of exclosure versus open plots (Table 2).

**Discussion**

The decrease in biomass is probably a short-term response to muskrat eat-outs, and vegetative productivity will likely recover for these areas when muskrat eat-out pressure has lessened [this indeed did happen in 2002]. The majority of studies conducted on aquatic rodent eat-outs have been in coastal areas where tidal effects cause erosion and eventually marsh loss (Taylor et al. 1997; Grace and Ford, 1996; Carter et al. 2000). This study is unique in its attempt to quantify vegetative loss due to muskrat eat-outs in inland marshes, and to separate the effect of subsequent muskrat herbivory from the effect of muskrat eat-outs. Figure 5 shows number of muskrat lodges at the ORWRP for all winters since muskrats invaded the site in 1996, macrophyte biomass for July 2000 in eatout and control plots, and macrophyte coverage for each year. The number of muskrat lodges increased significantly in winter 1999-2000, 3 years after muskrat invasion. Following the large muskrat pulse in 1999-2000, macrophyte cover was reduced in wetland 2 from 66% in 1999 to 48.6% in 2000. In wetland 1, macrophyte biomass was significantly reduced following muskrat invasion and did not return to levels found in 1999.

![Figure 3. Above ground biomass in mid-summer (July 2000) eat-out and control plots for wetlands 1 and 2](image-url)

![Figure 4. Above ground biomass in mid-summer (July 2000) in open and exclosure plots for wetlands 1 and 2](image-url)
cover decreased from 63% in 1999 to 45.7% in 2000. More specifically, emergent vegetation in eat-out areas showed less re-growth than vegetation in control areas during the growing season 2000 following muskrat invasion (Figure 5 middle). In August 2001, the second growing season after continued muskrat dominance, macrophyte cover reduced to 17.3% of the Typha-dominated Wetland 2 and 27.6% in the more diverse Wetland 1 (see Mitsch and Zhang, 2002, this report). This precipitous decrease in vegetation in 2001, essentially an “eatout” in terms of vegetation loss led to a crash in the muskrat activity in the basins in the winter of 2001-02 (Figure 5 top) in both basins.

Muskrat Role

Effects of muskrat engineering do not end at decreased biomass. Svenson (1995) reported that Sphagnum fuscum acted like a small-scale engineer by capturing mineral nutrients quickly, and limiting Drosera rotundifolia growth in a Swedish bog. Svenson’s (1995) results support the idea that muskrat eat-out activity positively or negatively influence other organisms in a marsh by changing the abundance and state of marsh vegetation.

Muskrats in this study cleared dense Typha stands in a naturally colonizing Wetland 2. The highly aggressive Typha achieves dominance in many naturally colonizing wetlands in the United States. Communities of dominant macrophytes serve many direct and indirect functions: provide food for animals, compete for resources, provide shelter for other species, capture food, cast shade, reduce the impact of rain, and oxygenate soil (Svenson, 1995).

Though muskrat herbivory in this study was not correlated with an increase in emergent macrophyte species richness several other studies have noted such relationships (Nyman et al., 1997). Wilby et al. (2001) depict many interactions between herbivores and plant communities occurring simultaneously, and that ecosystem engineering and tropic processes can be closely associated, resulting from single interactions of herbivores. Through feeding and digging, muskrats create open areas for seed and resource accumulation, allowing invasive species establishment.

References


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